



Near-bottom zooplankton over three seamounts in the east Canary Islands: Influence of environmental variables on distribution and composition.

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ABSTRACT

The near-bottom zooplankton over three seamounts of the eastern Canary Islands (Amanay, El Banquete and Concepción) was analyzed, identifying the environmental variables that explain biomass distributions over them. Zooplankton composition changed between adjacent water masses, except for the two deepest assemblages associated with Atlantic Antarctic Intermediate Water (AAIW) and Mediterranean Water (MW). The highest biomass of total zooplankton and of main taxa (e.g. copepods, chaetognaths, siphonophores) were recorded at the seamount summits, i.e., over Amanay-El Banquete (summit depths of 23–24 m) associated with Surface Water (SF) and over Concepción (150 m) in upper levels of the North Atlantic Central Water (NACW). Biomass minima at the three banks were found at ca. 250–650 m, in the deepest levels of NACW. At ca. 700–1000 m (the level occupied by AAIW) and below 1000 m (MW level) biomass increased again. Near-bottom fluorometry (f_{5mab} , 5 m above bottom) and dissolved oxygen ($O_{2\ 5mab}$) were the main variables explaining changes of total zooplankton/main taxa biomass. Biomass minima (250–650 m) coincided with decreases of $O_{2\ 5mab}$ (3.30–3.99 ml/l at 400–700 m) at deepest depths occupied by NACW. Other variables not included in our models like turbidity (resuspension of particles) may have locally enhanced zooplankton aggregation, as they may locally occur alongside Concepción at the NACW-AAIW confluence (at ca. 700 m), probably from the effects of internal waves. Our results suggest that observations regarding the attraction of organisms to the stationary substrates of seamounts could be related to elevated chlorophyll fluorescence and $O_{2\ 5mab}$ concentration. Peaks in those variables apparently enhance zooplankton aggregation.

1. Introduction

Visual techniques (e.g., ROVs) and multi-beam sonars have given us detailed information about the seafloor, even at great depths, allowing us to identify and characterize seamounts and similar submarine promontories like banks and knolls. These are among the most intriguing benthic features, as indicated by the increasing number of studies on the distribution of fauna and the operation of their ecosystems (see Pitcher et al., 2007, for a review). One reason is that seamounts are distributed worldwide (Rogers, 1994; Butler et al., 2001; Gubbay, 2003; Baco, 2007; Pitcher et al., 2007), including semi-enclosed seas such as the deep Mediterranean (Mitchell and Lofi, 2008). Also, seamounts support communities that on mainland slopes are severely damaged, specifically, those established among cold-water corals. A third aspect of interest relates to biological productivity over and around seamounts.

Despite often being isolated far from the nearest coasts, some seamounts can support high biological productivity (White et al., 2007) and substantial fisheries (Rogers, 1994; Koslow et al., 2000). For some taxa seamounts have acquired high levels of biodiversity and endemism (Parin et al., 1997; Clark et al., 2010; Rowden et al., 2010). High productivity explains, among other factors, the greater abundance in their vicinity of seabirds and large nekton like cetaceans and sharks, and it explains aggregation of benthopelagic fish over seamounts for feeding and spawning (Hui, 1985; Blaber, 1986; Hyrenbach et al., 2000; Morato and Clark, 2007). However, increase of zooplankton biomass over seamounts is not general (Dower and Mackas, 1996; Martin and Christiansen, 2009). Where zooplankton do increase over seamounts, it relates to bottom trapping of vertically migratory species in daytime (by seamount topography), and by enhanced resuspension of food particles by strong currents impinging on the summits and slopes (Genin and Dower, 2007).

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Currents and water mass circulation around seamounts (e.g. Roden, 1987; Dower et al., 1992; Kunze and Sanford, 1986; Genin and Dower, 2007) can have strong effects on the sediments covering them, by resuspending them and the associated particulate organic matter (POM). One effect is low organic matter content (%OM) on seamount summits (e.g. ca. 1.5–2 %OM on the summit of Galicia bank; Serrano et al., 2017a). Possibly, as a consequence, zooplankton are important in trophic webs over North Atlantic seamounts (Fock et al., 2002; Colaço et al., 2013) and specifically in the Cantabrian Sea (Preciado et al., 2009, 2016). In contrast, epibenthos and infaunal deposit feeders, dependent on both the quantity and quality of POM in deposited sediments, are often at reduced densities (Samadi et al., 2007; Serrano et al., 2017a). This has been found especially on seamounts and bank summits (e.g. at Le Danois Bank - Cartes et al., 2007, and Galicia Bank, Cartes et al., 2014, Serrano et al., 2017a). The enhanced currents around seamounts also provide favourable living space for sessile filter-feeding sponges and corals and for suspension feeders (Rogers, 1994; Gubbay, 2003; Samadi et al., 2007; Serrano et al., 2017b). Pelagic and benthopelagic fish (Porteiro and Sutton, 2007; Preciado et al., 2016) and sessile filter feeders are directly or indirectly dependent on zooplankton. To date, practically all studies on zooplankton over seamounts have been done in the water column. Zooplankton dwelling over seamounts can differ significantly from those found in the neighbouring open ocean (Rogers, 1994; Genin and Dower, 2007). However, such comparisons often ignored the near-bottom domain, with the consequent bias due to quite different compositions of zooplankton near the bottom from those in midwater (e.g. increase of gelatinous forms at the Benthic Boundary Layer (BBL); Martin and Christiansen, 2009). Therefore, it is important to understand the dynamics of zooplankton living in near contact with seamount, in their benthic boundary layer.

The sources of available food and the environmental variables that favour zooplankton aggregation around seamounts are not well known (e.g., Nellen, 1973; Parin et al., 1997; Genin, 2004). Temperature and salinity, defining water masses, have been the variables explored most (e.g. Hanel et al., 2010). Benthopelagic decapods were distributed over Galicia Bank in assemblages associated with water masses surrounding it: Mediterranean Outflow Water (MOW) and Labrador Sea Water (LSW) (Cartes et al., 2014). However, variables with more direct biological effects, e.g., Chl *a* and O₂, have been less frequently considered in distributional analysis of zooplankton (Dower and Mackas, 1996; Genin and Dower, 2007; Denda and Christiansen, 2013) or benthopelagic micronekton, such as decapod crustaceans, living over seamounts (Fock et al., 2002; Preciado et al., 2009; Colaço et al., 2013).

Processes like upwelling and Taylor columns/caps, waves, and internal waves have been found to be shaping and driving biological distribution patterns over seamounts (White et al., 2007; Genin and Dower, 2007; Lavelle and Mohn, 2010; Denda and Christiansen, 2013; Turnewitsch et al., 2016). Taylor columns are known to enhance the trapping of small particles and organisms above seamounts (Rogers, 1994; White et al., 2007). All these hydrographic phenomena can be important depending on seamount shape, summit depth and water mass homogeneity and stratification over them. Because of this complexity, comparative studies of the distributions of zooplankton over two or more seamounts have been designed in recent years (Martin and Christiansen, 2009; Denda and Christiansen, 2013).

There are several, differing banks distributed in the eastern Canary Islands (N Atlantic Ocean). Amanay and El Banquete banks are shallow (23–24 m summits) and located in a region influenced by both the Canary current and trade winds (Knoll et al., 2002; Hernández-Guerra et al., 2003; Machín et al., 2006; Troupin et al., 2010; Benítez-Barrios et al., 2011). The summit of Concepción Bank (located to the northeast of Lanzarote) is at 150 m depth. Canary waters are generally considered oligotrophic (Davenport et al., 2002). Due to the location of the eastern Canary Islands, relatively close to the mainland, water from coastal upwelling off Northwest Africa arrives in the region SE of El Banquete

as plumes or filaments (Barton et al., 2004; Brochier et al., 2008). Meso-scale structures like eddies occur also to the SE of Fuerteventura (Barton et al., 2004; Yebra et al., 2004; Rodríguez et al., 2008). Anticyclonic eddies, with small ascending flow in their cores (Gubbay, 2003) bring some deeply sourced water to the surface in the archipelago (Aristegui et al., 1993).

Aiming to learn from this complex physical context, the aim of our study was to determine the structure, composition and ecology of near-bottom zooplankton communities dwelling over Concepción, Amanay and El Banquete banks in the eastern Canary Islands. They are characterised by different summit depths and morphologies. Based on a multidisciplinary approach covering wide depth ranges (samples from 32 to 1584 m), our specific questions were: 1) What were the distributional patterns of near-bottom zooplankton over the banks? 2) What factors condition the distributions and structures of assemblages? And 3) what specific environmental variables (mainly of biological/trophic nature) explain the patterns found in near-bottom zooplankton assemblages? We also discuss the influence of complex hydrographic phenomena (internal/tide waves, eddies and Taylor caps) related to water mass dynamics around and over seamounts.

2. Material and methods

2.1. Study area: characteristics

Two cruises were performed in 2011 within the LIFE + INDEMARES project around the eastern Canary Islands (NE Atlantic) over the Concepción (8-23/06/2011) and Amanay-El Banquete (25/06-06/07/2011) Banks.

Concepción Bank is a submarine rise located 75 km to the north of Lanzarote Island, rising 2000 m from the surrounding seafloor, with a rather conical summit at 150 m depth (Fig. 1). Amanay and El Banquete banks are ca. 225 km to the southwest of Concepción, on the Canary Ridge (between the islands of Fuerteventura and Gran Canaria). El Banquete is ca. 7 km west from the southwestern point of Fuerteventura Island, west of the Jandía Peninsula and connected to it by a flat and shallow platform. Both seamounts, similar in size and with flat summits at 24 and 23 m depths, respectively, exceed 2000 m height with basal diameters of ca. 30 km (Ancochea and Huertas, 2004). They are separated by a narrow channel with depths > 1000 m (Fig. 1).

The main (permanent) water masses in the area are: 1) Surface Water (SF), distributed to 150 m depth; 2) North Atlantic Central Water (NACW, ENACW at Concepción), between SF and ca. 600–700 m, that flows toward the SW; 3) Atlantic-Antarctic Intermediate Water (AAIW) that occupies depths below NACW to ca. 1000–1100 m (Knoll et al., 2002; Vélez-Belchí et al., 2015), and 4) the Mediterranean Water (MW) distributed at ca. 1100–1500 m (Knoll et al., 2002). AAIW includes minimum values in the water column of salinity (35.05) and temperature (4.03 °C); it originates in the Antarctic Ocean, and it advects northward. At its northward penetration, with important intra- and interannual oscillations (Fraile-Nuez et al., 2010), AAIW sinks deeper due to its high density. It has marked seasonal variability in the Canary Islands appearing in autumn east of Concepción, decreasing to be barely detectable in June 2011. The MW is characterized by the relative maximum values of salinity and temperature (Knoll et al., 2002) and it flows primarily to the south in the Canary Islands, with less flow in summer (June, in our study) than in other seasons (Knoll et al., 2002).

