# Trophic position of twelve dominant pelagic copepods in the eastern tropical Pacific Ocean

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## ABSTRACT

In this study, the trophic structure of the pelagic copepod community was analyzed in six geographical zones in the eastern tropical Pacific Ocean. Zooplankton samples were collected on two oceanographic cruises from August to December 2003 using a bongo cone net (333 μm mesh light). The isotopic signatures were measured as $\delta^{15}N$ and $\delta^{13}C$ in twelve selected species based on their dominance and their feeding types. We observed a significant latitudinal gradient in $\delta^{15}N$ values, generally increasing northwards. The values of $\delta^{13}C$ isotopes did not show a significant longitudinal gradient, but geographical differences occurred in some species. *Pleuromamma robusta* was recognized as the species with the highest trophic position in the copepod community. In general, there was a positive relationship between average body size and trophic position, except for the herbivorous species *Eucalanus inermis*, which was detected in the lowest trophic position. The isotopic niche was similar for each of the 12 species of copepods studied, but in most cases, the niche overlap between each pair of species was low and not higher than 50%. While the differences in isotopic signatures can be attributed mainly to the dominant nutrient sources in each zone, the low trophic niche overlap may be explained by the differential spatial distribution of species, reducing competition for food resources.

## 1. Introduction

The study of trophic relationships in zooplankton has generally been based on inferences made from different methodological approaches that include analyses of the comparative morphology of organisms (Giesecke and González, 2004), observations of feed rates (Saiz et al., 2014), analyses of stomach or intestinal contents by microscopic (Natori et al., 2017) or molecular methods (Durbin et al., 2012) and the use of biochemical markers such as stable isotopes and fatty acids (El-Sabaawi et al., 2009). However, zooplankton is often small (< 1 cm), making trophic studies complicated and relatively infrequent (El-Sabaawi et al., 2009, 2013; Henschke et al., 2015; Yang et al., 2017). Therefore, common species are grouped together either by taxonomic group or size class or as members of a single second trophic level (herbivores-omnivores). However, copepods represent a zooplankton group that makes a substantial contribution to secondary marine productivity, since they are the most abundant component of mesozooplankton. The main ecological role of this community in the pelagic food web is the transfer of energy between the primary producers and successive trophic levels. In this sense, the trophic spectrum of copepods is very diverse, including both primary and secondary consumers, with feeding habits ranging from detritivores to highly specialized parasites. In fact, the determination of feeding habits of copepods is often made based on the morphology of their feeding structures, which are adapted according to the type of food they ingest (Raymont, 1983; Schmidt et al., 2004; Giesecke and González, 2004; Michels and Schnack-Schiel, 2005; Michels and Stanislav, 2015).

Alternatively, the quantification of trophic markers as the stable isotopes of C and N (e.g. Tiselius and Fransson, 2016) is useful for determining feeding habits, for defining, in a relative way, the trophic levels in the trophic network and for estimating the overlap of trophic niches of planktonic organisms. The isotopic composition of an organism is mainly determined by the isotopic value of the food it consumes (DeNiro and Epstein, 1978, 1981). In this sense, several studies have measured $\delta^{15}N$ and $\delta^{13}C$ in order to understand the trophic relationships within marine food webs, detecting an isotopic enrichment along trophic levels (Fry, 1988). This method is used because the heavy isotopes ($^{15}N$ and $^{13}C$) tend to accumulate in consumers as the light isotopes ($^{14}N$ and $^{12}C$) are preferentially excreted. An enrichment of approximately 3–5‰ has been detected in the nitrogen isotopic ratio

(DeNiro and Epstein, 1981; Fry, 1988; Minagawa and Wada, 1984; Peterson and Fry, 1987) and 0–1‰ for the isotopic ratio of carbon per trophic level (Post, 2002). Thus, in general, the higher enrichment of the stable isotopes of $^{15}N$ is indicators of the trophic position of an organism because the isotopic value of the predator and its prey does not overlap (Minagawa and Wada, 1984; Vander Zanden and Rasmussen, 1999). In contrast, due to the lower enrichment of the $^{13}C$ isotopes, they are useful as an indicator of the original carbon source in the food web (Peterson and Fry, 1987; Fry, 1988; Perry et al., 1999).

The pelagic environment of the eastern tropical Pacific Ocean is a highly productive area with species of commercial interest, particularly large pelagic species such as tunas and billfishes (e.g. Popp et al., 2007). In this zone, there are several marine currents (California Current and Costa Rica Current), upwelling processes and other large-scale events such as ENSO (Fiedler and Talley, 2006; Kessler, 2006). All these phenomena influence the distribution and abundance of species, primary productivity and fixation of carbon and nitrogen (e.g. Kienast et al., 2002). The distribution of pelagic copepod communities in these regions were described in López-Ibarra et al. (2014). In this study, we test whether the predefined feeding types based on feeding structure morphology differ in trophic position, and the dependence of trophic position on the mean individual size of the species. Therefore, the main objective of this study was to determine the existence of differences in the position and trophic niches of the dominant pelagic copepod species in the pelagic environment of the eastern tropical Pacific Ocean.

## 2. Materials and methods

### 2.1. Field sampling

Ninety-six zooplankton samples were collected along sampling stations in the eastern tropical Pacific Ocean from July to December 2003 aboard the NOAA David Starr Jordan and MacArthur II vessels. Sampling was done with oblique tows of bongo net of 0.6 m in diameter and with a mesh light of 333 μm from 200 m deep to the surface. A flowmeter was used on the out-board net, and an average of 438 $m^3$ of water was filtered per tow. The samples were immediately frozen on board the vessel and kept frozen in the laboratory for subsequent isotopic analysis. The study area encompassed coastal and oceanic regions, upwelling areas, and regions influenced by the California Current (cold waters) and the Coastal Current of Costa Rica (warm waters). In this sense, the area is highly heterogenous with different physical and chemical characteristics that influence the structure of the pelagic copepod community and therefore, the complexity of food webs. To contrast the results spatially, we used the six geographical zones identified by López-Ibarra et al. (2014) and based on the structure of the pelagic copepod community: zone a: western coast of the Baja California peninsula (southern part of the California Current), zone b: Mexico's coastal region, zone c: Mexico's oceanic region, zone d: central coastal region, zone e: central oceanic region and zone f: equatorial oceanic region (Fig. 1).

### 2.2. Stable isotope analysis of C and N

For this study, 12 species of pelagic copepods were selected. The species met one or both of the following criteria: a) being a dominant species, and b) having a feeding type that was previously defined from comparative morphology or direct observations. The dominance of the species was determined by López-Ibarra et al. (2014), and the feeding type was assigned according to the criteria established by Raymont (1983) and Benedetti et al. (2016). The selected omnivorous species were *Acartia danae*, *Centropages furcatus*, *Subeucalanus subcrassus* and *S. subtenuis*; herbivores, *Paracalanus parvus*, *P. aculeatus*, *Eucalanus inermis*; and carnivores, *Euchaeta indica*, *E. marina*, *Pleuromamma abdominalis*, *P. gracilis* and *P. robusta*.

