Distribution of calanoid copepods across the mesoscale frontal zone of tropical-subtropical convergence off México.

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ABSTRACT

The distribution of calanoid copepods was investigated in the convergence zone between the California Current Water and Transitional Tropical Water in June 2010 to understand how this zooplankton community responds to mesoscale environmental structure.

Hydrographic conditions and zooplankton profiles were measured along two transects which crossed a mesoscale front and adjacent structures, visible in sea surface temperature and ocean color satellite images. The hydrographic structure showed strong temperature ($\sim 2^\circ\text{C}$) and oxygen ($50\ \mu\text{mol kg}^{-1}$) gradients in the frontal zone ($\sim 90\ \text{km}$) associated with a sinking of the thermocline and oxycline, from $\sim 30\ \text{m}$ depth in the Transitional Tropical Water, to $\sim 90\ \text{m}$ depth in the California Current Water. The front was marked by a salinity minimum ($<34.3\ \text{g kg}^{-1}$) that sank along the sloping thermocline. High chlorophyll-*a* concentrations associated with the thermocline were detected in the Transitional Tropical Water, where a cyclonic eddy was defined. These concentrations decreased as the thermocline depth increased. Multivariate analysis defined three calanoid copepod habitats related to the hydrographic structure. A habitat with the highest copepod concentration ($24,704\ \text{copepods } 1000\ \text{m}^{-3}$) was found on the tropical water side associated with a cyclonic eddy. *Subeucalanus subtenius* and *Centropages furcatus*, indicator species, were concentrated between the thermocline ($\sim 30\ \text{m}$ depth) and the sea surface. On the subtropical water side, where the thermocline was deeper, a habitat with the lowest copepod concentration ($3304\ \text{copepods } 1000\ \text{m}^{-3}$, an order of magnitude smaller), characterized by *Euchaeta indica* and *Centropages elongates*, was observed. As an unexpected result, the habitat located in the frontal zone, characterized by *Scolecithrix*

bradyi and *Heterorhabdus papilliger* had low copepod concentration (4453 copepods·1000 m⁻³). This low concentration could be due to the steep thermocline slope in the frontal zone, which could cause the thermocline depth to rapidly exceed the photic zone depth, and therefore affect the availability of food for calanoid copepods. It is concluded that the definition of the calanoid copepod habitats, was not only caused by the front itself, but by its interaction with other fine-scale mechanisms that generate oceanographic conditions leading to development of different food webs depending on the structure of water column.

Keywords: Calanoid copepods, Vertical distribution, Frontal zone, Mesoscale, Pacific off Mexico.

1. Introduction

Calanoid copepods are one of the most abundant groups in the marine zooplankton in the tropical and subtropical oceans, serving as a link between primary producers and higher trophic level species (e.g. Longhurst, 1967; Mackas et al., 2005; Palomares-García et al., 2013). The fluctuations in concentration of this group of copepods may be a good indicator of the biological response to hydrographic processes in the ocean (Urban-Rich et al., 2001; Cruz-Hernández et al., 2018).

Ocean fronts play an important role in marine ecosystem structure and function. The physical processes in frontal zones, mainly zones of convergence, may act as mechanisms of enrichment, concentration, and retention of zooplankton organisms (Bakun, 1996; Bakun and Csirke, 1998). While there are several categories of fronts generated under a variety of conditions (e.g. estuarine fronts, river plume fronts, tidal fronts, shelf-break fronts, thermohaline fronts), most of them are characterized as locations of enhanced primary productivity and blooms of zooplankton organisms (Bakun, 1996; Trudnowska et al., 2016), which constitute feeding areas for organisms of higher trophic levels (Etnoyer et al., 2006).

The general responses of planktonic crustaceans to oceanic fronts have been documented in other regions of the world where water masses converge, e.g. off Pt. Conception, California (Smith et al., 1986), in the Antarctic Polar Sea (Urban-Rich et al., 2001), in the Mediterranean Sea (Molinero et al., 2008) and off the Angolan coast (Loick et al., 2005). These authors recorded greater zooplanktonic biomass and copepod concentration in the frontal zone than in the adjacent areas, and proposed that oceanic

fronts may act as retention areas for most zooplankton organisms, including the calanoid copepods. However, the effect of mesoscale frontal zones on the vertical distribution of the zooplankton organisms has been poorly studied.

The Eastern Tropical-Subtropical Convergence off Mexico is a region known as a nursery and feeding area of species of fish and squid of commercial importance (Etnoyer et al., 2006; Davies et al., 2015), which is associated with a complex oceanographic context. This is a region of seasonal confluence of three different water masses in the upper layers namely: The Gulf of California Water (GCW); Tropical Surface Water (TSW); and Transitional Tropical Water (TTW) (Fiedler and Talley, 2006; Portela et al., 2016). The last of these results from mixing between California Current Water (CCW), Tropical Surface Water (TSW) and Gulf of California Water (GCW). Subsurface water characterized by Subtropical Subsurface Water (StSsW) is brought by the Mexican Coastal Current from the south (Portela et al., 2016). The intensification of the California Current from spring to early summer creates complex unstable boundaries, characterized by mesoscale structures like eddies and fronts, between these water masses (Kurczyn et al., 2012; Lavín et al., 2013). These unstable mesoscale processes might modulate primary productivity and zooplankton blooms on different time-scales than observed in the ocean fronts found in the Antarctic Polar Sea (Urban-Rich et al., 2001) and off the Angolan coast (Loick et al., 2005).

