VERTICAL DISTRIBUTION OF CALANOID COPEPODS IN A MATURE
CYCLONIC EDDY IN THE GULF OF CALIFORNIA

BY

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ABSTRACT

29 The distribution of calanoid copepod habitats in a cyclonic eddy in the Gulf of California was
30 examined. Direct velocity observations revealed that the eddy extended to approximately 550 m
31 depth and 150 km diameter. The established thermocline suggested that active vertical pumping
32 was not occurring because the eddy was in mature phase. A copepod habitat located in the
33 surface mixed layer, showed high abundances, dominated by *Subeucalanus subtenius*
34 (Giesbrecht, 1888), whose abundances decrease towards the centre of the eddy. A second habitat,
35 situated in thermocline, had the highest abundances dominated by *Nannocalanus minor* (Claus,
36 1983) and *Temora discaudata* (Giesbrecht, 1889). Another habitat, beneath the thermocline, was
37 dominated by most of species recorded in thermocline, but with the lowest abundance. Results
38 suggest that in the mature phase of a cyclonic eddy, the water column stratification induces
39 layering of the calanoid copepod habitats, with the most propitious conditions for their feeding in
40 thermocline.

RESUMEN

44 Se determinó la distribución de hábitats de copépodos calanoides en un remolino ciclónico en
45 el Golfo de California. Datos de velocidad mostraron que el remolino midió 550 m de
46 profundidad y 150 km diámetro. El establecimiento de la termoclina sugirió que no hubo
47 bombeo vertical activo debido a que el remolino estuvo en etapa madura. Se localizó un hábitat
48 en la capa de mezcla, siendo dominado por *Subeucalanus subtenius* (Giesbrecht, 1888), cuya
49 abundancia disminuyó hacia el centro del remolino. El hábitat termoclina fue el más abundante,
50 dominado por *Nannocalanus minor* (Claus, 1983) y *Temora discaudata* (Giesbrecht, 1889). Otro
51 hábitat, localizado por debajo de la termoclina, fue dominado por especies registradas en la
52 termoclina, pero con menor abundancia. Los resultados sugieren que en fase madura de un
53 remolino ciclónico, la estratificación de la columna de agua induce la estratificación de los
54 hábitats de copépodos calanoides, con condiciones propicias para su alimentación en termoclina.

INTRODUCTION

57 Zooplankton plays a central role in the transfer of energy from primary producers to upper
58 trophic levels (Mackas & Coyle, 2005). In tropical and subtropical oceans, calanoid copepods are
59 frequently the most abundant group in the marine zooplankton, having a key trophic position in
60 the ecosystems as a link between primary producers and secondary consumers (e.g. Wiebe, 1976;
61 Palomares-García et al., 2013). Calanoid copepods are deemed to be a valuable indicator of
62 environmental variability because their abundance and distribution is strongly influenced by
63 mesoscale activity and environmental conditions (Ashjian & Wishner, 1993; Beaugrand &
64 Ibanez, 2004; Kozak et al., 2014).

65 Mesoscale hydrographic structures, such as eddies, may act as mechanisms of enrichment,
66 concentration and retention of zooplankton (Iles & Sinclair, 1982; Bakun, 1996). The biological
67 structure within mesoscale eddies is a product of both the initial entrainment of zooplankton
68 from the source waters of the eddy and the succession of these assemblages over time (Griffiths
69 & Wadley, 1986; Mackas & Coyle, 2005). Early phases of cyclonic eddies are characterized by
70 an upwelling of cooler, nutrient-rich waters from depth and subsequent phytoplankton growth. In
71 the mature phase, after the eddy is spun up, isosurfaces remain domed in near-geostrophic
72 equilibrium with a rotating flow but the vertical pumping is absent. As cooler water is no longer
73 introduced to the surface layers, surface heating induces the re-establishment of the thermocline
74 (Bakun, 2006; Sangrà et al., 2009).

75 Traits of copepod distributions relative to eddies in the open sea have been observed in
76 different ecosystems, such as the Gulf Stream system (Wiebe, 1976), the Gulf of Mexico
77 (Cummings, 1984; López-Salgado et al., 2000), the California Current (Haury et al., 1986) and
78 the Gulf of Alaska (Mackas & Galbraith, 2002; Mackas & Coyle, 2005; Batten & Crawford,

792005). These authors described that in eddies that travel from coastal origins to the open ocean,
80the zooplankton community composition within the eddy changes as the eddy ages. The coastal
81community is out-competed by oceanic species ones as conditions in the eddy become gradually
82more oceanic. However, the influence of mesoscale eddies upon ecological aspects linked to the
83vertical distribution of the copepods is still poorly understood.