It has been observed that the variance in the isotopic composition is

comparatively lower from a sample of several organisms than from individual samples. Therefore, for the isotopic analysis, each collected sample was defrosted, and 50 to 200 individuals of each species were subsampled, yielding a total of 237 subsamples. Additionally, to eliminate the possible influence of lipids and carbonates on the $\delta^{13}C$ values (Fry, 1988; Post et al., 2007), an experiment was performed with 15 subsamples to compare the results. The experiments consisted of comparing the values of $\delta^{13}C$ in the subsamples 1) with and without extracted lipids, 2) with and without extracted carbonates, and 3) in a control subsample without extracting lipids or carbonates. The lipids were extracted using a 2:1 mixture of chloroform:methanol and dried for 20 min at 60 °C. The carbonates were extracted by adding 1 mol l$^{-1}$ hydrochloric acid dropwise until no $CO_2$ was released and dried for 20 min at 60 °C. An analysis of variance showed that there were no significant differences in the values of $\delta^{13}C$ between the values obtained in the experiments and the control (F = 0.022, $p > 0.5$). Thus, the rest of the samples were processed without elimination of lipids or carbonates and were dried at 60 °C for 24 h to remove water (Mullin et al., 1984). As the specimens were frozen immediately after sampling, the determinations of stable isotopes include also their gut contents. This practice was also followed in other studies with mesozooplankton (e.g. Bode et al., 2015) as it was assumed that the contribution of the gut content to total biomass is small. Once the subsample was dry, it was reduced into a fine powder inside a vial with a spatula under a laminar flow bell. From the pulverized sample, 0.3 mg was weighted on an analytical balance and placed in a tin capsule. The $^{13}C$ and $^{15}N$ determination was performed on an isotope ratio mass spectrometer interfaced with an elemental analyzer at the University of Hawaii, Stable Isotope Biogeochemistry Laboratories.

The $\delta^{13}C$ and $\delta^{15}N$ values, expressed in (‰), were calculated according to the formula:

$$\delta X (‰) = \left[ \frac{R_s}{R_{std}} - 1 \right] \times 1000$$

where $X$ is the stable isotope ($^{13}C$ or $^{15}N$), and $R_s$ and $R_{std}$ are the isotopic ratios ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) of the sample and the standard, respectively. The standard used for $^{13}C$ was Vienna Pee Dee Belemnite (VPDB), and the standard for $^{15}N$ was the atmospheric $N_2$ (Coplen, 2011). The raw data set used in this study is available at López-Ibarra et al. (2018).

A Kruskal-Wallis test was used to compare the isotopic signatures of $\delta^{13}C$ and $\delta^{15}N$ between species and between geographic zones as reported by López-Ibarra et al. (2014). In addition, we used a Spearman rank correlation test to analyze longitudinal and latitudinal trends in the values of $\delta^{13}C$ and $\delta^{15}N$, respectively.

### 2.3. Trophic position

The trophic position (TP) was calculated according to Hannides et al. (2009).

$$TP = 1 + (\delta^{15}N_{zoo} - \delta^{15}N_{PN})/2$$

where $\delta^{15}N_{zoo}$ and $\delta^{15}N_{PN}$ are the values of $^{15}N$ in zooplankton and particulate organic matter, respectively. In the absence of specific measurements of $\delta^{15}N_{PN}$ for this study, we used the mean value of 4.05‰ between the values reported for upwelling (7.5‰, Meador et al., 2007) and oligotrophic areas (0.6‰, Hannides et al., 2009) in the eastern tropical Pacific Ocean. While more realistic TP estimations would result from the use of zonal $\delta^{15}N_{PN}$ values, in this study we focus on the differences among species rather than between zones. A value of 2‰ has been suggested for the isotopic fractionation between the trophic levels in copepods, considering that they are poikilotherm animals with a mixed diet of algae and other animals (McCutchan et al., 2003). The calculated trophic position was compared with the average individual size of each species and the feeding type previously reported
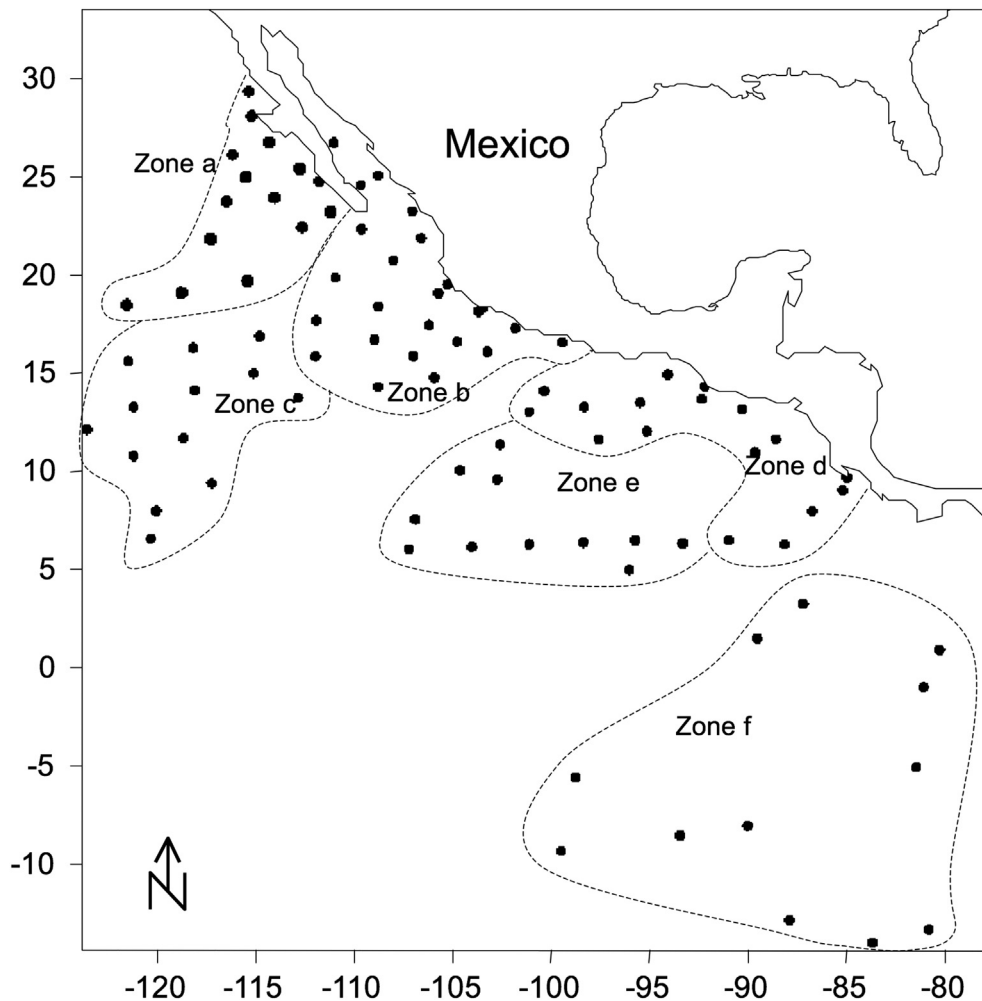
**Fig. 1.** Study area and sampling stations in the six geographical zones. Zone a: western coast of the Baja California peninsula (southern part of the California Current), zone b: Mexico's coastal region, zone c: Mexico's oceanic region, zone d: central coastal region, zone e: central oceanic region and zone f: equatorial oceanic region.