In water mass convergence regions with intense mesoscale activity, like the Eastern Tropical-Subtropical Convergence off Mexico (Kurczyn et al., 2012; Lavín et al., 2013), two factors may be considered: i) mesoscale fronts located between unstable boundaries of water masses can generate physical conditions that persist long enough to provide and define zooplanktonic habitats; and ii) species of calanoid copepods can be indicators of

different zooplanktonic habitats. Based in this scenario, we hypothesized that one calanoid copepod habitat will be associated with the frontal zone, and two calanoid copepod habitats located either side of the front, with copepod calanoid concentration associated with the water mass properties and related to the mesoscale structures in each. It seemed likely that the different origins and histories of water masses on either side of the front would be reflected in different habitats, and that the mesoscale structures associated with the front itself persist for long enough to support the development of a distinct calanoid copepod habitat. To gain insight into relationships between the mesoscale activity and the biological response of the first levels of the marine trophic chains, the aim of this study was to identify the three-dimensional distribution of calanoid copepods across a mesoscale front in the convergence zone of CCW and TTW in the Pacific off Mexico, a region with high commercial importance.

2. Material and methods

2.1. Sampling strategy and data handling

Using daily satellite images of sea surface temperature (SST) and chlorophyll-*a* concentration from the Moderate Resolution Imaging Spectrum radiometer (MODIS) sensors on board the satellites Aqua and Terra, the position of an oceanic front in the convergence zone of CCW and TSW was monitored during 2 months prior to the start of the cruise from 15 June to 1 July 2010. The images with a spatial resolution of 1 km/pixel (Local Area Cover (LAC)) were processed using Level 1Bit data for NASA (<http://oceancolor.gsfc.nasa.gov>) to Level 2 with SeaDAS, version 5.5, and using standard algorithms. Level 3 imagery was

constructed through an equidistant cylindrical projection. The Absolute Dynamic Topography (ADT) variable was produced by the *Segment Sol multimissions d'ALTimétrie, d'Orbitographie et de localisation précise* and the Data Unification and Altimeter Combination System in France. Access to ADT weekly means at a spatial resolution of $1/3 \times 1/3$ -degree cells, spanning the period 1992–2013, was granted by the Archiving, Validation, and Interpretation of Satellite Oceanographic Data program (AVISO; <http://www.aviso.oceanobs.com/en/>).

Two transects of physical and biological sampling stations were made aboard the RV “Francisco de Ulloa” (Fig. 1). The first transect (stations A07 to A01) extended from $22^{\circ}46'N$, $109^{\circ}44'W$ to the southeast as far as $21^{\circ}31'N$, $108^{\circ}46'W$. The second transect (stations B10 to B01) was located from $21^{\circ}18'N$, $108^{\circ}58'W$ to $21^{\circ}56'N$, $112^{\circ}36'W$. Vertical profiles of temperature and conductivity were obtained at ± 50 km intervals along the transects with a Sea Bird 911plus CTD probe which was also equipped with dissolved oxygen (DO) and fluorescence sensors. The data were processed using the manufacturer’s software and averaged to 1 dbar (Godínez et al., 2010). Absolute Salinity (S_A , $g \cdot kg^{-1}$), Conservative Temperature ($^{\circ}C$) and density anomaly ($kg \cdot m^{-3}$) were calculated from in situ temperature and salinity with the TEOS-10 (Thermodynamic Equation of Seawater-2010) software which was downloaded from <http://www.TEOS-10.org> (IOC et al., 2010; Pawlowicz et al., 2010). The phytoplankton biomass ($mg \text{ Chl-}a \cdot m^{-3}$) was estimated indirectly from the in situ fluorescence with the manufacturer’s nominal calibration.

The geostrophic velocity relative to the maximum common sampling depth of pairs of stations (usually 1000 m) was calculated from objectively mapped conservative temperature and Absolute Salinity by the TEOS-10 software. A standard objective mapping interpolation was applied using a classic Gaussian correlation function with relative errors of

0.1, a 70-km horizontal length scale and a 30-m vertical scale. The thermocline was defined as the temperature band $\pm 1^{\circ}\text{C}$ centered on the depth of the maximum temperature gradient ($\delta T/\delta z$).

Oblique zooplankton hauls were made during day and night by using opening-closing conical zooplankton nets with a mouth diameter of 60 cm, 250 cm net length, and 505 μm mesh size (<http://www.generaloceanics.com>). The towing speed was 5 knots as in Smith and Richardson (1979). Six strata were sampled over the upper 200 m of the water column (0–15, 15–30, 30–50, 50–100, 100–150 and 150–200). The nets were opened with manual brass messengers at the start of the haul and closed when the upper level of the sampling strata was reached, and the haul was concluded. To ensure the accurate sampling of each depth stratum, the depth of the net was calculated with the cosine of the wire angle method following the standard specifications by Smith and Richardson (1979). This stratified sampling technique has been successfully used in previous studies (e.g. Sánchez-Velasco et al., 2017; Cruz-Hernández et al., 2018).

