

Zooplankton and the oceanography of the eastern tropical Pacific: A review [☆]

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Quiero dedicar mi trabajo a la memoria de José Rodolfo Färber Holderness (1912–2006), mi Padre. Su honestidad, sencillez, franqueza, sentido de justicia e inquebrantable buena voluntad, fueron siempre un ejemplo para mí, eso me permitió entender que solo siguiendo estos simples principios, me podría ver en el espejo cada mañana con tranquilidad y sin remordimientos. Siempre estará presente en todo lo que haga.

Abstract

We review the spatial and temporal patterns of zooplankton in the eastern tropical Pacific Ocean and relationships with oceanographic factors that affect zooplankton distribution, abundance and trophic relationships. Large-scale spatial patterns of some zooplankton groups show broad coincidence with surface water masses, circulation, and upwelling regions, in agreement with an ecological and dynamic partitioning of the pelagic ecosystem. The papers reviewed and a new compilation of zooplankton volume data at large-scale show that abundance patterns of zooplankton biomass have their highest values in the upwelling regions, including the Gulf of Tehuantepec, the Costa Rica Dome, the equatorial cold tongue, and the coast of Peru.

Some of the first studies of zooplankton vertical distribution were done in this region, and a general review of the topic is presented. The possible physiological implications of vertical migration in zooplankton and the main hypotheses are described, with remarks on the importance of the oxygen minimum zone (OMZ) as a barrier to both the vertical distribution and migration of zooplankton in the region. Recent results, using multiple-net gear, show that vertical distribution is more complex than previously thought. There are some well-adapted species that do live and migrate within the OMZ.

Temporal patterns are reviewed and summarized with historical data. Seasonal variations in zooplankton biomass follow productivity cycles in upwelling areas. No zooplankton time series exist to resolve ENSO effects in oceanic regions, but some El Niño events have had effects in the Peru Current ecosystem. Multidecadal periods of up to 50 years show a shift from a warm sardine regime with a low zooplankton biomass to a cool anchovy regime in the eastern Pacific with higher zooplankton biomasses. However, zooplankton volume off Peru has remained at low values since the 1972 El Niño, a trend opposite to that of anchoveta biomass since 1984.

Studies of trophic relations emphasize the difference in the productivity cycle in the eastern tropical Pacific compared to temperate or polar ecosystems, with no particular peaks in the stocks of either zooplankton or phytoplankton. Productivity is more dependent on local events like coastal upwelling or water circulation, especially in the equatorial countercurrent and around the equatorial cool-tongue. Micrograzers are very important in the tropics as are predatory mesozooplankton.

[☆] The order of authorship was determined by the flip of a coin. Sections 1–2.2 by M.A.F. and Sections 2.3–4.4 by J.F.

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Up to 70% of the daily primary productivity is consumed by microzooplankton, which thus regulates the phytoplankton stocks. Micrograzers are an important link between primary producers, including bacteria, and mesozooplankton, constituting up to 80% of mesozooplankton food. Oceanography affects zooplankton trophic relationships through spatial–temporal effects on primary productivity and on the distributions of metabolic factors, food organisms, and predators. This paper is part of a comprehensive review of the oceanography of the eastern tropical Pacific.

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1. Introduction – History of research in region

The pelagic environments of the Pacific Ocean encompass a broad complex of zooplankton populations (Brinton, 1962). Knowledge of these groups in the eastern tropical Pacific has been restricted to some well-sampled regions, notably the EASTROPAC (Love, 1972–1978; Ahlstrom, 1971, 1972a) area from about 20°N to 20°S and from 80°W to 130°W. These studies, although generally important, were isolated efforts without continuity. Furthermore, only several taxonomic groups and collections have been studied from the great diversity of zooplankton, a situation not much improved since the assessment of Bogorov (1958). Here, we describe the main findings in the eastern tropical Pacific. This paper is not an exhaustive review of all zooplankton information, but we attempt to document the present state of our knowledge of these animals in relation to spatial and temporal oceanographic patterns in the eastern tropical Pacific.

For this review, the eastern tropical Pacific region extends from the southwestern coast of Baja California to northern Peru (see Fig. 1 in Fiedler and Lavín, 2006). It includes the equatorial current systems of the eastern Pacific and the eastern Pacific warm pool to the west of Central America and southwestern Mexico. Eastern boundary currents flowing into the region from the north (California Current) and south (Peru Current) also have influences in the eastern tropical Pacific region (Fiedler and Lavín, 2006).

The British *Challenger* Expedition (1873–1876) is conventionally cited as the beginning of dedicated scientific studies of the seas, including the Pacific Ocean (Hedgpeth, 1974). The zooplankton collections taken by this cruise provided the first extensive taxonomic and distributional information of some zooplankton groups in this ocean (Brinton, 1962). However, this expedition never reached the eastern tropical region of the Pacific (see Thomson and Murray, 1885).

The Italian circumnavigation voyages by the *Vettor Pisani* (1882–1884) and *Liguria* (1903–1905) included several localities in the eastern tropical Pacific: the coast of Peru, Galapagos Islands, and Mexico. From these expeditions Rosa (1907, 1908), Granata (1911), and Baldasseroni (1915) described species of the holoplanktonic Polychaeta (Tomopteridae and Alciopidae), and Chaetognatha, respectively.

The voyages of the U.S. Fish Commission Steamer *Albatross*, between 1888 and 1905, marked the beginning of more systematic oceanographic and biological studies in the region. The last three of these expeditions were in charge of the prestigious naturalist Alexander Agassiz, whose main interest was the relationship between the marine fauna on the Pacific side of the Panama Isthmus with that of the Caribbean and Gulf of Mexico. Plankton collections were taken with both open and open-closing nets (Hedgpeth, 1974). Basic and important taxonomic information on several zooplankton groups from these *Albatross* collections have been published: for example, Euphausiacea and Mysidacea (Ortmann, 1894; Hansen, 1912), Copepoda (Giesbrecht, 1895), Medusae and Siphonophorae (Maas, 1897; Agassiz and Mayer, 1902; Bigelow, 1909, 1911, 1913), Polychaeta (Chamberlin, 1919), and Tintinnoidea (Kofoid and Campbell, 1939).

From 1923 to 1938, the Department of Tropical Research of the New York Zoological Society organized various expeditions to the eastern Pacific in the ships *Noma*, *Arcturus*, *Antares*, *Templeton Crocker*, and *Zaca* that collected numerous zooplankton samples (Tee-Van, 1926). Beebe (1926) gave some preliminary results of the plankton hauls with data for the more easily recognizable groups of invertebrates and their relative abundance. Treadwell (1928, 1941, 1943) described the Polychaeta from some of these expeditions, including the pelagic species. Eastern Pacific collections made by the Allan Hancock Foundation cruises dating from 1931 to 1941 provided information about fauna and flora from the rich area between the low-tide mark and the 100-fathom line (Fraser, 1943; Squires, 1959).

Blackburn (1966a) reviewed the information on biological oceanography in order to state the main results obtained on 29 biological-oceanographic expeditions made between 1952 and 1964. His main purpose was to describe the oceanic circulation features and the associated distribution of variables, particularly those features having significant influence on the distribution and abundance of the biota.

One of the most fruitful periods in the exploration of the eastern tropical Pacific was the multi-institutional and international EASTROPAC project during 1967–1968. It has been the only survey in this region that studied a large area repeatedly throughout the year (seven bimonthly periods). The publication of atlases that included physical, chemical, and biological data, edited by Love (1972–1978, <http://swfsc.nmfs.noaa.gov/PRD/atlas>) is among the most important results of this survey. An important part in the success of these expeditions was the prospecting of commercial species in relation to areas of high abundance of plankton in upwelling regions.

2. Spatial pattern

2.1. Large-scale: water masses, currents, and upwelling

Knowledge of large-scale geographical distribution of plankton began to be obtained during the great transoceanic expeditions made at the end of the 19th and during the 20th centuries (see above and Fiedler and Lavín, 2006). Studies of oceanic biogeography have shown that distributions of pelagic animals are linked with the patterns of large-scale circulation as characterized by the distribution of water masses, in particular with the surface water masses, which are often considered as different epipelagic biogeographic provinces (Steuer, 1933; Sverdrup et al., 1942; McGowan, 1960a,b, 1974; Bogorov, 1958; Beklemishev, 1961, 1971, 1981; McGowan and Williams, 1973; Johnson and Brinton, 1963; Semenov and Berman, 1977; Reid et al., 1978; Van der Spoel and Pierrot-Bults, 1979; Van der Spoel and Heyman, 1983).

Important contributions to the knowledge of large-scale spatial patterns of zooplankton groups in the Pacific Ocean also show the broad coincidence with the oceanographic features. From this biogeographic point of view, the eastern tropical region of the Pacific has often been considered as a distinct province (Ebeling, 1967; McGowan, 1971, 1974, 1986; Briggs, 1975; Vermeij, 1978; Backus, 1986; White, 1994; Hastings, 2000; Longhurst, 2001). Fig. 1, modified from McGowan (1971), shows the core areas of biogeographic distributions of zooplankton in the Pacific. The core of the *Eastern Tropical Pacific* fauna corresponds almost exactly to the eastern Pacific warm pool (Fiedler and Talley, 2006), while some of the *Equatorial* fauna extends into the eastern equatorial Pacific where it mixes with species from the *Eastern Tropical Pacific* and other groups (McGowan, 1971). On a finer spatial scale, Blackburn (1966b) compiled biological oceanography results from the period 1952–1964 and proposed a division of this province into 14 areas for the periods of January–June and July–December on the basis of certain physical oceanographic properties such as upwelling and thermocline depth. He discussed seasonal variations, relationships within and between trophic levels, taxonomic composition of phytoplankton, zooplankton, and micronekton, and ecological aspects of some groups.

Longhurst (1998) reviewed the current state of pelagic biogeography and concluded that the available information on the distribution of the species of the pelagic ecosystem is inadequate to define the distribution of pelagic biomes. He proposed an ecological analysis utilizing spatial and temporal patterns discernable with satellite imagery, in order to define ecological provinces in the pelagic realm of the oceans. He included the eastern tropical Pacific in the “*Pacific Trade Wind Biome*”, formed by two provinces that correspond to oceanographic subregions described by Fiedler and Talley (2006). The “*North Pacific Equatorial Countercurrent Province*” coincides with the eastern Pacific warm pool and the “*Pacific Equatorial Divergence Province*” is related to the equatorial cold tongue. During El Niño-Southern Oscillation (ENSO) events, these provinces lose their characteristics partially or completely and the entire region might be considered a *trans-Pacific WARM-ENSO Province* (see Section 3.3). Platt and Sathyendranath (1999) proposed a dynamic partition of the pelagic ecosystem into functional subunits with ecophysiological or biochemical parameters and elastic boundaries that vary at the interannual, seasonal, and shorter time scales. These ecological and functional approaches to biogeography are more useful than earlier descriptions based only on presence/absence of species and agree with the focus of this review.

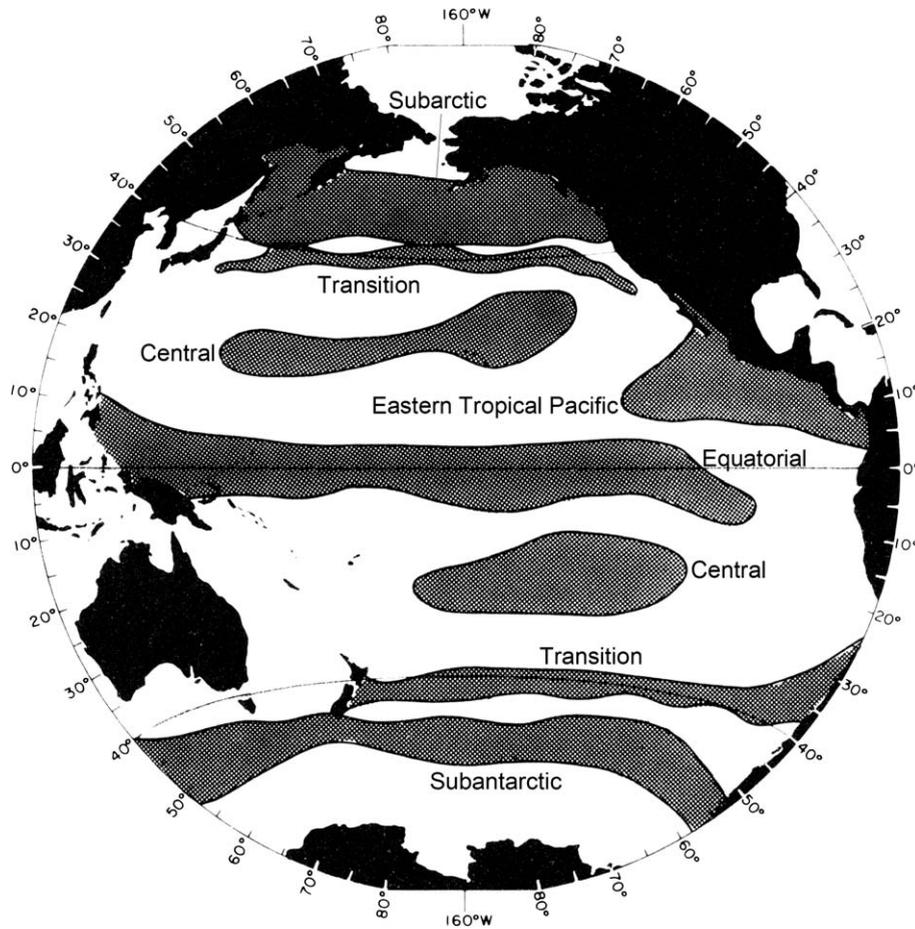


Fig. 1. Zoogeographic centers of some species distribution patterns in the pelagic region of the Pacific Ocean (modified from McGowan, 1971, with permission of the author and publisher).

2.1.1. Zooplankton biomass

Large-scale distribution patterns of zooplankton in this region are best known in terms of total biomass, which has been systematically documented from the end of the 1950s. In general, the patterns of distribution of standing stocks of zooplankton are in agreement with the physical features, such as surface water masses, upwelling regions, and major currents, present in the eastern tropical Pacific (e.g. Holmes, 1958a,b; Brandhorst, 1958; Reid, 1962; Forsbergh and Reid, 1964). Some of these studies have examined relationships of zooplankton biomass with other chemical and biological data, such as the distribution of nutrients, phytoplankton, micronekton, fish, birds and mammals.

Holmes et al. (1957), Holmes (1958b), and Holmes and Blackburn (1960) studied the area between 30°N and 9°S out to 120°W. They found a fair general agreement between the geographical distribution of surface chlorophyll, primary production, standing crop of zooplankton, the circulation features, and the hydrographic structure. Brandhorst (1958) discussed the relations between the topography of the thermocline, the circulation, and the zooplankton standing crop. In these results, the enrichment of the surface layers was in general associated with a shallow thermocline, which is characteristic of the equator, the northern boundary of the North Equatorial Countercurrent, the Costa Rica Dome, and several places along the coast of Central America.

Reid (1962) analyzed the circulation, phosphate, and zooplankton biomass distribution for the entire Pacific Ocean, and demonstrated the high fertility of the eastern equatorial region. The geographic distribution of standing crop and production of phytoplankton in the area of 10°N to 33°S and west to 130°W

was analyzed and discussed by Forsbergh and Reid (1964). They found general relationships among thermocline topography, nutrient concentration, and various trophic levels from primary producers to fish and mammals. They also observed high values of zooplankton biomass associated with high values of chlorophyll, productivity and concentrations of phosphate, and an inverse relationship with depth of the thermocline.

Blackburn (1962, 1966a,b, 1968) discussed relations between the biota and oceanographic features, with a view to finding possible ways of predicting tuna abundance. Blackburn et al. (1970) extended this work with EASTROPAC data, comparing standing stocks of chlorophyll-*a*, zooplankton and micronekton in three areas of the eastern tropical Pacific in order to understand patterns of seasonal and areal variability. Results show that the seasonal variability in the western area was low, but moderate in southern and eastern areas. In addition, it was clear that spatial differences in the standing stocks agreed with differences in the physical conditions: the stocks generally declined from east to west and were higher in upwelling and shallow thermocline areas. Blackburn (1973) studied data of standing stocks of chlorophyll-*a*, zooplankton, and micronekton collected in the western area of the eastern tropical Pacific (16°N–3°S and 100°–120°W), that received better seasonal coverage during EASTROPAC cruises. The results of regression analysis showed that stocks of phytoplankton and zooplankton were significantly correlated in the same way throughout the year in all parts of the studied area.

Beers and Stewart (1971) analyzed samples from a transect along 105°W, between ~10°N and 12°S, during the EASTROPAC program and described taxonomic composition and abundance of microzooplankton. They found a highly significant positive correlation between chlorophyll-*a* and microzooplankton biomass in data averaged over the euphotic zone. Vertical distribution of this community was also studied and related to the hydrographic features. The authors concluded that microzooplankton must have important roles in controlling the extent of the phytoplankton blooms in the survey region.