84 Mesoscale physical phenomena such as fronts and eddies are common features in the Gulf of
85California, which is a semi-enclosed sea 150 – 200 km wide in the inner region (Lavín &
86Marinone, 2003). Its surface circulation reverses seasonally from cyclonic in summer to
87anticyclonic in winter (Beier, 1997; Lavín & Marinone, 2003; Sánchez-Velasco et al., 2009). The
88circulation has a strong mesoscale component, related to the seasonality of the currents and their
89interaction with the bathymetry (Lavín et al., 2013; 2014). The poleward-flowing Mexican
90Coastal Current, which enters the Gulf of California from the central Mexican coast, interacts
91with specific topographic irregularities and capes to generate eddies of width similar to the gulf.

92 Previous sampling efforts to study copepod species composition and distribution in the Gulf
93of California have been made using oblique hauls of bongo nets that integrate the zooplankton of
94the upper 200 m (e.g. Fleminger, 1975; Brinton et al., 1986; Jiménez-Pérez and Lara-Lara,
951988). Recently, Palomares-García et al. (2013), who analyzed the copepod vertical structure in
96the northern Gulf, recorded the highest copepod abundance near the thermocline. However, in
97view of the oceanographic variability of the Gulf of California (Lavín et al., 2013; 2014), which
98promotes heterogeneity of the zooplankton, the vertical distribution of copepods, is practically
99unknown.

100 Despite the frequent occurrence of eddies in the Gulf of California (Lavín et al., 2013), their
101effects on holoplanktonic organisms have not been investigated. The hypothesis of this study, is

102that in the eddy's mature phase, when the thermocline is re-established, the stratification of the
103water column largely determines the distribution of the copepod habitats. The objective of this
104paper is to examine the distribution of habitats of calanoid copepods in a mature cyclonic eddy in
105the southern Gulf of California during summer (2011), as a contribution to holoplankton
106ecology.

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METHODS

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Sampling strategy and data handling

110 The position of eddies in the southern Gulf of California was monitored from April to August
1112011 (not shown), before and after the oceanographic cruise, using daily satellite images of
112chlorophyll a concentrations from the Moderate Resolution Imaging Spectro radiometer
113(MODIS) sensors on board the satellites Aqua and Terra. (<http://oceancolor.gsfc.nasa.gov>). A
114system of four mesoscale eddies was detected with the chlorophyll a images (see details in
115Sánchez-Velasco et al., 2013); however the study is focused on the largest and most persistent
116cyclone during the period, which was located at approximately 26°21'N, 110°22'W (fig. 1).

117 A transect with 19 physical and biological sampling stations and two more on the mainland
118coast was made aboard the R.V "El PUMA" from 26 July to 6 August 2011 across the cyclonic
119eddy from coast to coast (fig. 1). Vertical profiles of temperature and conductivity were obtained
120at 10 km intervals along the transect with a Sea Bird 911plus CTD (conductivity, pressure,
121depth) probe, which was also equipped with dissolved oxygen and fluorescence sensors. The
122data were processed using the manufacturer's software and averaged to 1 dbar (Godínez et al.,
1232011). Conservative Temperature $\theta(^{\circ}\text{C})$, Absolute Salinity ($S_A, \text{g}\cdot\text{kg}^{-1}$) and density anomaly (σ_{θ}
124 $\text{kg}\cdot\text{m}^{-3}$) were calculated from in situ temperature and salinity with the TEOS-10

125(Thermodynamic Equation of Seawater-2010) software, which was downloaded from
126<http://www.TEOS-10.org> (IOC et al., 2010; Pawlowicz, 2010). The phytoplankton biomass (mg
127Chl a·m⁻³) was estimated indirectly from the in situ fluorescence with the manufacturer's nominal
128calibration.

129 Velocity profiles were measured with a broadband Teledyne- RDI 300 kHz lowered acoustic
130Doppler current profiler (LADCP) attached to the CTD protection frame. The sampling bins
131were 8m in size and the absolute velocity profiles were obtained with the methods described by
132Visbeck (2002).

133 The ocean surface mixed layer depth was calculated following the methodology of Kara et al.
134(2000) which consists of a gradient-based criterion having a fixed temperature difference of 0.8
135°C and variable salinity. The thermocline was defined as the temperature band $\pm 1^\circ\text{C}$ centered on
136the depth of the maximum temperature gradient ($\delta T/\delta z$) following the procedure of Kara et al.
137(2000).