The volume of filtered water was calculated using calibrated flow meters that were placed at the mouth of each net. Samples were fixed with 4% formalin in seawater and buffered with sodium borate. The zooplankton biomass, estimated with the displacement volume method (Kramer et al., 1972), was standardized to $\text{mL} \cdot 1000 \text{ m}^{-3}$. Zooplankton subsamples (aliquots of 30 mL, typically with ≥ 500 copepods) were obtained with a Stempel pipette of 30 mL volume. Adult calanoid copepods were sorted and identified using the taxonomic keys (Palomares-García et al., 1998; <http://copepodes.obs-banyuls.fr/en/index.php>; <http://www.marinespecies.org/aphia.php?p=taxlist>). The calanoid copepod concentration in each sample was standardized to the number of organisms per

1000 m³ (Smith and Richardson, 1979), but the distribution of the integrated total concentration of the calanoid copepods are shown as number of organisms per 10 m².

Because of the use of 505 µm mesh size, this study was focused on adult calanoid copepods which range between 1500 and 5000 µm in length (Palomares-García et al., 1998; <http://copepodes.obs-banyuls.fr/en/>), taking advantage of the samples collected in a multidisciplinary study.

2.2 Considerations of the copepod sampling

As pointed out by Hopcroft et al. (2001), small copepods and early development stages dominate copepod communities from polar to tropical waters, including in our study area. In this context, it is evident that the net used in this study (505 µm) undersampled the copepod community. However, copepod concentration differences appear to be correlated to water mass properties related to inherent conditions that would be expected to impact all life-history stages in the same manner.

2.3. Statistical analysis

The non-parametric Kruskal-Wallis test (Sokal and Rohlf, 1985; Siegel and Castellón, 1988) was used to assess the statistical significance of the differences in calanoid copepod concentration between day and night-time.

The data matrix of the concentration of calanoid copepods with ≥ 0.6 % of the frequency from the two transects was log₁₀ transformed to reduce the data variance and to apply the numerical classification techniques (Clarke and Ainsworth, 1993). The Bray–

Curtis dissimilarity Index was used to define calanoid copepod habitats which differed statistically in the nonparametric tests. This index is not affected by multiple absences and gives more weight to abundant species than to rare ones (Bray and Curtis, 1957; Fieldet al., 1982). The copepod habitats were defined by a dendrogram using a simple average link (Sokal and Sneath, 1963). The cut line in the dendrogram was visually chosen according to the common practice in zooplankton and copepod studies (e.g. Yang-Chi et al., 2004; Zuo et al., 2006). To detect significant differences among the dissimilarity of the distinct calanoid copepod habitats, we applied a one-way ANOSIM. The null hypothesis is therefore that there are no differences between the members of the habitats (Clarke and Ainsworth, 1993).

The Phi coefficient (Tichy and Chytrý, 2006) was applied in order to obtain the indicator (or diagnostic) value of a species with respect to the components of each copepod habitat. This coefficient considers only the presence / absence data. The Phi coefficients range from -1 (perfect negative indication) to 1 (perfect positive indication). The null hypothesis is that the Indicator Value is not larger than would be expected at random i.e. the species has no indicator value. If the absolute value of the Phi is greater than 0.05, the null hypothesis is rejected, i.e. the species has value as an indicator.

3. Results

3.1. Synoptic view of the frontal zone

Satellite imagery of SST and ocean color showed environmental variations at the time of the cruise around the southern tip of the Baja California Peninsula (Fig. 1). The minimum SST in the cruise area was $\sim 20^{\circ}\text{C}$ in the California Current area, in the northwest and in the upwelling zone off Magdalena Bay (Fig. 1a). The highest SST ($\sim 30^{\circ}\text{C}$) was observed east and south of the cruise sampling, along the mainland coast; and in the Gulf of California. A narrow cold tongue ($\sim 22^{\circ}\text{C}$), suggestive of a jet-like current, extended southward near 110°W , originating in the coastal upwelling on the western side of Baja California and separating from the tip of the peninsula. Chlorophyll-*a* concentration ranged from 0.03 in the oligotrophic open ocean increasing up to 0.6 mg m^{-3} in the narrow filament extending $\sim 230\text{ km}$ ($\sim 20.5^{\circ}\text{N}$ and 110°W) and coincident with the cooler, jet-like feature (Fig. 1b). This filament marked a surface mesoscale front between the relatively high ($\sim 0.6\text{ mg m}^{-3}$) chlorophyll-*a* concentration to its east and low concentrations ($< 0.1\text{ mg m}^{-3}$) to its west.

