



Distribution of Atlantidae species (Gastropoda: Pterotracheoidea) during an El Niño event in the Southern California Current System (summer–fall 2015)

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ABSTRACT: Atlantids are holoplanktonic gastropods present in tropical to sub-polar waters, and have gained an increasing interest due to their potential use as biological indicators of climate change and ocean acidification. However, there is a lack of information regarding their distribution for large areas of some oceans, particularly in the California Current System (CCS), which has been used as a model for many acidification studies and where intense warming events occur. The distribution patterns of 18 species of Atlantidae off the west coast of the Baja California Peninsula, Mexico, representing 90 % of the atlantid species registered for the Pacific Ocean, were analyzed during a period of warm anomalies associated with the El Niño of 2015–2016 and the 2014–2016 marine heat wave (MHW). The species distribution showed 3 groups: 2 in the north (coastal and oceanic) and 1 in the south. The limit of distribution between these 3 groups was found in the vicinity of Punta Eugenia (PE). The southernmost community of atlantids was characterized by tropical and subtropical species that were transported northward due to coastal advection of warm waters associated with the El Niño of 2015–2016. North of PE, the warm-water affinity oceanic species *Atlanta rosea* and *A. fragilis* were found, evidencing the entrance of water from the Central Pacific related to MHW which affected the oceanic region off the coast of PE. The response of the distribution patterns proves that atlantids can be used as biological indicators, as they reflect the effect of environmental anomalies in the southern CCS.

KEY WORDS: El Niño 2015–2016 · Heteropods · Northeastern Pacific

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1. INTRODUCTION

Atlantidae (Gastropoda: Pterotracheoidea) are small (<14 mm) marine mollusks that spend their entire life cycle in the water column of tropical to sub-polar waters, yet they are often overlooked in zooplankton studies (Lalli & Gilmer 1989, Wall-Palmer et al. 2016b, 2018a). They are important components of the marine food web (Wall-Palmer et al. 2016b) and transport energy through the water column due to

their vertical migrations (Seapy 1990, Wall-Palmer et al. 2018b). They are also key elements in the oceanic carbon system because they have an aragonitic (calcium carbonate) shell, which is prone to dissolution due to ocean acidification (Lalli & Gilmer 1989, Bednaršek et al. 2012).

The detailed distribution patterns of these organisms are not well understood, and no data regarding atlantids are available for large areas of the oceans, specifically for much of the Pacific Ocean (Wall-

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Palmer et al. 2018a). However, the Pacific Ocean has the highest species richness of atlantids (Seapy & Skoglund 2001). For the northeastern Pacific, off the western coast of the Baja California Peninsula (WBCP), in the southern region of the California Current System (CCS), recent work recorded 18 species (Moreno-Alcántara et al. 2020), which represent 90% of the known species in the Pacific Ocean and 78% worldwide (Moreno-Alcántara 2019). The species found in this area were *Oxygyrus inflatus*, *Protatlanta souleyeti* and 16 species of the genus *Atlanta*. This makes the WBCP the area with the highest species diversity of atlantids recorded in the American Pacific (Angulo-Campillo et al. 2011, Moreno-Alcántara et al. 2014, 2017, Moreno-Alcántara 2019).

Most atlantids have tropical and subtropical affinity (Lalli & Gilmer 1989), but almost two-thirds of the known species are widely distributed from the tropics to transitional or temperate regions (McGowan 1967, Wall-Palmer et al. 2016b, Moreno-Alcántara 2019). Since this group of mollusks has a completely planktonic life cycle, their horizontal distribution is entirely dependent on currents (Lalli & Gilmer 1989, Suárez-Morales & Rivera 1998). Because of the lack of studies focused on atlantids, the main environmental variables that determine their distribution and affect their abundance in the oceanic ecosystems are still unknown (Wall-Palmer et al. 2016b). However, their short life cycle as well as the apparent affinity for specific conditions makes them potential biological indicators of the environment (Furnestin 1979), as it has been seen for species such as *A. californiensis*, which is exclusive to the northeastern Pacific (Seapy & Richter 1993, Moreno-Alcántara 2019), or *A. ariejansseni*, which has a narrow latitudinal distribution (37–48° S) in the Southern Subtropical Convergence Zone of the Atlantic and Indo-Pacific Oceans (Wall-Palmer et al. 2016a).

In the central portion of the WBCP, near Punta Eugenia (PE), the Subarctic, transitional, Central Pacific and Tropical Pacific water masses converge (Durazo 2009), as do the eco-regions of the California Current (CC), North Central Pacific and Eastern Tropical Pacific (Sutton et al. 2017). Subarctic water (SAW) prevails in the area in winter, spring and early summer, while tropical surface water (TSW) and subtropical surface water (StSW) prevail from late summer through fall, mainly south of PE (Durazo 2009). The area surrounding PE is also recognized as the boundary between the San Diego and Mexican biogeographic provinces (Briggs & Bowen 2012); because of its transitional nature, fauna of temperate/subarctic and tropical/subtropical affinity often

overlap (Lavaniegos et al. 2003, Durazo 2015, Aceves-Medina et al. 2018). However, the latitudinal location of the transitional area between northern temperate and southern tropical fauna assemblages is dependent on the intensity of the equatorward flow of the CC, the poleward flow of the California Undercurrent, the seasonally intermittent coastal California Countercurrent, mesoscale dynamics and anomalous conditions or events like El Niño (EN) (Moser & Smith 1993, Durazo et al. 2005, Aceves-Medina et al. 2018).

The 2015–2016 EN event is among the 3 most intense in historical records (Fiedler & Mantua 2017). It affected the WBCP during the fall of 2015 and caused an anomalous near-surface poleward coastal countercurrent and northward advection of TSW and StSW (Durazo et al. 2017). Prior to this event, the WBCP was also affected by a marine heatwave (MHW) that reached the northern portion of the WBCP during 2015 (Di Lorenzo & Mantua 2016, Jacox et al. 2016, Gentemann et al. 2017, Wells et al. 2017). These warming events produced anomalies in sea temperature, strong stratification of the water column, deeper thermoclines, lower nutrients, reduced productivity and an unprecedented distribution of tropical species north of 30° N (Leising et al. 2015, Cavole et al. 2016, Jacox et al. 2016, McClatchie et al. 2016, Zaba & Rudnick 2016). However, to our knowledge, it is unknown if the North Pacific MHW had any impact on the structure of the pelagic ecosystem communities off the WBCP (southern region of the CCS) and if there was any combined effect between the MHW and the EN events that occurred between 2014 and 2016.

Because of the potential usefulness of atlantids as indicators of changes in different variables and environmental processes, as well as on different time scales, the aim of this work was to investigate the main environmental variables related to the distribution, abundance and assemblage formation of atlantid mollusks in the southern CCS off the WBCP, during a period of warm anomalies caused by the North Pacific MHW and EN of 2015–2016.

2. MATERIALS AND METHODS

2.1. Study area

Environmental data and zooplankton samples were collected during an oceanographic survey on board the RV 'Buque de Investigación Pesquera y Oceanográfica' (BIPO-INAPESCA) during summer-fall 2015 off the WBCP. The survey (BIPOCO-1509)

began on 17 September and finished on 11 November 2015. The 214 sampling stations were arranged in 18 lines perpendicular to the coast (from line 97 to 153), separated by 40.5 nautical miles (n miles) each, with stations separated by 20 n miles within the Mexican Exclusive Economic Zone from Ensenada to Cabo San Lucas, Mexico (Fig. 1).

2.2. Sample collection and processing

At each sampling station, we measured conductivity, temperature and fluorescence in the water column down to a maximum depth of 1500 m with a conductivity-temperature-density (CTD) probe (Itronaut Ocean Seven 320 plus). Along with the CTD data, salinity, chlorophyll *a* (chl *a*) concentration, mixed layer depth (MLD) and dynamic height were estimated at each station.

Zooplankton samples were collected following the standard methods of the California Cooperative Oceanic Fisheries Investigations program for ichthyoplankton studies, using oblique trawls with 2 cylindrical-conical Bongo nets with a mouth diameter of 0.71 m and mesh of 505 μm . These sampling gears have proven to be useful in composition and abundance analyses of Atlantidae, since their frequency of capture (both juvenile and large specimens) and abundance is high, and they have proved useful in estimating species diversity in different areas of the ocean (Moreno-Alcántara et al. 2014, 2020). Both Bongo nets were equipped with a General Oceanics digital flow meter to estimate the volume of filtered water. Trawls were made at a maximum depth of 210 m, or 15 m above bottom at shallower stations (Smith & Richardson 1977). The zooplankton volume (ZV) was obtained through the displaced volume method (Beers 1976), and the volume was standardized to ml 1000 m^{-3} of filtered water (Smith & Richardson 1977). Zooplankton was fixed in 4% formalin neutralized with sodium borate.