2.2. Sampling

Large mesozooplankton, macroplankton and small micronekton (hereafter all referred to as zooplankton) were collected near the bottom with a 1 m² ring net of the type WP2-WP3, a cylindro-conical plankton net with 0.5 mm mesh (hereafter named WP2). Our WP2 net was equipped with a net depressor (weight: 25 kg) to help maintain it near the bottom during horizontal (oblique in fact) hauls. The net was

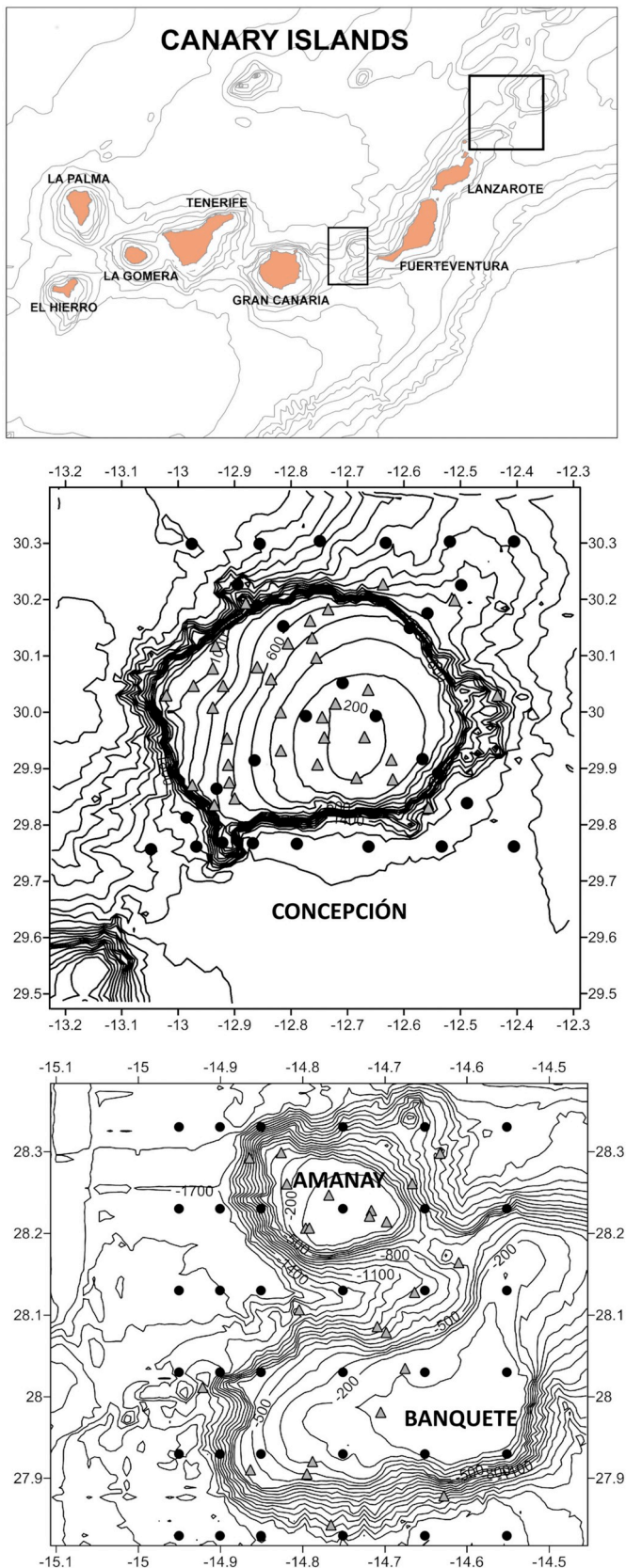


Fig. 1. Maps of the Concepción and Amanay-El Banquete seamounts located to the northeast of Lanzarote and west of Fuerteventura in the eastern Canary Islands, with the locations of near-bottom WP2 net hauls (▲) and CTD (●) deployments (grid structure) indicated. X and Y axes are decimal latitudes/longitudes.

also equipped with choke and rope bands and a 1000DT opening-closing mechanism (General Oceanics). It was always deployed closed (ship at a standstill), it was opened near the bottom and then closed before recovery using mechanical messengers, reducing sample contamination through the water column. Trawling was carried out at an initial distance of 5 m above the bottom (mab) for ca. 10 min (to 15 min in some hauls) at an average speed of ca. 1.1 knots (range 0.9–1.6 knots; mean distances to the bottom ca. 5–50 mab, greater at greater depths). Distances of the WP2 to the bottom were recorded by Simrad ITI Trawl monitoring sensors attached to the depressor. The depressor has a flat fin at the back allowing control of net orientation during trawling (Cartes et al., 2010, 2013). The WP2 was equipped with sensors to measure its distance above the seafloor providing greater manoeuvrability close to the bottom in deep-sea sampling compared with multi-net systems (MOCNESS, BIONESS). Standard 2030 flowmeters (General Oceanics) were attached to the net mouth to estimate the amount of water filtered (ranging in most cases between 400 and 1100 m³ per haul) and to measure the distance covered by each haul. Thirty-six WP2 hauls were made over Concepción Bank and 24 over the Amanay-El Banquete Banks, all performed during daytime. The mean depths (soundings) of hauls performed ranged between 32 and 1584 m, and their distributions around each bank are listed in Table S1 and shown in Fig. 1. All hauls sampled the SF, NACW, AAIW and MW water masses, except that the deepest sample at 1584 m (El Banquete) was in North Atlantic Deep Water. The sampling design for near-bottom zooplankton was necessarily adapted to the bottom shape of seamounts (we could not follow a pre-established regular grid as for surface zooplankton). In addition, near-bottom sampling was not possible along practically vertical walls like those found on SE Banquete and S-SE Concepcion.

Zooplankton were fixed in buffered formaldehyde (4%) on board. Samples were sorted and the organisms identified in the laboratory at 10X to 40X (see Cartes et al., 2013). All taxa were counted and weighed (wet weight after blotting out water on blotting paper for a fixed time). Zooplankton were identified to broad taxa (e.g. siphonophores, polychaetes, euphausiids, and calanoid copepods) and to genus/species for some large crustaceans (e.g. euphausiids, decapods or hyperiids), fish and jellyfish, excluding groups such as copepods and ostracods, due to limitations of the authors' knowledge of those groups. Aliquots from 1/2 to 1/8 of samples were sorted for the very numerous smaller organisms, those < 2 mm, e.g. copepods, ostracods, and euphausiid/decapod larvae. Both broad taxa and species were standardized prior to statistical analyses to individuals/1000 m³ or gWW (wet weight)/1000 m³ for each haul.

Grids of CTD profiles were performed in the same areas as the zooplankton sampling with an SBE25 CTD profiler. The CTD was deployed to ca. 5–10 m above the seafloor, the same depths sampled by the opening-closing WP2. Four environmental parameters were recorded by the CTD profiler: T (temperature in °C), S (salinity), O₂ (oxygen concentration in ml/l) and f (fluorescence in voltage units). The CTD recorded at 24 data sets per second, and a mean of each variable was calculated for each 1 m down the water column. Mean values of T, S, O₂ and f near the bottom (same levels sampled by WP2) were included in data matrices for the environmental analyses.

3. Data analysis

3.1. Environmental variables analysed

We analysed zooplankton abundance as a function of hydrographic, geographic and biological variables. Hydrographic variables were temperature (T) and salinity (S). Geographic data were latitude (LAT) and longitude (LONG) of each haul. Fluorescence (f) and dissolved oxygen (O₂) recorded by sensors were the best available proxies for biological variables. The T, S, f and O₂ near the bottom were taken from the CTD cast nearest (at the same levels of the water column) to each

WP2 sample. Near-bottom O_2 values obtained for all hauls were plotted as function of depth. The hydrographic data defining water masses (T-S profiles) over Concepción and El Banquete-Amanay confirmed in our cruises the general distribution of water masses listed above (Fig. S1; Martín-Sosa, 2013a, b); those were adopted for MDS analyses. Results on f and O_2 are presented and discussed in conjunction with zooplankton distribution results.

In addition we considered (over the three banks): 1) profiles of fluorescence from surface to 200 m over each bank, averaging the information from 2 to 5 CTD profiles over each bank summit from June 2011; and 2) Chlorophyll a concentration at the surface ($mg\ Chl\ a/m^3$) downloaded from satellite imagery (<http://gdal1.sci.gsfc.nasa.gov/>) simultaneous with the sampling date (June) and from 1 to 4 months before. Those variables served as a proxies for phytoplankton biomass. Chl a was recorded for the location (LAT, LONG) of each haul and for the two nearest haul locations with Chl a data available, and means per month were calculated. Distances between WP2 hauls and CTD profiles were typically less than 1 km (within the range of 300–500 m travelled in WP2 sampling). However, in 15% of cases the distance between a WP2 haul and its nearest CTD was greater than 1 km (all at Concepción).

3.2. Analysis of abundance and biomass

Abundances of the main broad taxa and species of zooplankton were calculated per haul (each WP2 sample) for each of the three banks. Haul compositions (abundances) were analysed by non-metric Multidimensional Scaling (nMDS; Clarke and Warwick, 2001) to examine sample relationships among banks and water masses on a 2-dimensional ordination plane. We used Bray-Curtis distances after log-transformation of the data as the nMDS entries. Taxa (either broad taxa or species) with low frequencies of occurrence (once or twice, less than 5% of samples) were removed from the matrices to prevent an undue influence on the results (Gauch, 1982).

PERMANOVA tests (distance-based Permutational Analysis of Variance; Anderson et al., 2008) were performed on the same abundance matrices (999 permutations) to evaluate whether assemblages differed among the three banks and among the different water masses found in the area. The PERMANOVA designs were based on two factors with a crossed design: Factor I was the water mass in which each haul was located based on comparison of T-S properties in the haul depth interval to values in the literature for water masses distributed in the eastern Canary Islands. Levels for Factor I were: 1) Surface Water (SF), from surface to depths of 150 m; 2) North Atlantic Central Water (NACW, called ENACW over Concepción area) below SF and to depths of 700 m; 3) Atlantic-Antarctic Intermediate Water (AAIW) below NACW to 1000 m, and 4) Mediterranean Water (MW) covering all hauls performed below 1000 m in the current study. The WP27 haul from El Banquete (at 1584 m) fell within the limits of the North Atlantic Deep Waters (NADW), but it was included as belonging to the MW group. Factor II was “bank”, with three levels: Concepción, Amanay and El Banquete.

A SIMPER (SIMilarity of PERcentages) routine was performed on the Bray-Curtis matrix (Clarke, 1993) to identify those taxa that most typify each of the taxon groups that were significantly different based on the nMDS results. Results on the abundance ($ind./1000\ m^3$, log-transformed) and of the contribution of the main zooplankton taxa to the average Bray-Curtis similarity within each group were included. All the analyses were performed using PRIMER 6 & PERMANOVA + software (Clarke and Warwick, 2001; Anderson et al., 2008).

Biomass of total zooplankton and of the 14 broad or major taxa of zooplankton dominant in biomass in the eastern Canary Islands were calculated for each haul. Biomass provides a trophic approach, related with the energy flux in ecosystems.

Relationships between main taxa biomass and environmental variables (cited above) were explored by the multivariate Canonical

Correspondence Analysis technique (CCA; ter Braak, 1986). CCA extracts synthetic environmental gradients from ecological data (ter Braak and Verdonschot, 1995). Ordination axes (often two are represented) in CCA are linear combinations of the environmental variables considered. The individual variables are represented on the ordination plots by arrows with lengths proportional to their importance for explaining in this case- biomass variability (ter Braak, 1986). Data were log-transformed. The software XLStat (AddinSoft Inc.) was used for CCA. For those taxa that appeared in the CCA to be associated with specific environmental variables, we tested the significance of those relationships using non-parametric Spearman's rank correlation coefficients.

Finally, biomass from the WP2 hauls ($gWW/1000\ m^3$) was evaluated as a function of environmental explanatory variables using Generalized Linear Models (GLMs, Gill, 2001) and Generalised Additive Models (GAMs, Yee and Mitchell, 1991). In a preliminary analysis we explored possible correlations among explanatory variables by Draftsman plots of Pearson correlations – r – between explanatory variables. Temperature was strongly correlated with near-bottom fluorescence and O_2 ($r \geq 0.7$). Thus, GLMs were built for both biological and hydrographic variables separately. We put emphasis on the results for biological variables, because the relationships of water masses (T and S) with zooplankton had already been explored by MDS (and CCA) results. GLMs are flexible generalizations of ordinary least squares regressions, in which the environmental variables significantly related to the distributions of the dependent variables (in this case total biomass of zooplankton, copepods, etc.) are identified. Tests of relationships derived from the GLMs were based on a Gamma distribution using a log link function. GLMs were built using R software (see <http://www.r-project.org>). Best models generated from our dataset were selected based on the A.I.C. (Akaike information criterion). GAMs are a more flexible expansion of GLMs that use non-parametric smoothers to model species – environment relationships. We applied a smoother to variables in the GAM and used a stepwise GAM model builder (step.GAM).

4. Results

Water column data of fluorescence, satellite Chl a data and O_2 .