3.2. Geostrophic circulation and hydrography of the mesoscale frontal zone

Absolute Dynamic topography and the associated surface geostrophic velocities are shown in Fig. 1c, where the jet-like feature, a mesoscale front, with high values of chlorophyll-*a* ($\sim$ stations B02 and B04) coincides with the southward flux produced by a cyclonic eddy on the eastern side of the jet and an anticyclonic circulation on the western side. The southward jet-like flow is connected with a current that meanders along the western coast of Baja California Peninsula. We can identify this current as the Tropical Branch of the California Current, which carries CCW from the north. The California Current is strong mainly during June and July (Portela et al., 2016).

The vertical distribution of geostrophic velocities along the transects are shown in Fig. 2, where positive velocities were entering the triangle given by stations A01-A07-B01-B10-A01 (positions in Figs. 1 and 2). The jet-like negative velocities can be seen between stations B03 and B04 and the positive velocities between stations A01-A03. Both jets correspond to the cyclonic eddy south of the tip of Baja California Peninsula. The jet-like negative velocities were located between the boundary of the TTW, which included the cyclonic eddy, and the CCW.

The θ - S_A diagram shows the water masses usually present in the area (Fig. 3): GCW, TTW, TSW (not detected in this cruise), CCW; StSsW, and two deeper water masses. Each side of the frontal zone (stations B03 to B04) presents different water masses. On the eastern side, TTW and StSsW were dominant, while on the western side CCW, StSsW and TTW were dominant. The maximum DO concentrations ($DO > 100 \mu\text{mol kg}^{-1}$) were found in the surface water masses. The CCW had the highest values of DO compared to the low subsurface concentration and the StSsW ($DO < 44 \mu\text{mol kg}^{-1}$).

On the western side of the frontal zone (CCW), the temperature distribution exhibited a deep mixed layer (~ 80 m depth) with temperatures from 23 to 24 °C, while on the eastern side of the front (TTW) the mixed layer was shallower (~ 10 -15 m depth) (Fig. 4a). The thermocline sloped upward from station B05 (at 80 m depth) as far as B03 (~ 30 m depth). The strong changes in thermocline depth were detected in the frontal zone (stations B05 to B03), while below the thermocline, the temperatures < 18 °C extended along the whole transect.

In addition, a strong contrast in the salinity was evident across the frontal zone (Fig. 4b). The salinity increased from $34.5 \text{ g}\cdot\text{kg}^{-1}$ in the western side of the front (B05) to $35.25 \text{ g}\cdot\text{kg}^{-1}$ in the eastern side (B03). The higher salinity values in the surface layer were

indicative of the presence of TTW. Furthermore, two separated cores of low salinity concentration at stations B01-A07 and A05-A01 ($\sim 34.7 \text{ g}\cdot\text{kg}^{-1}$) near 50-m depth probably indicated the recirculation of the Tropical Branch of CC bringing CCW from the northwest. At greater depths, the salinity had a relative uniform value of $\sim 34.75 \text{ g}\cdot\text{kg}^{-1}$ which typically indicates StSsW.

The DO in the TTW showed stronger vertical gradients (Fig. 4c) between 25 and 50 m depth on the eastern side of the frontal zone. The shallower mixed layer and the thermocline were highly oxygenated with values $> 225 \mu\text{mol kg}^{-1}$, but the dissolved oxygen dropped quickly to hypoxic conditions below 50-m depth. These hypoxic conditions were even stronger ($\leq 44 \mu\text{mol kg}^{-1}$) below the thermocline depth (25 to 80 m depth) in the frontal zone. The low values of DO concentrations observed near the surface ($\leq \sim 50$ m of depth) indicated the presence of StSsW. In the CCW, the surface water was oxygenated (130 to $220 \mu\text{mol kg}^{-1}$) down to 70-m depth. However, hypoxic conditions (20 to $44 \mu\text{mol kg}^{-1}$) were present below ~ 180 -m depth.

The chlorophyll-*a* concentration showed mainly oligotrophic conditions (Fig. 4d) on the western side of the front. To the east, the highest values (2 mg m^{-3}) were detected at the thermocline depth (~ 25 m) from stations B03 to A01. The chlorophyll-*a* concentration decreased drastically where the thermocline sank ($\sim$ B04) across the frontal zone from 25 to ~ 80 -m depth.

3.3. Copepod composition

Differences in calanoid copepod concentration between day and night were not statistically significant ($P > 0.05$) within an overall concentration range from 3 to 124,320 ind 1000 m^{-3} . The calanoid copepods were represented by 78 copepod species belonging to 16 families and 36 genera (See the calanoid copepod species identified in this study in the Supplementary material I).

The distribution of the integrated total concentration of the calanoid copepods is shown in Fig. 5. Away from the coast, the highest copepod concentrations were found to the eastern side of the chlorophyll-*a* jet, in the frontal zone, and in the cyclonic eddy visible in the geostrophic currents in the same figure. The lowest concentrations were observed to the western side of the front in the domain of the Tropical Branch of the California Current.

Bray-Curtis dissimilarity Index defined three groups of samples or calanoid copepod habitats to a cut of 57 % of information remaining in the dataset (Fig. 6). The habitats were significantly different (ANOSIM: $R = 0.71$, with 95% confidence level) and were named according to their location as i) “Tropical Transitional Habitat”, ii) “California Current Habitat” and iii) “Frontal Habitat”.