The papers reviewed above generally show that zooplankton biomass has spatial and seasonal biogeographical patterns positively related to chlorophyll, primary production and concentration of phosphate, and inversely related to depth of the thermocline. Spatial patterns of oceanic upwelling and productivity in the eastern tropical Pacific have been reviewed by Fiedler (1994, 2002a) and Fiedler et al. (1991). They found high values of chlorophyll, phytoplankton productivity, productivity index, nutrients, and phytoplankton biomass along the equatorial and countercurrent divergences, around the Galapagos Islands and at the Costa Rica Dome. These results agree with the high zooplankton biomass reported in the papers reviewed above and with the compiled data (Fig. 2) obtained from a modified version of the World Ocean Database 2001 plankton dataset (see Appendix).

2.1.2. Community patterns

The distribution patterns of species or other taxa are more complicated than the pattern of standing stock or plankton volume, since the species do not react uniformly to a given environment (Beklemishev, 1981). However, as discussed above, biogeographic studies have shown zooplankton communities or recurrent groups with spatial patterns corresponding to large-scale oceanographic features (Fig. 1). It should be noted that water mass definitions and resolution of smaller-scale oceanographic features have evolved since the writing of many of the papers reviewed here (see Fiedler and Talley, 2006; Willett et al., 2006). For example, the differentiation of Tropical Surface Water and Equatorial Surface Water across the Equatorial Front (Wyrski, 1966) was not appreciated by earlier authors who related species distributions to an Equatorial Water mass described by Sverdrup et al. (1942) that covered the entire tropical Pacific. This does not invalidate, however, the past observations of relationships between species distributions and oceanographic patterns known at the time.

Studies of several zooplanktonic groups have shown that large-scale distribution patterns of some species are closely related to the principal water masses or the main currents in the eastern tropical Pacific. For example, Kofoed and Campbell (1939) studied microzooplankton samples taken at 130 localities during the *Albatross* cruise of 1904–1905. A total of 347 species of Tintinnoidea protists were identified and showed a generally higher abundance in the Peru Current. They also quantified the species richness in this and the other oceanic currents that were studied in the cruise. Boltovskoy and Jankilevich (1985) studied radiolarian protists from the water column in the eastern equatorial Pacific, describing the distribution patterns of 141 taxa and discussing the utility of species assemblages of this group in relation to the zoogeographical schemes of the survey region.

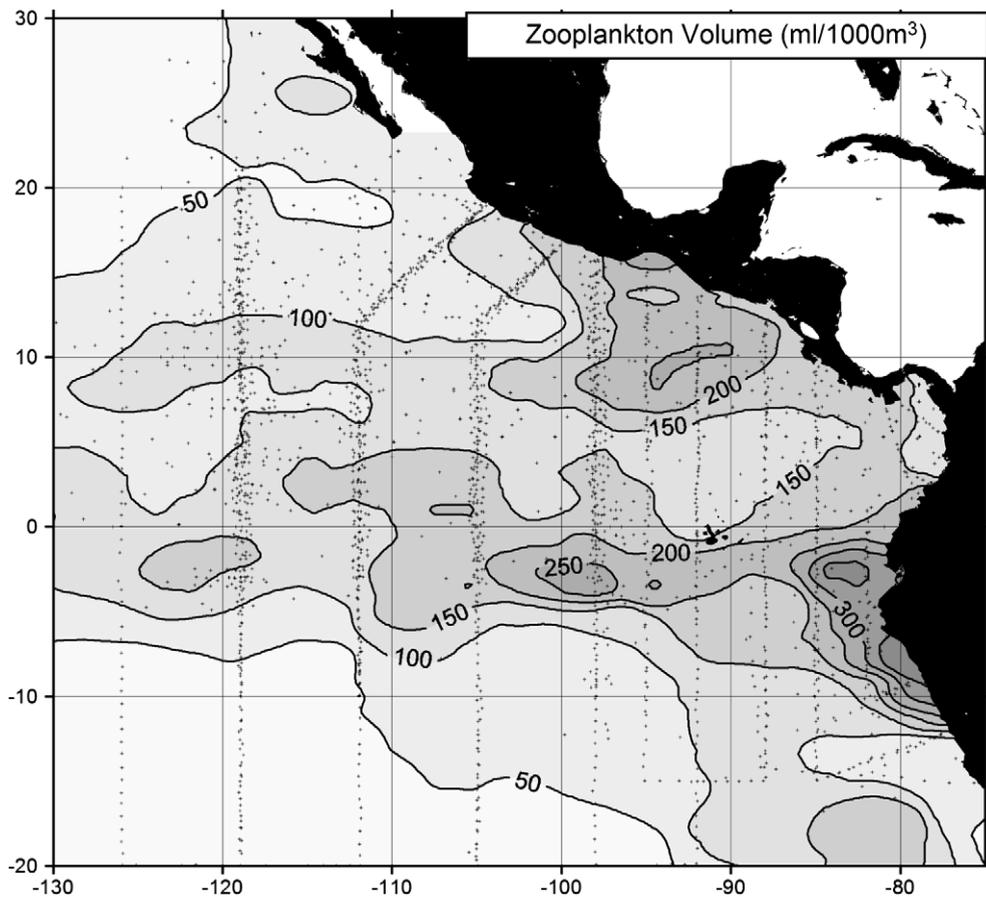


Fig. 2. Mean zooplankton volume from 333- μ m mesh net tows, 0–200 m (see Appendix for data sources).

Among the macrozooplankton groups, Bigelow (1911) found that the distribution and abundance of several species of siphonophores were related to the temperature gradient along the northern border of the Peru Current, occurring more frequently and abundantly to the north where the waters were warmer. The Hydro-medusae and Scyphomedusae from samples collected during the EASTROPAC program were studied by Segura-Puertas (1984). The distributions of 61 and 2 species, respectively, were related to the main water masses present in the eastern tropical Pacific. Larson (1990) reviewed the literature on Scyphomedusae (43 spp.) and Cubomedusae (1 sp.) from the eastern Pacific, providing a discussion of their distribution and an analysis of the taxonomic status of some species. Among these 44 species, three were defined as cosmopolitan and 14 have been observed at localities within the eastern tropical Pacific.

Arcos and Fleminger (1986) studied the distribution of copepods in the eastern equatorial Pacific, using samples obtained during two EASTROPAC cruises. They concluded that distribution of individual species and species groups were related to surface water masses and the Peru Current and equatorial current system in the region. Grice (1961) and Gueredrat (1971) studied an equatorial transect, from the Galapagos Islands to the north of the Solomon Islands, and found that the distribution of copepods showed distinct differences between the eastern, central, and western regions. Dessier (1983) and Dessier and Donguy (1985, 1987) analyzed the seasonal and areal distribution of copepod populations in the eastern equatorial Pacific from ship of opportunity sampling. These samples constitute the best oceanic zooplankton time series from the region (see Sections 3.1 and 3.3).

Longhurst and Seibert (1972) studied the distribution of cladocerans of genus *Evadne* from samples of the EASTROPAC cruises. *Evadne tergestina* was observed to be widely but irregularly distributed in warm waters at low latitudes (coincident with the Tropical Surface Water, Fiedler and Talley, 2006), and *E. spinifera* was

located in the central gyral waters (Subtropical Surface Water) of the eastern Pacific in relatively cool water (<24 °C). These results showed that these species of cladocerans are epiplanktonic with an ocean-wide distribution in the Pacific, similar to distributions observed in the North Atlantic.

Euphausiids are one of the best-known groups of macrozooplankton. Ortmann (1894) and Hansen (1912) were the first to report this group in the eastern tropical Pacific, recording the horizontal and vertical distribution of species collected by *Albatross* in 1891 and 1904–1905, respectively. Most of the samples were collected at stations located in the Gulf of Panama, around the Galapagos Islands, near Acapulco, and from the Gulf of California. Brinton (1962) described quantitative aspects of the horizontal and vertical distribution and abundance of Pacific euphausiids including several localities in the eastern tropical Pacific. Brinton (1979) studied samples taken on a transect from 23°N to 3°S defining the principal physical–chemical environments that influence the horizontal distribution patterns and vertical migration of euphausiids. For example, in the transition region from California Current to the Eastern Tropical Pacific, the dominant species were *Euphausia eximia* and *Nyctiphanes simplex*, associated with the crustacean galatheid crab *Pleuroncodes planipes* (Brinton, 1979), while the region of extreme subthermocline oxygen deficiency from 21° to 10°N was characterized by *Stylocheiron affine*, *S. carinatum*, *Euphausia tenera*, *E. distinguenda* and *E. lamelligera*. Brinton (1962, 1979) considered the last two as characteristic species, well adapted to the special hydrographic conditions of the eastern Pacific surface water masses known at that time and reviewed by Fiedler and Talley (2006).

Bieri (1957) made the first records of chaetognaths in the eastern tropical Pacific, although he mentions that Baldasseroni (1915) recorded *Sagitta enflata*, *S. lyra*, and *S. serratodentata* from a single locality off Chile. He studied samples from the surface waters off the Peruvian coast and found interesting differences in the distribution of 15 species when a strong El Niño was present (1941) compared with a year of cool water conditions (1952). Bieri (1959) analyzed the distribution of 27 species from the Pacific Ocean, determining their relationship with circulation and water masses and discussing their distinctive assemblages. He observed that the agreement between species distributions and surface water masses was best in the eastern Pacific, with a clear boundary of the chaetognath fauna southwest of Baja California (at 18–20°N), corresponding to the boundary between California Current Water and Tropical Surface Water (Fiedler and Talley, 2006). He compared these patterns with analogous distributions of other groups (euphausiids, copepods, and dinoflagellates). Sund and Renner (1959), Sund (1961), and Sund (1964) made other studies of chaetognath distribution and hydrographic features in the eastern tropical Pacific, notably the Costa Rica Dome and Peru upwelling and also described the influence of El Niño 1958.

The occurrence of some species of holoplanktonic polychaetes in upwelled or subtropical waters has been documented by Ekman (1953), Dales (1957), Tebble (1962), Fernández-Alamo (1983, 1987), and Vicencio-Aguilar and Fernández-Álamo (1996). A general perspective of the large-scale patterns of distribution and abundance was obtained from a study of samples taken during the EASTROPAC program (Fernández-Alamo, 1983). Some of the 44 species identified in this study show patterns of abundance that are closely similar to patterns of productivity and zooplankton biomass. For example, *Pelagobia longicirrata* (Fernández-Álamo, 2002), *Tomopteris planktonis* and *T. elegans* (Fernández-Álamo, 2000) were present in higher abundances in upwelling regions: the Gulf of Tehuantepec, the Costa Rica Dome, the coasts of Panama–Colombia, the equatorial cold tongue, the coast of Peru, and the Galapagos region (Kessler, 2006). Other species – *Vanadis tagensis*, *Plotohelmis alata*, *Watelio gravieri*, *Maupasia coeca*, *Maupasia gracilis*, *Phalacrophorus pictus*, and *Tomopteris septentrionalis* – were scarce in the EASTROPAC samples, but also show a direct relationship with upwelling regions. On the other hand, *Naiades cantraini*, *Vanadis formosa*, *Tomopteris krampfi* and *Travislopsis lanceolata* were present exclusively in the southeastern Pacific in high salinity (35.5–36.5) waters. Localization of these species coincides with the distribution of Southern Subtropical Surface Water described by Wyrski (1966) and Fiedler and Talley (2006). Fernández-Alamo (1983, 2004) suggested that these species could be indicators of this water mass in the survey region. Similar records were observed for *Pedinosoma curtum*, *Vanadis crystallina* and *Vanadis longissima*, however, they were also found in localities with relatively high salinity at the equatorial cold tongue and near the Costa Rica Dome (Fernández-Alamo, 1983).

Ahlstrom (1971, 1972b) described the composition, distribution, and abundance of fish larvae from the zooplankton samples taken over an extensive area during EASTROPAC. Eighty-two families were identified, of

which 10 account for over 90% of the total. An analysis of seasonal variation was included with the aim of determining the annual reproductive cycles of fishes in tropical waters. Ahlstrom and Moser (1969) described a new species of gonostomatid fish from the ichthyoplankton taken during one EASTROPAC cruise, and named it *Araiphos eastropas* to commemorate the program.

A distinctive feature of the eastern tropical Pacific is the Costa Rica Dome, an oceanic upwelling center. Here, the thermocline ascends to very near the sea surface, with the 20 °C isotherm at about 25 m (Wyrski, 1964; Barberan et al., 1984; Fiedler and Talley, 2006; Kessler, 2006). The Costa Rica Dome supports a mean zooplankton biomass as high as or higher than the equatorial upwelling zone (Fig. 2). Vicencio-Aguilar and Fernández-Alamo (1996) presented lists of several groups from the zooplankton collections taken during four DOMO cruises in this region between 1979 and 1982 and noted the presence of species with different zoogeographical affinities influenced by upwelled waters, such as the cosmopolitan cold water amphipod *Prinno macropa* and polychaete *Tomopteris septentrionalis* (Ekman, 1953) and several meso- and bathypelagic species: the polychaete *Vanadis tagensis* (Tebble, 1962; Fernández-Alamo, 1983), the amphipods *Paraphronima gracilis* and *Phronima sedentarius* (Ekman, 1953) and the chaetognath *Sagitta decipiens* (Sund, 1961; Alvarino, 1965).

It has been established that pelagic faunal communities are not as geographically isolated as shelf or terrestrial communities (Ekman, 1953), due to the general patterns of currents and countercurrents that give a dynamic nature to the pelagic realm and connect the waters of all oceans with very few definite boundaries. However, endemism has been recorded in this region for copepods such as *Eucalanus inermis* by Fleminger (1973), *Pontellina sobrina* by Fleminger and Hulsemann (1974), and *Pleuromamma johnsoni* by Ferrari and Saltzman (1998); and for euphausiids such as *Euphausia eximia*, *E. distinguenda*, and *E. lamelligera*, which are well adapted to O₂ deficient waters, by Brinton (1962, 1979). Shih (1979) infers that the high number of endemic species that occur in this tropical region, may be closely related to the oceanographic and hydrographic complexity of the physical environment (reviewed by Kessler, 2006; Fiedler and Talley, 2006). These endemic species add evidence to that the eastern tropical Pacific is an isolated segment in the Pacific Ocean, from a zoogeographic point of view. As reviewed above, this zoogeographic subdivision has been discussed in detail by Sverdrup et al. (1942), Beklemishev (1961, 1971, 1981), McGowan (1971, 1974, 1986), McGowan and Williams (1973), and Reid et al. (1978).

2.2. Small-scales: eddies, jets, nearshore

The most distinctive mesoscale features of the eastern tropical Pacific are associated with the wind jets blowing through three gaps in the Central American cordillera: at the Isthmus of Tehuantepec in Mexico, the Papagayo region of Nicaragua, and the Isthmus of Panama (Amador et al., 2006). The jets force strong mixing and upwelling phenomena (Kessler, 2006; Willett et al., 2006) that result in high biological productivity (Blackburn, 1962; Blackburn et al., 1962; Färber-Lorda et al., 1994, 2004a; Gonzalez-Silvera et al., 2004; Pennington et al., 2006). These intense wind events generate dynamic cyclonic and anticyclonic eddies, the latter moving long distances offshore and influencing the biological productivity of the adjacent regions (Gonzalez-Silvera et al., 2004).

The ability to study oceanic eddies is linked with the development of satellite remote sensing (Willett et al., 2006). This tool has permitted the study of the origin, development and evolution of eddies and confirmed that their special characteristics can be maintained over sufficient time to affect plankton processes (Gonzalez-Silvera et al., 2004; Färber-Lorda et al., 2004a). Although the dynamics of mesoscale eddies associated with the wind jets, and other coastal processes have been studied for some time in the eastern tropical Pacific, zooplankton data related directly to the offshore eddies have not yet been generated. However, there are some papers about ichthyoplankton and zooplankton associated with mesoscale dynamics (frontal eddies) in the North Pacific, for example Lobel and Robinson (1986, 1988), Kimura et al. (2000), Nakata et al. (2000), Mackas and Galbraith (2002), and Okazaki et al. (2001, 2002). Zooplankton patterns in North Atlantic eddies have been particularly well documented (The Ring Group, 1981; Wiebe et al., 1992). Gasca et al. (2001) compared the dominance of some species of euphausiids in an offshore warm-core eddy and in the Bay of Campeche in the Gulf of Mexico, finding important differences.

Coastal waters of the eastern tropical Pacific are not the focus of this review, but they will be considered briefly to conclude this section. Nearshore studies of eastern tropical Pacific zooplankton have been made mainly in relation to coastal upwelling regions. These areas are very important in the tropical regions because the horizontal and vertical transport of upwelled water modulates nutrient supply in these generally well-stratified surface waters, increasing their productivity compared with the adjacent regions. For example, the Peru and Baja California upwelling regions support important anchovy, sardine and tuna fisheries (Blackburn, 1966c; Longhurst and Pauly, 1987). In the Gulf of Panama, Schaefer et al. (1958) found that strong coastal upwelling and mixing occurs regularly each year during January–April when strong northerly winds are blowing offshore. This upwelling is responsible for high phytoplankton and zooplankton volumes that support sizeable stocks of commercially important organisms, for example the tuna *Cetengraulis mysticetus* and a shrimp fishery (Burkenroad et al., 1955).