138 Oblique zooplankton hauls were made during day and night in three depth strata from the
139surface to just below the thermocline (approximately 45 m depth) and three 50 m strata below
140that depth to a maximum of 200 m (i.e. 0-15, 15-30, 30-50, 50-100, 100-150, 150-200 m depth)
141or to some 10 m off bottom where the water was shallower. Opening–closing conical
142zooplankton nets were used, with a mouth diameter of 60 cm, 250 cm net length, and 505 μm
143mesh size (<http://www.generaloceanics.com>). Two hauls were made at each station, each haul
144sampling three strata. The nets were opened with manual brass messengers at the start of the haul
145and closed when the upper level of the sampling strata was reached, and the haul concluded. To
146ensure accurate sampling of each depth stratum, the depth of the net was calculated with the
147cosine of the wire angle method, following the standard specifications by Smith & Richardson

148(1979). This stratified sampling technique has been used successfully in previous studies (e.g.,
149Sánchez-Velasco et al., 2013; Sánchez-Velasco et al., 2017).

150 The volume of filtered water was calculated using calibrated flow meters that were placed at
151the mouth of each net. Samples were fixed with 5% formalin, buffered with sodium borate. The
152zooplankton biomass, estimated with the displacement volume method (Kramer et al., 1972),
153was standardized to $\text{mL} \cdot 1000 \text{ m}^{-3}$. Zooplankton subsamples (aliquots of 30 mL, typically with
154 ≥ 500 copepods) were obtained with a Stempel pipette of 30 mL volume. Adult copepods were
155sorted and identified using taxonomic keys (Palomares-García et al., 1998; [http://copepodes.obs-](http://copepodes.obs-banyuls.fr/en/index.php)
156**banyuls.fr/en/index.php**). Because of the mesh size of 505 μm , this study was focused on
157calanoid copepods, which fluctuate between 1,500 and 5,000 μm in length (Palomares-García et
158al., 1998; <http://copepodes.obs-banyuls.fr/en/>). The calanoid copepod abundance in each sample
159was standardized to the number of organisms 1000 m^{-3} (Smith & Richardson, 1979).

160

161 Statistical analysis

162 The non-parametric Kruskal-Wallis test (Sokal & Rolf, 1985; Siegel & Castellón, 1988) was
163used to assess the statistical significance of the differences in calanoid copepod abundance
164among daytime and nighttime.

165 The data matrix of the abundance of calanoid copepods with $\geq 0.04\%$ of total abundance
166from the eddy transect was $\log_{10}$ transformed to reduce the data's variance and to apply
167numerical classification techniques (Clarke & Ainsworth, 1993). The Bray–Curtis dissimilarity
168Index was applied to define calanoid copepod habitats that differed statistically in the
169nonparametric tests. This index is not affected by multiple absences and gives more weight to
170abundant species than to rare ones (Bray & Curtis, 1957; Field et al., 1982). The copepods

171habitats were defined by a dendrogram using a simple average link (Sokal & Sneath, 1963). The
172cut line in the dendrogram was chosen visually, according to common practice in zooplankton
173and fish larvae studies (e.g. Doyle et al., 1993; Moser & Smith, 1993; Atwood et al., 2010). To
174detect significant differences among the dissimilarity of the distinct calanoid copepod habitats,
175we applied a One-way ANOSIM as a test of the significance of the habitats that was defined a
176priori. The null hypothesis is therefore that there are no differences between the members of the
177habitats (Clarke & Ainsworth, 1993).

178 The Olmstead–Tukey test ranked the species of each habitat of calanoid copepods as
179dominant, frequent, constant or rare (Sánchez-Velasco et al., 2009; Mahadevan et al., 2008). This
180test considered the average relative abundance against the frequency of occurrence of each
181species (Sokal & Rohlf, 1985). Average similarity and the percentage contribution of specific
182species to the identity of each habitat were determined using the Similarity Percentage
183(SIMPER) routine. This analysis calculates the contribution of each species (or other variable) to
184the observed similarity between samples. Diversity was calculated with the Shannon Wiener
185Index (Ludwig & Reynolds, 1988). Canonical correspondence analysis (Ter-Braak, 1986) was
186applied to define if relations exist between calanoid copepod habitats and environmental
187variables. Before executing the canonical correspondence analysis, the standardized biological
188data were $\log_{10}(N + 1)$ transformed to reduce the spread of the data. The biological matrix
189contained the abundance of copepod species (ind. 1000 m⁻³) of each sample, while the
190environmental matrix contained the average of the values of Conservative Temperature ($\theta^{\circ}\text{C}$),
191Absolute Salinity (S_A , g·kg⁻¹), Chlorophyll a (mg Chl a·m⁻³) and dissolved oxygen ($\mu\text{mol}\cdot\text{kg}^{-1}$) of
192each stratum.