Fluorescence (f) profiles were the best available proxy indicating phytoplankton biomass/production in the water column surrounding the three banks during the June sampling period. Chlorophyll a distributions and locations of fluorescence peaks (Fig. 2) differed among the banks, both up in the water column and near the bottom. In the water columns over the banks, average f was clearly greater at Amanay than at El Banquete (t tests were significant, $p < 0.001$), and the average peak depth of f was shallower at Amanay, 76 m versus 110 m at El Banquete. Concepción had similar f distributions to Amanay, but the peak of f was even closer (51 m) to the sea surface (but farther away from its summit at 150 m). Near the bottom, the highest f values were found at 32–43 m near Amanay's summit at 24 m, at 71 m beside El Banquete's summit at 23 m. At Concepción peak of near-bottom f were at 194 m and 279 m (Fig. 2), well off its summit at 150 m. Finally, near-surface satellite data showed very similar Chl a over the three banks (0.095 – $0.109\ mg\ Chl\ a/m^3$; with no significant differences: t tests, $p > 0.05$) in June, as also was observed in the near-surface portions of the fluorometer profiles (Fig. 2). Satellite Chl a data taken before the sampling dates were on average greater at Concepción in February ($0.315\ mg\ Chl\ a/m^3$) than at Amanay or El Banquete (0.266 and $0.263\ mg\ Chl\ a/m^3$, respectively; t -test significances, $p < 0.05$). The seasonal peak of Chl a was delayed at Amanay (March) compared to El Banquete (February, Fig. 2).

The profiles of near-bottom O_2 vs. depth showed parallel tendencies over the three banks (Fig. 3). In SF to 150 m, near-bottom O_2 ranged between 4.82 and 4.97 ml/l. It decreased to 3.30–3.99 ml/l in the deepest layers occupied by NACW (400–700 m), and to 3.16–3.34 ml/l at depths occupied by AAIW (ca. over 700–1000 m). Below that it

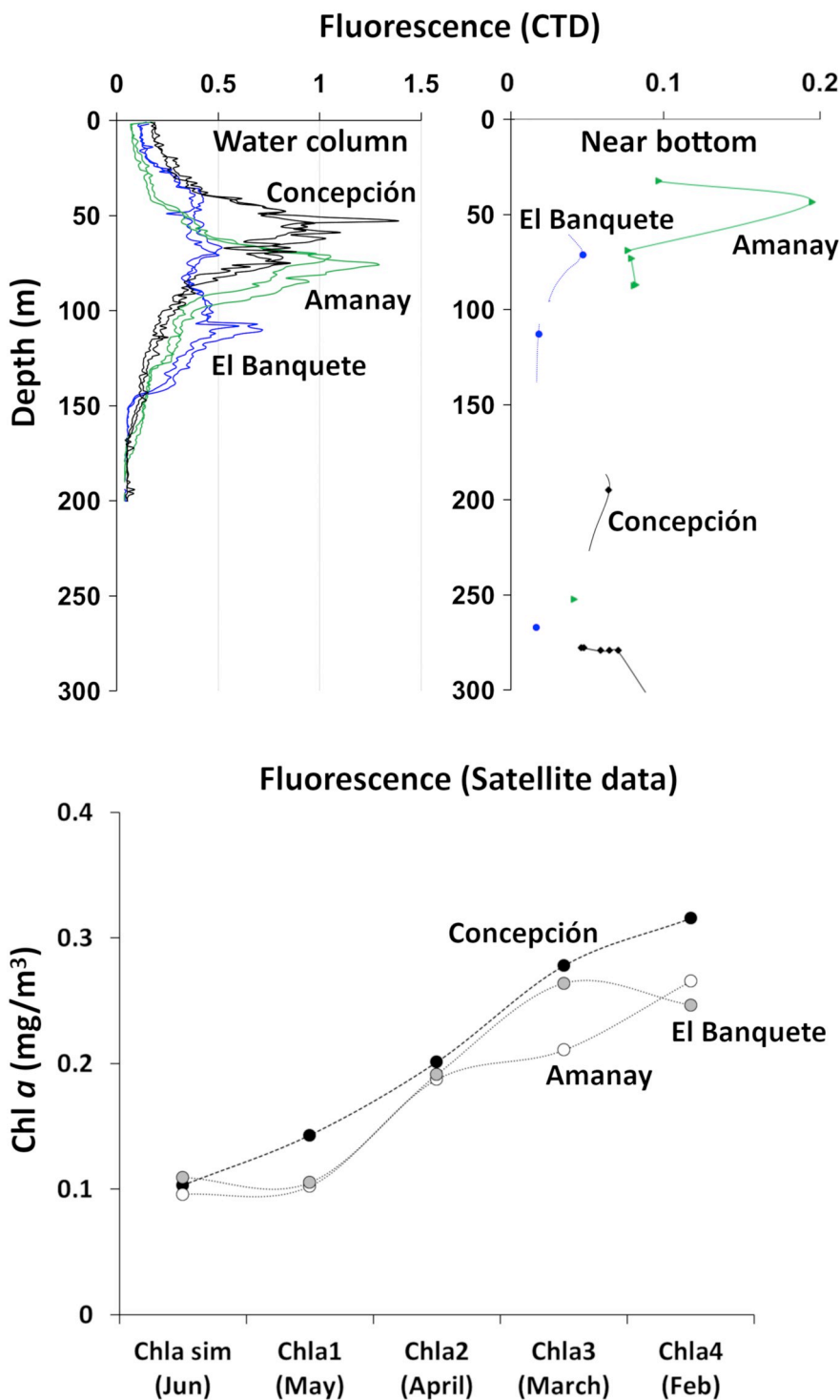


Fig. 2. Distribution of fluorescence (from sensors attached to the CTD) and Chl *a* (from satellite imagery) over Concepción (●), Amanay (●) and El Banquete (●) seamounts (eastern Canary Islands). Each symbol (●, ●, ●) indicates the mean fluorescence value in each haul. Surface satellite Chl *a* calculated for the time of sampling (June) and 1 (e.g. Chla 1) to 4 months before that; fluorescence profiles from in the open water surrounding each bank and from near bottom sensor.

increased again to 4.32–4.39 ml/l within the MW (significant ANOVA and post-hoc comparisons all with $p < 0.001$, comparing O₂ between adjacent water masses: SF vs NACW, NACW vs AAIW, AAIW vs MW). Oxygen concentration was lower over El Banquete seafloor at levels occupied by NACW and AAIW, compared with concentrations in those water masses at the other two banks (Fig. 3).

4.1. Distribution of zooplankton abundance

A total of 216 taxa, most of them classified to species or genus level, were identified in the near-bottom zooplankton of the three banks.

Since taxa with less than 5% of frequency of occurrence were removed from the data matrix, the resulting matrix comprised 112 taxa, 82 of them determined at species or genus level (Table 1). In terms of mean abundance (ind./1000 m³), the highest totals for zooplankton were from Surface Water (SF) level: 28367 ind./1000 m³ over Amanay Bank and 17194 ind./1000 m³ over El Banquete (Table 1). Near-bottom zooplankton abundance decreased at intermediate levels. Within the NACW, it was 3021–5199 ind./1000 m³ (range at all three banks). At AAIW levels it was 2055–2693 ind./1000 m³ (Table 1). Near-bottom zooplankton mean abundance reached minimum values in AAIW over the slopes of Concepción Bank. At MW levels zooplankton abundance

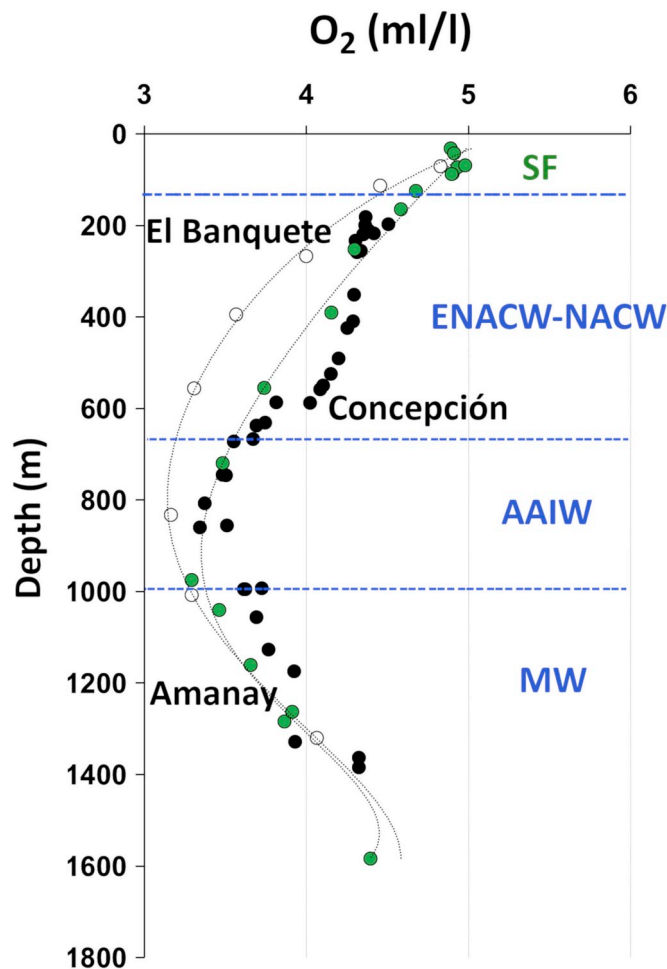


Fig. 3. Distribution of near-bottom O_2 (recorded by oxygen sensors attached to the CTD, ml/l), over Concepción (●), Amanay (●) and El Banquete (○) seamounts (eastern Canary Islands). Water masses found around the Canary Islands are indicated: SF— Surface Water; NACW-ENACW - (Eastern) North-Atlantic Central Water; AAIW - Atlantic-Antarctic Intermediate Water; MW - Mediterranean Water. Each symbol (●, ●, ○) indicates the mean O_2 value associated with a particular haul.

reached similar values (1555–3272 ind./1000 m^3) to those in the NACW-AAIW, increasing to 3272 ind./1000 m^3 near Concepción Bank. Increase of zooplankton biomass at MW level was general, especially adjacent to Amanay-El Banquete (see below).

Calanoid copepods were generally the dominant group (in number and biomass), being 43.8–48.9% of total zooplankton abundance in SF, with proportions increasing deeper, to maximum percentage of abundance in MW, e.g., to 88.5% of total zooplankton beside Concepción Bank. In SF (only sampled over Amanay and El Banquete), decapod and euphausiid larvae were also important, with 9.6% of abundance at El Banquete and 14.7% at Amanay, respectively. Juvenile mysids, mainly *Anchialina* sp., contributed 2.3% to abundance at Amanay.

The most remarkable trends for the remaining taxa significant in terms of abundance, but also some large animals important in respect to biomass, were:

1) Chaetognaths were especially abundant in SF at Amanay-El Banquete and in NACW at Concepción (1136.9 ind./1000 m^3). In AAIW and MW levels densities were less by an order of magnitude.

2) Decapod larvae were mainly distributed in SF at Amanay-El Banquete, where 97% of them were collected. Abundance of euphausiid larvae (*Calypotopsis* and *Furcilia*) showed a similar trend, 77% of larvae

were in samples from SF layers.

3) Siphonophores were most abundant in SF over Amanay-El Banquete, then fewer in deeper hauls. Considering taxa classified at family or genus/species level, they were more abundant in NACW and AAIW levels, less so in MW. However, they were more diverse in MW, especially adjacent to Concepción Bank where 11 taxa were identified. That compared to only 4 at Amanay-El Banquete, where *Eudoxoides* sp. reached 46.7 ind./1000 m^3 . *Chelophyes appendiculata* was distributed mainly in SF and NACW levels, while *Lensia* spp. were found mainly deeper, in NACW-AAIW.

4) Small pelagic pteropods, mainly *Creseis acicula* and *Limacina inflata*, were abundant (to 417.9 ind./1000 m^3) in SF at Amanay-El Banquete and in NACW levels, with abundance decreasing with depth. However, they also reached moderate abundances in some samples (to 50.7 ind./1000 m^3) from MW adjacent to Concepción.