according to the morphology of their feeding structures (maxilla and maxillulae). The average species size was calculated from female and male individual sizes obtained from the Marine Planktonic Copepods online database (http://copepodes.obs-banyuls.fr/en/; Razouls et al., 2005–2017), and the feeding type was defined according to Anraku and Omori (1963), Raymont (1983), Schmidt et al. (2003) and Benedetti et al. (2016).

### 2.4. Isotopic niche

The SIBER (Bayesian Ellipses of Stable Isotopes) routine from SIAR for R (Jackson et al., 2011; Parnell and Jackson, 2013) was used to estimate the potential isotope niche width and overlap for the dominant copepod species in the eastern tropical Pacific Ocean. This method generates standard probability ellipses in a bivariate plane defined by the observed isotopic values of $\delta^{13}C$ and $\delta^{15}N$ for each species. The size and shape of these ellipses depend on the niche breadth of each species, so that if the ellipses overlap, the trophic niche overlap between each pair of species can be quantified (Jackson et al., 2011). In this analysis, the data were not separated by zone, because the number of samples available by zone was reduced. Although the isotopic values of $\delta^{13}C$ and $\delta^{15}N$ may be different between zones, this analysis allowed us to explore the potential niche breadth in the region and analyze the potential overlap between species.

## 3. Results

### 3.1. Geographic distribution of analyzed species

The majority of the 12 species selected for stable isotope analysis were found in all areas but with highly variable abundances (between 50 and 2500 ind/1000 m³). Some species had a high abundance in some areas, while in other areas, they were less abundant and even absent, as was the case of *E. inermis*, which had a high abundance in zone e, while in zone a, b, c and f, it was less abundant or absent (Fig. 2).

### 3.2. Species differences in isotopic composition

In addition to the differences presented for the abundance of the species, differences in the isotopic signature values were also observed depending on the geographic zone where they were collected. A Kruskal-Wallis test revealed that the $\delta^{15}N$ isotopic values showed significant differences by zone and species ($p < 0.05$). It was observed that in zones a and b, the species presented higher values of $\delta^{15}N$ than in zones c, d, e and f (Fig. 3). In addition, a latitudinal gradient was found for the $\delta^{15}N$ values with a significant tendency to increase towards the north (correlation between $\delta^{15}N$ and latitude, Spearman's rho = 0.6, $p < 0.05$) and to the south (Spearman's rho = 0.7, $p < 0.05$) from the equator. Regarding the values of $\delta^{13}C$, the Kruskal-Wallis test revealed that these values were significantly different by zone and by species ($p < 0.05$). Although values tended to be higher in
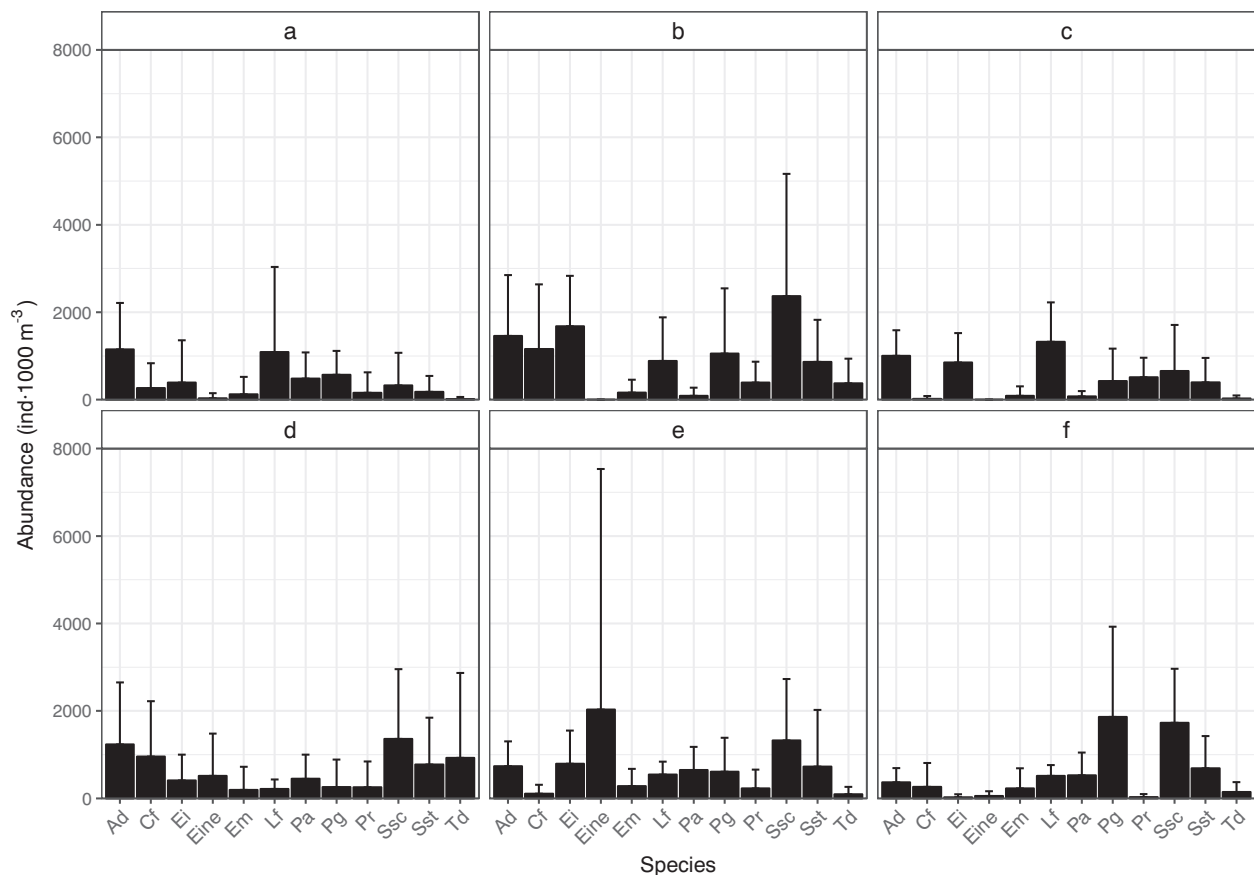
**Fig. 2.** Average abundance and standard deviation in each zone of the 12 species of copepods selected for isotopic analysis (Ad = *Acartia danae*, Cf = *Centropages furcatus*, Ei = *Euchaeta indica*, Eine = *Eucalanus inermis*, Em = *E. marina*, Lf = *Lucicutia flavicornis*, Pa = *Pleuromamma abdominalis*, Pg = *P. gracilis*, Pr = *P. robusta*, Ssc = *Subeucalanus subcrassus*, Sst = *S. subtenuis*, and Td = *Temora discaudata*).