The “Tropical Transitional Habitat” (Fig. 7a, white circles) was located mainly on the eastern side of the front in the domain of the cyclonic eddy defined by 54 samples. This habitat was made up of forty species of copepods with a mean concentration of 24,704 ind 1000 m^{-3} (Table 1). Vertically, the highest copepod concentration occurred between the thermocline and the surface. The average concentration of most dominant species was higher than in the other habitats. For example, *Nannocalanus minor* (Claus, 1863), exhibited a high concentration of seven times higher in this habitat than in the “Frontal Habitat” (Table 1). The species *Subeucalanus subtenuis* (Giesbrecht, 1888) and *Centropages furcatus* (Dana, 1849) were indicator species of this “Tropical Transitional

Habitat” i.e. they were only recorded in this habitat (Table 1). The distribution of *S. subtenuis* was represented in the Θ - S_A diagram with DO concentrations (Fig. 3, white circles). This species was observed mainly in salty water masses like the TTW and StSsW in a wide range of DO concentrations.

The “California Current Habitat” (Fig. 7b, red circles) was defined on the western side of the front. It was formed by 29 samples and 36 species and had the lowest mean copepod concentration (3304 ind 1000 m⁻³), an order of magnitude less than the habitat located in the TTW (Table 1). This habitat extended throughout the sampled water column. The average concentration of most dominant species was lower than in the “Frontal Habitat”. *Euchaeta indica* (Wolfelden, 1905), *Centropages elongatus* (Giesbrecht, 1896) and *Candacia catula* (Giesbrecht, 1889) were the indicator species of this habitat (Table 1). The distribution of *C. elongatus* was represented in the Θ - S_A diagram with DO concentrations (Fig. 3, red circles). This species was observed mainly in surface and oxygenated water masses like the CCW and TTW, but it was also present in StSsW.

The “Frontal Habitat” (Fig. 7c, black circles) was defined by 14 samples. This habitat contained 39 species and a copepod mean concentration of 4453 ind 1000 m⁻³ (Table 1). This habitat was distributed throughout the observed water column in stations B03, B04 and B05, corresponding to the frontal zone. Most of the dominant species presented lower concentration than in the “Tropical Transitional Habitat”, and were practically absent in the “California Current Habitat”. The “Frontal Habitat” had species that were recorded only in the front; indicator species for this habitat were *Scolecithrix bradyi* (Giesbrecht, 1888) and *Heterorhabdus papilliger* (Claus, 1863). The distribution of *S. bradyi* was represented in

the Θ -SA diagram superimposed to DO (Fig. 3, black circles). This species was concentrated in the StSsW, characterized by low DO concentrations ($< 100 \mu\text{mol kg}^{-1}$).

4. Discussion

This is one of first studies that demonstrates the existence of mesoscale zooplankton habitats in a Tropical-Subtropical water mass convergence region, indicated by calanoid copepods. Many mesoscale activity, like eddies, last several months (Kurczyn et al., 2012) which allows for at least one complete reproduction cycle of most of holoplanktonic organisms (Brinton et al., 1996). In this context, this study considered that i) mesoscale fronts located between boundaries of water masses can generate physical conditions that persist long enough to generate and define zooplanktonic habitats, and ii) species of calanoid copepods can be indicators of different zooplanktonic habitats. The definition of three calanoid copepods habitats across a front and an adjacent cyclonic eddy implies the acceptance of the hypothesis.

The monitoring of the study region by satellite images (not shown) showed that the oceanographic conditions established during the sampling time were present from May 2010 to August 2010. The mesoscale front and the adjacent cyclonic eddy embedded in the TTW as sampled here (Fig. 1) formed part of a system of fronts resulting from the transport of waters of different origins by the tropical branch of the California Current and by the Mexican Coastal Current. The former transports subpolar water to tropical latitudes (Godínez et al., 2010; Portela et al., 2016), while the latter transports tropical waters poleward (Willett et al., 2006; Portela et al., 2018). These current systems converge in and

around the study area, where they mix and interact with Gulf of California waters intensifying the mesoscale processes in the region (Fiedler and Talley, 2006; Portela et al., 2018). Biologically, this water mass convergence region has been little studied to date, but some authors like Etnoyer et al. (2006) have suggested that the contribution of the mesoscale activity to primary productivity could be high, given the high frequency and abundance of top predators in the region.

In these environmental circumstances, as mentioned above, multivariate analysis defined three calanoid copepod habitats related to the hydrographic structure of the front and the cyclonic eddy that was also sampled. A habitat with the highest copepod concentration (24,704 copepods 1000 m⁻³) was defined in the area influenced by the cyclonic eddy embedded in the TTW. Vertically, it was concentrated mainly between the shallow thermocline (~ 30-m depth) and the surface. The most abundant species like *N. minor* and *T. discaudata*, and the indicator species, *S. subtenuis* and *C. furcatus*, are herbivorous and omnivorous species (Longhurst, 1985; Cruz-Hernández et al., 2018). These species appeared to take advantage of the high food availability around the shallow thermocline, as indicated by the highest chlorophyll-*a* concentrations, corresponding with observations in similarly stratified conditions in other oceans (Cummings, 1984; Longhurst, 1985).