RESULTS

Eddy physical characteristics

196Details of the series of eddies observed during the survey may be consulted in Sánchez-Velasco
197et al. (2013). The LADCP velocity distribution and the domed isopycnals (fig. 2) indicate that
198the eddy was cyclonic, with maximum azimuthal speeds on the mainland side of $\sim 40 \text{ cm}\cdot\text{s}^{-1}$
199(stations A14 to A16) and $\sim 20 \text{ cm}\cdot\text{s}^{-1}$ on the peninsula side (stations A06 to A10). Weaker
200velocities ($< 10 \text{ cm}\cdot\text{s}^{-1}$) were observed at stations A01 to A04 on the peninsula side outside the
201eddy. The total width of the eddy was $\sim 140 \text{ km}$ from stations A05 to A19, and its depth was $\sim$
202470 m as shown in fig. 2. The center of the eddy, where the surface current speed was near zero,
203was located between stations A11 and A13.

204 The temperature distribution (fig. 3A) revealed strong uplift of isotherms below the
205thermocline in the eddy center; for instance, the 14°C isotherm rose from $\sim 180 \text{ m}$ at station A05
206to $\sim 100 \text{ m}$ depth at station A11. The surface mixed layer (blue line) was 10–15 m deep and its
207temperature was close to 30°C . The thermocline, roughly located between the isotherms 24 and
208 26°C , fluctuated in depth from 20 to 40 m depth across the eddy. Most of the isotherms in and
209above the thermocline were practically flat, showing that upwelling in the eddy center was
210insignificant and probably dominated by surface layer exchanges and dynamics.

211 The high chlorophyll a was concentrated in a subsurface maximum ($> 2 \text{ mg}\cdot\text{m}^{-3}$) near the
212thermocline (fig. 3B). Values $> 1 \text{ mg}/\text{m}^3$ were found between 25 and 60 m depth along the
213transect. The maximum chlorophyll a occurred just inside the northeastern boundary of the eddy
214and close to the peninsular coast (samples A14 and A01-A03).

215 The salinity distribution in the eddy (fig. 3C) illustrates the typical decrease with depth in the
216Gulf of California. The maximum salinities ($35.5\text{--}35.6 \text{ g}\cdot\text{kg}^{-1}$) occurred from the surface to 100

217m depth within the eddy between stations A05 and A16. At deeper levels, the 35.0 isohalines
218were uplifted under the eddy.

219 The dissolved oxygen (fig. 3D) was highest ($\geq 120 \mu\text{mol}\cdot\text{kg}^{-1}$) near to the surface and
220decreased with depth. Hypoxic water, delimited by the oxypleth of $44 \mu\text{mol}\cdot\text{kg}^{-1}$, was uplifted
221under the eddy center at stations A11, A12 and A13 from ~ 200 m to ~ 100 m depth.

222 In the coastal stations (Supplementary Material I), the depth of the surface mixed layer and
223thermocline were similar to the eddy transect, and the isotherms were also completely flat. The
224high chlorophyll a was also concentrated in the thermocline. The salinity and dissolved oxygen
225values decreased to depth.

226

227 Copepod composition

228 In the eddy transect, calanoid copepods accounted for > 80 % of the total relative abundance.
229Differences in calanoid copepod abundance between day and night were not statistically
230significant ($P > 0.05$), within an overall abundance range from 4 to 46,697 ind. 1000 m^{-3} . The
231calanoid copepods were represented by 57 copepod species belonging to 14 families and 38
232genera (Supplementary material II). Most of the species were oceanic (64.9%) and carnivorous
233(49.1%), but the dominant species were herbivorous and omnivorous. The species *Nannocalanus*
234*minor* (Claus, 1983) (23.2 %, herbivorous and oceanic), *Scolecithrix danae* (Lubbock, 1856)
235(19.6 %, omnivorous and oceanic), *Temora discaudata* (Giesbrecht, 1889) (12.3 %, herbivorous
236and neritic), *Subeucalanus subtenuis* (Giesbrecht, 1888) (7.3 %, herbivorous and oceanic),
237*Undinula vulgaris* (Dana, 1849) (7.1 %, herbivorous and neritic) contributed > 69 % to the
238abundance of the entire study (Supplementary material II).