the geographic zones near the coast (a, b, d and f), they were lower in the oceanic zones (c and e), and in this case, no significant trend with geographic longitude was found (Spearman's rho = 0.13, $p = 0.07$). In the case of some species with higher coastal affinities (e.g., *E. indica* and *C. furcatus*), the $\delta^{13}C$ values were relatively high but not significant (Fig. 4).

### 3.3. Trophic position and individual size

There was a marked association between the estimated trophic position and the average size and reported feeding type of species (Fig. 5). The species with the highest trophic position was *P. robusta*, coinciding with the feeding type previously reported (carnivorous). However, these high values were not observed in other species previously considered as carnivorous, as in the case of *P. gracilis* and *P. abdominalis*. For these species, the estimated trophic position was relatively low, suggesting that these species tend to be more omnivorous and not strictly carnivorous. Similarly, *C. furcatus* has previously been described as omnivorous, but its trophic position indicates a tendency towards being carnivorous compared with other omnivorous species. On the other hand, there is a positive relationship between body size and trophic position, except for *E. inermis*. In fact, if this species is not considered, the correlation is significant (Spearman's rho = 0.71, $p < 0.05$).

### 3.4. Isotopic niche overlap

Most species potentially occupy a similar isotopic niche (Fig. 6a). However, in most cases, the niche overlap between each pair of species was low and was not > 50% (Table 1). In fact, only 16% of the

comparisons between each pair of species had a value above 50%. The isotopic niche overlap forms a network of interactions between the species in the bivariate plane of $\delta^{13}C$ and $\delta^{15}N$ (Fig. 6b). It was observed that the greatest interactions occur among the group of species *A. danae*, *P. abdominalis*, *P. gracilis*, *S. subcrassus* and *S. subtenuis*.

## 4. Discussion

### 4.1. Species differences in isotopic composition

In this study, it was possible, through the stable isotope analysis, to redefine the trophic position of some dominant species of the eastern tropical Pacific by taking into account its variability along a large productivity gradient. This is one of the few studies related to the transfer of energy and the functional role played by zooplankton, and in particular by copepods, carried out in tropical oceans (Hannides et al., 2009, 2013; Williams et al., 2014). Other studies have addressed this topic in oceanic areas with wide spatial coverage (McMahon et al., 2013; Mompeán et al., 2016) but mostly in temperate zones (Mullin et al., 1984; Sato et al., 2002; Schmidt et al., 2003; Giesecke and González, 2004; El-Sabaawi et al., 2009), in the Atlantic (Montoya et al., 1990; Bode et al., 2003; Bode and Alvarez-Ossorio, 2004; Bode et al., 2007; Bode et al., 2015; Basedow et al., 2016), and in upwelling areas (Kibirige et al., 2002; Rau et al., 2003).