In contrast, the second habitat was defined in the CCW, where the copepod concentration was lowest (3304 copepods 1000 m⁻³) and the thermocline was deepest (~ 90-m depth). This habitat occurred through the water column (0-200 m). Even though herbivorous species were found in this habitat, omnivorous and carnivorous species predominated, e.g. *P. gracilis*, and the indicator species, *E. indica* and *C. elongatus* (Longhurst, 1985; Cruz-Hernández et al., 2018). This species composition could be a

response to the greater thermocline depth allowing species less dependent on the concentration of phytoplankton to flourish in the water column (Palomares-García et al., 2013).

As an unexpected result, the habitat located in the mesoscale frontal zone had low concentrations of calanoid copepods (4453 copepods 1000 m^{-3}), in contrast to the copepod accumulations recorded in most oceanic fronts (Smith et al., 1986; Uye et al., 1992; Molinero et al., 2008; Trudnowska et al., 2016). In this study, it was observed that the sinking of the thermocline and oxycline, from $\sim 30\text{ m}$ depth on the tropical side (TTW) to $\sim 90\text{ m}$ depth on the subtropical side (CCW) (Fig. 4a,c) contributed significantly to the decrease in the concentration of calanoid copepods. The chlorophyll-*a* concentrations related with the thermocline, decreased as thermocline depth increased (Fig. 4d). It is possible that the depth of the thermocline in the frontal zone was deeper than the euphotic zone, and therefore the primary productivity and food availability for zooplankton organisms decreased. The environmental gradients recorded in this habitat are associated with a mix of omnivorous and herbivorous species, but with lower concentrations than in their preferential habitats, that is, the habitats defined to each side of the front (Table 1). The “Frontal habitat” had its own indicator species like *S. bradyi* and *H. papilliger*, which could result from the front’s persistence for enough time for the development of an independent habitat where the indicator species can reproduce favorably.

The interaction of physical processes on different time-scales is complex in a region of water mass convergence (Godínez et al., 2010; Portela et al., 2016). However, our results suggest that, in addition to a drastic sinking of the thermocline with the inherent reduction of the primary productivity, as we explain above, the role of the cyclonic eddy could be to create a hotspot by the recirculation of the California Current at $\sim 50\text{-m}$ depth in

the tropical side of the front, thus increasing the zooplankton concentration, as was the case of the calanoid copepods. In this scenario, the mechanism that defined the calanoid copepod habitats, and possibly those of all the zooplankton communities, was not the front itself but its interaction with other fine-scale mechanisms that generate oceanographic conditions leading to development of different food webs depending on the structure of the water column. Therefore, in Tropical-Subtropical convergence regions, where strong mesoscale activity is generated in the boundaries of water masses, different zooplanktonic trophic habitats are established. The herbivorous species may proliferate by taking advantage of the high food availability in the water mass where the thermocline is shallow and the primary productivity is high, while the carnivorous species may proliferate in the water mass where the thermocline is depressed and the food availability is reduced. However, in the frontal zone, where the instabilities of the convergence such as eddies and filaments affect also the structure of the water column, the trophic conditions will vary as the mesoscale structure changes in time. Thus, the near-frontal mesoscale structure provides the perfect laboratory to study the ecology of calanoid copepods and other zooplankton organisms.

5. Conclusions

The results of this study showed relationships between the interaction of physical processes on different spatial scales and the biological response of the first trophic levels of the marine food chain, indicated by the distribution of calanoid copepod habitats in the Eastern Tropical-Subtropical Convergence off Mexico. Three different calanoid copepod

habitats were defined around a mesoscale front with a concentration gradient from the east side of the front, TTW, to the west side of the front, CCW. In addition to a drastic sinking of the thermocline from the TTW to CCW, with the inherent reduction of the primary productivity, the role of a cyclonic eddy adjacent to the front and embedded in the TTW could create a hotspot that increased the copepod concentrations there. In this scenario, the factor that defined the calanoid copepod habitats, and possibly those of all the zooplankton community, was not the front itself but its interaction with other fine-scale mechanisms that generate oceanographic conditions leading to development of different food webs depending on the structure of the water column.

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Caption of figures

Fig. 1. Sampling station locations in the Tropical-Subtropical convergence off Mexico.

Aqua/MODIS daily satellite images: a) Mean sea surface temperature ($^{\circ}\text{C}$) and black dotted line, indicates the position of the front; b) Mean CHL (mg m^{-3}) and red vectors indicate velocity vectors averaged over 0 – 50-m depth June 15 – July 1, 2010; c) Absolute Dynamic topography (ADT) and surface geostrophic velocities (black vectors) derived from AVISO in the Tropical-Subtropical convergence off Mexico. White circles indicate zooplankton and CTD sampling stations. Red arrows indicate current normal to the transect averaged over 0 – 50-m depth.