As summarized above, spatial and temporal variability of primary production in the Gulf of Tehuantepec is driven by seasonal local winds. Values of zooplankton biomass in the Gulf of Tehuantepec have been documented by Blackburn et al. (1962) from three cruises made in 1958–1959, Alameda-de la Mora (1980), Färber-Lorda et al. (2004a,b) and Ayala-Duval et al. (1996). Some papers on distribution and abundance of several zooplankton taxa have been published: for example, copepods (Alameda-de la Mora, 1980; Fernández-Álamo et al., 2000), medusae (Segura-Puertas, 1987), euphausiids (López-Cortés, 1990); holoplanktonic polychetes (Fernández-Álamo, 1987), and ichthyoplankton (Ayala-Duval et al., 1998). Färber-Lorda et al. (2004a,b) defined three different water masses in the Gulf of Tehuantepec, and analyzed how these features influence distributions of euphausiid species and of their early larval stages. These works demonstrate that both zooplankton biomass and the distribution and abundance of species were related to the presence of the strong winds in winter and the particular hydrographic conditions generated by these winds.

The southern and northern regions of the California and the Peru Currents, respectively, represent apparent ecotones between at least three biogeographic provinces, with biotas from the boundary currents, from the tropical zone and from subtropical waters. The distributions of zooplankton species reviewed here are consistent with this pattern. A good example was observed for euphausiids by Brinton (1979), who found species with temperate affinities (*Euphausia pacifica* in the north and *E. mucronata* in the south) which decreased in dominance within the transition regions towards the equator. At the western edge of the currents occur species of the subtropical central and western Pacific, such as *E. hemigibba*, and finally, there are a few records of the tropical species *Nematocelis gracilis*, *Euphausia distinguenda*, and *E. lamelligera*. More examples are found in the following lists of studies from the eastern boundary currents to the north and south of the eastern tropical Pacific.

Systematic studies of fish larvae and zooplankton along the Peruvian coast between 3°S and 18°S are conducted by the Instituto del Mar de Peru. Data on these groups have been published by Alamo and Bouchon (1987), Sandoval de Castillo (1979, 1985), Carrasco and Lozano (1989), Girón (1996, 1998), Girón et al. (1997), Ayón and Aronés (1997a,b), Ayón and Girón (1997), Aronés and Ayón (1998), Ayón and Quesquén (1998), Ayón et al. (1997, 2004), and Gusmán et al. (1998). All give information about the composition, distribution, abundance, biomass, and temporal variations (including El Niño 1982–1983 and 1997–1998) of ichthyoplankton and zooplankton.

In the southern region of the California Current System off the Baja California peninsula, zooplankton biomass and the distribution of some zooplankton groups have been studied repeatedly since the 1950s. Much information is found in the atlases of distribution and abundance published by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) Program: zooplankton biomass (Isaacs et al., 1969, 1971; Smith, 1971; Fleminger et al., 1974), copepods (Fleminger, 1964, 1967; Bowman and Johnson, 1973), chaetognaths (Alvariño, 1965), pelagic molluscs (McGowan, 1967), euphausiids (Brinton, 1967, 1973; Brinton and Wyllie, 1976), and ichthyoplankton (Ahlstrom, 1972a,b; Ahlstrom and Moser, 1975; Moser et al., 1993, 1994, 2001). Also, some contributions in ichthyoplankton have been published by the Instituto Nacional de la Pesca, Mexico (Olvera-Limas et al., 1983; Padilla and de la Campa, 1981).

Since 1982, systematic studies of zooplankton (biomass, ichthyoplankton, copepods and euphausiids) from the most southern region of the California Current System have been conducted by Departamento de Plankton y Ecología del Centro Interdisciplinario de Ciencias Marinas (CICIMAR) in La Paz, Baja California Sur. Several examples of results of these investigations are: for zooplankton biomass (Hernández-Trujillo et al.,

1992); for ichthyoplankton (Esqueda-Escárcega et al., 1984; Funes-Rodríguez et al., 1991, 1995, 1998, 2000, 2002; Hernández-Rivas et al., 2000); for copepods (Hernandez-Trujillo, 1999a,b; Hernandez-Trujillo and Suarez-Morales, 2000, 2002); and for euphausiids (Gómez-Gutiérrez et al., 1995a,b; Cortés-Verdín, 1997).

Investigaciones Mexicanas de la Corriente de California (IMECOCAL) is a program created in 1997 with the goal of understanding the pelagic resources inhabiting waters of the southern region of the California Current System (Baumgartner et al., 2000). Some results of these surveys have been published by Lavaniegos et al. (1998, 2002, 2003), Jiménez-Pérez and Lavaniegos (2004). Fernández-Álamo et al. (2003) studied samples taken on a transect that included the coasts of California and the Baja California peninsula and found three assemblages of holoplanktonic polychaetes clearly related with the principal water masses. The southern group from Bahía Magdalena to Cabo San Lucas had the highest species richness, low abundance, and some species of tropical affinity that are more common in the eastern tropical Pacific.

Between the eastern boundary current systems at the northern and southern edges of the eastern tropical Pacific, there have been few oceanographic studies of zooplankton other than the work in the Gulf of Tehuantepec reviewed above. From the coastal region of Costa Rica, in the Gulfs of Nicoya and Dulce, Molina-Ureña (1996) analyzed the ichthyoplankton assemblages during rainy (December) and dry (February) seasons, reporting 22 families. Wangelin and Wolf (1996) studied the zooplankton communities and biomass, and Hossfeld (1996) reported the distribution and biomass of chaetognaths during the same periods, while Morales-Ramírez (1996) included a list of 54 species of copepods.

The few publications on zooplankton from the coastal region of southern Mexico are mainly about the composition, distribution and abundance of ichthyoplankton, as in Olvera-Limas et al. (1990). Acal (1991) conducted an ichthyoplankton survey in the neritic region of the Pacific Ocean off southwest Mexico, recording the abundance and diversity of larvae: 40 families and 129 species. Higher diversity was found during the night in one of the three areas analyzed and this was related to vertical migration. The most abundant species were *Bregmaceros bathymaster* and *Viciguerria lucetia*, the first being a mesopelagic species that was largely dominant in the area and was more abundant onshore in the two areas where the continental shelf is narrow. From the coasts of Colima and Jalisco, Mexico Franco-Gordo et al. (1999, 2001), Franco-Gordo (2001), and Navarro-Rodríguez et al. (2001) described the seasonal zooplankton biomass and ichthyoplankton composition. Finally, Hendricks and Estrada-Navarrete (1989) discussed the biogeographical affinities of 86 pelagic species of decapod crustaceans from the Mexican coast; since this group has planktonic larvae (and some are holoplanktonic), this information has value to zooplankton studies. It is apparent that data on zooplankton distribution in coastal regions within the eastern tropical Pacific are not sufficient to reach final conclusions about their zoogeographical patterns.

2.3. Vertical patterns

2.3.1. Vertical distribution

The vertical distribution of zooplankton has been studied for long time and a variety of classifications of vertical distribution have been proposed, usually consisting of three or more divisions that are narrower near the surface (Haeckel, 1887; Dahl, 1894; Fowler, 1898). Vertical distribution is important because of the marked anisotropy of the pelagic environment, a realm in which plankton diversity and environmental homogeneity have seemed to contradict ecological theory based on terrestrial systems (Longhurst, 1985a). Russell (1927) wrote “At the same time different species each appear to have their own definite vertical regions of distribution with upper and lower depth limits: this is only to be expected on account of the different environmental changes which occur from the surface downwards”. Thus, at that time, it was already evident that vertical distribution was a complex combination of species-specific tolerance and environmental conditions, together with food requirements and other factors such as light. But these factors are not yet completely understood.

Studies of vertical distribution patterns of zooplankton biomass or species are influenced by sampling methodology. At the very least, a net that can be closed is required, but detailed study requires net systems that can sample multiple depth intervals. For example, Longhurst (1976) analyzed EASTROPAC samples and, following Fowler (1898) and Vinogradov (1968), defined *epiplankton* as those species in the layer where zooplankton are most abundant, from the surface to depths from 50 m to 150 m. According to his results, Longhurst (1976)

also defined the *planktocline* as the layer where the zooplankton decrease by about 100–1000 animals m^{-3} per meter of depth and, also, the *planktostad* as the layer where the zooplankton biomass changes very little with increasing depth. These definitions were made possible by the type of sampling he performed with the Longhurst-Hardy Plankton Recorder. Thus, *planktocline*, even if it is a valid definition, does not have much use when the samples are taken with other types of nets with less resolution and precision in the depth of occurrence of the populations. However, recent advances in zooplankton sampling and surveillance with acoustic and visual methods could find this definition useful or even refine it, because a very good resolution of vertical distributions can be obtained.

In the eastern tropical Pacific, important factors influencing vertical patterns are the unusually strong thermocline and low oxygen concentration in subthermocline waters (Fiedler and Talley, 2006). Vertical distribution and migration are often restricted by the oxygen minimum zone, which extends vertically from about 50 m to 1200 m in the eastern Pacific, but varies considerably, depending on the location, currents and other factors. This zone can be defined as the area where the oxygen falls below $\sim 45 \mu\text{mol kg}^{-1}$. It can constitute an effective barrier for many organisms, but it also offers increased food supply and refuge to many species adapted to these conditions (Wishner et al., 1995). Considerable amounts of biota aggregate in these oxygen-deficient zones (Longhurst, 1967; Mullins et al., 1985).

Low oxygen waters, common in low latitudes, are more widely developed in the eastern tropical Pacific “because here the horizontal advection is weakest and biological consumption greatest” (Longhurst, 1967). Kamykowski and Zentara (1990) described the historical data obtained up to 1986 and found that the typical levels for most of the hypoxic areas were $<1.5 \text{ ml l}^{-1}$ or $<20\%$ oxygen saturation, whereas for the eastern Pacific they reduce to 0.5 ml l^{-1} or $\sim 7.5\%$ saturation. Fiedler and Talley (2006) explain that the shallow OMZ in the eastern tropical Pacific lies below the high near-surface biological productivity layer, where oxygen production and exchange are highest, at intermediate depths where replenishment by advection/diffusion is lowest. Low oxygen waters extend to deeper waters because organic particles settle through the water column and are degraded by respiration and bacterial decomposition, further depleting oxygen. These authors also show that the transport of oxygenated waters from the western Pacific along the equator results in a thinner OMZ and higher oxygen concentrations than to the north and south of the equator in the eastern Pacific. The OMZ north of the equator extends to more than 1000 m depth and is more pronounced in thickness and reduced concentration, because there is no source of oxygenated, high-density water at the surface in the North Pacific. The thickness of the OMZ varies from 600 m to 200 m in the south Pacific and from 1100 m to 400 m in the north Pacific. Fiedler and Talley (2006) also emphasize the low oxygen concentrations in relatively shallow waters. Fig. 3 shows the depth of the $1 \text{ ml O}_2 \text{ l}^{-1}$ isocline, representing the upper boundary of the OMZ, at 40–60 m off Central America, around the Costa Rica Dome and Peru, but considerably deeper along the equator at $\sim 200 \text{ m}$.

Zooplankton sampling has evolved, since the first samplings were performed with simple conical nets, as more sophisticated apparatus has been invented. Thus, qualitatively different data have been obtained, which render both spatial and temporal comparisons among studies difficult. In the remainder of this section, we review some results from the eastern tropical Pacific, mostly sampled with different methods or nets, to demonstrate the influence of sampling methodology on results.

Longhurst (1967) published results obtained with the aid of the then recently invented Longhurst-Hardy plankton recorder. He related the oxygen minimum to the vertical distribution of zooplankton in the southern California Current off southern Baja California, showing that many species can live at concentrations as low as 0.5 ml l^{-1} and migrate within an oxygen range from 5.0 ml l^{-1} near surface during the night to 0.5 ml l^{-1} at 300 m during the day. It was shown that the limiting oxygen concentration for zooplankton is apparently lower than 0.2 ml l^{-1} . Comparatively higher concentrations of zooplankton were found in this area than in other low oxygen areas, such as the northern Arabian Sea (Vinogradov and Voronina, 1962), because in the southern California Current there is a more pronounced annual productivity cycle caused by the seasonal upwelling typical of the eastern boundary currents. Vinogradov et al. (1985) studied the Black Sea and Vinogradov and Voronina (1962) the northern Arabian Sea, showing that zooplankton were also present at oxygen concentrations as low as 0.15 ml l^{-1} , and suggesting that sulfide could be as important as oxygen deficiency in restricting the vertical distribution of zooplankton. The absence of sulfide in the eastern Pacific OMZ (Muromtsev, 1963) is probably another factor that permits the development of more abundant zooplankton

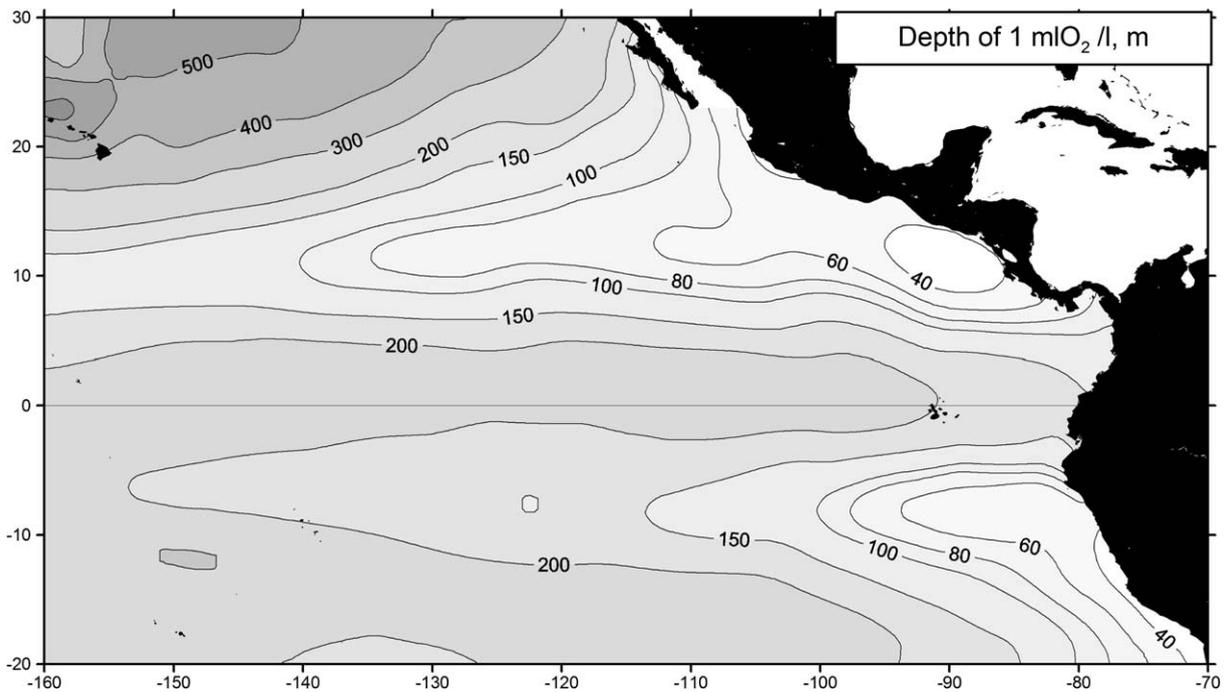


Fig. 3. Depth of the top of the oxygen minimum zone ($1 \text{ ml O}_2 \text{ l}^{-1}$ isocline). Based on Fiedler and Talley (2006).

populations. Longhurst (1967) suggested that the subthermocline low-oxygen layer is a suitable place for resting stocks of copepods, because the low temperature will reduce the metabolism of the animals, which, at that depth, will be transported northward beneath the southward and offshore surface current, and thus will be advected back to the more productive waters.

Longhurst (1985a) postulated that there are six depth zones in the upper 250 m of the water column at a station in the eastern tropical Pacific, each having different ecological characteristics. Each zone is the domain of plankton species having similar feeding requirements. Table 1 lists the different zones, which are greatly determined by the depth of the thermocline and are closely related to the concept of a *planktocline*. Longhurst (1985a) also described differences in how the herbivorous, omnivorous and predatory copepods are distributed in relation to the thermocline. Most herbivores are present within or near the thermocline and within the chlorophyll maximum during the day with very small nighttime migration; they do not cross the $1.0 \mu\text{l l}^{-1}$ oxygen concentration barrier. However, most omnivorous copepods are distributed in deeper waters, at the lower base of the thermocline and below, and migrate to deeper or shallower water during the night, performing more extensive migrations than the herbivorous copepods (see Fig. 4). The fine-resolution sampling possible with the LHPR enabled the description of these patterns.