The variability in the isotopic values of carbon and nitrogen has been recognized for the same species (e.g. Montoya et al., 1990; Buskey et al., 1999; Hasegawa et al., 2001; Sato et al., 2002; Schmidt et al., 2003; Tiselius and Fransson, 2016) as well as for different plankton assemblages (e.g. McMahon et al., 2013). This variability can be attributed mostly to the different sources of nutrients available in the
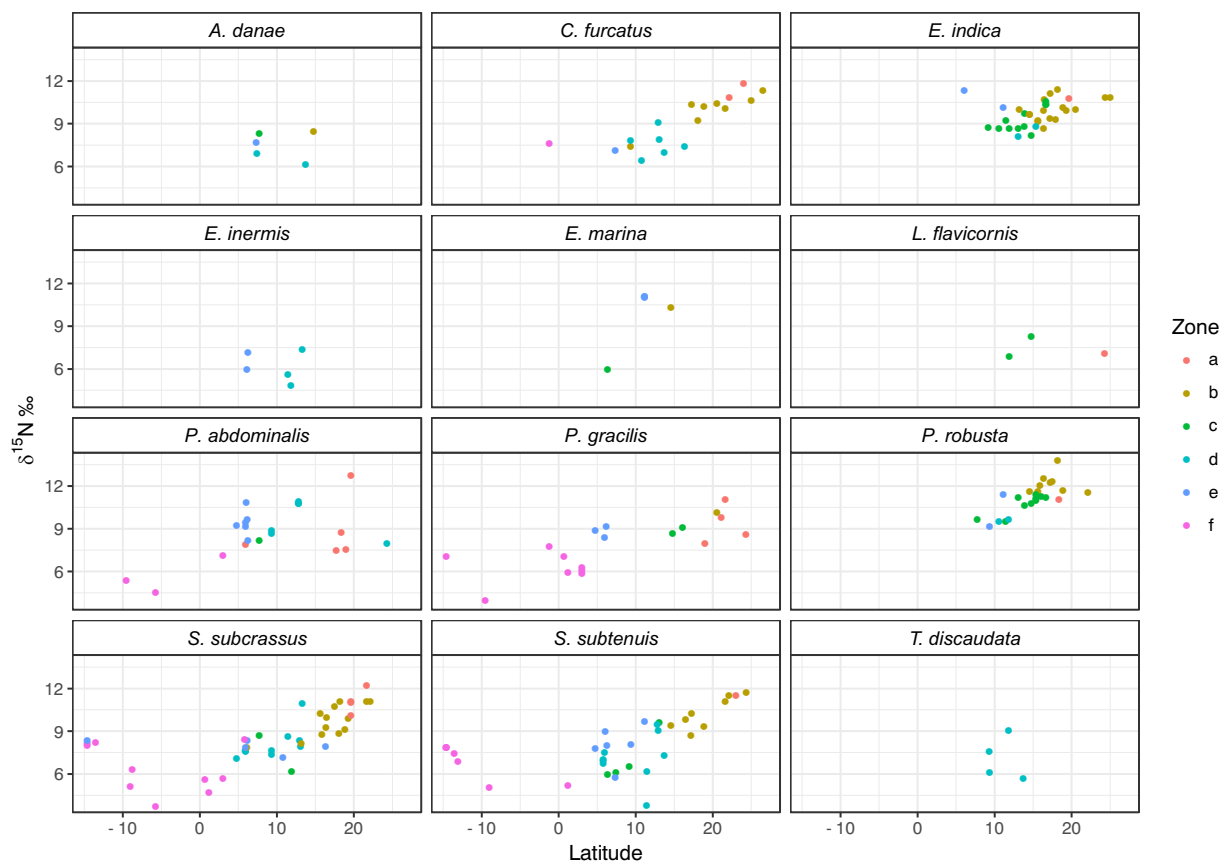
**Fig. 3.** Isotope values of $\delta^{15}N$ recorded in selected copepod species in different geographic zones in the tropical eastern Pacific Ocean.
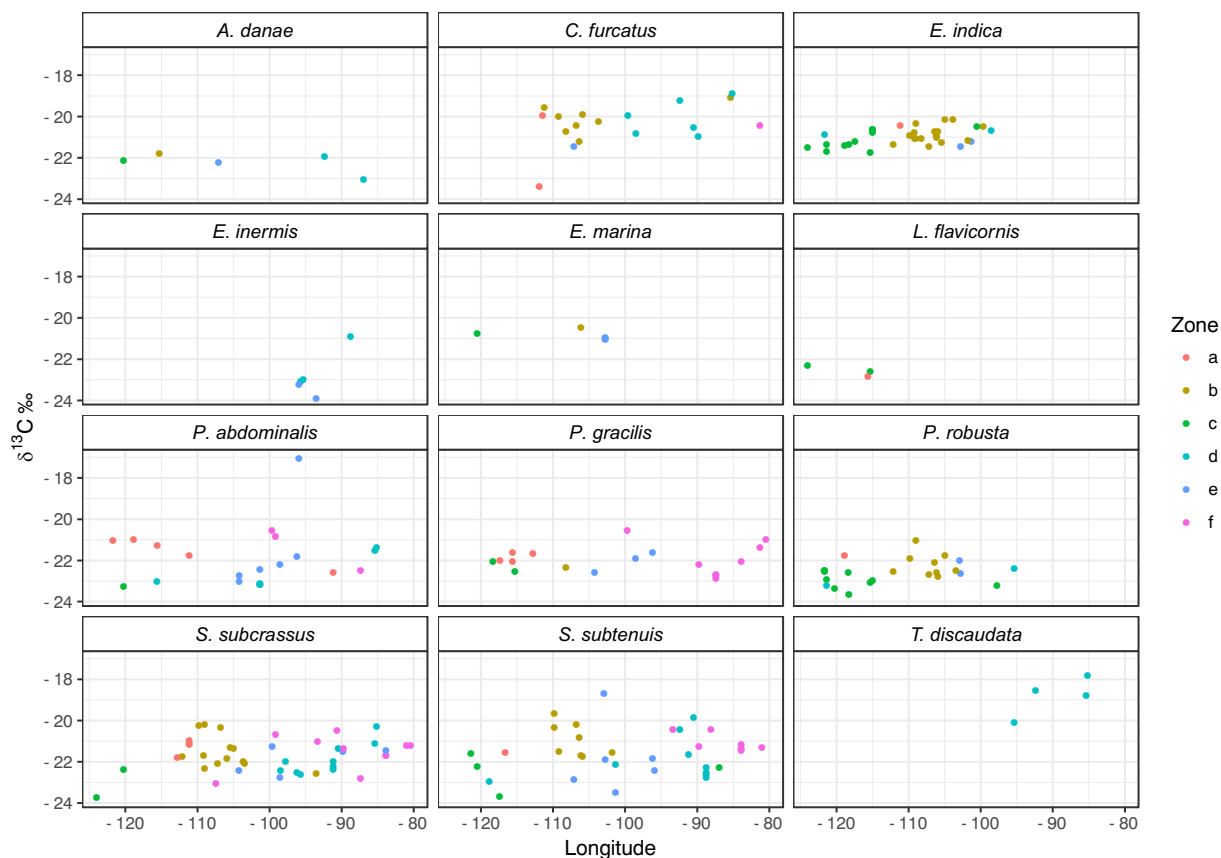


**Fig. 4.** Values of $\delta^{13}C$ isotopes recorded in selected copepod species in different geographic zones in the tropical eastern Pacific Ocean.
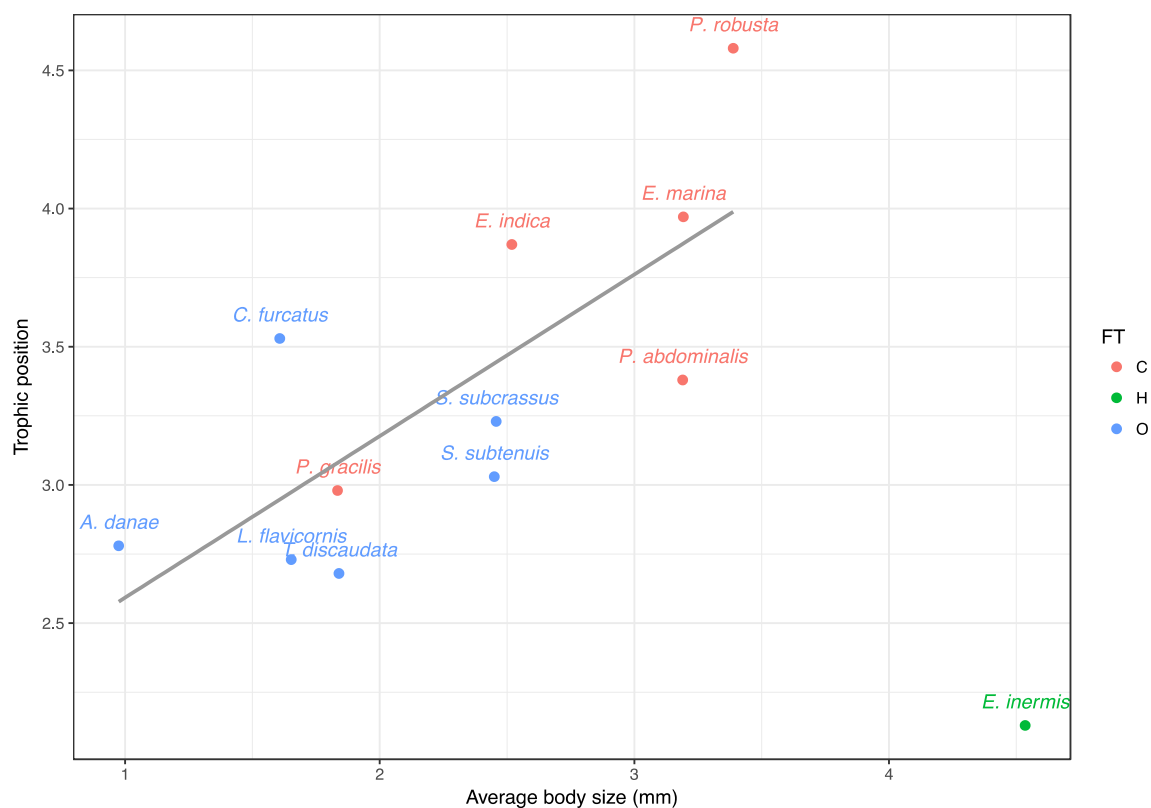
**Fig. 5.** Trophic position calculated in relation to the average size and reported feed rate of the 12 selected species. FT: feeding type. The trendline excluding *E. inermis* is shown.