Fig. 2. Geostrophic velocities (m s^{-1}) normal to both transects in the Tropical-Subtropical convergence off Mexico. The green tones indicate positive velocities and the brown and magenta color negative velocities. Vertical brown line indicates change of direction of the transect.

Fig. 3. Θ - S_A diagram and copepods with Dissolved oxygen concentrations ($\mu\text{mol kg}^{-1}$). The water mass limits were graphed as in Portela et al. (2016). TSW, Tropical Surface Water; GCW, Gulf of California Water; TTW, Tropical Transitional Water; CCW, California Current water; StSsW, subtropical subsurface water; PIW, Pacific intermediate water; PDW, Pacific Deep Water. Symbols indicate presence of copepod species of each Calanoid Copepod Habitat: Red circles, *Centropages elongatus* (“California Current Habitat”); black circles, *Scolecithrix bradyi* (“Frontal Habitat”) and white circles, *Subeucalanus subtenuis* (“Tropical Transitional Habitat”).

Fig. 4. Vertical distribution of hydrographic conditions along transects in the Tropical-Subtropical convergence off Mexico. a) Conservative temperature $\theta(^{\circ}\text{C})$, the heavy blue curve indicates the position of the thermocline, b) absolute salinity (S_A , g kg^{-1}); c) dissolved oxygen ($\mu\text{mol kg}^{-1}$); and d) chlorophyll-*a* (mg m^{-3}) concentrations. Vertical brown line indicates change of direction of the transect.

Fig. 5. Aqua/MODIS daily satellite images (Mean CHL mg m^{-3}) and geostrophic surface velocity vectors derived from AVISO in the Tropical-Subtropical convergence off Mexico. The white symbols indicate the integrated total calanoid copepod concentration ($\text{ind } 10 \text{ m}^{-2}$). Circle size indicates the copepod concentration.

Fig. 6. Dendrogram of calanoid copepod samples defined by the Bray-Curtis dissimilarity Index and the flexible agglomerative methods from copepod data collected in the Tropical-Subtropical convergence off Mexico.

Fig. 7. Vertical distribution of hydrographic conditions along transects in the Tropical-Subtropical convergence off Mexico. a) Conservative temperature $\theta(^{\circ}\text{C})$ and concentration of “Tropical Transitional Habitat” copepods (white circles), the heavy blue curve indicates the position of the thermocline; b) absolute salinity (S_A , g kg^{-1}) and concentration of “California Current Habitat” copepods (red circles); and c) dissolved oxygen ($\mu\text{mol kg}^{-1}$) and concentration of “Frontal Habitat” copepods (black circles). Copepod concentrations standardized to $\text{ind } 1000 \text{ m}^{-3}$. Vertical brown line indicates change of direction of the transect.

		California Current			Front			Tropical Transitional		
		Habitat			Habitat			Habitat		
Dominant	FS	X	% F	p<0.05	X	% F	p<0.05	X	% F	p<0.05
<i>Nannocalanus minor</i>	H	270	29		804	14		5,537	56	
<i>Rhincalanus nasutus</i>	Om				711	9		1,733	49	
<i>Subeucalanus subcrassus</i>	H	870	26		614	13		2,023	33	
<i>Scolecithrix bradyi</i>*	Om				517	8	0.0002			
<i>Temora discaudata</i>	H				506	13		2,142	55	
<i>Undinula vulgaris</i>	H	277	30		492	12		1,854	52	
<i>Pleuromamma gracilis</i>	Om	633	23		466	5				
<i>Pleuromamma abdominalis</i>	Om				448	10		370	33	
<i>Pareucalanus sewelli</i>	Om	220	27		391	13		1,772	54	
<i>Calanus pacificus</i>	H				367	11		340	41	
<i>Euchaeta rimana</i>	Ca	214	27		313	13		212	51	
<i>Heterorhabdus papilliger</i>*	Ca				246	13	0.0026			
<i>Scolecithrix danae</i>	Om	283	22		236	10		680	53	
<i>Euchaeta indica</i>*	Ca	646	27	0.0006						
<i>Euchaeta longicornis</i>	Ca	228	25					339	46	
<i>Centropages elongatus</i>*	Om	162	28	0.0002						
<i>Candacia catula</i>*	Ca	153	23	0.0004						

<i>Subeucalanus subtenuis</i> *	H		1596	34	0.0100
<i>Centropages furcatus</i> *	Om		755	52	0.0002
Mean copepod abundance		3,304	4,453	24,704	
Total of number of taxa		36	39	40	
Number of samples		29	14	54	

Table 1. Abundance is expressed as number of copepods per 1000 m⁻³. FS, feeding strategy: herbivorous (H), omnivorous (Om), carnivorous according to Palomares-García et al. (1998). (Ca); X, mean abundance; %F, percentage of occurrence; *, Indicator Value of a Species ($P<0.05$).