Among large taxa (crustaceans and fish), we found:

1) More euphausiid species were caught in intermediate and deeper waters below SF, especially in MW at Concepción, where nine species were identified. At Amanay and El Banquete we found the highest abundance of euphausiids at NACW levels. At Amanay, *Euphausia pseudogibba* and juveniles of *Nematoscelis* spp. reached 24.7 and 12.6 ind./1000 m^3 , respectively. No other euphausiids reached similar densities, and only *Nematoscelis atlantica* reached 4.5 ind./1000 m^3 at Concepción. It was also found in lower densities over the other two banks (Table 1).

2) Hyperiid amphipods reached high densities only in SF, specifically *Hyperoides longipes* (21.3 ind./1000 m^3) and *Lanceola loveni* (13.8 ind./1000 m^3) over El Banquete. Deeper, only *Primno* spp. reached significant densities (3.9–6.8 ind./1000 m^3), with some changes in species composition depending on the bank sampled: *Primno macropa* at Amanay-El Banquete, *Primno brevidens* at Concepción.

3) Adult meso- to bathypelagic decapods were collected almost exclusively from the level of MW, with different species appearing over each bank and greater species numbers at Concepción, most abundantly *Systellaspis debilis*, *Sergestes sargassi* and *Sergestes japonicus*.

4) Meso- and bathypelagic fish, mostly juveniles (not larvae), were part of the micronekton community and underestimated by our sampling technique. However, the specimens caught indicate distributions similar to those for decapods. They were collected at AAIW and MW levels, with higher species numbers at Concepción (9 species identified), than at Amanay-El Banquete combined (6 species).

4.2. Multivariate analyses of zooplankton abundance

Multi-Dimensional Scaling (nMDS) showed some ordination (Stress = 0.14) of WP2 samples, separating the different banks and water masses (Fig. 4). Concepción zooplankton hauls were in the right-upper part of the plot, Amanay zooplankton hauls in the left-lower, and El Banquete hauls were on average in an intermediate position. Regarding water masses, WP2 samples from Surface Water (SF) appeared (well grouped) to the left of the nMDS plot (Fig. 4). The other hauls were placed progressively farther to the right with increasing water mass depth, although zooplankton hauls from AAIW and MW were mixed together. The composition of near-bottom zooplankton was significantly different by factor “bank” according to the two-way PERMANOVA (pseudo- F = 2.55; p = 0.02). Paired comparisons revealed significant differences of zooplankton over Concepción from those over Amanay (t = 3.69; p = 0.001), similarly but less strongly between Concepción and El Banquete (t = 2.42; p = 0.001) and between El Banquete and Amanay (t = 1.45; p = 0.04). Average similarity of zooplankton composition for the three banks was between 46.1 and 60.1%, and composition was moderately different (dissimilarity range was 52.2–54.5%) among the three banks. The composition of zooplankton was also significantly different by factor “water mass” (pseudo- F = 2.71; p = 0.003). The factor “water mass” gave significant results (pairwise- t from PERMANOVA) when we compared the zooplankton

Table 1
Mean abundance (ind./1000 m³) of main zooplankton taxa (classified to broad taxa or to genus/species) from the WP2 collections taken close to the bottom over Concepción and Amanay-El Banquete seamounts. Results are presented by depth ranges occupied by water masses found around the Canary Islands: SF - Surface Water - NACW-ENACW - North-Atlantic Central Water; AAIW - Atlantic-Antarctic Intermediate Water; MW - Mediterranean Water. L: larvae; J: juveniles. Taxa found only one time in the sampling are not listed.

	SF			NACW-ENACW			AAIW			MW		
	Amanay	El Banquete	Concepción	Amanay	El Banquete	Concepción	Amanay	El Banquete	Concepción	Amanay	El Banquete	Concepción
	32-87 m	71-113 m		252-555 m	257-566 m	257-566 m	720-1041 m	833-1008 m	667-995 m	1161-1284 m	1269-1575 m	1105-1648 m
	n=6	n=2		n=3	n=3	n=20	n=3	n=2	n=10	n=2	n=3	n=6
Decapoda												
Alpheidae (L)	238.5	12.1		0.9	0.6	0.2	2.2	0	0	0	0	0.2
zoea Brachyura	214.6	18.7		21.7	0	1.0	6.6	0	0.8	6.9	0	0.1
megalopa Brachyura	14.6	9.7		7.3	0	0.8	0	0	0.4	1.7	0	0.1
Caridea (L)	1565.6	11.6		41.7	0	2.6	4.5	10.9	0.9	1.0	0	0.9
Galatheididae (L)	779.9	29.0		0	0	0	6.1	0	0	0.3	0.2	0
megalopa Natantia	308.6	0		6.7	0	1.5	0	0	0.1	0	0.5	0.1
megalopa Paguridae	180.7	2.9		0	0	0	0	0	0	0	0	0
Decapoda larvae unid.	397.5	1657.5		4.2	34.2	0	0	0	0	0	0	0.8
<i>Acanthephyra pelagica</i>	0	0		0	0	0	0	0	0	0.4	0.3	0
<i>Gennadas valens</i>	0	0		0	0	0	0	0	0	0.3	0	0.1
<i>Gennadas brevisrostris</i>	0	0		0	0	0	0	0	0	1.0	0	0
<i>Sergestes atlanticus</i>	0	0		0	0	0	0	0	0	0	0.2	0
<i>Sergestes japonicus</i>	0	0		0	0	0	0	0	0	0	0	0.2
<i>Sergestes pectinatus</i>	0	0		0.6	0	0	0	0	0	0	0	0
<i>Sergestes sargassi</i>	0	0		0	0	0	0	0	0	0	0	0.3
<i>Systellaspis debilis</i>	0	0		0	0	0	0	0	0	0	0	0.2
Euphausiacea												
Furcilia + Calyptopis larvae	4169.2	415.6		569.3	66.0	203.3	110.4	62.6	98.6	124.1	41.6	45.4
<i>Thysanopoda</i> sp. (J)	0	0		0	0	0	0.3	0.8	0.2	0	3.9	0
<i>Euphausia hemigibba</i>	0	2.9		26.9	0	0.4	3.9	2.4	2.4	0	1.1	0.9
<i>Euphausia krohni</i>	0	0		1.0	0	0	0	2.0	0	0	0	0
<i>Euphausia</i> sp. (J)	4.2	0		10.8	0	1.5	3.4	0	1.2	2.4	0	0.4
<i>Nematobrachion boopis</i>	0	0		0	0	0.2	0	0	0	0	0	0
<i>Nematobrachion flexipes</i>	0	0		0.6	0	0	0	0.4	0	0	0	0
<i>Nematoscelis atlantica</i>	0	0		1.2	0	1.1	1.0	0	1.6	0	0.5	4.5
<i>Nematoscelis megalops</i>	0.4	0		0	0.9	0	1.3	0.8	0	2.8	0	0
<i>Nematoscelis microps</i>	0	1.3		0.5	0	0	2.0	0	0	1.4	1.3	0
<i>Nematoscelis</i> sp. (J)	0	0		12.6	2.8	0.7	0	0	0.2	1.3	0	0.4
<i>Nematoscelis tenella</i>	0	0		0	0	0	0	2.1	0.2	0	0	0.2
<i>Stylocheiron affine</i>	0	0		0	0	0.6	0	0	0.1	0	0.2	0.1
<i>Stylocheiron elongatum</i>	0	0		1.2	0	0.1	0.7	0.4	0.1	0.3	0	0
<i>Stylocheiron longicorne</i>	0.9	0		1.1	0	0.2	0.4	0.4	0.3	0	0	0.2
<i>Stylocheiron</i> sp. (J)	0.5	0		0	3.8	0.6	0	0	0	0	0.2	0.4
<i>Thysanoessa parva</i>	0	0		0	0	0	0.3	0.4	0	0	0.2	0
<i>Thysanopoda aequalis</i>	0	0		0	0	0.1	0.4	0.4	0.2	0.7	0.5	0.5
<i>Thysanopoda obtusifrons</i>	0	0		0	0	0	0	0	0.3	0.3	0.2	0.3
<i>Thysanoessa</i> sp. (J)	0	6.8		0	0	0.9	0	0	0.1	0	0	0.1
<i>Thysanopoda</i> cf. <i>microphthalma</i>	0	0		0	0	0	0	0	0	0	0	0.2
<i>Thysanopoda monacantha</i>	0	0		0	0	0	0	0	0	0	0	0.5
Lophogastrida (<i>Eucopia unguiculata</i>)	0	0		0	0	0	0.3	0.4	0	0.7	0	0.9
Mysidacea												
<i>Gastrossacus</i> sp.	39.4	0		0	0	0	0	0	0	0	0	0
<i>Anchialina</i> sp. (J)	662.9	68.6		0	3.0	0	0	0	0	0	0	0
Amphipoda												
<i>Cyphocaris challengerii</i>	0	0		1.2	0	0	0	0	0	0	0	0.2

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Table 1 (continued)

	SF			NACW-ENACW			AAIW			MW		
	Amanay	El Banquete	Concepción	Amanay	El Banquete	Concepción	Amanay	El Banquete	Concepción	Amanay	El Banquete	Concepción
	32-87 m	71-113 m		252-555 m	257-566 m	257-566 m	720-1041 m	833-1008 m	667-995 m	1161-1284 m	1269-1575 m	1105-1648 m
	n = 6	n = 2		n = 3	n = 3	n = 20	n = 3	n = 2	n = 10	n = 2	n = 3	n = 6
<i>Cyphocaris anonyx</i>	0	0		0	0	0.2	0	0	0.2	0	0	0.7
<i>Cyphocaris</i> sp. (J)	0	0		0	0	0	2.7	0	0	0.4	0	0
<i>Trischizostoma nicaense</i>	0	0		0	0	0	0.3	0	0	0	0	0.1
<i>Cystisoma fabricii</i>	0	0		0	0	0	0	0	0.2	0	0	0
Hyperiididae	0.8	0		0	0	0.6	0	0	0.1	0	0	1.0
<i>Hyperoides longipes</i>	0	21.3		0	0	0.7	0	0	0.1	0.4	0	0.1
<i>Lanceola loveni</i>	0	13.8		0	0	0	0	0	0	0	0	0
<i>Lestrigonus schizogeneios</i>	3.1	0		0	0	0.2	0.4	0	0.5	0	0	0
<i>Parapronoe cruscum</i>	0	0		0	0	0	0	0	0	0	0	0.4
<i>Phronima sedentaria</i>	0	1.0		0	0	0	0	0	0	0	0	0.1
<i>Phrosina semilunata</i>	0	1.0		0	0	1.2	0	0	0.1	0	0.2	1.3
Platyscelidae (J)	0	4.8		0	0	0	0	0	0	0	0.2	0.1
<i>Primno brevidens</i>	0	0		0.6	0	0.6	0.3	0	4.2	0	3.9	2.3
<i>Primno johnsoni</i>	0	1.0		0	0	0	0	0	0	0	0	0.1
<i>Primno latrellei</i>	0	1.9		0	0.6	0.1	0	0	0.1	0	0	0.3
<i>Primno macropa</i>	0	2.9		0	0	0	6.7	4.2	0.9	6.8	0.3	0.8
<i>Scina stenopus</i>	0	1.3		0	0	0	0	0	0	0	0	0
<i>Streetsia challengerii</i>	0.7	0		0	0	0.1	0	0	0.1	0	0	0.1
<i>Vibilia armata</i>	0	0		0	0.5	0.2	0	0	0.5	0	0.5	1.1
Isopoda (<i>Gnathia</i> sp. - <i>pranizza</i>)	5.9	0		0	0	0	0.4	0	0	0	0	0
Ostracoda (<i>Conchoecia</i> sp.)	260.0	122.1		209.5	77.0	132.3	42.4	124.9	102.5	86.6	11.3	69.3
Calanoidea	12420.3	8421.8		3444.3	1949.2	3470.7	2120.9	1333.5	1405.4	1712.4	1252.7	2894.3
Cyclopoidea	236.6	381.5		67.8	51.6	21.9	11.1	43.5	13.0	30.5	9.7	7.5
Harpacticoida	0	0		0	0	1.7	0	0	2.2	0	0	0
Siphonophora												
<i>Abylopsis tetragona</i>	0	0		0	0	0	0.3	0	0.2	0	0	0.2
<i>Chelophyes appendiculata</i>	1.4	6.3		6.7	25.3	3.9	0.3	0	0.3	0	0	1.0
<i>Lensia</i> spp.	0	0		16.4	0	4.2	2.0	7.8	3.9	0.3	0.7	0.2
Other siphonophora	1166.8	850.6		53.0	69.2	14.4	43.9	36.4	7.1	45.8	21.4	3.2
Abylidae	0	0		0	0	0.1	0	0	0.1	0	0	0.2
Agalmidae	0	1.0		0	0	0.1	0	0	0	0	0	0
Dyphidae (<i>Eudoxoides</i> sp.)	0	0		26.7	0	45.7	0	0	39.8	0	0.4	12.1
<i>Forskalia</i> sp.	0	0		0	0	0.1	0	0	0.2	0	0	0
Hyppodidae	0	0		0	0	0.1	0	0	0	0	0	0.2
Prayidae	0	0		0	0	0	0	0	0	0	0	0.1
<i>Vogtia spinosa</i>	0	0		0	0	0	0	0	0.6	0	0	1.2
Ctenophora	0.5	0		13.3	7.4	0	0	0.4	0	0	9.5	0
Scyphozoa												
<i>Solmissus</i> sp.	12.5	0		0	0	0.4	0	0	0	0	0.3	0
unident. Scyphozoa	0	0		0.6	3.9	0.3	0	0	2.0	0	2.5	0.3
Polychaeta												
Tomopteridae	4.4	8.4		1.2	0	1.2	0.4	0	1.0	1.7	0	0
Alciopidae	0	0		0.5	0	0	0	0	0	0	0.5	0
Gastropoda												
<i>Atlanta</i> sp.	5.1	15.8		6.7	6.1	5.4	0	0	1.7	0	3.7	1.6
Gastropoda larvae	0.5	9.4		0	0	0	0	0	0	0	0	0
Gastropoda unid.	8.9	453.4		0	37.4	0	0	0	0	0	0.8	0
<i>Peracelis triacantha</i>	0	0		0	0	0	0	0	0.2	0	0	0
<i>Cavolinia inflexa</i>	0	0		0	0	0	0	0	0.2	0	0	0.5