239 In the coastal samples, calanoid copepods accounted for > 87 % of the total relative
240abundance. Differences in calanoid copepod abundance between day and night were not
241statistically significant ($P > 0.05$). The composition of the calanoid copepods was similar to that
242of the eddy transect, but the abundance was almost of the double that in eddy (from 44 to 72,471
243ind. 1000 m⁻³).

244

245 Vertical distribution of calanoid copepod habitats in the eddy transect

246 Bray-Curtis dissimilarity Index defined three calanoid copepod habitats related to the
247stratified water column and the eddy structure to a cut of 50 % of information remaining of the
248dataset (fig. 4). The habitats were significantly different (ANOSIM: $r = 0.5$, with 95% confidence
249level) and were named according to their location as i) “Surface mixed layer habitat”, ii)
250“Thermocline habitat” and iii) “Hypoxic habitat”.

251 The “Surface mixed layer habitat” was located in the surface layer above the thermocline all
252along the transect (fig. 3B, blue circles). This habitat was defined by 22 samples and 37 species
253of copepods with a mean abundance of 9,003 ind. 1000 m⁻³ and 0.85 of diversity (Table I).
254Copepod abundance was high at the periphery of the eddy, and low near to its center (stations
255A09 to A11). *U. vulgaris*, *S. subtenuis* and *Euchaeta indica* (Wolfenden, 1905), although
256recorded throughout the water column, had high abundance in this habitat, and decreased at
257greater depth (fig. 5D-F). All the dominant species are shown in Table I.

258 The “Thermocline habitat”, located mainly around the thermocline in most of the transect
259(fig. 3C, red circles), and down to 150 m depth in the eddy center (stations A08 to A12), was
260defined by 46 samples and 39 species of copepods. The highest copepod abundance of 17,406
261ind. 1000 m⁻³ with 0.89 of diversity occurred in this habitat (Table I). The most abundant species

262of the study, *N. minor*, *S. danae*, and *T. discaudata*, were also distributed throughout the water
263column and decreased with depth (fig. 5 A-C), dominated in this habitat. Other species like
264*Euchaeta rimana* (Bradford, 1974), *Heterorhabdus papilliger* (Giesbrecht, 1898), *Pareucalanus*
265*sewelli* (Fleminger, 1973) and *Rhincalanus nasutus* (Giesbrecht, 1888) (fig. 5 G-J) were also
266dominant in the thermocline habitat (Table I).

267 The “Hypoxic habitat” (fig. 3D, black circles), defined beneath the thermocline habitat, was
268formed by 40 samples and 39 species with 1.03 of diversity, and had the lowest mean copepod
269abundance (3,199 ind. 1000 m⁻³) of the study (Table I). The abundance was slightly greater in the
270eddy center (stations A12 to A14) and at its edge at stations A17 and A01 than elsewhere in the
271habitat. The same species dominated here as in the thermocline, but with a quarter of the
272abundance. Species like *Aetideus bradyi* (Scott A., 1909) (fig. 5I) and *Pleuromamma*
273*abdominalis* (Lubbock, 1856) were important in this habitat, but not in thermocline habitat.

274 The Canonical Correspondence Analysis (fig. 6) detected high correlation between the
275distribution of the calanoid copepod habitats and the environmental variables. Axis 1 had a
276Pearson correlation of 0.89 with a percentage of variance explained of 7.9, while Axis 2 had a
277correlation of 0.56 with a percentage of variance explained of 1.9. The first canonical axis was
278related to vertical gradients, in which the temperature was the best correlated (0.89). The second
279canonical axis was related to horizontal gradients, where the dissolved oxygen was the variable
280with major correlation (0.79).

281 The ordination of the copepod habitats confirmed their location in the eddy. The habitat
282centroids were designated by green stars. “Surface mixed layer habitat” (blue circles) was
283correlated significantly with high values of temperature and dissolved oxygen. The “Thermocline
284habitat” (red circles), which was the most dispersed, overlapping with the other two habitats, was

285 correlated with intermediate values of most of the variables. The “Hypoxic habitat” (black
286 circles) was inversely correlated with all the variables as it was the deepest.

287

288

DISCUSSION

289 This study has shown the distribution of three calanoid copepod habitats in a cyclonic eddy
290 in the Gulf of California. The domed iso-surfaces, lack of any surface cool anomaly and the well-
291 established thermocline indicated that the cyclonic eddy sampled was in its mature phase (fig.
292 3A). It is likely therefore that vertical pumping was not occurring, in contrast to the face of early
293 phase cyclonic eddies, in which active upwelling characterizes their center (Bakun, 1996; Sangrà
294 et al., 2009). The re-established near-surface stratification appeared related to layering in the
295 calanoid copepod habitats, with the most propitious conditions for calanoid copepod survival in
296 the thermocline.