Atlantidae were separated from the zooplankton samples using a stereoscopic microscope (ZEISS Discovery V8) and were preserved in 96% ethanol. Atlantids were identified according to Seapy (1990) on the basis of spires, general shell morphology and eye

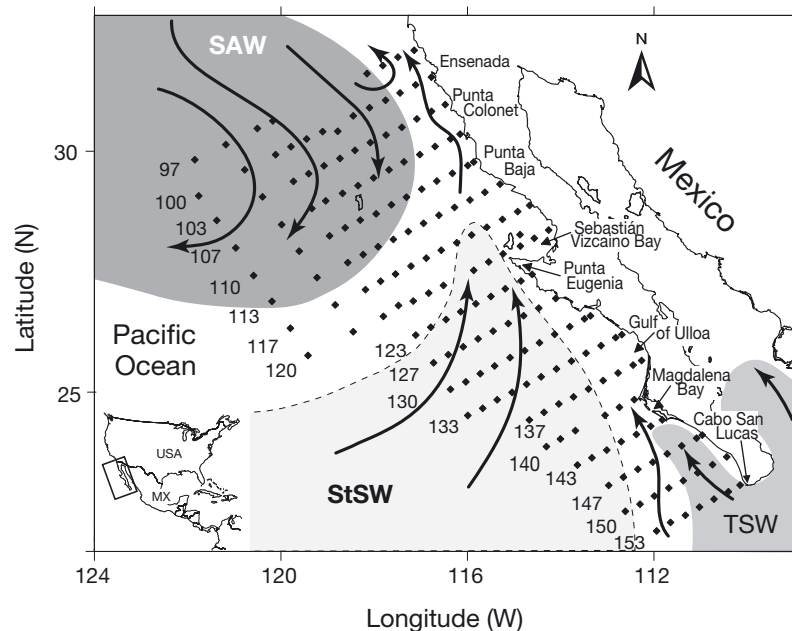


Fig. 1. Study area with sampling stations (dots) and transect number of the BIPOCO-INAPESCA survey during summer–fall, 2015. Superficial distribution of water masses (grey shaded areas) and flow direction (bold arrows) for summer–fall following Durazo & Baumgartner (2002). SAW: subarctic water; StSW: subtropical surface water; TSW: tropical surface water

type, and confirmed with keys by Richter & Seapy (1999), Wall-Palmer (2017) and Moreno-Alcántara (2019). Distribution maps of the standardized abundance of organisms (organisms 1000 m^{-3}) for each species were created using the software Surfer v.13.3.

2.3. Data analysis

To estimate which factors determined environmental variability, a principal component analysis (PCA) was performed using a data matrix obtained from the measurements of each environmental variable at 10 m depth, including sea surface temperature (SST) and salinity (SSS), and chl *a*; MLD and ZV were also included. The 10 m value was selected, as it is representative of the processes occurring in the mixed layer, and avoids the environmental effect of micro- to sub-mesoscale structures and wind in the surface layer. The values of each environmental variable were transformed to standard error (SE) using:

$$SE = \frac{X - \mu}{\sigma \sqrt{n-1}} \quad (1)$$

where X is the environmental variable with mean μ and standard deviation σ , and n is the number of observations of X . To test whether there was a statis-

tically significant difference between station groups, a multi response permutation procedure (MRPP) was performed using PC-ORD v. 6.0 (McCune & Mefford 2011).

From the CTD data, the water masses were determined using temperature–salinity (T–S) diagrams following Durazo & Baumgartner (2002). Horizontal distribution maps of the environmental variables were created using Surfer v.13.3. In addition, remotely sensed SST anomalies (SSTa) and the associated geostrophic flows were obtained from the Copernicus Marine Environment Monitoring Service.

The community description was based on the species composition as reported by Moreno-Alcántara et al. (2020) and the standardized abundance for each species, as well as species richness (S), the Shannon Index ($\log_2 H'$) and Pielou's evenness (J) that were calculated with BioDiversity Pro V.2 software. Distribution maps of standardized abundance, S , H' and J were made with Surfer v.13.3.

A cluster analysis (CA) was performed using the Bray-Curtis similarity index and the simple averaging link method with BioDiversity Pro V.2 to establish the relations of the sampling stations according to species abundance.

To establish the effect of the environmental gradients on Atlantidae distribution and abundance, a canonical correspondence analysis (CCA) was performed using the software PC-ORD V. 6.0 (McCune & Mefford 2011). For the CA and the CCA, matrices were obtained with the most abundant species that together comprised 80% of the grand total of all atlantids captured, plus those that were present in at least 10% of the total sampling stations. In order to minimize differences in the extreme abundance values between species and to reduce variance, abundances for the main matrix were transformed to $\log_{10}(x_{ij} + 1)$, where x is the abundance of species i at station j . The same environmental matrix used in the PCA was used as the secondary matrix with SST, SSS, chl a , ZV and MLD as variables. Dispersion diagrams were obtained for the sampling stations and the species abundance.

3. RESULTS

The results of the PCA (Table 1) show that the first 3 components (PC) explained 85% of the total variance. The first component (PC1) explained 44.5% of the variance with high correlation values for SST and SSS, while the second (PC2) and third (PC3) component explained 25.8 and 14.5% of the variance, re-

Table 1. Principal component analysis performed with environmental variables. Percentage of explained variance of each component, cumulative explained variance and eigenvectors scaled to unit length for each component (PC1–PC3). ZV: zooplankton volume; SST (SSS): sea surface temperature (salinity); Chl a : chlorophyll a concentration; MLD: mixed layer depth

	PC1	PC2	PC3
Variance (%)	44.585	25.873	14.499
Cumulative variance (%)	44.585	70.458	84.957
ZV	0.0978	-0.6856	0.6548
SST	-0.6113	-0.1098	0.1777
SSS	-0.5950	-0.2919	-0.1353
Chl a	0.2145	-0.6539	-0.6820
MLD	-0.4655	0.0717	-0.2372

spectively, and both components had the highest correlation values with chl a and ZV. The PCA dispersion diagram depicts the separation of the northern and southern stations with respect to PC1 (Fig. 2a), which is related to the latitudinal gradients observed for SST and SSS (Fig. 3a,b). Environmental variables related to PC2 and PC3 (chl a and ZV) had a coastal-oceanic gradient (Fig. 3c,d).

The difference between the groups of northern and southern stations was statistically significant according to the MRPP ($A = 0.048$; $p < 0.01$). The T–S diagrams (Fig. 2b,c) showed predominance of SAW in the northern region, while in the south there was a predominance of transitional water (TrW) and equatorial subsurface water (ESSW) and an increase in StSW; however, there was no evidence of TSW.

Cruise-mean geostrophic currents derived from sea level anomaly gradients, overlaid on cruise-mean SST deviations from the climatological mean (Fig. 4), depict the largest SSTa nearshore in PE. Sea surface currents show the presence of 4 cyclonic eddies: one near 30°N, the second between 30 and 27°N, the third in the oceanic region facing the Gulf of Ulloa at 24°N and the fourth near the tip of the peninsula between 21 and 22°N. A single anticyclonic eddy was present off PE at 27°N.

The distribution of the total Atlantidae mollusks (Fig. 5a) showed relatively high abundance values at some oceanic stations at the northern limit of the study area off Ensenada, and at some oceanic stations in the south off Cabo San Lucas. However, the latter did not exceed the densities found in the coastal region, where they showed the highest abundance mainly in Sebastian Vizcaino Bay (BSV), the Gulf of Ulloa and Magdalena Bay. Stations with very low abundance or absence of atlantids had temperatures between 22 and 26.7°C and salinity between