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Table 1 (continued)

SF	NACW-ENACW						AAIW						MW					
	Amanay	El Banquete	Concepción	Amanay	El Banquete	Concepción	Amanay	El Banquete	Concepción	Amanay	El Banquete	Concepción	Amanay	El Banquete	Concepción	Amanay	El Banquete	Concepción
32-87 m	71-113 m	252-555 m	257-566 m	257-566 m	833-1008 m	667-995 m	1161-1284 m	1269-1575 m	1105-1648 m									
n = 6	n = 2	n = 3	n = 3	n = 3	n = 2	n = 10	n = 2	n = 3	n = 6									
<i>Clyo pyramidata</i>	2.9	0	20.0	13.5	0	0.7	6.1	0	0.2	1.7	0	0	0	0	0	0	0	0
<i>Cresis actula</i>	613.3	59.7	28.4	0	0	1.3	3.9	5.4	0.3	2.1	0	0	0	0	0	0	0	0
<i>Hyalocitis striata</i>	0	28.7	17.5	0	0	0	0	10.0	0	0	0	0	0	0	0	0	0	0
<i>Limacina inflata</i>	300.8	417.9	212.2	47.9	0	53.1	6.1	41.3	20.7	1.7	17.7	0	0	0	50.7	0	0	0
<i>Peracelis reticulata</i>	0	0	0	0	0	0.1	0	0	0	0	3.9	0	0	0	0.2	0	0	0
Cephalopoda	1.8	19.0	0	1.1	0	0	0	0.4	0.1	0	0	0	0	0	0	0	0	0
Chaetognata	1957.5	3110.6	391.0	427.5	0	1136.9	271.7	364.6	329.4	211.4	121.5	0	0	0	158.2	0	0	0
Thaliacea (<i>Salpa</i> spp.)	2199.1	138.8	311.7	141.0	0	4.6	16.0	58.1	3.4	30.5	28.1	0	0	0	0.9	0	0	0
Appendicularia	268.3	442.4	13.3	2.5	0	3.8	0	4.2	1.4	0	0	0	0	0	0.7	0	0	0
Echinodermata larvae	1.5	129.1	0	4.9	0	0	0	0	0	0	1.8	0	0	0	0	0	0	0
Teleostei																		
<i>Argropelecus sladeni</i>	0	0	0	0	0	0.1	0	0	0.4	0	0	0	0	0	0	0	0	0
<i>Bathophilus vaillanti</i>	0	3.9	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0
<i>Chauliodus danae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0
<i>Cyclothone braueri</i>	0	0	0	0.5	0	1.0	0.3	3.4	2.9	1.7	1.2	0	0	0	1.7	0	0	0
<i>Cyclothone livida</i>	0	0	0	0	0	0	0.6	0	0	0	0.7	0	0	0	0.2	0	0	0
<i>Cyclothone microdon</i>	0	0	0	0	0	0	0	0.9	0.1	0	0	0	0	0	0.5	0	0	0
<i>Cyclothone pseudopalpida</i>	0	0	0	0	0	0	2.2	0.9	0.1	0	0	0	0	0	0.1	0	0	0
<i>Cyclothone</i> spp. (J)	0	0	0	0	0	0	1.6	0	0	1.1	0.3	0	0	0	0	0	0	0
<i>Diogenichthys atlanticus</i>	0	0	0	0	0	0	0	0	0	0	0.3	0	0	0	0.1	0	0	0
Sternoptychidae	0	0	0	0	0	0.1	0	0	0	0.3	0	0	0	0	0	0	0	0
<i>Sternoptyx diaphana</i>	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0.2	0	0	0
Fish eggs	146.4	197.7	33.0	38.2	0	5.2	2.0	0	0	0	5.5	0	0	0	0	0	0	0
Fish larvae	170.8	90.9	16.8	4.3	0	0.4	6.9	0.8	0.1	0.4	0.2	0	0	0	0	0	0	0
	28367.2	17194.3	5600.8	3021.0	5129.4	2054.6	2693.2	2124.6	2054.6	2281.4	1551.2				3271.7			

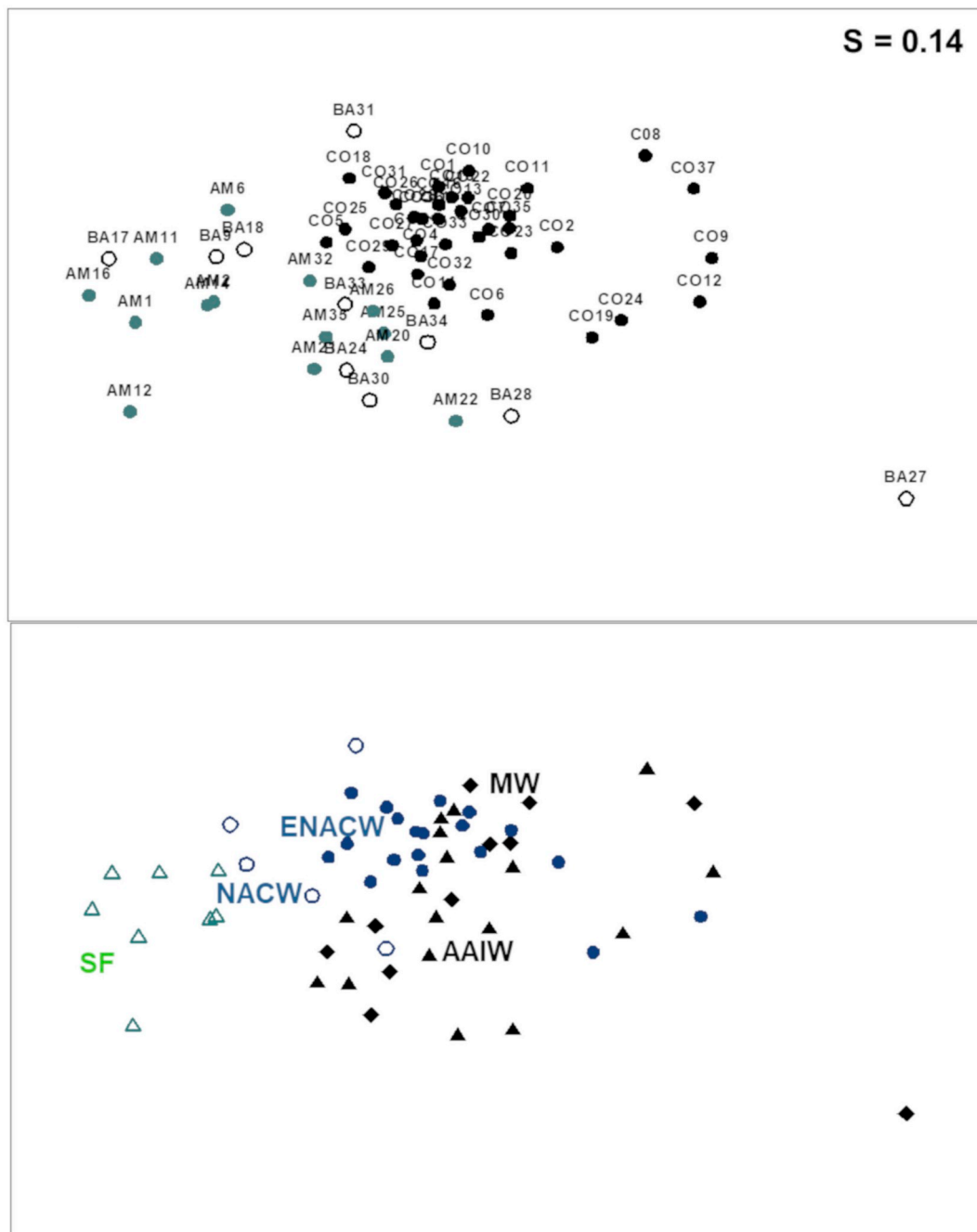


Fig. 4. nMDS ordination plot of abundance data from WP2 samples collected over the seamounts Concepción (CO, ●) Amanay (AM, ●) and El Banquete (BA, ○) (top). Results are also presented as a function of the water masses found around the Canary Islands: SF - Surface Water (△); NACW-ENACW (○, ●) - North-Atlantic Central Water (▲); AAIW - Atlantic-Antarctic Intermediate Water; MW - Mediterranean Water (◆) (bottom). The nMDS was performed on the standardized abundance (ind./1000 m³) results for the main zooplankton taxa as shown in Table 1.

Table 2

PERMANOVA statistics comparing the composition of zooplankton (abundance, ind./1000 m³) associated to the different water masses surrounding the eastern Canary Islands: SF - Surface waters; NACW-ENACW - North-Atlantic Central Water; AAIW - Atlantic-Antarctic Intermediate Water; MW - Mediterranean Water. Values of *p* for each paired comparison are between parenthesis.

t pairwise	NACW-ENACW	AAIW	MW
SF			
NACW-ENACW	3.73 (0.001)	3.79 (0.001)	3.26 (0.001)
AAIW		1.58 (0.010)	1.60 (0.016)
			0.98 (0.475)

compositions of adjacent shallower water masses (SF vs. NACW-ENACW, *p* = 0.001, Table 2), and also when comparing NACW-ENACW vs. AAIW (*p* = 0.01). However, differences between zooplankton composition in AAIW and MW were not significant. Interaction between the two factors in two-way PERMANOVA was not significant (pseudo-*F* = 1.52; *p* = 0.05).