Table 1

Principal ecological characteristics of six depth zones in the eastern tropical Pacific (Longhurst, 1985a)

Zone	Depth (m)	Salinity (psu)	Temperature ($^{\circ}\text{C}$)	NO_3 ($\mu\text{g l}^{-1}$)	Chl-A ($\mu\text{g l}^{-1}$)	PP h-1 ($\text{mg C m}^{-3} \text{ h}^{-1}$)	POC ($\mu\text{g C l}^{-1}$)	Zooplankton species (m)	
								Day	Night
Neuston layer	0–15	34.13	>28.0	–	<0.02	<0.20	0.34	0.0	15.90
Mixed layer	10–35	34.29	>28.0	–	0.18	0.29	0.46	9.20	15.30
Upper thermocline	35–55	34.84	27.20	9.85	0.48	1.10	0.44	14.80	16.70
Lower thermocline	55–85	34.73	22–15	25.55	<0.40	<0.36	<0.30	13.90	18.80
Upper mesopelagic	85–110	34.80	15–13	31.40	–	–	0.03	14.10	12.90
Lower mesopelagic	110–150	34.89	13–11	32.00	–	–	–	5.50	4.90

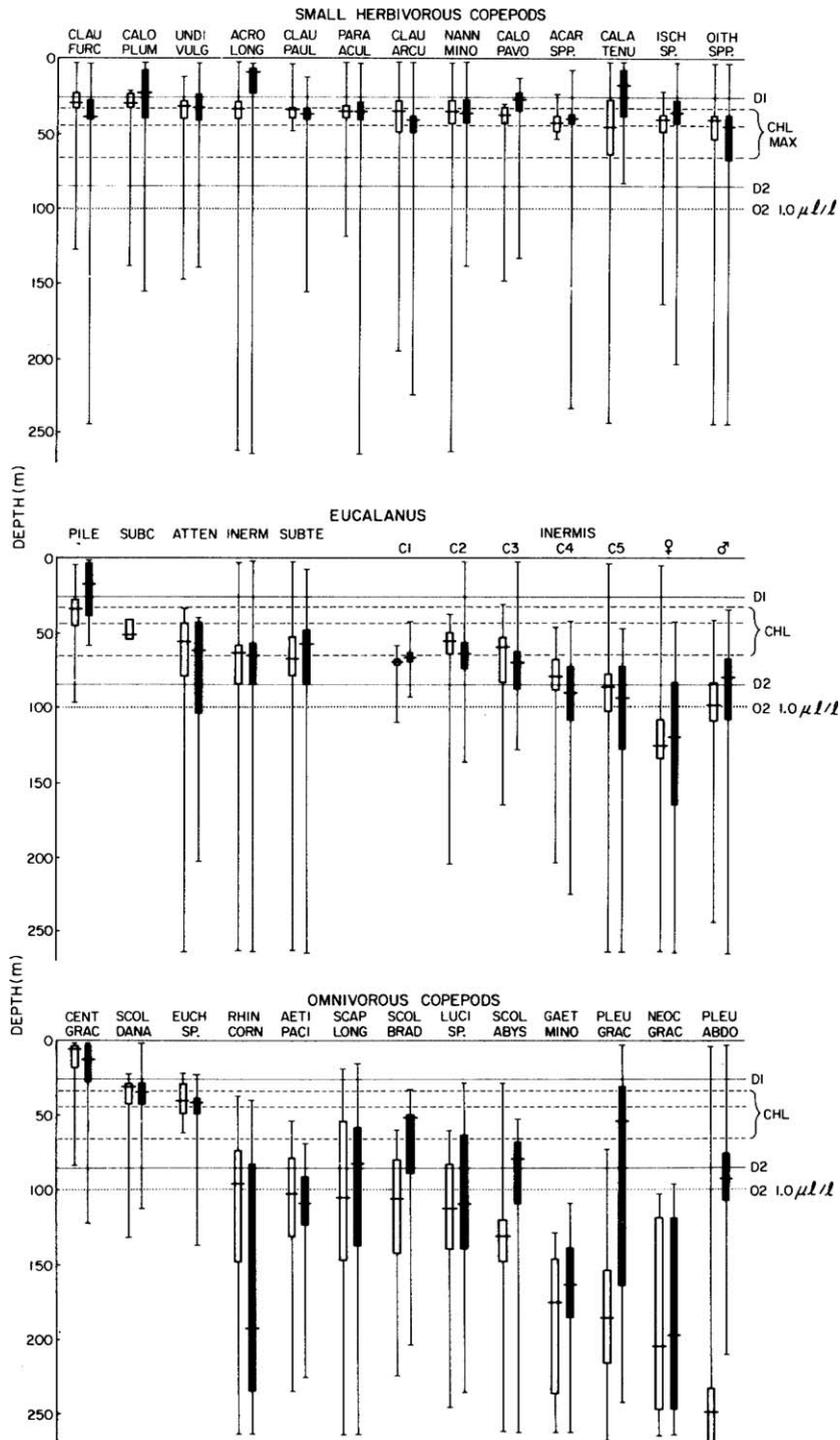


Fig. 4. Vertical distribution of small and large herbivorous copepods and of omnivorous copepods. Each species is illustrated by: total depth range, range of central 50% of population (open for day and closed for night), and modal depth. Top (D1) and bottom (D2) of the thermocline, the top, peak and bottom of the chlorophyll maximum and the isopleth of 1.0 mg Chl m⁻³ are also shown. From Longhurst (1985a, Fig. 13), which should be consulted for the full species names.

Vinogradov et al. (1991) made visual observations from a manned submersible, with the aid of net and bottle samples, to study the mesozooplankton and macrozooplankton in the region of the Costa Rica Dome, an area of low oxygen. They found that zooplankton biomass peaks at 20–35 m, then decreases in the lower part of the thermocline and below it; at ~100 m the biomass was 10-fold less. Mesozooplankton had high biomasses; the copepod *Eucalanus inermis* was the dominant species. They also found a daytime peak of meso- and macrozooplankton biomasses within the OMZ at around 600 m. The copepod *E. inermis* was found well within the OMZ and euphausiids like *Euphausia distinguenda* and *E. eximia* were also found in the OMZ. Some large chaetognaths were found from 1400 m to 2000 m but species were not identified.

Saltzman and Wishner (1997a), using a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS), found a unique vertical distribution of zooplankton in the eastern tropical Pacific: two maxima of zooplankton biomass, one near the thermocline (40–50 m) at the upper boundary of the OMZ and another in the lower OMZ (600–1000 m). They assumed that the OMZ acts as a barrier to many zooplankton species, and hypothesized that zooplankton concentrate just below the OMZ because particles found there have settled through the OMZ without degradation and, thus, they retain good nutritional value. They also proposed four different vertical distribution patterns of zooplankton taxa in that area, based on cluster analysis, patterns related to the tolerance of the species to low oxygen concentrations. The depth and vertical resolution of this MOCNESS sampling is unusual, but this classification may represent the vertical distribution patterns of zooplankton in the eastern tropical Pacific in general:

- (1) The most common pattern includes copepods, amphipods, chaetognaths and unidentified gelatinous animals, that are common to very common at all depths, with maximum abundance in the mixed layer and the thermocline and a secondary peak of biomass at the lower OMZ interface, with minimum abundances in the OMZ and below the lower OMZ interface.
- (2) Euphausiids are part of the same group, but represent a different vertical pattern, migrating from the surface waters at night to the upper OMZ during the day (but see Antezana, 2002a,b).
- (3) A cluster group formed by ostracods, polychaetes, salps and doliolids, had low abundance near the surface, with a peak in abundance at 40–75 m and a secondary peak at 600–1000 m, depending on the thickness of the OMZ. This group was also dominant in the upper OMZ, at 100–300 m, with a mean fraction of total zooplankton abundance of 43%.
- (4) Larvaceans and molluscs with maximum abundances in the mixed layer and decreasing abundances with increasing depths. They did not present a secondary maximum abundance at the lower OMZ interface zone.

2.3.2. Vertical migration

One of the most important characteristics of zooplankton is that many species perform vertical migration. There is not a clear explanation for this behavior. Mangel and Clark (1988) described 13 possible hypotheses for vertical migration presented in literature. These can be grouped into three main categories, which are not alternatives and may be complementary:

- (1) *Metabolic-demographic advantage*. Zooplankton obtain a physiological and reproductive advantage by spending part of their time in cooler waters during the day (McLaren, 1974; Enright, 1977), feeding during the night near the surface where they find more food available, especially phytoplankton, and assimilating food at cooler deep temperatures allowing greater growth efficiency and larger individual size.
- (2) *Sunlight avoidance*. Zooplankton are damaged by sunlight (Huntsman, 1924; Williamson et al., 1996) and retreat to dim depths during daylight hours.
- (3) *Predator avoidance*. Zooplankton stay in deeper waters during the day to reduce predation mortality, because they are more visible in daylight near the surface (Zaret and Suffern, 1976).

One way to detect vertical migration without vertically-stratified sampling is by day–night differences of abundance or biomass in surface waters. Historical data (see Appendix) were analyzed to better understand the day/night differences in zooplankton volume in the eastern tropical Pacific (Fig. 5). Zooplankton biomass

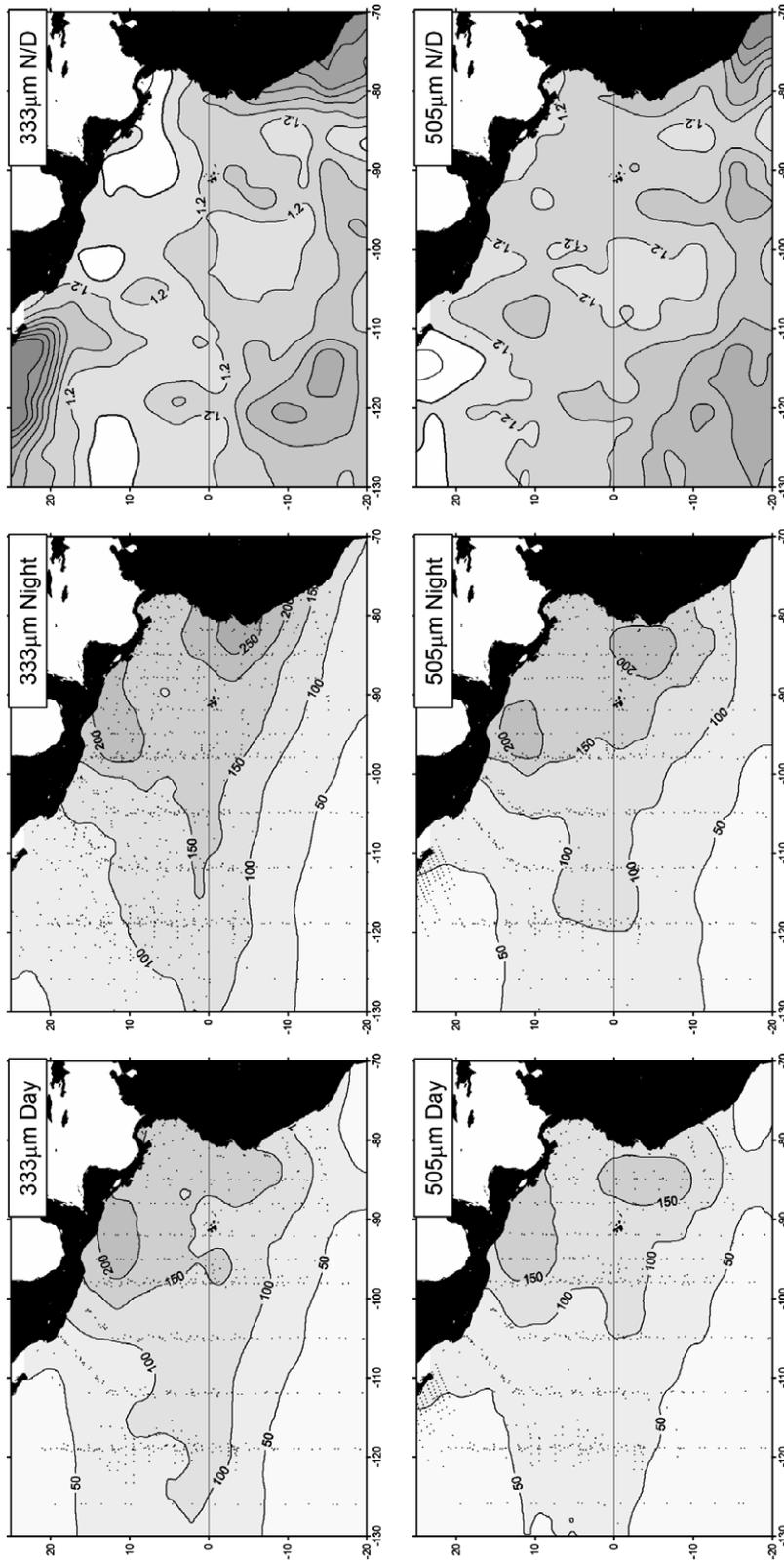


Fig. 5. Night and day distribution and night/day ratios of zooplankton volumes, $\text{ml } 1000 \text{ m}^{-3}$, from 333- to 505- μm mesh net tows, 0–200 m (see Appendix for data sources).

in the upper ~200 m increases by 20–60% at night, with greater increases evident for the larger zooplankton. These findings are being further analyzed (Färber-Lorda et al., in preparation).

Longhurst (1985a) classified the diel vertical migrations of tropical zooplankton into two types:

- (1) The interzonal migration of plankton and nekton which reside during the day in species-specific layers from 250 m to 500 m. These are euphausiids, sergestid shrimps, small bathypelagic fish, and copepods often of the genera *Metridia* and *Pleuromamma*. These layers migrate to the surface in the night and descend again at dawn. They constitute the most important element of the food chain in the tropical ocean; because they can move up to 20% of the total biomass to the epipelagic zone during the night.
- (2) Zonal migration, in which individual species perform short vertical migrations, characteristic of each species, that do not carry them to another zone.

Loeb and Nichols (1984) studied the zooplankton and ichthyoplankton of the region and found that a maximum abundance of invertebrate zooplankton occurs at the bottom of the mixed layer during the day, whereas during the night the maximum is in the upper mixed layer. Maximum abundance and diversity of ichthyoplankton occurs in the upper thermocline, and most ichthyoplankton species live below the depth of the maximum abundance of invertebrate zooplankton. The authors hypothesize that this population structure probably reflects the high surface concentrations of invertebrate zooplankton, which provide abundant food for the actively migrating adults and intense food competition and/or predation upon shallow-living larvae. Vertical migration within the shallow thermocline and mixed layer is not detectable by day–night differences of oblique tows between night and day (as in Fig. 5).

2.3.3. Copepods

Even if copepods are less dominant in tropical waters than in temperate or polar waters (Longhurst, 1985b), they constitute about one-third of the mean plankton carbon biomass. Thus, understanding their vertical migration is important to understanding zooplankton vertical distribution in general. They are also more important in the eastern tropical Pacific than in other tropical areas (Longhurst, 1985a). Vertical distribution of pelagic copepods was studied by Chen (1986). In samples obtained in May–June 1974 during the Krill cruise (see also Brinton, 1979), 63 of the 140 known species of copepods for the area were identified. Abundance was dominated by *Eucalanus subtenuis* and *Eucalanus subcrassus*, with a mean relative abundance of 33.5% and 12.8%, respectively. *Eucalanus subtenuis* was more abundant during the day than during the night and had great concentrations from 25 m to 175 m. Diel vertical migration was not apparent: the species was present from the surface to 630 m. *Eucalanus subcrassus* had a similar vertical pattern, occurring mainly above the 200 m, but the vertical range was deeper for juveniles. Vertical range of males was shallower than that of females. A comparison of day and night samples did not show vertical migration.

Saltzman and Wishner (1997b) also proposed four general patterns of vertical distribution for copepods, relating to their apparent tolerance of oxygen concentrations. These patterns are slightly different than the patterns described for zooplankton in general (Saltzman and Wishner, 1997a, see above):

- (1) The most common pattern was maximum abundance in the mixed layer and thermocline, with a secondary maximum in the lower OMZ interface layer, exhibited by copepod genera such as *Clausocalanus*, *Oncaea*, *Eucheta*, *Oithona* and *Corycaeus*. Low oxygen apparently did not restrict these groups, since they were present throughout the OMZ.
- (2) Vertical migration between the thermocline and the low oxygen zone was considered the second vertical distribution pattern. *Pleuromamma robusta* displayed this pattern, showing maximum abundance at night in the thermocline and at the core of the OMZ during the day. A secondary maximum of abundance was present at the lower OMZ interface.
- (3) The third distribution pattern was shown by copepods that were abundant in the upper OMZ and at the lower OMZ interface. This pattern was separated into two subpatterns. First, *Eucalanus inermis*, *Haloptilus paralongicirrus*, *Mormonilla* spp., *Spinocalanus abyssalis* and *Lucicutia flavicornis* were abundant in the upper OMZ and in the lower OMZ interface zone, but dominant in the upper OMZ. Second, *Heterostylites longicornis* was present throughout the OMZ, but with maximum abundances below the

thermocline and in the lower OMZ interface zone. These copepod species apparently tolerate the low oxygen concentrations and maintained viable populations in low oxygenated waters. Some species like *Rhincalanus cornutus* and *Rhincalanus nasutus* are apparently restricted by the oxygen minimum.

- (4) A fourth pattern was represented by the species that live mainly above the OMZ day and night. For this group a secondary maximum at the lower OMZ interface was sometimes present.