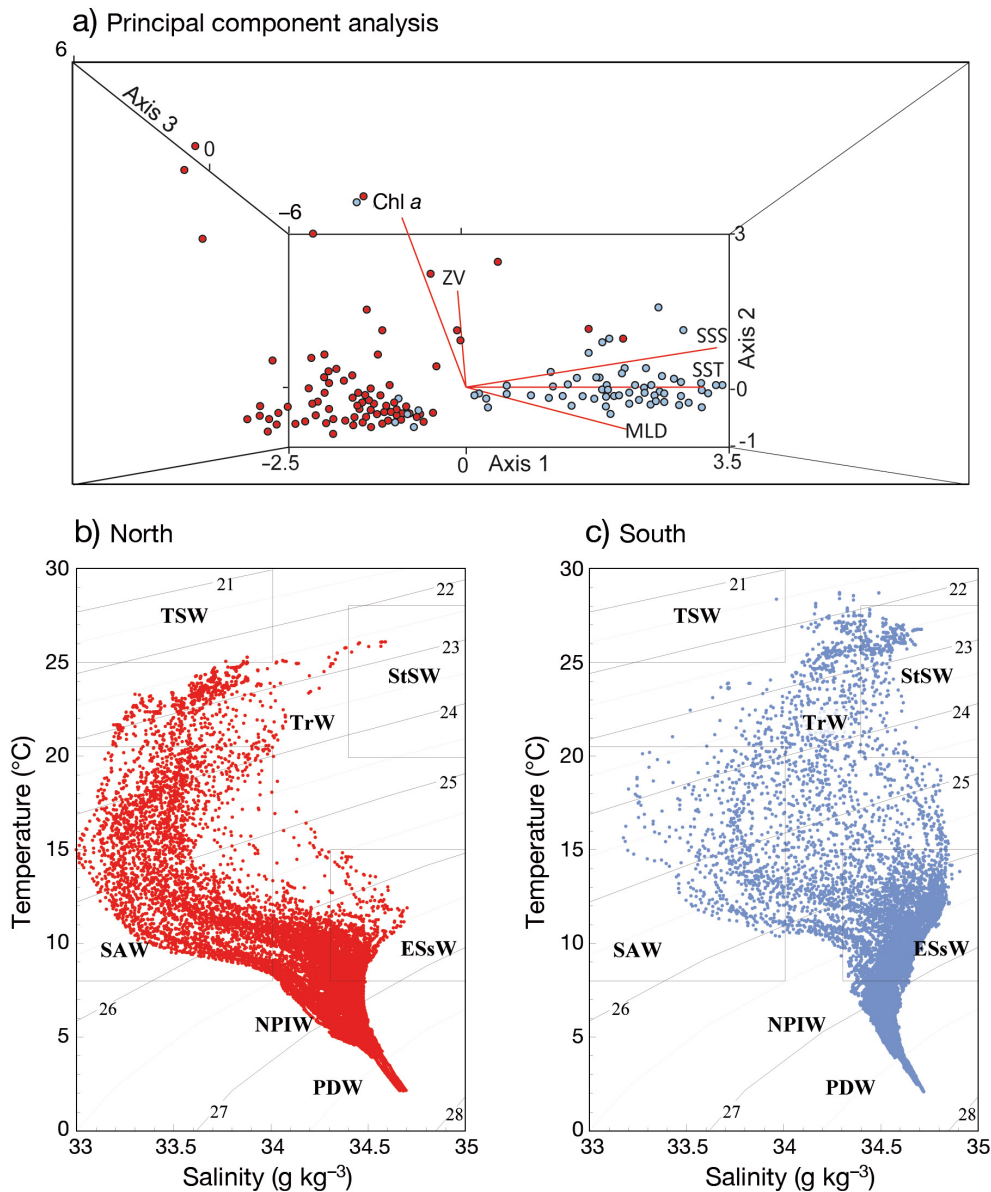


Fig. 2. (a) Dispersion diagram of components 1, 2 and 3 eigen-vectors, obtained from the principal component analysis of the environmental variables. Blue circles represent stations south of Punta Eugenia (transects 97.7–120). Red circles represent stations north of Punta Eugenia (transects 123.3–153.3). SST (SSS): sea surface temperature (salinity); ZV: zooplankton volume; MLD: mixed layer depth. (b) Temperature–salinity (T–S) diagram of water masses found north of Punta Eugenia; (c) T–S diagram of water masses found south of Punta Eugenia. TSW: Tropical surface water; StSW: subtropical surface water; TrW: transitional water; SAW: sub-arctic water; ESsW: equatorial subsurface water; NPIW: North Pacific intermediate water; PDW: Pacific deep water. Numbered contours represent density isolines

33.3 and 34.7, and were found off Punta Baja as well as in the central region of the study area between PE and the oceanic region off the Gulf of Ulloa. In contrast, high values of species richness, diversity and evenness were found at oceanic stations north and south of the study area (Fig. 5b–d). The highest values of species richness and diversity were observed off the southern portion of the peninsula.

The most abundant species were *Atlanta oligogyra* (26.4%), *A. californiensis* (24.6%), *A. inflata* (12%), *A. lesueurii* (8%), *A. peronii* (6.5%), *A. helicinoidea* (6.4%), *Atlanta* sp. 1 (3.5%) and *A. turriculata* (2.2%), which together accounted for 89.6% of the total abundance (Table 2).

The CA (Fig. 6) revealed 3 groups of sampling stations with 38% similarity. The first group included all of the northern oceanic stations, while a second group included the northern coastal stations, both with a southern distribution limit off PE. A third group, located south of PE, consisted of oceanic and coastal stations from Cabo San Lucas to Magdalena Bay and only coastal stations between the Gulf of Ulloa and BSV. Spatially, high species richness, diversity and evenness values in the north characterize the northern oceanic group; high values for these 3 same community parameters south of PE belong to the southern oceanic-coastal group (Fig. 5b–d). An important result is the strong similitude between the

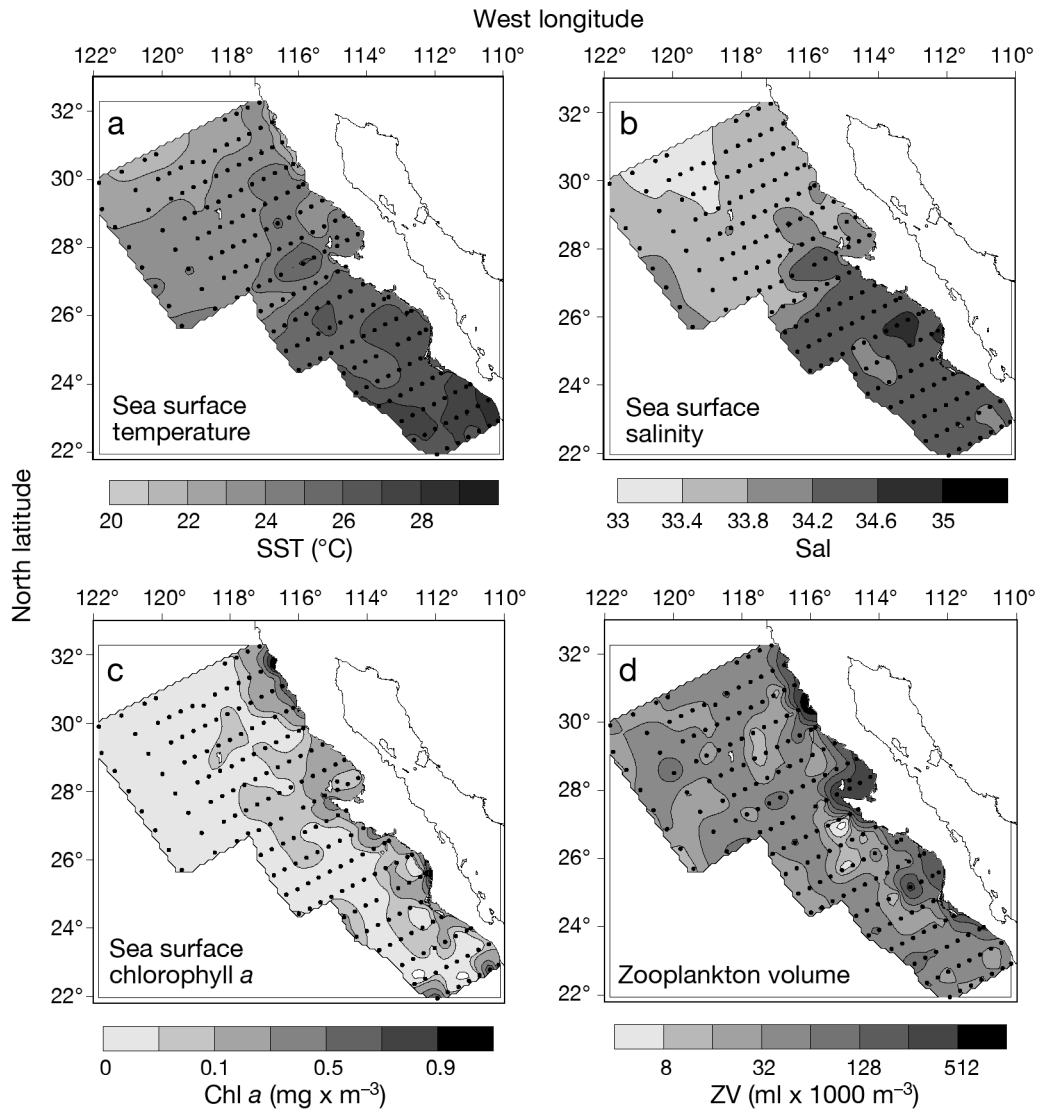
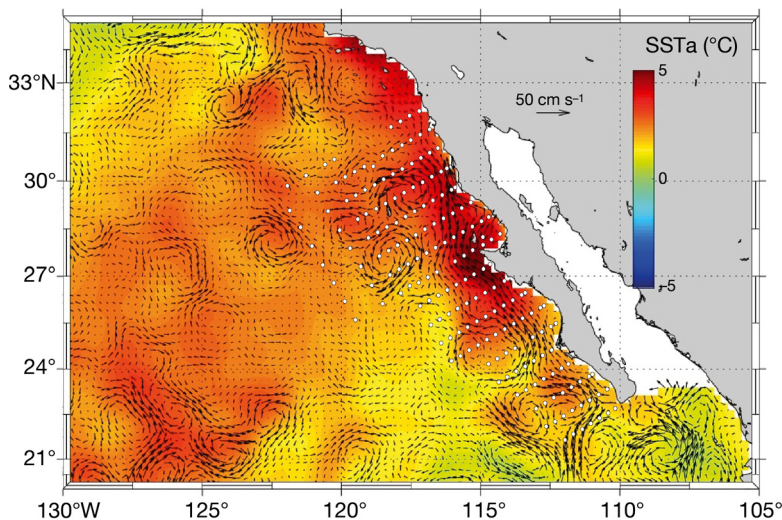


Fig. 3. Sea surface distribution of (a) temperature, (b) salinity, (c) chlorophyll *a* and (d) zooplankton volume



southern distribution limits of the northern assemblages with the 24.5°C isotherm, as well as the northern distribution limits of the southern assemblage with the 26°C isotherm (Fig. 6), which seems to be an important physical indicator of the distribution limits of both northern and southern communities.