SIMPER results from the assemblages associated with each water mass (Table S2), showed changes in the contributions of different groups to similarity that generally fit with the abundance patterns (see above). Briefly, copepods were always the taxon with the highest contributions to similarity, especially for comparisons between samples from NACW, AAIW and MW (25.3–30.9%), less strongly contributing

among SF samples (13.3%). Chaetognaths were always abundant and with similar contributions in all water masses. The main distinctive feature within SF was the large contribution of decapod larvae (e.g. Alpheidae, Galatheidae, Caridea) to similarity. *Creseis acicula* made the largest contribution to similarity among pteropods, while other pelagic gastropods (pteropods *Limacina inflata* and *Clio pyramidata*, the heteropod *Atlanta* sp.) were more important in NACW-ENACW. *Conchoecia* spp. also increased in contribution to total similarity at these deeper levels. Finally, at the deepest level (AAIW-MW) several taxa of siphonophores, i.e. *Eudoxoides* sp. (also present in ENACW) and *Lensia* sp. contributed substantially to similarity, as to a lesser extent did some euphausiids and hyperiids (Table S2). Results of similarity per bank (not included) showed greater contributions to similarity by copepods and chaetognaths in all banks, from Amanay (32.9%) to Concepción (47.3%). The greatest differences between the banks were the higher contributions of decapod and fish larvae and salps at Amanay-El Banquete and by *Eudoxoides* sp. at Concepción.

4.3. Distribution of zooplankton biomass

Mean biomass (gWW/1000 m³) of near-bottom zooplankton collected over the Canary Island seamounts showed minimum values of biomass at intermediate depths. Hence, over Amanay-El Banquete (with summits at 23–24 m), mean biomass of total zooplankton and of main taxa (copepods, chaetognaths) followed the same depth-related trend (Fig. 5), with higher biomass of near-bottom zooplankton in the SF, i.e. close to the mount summit. Mean total biomass reached significant minima at levels occupied by NACW compared to SF biomass (one-way ANOVA (2,20) = 8.47; Tukey test $p = 0.001$). At depths of ca. 700–1600 m biomass significantly increased again, at AAIW-MW (Tukey test $p = 0.02$). Copepod and chaetognath biomass followed the same trend (copepods: 1-way ANOVA (2,20) = 8.23; Tukey test SF vs NACW $p = 0.001$; NACW vs AAIW-MW $p = 0.05$; chaetognaths: 1-way ANOVA (2,20) = 8.10; Tukey test SF vs NACW $p = 0.02$; NACW vs AAIW-MW $p = 0.0006$). Other taxa, particularly cnidarians – mainly siphonophores – showed a similar trend of minimum biomass at intermediate depths, though not significantly so.

Mean total biomass was higher over Amanay than over El Banquete (Fig. 5), e.g. biomass of (all) zooplankton reached a maximum of 15.2 gWW/1000 m³ at Amanay and only 7.3 gWW/1000 m³ at El Banquete. A similarly significant tendency (t -test 3.73, $p = 0.002$) was observed for copepods (6.7 gWW/1000 m³ at Amanay, 2.8 gWW/1000 m³ at El Banquete).

Although over Concepción (summit at 150 m) we found higher variability in depth-related distribution of near-bottom zooplankton biomass than over Amanay-El Banquete, some common trends were also observed (Fig. 6). In this sense, the highest biomass of total zooplankton (3.5 gWW/1000 m³), copepods (2.6 gWW/1000 m³) cnidarians (0.12 gWW/1000 m³) and chaetognaths (0.71 gWW/1000 m³) were collected by the shallowest haul (at 182 m at ENACW levels; Fig. 6). Also, significant minima of biomass were found at intermediate depths (ENACW levels between 559 and 663 m) for both total zooplankton biomass ($F_{(2,33)} = 46.6$; Tukey test $p = 0.01$ for shallower ENACW, $p = 0.0001$ for AAIW-MW hauls), and for main taxa biomass (copepods: $p = 0.05$ for shallower ENACW hauls; cnidarians: $p = 0.05$, $p = 0.01$ for shallower ENACW and AAIW-MW hauls), while chaetognaths and other taxa showed non-significant minimum biomass values at intermediate depths (Fig. 5). Finally, over Concepción we found downward sharp increases of total biomass (also for copepods and chaetognaths) at depths where ENACW and AAIW met (ca. at 700 m, Fig. 6).

4.4. Relationships of environmental variables with near-bottom zooplankton

The CCA was performed separately for Amanay-El Banquete (geographically close, with summits at 23–24 m) and Concepción (Fig. 7). Over Amanay-El Banquete 80.1% of constrained variance was

explained by the first 2 axes. Larvae of decapods, fish and euphausiids, mainly distributed in SF, were positively related with near-bottom fluorescence ($f_{5\text{mab}}$) and near-bottom O₂. Spearman's ρ was significant for these relationships (for decapod larvae vs $f_{5\text{mab}}$, $n = 23$, $\rho = 0.567$, $p < 0.01$; vs O₂, $n = 24$, $\rho = 0.651$, $p < 0.001$; for fish larvae vs $f_{5\text{mab}}$, $n = 23$, $\rho = 0.669$, $p < 0.001$; vs O₂, $n = 24$, $\rho = 0.529$, $p < 0.01$; for euphausiid larvae vs $f_{5\text{mab}}$, $n = 23$, $\rho = 0.533$, $p < 0.01$; vs O₂, $n = 24$, $\rho = 0.551$, $p < 0.01$). Some groups showed inverse trends, that is distributions in lower oxygen and lower $f_{5\text{mab}}$ levels: adult fish, euphausiids and chaetognaths (Fig. 7). Fish and euphausiids showed significant relationships with some of these variables (fish vs $f_{5\text{mab}}$, $n = 23$, $\rho = -0.414$, $p < 0.05$; euphausiids vs O₂, $n = 24$, $\rho = -0.360$, $p < 0.05$). Those groups were mainly associated with NACW (chaetognaths) and AAIW (fish). Euphausiids and adult decapods were more strongly associated with MW (upper right in Fig. 7), and scyphozoans were mainly distributed on the eastern side of the Amanay-El Banquete area. Over Concepción, the relationships identified were rather geographic, with scyphozoans, fish and decapod larvae more abundant over the north-eastern sector of the Bank. Scyphozoans and fish showed significant relationships with some of the geographic variables (scyphozoans vs LAT, $n = 36$, $\rho = 0.395$, $p < 0.05$; fish vs LONG, $n = 36$, $\rho = 0.420$, $p < 0.01$). Total biomass, however, did not show any clear geographic trend over Concepción (Fig. 8). Fish larvae were found at depths with higher T, higher $f_{5\text{mab}}$ and near-bottom O₂, mainly within the ENACW. Relationships with $f_{5\text{mab}}$ and near-bottom O₂ were significant (vs $f_{5\text{mab}}$, $n = 36$, $\rho = 0.393$, $p < 0.01$; vs O₂, $n = 36$, $\rho = 0.30$, $p < 0.05$). Explained variance was 79.8%. Adult decapods were more associated with colder waters, MW-AAIW, (upper left in the plot).

4.5. Generalized linear models (GLM) and Generalized Additive models (GAM).

Once conditions of independency among variables, variance homogeneity and normality were checked and accomplished for data residuals, the best GLM based on biological variables (fluorescence - $f_{5\text{mab}}$, O₂ 5mab and Chl a 1) explained 42.3% of variance for total zooplankton biomass (Table 3). In all cases (total zooplankton, main taxa) the main explanatory variables were $f_{5\text{mab}}$ and O₂ 5mab (both having a positive relationship with biomass) and Chl a 1 (negatively correlated with biomass).

At Amanay-El Banquete, explained variance for total zooplankton biomass was 77.8%. In the best model obtained (lowest AIC = 73.6), total zooplankton biomass was greater with increasing O₂ 5mab and greater when the peak of surface Chl a was recorded 4 months before sampling (Table 3). In other models (AIC 75.6) $f_{5\text{mab}}$, O₂ 5mab and Chl a-4 months also explained 77.8% of variance for total zooplankton biomass, with $f_{5\text{mab}}$ accumulating 46.6% of variance.

We found few significant relationships for Concepción Bank, and GLMs (for each taxon) hardly accumulated < 15% of variance. Calanoid copepods did show higher biomass in depths with high $f_{5\text{mab}}$ ($p < 0.01$).

A Generalized Additive model (GAM) based on the same biological variables ($f_{5\text{mab}}$, O₂ 5mab and Chl a-4 months) used to build the GLM for total zooplankton biomass (all Banks, Table 3) detected significant associations (Fig. 9) between biomass and O₂ 5mab ($p = 0.03$) and $f_{5\text{mab}}$ ($p = 0.02$). AIC was 183.9 and GVC = 0.515 (Generalized Cross Validation criteria for prediction error), with 54.1% of total variance explained (28.5% by O₂ 5mab and 25.6% by $f_{5\text{mab}}$, Table 3).

Temperature (T) was the more significant explanatory variable in GLMs based on T and S, accumulating (results for the 3 Banks) between 18% (euphausiid larvae) and 26.4% (fish larvae) of variance. Temperature was also positively correlated with zooplankton (total) biomass, and 25.2% of the variance of total biomass was explained by T, and it was the only explanatory variable for total biomass (41% of variance) in GLM models from Amanay-El Banquete.

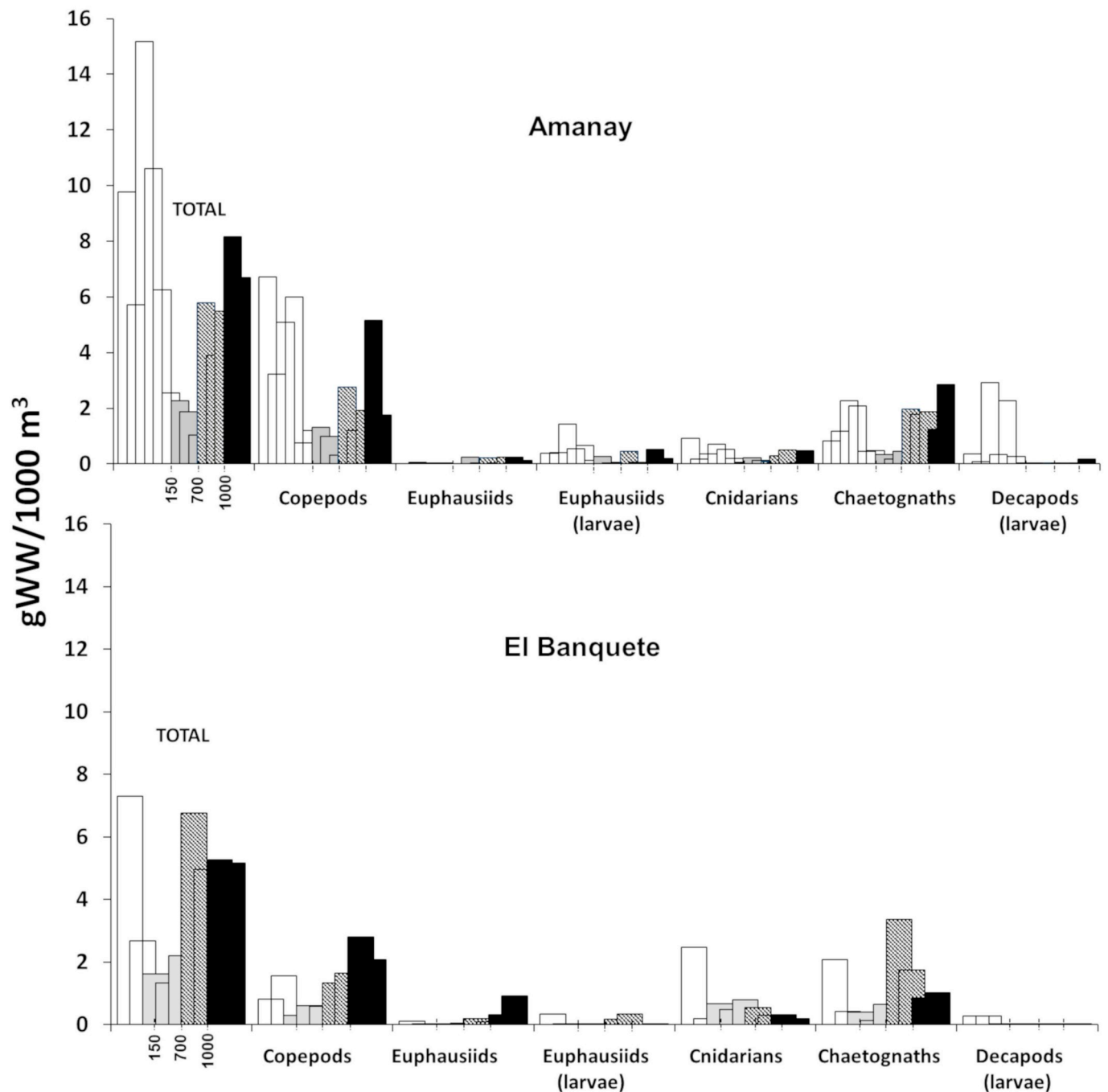


Fig. 5. Plots of biomass (gWW/1000 m³) of the most important groups of near-bottom zooplankton collected over Amanay and El Banquete seamounts (eastern Canary Islands). Bars were ordered by increasing depth, with corresponding water masses indicated. Scales on abscissae for each taxon represent the depths delimiting the different water masses: SF - Surface Water (□); NACW - North-Atlantic Central Water (▨); AAIW-MW - Atlantic-Antarctic Intermediate and Mediterranean Water (■).