297 The near-synoptic vision of the distribution of the three copepod habitats revealed a clear
298 relation with the water column stratification, but little detectable effects along horizontal
299 gradients, which were associated with the mature phase of the eddy described above (fig. 3). The
300 “Thermocline habitat” located in the layer between ~ 17 and 51 m depth was defined by the
301 highest calanoid copepod abundance, predominantly oceanic species, herbivorous and
302 omnivorous, like *N. minor*, *S. danae* and *T. discaudata*, which although distributed throughout
303 the water column, presented massive abundances in this layer (fig. 5). The feeding strategies of
304 these species appeared to take advantage of high food availability near the thermocline, as
305 indicated by the highest chlorophyll a concentrations there. A distinct “Surface mixed layer”
306 calanoid copepod habitat was identified at shallower levels, although some of the dominant
307 species of the “Thermocline habitat” were present in both habitats, but with different abundance

308and frequency (figs. 3, 5). In this “Surface mixed layer” habitat, located in warm and oxygenated
309waters, the number of significant species decreased, but herbivorous species were predominant
310even though carnivorous species like *E. indica* were present. In the third, “Hypoxic habitat”,
311located below the thermocline and immersed in cold and hypoxic water, the lowest calanoid
312copepod abundance was found, possibly as a result of the stressful environmental conditions.
313Species like *A. bradyi* recorded in this habitat (fig. 3d), might be an example of a species adapted
314to conditions of low dissolved oxygen concentrations.

315 Despite no significant differences in calanoid copepod abundance between light and dark
316hours, the highest abundance of copepods in the thermocline suggests that most of them
317gradually accumulated in this layer probably for feeding and reproduction during the mature
318phase of the sampled eddy. This vertical structure, both physical and biological, likely changes
319during the eddy development. During the early phases of the eddy, when its center experiences
320active upwelling (Bakun, 1996; McGillicuddy et al., 2007), the thermocline could disappear.
321Contrary to the results obtained in this study, the impact on calanoid copepod distributions would
322be strong, probably dispersing the organisms to the eddy edges, and decreasing their abundances,
323compared to later phases. Studies focused on the 3D-distribution during the development of these
324mesoscale eddies would shed light on these issues.

325 Few studies of the vertical distribution of copepods in eddies have been complemented by
326oceanographic information. The present results support some earlier findings focused mainly on
327their vertical distribution. Cummings (1984), on the basis of zooplankton sampling in the
328northwestern Gulf of Mexico, proposed that the vertical structure of the copepod species was
329related to the "nutrient-limited" and "light-limited" physiological regimes documented for
330oceanic phytoplankton species. In addition, Longhurst (1985) reported two locations in the

331eastern Tropical Ocean where the greatest abundance and diversity of copepod species were in
332and around the thermocline, with a dominance of herbivorous species during hours of both light
333and dark. Recently Palomares-García et al. (2013) also showed that vertical distribution and
334abundance of copepods were associated with vertical temperature structure and thermocline
335depth in the central Gulf of California. The similarity of the vertical distribution of the copepod
336community observed in stratified conditions in different regions suggests that the vertical
337distribution of copepods is defined mainly as a response to trophic order, independently of the
338mesoscale activity.

339 This consideration conforms with previous studies on the behavior of copepods (Clarke,
3401934; Longhurst, 1985), which have shown that these are active swimmers reaching speeds up to
341136 cm · min⁻¹. The direction of swim and the copepod location are governed by the interaction of
342physical and biological factors. Among the physical ones are gravity, which naturally sinks
343organisms, light and gradients of temperature, salinity, and in some cases, dissolved oxygen.
344Among the biological factors are the availability of food and the avoidance of predation. It seems
345likely that feeding is one of the most important factors that determine the swim direction and
346their location in the water column. The calanoid copepods tend to migrate to the thermocline,
347which maintains a high availability of food.