For the northern oceanic group, the most abundant species were *A. oligogyra*,

Fig. 4. Superficial geostrophic currents (arrows) and sea surface temperature anomaly (SSTa, color scale) calculated from 17 September to 10 October 2015. Sampling stations are indicated by white solid circles

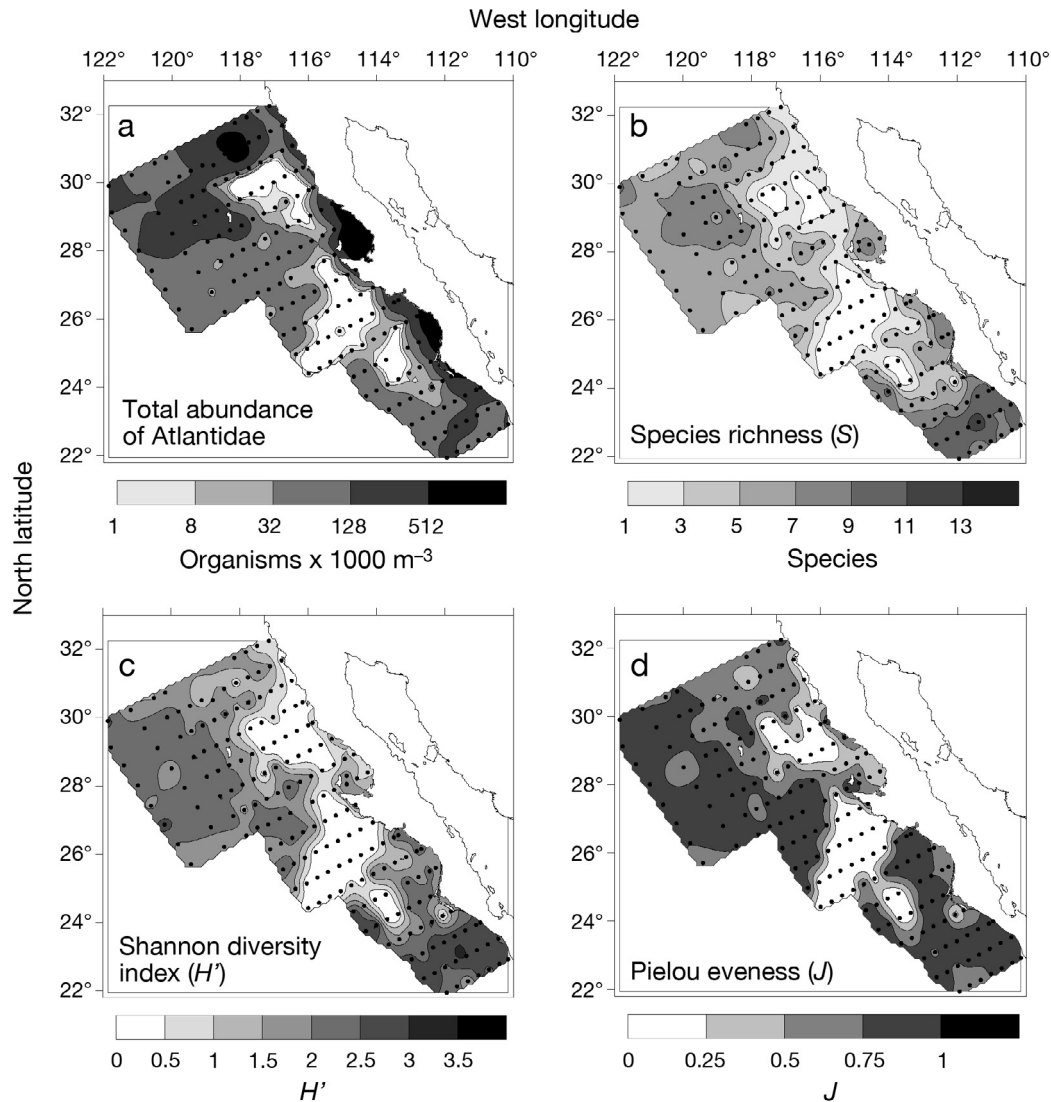


Fig. 5. (a) Distribution of standardized abundance (organisms 1000 m^{-3}) of total atlantids found; (b) species richness (S); (c) Shannon index (H'); (d) Pielou's evenness (J)

A. inflata, *A. helicinoidea*, *A. turriculata*, *Protatlanta souleyeti* and *A. peronii*, which were distributed across almost the entire study area, although they were more abundant and frequent north of PE (Fig. 7a–f). In this same northern oceanic group, *A. rosea* and *A. fragilis* were almost exclusively from the northern region (Fig. 7g,h). The group of northern coastal stations was mainly defined by *A. californiensis*, which was more abundant at coastal stations, particularly in BSV (Fig. 7i). The group of southern stations was characterized by *A. lesueurii*, *A. echinogyra*, *A. plana*, *A. frontieri*, *A. inclinata*, *A. brunnea*, *A. gibbosa*, *A. tokiokai*, *Atlanta* sp. 1 and *Oxygyrus inflatus* (Fig. 8). Except for *A. brunnea*, which had wide distribution but was more abundant south of PE (Fig. 8f), the remaining species had their

northern distribution limit south of PE. Distribution limits of almost all species were spatially coincident with the 24.5°C isotherm for the northern group species, and with the 26°C isotherm for the southern group species, with the exception of *A. lesueurii* and *Atlanta* sp. 1, whose distribution was coincident with the $100\text{ ml } 1000\text{ m}^{-3}$ ZV isoline (Figs. 7 & 8).

The distribution of the abundance of Atlantidae among the temperature and salinity intervals show a clear separation between the northern and southern groups of species. For species found mainly in the north, between 85 and 95% of individuals were collected at temperatures below 24.5°C and salinities below 34 (Fig. 9a), whereas 90–100% of individuals from the southern group were found at temperatures above 26°C and salinities above 34.3 (Fig. 9b). The

Table 2. Standardized abundance of Atlantidae species present along the western coast of the Baja California Peninsula and percentage of positive samples (% PS)

Species	Abundance	%	% PS
<i>Atlanta oligogyra</i> Tesch, 1806	7239	26.4	76
<i>Atlanta californiensis</i> Seapy & Richter, 1993	6761	24.6	41
<i>Atlanta inflata</i> J.E. Gray, 1850	3284	12.0	76
<i>Atlanta lesueurii</i> Gray, 1850	2202	8.0	27
<i>Atlanta peronii</i> Lesueur, 1817	1796	6.5	41
<i>Atlanta helicinoidea</i> Gray, 1850	1745	6.4	59
<i>Atlanta</i> sp. 1	963	3.5	15
<i>Atlanta turriculata</i> d'Orbigny, 1836	599	2.2	40
<i>Atlanta frontieri</i> Richter, 1993	511	1.9	18
<i>Atlanta</i> spp.	510	1.9	27
<i>Atlanta inclinata</i> Gray, 1850	306	1.1	20
<i>Atlanta plana</i> Richter, 1972	254	0.9	13
<i>Atlanta tokiokai</i> Spoel & Troost, 1972	240	0.9	19
<i>Atlanta brunnea</i> Gray, 1850	237	0.9	19
<i>Protatlanta souleyeti</i> (Smith, 1888)	192	0.7	24
<i>Atlanta fragilis</i> Richter, 1993	176	0.6	16
<i>Atlanta rosea</i> Gray, 1850	159	0.5	13
<i>Atlanta echinogyra</i> Richter, 1972	128	0.5	12
<i>Oxygyrus inflatus</i> (Lesueur, 1817)	126	0.4	15
<i>Atlanta gibbosa</i> Souleyet, 1852	18	0.1	3
TOTAL	27449		

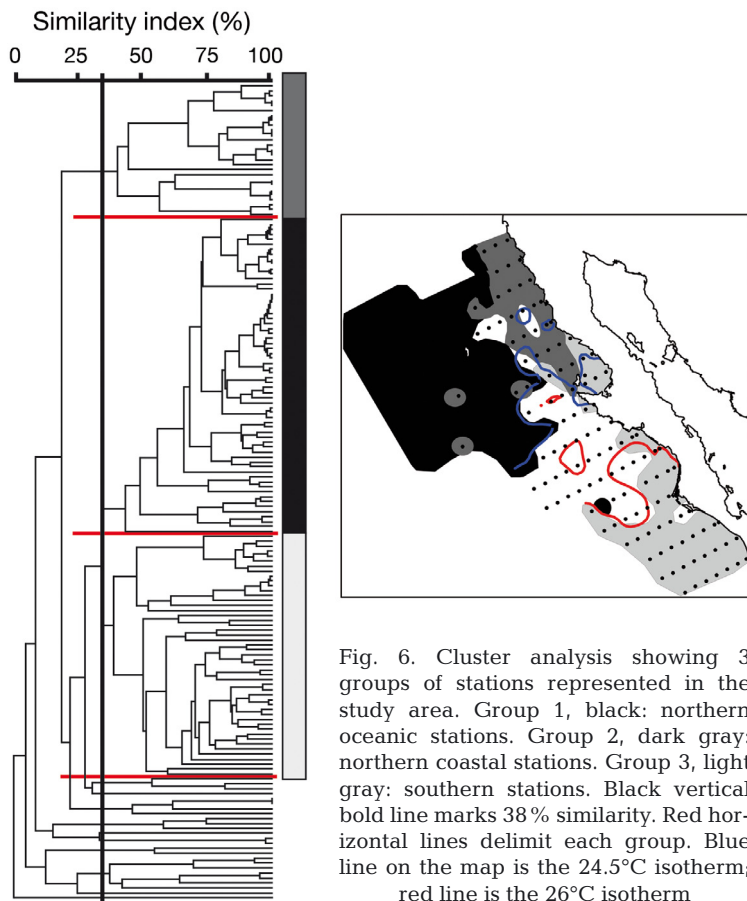


Fig. 6. Cluster analysis showing 3 groups of stations represented in the study area. Group 1, black: northern oceanic stations. Group 2, dark gray: northern coastal stations. Group 3, light gray: southern stations. Black vertical bold line marks 38% similarity. Red horizontal lines delimit each group. Blue line on the map is the 24.5°C isotherm; red line is the 26°C isotherm

mentioned interval of temperature and salinity that limits the maximum abundance of each group represents a thermohaline range of transition between the northern and southern fauna where they coexist in lower abundance. The species that had a wide distribution throughout the study area apparently were not affected by this thermohaline gap (Fig. 9c).

The PCA, along with environmental variables, composition of water masses, diversity descriptors and the grouping of the stations obtained through the CA, revealed different environmental characteristics and community structures between the northern and southern regions, with PE as their common boundary. Additional analyses were performed separately for each region.

The CCA for the northern region (Table 3) explained 27.5% of the accumulated variance along the first 2 axes. For axis 1 (20.2%), Pearson's correlation value was 0.74 and the variables that determined the distribution were chl *a* ($r = -0.867$) and ZV ($r = -0.625$). Along the second axis (7.3%), Pearson's correlation was 0.68 and the variables with the highest correlation were SST ($r = -0.864$), SSS ($r = -0.852$) and MLD ($r = -0.554$).