Vertical migration patterns may vary between locations. For example, in a comparative study at the end of winter/beginning of spring, at two contrasting eastern tropical Pacific stations (BIOSTAT, with stable conditions and DOME, with upwelling conditions), Sameoto (1986) found that only 8 of the 58 common copepod species were vertical migrators. In contrast, during autumn, at the Volcano 7 site of Saltzman and Wishner (1997a), 24 copepod species were vertical migrators. This difference was probably related to different hydrographic conditions during different seasons. Some species that showed vertical migration in some areas, were restricted to waters above the OMZ in other areas, or were absent from low oxygen concentration areas (Sameoto, 1986). In many cases, species present completely different patterns at different locations. At the DOME site, he found that mesozooplankton showed from 2 to 4 times the biomass that he observed at the BIOSTAT site, and very few species were present in the low oxygen layer. The vertical patterns might also change in relation to events like El Niño/La Niña, since physical conditions such as thermocline depth will change (Fiedler and Talley, 2006; Wang and Fiedler, 2006). However, we are aware of no observations of an ENSO effect on zooplankton vertical distribution in the region.

2.3.4. Macrozooplankton and micronekton

Euphausiids constitute an important group of large zooplankters and are, in general, both vertical and horizontal migrators (Brinton, 1962; Baker et al., 1990). They can form up to 50% of the total zooplankton biomass in the eastern tropical Pacific (Brinton, 1979). Support for one hypothesis to explain vertical migration, metabolic-demographic advantage (see above), comes from studies of euphausiids and other macrozooplankton groups. Childress (1968, 1971, 1975, 1977) found that the respiratory rate declines as depth increases, which is a very advantageous adaptation to the general reduction in food supply at depth. This reduction of metabolism is more related to the low temperature than the hydrostatic pressure. Small and Hebard (1967) and Percy and Small (1968) did not find significant differences in the respiratory rate of euphausiids at 1 atm and at 16–50 atm, which is the normal range for their vertical distribution. The results of Teal and Carey (1967a,b) support the same hypothesis. Childress and Thuesen (1993) analyzed the respiratory rate of deep-water species at hydrostatic pressures equivalent to 1000 m and at the surface and found that the relationships between animal weight and oxygen consumption at the two pressures were not significantly different. However, work by Bailey et al. (1994) showed that respiration in situ of gelatinous zooplankton, measured with a submersible, was 2–5 times higher than in shipboard incubations. This was attributed to the higher activity of the animals in deep waters; the authors suggest that there is a loss of motor activity due to decompression.

Brinton (1979) described the migratory behavior of euphausiid species within the zone from 22°N to 10°N in the eastern tropical Pacific and classified them in two groups: (1) species like *Euphausia diomedea* and *Euphausia mucronata* that migrate from the very low-oxygen waters in the day to oxygenated waters near the surface during the night; and (2) non-migrating species like *Stylocheiron* spp. with a vertical distribution within the mixed layer. He described the vertical distribution of euphausiids by stage of development for some species. Among migrating species, early larval stages have a shallower vertical distribution during both day and night than do the adults and juveniles. Another important fact is that adults and juveniles of most euphausiid species migrate within the oxygen minimum layer. In general, vertical distributional ranges become wider with maturation, being shallowest for larvae and deeper for adults. Non-migrating *Stylocheiron* spp. are most abundant near the depth of the thermocline, and their vertical distribution is apparently restricted by the 0.5 ml O₂ l⁻¹ isocline (Brinton, 1979).

The vertical distribution of euphausiids in the eastern tropical Pacific was studied by Sameoto (1986) and Sameoto et al. (1987) using a BIONESS multiple net sampling system. They found that the thermocline was the most important factor limiting vertical distribution, and that the vertical distribution is interrupted by the oxygen minimum. Highest zooplankton biomasses were found in an area of continuous upwelling as com-

pared to another non-upwelling area; biomasses at the upwelling station were among the highest recorded for tropical oceans. Twenty-two species were found at either or both locations, however, only two or three species were dominant at each. They found that euphausiid vertical distribution was greatly influenced by the oxygen minimum. Low concentrations of only a few species (*Euphausia eximia*, *E. diomedea*, *E. distinguenda*, *E. lamelligera*, *Nematocelis gracilis* and *Nematobranchion flexipes*) were found below the oxygen minimum down to 1000 m. Only two species were found within the depth zone with O_2 concentration $<0.1 \text{ ml l}^{-1}$, in opposition to findings of Brinton (1979). One possible reason for this discrepancy is the difference in sampling gear, the BIONESS net providing better vertical definition.

Antezana (2002a) found that *Euphausia mucronata* is capable of migration within the oxygen minimum zone in the southeastern tropical Pacific, from 7°S to 39°S, in oxygen concentrations as low as $0.1 \text{ ml O}_2 \text{ l}^{-1}$. All developmental stages of this species performed vertical migration within the OMZ. *Euphausia mucronata* is the dominant species in the Peru Current and shows striking adaptations to low oxygen (Antezana, 2002b), including enlarged gill surface, active swimming and respiration under anoxic conditions. It is capable of feeding within the OMZ. These adaptations permit the active utilization of the habitat by *E. mucronata*.

3. Temporal variability

3.1. Seasonal

Seasonality in the tropical oceans is weak compared to temperate and polar oceans, but seasonal changes in physical forcing are significant (see reviews in this volume: Amador et al., 2006; Fiedler and Talley, 2006; Kessler, 2006). In general, seasonal changes in local biological communities are rather small, except in upwelling regions. Seasonality in the tropical oceans, in general, is driven by the twice-yearly passage of the sun across the equator (Kessler et al., 1998). Seasonality in the eastern tropical regions also generally involves changes in the velocity and extent of the Equatorial Countercurrents (Longhurst and Pauly, 1987): the North Equatorial Countercurrent in the eastern tropical Pacific does not extend farther east during winter than about 120°W, but from May to November it extends nearly to the coastline of the American continent, where it is deflected to the north and south (Kessler, 2006).

Seasonal variability of zooplankton in the eastern tropical Pacific has not been adequately sampled since the EASTROPAC program in 1967 and 1968, when bimonthly samples were obtained from a huge area, from 20°S to 20°N and 127°W to the American coast. From these data, Blackburn et al. (1970) showed that standing stocks of phytoplankton, zooplankton, micronekton and fish varied seasonally by factors of 2 or 3 to the west of 100°W, and 3–5 in the coastal zone. Zooplankton varied synchronously with chlorophyll, or at least lagged by less than the 2-month sampling interval, while micronekton lagged by about 2 months.

Zooplankton biomasses obtained from EASTROPAC and other cruises in the years 1955, 1967–1968, 1970, 1971, 1973, and 1998–2000 are presented in Fig. 2. This constitutes an accumulation of a large amount of data ($N = 2371$, see Appendix). The quarterly fields (Fig. 6) show increased zooplankton in coastal upwelling regions after winter wind-driven production along Central America (January–March) and Peru (October–December; Carrasco and Lozano, 1989; Ayón et al., 2004), and along the equator when equatorial upwelling increases in late northern summer (July–September). This equatorial increase is maintained into autumn (October–December), when trade winds along the equator begin to decrease and upwelling weakens. Very similar seasonal patterns are seen in quarterly fields of zooplankton volume from 505- μm mesh nets (not shown).

Dessier and Donguy (1985) described the seasonal and areal distribution of copepod populations in the eastern equatorial Pacific. Near the equator (from 4°N to 4°S) an August maximum of chlorophyll was found during the peak of the upwelling season and another less distinct peak, between March and May; copepods also showed peak abundances at these times. Herbivorous copepods became more abundant relative to carnivorous species during the upwelling season. The diversity of copepods was higher in oligotrophic subtropical waters from 10°S to 14°S than in more productive equatorial waters. Few studies on the distribution of ichthyoplankton have been published, however, the EASTROPAC study showed that the species dominance of the eastern equatorial Pacific ichthyoplankton was not seasonally variable (Ahlstrom, 1971, 1972b). During February–March 1967, the most abundant groups were the families Myctophidae, followed by the Gonostomatidae, Sternoptychidae and Bathylagidae. However, in samples from near Central America to Peru, and in

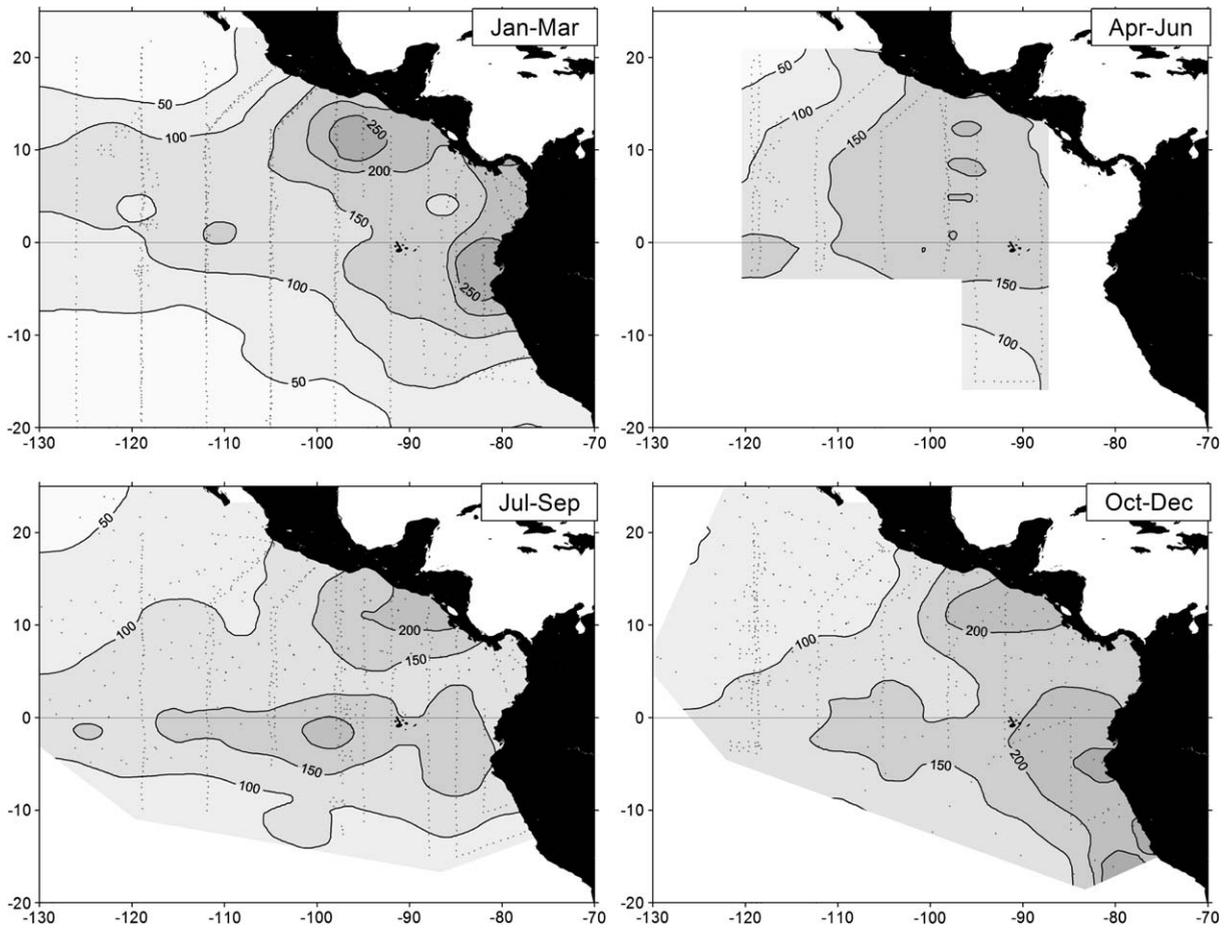


Fig. 6. Mean quarterly fields of zooplankton volumes, $\text{ml } 1000 \text{ m}^{-3}$, from 333- μm mesh net tows, 0–200 m (see Appendix for data sources).

part of the Peru upwelling area, the third most abundant group of fish larvae was the Bathylagidae. Six months later (September–October, 1967), a similar spatial distribution pattern was found, with the same families of larvae dominating the samples, although abundances were higher during this time of year. In general, higher abundances were found in the area around the Peru Upwelling system and around the Galapagos Islands and along the equator, except for the Gonostomatidae, for which the maxima were found in the area around 120°W and south of 10°S.

3.2. Interannual (*El Niño* and *La Niña*)

Interannual variability in the eastern tropical Pacific is dominated by the El Niño/Southern Oscillation (ENSO) with a period of 2–7 years. Wang and Fiedler (2006) review the differences between periods when trade winds are well developed, considered as normal conditions, and El Niño periods when easterly trade winds are weak or even replaced by westerly winds at low latitudes. From an ecological geography point of view, Longhurst (1998) recognized the influence of two principal modes of circulation depending on ENSO variability in the Pacific. These modes have important consequences in the distribution patterns of the biota in the eastern tropical Pacific. During normal conditions, Longhurst (1998) recognized three tropical provinces within the Pacific Trade Wind Biome: (a) the North Pacific Equatorial Countercurrent; (b) the Pacific Equatorial Divergence; and (c) the Western Pacific Warm Pool. During an ENSO event, these provinces lose their characteristics partially or completely to the extent that the entire tropical Pacific can be characterized as a

single trans-Pacific WARM-ENSO province with warm surface water, a deep thermocline and low productivity.

Zooplankton sampling has not covered ENSO variability in the region, except for local areas or single events. Dessier and Donguy (1987) used samples and data obtained by ships of opportunity to study the response of the epipelagic copepod populations to ENSO in the eastern tropical Pacific. The sampling period was from 1979 to 1984, from 20°S to 10°N along a track from New Caledonia to Panama. During the 1982–1983 El Niño event, the authors distinguished two phases: during the first phase, from November 1982 through the end of 1984, the thermocline deepened, resulting in strong declines of primary productivity and abundance of total copepods along the equator. This phase also included an anomalous eastward flux along the equator carrying impoverished populations with low abundance from the west. The second phase, beginning in April 1983, was characterized by a new areal distribution of copepods, which was related to the southwestward extension of the low salinity surface waters from the Gulf of Panama. During the 1982–1984 El Niño period, no seasonal signal was detected in the region. Vecchione (1999) recorded an unusual abundance of paralarval cephalopods in surface plankton samples during El Niño 1987 in the eastern tropical Pacific.

Hydrography, zooplankton biomass, and zooplankton community changes along the coast of Peru were followed by Carrasco and Santander (1988) during the El Niño event of 1983. A warming of surface waters was found, accompanied by a general decrease of zooplankton biomass during El Niño. However, in some areas, such as the central Peru coast, zooplankton biomass increased. Copepods, appendicularians, siphonophores and other groups of zooplankton showed a pronounced decrease in 1983, in relation to the “normal” years of 1981 and 1977. Larval stages of the common zooplankton species also decreased in abundance. Furthermore, Penaeid shrimp larvae, which are not common to the area, were present in 1983. A long time series from Peru coastal waters shows no consistent effect of El Niño events on zooplankton volume (Ayón et al., 2004): some events are associated with declines (1972–1973, 1982–1983), but others are not (1986–1987, 1997–1998). Fig. 7 shows this time series in relation to positive sea surface temperature anomalies. It is clear that after the 1972 El Niño, the zooplankton volume has remained lower than before and also that the last two El Niño events did not produce a decrease in zooplankton mean volume.

A comparative study of the changes in trophic relationships and abundances of zooplankton groups of different sizes, during El Niño and non-El Niño conditions was conducted by González et al. (2000). They studied the composition, biomass and grazing impact of crustaceans and tunicates in the northern Peru Current

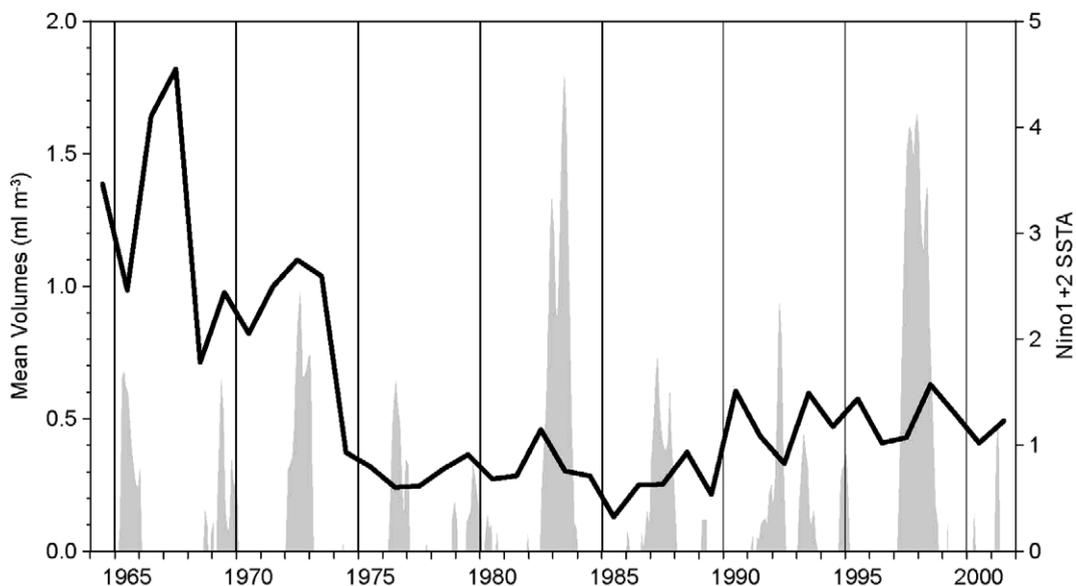


Fig. 7. Mean annual zooplankton volumes, $\text{ml } 1000 \text{ m}^{-3}$, from 300- μm mesh net tows, 0–50 m (the bold line; Ayón et al., 2004) and corresponding positive monthly sea surface temperature anomalies (gray) in Peru coastal waters. (NINO1+2 SSTA is sea surface temperature anomaly, 0–10°S, 90–80°W).

during El Niño and non-El Niño years: before the El Niño (January 1997) during the El Niño (July 1997) and at the maximum of El Niño (January 1998). Crustaceans were divided into large, medium and small size categories. Small calanoid copepods represent a minor fraction of the crustacean zooplankton biomass (4–20%), but accounted for a relatively large portion of total ingestion (26–68%) by the crustacean community. Large euphausiids represented a large fraction of total zooplankton carbon (28–73%) and contributed 5–61% of total crustacean grazing. Specific ingestion rate was negatively correlated with animal size. Ingestion by copepods exceeded respiratory needs for the three periods sampled. For euphausiids, in contrast, respiratory needs exceeded ingestion, which leads to the conclusion that they have other sources for food. During El Niño, the thermocline deepened with consequently lower primary productivity. No significant difference was found between the El Niño and non-El Niño zooplankton biomasses, but a shift in the size spectrum toward smaller sized copepods occurred during El Niño conditions.