348 This vision of the vertical distribution is difficult to compare with earlier studies focused on
349copepods in relation to mesoscale eddies because these were based on integrated sampling from
350200 m depth to the surface, with no possibility of observing the vertical structure of the
351zooplankton community. Studies that analyzed cyclonic and anticyclonic eddies, for example,
352López-Salgado et al. (2000) in the western Gulf of Mexico and Batten & Crawford (2005) in the
353eastern Gulf of Alaska, concluded that the copepod abundance was higher in cyclonic eddy

354centers than in anticyclonic ones. The results of the present study are consistent with the idea
355that eddies are favorable habitats for the copepod communities in terms of the abundance in the
356open sea, where the thermocline layer might be the preferential habitat dominated by herbivorous
357species, at least in the eddy's mature phase. The high abundance of the calanoid copepod
358reported in eddies shows that mesoscale hydrographic structures contribute to the productivity of
359the pelagic ecosystems in the open oceans. However, studies of the effects of the succession of
360hydrographic structures on the vertical distribution of the holoplankton organisms within eddies
361are needed for a better understanding of holoplankton ecology.

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363

CONCLUSIONS

364 A near-synoptic sampling of the vertical distribution of copepods defined three statistically
365different habitats in a mature cyclonic eddy in the Gulf of California, a semi-enclosed sea, during
366the summer period of strongest stratification. Vertical separation of the calanoid copepod
367habitats was related to the water column stratification. Better conditions for calanoid copepod
368survival were found in the thermocline, where herbivorous and omnivorous species
369(*Nannocalanus minor* and *Scolecithrix danae*) were highly abundant. Based in the results
370presented here and previous studies, it can be supposed that this vertical structure, physical and
371biological, changes during the eddy evolution.

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CAPTIONS

541 Fig. 1. Aqua/MODIS Chlorophyll a satellite image and sampling stations (26 July to 6
542 August 2011). Red circles: CTD data and biological samples.

544 Fig. 2. LADCP velocities ($\text{cm}\cdot\text{s}^{-1}$) normal to the eddy transect in the southern Gulf of
545 California. Yellow colors indicate positive velocities, and blue colors indicate negative
546 velocities.

548 Fig. 3. Vertical distribution of hydrographic conditions along the eddy transect in the
549 southern Gulf of California; A) Conservative Temperature $\theta(^{\circ}\text{C})$. The heavy red curve
550 marks surface mixed layer depth, and the blue curve is mixed layer depth; B) Chlorophyll a
551 (mg/m^3) with “Surface mixed habitat” (blue circles); C) Absolute Salinity (S_A , $\text{g}\cdot\text{kg}^{-1}$) with
552 “Thermocline habitat” (red circles), and D) dissolved oxygen ($\mu\text{mol}\cdot\text{kg}^{-1}$), with “Hypoxic
553 habitat” (black circles).

555 Fig. 4. Dendrogram of calanoid copepod samples defined by the Bray-Curtis
556 dissimilarity Index and the flexible agglomerative methods from copepod data collected in
557 the eddy transect in the southern Gulf of California.

559 Fig. 5. Vertical distribution of the mean abundance of dominant calanoid copepod
560 species from copepod data collected in the eddy transect in the southern Gulf of California.
561 The mean depth of upper and lower limits of the thermocline are represented by black
562 dashed lines.

564Fig. 6. The Canonical Correspondence Analysis (CCA) results show copepod habitats in
565relation to hydrographic conditions in the eddy transect during July 2011. The three habitats
566are “Surface mixed habitat” (blue circle), “Thermocline habitat” (red circle) and “Hypoxic
567habitat” (black circle). Copepod habitat centroids (green stars) and environmental data
568(arrows); first axis is horizontal and second axis vertical.

Table I

571 Dominant taxa per calanoid copepod habitats from the eddy transect in the southern Gulf
 572 of California (July 2011). Abundance is expressed as number of copepods per 1000 m⁻³.
 573 FS: Feeding Strategy, herbivorous (H), omnivores (Om), carnivores (Ca); X: mean
 574 abundance; %F: percentage of occurrence; %C: percentage of contribution.

Dominant	FS	Surface mixed habitat			Thermocline habitat			Hypoxic habitat		
		X	%F	C%	X	%F	C%	X	%F	C%
<i>Euchaeta indica</i> (Wolfenden, 1905)	Ca	11,927	95	4						
<i>Aetideus bradyi</i> (Scott A., 1909)	Om							6,911	83	6
<i>Pleuromamma abdominalis</i> (Lubbock, 1856)	Om							4,324	74	5
<i>Euchaeta rimana</i> (Bradford, 1974)	Ca				18,084	89	10			
<i>Subeucalanus subtenuis</i> (Giesbrecht, 1888)	H	53,793	100	6	23,525	93	12			
<i>Nannoclanus minor</i> (Dana, 1852)	H	32,727	91	10	204,036	100	15	17,713	87	10
<i>Scolecithrix danae</i> (Lubbock, 1856)	Om	56,567	86	9	138,475	100	11	19,244	87	9
<i>Temora discaudata</i> (Giesbrecht, 1889)	H	63,367	100	6	64,199	93	10	6,843	86	6
<i>Undinula vulgaris</i> (Dana, 1849)	H	40,183	95	4	26,523	86	10	10,667	76	4
<i>Heterorhabdus</i>	Ca				19,180	83	5	12,948	85	5