The dispersion diagram showed a separation between *A. californiensis* (the only abundant species in the coastal region) from the rest of the oceanic-distributed species attributed to high values of chl *a* and ZV (Fig. 10). The species *A. oligogyra*, *A. fragilis*, *A. peronii*, *A. rosea* and *A. brunnea* were associated with low SST and SSS values, while *A. helicinoidea*, *A. inflata*, *A. turriculata* and *P. souleyeti* were related to high SST and SSS values. The station dispersion diagrams showed an ocean–coast segregation with high values of SST, SSS, ZV and chl *a* at coastal stations and low values at oceanic ones.

The CCA for the southern region (Table 4) showed that the first 2 axes explained 28.4% of the accumulated variance. The first axis had an explained variance of 14.5% with a Pearson's correlation value of 0.809; it was related to SSS ($r = -0.827$) and SST ($r = -0.567$). The second axis had an explained variance of 10.3% with a Pearson's correlation value of 0.793.

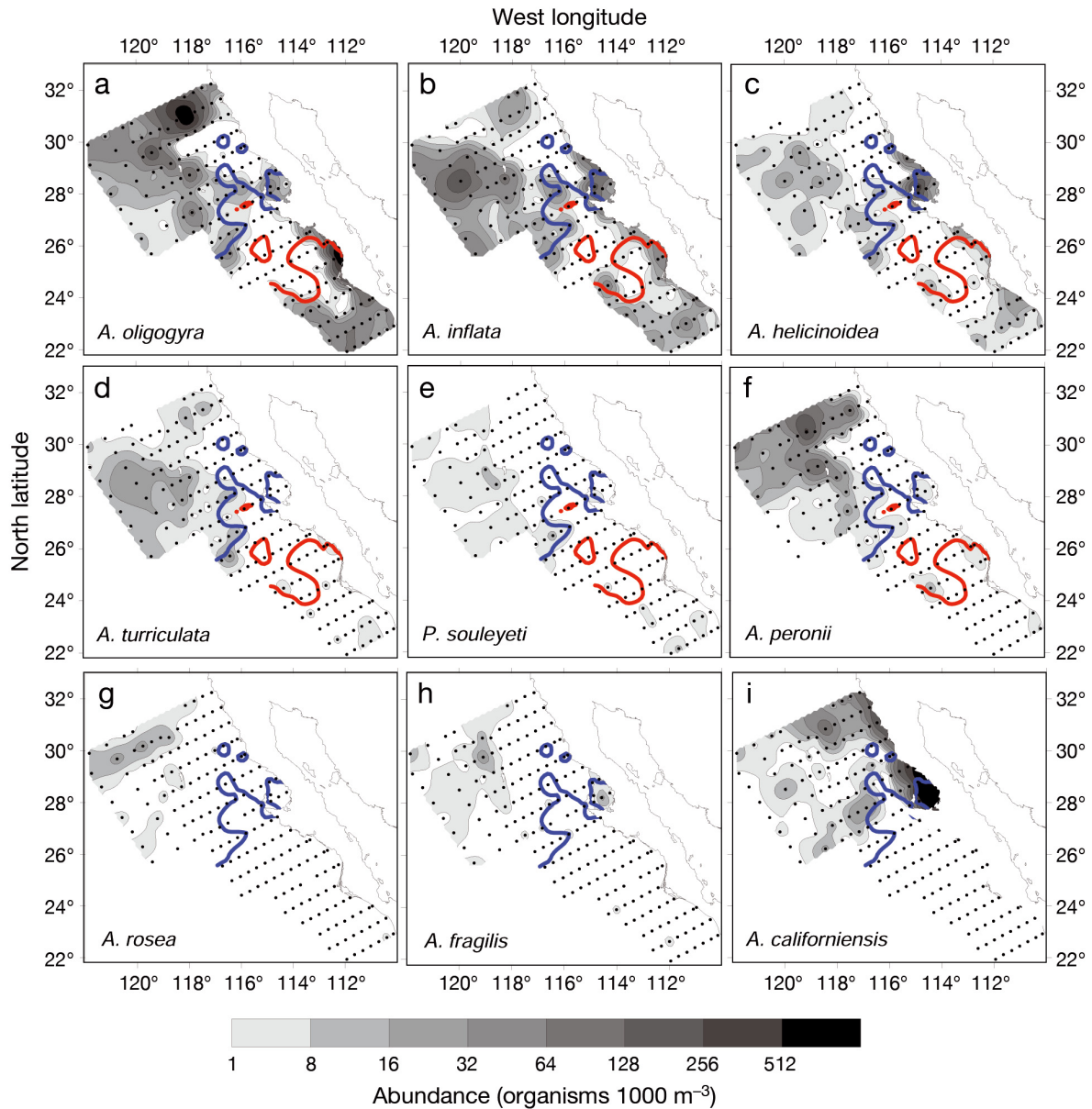


Fig. 7. Distribution of Atlantidae species (*Atlanta* spp. and *Protatlanta souleyeti*) off the west coast of the Peninsula of Baja California (summer–fall 2015). Blue line: 24.5°C isotherm; red line: 26°C isotherm

The environmental variable with the highest correlation value with the second axis was ZV ($r = 0.876$).

The dispersion diagram for the species in the southern region (Fig. 11) showed that *A. lesueurii* and *Atlanta* sp. 1 (Fig. 8a,i) correlated with the highest values of ZV and SSS at the coastal stations north of Magdalena Bay (Fig. 3b,d). *A. brunnea*, *A. echinogyra*, *A. plana*, *A. frontieri*, *A. inclinata*, *O. inflatus* and *A. tokiokai* (Fig. 8) were distributed both in the coastal and oceanic regions only south of Magdalena Bay, associated with stations with the highest SST (Fig. 3a). *A. oligogyra*, *A. inflata*, *A. helicinoidea*, *A.*

turriculata, *P. souleyeti* and *A. peronii* (Fig. 7a–f) showed a similar distribution pattern both on the coast and in the oceanic region south of Magdalena Bay, but they were also found off PE.

4. DISCUSSION

Given the magnitude of the climatic indices for EN 2015–2016, significant changes in the structure of the pelagic communities were predicted (Leising et al. 2015, McClatchie et al. 2016, Varotsos et al. 2016).

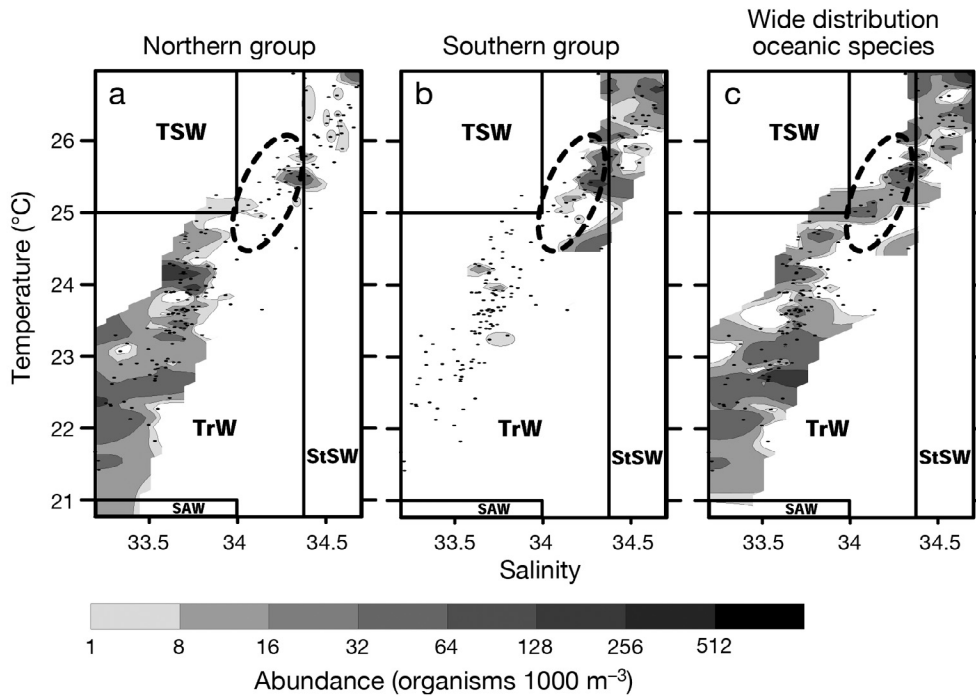


Fig. 9. Abundance of Atlantidae vs. salinity and temperature, and the corresponding water masses. (a) Northern group, (b) southern group, (c) wide-distribution oceanic species. Black dots: sampling stations; oval: transitional thermohaline interval. Limits of water masses follow Durazo & Baumgartner (2002). TSW: tropical surface water; StSW: subtropical surface water; TrW: transitional water; SAW: subarctic water

Table 3. Canonical correspondence analysis performed for the region north of Punta Eugenia, Mexico

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.183	0.056	0.014
Explained variance (%)	20.2	7.3	0.8
Cumulative variance (%)	20.2	27.5	28.3
Pearson's correlation (species–environment)	0.74	0.68	0.31
Correlations			
Sea surface temperature	-0.370	-0.864	-0.031
Sea surface salinity	-0.422	-0.852	-0.278
Chlorophyll <i>a</i>	-0.867	0.275	0.014
Mixed layer depth	0.392	-0.554	0.164
Zooplankton volume	-0.625	0.052	0.623

continuously. Previous studies related to EN-induced changes have shown positive temperature and salinity anomalies of up to 5°C and ~0.7, respectively, along the Baja California coast (Durazo & Baumgartner 2002, Durazo 2009, Gaxiola-Castro et al. 2010, Durazo 2015) and a deepening of the CC core to depths of 100 m or more (Durazo et al. 2017) during the anomalous 2014–2015 warming period. In summer 2014, advection of TSW and StSW related to a coastal poleward flow was detected south of PE, which is characteristic of EN years (Durazo 2015, McClatchie et al. 2016, Durazo et al. 2017). As this coastal flow intensified, it reached the northern region of the WBCP in 2015 (Fig. 4), modifying the

hydrographic conditions with warmer water from the south and explaining the wide dispersion of the data shown in the T–S diagrams (Fig. 2b,c).