environment and incorporated into the food web through the fixation of N and C by autotrophs and grazing by zooplankton and other consumers. In the eastern tropical Pacific in $\delta^{15}N$ variability in the pelagic food web is mostly driven by nitrogen dynamics, as trophic positions are uniform despite the marked spatial gradient (Hetherington et al., 2017). In our study, this geographic variability is reflected as a marked latitudinal pattern from north to south for the values of $\delta^{15}N$ and a less marked longitudinal pattern from the coastal zone to the open ocean for the values of $\delta^{13}C$, both in general level and at the species level. These results agree with those reported for other regions of the Pacific (Table 2) and stress the importance of the dominant nutrient sources in each region. In the case of $\delta^{15}N$, isotopic studies of organic matter and nitrogenous nutrients have shown a latitudinal pattern with elevated values of $\delta^{15}N$ in the region of California and Baja California decreasing towards Ecuador (Farrell et al., 1995; Altabet et al., 1999; Voss et al., 2001; Kienast et al., 2002; Aguíñiga et al., 2010). Because the study area is an extensive region affected by different oceanographic processes (upwelling, minimum oxygen zone), the confluence of the different water masses (Lavín and Marinone, 2003; Rau et al., 2003; Fiedler and Talley, 2006) and by nitrification-denitrification processes that have associated a high isotopic fractionation (Montoya, 2008), there is substantial variability in the isotopic signatures recorded in the organisms of the food web. This variability is first detected in primary producers (Farrell et al., 1995; Altabet et al., 1999; Voss et al., 2001; Kienast et al., 2002), is reflected in the successive trophic levels (Hannides et al., 2009, 2013; Popp et al., 2007; Hetherington et al., 2017). For example, the zones influenced by the California Current (as our zone a) had the highest minimum values of $\delta^{15}N$ (Table 2), likely a consequence of input of subsurface nitrate and low denitrification rates (Voss et al., 2001). In contrast, in the southern region of the study area (as our zone f), the low $\delta^{15}N$ values recorded in copepods (Table 2) are probably due to the transport of water with low nitrate $\delta^{15}N$ values (Kessler, 2006; Sutka et al., 2004) because the fixation of atmospheric N

with $\delta^{15}N = 0$ (Luo et al., 2012). These results are consistent with the negative correlation found between surface nitrate concentrations and $\delta^{15}N$ in the pelagic food web (Hetherington et al., 2017).

A marked latitudinal pattern of the $\delta^{13}C$ isotopic signature has been found in samples of seston and zooplankton at the scale of oceanic basin, with the highest values at low latitudes (Rau et al., 1982; Chen et al., 2006; McMahon et al., 2013) This pattern is less clear in Pacific zooplankton (Table 2). Since our sampling area was restricted to the tropical waters, we focused on the variation of $\delta^{13}C$ along the longitudinal gradient. An overall longitudinal pattern in $\delta^{13}C$ was not significant but some species were depleted in $^{13}C$ in oceanic zones. For instance, $\delta^{13}C$ of *P. robusta* was $-22.7‰$ in the stations near the coast (zone b) and of $-23.6‰$ in the oceanic stations (zone c). This difference could be due to a different content in lipids, that are associated to characteristically low $\delta^{13}C$ values (Post et al., 2007) or to the use of organic matter from continental origin (Perry et al., 1999). Lipid influence seem to have been low in our samples (see Materials and methods) and therefore $\delta^{13}C$ signatures indicate a variability in the different carbon sources that copepods use in different regions of the study area. Thus, at least in some species, $\delta^{13}C$ isotopic signatures are consistent with the differential use of oceanic vs. coastal carbon sources.

### 4.2. Trophic position

According to the average trophic position estimated from $\delta^{15}N$ for each species, *E. inermis* had the lowest trophic position, suggesting a predominantly herbivorous feeding type, as previously described in the literature based on their feeding structures (Raymont, 1983; Benedetti et al., 2016). Most of the species had intermediate trophic positions, thus in agreement with previous classification as omnivores (Raymont, 1983). However, in the case of *P. gracilis* and *P. abdominalis*, previously described as carnivores (Schmidt et al., 2004; Giesecke and González,
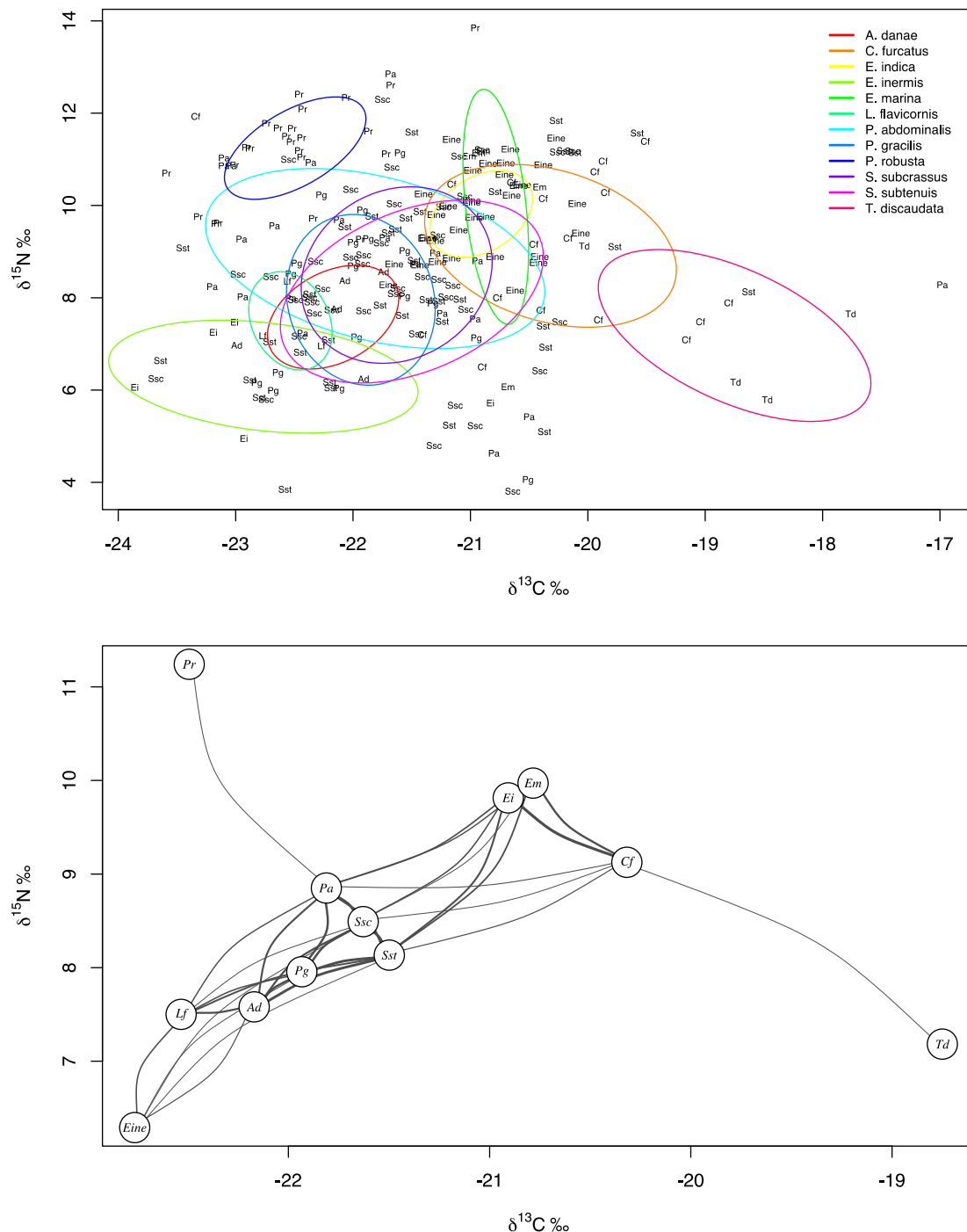
**Fig. 6.** Potential isotopic niche defined by δ¹³C and δ¹⁵N (upper panel) and isotopic niche overlap network (bottom panel) of the 12 dominant pelagic copepod species of the tropical eastern Pacific Ocean. The thickness of the lines between each pair of species is proportional to the degree of isotopic niche overlap (Ad = *Acartia danae*, Cf = *Centropages furcatus*, Ei = *Euchaeta indica*, Eine = *Eucalanus inermis*, Em = *E. marina*, Lf = *Lucicutia flavicornis*, Pa = *Pleuromamma ab-dominalis*, Pg = *P. gracilis*, Pr = *P. robusta*, Ssc = *Subeucalanus subcrassus*, Sst = *S. subtenuis*, and Td = *Temora discaudata*).