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Species	MA ind 1000 m ⁻³	R F (%)
<i>Nannocalanus minor</i>	3311	98.97
<i>Temora discaudata</i>	1450	86.60
<i>Rhincalanus nasutus</i>	1449	63.92
<i>Subeucalanus</i> <i>subcrassus</i>	1349	72.16
<i>Subeucalanus</i> <i>subtenuis</i>	1215	45.36
<i>Undinula vulgaris</i>	1172	93.81
<i>Pareucalanus sewelli</i>	1131	93.81
<i>Centropages furcatus</i>	684	57.73
<i>Euchaeta plana</i>	560	1.03
<i>Scolecithrix danae</i>	524	84.54
<i>Pleuromamma</i> <i>gracilis</i>	510	50.52
<i>Pleuromamma</i> <i>quadrangulata</i>	395	5.15
<i>Scolecithrix bradyi</i>	390	15.46
<i>Euchaeta indica</i>	386	56.70
<i>Centropages</i> <i>elongatus</i>	370	38.14
<i>Pleuromamma</i> <i>abdominalis</i>	338	59.79
<i>Calanus pacificus</i>	305	70.10
<i>Euchaeta longicornis</i>	296	77.32
<i>Candacia</i> <i>pachydactyla</i>	268	8.25
<i>Acartia lilljeborgii</i>	260	7.22
<i>Subeucalanus</i> <i>pileatus</i>	240	14.43
<i>Euchaeta rimana</i>	228	90.72
<i>Haloptilus</i> <i>mucronatus</i>	226	32.99
<i>Candacia discaudata</i>	214	12.37
<i>Scolecithricella</i> <i>abyssalis</i>	199	1.03
<i>Calanopia minor</i>	183	5.15

<i>Pleuromamma</i>		
<i>xiphias</i>	182	13.40
<i>Acartia Clausi</i>	167	3.09
<i>Candacia catula</i>	165	42.27
<i>Clausocalanus</i>		
<i>arcuicornis</i>	154	29.90
<i>Haloptilus</i>		
<i>longicornis</i>	147	56.70
<i>Heterorhabdus</i>		
<i>papilliger</i>	140	56.70
<i>Acrocalanus gracilis</i>	136	27.84
<i>Aetideus bradyi</i>	136	48.45
<i>Acartia danae</i>	124	21.65
<i>Calanopia elliptica</i>	117	4.12
<i>Mesocalanus</i>		
<i>tenuicornis</i>	115	2.06
<i>Candacia ethiopica</i>	114	15.46
<i>Labidocera acuta</i>	111	16.49
<i>Labidocera</i>		
<i>acutifrons</i>	108	25.77
<i>Candacia bipinnata</i>	104	8.25
<i>Pontellina plumata</i>	103	15.46
<i>Aetideus giesbrechti</i>	100	11.34
<i>Scolecithricella</i>		
<i>marginata</i>	98	2.06
<i>Candacia truncata</i>	96	13.40
<i>Haloptilus acutifrons</i>	94	45.36
<i>Candacia armata</i>	92	51.55
<i>Lucicutia flavicornis</i>	87	22.68
<i>Labidocera</i>		
<i>detruncata</i>	80	5.15
<i>Aetideus armatus</i>	78	4.12
<i>Clausocalanus</i>		
<i>mastigophorus</i>	73	3.09
<i>Euchirella pulchra</i>	69	7.22
<i>Euchaeta magniloba</i>	66	25.77
<i>Euchaeta acuta</i>	65	15.46
<i>Gaetanus miles</i>	65	17.53
<i>Neocalanus cristatus</i>	64	8.25
<i>Metridia princeps</i>	63	1.03
<i>Pleuromamma</i>		
<i>johnsoni</i>	62	3.09
<i>Clausocalanus</i>		
<i>furcatus</i>	61	2.06
<i>Euchirella curticauda</i>	61	6.19

<i>Scaphocalanus</i>		
<i>elongatus</i>	50	5.15
<i>Candacia pofi</i>	46	2.06
<i>Calocalanus minor</i>	45	3.09
<i>Gaetanus pileatus</i>	45	3.09
<i>Euchaeta media</i>	44	1.03
<i>Scaphocalanus</i>		
<i>echinatus</i>	41	2.06
<i>Euchaeta tenuis</i>	38	6.19
<i>Phaenna spinifera</i>	34	7.22
<i>Haloptilus spiniceps</i>	31	3.09
<i>Cosmocalanus</i>		
<i>darwinii</i>	28	1.03
<i>Rhincalanus</i>		
<i>rostrifrons</i>	26	1.03
<i>Euchirella venusta</i>	19	1.03
<i>Lucicutia gaussae</i>	19	1.03
<i>Calocalanus pavo</i>	9	1.03
<i>Pontellina sobrina</i>	9	1.03
<i>Augaptilus</i>		
<i>longicaudatus</i>	9	1.03
<i>Paraeuchaeta</i>		
<i>birostrata</i>	7	1.03
<i>Pontellopsis yamadae</i>	4	1.03

Supplementary material I

Calanoid copepod species identified in the frontal zone of tropical-subtropical convergence off México (15 June to 1 July 2010). MA: Mean Abundance, RF, Relative Frequency.

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Dear editor

The authors declare that we have no conflict of interest

Laura Sánchez Velasco

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