Very low values of chl *a* and ZV observed in this study were consistent with the observed sinking of the thermocline and broadening of the MLD (~40 and 27 m in oceanic and coastal zones, respectively; data not shown). Additionally, the decreasing trends of chl *a* and ZV throughout the Northeast Pacific (Leising et al. 2015, Cavole et al. 2016, McClatchie et al. 2016) were associated with an increase in the vertical stratification of the water column, the sinking of the pycnocline (~30 m) and a reduced supply of nutrients to the surface (Gómez-Ocampo et al. 2017, 2018, Wells et al. 2017). All of these changes have been associated with the presence of the MHW 2013–2015, EN 2014 and EN 2015–2016 (Bond et al. 2015, Kintisch 2015, Peterson et al. 2015, Di Lorenzo & Mantua 2016).

Despite recurring warming events from 2013 to 2016, the environmental variables in the pelagic ecosystem off the WBCP (Fig. 3) showed a typical latitudinal gradient during the summer–fall season of 2015 (Durazo & Baumgartner 2002, Durazo et al. 2010). Statistical analyses confirmed 2 regions with distinct hydrographic characteristics (north and south) and a transition area off PE, which is consistent with the previously proposed regionalization using hydrography and productivity under different climatic conditions (Durazo & Baumgartner 2002, Durazo 2009,

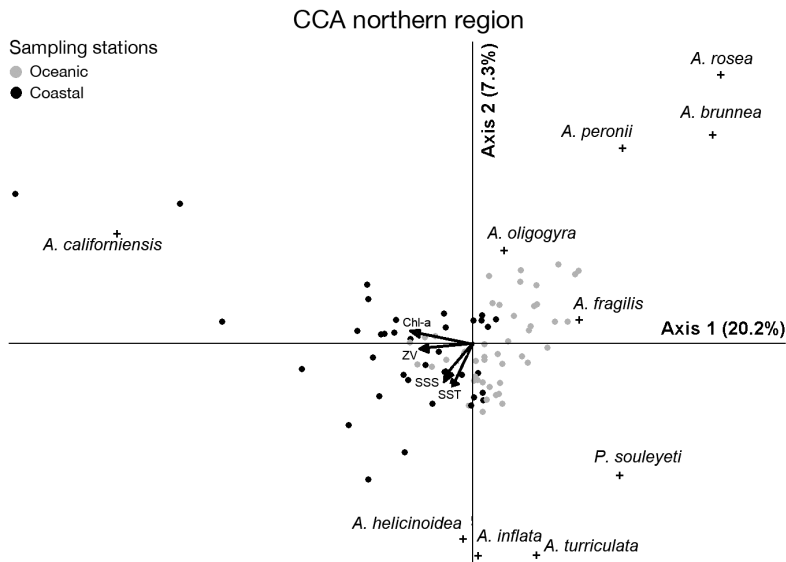


Fig. 10. Canonical correspondence analysis (CCA) for the species and stations of the northern region. Explained variance for each axis in parentheses. Plus symbols: species; black circles: coastal stations; gray circles: oceanic stations; arrows: eigenvector for each variable. SST (SSS): sea surface temperature (salinity); ZV: zooplankton volume; chl a: chlorophyll a

2015, Durazo et al. 2010, Gaxiola-Castro et al. 2010). The distribution patterns of Atlantidae (Figs. 9 & 10) as well as the community parameters (Fig. 7b–d) demonstrated the presence of 3 main communities in the WBCP that were determined by the distribution of water masses and their environmental characteristics (mainly temperature and salinity). However, mesoscale structures such as the coastal upwelling in areas north of PE, as well as cyclonic and anticyclonic eddies in front of PE, were also determinant. These findings were supported by the groups formed in the CA (Fig. 8), which were separated by a transitional area evidenced by the absence of organisms off the middle portion of the peninsula and characterized by

Table 4. Canonical correspondence analysis performed for the region south of Punta Eugenia, Mexico

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.207	0.146	0.024
Explained variance (%)	14.5	10.3	1.7
Cumulative variance (%)	14.5	28.4	26.5
Pearson's correlation (species–environment)	0.809	0.793	0.481
Correlations			
Sea surface temperature	–0.567	–0.238	–0.266
Sea surface salinity	–0.827	0.122	0.450
Chlorophyll a	–0.235	0.074	0.202
Mixed layer depth	–0.056	0.079	0.343
Zooplankton volume	–0.041	0.876	–0.457

temperatures between 24.5 and 26°C, and salinities between 34 and 34.3.

The first group of atlantid mollusks identified corresponded to species with tropical-subtropical affinity (*Atlantia oligogyra*, *A. inflata*, *A. helicinoidea*, *A. rosea*, *A. fragilis*, *A. peronii*, *A. turriculata* and *Protatlanta souleyeti*) distributed mainly in the northern oceanic region in an area characterized by high values of species richness, diversity and evenness (Fig. 5) that had values of chl a of less than 0.1 mg m⁻³ and of ZV less than 32 ml 1000 m⁻³, which reflects their affinity to conditions of low primary and secondary production in the oceanic region of the study area (Gómez-Ocampo et al. 2017). This group is of particular interest since it includes *A. rosea* and *A. fragilis*, which correspond to new distribution records for the American Pacific

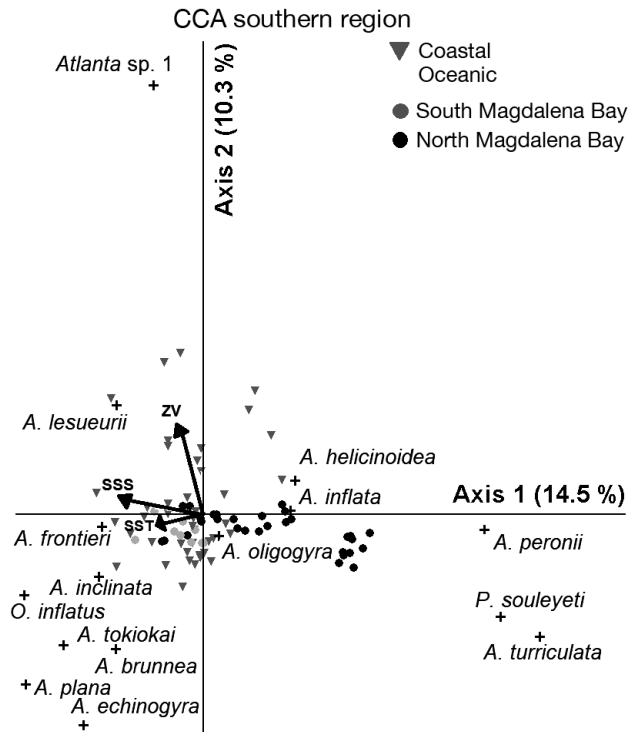


Fig. 11. Canonical correspondence analysis (CCA) for the species and stations of the southern region. Explained variance for each axis in parentheses. Plus symbols: species; black (gray) circles: oceanic stations north (south) of Magdalena Bay; gray triangles: coastal stations; arrows: eigenvector for each variable. SST (SSS): sea surface temperature (salinity); ZV: zooplankton volume

(Moreno-Alcántara et al. 2020). *A. rosea* is considered a rare species with circumtropical distribution, including the central Pacific (Richter & Seapy 1999, Wall-Palmer et al. 2018a). Similarly, the warm-water species *A. fragilis* was recently recorded in the Indian and Central Pacific Oceans (Wall-Palmer et al. 2018a).

At least 5 species (*Atlanta rosea*, *A. fragilis*, *A. peronii*, *A. turriculata* and *P. souleyeti*) presented between 90 and 95% of their abundance in areas with temperatures lower than 24.5°C and salinities lower than 34 (Fig. 9a), which correspond to the TrW and the northern SAW water masses (Durazo & Baumgartner 2002)

The narrow northern oceanic distribution observed for *A. rosea* and *A. fragilis*, as well as their affinity for warm water, suggests that they do not enter the CCS from the south, where they are absent, but instead they reach the CCS from the Central Pacific, where the nearest known record exists (Wall-Palmer et al. 2018a, Moreno-Alcántara et al. 2020). This finding is substantiated by the presence of a surface geostrophic flow towards the northeast over the oceanic region north of 33° N (Fig. 6). This flow also explains the presence of 3 other warm-water species (*A. peronii*, *A. turriculata* and *P. souleyeti*) which do not seem to arrive from south of the peninsula, although these species have previously been recorded in the area (McGowan 1967, Moreno-Alcántara 2019).

A. oligogyra, *A. inflata* and *A. helicinoidea*, although more abundant towards the north, were also found in the southern region of the peninsula. However, their distribution was continuous in a narrow strip along the coast and was interrupted towards the oceanic region off PE. Even though the distribution limit between the northern populations of these 3 species was also limited by the 24.5°C isotherm and the 34 isohaline, the southern populations were found again where values for temperature and salinity were above 26°C and 34.3, respectively.