2004; Michels and Schnack-Schiel, 2005), our results suggested a trophic position similar to other omnivorous species. Similar results have been reported in other studies using stable isotopes, as for the carnivorous copepod *Heterocope septentrionalis*, which was typically defined as predator, but its δ¹⁵N indicated an omnivorous feeding type (Paffenhöfer and Knowles, 1980). In contrast, *C. furcatus*, with a trophic position closer to carnivorous species, although this species has been described as omnivore (Raymont, 1983; Benedetti et al., 2016). Experimental evidence also supports a dominance of N sources derived from carnivory in *C. furcatus* (Paffenhöfer and Knowles, 1980).

The highest trophic position of *P. robusta*, in comparison to the rest of the species, is related to its body size and the morphology of its maxilla and maxillulae, which have a relevant function in the trapping of mobile prey (Schmidt et al., 2004; Giesecke and González, 2004; Michels and Schnack-Schiel, 2005). In addition, it was collected in oceanic regions with low concentrations of chlorophyll *a* (López-Ibarra et al., 2014), so predation must have been its main feeding mechanism as opposed to filtration, which is likely similar for the other species of the same genus. In Antarctica, δ¹⁵N values in *P. robusta* were higher than those recorded in other copepods and euphausiids, indicating that

**Table 1**

Isotopic niche overlap ratio of the 12 species of selected copepods. The upper right triangle represents the overlapping of each species with respect to the species in the column. The lower left triangle represents the overlap of each species with respect to the species in the row. Ad = *Acartia danae*, Cf = *Centropages furcatus*, Ei = *Euchaeta indica*, Eine = *Eucalanus inermis*, Em = *E. marina*, Lf = *Lucicutia flavicornis*, Pa = *Pleuromamma abdominalis*, Pg = *P. gracilis*, Pr = *P. robusta*, Ssc = *Subeucalanus subcrassus*, Sst = *S. subtenuis*, and Td = *Temora discaudata*.

| | Ad | Cf | Ei | Eine | Em | Lf | Pa | Pg | Pr | Ssc | Sst | Td |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ad | – | 0 | 0 | 0.11 | 0 | 0.66 | 0.14 | 0.42 | 0 | 0.25 | 0.26 | 0 |
| Cf | 0 | – | 1 | 0 | 0.69 | 0 | 0.19 | 0 | 0 | 0.18 | 0.27 | 0.14 |
| Ei | 0 | 0.21 | – | 0 | 0.37 | 0 | 0.07 | 0 | 0 | 0.11 | 0.12 | 0 |
| Eine | 0.3 | 0 | 0 | – | 0 | 0.42 | 0 | 0.17 | 0 | 0.03 | 0.12 | 0 |
| Em | 0 | 0.25 | 0.64 | 0 | – | 0 | 0.1 | 0 | 0 | 0.05 | 0.16 | 0 |
| Lf | 0.41 | 0 | 0 | 0.1 | 0 | – | 0.06 | 0.13 | 0 | 0.04 | 0.1 | 0 |
| Pa | 0.63 | 0.27 | 0.49 | 0 | 0.4 | 0.4 | – | 0.77 | 0.2 | 0.93 | 0.76 | 0 |
| Pg | 0.83 | 0 | 0 | 0.13 | 0 | 0.42 | 0.34 | – | 0 | 0.59 | 0.51 | 0 |
| Pr | 0 | 0 | 0 | 0 | 0 | 0 | 0.04 | 0 | – | 0 | 0 | 0 |
| Ssc | 0.64 | 0.15 | 0.42 | 0.03 | 0.12 | 0.15 | 0.54 | 0.77 | 0 | – | 0.65 | 0 |
| Sst | 0.92 | 0.31 | 0.63 | 0.16 | 0.5 | 0.54 | 0.6 | 0.89 | 0 | 0.88 | – | 0 |
| Td | 0 | 0.14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | – |

**Table 2**

Range of natural abundance of carbon and nitrogen isotopes in mesozooplankton of different regions in the Pacific Ocean as reported in the literature and in this study. The depth range (m) is indicated. The sample type indicates whether copepods or whole plankton (mesh size) were collected. OC: Oyashio Current, NECC: North Equatorial Counter Current, STCC: Subtropical Counter Current, CB: California Bight, CC: California Current, OMZ: oxygen minimum zones.