5. Discussion

Zooplankton aggregations near the bottom over continental margins may have special significance, with groups like euphausiids, decapods and lanternfishes playing key roles as prey of benthopelagic fish (Mauchline and Gordon, 1991). Zooplankton/micronekton becomes the main food resource exploited by deep-water species around islands (hake: Cartes et al., 2008a; red shrimp: Cartes et al., 2008b) and also over submarine mounts (Preciado et al., 2009, 2016). Hence to know thoroughly the dynamics of marine food webs over seamounts requires sampling of near-bottom zooplankton over their slopes, as it has been

performed in previous studies over banks (Papiol et al., 2014), submarine canyons, and along continental margins (Cartes et al., 2008a,b; 2010, 2013). Sampling of zooplankton near seamount bottoms, i.e. in the Benthic Boundary Layer (BBL), has not been specifically performed in conventional midwater zooplankton studies over seamounts (Dower and Mackas, 1996), in which hauls were only occasionally taken close to the bottom (Martin and Nellen, 2004; Martin and Christiansen, 2009). It is, however, documented that zooplankton composition can be different at the BBL than in midwater (Mauchline and Gordon, 1991; Vereshchaka, 1995). In the northeast Atlantic, local increase of zooplankton biomass, basically gelatinous forms, was evident in the BBL of

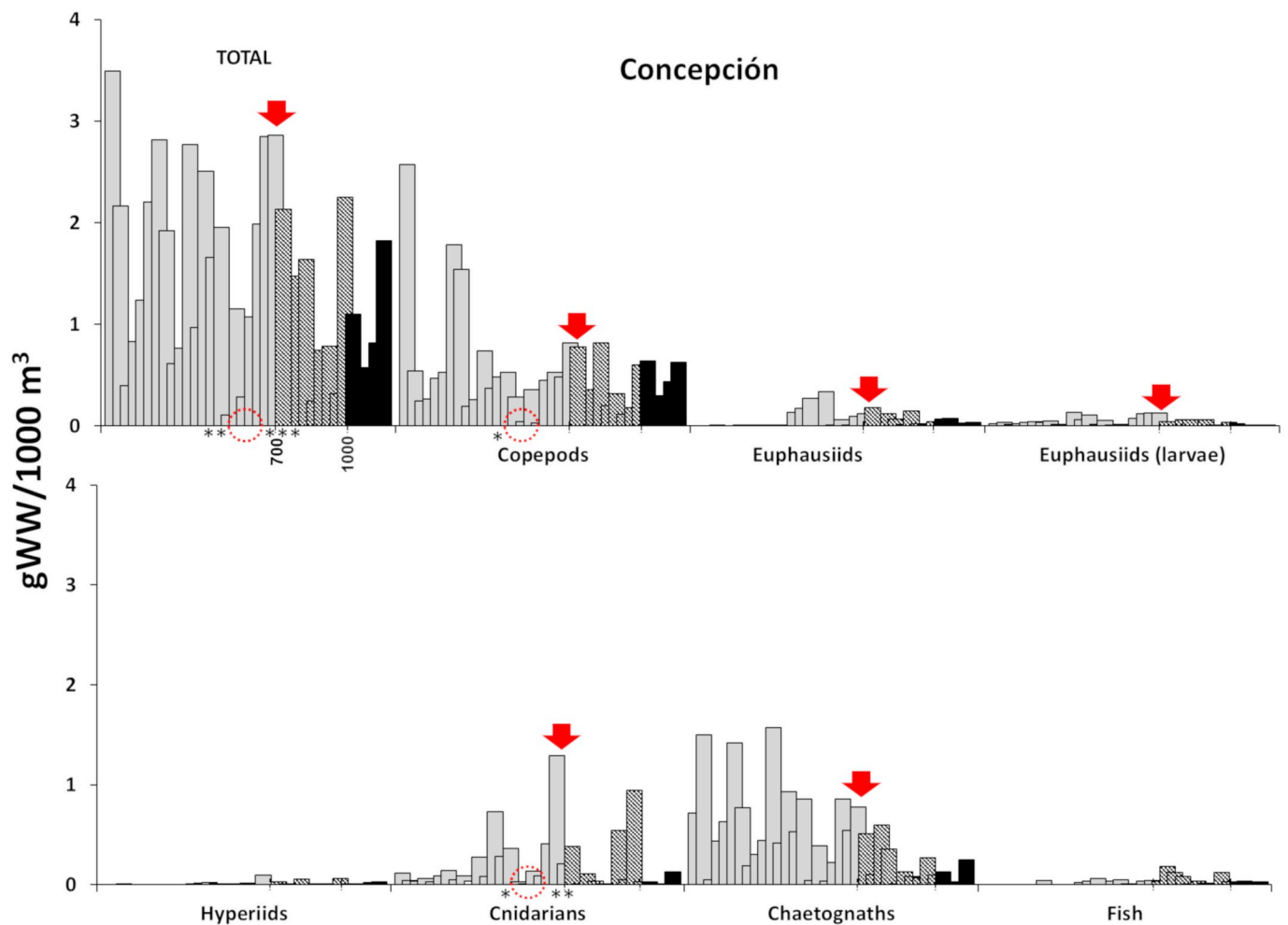


Fig. 6. Plots of biomass ($\text{gWW}/1000 \text{ m}^3$) of the most important groups of near-bottom zooplankton collected over Concepción seamount (eastern Canary Islands). Bars ordered by increasing depth indicating the corresponding water masses. For each taxon, scales on the abscissae represent the depths delimiting the different water masses: ENACW - Eastern North-Atlantic Central Water (□); AAIW-MW - Atlantic-Antarctic Intermediate and Mediterranean Water (▨, ▩). Circles indicate significant minima of biomass at intermediate depths (559–633 m), close to the deepest part of the ENACW level. Asterisks indicate the significance levels of biomass comparisons between the level 559–633 m and the shallowest (ENACW) hauls or deepest (mainly AAIW-MW) hauls: (*) $p < 0.05$; (**) $p < 0.01$; (***) $p < 0.001$. Arrows indicate the sharp increases of biomass for different taxa at the confluence of ENACW with AAIW.

the Seine/Ampère seamounts (Martin and Christiansen, 2009). In the Bay of Biscay over Le Danois Bank summit we found aggregations of *Cymbulia peroni* ($55.1 \text{ ind.}/1000 \text{ m}^3$) and other gelatinous zooplankton in a collapsed muddy depression at 503 m depth, whilst in the midwater column maximum densities were only $15.1 \text{ ind.}/1000 \text{ m}^3$ (authors, unpublished). Over the Middle Atlantic Ridge ($42^\circ 52' - 43^\circ 53' \text{N}$), as deep as 2335 m, siphonophores, doliolids and salps were a main component of this near-bottom zooplankton (Youngbluth et al., 2008). So, comparisons of the on-seamount and off-seamount zooplankton compositions can be biased due to this “bottom effect” (e.g. see Dower and Mackas, 1996, comparing 250 m-surface zooplankton over quite different depths).

5.1. Long-term and spatial changes in zooplankton communities

Because studies on zooplankton at species level are few around the Canary Islands, long-term comparisons are difficult. The most complete studies at species level were carried out in 1965 (the SOND cruise, SE Fuerteventura, see Foxton, 1970a, b; Baker, 1970, Badcock, 1970; Pugh, 1974; Thurston, 1976a, b), supplemented by a few recent studies on specific taxa by Wienerroither et al. (2009) and Vereshchaka et al. (2016). All these studies were performed in the water column (not near the bottom), with different samplers (including an IKMT for

micronekton in 1965) and in different seasonal periods, all of which may introduce important biases in zooplankton composition.

Despite all these considerations, we found generally similar compositions comparing our sampling and previous studies in the area among different taxa. Hence, practically all crustaceans (decapod shrimps, euphausiids and amphipods) collected had already been documented in the area (Foxton, 1970a, b; Baker, 1970, Thurston, 1976b). This seems applicable also to other taxa. Among siphonophores, *Eudoxiodes* spp., characteristic of warm waters south of 40°N (Pugh, 1974), was a dominant taxon both ca. 50 yrs ago and in our sampling.

Among fish, gonostomatids (with only a few myctophids) were dominant in our sampling at the BBL, rather than the dominance of myctophids reported from the mesopelagic domain (Wienerroither et al., 2009). Dominance by non-migratory gonostomatids does characterize the BBL in neighbouring regions, e.g., the deep Mediterranean (Fanelli et al., 2013). The same *Cyclothone* spp. found by Badcock (1970) and Wienerroither et al. (2009) were collected in our study, with the same dominance ranking, i.e. (by decreasing abundance) *Cyclothone braueri*, *C. pseudopallida* and *C. livida*. We found in addition *C. microdon* linked to AAIW-MW close to and deeper than 1000 m, the maximum depth sampled by Badcock (1970). Among euphausiids *Euphausia hemigibba* was the most abundant species ca. 50 yrs ago and currently,

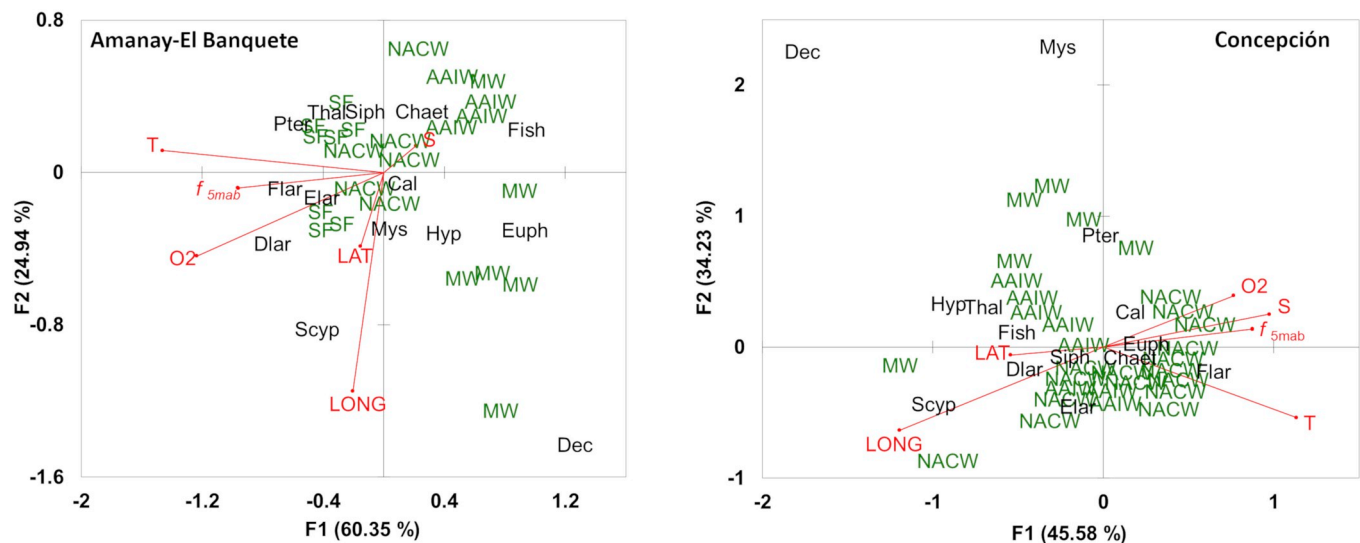


Fig. 7. Canonical Correspondence Analysis (CCA) for the composition of main broad taxa of near-bottom zooplankton over Concepción and Amanay-El Banquete seamounts (eastern Canary Islands). Water masses as in Fig. 3. Taxa: Cal (calanoid copepods); Dlar (decapod larvae); Dec (decapods); Elar (euphausiid larvae); Euph (euphausiids); Mys (mysids); Hyp (hyperiid amphipods); Siph (siphonophores); Scyp (scyphozoans); Thal (thaliacans); Chaet (chaetognaths); Pter (pteropods); Flar (fish larvae). Environmental (near-bottom) variables: T (temperature); O₂ (dissolved oxygen); S (salinity); f (fluorescence). Haul latitude (LAT) and longitude (LONG) are also included.

while other *Euphausia* identified by Baker (1970) as abundant in mid-water were scarcely collected (*E. gibboides* in a single haul at 587 m) or absent from our samples (e.g. *E. brevis*). *Euphausia krohni*, by contrast, was more abundant in our BBL sampling, as happens in near-bottom zooplankton of other areas (Cartes et al., 2010). *Nematoscelis microps/atlantica* was abundant in Baker (1970) study, while in our sampling *N. megalops* was more abundant, probably because it has more strictly benthopelagic habits (Casanova, 1974; Cartes, 2011; Cartes et al., 2010, 2013; 2014). Among hyperiids, low contributions of *Primno macropa* and *Hyperoides longipes* in our sampling could also be a consequence of the different habitat sampled. Most specimens of these species were collected near the surface (to 85–100 m) by Thurston (1976b), a level not sampled in our study. In conclusion, the near-bottom community of micronekton (fish, crustaceans) dwelling in the BBL of the Canary Islands seamounts seems to have a distinctive species composition and, in general, lower species richness than does the water column.