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papilliger
(Giesbrescht,
1898)

Pareucalanus
sewelli

(Fleminger, 1973) Om

29,026

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4,312

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Rhincalanus
nasutus
(Giesbrescht,
1888)

Om

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12,248

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Mean copepod
abundance

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003

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,406

3,
199

Total number of
taxa

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Number of
samples

22

46

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Diversity bits/ind.

0.85

0.89

1.03

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585 Fig. 1. Aqua/MODIS Chlorophyll a satellite image and sampling stations (26 July to 6
586 August 2011). Red circles: CTD data and biological samples.

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 592 California. Yellow colors indicate positive velocities, and blue colors indicate negative
 593 velocities.

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606 Fig. 3. Vertical distribution of hydrographic conditions along the eddy transect in the
 607 southern Gulf of California; A) Conservative Temperature θ ($^{\circ}\text{C}$). The heavy red curve
 608 marks surface mixed layer depth, and the blue curve is mixed layer depth; B) Chlorophyll *a*
 609 ($\text{mg}\cdot\text{m}^{-3}$) with "Surface mixed habitat" (blue circles); C) Absolute Salinity (S_A , $\text{g}\cdot\text{kg}^{-1}$) with
 610 "Thermocline habitat" (red circles), and D) dissolved oxygen ($\mu\text{mol}\cdot\text{kg}^{-1}$), with "Hypoxic
 611 habitat" (black circles).

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617 Fig. 4. Dendrogram of calanoid copepod samples defined by the Bray-Curtis
618 dissimilarity Index and the flexible agglomerative methods from copepod data collected in
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632 species from copepod data collected in the eddy transect in the southern Gulf of California.

633 The mean depth of upper and lower limits of the thermocline are represented by black
634 dashed lines.

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Fig. 6. The Canonical Correspondence Analysis (CCA) results show copepod habitats in relation to hydrographic conditions in the eddy transect during July 2011. The three habitats are “Surface mixed habitat” (blue circle), “Thermocline habitat” (red circle) and “Hypoxic habitat” (black circle). Copepod habitat centroids (green stars) and environmental data (arrows); first axis is horizontal and second axis vertical.

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653 Supplementary material I. Vertical distribution of hydrographic conditions in the
 654 coastal stations in the southern Gulf of California; A) Conservative Temperature $\theta(^{\circ}\text{C})$. The
 655 heavy red curve marks surface mixed layer depth, and the blue curve is mixed layer depth,
 656 and black circles, abundance of calanoid copepods; Chlorophyll *a* ($\text{mg}\cdot\text{m}^{-3}$); C) Absolute
 657 Salinity (S_A , $\text{g}\cdot\text{kg}^{-1}$), and D) dissolved oxygen ($\mu\text{mol}\cdot\text{kg}^{-1}$).

658

662Supplementary material II. Calanoid copepod species identified in the eddy transect in the
663southern Gulf of California (July 2011). Feeding Strategyⁱ (FS) is indicated as herbivorous
664(H), omnivorous (Om), or carnivorous (Ca). Ecology Affinitiesⁱⁱ (EA) categories are shown
665as neritic (N), coastal (C), or oceanic (O). Biogeographic Affinitiesⁱⁱⁱ (BA) are indicated as
666tropical-subtropical (Trop-subtrop), subtropical (subtrop), subpolar-subtropical (subpolar-
667subtrop), equatorial (Equat), cosmopolitan (Cos), tropical (Trop). % Abu, percentage of
668abundance per species; MA, Mean abundance; %F, percentage of frequency of occurrence.

79i According to Longhurst, 1985; Broglio et al., 2001; Cruz-Hernández & S. Hernández-Trujillo, 2007.
80

81ii Brinton, 1985; Jiménez-Pérez, L. C., & B. E. Lavaniegos, 2004; Kozak et al., 2014; Suárez-Morales
82et al., 2000.

83iii Brinton, 1985; López-Salgado et al., 200; Kozak et al., 2014; [http://copepodes.obs-](http://copepodes.obs-banyuls.fr/en/fichesp.php?sp=1250)
84banyuls.fr/en/fichesp.php?sp=1250.

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