The thermal and saline intervals, as well as the water masses where the previous 3 species (*A. oligogyra*, *A. inflata* and *A. helicinoidea*) of the northern oceanic groups are distributed, in addition to their preference for waters with low primary and secondary production, suggest 2 possibilities for their disjunct distribution. The first is that the northern populations, together with *A. rosea*, *A. fragilis*, *A. peronii*, *A. turriculata* and *P. souleyeti*, entered with the flow from the Central Pacific, which was associated to the MHW that occurred in the area during 2015 (Di Lorenzo & Mantua 2016, Jacox et al. 2016, Gentemann et al. 2017, Wells et al. 2017), while the southern populations penetrated with the advance of warm

water masses associated with EN 2015–2016, and were limited by the 26°C isotherm. A second possibility is that the observed distribution originated from a population that was initially widely distributed and was later fragmented in the oceanic region by the mesoscale circulation processes in front of PE. This process corresponded mainly with the presence of a system of 3 eddies (1 anticyclonic and 2 cyclonic) between Punta Baja and PE off BSV.

The second group was defined by the almost exclusive presence of *A. californiensis*, associated with the highest values of chl *a* according to the CCA (Fig. 10, Table 4). This is the only species registered as an indicator of the temperate transition zone of the North Pacific (Seapy & Richter 1993). Although this species was distributed throughout most of the study area north of PE, its greatest abundance coincided with the lowest values of species richness, diversity and evenness found at coastal stations from Ensenada to PE, where coastal upwelling can be observed throughout the year (Durazo 2015). In the same way as the northern oceanic group, the distribution of *A. californiensis* was limited to the south by the 24.5°C isotherm and the isohaline of 34. In general, this species inhabited colder and more productive areas associated with the temperate CCS.

The third group was formed by *Atlanta* sp. 1, 5 tropical species (*A. echinogyra*, *A. plana*, *A. frontieri*, *A. gibbosa* and *Oxygyrus inflatus*), which dominated the pelagic ecosystem south of Magdalena Bay (oceanic and coastal), and 3 tropical-subtropical species (*A. tokiokai*, *A. inclinata* and *A. lesueurii*) that were distributed further north. The distribution limits of this group corresponded to the northward geostrophic flow observed (Fig. 4), where at 24° N, the presence of a cyclonic eddy caused the flow to shift eastward, becoming coastal. This circulation pattern limited the distribution of tropical species to the north of Magdalena Bay and apparently allowed passage to the north of *A. lesueurii* and *Atlanta* sp. 1, only over the coastal region of the Gulf of Ulloa to BSV. This is consistent with the CCA results (Fig. 11, Table 4), which related these 2 species to high ZV values, and the Gulf of Ulloa and BSV regions are known to have high productivity (Lluch-Belda 2000). Additionally, the CCA associated the species in this group to high SST values, which coincides with the dominance of StSW and ESsW observed in the southern region (Fig. 2b). The distribution of this community also corresponded with the highest values of species richness, diversity and evenness expressing the warm-water affinity of this group (Wall-Palmer et al. 2016b, 2018a). Therefore, we define this group as

a tropical community associated with the advection of StSW warm waters (Fig. 9b) coming from the south due to the effect of EN 2015–2016.

The environmental parameters in the area in front of PE that is characterized by the absence of Atlantidae coincide with the thermohaline interval of faunal transition (24.5–26°C and 34–34.3). However, this thermal interval was also found in other parts of the study area, such as in BSV and Gulf of Ulloa, where atlantids were present. Another similar situation was observed in areas influenced by mesoscale eddies (Fig. 4), as in the case of the area surrounding Punta Baja, where there was an absence of organisms (Fig. 5) and the temperature in the area was between 23 and 26°C (Fig. 3a). This thermal interval was also registered in areas without the influence of eddies and where high abundance was observed.

The distribution of groups of atlantids highlights the transitional character of the coastal area of PE, where communities of temperate–subarctic ecosystems associated with the subarctic flow of the CC, tropical components of StSW and ESsW water masses and components from the Central Pacific meet. This transitional zone has already been registered for other taxonomic groups of zooplankton, such as fish larvae (Aceves-Medina et al. 2018). Since the 3 Atlantidae communities identified and described herein were separated by areas where no Atlantidae species were found in the oceanic region in association with the presence of mesoscale eddies south of PE, off the Gulf of Ulloa and off Punta Baja, we propose that eddies in the oceanic region apparently function as barriers against the dispersion of species between northern and southern parts of the pelagic ecosystem off the WBCP, in a way similar to that of other zooplankton groups (Lavaniegos & Hereu 2009, Lavaniegos 2014, Aceves-Medina et al. 2018). To support this argument, it is to be noted that the atlantids perform important vertical migrations in the epipelagic zone (0–200 m depth) associated with the diel cycle (Lalli & Gilmer 1989, Wall-Palmer et al. 2016b). In the area of the southern region of the CC, the main superficial water masses are distributed in this same depth range (SAW: 0–100 m, ESsW: 100–150 m; Durazo & Baumgartner 2002), as are the most intense effects associated with mesoscale eddies and coastal upwelling (down to 400 m depth; Soto-Mardones et al. 2004, Kurczyn et al. 2012, Amos et al. 2019, Oyarzún & Brierley 2019). Because of this, we can establish that the distribution of Atlantidae in the southern CC is regulated mainly by the distribution of the water masses in the area and is influenced by mesoscale processes.

5. CONCLUSIONS

In this study, the community of Atlantidae mollusks off the WBCP showed that the limit of the distribution between southern and northern assemblages was located in the vicinity of PE, as has been seen in other zooplankton communities in the presence of anomalous environmental events of different nature (i.e. fish larvae during La Niña 1999; Aceves-Medina et al. 2018). This means that regardless of the intensity of the anomalous events (warm or cold) as well as the zooplankton group analyzed, the oceanographic processes and environmental gradients that occur in this area constitute effective environmental barriers in the latitudinal distribution of zooplankton species, which determine the biogeographic distribution of the marine epipelagic communities in the CCS off the WBCP.

In general, the distribution patterns of atlantids were determined by the distribution of currents and water masses in the area. The southern region of the WBCP was characterized by a community of tropical and subtropical species that were transported to Magdalena Bay and further up the coast to the south of Punta Baja (29.5°N) through the advection of warm water associated with EN 2015–2016. This northward transport of species happened only in the coastal region. The central portion of the study area, between PE and the oceanic region off the Gulf of Ulloa, was characterized by the absence of atlantids. These distribution patterns were attributed to the effects of a system of 1 anticyclonic and 2 cyclonic mesoscale eddies in the vicinity of PE, which apparently act as barriers that prevent transport of planktonic organisms into the oceanic realm, as has been seen with other zooplankton groups in the area (Moser & Smith 1993, Lavaniegos et al. 2003, Aceves-Medina et al. 2018). The narrow area of distribution of the tropical community in the coastal region and the presence of coastal upwelling in the area was reflected in the high abundance of atlantids and zooplankton in the Gulf of Ulloa.

North of PE, a mixture of southern and northern communities, which included the dominant species *Atlanta californiensis*, showed the highest abundance of atlantids in BSV. In the northern portion of the study area, the oceanic assemblage of species with warm-water affinity and the presence of *A. rosea* and *A. fragilis* evidence the advection of a water mass from the Central Pacific to the CCS, which we postulate is a consequence of the effect of the MHW in the region.

The confluence of tropical, Central Pacific and CC water masses have established the presence of 3 distinct communities off the WBCP, which contribute to the region's high diversity. In fact, 90% of all Atlantidae species recorded for the Pacific Ocean can be found here, lending insight into the usefulness of the Atlantidae community as indicators of environmental anomalies in the WBCP.