3.3. Interdecadal changes

Physical variability in the eastern tropical Pacific on scales of 10 years and longer is reviewed by [Mestas-Núñez and Miller \(2006\)](#). In the eastern boundary currents of the Pacific Ocean, the small pelagic fish community alternates on time scales of 10–50 years between dominance of anchovy, associated with cool water, and sardine, associated with warm water ([Chavez et al., 2003](#)). In the mid-1970s, the anchovy (cool) regime prevailing in the eastern Pacific changed to a sardine (warm) regime. This regime apparently changed back to an anchovy regime in the late 1990s. According to their findings, this return to a cool regime includes higher zooplankton biomasses, as a result of stronger upwelling and greater equatorward transport of cool water, and higher primary production. It is assumed that the changes in the Peru upwelling region are very similar to those of the California coast (however, see [Ayón et al., 2004](#), and discussion below). A long-term trend was reported by [Roemmich and McGowan \(1995\)](#) for the southern California section of the California Current: a decrease of 70% in macrozooplankton biomass from 1951 to 1993 was related to a warming of the surface layer and an increased stratification with a consequently lower input of inorganic nutrients that support a smaller zooplankton population. In the North Pacific, recent evidence of a regime shift following the 1997–1998 El Niño has shown a change in species composition to more boreal species than were seen during the earlier 1990s ([Batten and Welch, 2004](#); [Mackas et al., 2004](#)).

[McPhaden and Zhang \(2002\)](#) presented evidence that sea surface warming in the equatorial Pacific since the 1970s was associated with a decrease in equatorial upwelling that is part of the meridional overturning circulation forced by easterly trade winds. The authors suggest that the reduction in upwelling should have affected biological production in the region. Unfortunately, there are no long time series of zooplankton abundance or biomass in the region to test this hypothesis. Zooplankton sampling with bongo nets in 1998–2000 indicates no substantial change in zooplankton biomass compared to EASTROPAC ring net sampling of 1967 ([Fig. 8](#)), but the tropical shallow meridional overturning circulation apparently rebounded beginning in 1998 ([McPhaden and Zhang, 2004](#)).

[Carrasco and Lozano \(1989\)](#) described the long-term changes of zooplankton biomass off Peru, using data from 1964 through 1987. A clear decline of zooplankton biomass was found that was most pronounced after 1974. Seasonal changes are also analyzed, with highest biomasses in southern spring (October–December). The long-term study by [Ayón et al. \(2004\)](#) extended this time series through 2001. They describe zooplankton volume and anchoveta biomass trends for 35 years in the Peru Current ecosystem. The authors separate three periods, “highest” from 1964 to 1973, “lowest” from 1974 to 1989 and an “intermediate” period from 1990 to 2001. However, for anchoveta, the “intermediate” period began in 1984, coinciding with cooling of coastal waters off Peru, followed by five years of “highest” biomass (1991–1995). The seasonal spring peak of zooplankton biomass was less marked in the warm 1980s, compared to the 1960s and 1970s. There is general agreement between trends of zooplankton biomass and anchoveta biomass in the 1960s and the 1970s, with a sharp decline of both at the beginning of the 1970s. This was followed by an increase of anchoveta biomass after 1983, but not of zooplankton biomass, which remained low until 2001. The recent “intermediate” period has not shown a recovery of zooplankton biomass to the level of the 1960s. Since their biomass has increased considerably, anchoveta have shown either a remarkable adaptation to a lack of zooplankton for food by switching to more phytophagous feeding from 1985 until 2001, or there has been improved survival of larval

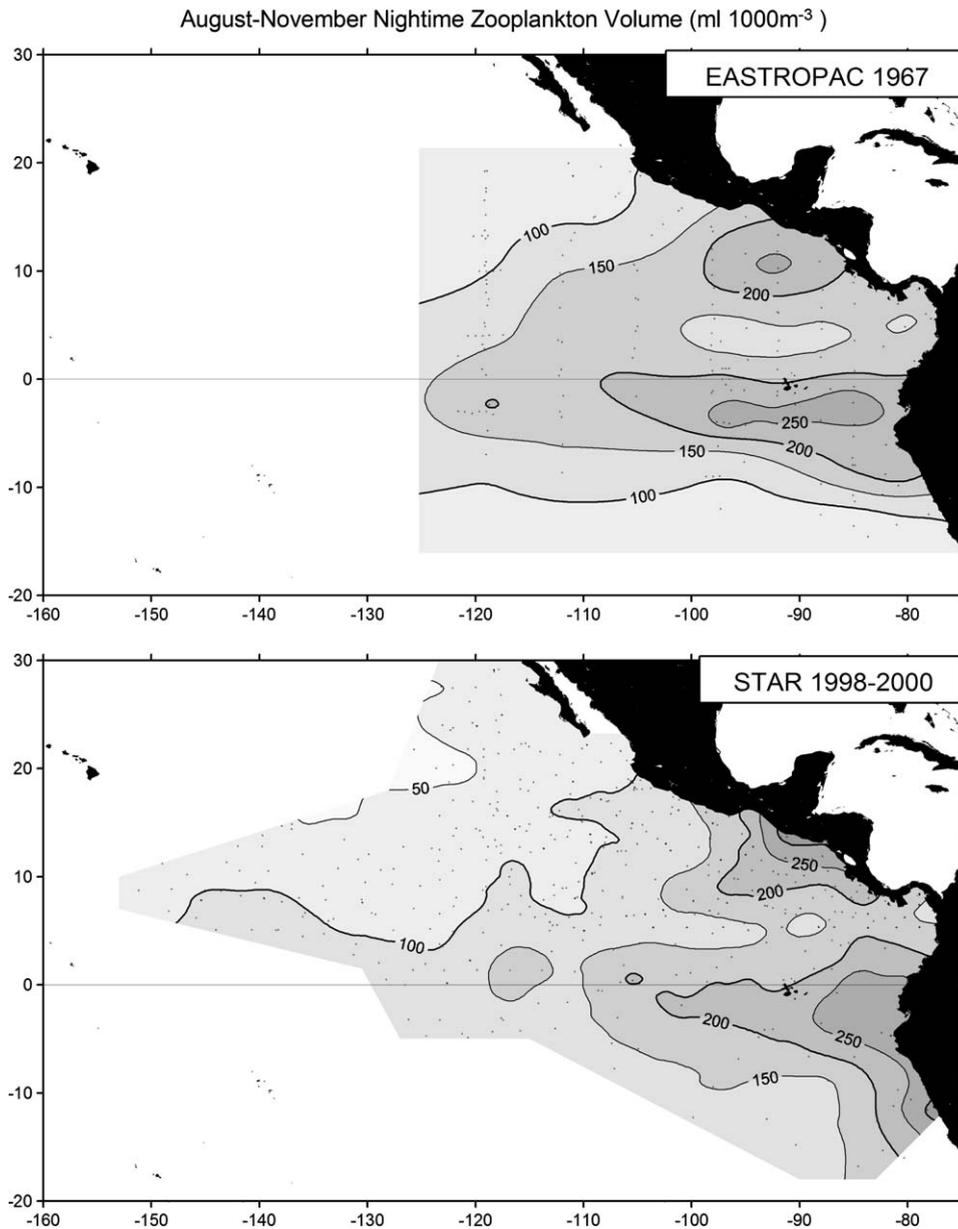


Fig. 8. Night zooplankton volumes for August–November 1967 compared to 1998–2000 (see Appendix for data sources).

stages due to a greater abundance of phytoplankton (Muck et al., 1989). Sea surface temperature (SST) decreased during the 1985–2001 period, but no significant correlation to anchoveta biomass or zooplankton volume could be established.

Changes during the early 1970s in zooplankton off Peru were coincidental with the anomalies of boreal and southern copepods in the North Pacific associated with the North Pacific regime shift of the early 1970s, as shown in Fig. 9 (from Mackas et al., 2004). However, no zooplankton changes have yet been observed off Peru corresponding to the apparent late 1990s shift to a colder regime and higher zooplankton biomass in coastal waters of the eastern North Pacific. However, in response to an El Niño off Peru, in 1997–1998 there was a reduction of anchoveta biomass, followed by an increase in 1999 toward pre-El Niño levels (Ayón et al., 2004). Färber-Lorda (2004) concluded that species composition modifications and lower productivity occurred during the El Niño, with coincident changes in species composition in different areas such as the Gulf

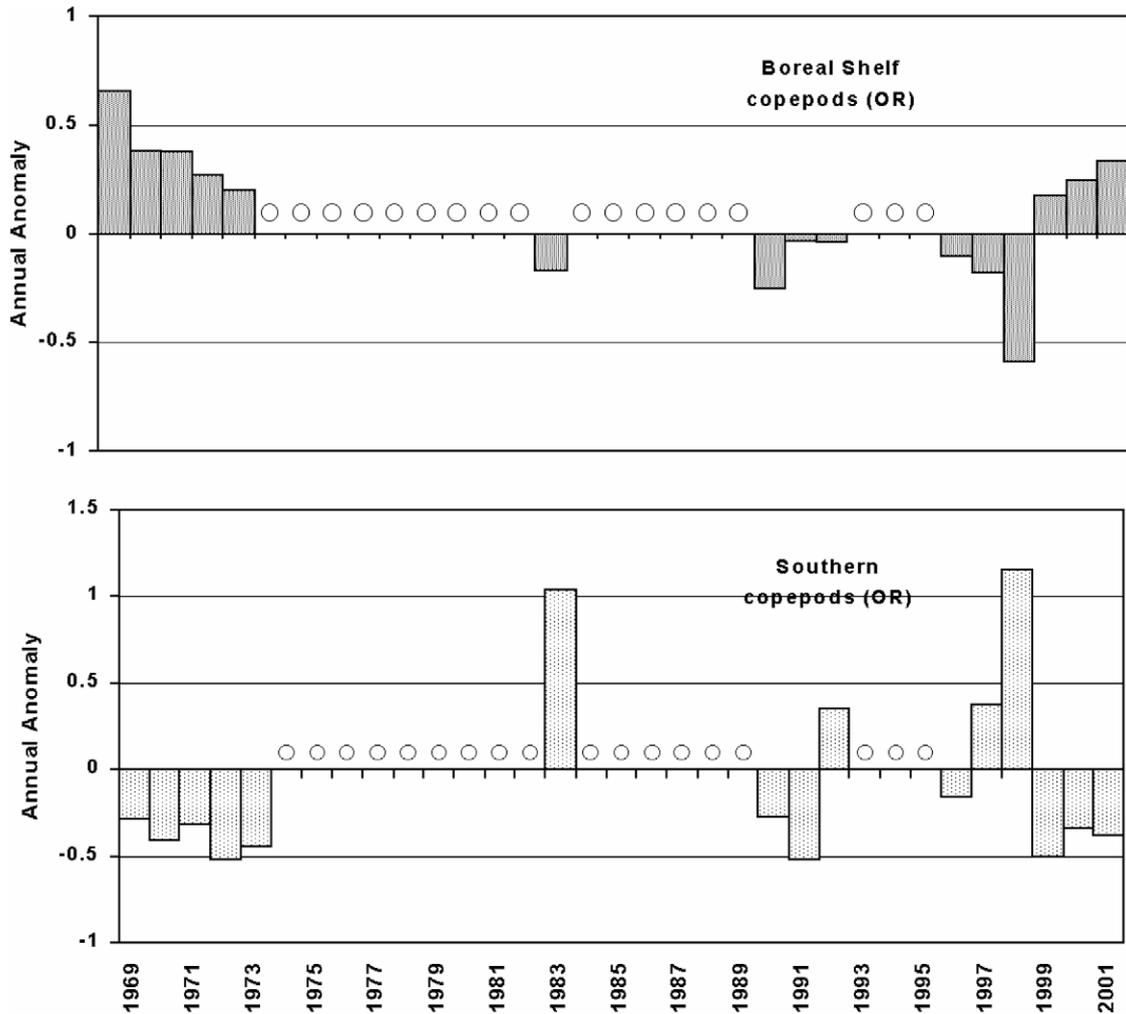


Fig. 9. Anomalies of Boreal and Southern copepods from Oregon (from Mackas et al., 2004, Fig. 4). Zero anomalies were found from 1973 (one year after the Peru sardine and zooplankton crash) until the 1982–1983 El Niño event, when a negative anomaly for boreal copepods and positive anomaly for southern copepods was found. Note that after the 1997–1998 El Niño/La Niña, Boreal copepods passed from a strong negative anomaly to a positive one in 1999, and the opposite for Southern copepods.

of California and the Peru upwelling. He suggested that the 1997–1998 El Niño triggered the 1998–1999 North Pacific regime shift (see also Yasunaka and Hanawa, 2005).

4. Trophic relationships

Oceanographic factors influence spatial and temporal patterns of zooplankton and phytoplankton, as reviewed above and in Pennington et al. (2006), and must therefore influence the trophic relationships that organize pelagic ecosystems. We will briefly review the characteristics of tropical, compared to higher-latitude, systems before reviewing oceanographic influences on trophic relationships in the eastern tropical Pacific.

4.1. Tropical pelagic ecosystems and food webs

There is often a clear functional relationship between annual cycles of zooplankton productivity and phytoplankton productivity. In polar and temperate ecosystems, the first lags the second by about two months,

but there are different cycles in different waters: there is only one annual peak of phytoplankton and zooplankton stocks in the polar oceans, due to a brief release from light limitation, while in the North Atlantic and other temperate waters there are typically two peaks in the annual cycle, one during spring and a smaller one during autumn. In the tropical oceans, as generalized by Sournia (1969), there are not always such obvious seasonal changes, but more a succession of small increases and decreases in phytoplankton and zooplankton stocks, determined by local weather conditions and the movement of water masses. However, when conditions of upwelling are present, as in the coastal and equatorial areas of the eastern tropical Pacific, seasonal variability is more pronounced (see Fig. 7 in Wang and Fiedler, 2006). Phytoplankton and zooplankton stocks vary in response to the seasonal upwelling cycle. Raymond (1983) gave a general review of the complex relationships between phytoplankton and zooplankton; however, it is apparent that, at that time, there were very few plankton studies in tropical regions, in particular about grazing.

Longhurst (1985b) analyzed the trophic groups of an idealized warm-water plankton ecosystem, shown schematically in Fig. 10. The relationship of these categories with their food supply is shown in Table 2, in which comparisons among polar, temperate, and tropical oceans are made. It is obvious that the tropical ecosystem is very different than high-latitude ecosystems. The relative number and biomass of predators in the tropical ocean is higher than in polar and temperate ecosystems: there is twice as much biomass of predators relative to herbivores and detritivores in tropical than in polar oceans, and on tropical shelves than on temperate continental shelves.

Microzooplankton (sizes $<202\ \mu\text{m}$) were studied by Beers and Stewart (1971), with samples obtained by pumping during the EASTROPAC cruise (Beers et al., 1967). Biomass varied from $15\ \text{ml}\ 1000\ \text{m}^{-3}$ in subtropical water south of the equator to $47\ \text{ml}\ 1000\ \text{m}^{-3}$ near the equator. Average microzooplankton biomass was 34% of phytoplankton biomass, a considerably higher value than that found in the California Current where it was on average 23%; however, the groups had basically the same composition. Three size categories were analyzed: ciliates, followed by tintinnids, dominated the $<35\ \mu\text{m}$ group; copepod nauplii and post-nauplii, followed by tintinnids, dominated the $35\text{--}103\ \mu\text{m}$ size group; and copepod nauplii and post-nauplii were most abundant in the $>103\ \mu\text{m}$ size group. These authors calculated that up to 70% of the daily phytoplankton organic production is consumed by microzooplankton. This indicated that microzooplankton were actively grazing on a greater proportion of the tropical phytoplankton than previously thought.