| Zone | $\delta^{13}C$ | | $\delta^{15}N$ | | Depth | Sample type | Reference |
|---|---|---|---|---|---|---|---|
| | Min | Max | Min | Max | | | |
| Arctic and subarctic Pacific (Alaska) | −24.0 | −17.6 | 4.6 | 11.9 | 0–100 | Copepods | Pomerleau et al. (2014) |
| Western north Pacific (OC) | – | – | 7.1 | 9.9 | 0–150 | Copepods | Chiba et al. (2011) |
| Central north Pacific (43–50°N, 180°E) | – | – | 1.2 | 4.5 | 0–150 | Copepods | Chiba et al. (2011) |
| Eastern north Pacific (45–50°N, 125–145°E) | – | – | 4.2 | 13.3 | 0–150 | Copepods | Chiba et al. (2011) |
| Western tropical north Pacific (NECC) | −19.8 | −19.3 | 6.1 | 7.4 | 0–300 | > 200 μm | Yang et al. (2017) |
| Western tropical north Pacific (STCC) | −20.9 | −20.1 | 1.9 | 3.8 | 0–300 | > 200 μm | Yang et al. (2017) |
| Eastern tropical Pacific (CB) | – | – | 8.1 | 12.3 | Euphotic | Copepods | Mullin et al. (1984) |
| Eastern tropical Pacific (CC) | – | – | 9.3 | 11.8 | Euphotic | Copepods | Ohman et al. (2012) |
| North Pacific subtropical gyre | – | – | 1.7 | 11.5 | Euphotic | Copepods | Hannides et al. (2009) |
| Eastern tropical north Pacific (OMZ) | −27.5 | −19.6 | 3.3 | 10.7 | 0–250 | > 153 μm | Williams et al. (2014) |
| Eastern tropical north Pacific (zone a) | −23.3 | −20.0 | 7.5 | 12.8 | 0–200 | Copepods | This study |
| Eastern tropical north Pacific (zone b) | −22.7 | −19.5 | 7.5 | 13.8 | 0–200 | Copepods | This study |
| Eastern tropical north Pacific (zone c) | −23.7 | −20.6 | 6.0 | 11.5 | 0–200 | Copepods | This study |
| Eastern tropical north Pacific (zone d) | −23.2 | −18.8 | 3.9 | 11.0 | 0–200 | Copepods | This study |
| Eastern tropical north Pacific (zone e) | −23.5 | −17.0 | 5.8 | 11.5 | 0–200 | Copepods | This study |
| Eastern tropical north Pacific (zone f) | −22.8 | −20.4 | 3.8 | 8.5 | 0–200 | Copepods | This study |
| Eastern tropical south Pacific (Australia) | −23.4 | −19.7 | 5.4 | 6.9 | 0–150 | > 200 μm | Waite et al. (2007) |
| Western south Pacific (New Caledonia) | – | – | 2.4 | 8.7 | 0–500 | > 200 μm | Hunt et al. (2015) |

this species is also strictly carnivorous (Schmidt et al., 2003). The significant increase in trophic position with copepod size found in this study is consistent with the pattern found in pelagic ecosystems where body size largely determines the access to prey (e.g. Bode et al., 2003; Jennings et al., 2008; Hunt et al., 2015; Yang et al., 2017). In some organisms, however, a large size does not prevent feeding on prey of low trophic position, as the planktivorous whales (Filatova et al., 2013) or the herbivorous salps (Banaru et al., 2014). These exceptions are generally due to the use of an efficient feeding mechanism allowing the capture of abundant but small prey. The exception in our case was the herbivore *E. inermis*, an efficient filter-feeder of relatively large size with high abundance in the zone e, characterized by relatively high chlorophyll concentrations (López-Ibarra et al., 2014). We also found species with similar body size, and even taxonomically related, that can occupy different trophic positions (e.g., species of the genus *Pleuromamma*).

### 4.3. Trophic niche overlap

Notwithstanding the variability in isotopic composition between zones, there was a relatively low overlap in trophic niches among the species, suggesting a specialization in feeding. Although these results may be influenced by the different sample size per species in each zone,

this could also reflect the differential abundance between the zones. This low niche overlap suggests a possible spatial segregation defined by the oceanographic conditions of the region. Even in the cases with large overlap, as the species *A. danae*, *P. gracilis* and *S. subcrassus* (Table 1), their spatial distribution is consistent with a low degree of actual competition for food, as their maximum abundances are reached in different zones (Fig. 2). The results of this study indicate a greater trophic plasticity of most species that would be able to exploit different resources depending on the availability of food in some areas as reported in other studies (Henschke et al., 2015). For instance, *S. subtenuis*, *S. subcrassus*, *E. indica* and *C. furcatus*, typically considered as omnivores (Raymont, 1983), had the highest isotopic values of $\delta^{15}N$ (10.9 to 11.6‰) in the zone influenced by the California Current, where they may have consumed prey enriched in $\delta^{15}N$ due to the effect of the upwelling (Rau et al., 2003) but also may have had access to a large variety of prey types living this productive environment (Pennington et al., 2006; Fernández-Álamo and Färber-Lorda, 2006). This suggests that species with mandibular appendages and that are morphologically similar and expected to have the ability to feed on prey of the same type are opportunistic species, even though they may occupy different trophic levels according to different environmental and trophic conditions. In areas where food may be a limiting factor, as in zone f, which has been characterized by low primary productivity,

intraspecific differences were observed. This means that trophic plasticity and opportunism occur in several species of pelagic copepods, such as *S. subtenuis*, *S. subcrassus*, *P. abdominalis* and *P. gracilis*. However, some species with lower trophic plasticity may be excluded from some areas, such as *P. robusta*, which is typically carnivorous and was not found in this zone.

## 5. Conclusions

Our results revealed a complex trophic structure in pelagic copepods of the eastern tropical Pacific waters have a complex trophic structure related to their ability to consume different types of prey. This agrees with studies in the tropical and subtropical Atlantic (Bode et al., 2015) indicating the existence of diverse trophic strategies, from species with broad plasticity to those that have an exclusive feeding type. In general, our results confirm the trophic classification of copepods based on the morphology of their feeding structures and observations on gut contents. We also confirm a general increase in the trophic position of copepods with body size. However, most species were omnivores with a large trophic plasticity in the different geographic areas, indicating that in fact few of the species can be described strictly on feeding habits and body size.

Because the spatial segregation of species due to the differential distribution of their abundance contributes to spatial segregation and reduced competition for food resources, reflecting a reduction in the actual overlap in trophic niche. Our results support the relevance of focusing isotopic studies of zooplankton are focused on the species level, both because of the great variety of feeding types and trophic plasticity they could have, as well as the fact that differential dominance of omnivorous or carnivorous species may contribute to an enormous variability of the stable isotope signature in grouped zooplankton samples. In this study, we demonstrated that the spatial distribution of the dominant copepod species is as variable as is their isotopic signature, reflecting differences in the food web structure of the eastern tropical Pacific.

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