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LITERATURE CITED

- ✦ Aceves-Medina G, Jiménez-Rosenberg SPA, Saldierna-Martínez RJ, Durazo R and others (2018) Distribution and abundance of the ichthyoplankton assemblages and its relationships with the geostrophic flow along the southern region of the California Current. *Lat Am J Aquat Res* 46:104–119
- ✦ Amos CM, Castelao RM, Medeiros PM (2019) Offshore transport of particulate organic carbon in the California Current System by mesoscale eddies. *Nat Commun* 10:4940
- ✦ Angulo-Campillo O, Aceves-Medina G, Avedaño-Ibarra R (2011) Holoplanktonic mollusks (Mollusca: Gastropoda) from the Gulf of California, México. *Check List* 7:337–342
- ✦ Bednaršek N, Tarling GA, Bakker DCE, Fielding S and others (2012) Extensive dissolution of live pteropods in the Southern Ocean. *Nat Geosci* 5:881–885
- Beers JR (1976) Determination of zooplankton biomass. In: Steedman HF (ed) *Zooplankton fixation and preservation*. Monographs on Oceanographic Methodology No. 4. The UNESCO Press, Paris, p 35–74
- ✦ Bond NA, Cronin MF, Freeland H, Mantua N (2015) Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophys Res Lett* 42:3414–3420
- ✦ Briggs JC, Bowen BW (2012) A realignment of marine biogeographic provinces with particular reference to fish distributions. *J Biogeogr* 39:12–30
- ✦ Cavole LM, Demko AM, Diner RE, Giddings A and others (2016) Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: winners, losers, and the future. *Oceanography* 29:273–285
- ✦ Di Lorenzo E, Mantua N (2016) Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nat Clim Change* 6:1042–1047
- ✦ Durazo R (2009) Climate and upper ocean variability off Baja California, Mexico: 1997–2008. *Prog Oceanogr* 83:361–368
- ✦ Durazo R (2015) Seasonality of the transitional region of the California Current System off Baja California. *J Geophys Res C Oceans* 120:1173–1196
- ✦ Durazo R, Baumgartner T (2002) Evolution of oceanographic conditions off Baja California: 1997–1999. *Prog Oceanogr* 54:7–31
- ✦ Durazo R, Gaxiola-Castro G, Lavaniegos BE, Castro-Valdez R, Gómez-Valdés J, Mascarenhas ADS Jr (2005) Oceanographic conditions west of the Baja California coast, 2002–2003: a weak El Niño and subarctic water enhancement. *Cienc Mar* 31:537–552
- Durazo R, Ramírez-Manguillar AM, Miranda LE, Soto-Mardones LA (2010) Climatología de variables hidrográficas. In: Gaxiola-Castro G, Durazo R (eds) *Dinámica del ecosistema pelágico frente a Baja California 1997–2007*. Diez años de investigaciones mexicanas de la Corriente de California. Instituto Nacional de Ecología, Ensenada, p 25–57
- ✦ Durazo R, Castro R, Miranda LE, Delgadillo-Hinojosa F, Mejía-Trejo A (2017) Anomalous hydrographic conditions off the northwestern coast of the Baja California Peninsula during 2013–2016. *Cienc Mar* 43:81–92
- ✦ Fiedler PC, Mantua NJ (2017) How are warm and cool years in the California Current related to ENSO? *J Geophys Res C Oceans* 122:5936–5951
- Furnestin ML (1979) Planktonic mollusks as hydrological and ecological indicators. In: Van der Spoel S, Van Bruggen AC, Lever J (eds) *Pathways in malacology*. Bohn, Scheltema & Holkema, Utrecht, p 175–194
- Gaxiola-Castro G, Cepeda-Morales J, Nájera-Martínez S, Espinosa-Carreón TL and others (2010) Biomasa y producción del fitoplancton. In: Gaxiola-Castro G, Durazo R (eds) *Dinámica del ecosistema pelágico frente a Baja California 1997–2007*. Diez años de investigaciones mexicanas de la Corriente de California. Instituto Nacional de Ecología, Ensenada, p 59–86
- ✦ Gentemann CL, Fewings MR, García-Reyes M (2017) Satellite sea surface temperatures along the West Coast of the United States during the 2014–2016 northeast Pacific marine heat wave. *Geophys Res Lett* 44:312–319
- ✦ Gómez-Ocampo E, Durazo R, Gaxiola-Castro G, De la Cruz-Orozco M, Sosa-Ávalos R (2017) Effects of the inter-annual variability of water column stratification on phytoplankton production and biomass at the north zone off Baja California. *Cienc Mar* 43:109–122
- ✦ Gómez-Ocampo E, Gaxiola-Castro G, Durazo R, Beier E (2018) Effects of the 2013–2016 warm anomalies on the California Current phytoplankton. *Deep Sea Res II* 151:64–76
- ✦ Jacox MG, Hazen EL, Zaba KD, Rudnick DL, Edwards CA, Moore AM, Bograd SJ (2016) Impacts of the 2015–2016 El Niño on the California Current System: early assessment and comparison to past events. *Geophys Res Lett* 43:7072–7080
- ✦ Kintisch E (2015) 'The Blob' invades Pacific, flummoxing climate experts. *Science* 348:17–18
- ✦ Kurczyn JA, Beier E, Lavín MF, Chaigneau A (2012) Mesoscale eddies in the northeastern Pacific tropical-subtropical transition zone: statistical characterization from satellite altimetry. *J Geophys Res* 117:C10021
- Lalli MC, Gilmer RW (1989) *Pelagic snails: the biology of holoplanktonic gastropod mollusks*. Stanford University Press, Stanford, CA

- Lavaniegos BE (2014) Pelagic amphipod assemblage associated with subarctic water off the West Coast of the Baja California peninsula. *J Mar Syst* 132:1–12
- Lavaniegos BE, Hereu CM (2009) Seasonal variation in hyperiid amphipod abundance and diversity and influence of mesoscale structures off Baja California. *Mar Ecol Prog Ser* 394:137–152
- Lavaniegos BE, Gaxiola-Castro G, Jiménez-Pérez LC, González-Esparza MR, Baumgartner T, García-Cordova J (2003) 1997–98 El Niño effects on the pelagic ecosystem of the California current off Baja California, Mexico. *Geofis Int* 42:483–494
- Leising AW, Schroeder ID, Bograd SJ, Abell J and others (2015) State of the California Current 2014–15: impacts of the warm water 'blob'. *Calif Coop Ocean Fish Invest Rep* 56:31–69
- Lluch-Belda D (2000) Centros de actividad biológica en la costa occidental de Baja California. In: Lluch-Belda D, Elorduy-Garay J, Lluch-Cota SE, Ponce-Díaz G (eds) *BAC: Centros de Actividad Biológica del Pacífico Mexicano*. Centro de Investigaciones Biológicas del Noroeste, La Paz, p 49–64
- McClatchie S, Goericke R, Leising A, Auth TD and others (2016) State of the California Current 2015–16: comparisons with the 1997–98 El Niño. *Calif Coop Ocean Fish Invest Rep* 57:5–61
- McCune B, Mefford MJ (2011) PC-ORD. Multivariate analysis of ecological data. Version 6.0. MjM Software, Glenden Beach, OR
- McGowan JA (1967) Distributional atlas of pelagic mollusks in the California Current region. *CalCofi Atlas No. 6*. State of California Marine Research Committee, La Jolla, CA
- Moreno-Alcántara M (2019) Atlantidae (Pterotracheoidea) of the northeast Pacific. *Zoosymposia* 13:139–146
- Moreno-Alcántara M, Aceves-Medina G, Angulo-Campillo O, Murad-Serrano JP (2014) Holoplanktonic molluscs (Gastropoda: Pterotracheoidea, Thecosomata and Gymnosomata) from the southern Mexican Pacific. *J Molluscan Stud* 80:131–138
- Moreno-Alcántara M, Giraldo-López A, Aceves-Medina G (2017) Heteropods (Gastropoda: Pterotracheoidea) identified along a coastal–oceanic transect in the Colombian Pacific. *Bol Investig Mar Costeras* 46:175–181
- Moreno-Alcántara M, Delgado-Hofmann D, Aceves-Medina G (2020) Diversity of Atlantidae mollusks (Gastropoda: Pterotracheoidea) from the southern region of the California current off Baja California peninsula, Mexico. *Mar Biodivers* 50:27
- Moser HG, Smith PE (1993) Larval fish assemblages of the California Current region and their horizontal and vertical distributions across a front. *Bull Mar Sci* 53: 645–691
- Oyarzún D, Brierley CM (2019) The future of coastal upwelling in the Humboldt current from model projections. *Clim Dyn* 52:599–615
- Peterson W, Robert M, Bond N (2015) The warm blob-conditions in the northeastern Pacific Ocean. *PICES Press* 23:36–38
- Richter G, Seapy RR (1999) Heteropoda. In: Boltovskoy D (ed) *South Atlantic zooplankton*, Vol 1. Backhuys, Leiden, p 621–647
- Seapy RR (1990) The pelagic family Atlantidae (Gastropoda: Heteropoda) from Hawaiian waters: a faunistic survey. *Malacologia* 32:107–130
- Seapy RR, Richter G (1993) *Atlanta californiensis*, a new species of atlantid heteropod (Mollusca: Gastropoda) from the California Current. *Veliger* 36:389–398
- Seapy RR, Skoglund C (2001) First records of Atlantid heteropod mollusks from the Golfo de California. *Festivus* 33:33–44
- Smith PE, Richardson SL (1977) Standard techniques for pelagic fish egg and larval surveys. *FAO Fish Tech Pap* 175. FAO, Rome
- Soto-Mardones L, Parés-Sierra A, Garcia J, Durazo R, Hormazabal S (2004) Analysis of the mesoscale structure in the IMECOCAL region (off Baja California) from hydrographic, ADCP and altimetry data. *Deep Sea Res II* 51:785–798
- Suárez-Morales E, Rivera A (1998) Zooplankton e hidrodinámica en zonas litorales y arrecifales de Quintana Roo, México. *Hidrobiologica* 8:19–32
- Sutton TT, Clark MR, Dunn DC, Halpin PN and others (2017) A global biogeographic classification of the mesopelagic zone. *Deep Sea Res I* 126:85–102
- Varotsos CA, Tzanis CG, Sarlis NV (2016) On the progress of the 2015–2016 El Niño event. *Atmos Chem Phys* 16:2007–2011
- Wall-Palmer D (2017) Shelled Heteropod Identification Portal. <https://www.planktonic.org/> (accessed 26 February 2019)
- Wall-Palmer D, Burrridge AK, Peijnenburg KT (2016a) *Atlanta ariejansseni*, a new species of shelled heteropod from the Southern Subtropical Convergence Zone (Gastropoda, Pterotracheoidea). *ZooKeys* 604:13–30
- Wall-Palmer D, Smart CW, Kirby R, Hart MB, Peijnenburg KTCA, Janssen AW (2016b) A review of the ecology, palaeontology and distribution of atlantid heteropods (Caenogastropoda: Pterotracheoidea: Atlantidae). *J Molluscan Stud* 82:221–234
- Wall-Palmer D, Burrridge AK, Goetze E, Stokvis FR and others (2018a) Biogeography and genetic diversity of the atlantid heteropods. *Prog Oceanogr* 160:1–25
- Wall-Palmer D, Metcalfe B, Leng MJ, Sloane HJ, Ganssen G, Vinayachandran PN, Smart CW (2018b) Vertical distribution and diurnal migration of atlantid heteropods. *Mar Ecol Prog Ser* 587:1–15
- Wells BK, Schoreder ID, Bograd SJ, Hazen EL and others (2017) State of the California Current 2016–2017: still anything but 'normal' in the north. *Calif Coop Ocean Fish Invest Rep* 58:1–55
- Zaba KD, Rudnick DL (2016) The 2014–2015 warming anomaly in the Southern California Current System observed by underwater gliders. *Geophys Res Lett* 43:1241–1248