Ikeda (1985) showed that zooplankton from low latitudes near the equator had higher metabolic rates, but lower total biomasses, compared to zooplankton from mid-latitudes. He concluded that 85–95% of the difference in metabolic rates can be attributed to body size and environmental temperature. It is well known that lower latitude zooplankton is composed of smaller animals, and their metabolism is more accelerated due to higher temperatures. He also showed that there is a strong negative correlation between adult body mass and

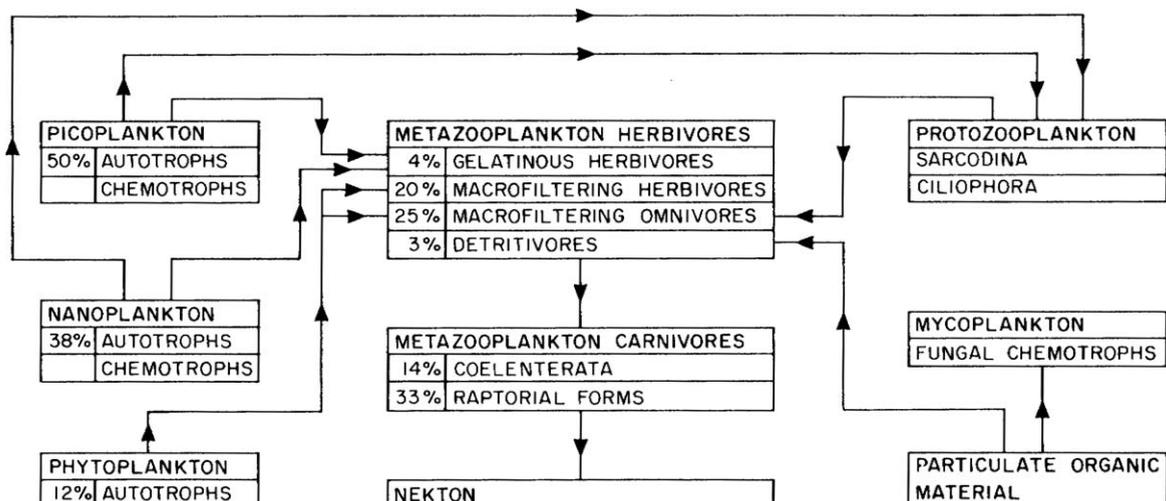


Fig. 10. Schematic trophic groups analysis for a warm-water ecosystem, from Longhurst and Pauly (1987).

Table 2

Latitudinal variation in relative importance of zooplankton trophic groups, as relative biomass (Longhurst, 1985b)

	Gelatinous predators (%)	Raptorial predators (%)	Gelatinous herbivores (%)	Grazing herbivores (%)	Grazing omnivores (%)	Detritivores (%)
Oceans						
Polar	0.88	21.72	0.21	56.13	18.08	2.98
Temperate	4.08	33.65	0.68	19.80	39.80	1.98
Tropical	14.30	33.05	4.12	20.48	26.64	3.44
Shelves						
Temperate	3.62	14.01	1.07	43.08	37.90	0.31
Tropical	9.84	28.14	6.28	7.84	42.58	5.31
Bays						
Temperate	0.00	21.61	0.29	26.24	39.18	0.4
Tropical	1.14	53.50	0.56	18.91	25.42	0.8
Reefs						
Tropical	4.30	21.54	1.00	6.94	38.53	1.27
Global (%)	4.77	28.40	1.78	24.93	33.27	2.06

temperature, and a strong positive correlation between body size and metabolism, especially for oxygen metabolism. Ikeda extrapolated the data to generate a geographical expression showing that, although relative zooplankton biomass is very high at high latitudes, relative secondary production rates per unit area are similar between high and low latitudes (see Fig. 11).

A “microbial loop” – consisting of dissolved organic matter, autotrophic and chemotrophic bacteria, viruses and protozoa – is now understood to be an important complement to the particulate “grazing food chain” in pelagic food webs (Landry, 2002). The food web in tropical waters is fundamentally different than

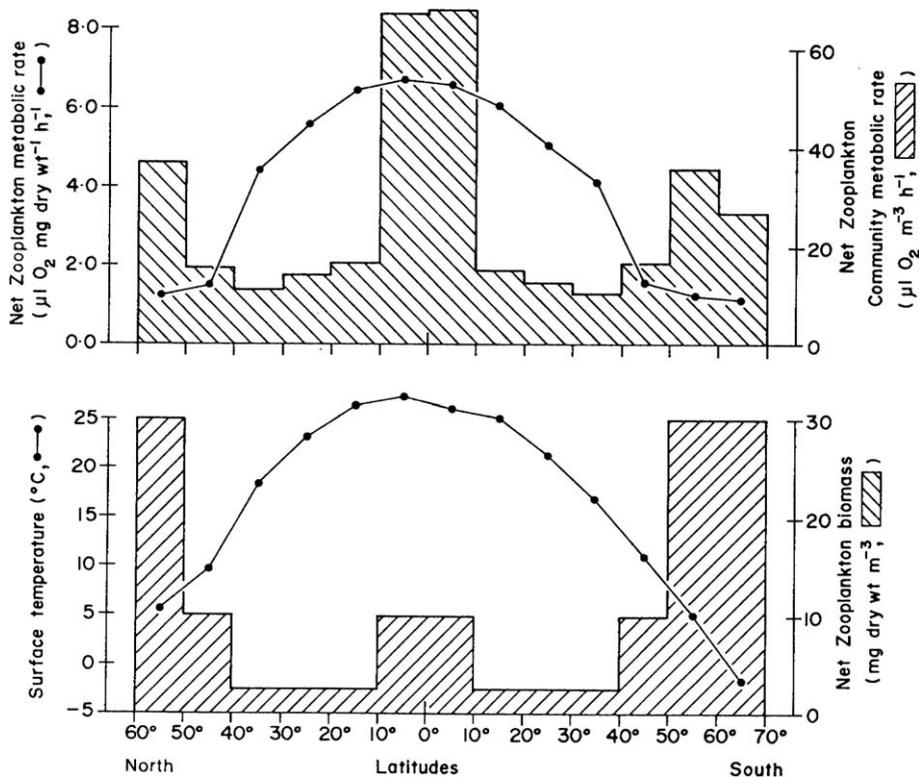


Fig. 11. Latitudinal variations in the western Pacific of (A) zooplankton-specific and total (community) metabolic rate and (B) zooplankton biomass (0–150 m) and surface water temperature. From Ikeda (1985, Fig 3, with permission from the author).

in other waters, because abundant smaller zooplankton grazers are able to feed on the production of this microbial loop. Bacteria are an important source of food for a great part of the microzooplankton that are, generally, smaller-sized species. The entire zooplankton community is composed of smaller individuals, and microzooplankton are very important in the transfer of energy to higher trophic levels. Frost (1991) discussed the general grazing hypothesis, including the role of microzooplankton in nutrient-rich areas of the open oceanic regions. A great variety of heterotrophic protists are consumers of bacterial and fungal cells. These single-cell organisms are the food of multicelled metazoan zooplankton. Calbet and Landry (2004) analyzed the impact of microplanktonic grazers on marine phytoplankton from literature data. They found that in tropical and subtropical areas, micrograzers consumed up to 75% of primary productivity as compared to ~59% for the polar, subpolar and temperate systems.

Gaudy et al. (2004) studied zooplankton trophic relationships between 8°S and 8°N along 180° in the central equatorial Pacific, representing the westward extension of the HNLC (high nutrient–low chlorophyll, see below) conditions of the eastern equatorial Pacific. Highest mesozooplankton biomasses occurred south of the equator; lower biomasses at some stations were attributed to the passage of a tropical instability wave (see Willett et al., 2006), which advected more oligotrophic waters with few zooplankton from the north. They concluded that since phytoplankton was insufficient, mesozooplankton must supplement their diet with other food sources such as microzooplankton, a hypothesis supported by their finding of low C:N ratios and a low level of O:N metabolic ratios suggesting food with high protein content. They also found higher proportions of carnivorous copepods at the equator. In another study at the equator in the central Pacific, Dam et al. (1995) concluded that up to 80% of the carbon ingested by mesozooplankton was not phytoplankton, and that the amount of carbon use by mesozooplankton corresponded to 23% of the primary production.

Gaudy et al. (2004) presented a budget for the photic layer in the central equatorial Pacific, in which bacteria are an important source of food for microzooplankton, which in turn could be the main source of food for mesozooplankton (Fig. 12). The authors used published information and their own data to construct this budget, thus it is one of the most current and complete budgets for an equatorial area. In general, micrograzers consume more phytoplankton and bacterioplankton than mesozooplankton, and mesozooplankton obtain most of their food from microzooplankton, less from phytoplankton than in temperate and polar areas. This budget illustrates the importance of the “microbial loop” in the area. A greater proportion of zooplankton feed on bacteria in these waters than in temperate or polar waters, and the entire zooplankton community is composed of smaller individuals. Also, microzooplankton, which make up a larger proportion of the mesozooplankton diet, have a higher nutritional value than the same amount of phytoplankton (by weight), thus transferring more energy between that trophic level and the next, than in temperate waters.

4.2. Trophic relationships and distribution of phytoplankton and zooplankton

Vertical and horizontal distributions of zooplankton (reviewed above) will obviously affect food availability for zooplankton consumers, as well as predation pressure on zooplankton populations. It has been argued that zooplankton vertical migration gives a physiological advantage: during the day, metabolic rates are lowered in cooler waters at depth, and, during the night, migration into the euphotic zone increases availability of phytoplankton food. However, this is based on the paradigm that food is more abundant near the surface, which is not always true (Dini and Carpenter, 1992; Williamson et al., 1996). Färber-Lorda et al. (2004b) found higher particulate protein at 10% and 1% light attenuation depths than at the surface in some stations in the entrance to the Gulf of California.

Longhurst (1985a) compared the diversity and vertical structure of two sites in the eastern tropical Pacific, one with a more stable hydrography (BIOSTAT) and one at the Costa Rica Dome (DOME) with almost constant upwelling, with data from the Longhurst-Hardy Plankton Recorder. He found greater variability of profiles of physical variables and plankton at DOME than at BIOSTAT. He showed how the different feeding groups of zooplankton have a coherent depth distribution (Fig. 13). Herbivorous copepods were present in the chlorophyll-rich layer, omnivorous calanoids had a slightly deeper, but wider distribution, and predatory copepods had a similar distribution to the omnivorous species. He also showed that other groups like chaetognaths and ostracods also followed these characteristic patterns.

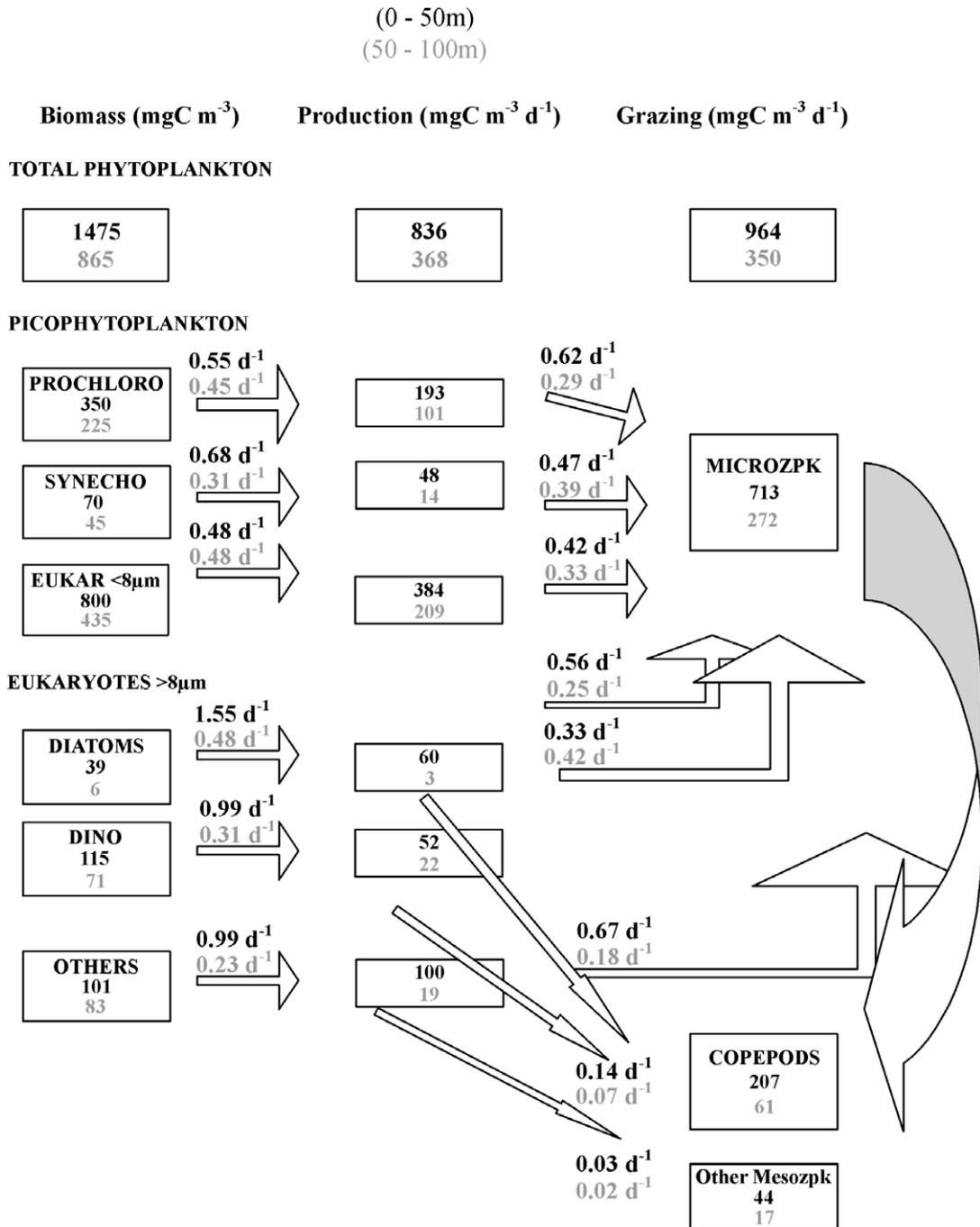


Fig. 12. Carbon budget of a zooplankton community in the equatorial central Pacific: (a) 0–50 m, (b) 50–100 m. Modified from Gaudy et al. (2004, Figs. 11 and 12). Feeding relations between the different compartments are indicated by arrows and the curved arrow indicates the possible trophic link between mesozooplankton and microzooplankton (not determined by the authors).

Longhurst (1976) analyzed interactions between 86 zooplankton and phytoplankton profiles obtained during EASTROPAC. He found that an epiplankton maximum at the base of the mixed layer corresponded with the depth of maximum carbon fixation, above the chlorophyll maximum. He concluded that the form of chlorophyll profiles may be influenced or determined by a depth-differential in herbivore grazing pressure, in addi-

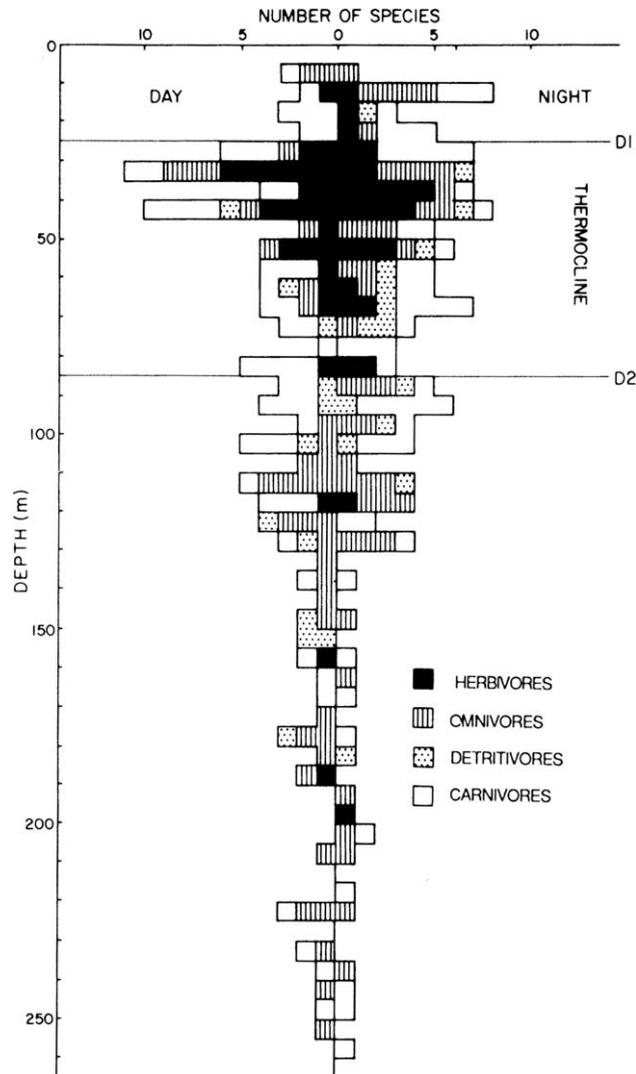


Fig. 13. Vertical distribution of functional groups of zooplankton from two stations in the eastern tropical Pacific (from Longhurst, 1985a, Fig. 6).

tion to the effects of differential cell-sinking rates as is assumed in some classical production models. King et al. (1978) studied the electron transport system (ETS) activity, a measure of respiration rate, of nanoplankton and zooplankton of the euphotic zone in the eastern tropical North Pacific. Results showed that most of the carbon fixed in the euphotic zone was respired there; 75% of the total water column respiration (0–3000 m) occurred within the euphotic zone and >90% above 200 m depth.

The vertical distribution and feeding of chaetognaths was studied by Terazaki (1996) at a station in the central equatorial Pacific using a Vertical Multiple Plankton Sampler net. Fourteen species were found, the most abundant being *Sagitta enflata*. In the 0–50 m layer, the fraction of the population containing food items was between 4.8% and 12.5%. The highest feeding activity was found from sunrise to noon, when vertical migrators had left surface waters. The stomach contents of the animals showed that copepods are the main food source. He calculated that *S. enflata* consumes 7.9% of the daily secondary production of the area.

Upwelling regions and frontal areas have hydrographic characteristics that affect both the distribution of zooplankton and the trophic conditions. Upwelling and mixing of deep nutrient-rich water into the euphotic zone results in higher primary and secondary productivity. Observations off the southwestern coast of

Mexico (Färber-Lorda and Lavín, in preparation) have shown contrasting patterns of productivity and zooplankton abundance in the wind-driven mixing and upwelling region of the Gulf of Tehuantepec, the advective mixing and frontal region at the entrance to the Gulf of California, and the more stratified and less productive coastline between these two productive regions (Fig. 14). POM, zooplankton biomass, euphausiid abundance, and lipid content of euphausiids were higher in the productive regions, indicating better

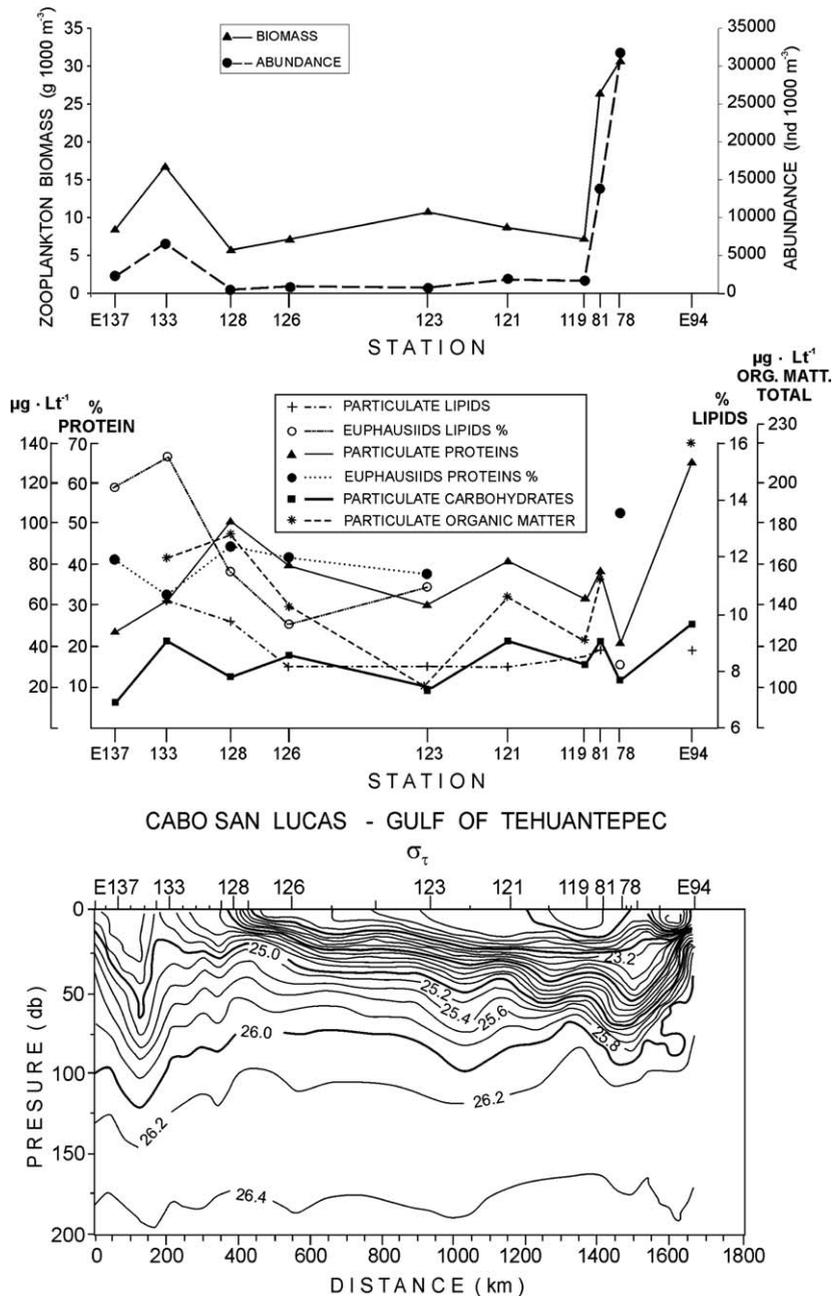


Fig. 14. Zooplankton biomass and euphausiid abundance (top), biochemical composition and potential food supply (middle), and 0–200 m sigma-t (bottom) measured along a transect from Cabo San Lucas (0 km) to the eastern side of the Gulf of Tehuantepec (1650 km). Productive areas at the Gulf of California mouth (0–400 km) and Gulf of Tehuantepec show increases in zooplankton abundance and nutritional status. Note upwelling in the middle of the Gulf of Tehuantepec (~1640–1650 km) and at Cabo Corrientes (350–400 km). From Färber-Lorda and Lavín (in preparation).

trophic conditions for the zooplankton (Färber-Lorda et al., 1994; Färber-Lorda, unpublished data). Färber-Lorda et al. (2004a,b) showed that zooplankton concentrations were coincident with higher productivity areas in the entrance to the Gulf of California. Multiple linear regressions between zooplankton biomass and POM were improved by separating different water masses and layers of light intensity, suggesting that changing hydrographic conditions, within short time periods, can result in different trophic conditions to which zooplankton can respond.

Ohman et al. (1982) analyzed biological and hydrographic data from two cruise sequences in the eastern North Pacific. They found important temporal changes in vertical patterns between winter and summer, which they attributed partially to seasonal cycles in vertical mixing and stability. Roman et al. (1995) described zooplankton variability on the equator at 140°W, contrasting El Niño conditions during March–April 1992 and non-El Niño conditions during October 1992. The average integrated zooplankton biomass in the upper 200 m was slightly, but not significantly, higher during October than during March–April. However, by October the thermocline had shoaled and zooplankton were more aggregated in the upper euphotic zone, copepods were more abundant and there were greater day/night differences as a result of vertical migration behavior. During the October cruise, a transient, nearly 5-fold increase of zooplankton biomass was attributed to the passage of a tropical instability wave.

4.3. Grazing and HNLC conditions

Much of the central and eastern tropical Pacific is classified as high nitrate, low chlorophyll (HNLC), meaning that primary production is limited by a factor or factors other than the intensity of light at the surface or the input of nitrate or phosphate across the nutricline (Cullen, 1991). Two general hypotheses to explain HNLC conditions are iron limitation and grazing limitation. Aumont et al. (2003) concluded that HNLC conditions in general could be explained by simultaneous iron limitation and grazing effects, where diatoms are limited by iron and nanophytoplankton is controlled by microzooplankton grazers.

Minas and Minas (1992) analyzed the relationships between water column chlorophyll contents and zooplankton grazing and concluded that grazing could be the main factor controlling the growth rates of phytoplankton populations in tropical upwelling systems. Mackey et al. (2002) suggested that even the picophytoplankton of the Pacific equatorial HNLC region might be controlled by macro-grazers.

Landry et al. (1997) reviewed the iron and grazing constraints on primary production in the central equatorial Pacific. They concluded that phytoplankton losses are dominated by microzooplankton grazing, which crops phytoplankton to a low stable level, but that remineralized iron from grazing sustains high total rates of phytoplankton production. Le Borgne and Rodier (2002) compared two sites in the central and western Pacific, the HNLC zone and the Warm Pool zone. Chlorophyll-*a* was 1.4 times higher and the mesozooplankton 2.6 times higher in the HNLC zone. They noted that the differences in standing stocks between these two sites were less than the difference in fluxes of the biological pump, which were higher in the HNLC zone by a factor of 2 to 4 times. That is consistent with the importance of grazing in the HNLC zone.

Strom et al. (2000) analyzed the great stability of phytoplankton productivity in all HNLC regions by a coupled experimental and modeling approach. They hypothesized that behavioral and physiological capabilities of the micrograzers hold the key for this until then unexplained stability, notably the highly plastic feeding capabilities of protist grazers switching from phytoplankton to bacteria and/or detritus.

A series of experiments to study the consequences of iron enrichment were performed in the eastern equatorial Pacific during the IronEx II experiment in May–June 1995. First, the dynamics of the phytoplankton growth and microzooplankton grazing were followed by Landry et al. (2000a) and Landry et al. (2000b): growth rates of phytoplankton quickly increased 2-fold, but grazing and growth were again balanced by the sixth day. Rollwagen-Bollens and Landry (2000) followed the biological response of mesozooplankton in this experiment. Mean carbon biomass increased 2–3-fold during the phytoplankton bloom, which they suggested was due to both a reproductive response (higher abundance of nauplii) and alteration of vertical migration, moving upwards due to the reduced light penetration. Although measured mesozooplankton growth rates were maximal, abundances and biomass declined before the end of the bloom, either

because of a quick response by predators or inadequate nutrition for viable young from the diatom-dominated bloom.

The IronEx II experiment was not only useful to demonstrate iron limitation in the equatorial Pacific HNLC areas, but also showed that the zooplankton community in tropical HNLC areas is able to respond rapidly to iron enrichment and achieve a new balance. This is probably related to the more complex trophic structure of the tropical areas compared to temperate and boreal waters. A wider range of more specialized plankton organisms, like bacterioplankton, microzooplankton and mesozooplankton, and the larger proportion of microzooplankton in these waters, rapidly compensate any sudden change in its “normal” balance. Similar results were reported by Chavez et al. (1991), who showed that microzooplankton grazers increased their heterotrophic activity and diversity when phytoplankton in incubated water samples were enriched with iron: the initial population was dominated by naked flagellates and ciliates, but assemblages with amoebae, heliozoans, heterotrophic dinoflagellates, and small calanoid copepods were observed in the final incubations.

4.4. Zooplankton as forage

Zooplankton are often the main source of food for fish. Tunas feed on micronekton, thus knowledge of the distribution of larger zooplankton might help to explain the variable distribution of tunas in the eastern tropical Pacific. In an early study of tunas and forage in the region, Blackburn (1968) analyzed the distribution, abundance and composition of micronekton and found in general that abundance was higher onshore than offshore and highest in onshore upwelling areas. He compared the micronekton caught with a net with the composition of stomach contents of yellowfin and skipjack tunas taken at the same stations and found broadly similar crustaceans but different fishes, indicating some selectivity by these predators.

Some fish species like sardine eat both zooplankton and phytoplankton. Alamo and Bouchon (1987) found that the food of the sardine *Sardinops sagax sagax* off Peru changed during El Niño years: stomach contents showed less phytoplankton, with an increased proportion of zooplankton and even small fish. The feeding coefficient (ratio of stomach contents to body weight) was lower and the mean weight of the sardine decreased.

Fiedler (2002b) showed that there is a good coincidence of surface nitrate enrichment with higher zooplankton biomasses in the region of the Costa Rica Dome, and that there is also a preponderance of blue whale sightings in this area. Blue whales might be feeding on large euphausiid stocks in the area around the Dome (Reilly and Thayer, 1990). Common dolphins are also abundant in the area, feeding on fish that eat zooplankton.

Spear et al. (2001), showed the response of seabirds to thermal boundaries in the eastern tropical Pacific. Concentrations of planktivorous birds increased or decreased in relation to the intensity of the semi-permanent Equatorial Front, because zooplankton are concentrated in the surface layer by physical processes. They further showed that planktivorous birds were more affected by these physical processes than piscivorous birds. Relationships between zooplankton and their predators are reviewed further in Ballance et al. (2006).

5. Future research

In general, zooplankton sampling and analysis are expensive and inevitably biased by the sampling gear. Remote sampling by acoustic methods is useful for larger zooplankton, but can identify species or functional groups only in low-diversity systems. Sampling in the huge eastern tropical Pacific area needs to be done more regularly. Special effort is specifically needed to (1) resolve seasonal variability in oceanic upwelling areas and separate it from ENSO-related variability, (2) repeat large-scale sampling like that of EASTROPAC with comparable or intercalibrated sampling methods to detect long-term trends, (3) take full advantage of new and more efficient technology to identify and enumerate zooplankton in local process studies where temporal consistency is not an issue, (4) study the consequences of the OMZ on vertical distribution of zooplankton and vertical fluxes of particulates including fecal pellets, and the importance of these fluxes for benthic populations, (5) further understand the apparent self-regulatory micro- and mesozooplankton response to iron enrichment.

6. Summary

- (1) Spatial abundance patterns of zooplankton in the eastern tropical Pacific are in good agreement with the principal characteristics of its hydrography and circulation. In particular, the higher values of biomass are clearly related to water masses where the thermocline is shallow, associated with coastal and oceanic upwelling processes. These areas include the Gulfs of Tehuantepec, Papagayo and Panama, Costa Rica Dome, equatorial cold tongue, west side of Galapagos, and the eastern boundary currents.
- (2) In general, during “normal” years, the two ecological provinces described for this region by Longhurst (1998), coincide with hydrographic subregions: the North Equatorial Countercurrent Province is related to the eastern Pacific warm pool and the Pacific Equatorial Divergence Province to the equatorial cold tongue.
- (3) Historical zooplankton biomass data show that seasonal changes of zooplankton biomass are not as important as in temperate and polar systems. Biomass is persistently larger around the Costa Rica Dome and in the Peru upwelling area, being higher in winter and lower during summer in both regions. Relatively higher values extend to the west along the equator during summer and autumn.
- (4) Changes in zooplankton biomasses during El Niño and La Niña are not well resolved by historical data, local studies give more coherent results. During El Niño events, the zooplankton biomasses decrease, as well as the presence of larval stages, and tropical species are present in normally cooler waters.
- (5) Interdecadal changes in Pacific ecosystems show that during “cool” periods, zooplankton biomasses are higher.
- (6) Vertical distribution of zooplankton in the eastern tropical Pacific is strongly restricted by the oxygen minimum zone (OMZ), but some species are adapted to these conditions and are found to reside within and migrate through the OMZ.
- (7) Zooplankton trophic relationships in the eastern tropical Pacific are very different from those of temperate and polar waters. Microzooplankton and bacterioplankton are more important and constitute a greater portion of mesozooplankton food than in temperate and polar areas.
- (8) Iron enrichment experiments demonstrate that even if productivity increased considerably at the beginning of the experiment, the ecosystem is self-regulated and rapidly returns to its original state by responses of zooplankton grazers.
- (9) Higher secondary productivity is found in the high nutrient low chlorophyll (HNLC) zone along the equator, where microzooplankton substitutes for phytoplankton as a food source for mesozooplankton.

Acknowledgements

This paper was very much improved by the suggestions and recommendations of Paul Fiedler and Miguel Lavín, for both text and interpretation of the results and we thank them for their patience. Thanks to Jose Maria Dominguez and Carlos Ponce (CICESE) for the adaptation of some figures. Carlos Cabrera (CICESE) prepared some figures and Maricela Vicencio (Laboratorio de Invertebrados UNAM) helped to check references. This is a contribution to the scientific agenda of the Eastern Pacific Consortium of the InterAmerican Institute for Global Change Research. This work was supported by CONACYT (Mexico) *SEP-2003-C02-42941A-1* and project *G34601-S*. Support was also provided by the Protected Resources Division of NOAA Fisheries, Southwest Fisheries Science Center.

Appendix. Zooplankton data

Zooplankton volume data were obtained from the NMFS Coastal and Oceanic Plankton Ecology, Production and Observation Database (COPEPOD, www.nmfs.noaa.gov/ST/plankton). COPEPOD is an updated version of the NODC World Ocean Database plankton data (O'Brien et al., 2002). Additional data were collected on NMFS Stenella Abundance Research (STAR) cruises in August–November of 1998–2000 (Fiedler and Philbrick, 2002) The data contain a total of 5785 volumes from net tows between ~200 m and the surface. 2405 of these samples were collected with mesh sizes of ~333 μm , 14 on FRONTS (1955, 300 μm mesh), 1757

during EASTROPAC (1967–1968), 162 during SKIPJACK (1970, 1971 and 1973), and 472 during STAR (1998–2000). STAR tows were conducted both with a bongo net and a 1/2-m ring net similar to the net used in EASTROPAC. Bongo net volumes were adjusted by a factor of 0.574 (in 89 paired STAR tows in 1998 and 1999, conducted in immediate succession, the ratio of ring net to bongo net volumes was 0.574 ± 0.056 SE). 3380 of these samples were collected with mesh sizes of $\sim 505 \mu\text{m}$: 1464 during CalCOFI (off southern Baja California, 1951–1980), 40 on FRONTS (1955, 650 μm mesh), 1765 during EASTROPAC (1967–1968), and 121 during SKIPJACK (1970 and 1971).

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