Among hyperiids, we found *Primno brevidens* and *Primno latreillei* as relatively abundant species linked to warmer waters than the typical habitat of *P. macropa*. Both species have been cited in the Gulf of Guinea, 3300 km to the south of the Canary Islands (Bowman, 1978). In our sampling they were more abundant in AAIW, which has a northward flux into the Canary Islands, but they were also present in the warmer MW (Knoll et al., 2002) during our sampling in June–July 2011. It is possible that advection of these deeper water masses along their slopes enhances the occurrence of such species adjacent to the Canary Islands banks. A hypothetical northward colonization by these species could be enhanced by long-term northward transport of AAIW, reported in the Canary Islands over the last two decades (Fraile-Nuez et al., 2010). The arrival of such species, rather secondary in the present assemblages, would be the only result that could be attributed to long-term changes. In general, however, the most abundant species changed very little, which fits with the lack of a strong warming trend in deep waters around the Canary Islands, a warming (of +0.25 °C decade⁻¹) restricted to waters shallower than ca. 200–600 m, the range of the permanent thermocline (Velez-Belchi et al., 2015). This slight warming has also been suggested to affect the nearby Canary Current upwelling ecosystem by decreasing productivity without an obvious effect on fisheries for small pelagic species (Aristegui et al., 2009). More detailed faunistic studies would help to identify possible indicator species for long-term changes.

5.2. Zooplankton biomass distribution and possible causes

Zooplankton biomass in the BBL adjacent to the Canary Island seamounts was sampled in summer: June. Total biomass of near-bottom zooplankton at El Banquete (7.3 gWW/1000 m³ on average) and Amanay (between 9.7 and 15.2 gWW/1000 m³) summits was similar to the biomass over the nearest seamount from which comparable data are available. That is Ampère Seamount, ca. 500 km north of the Canary banks north of Madeira (Martin and Christiansen, 2009), with its summit at 55 m. All these seamount summits are located within the epipelagic layer (cf. Porteiro and Sutton, 2007). Summit depth of Concepción (150 m) was more comparable to that of Seine seamount (summit at 170 m), and total biomass of near-bottom zooplankton was even lower (3.5 gWW/1000 m³ at 182 m) than near Seine's summit (9 mg/m³, Martin and Christiansen, 2009). Over Seine the increase of zooplankton near the bottom over the summit was moderate, while other authors have found higher concentrations of zooplankton near the bottom, over even deeper seamounts (e.g. Great Meteor, 35°N, 28°30'W, with its summit at 270 m, Martin and Nellen, 2004), to as deep as at 2335 m (Youngbluth et al., 2008). Over the eastern Canary Island seamounts, the biomass of gelatinous zooplankton (cnidarians) indicated by our samples was < 50% of that cited by Martin and Christiansen (2009) from Seine/Ampère. This could be due to seasonality, because sampling over Seine/Ampère was performed in spring, a period of higher abundance of gelatinous zooplankton.

In the eastern Canary Islands, with some exceptions (e.g., zooplankton associated with both AAIW and MW), near-bottom zooplankton composition changed as a function of which of the different water mass was impinging on the seamounts investigated. Such changes depending on water masses have been reported in previous studies comparing water-column zooplankton adjacent to northeast Atlantic seamounts (Denda and Christiansen, 2013), and affect benthopelagic communities of crustaceans, as also observed at Galicia Bank (Cartes et al., 2014), with particular fauna associated with water masses of quite different origins (e.g., Mediterranean vs. Labrador). Changes in zooplankton composition were also evident between nearby banks, with strong dissimilarities between Amanay and El Banquete (52.2%) in our area.

Regarding biomass changes, depth of the summit (the water mass overlapping bank summits) seems the most determining feature

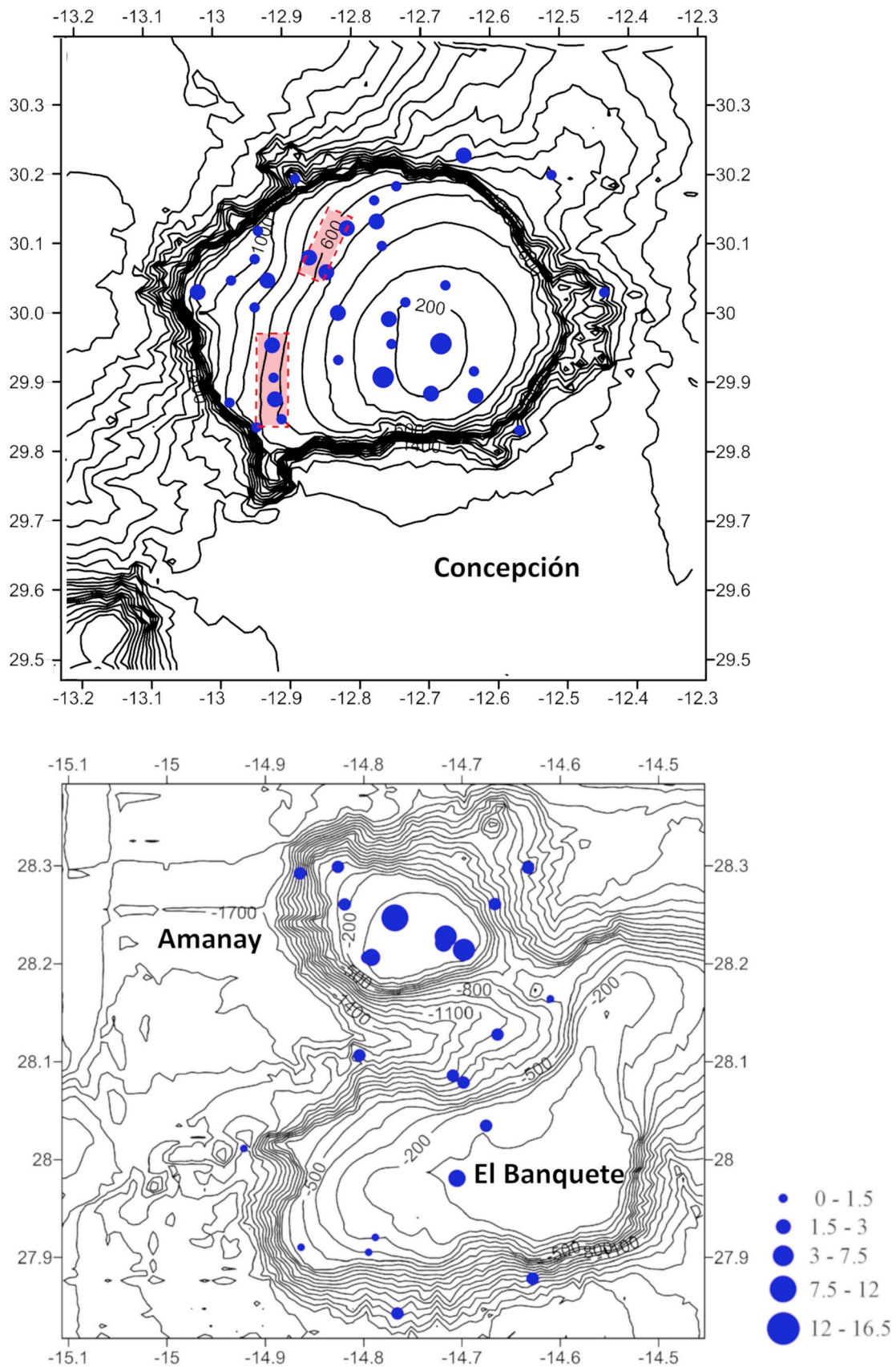


Fig. 8. Total biomass of zooplankton (gWW/1000 m³) near the bottom over Concepción Amanay and El Banquete seamounts (eastern Canary Islands). The shaded areas over the 600–700 m isobaths west of Concepción indicate the area of possible internal wave influence. Isobaths in meters, X and Y axes are decimal latitudes/longitudes.

Table 3

GLMs performed on the biomass of near-bottom zooplankton distributed over Concepción and Amanay-El Banquete seamounts (eastern Canary Islands) both for total zooplankton and for some dominant taxa. Explanatory biological variables included in the models were dissolved oxygen (O_2 5mab), fluorescence (f 5mab) and satellite Chl a taken in the month of sampling and taken 4 months before the sampling date. t is the estimate; p = level of significance. A.I.C. is Akaike information criterion. The best GAM for total biomass (All Banks) also included (see also Fig. 9).

GLM (Gamma distribution)	Dependent variable	Total Explained variance (r^2)	Explanatory variables	Estimate	t	Explained variance (%)	p	A.I.C.
The 3 Banks	Total Biomass	42.3	f	3.23	0.83	20.2	$2.2 \cdot 10^{-5}$	191.5
			O_2	0.75	2.87	11.1	0.001	
			Chla 1	-12.54	-3.71	11.0	0.001	
	Calanoidea	48.0	f	5.99	1.30	24.7	$1.1 \cdot 10^{-5}$	77.6
			O_2	0.82	2.66	10.3	0.002	
			Chla 1	-15.14	-3.77	12.9	$9.1 \cdot 10^{-4}$	
	Euphausiid larvae	39.5	f	2.03	0.32	16.7	$3.7 \cdot 10^{-5}$	185.4
			O_2	1.11	2.64	7.7	0.003	
			Chla 1	-32.11	-4.29	10.9	$6.3 \cdot 10^{-4}$	
			Chla 4	9.92	2.12	4.2	0.03	
Amanay-El Banquete	Total Biomass	77.8	O_2	0.78	5.67	62.9	$1.8 \cdot 10^{-5}$	73.6
			Chla 4	9.03	3.75	14.9	0.001	
			Chla 3	-8.12	-3.6	10.8	0.005	
	Calanoidea	78.5	O_2	0.77	4.66	55.6	$1.1 \cdot 10^{-6}$	38.5
			Chla 3	-8.12	-3.6	10.8	0.005	
			Chla 4	9.46	3.3	12.1	0.003	
GAM		variance (r^2)	variables			variance (%)		
The 3 Banks	Total Biomass	54.1	O_2			28.5	0.03	183.9
			f			25.6	0.02	

distinguishing near-bottom zooplankton dynamics of the three banks studied in the Canary Archipelago. Shallower depths at Amanay-El Banquete (24–23 m) were linked to greater biomass of zooplankton, especially the larvae of euphausiids, decapods and fish at SF levels. This was partially correlated with both near-bottom fluorescence (f) taken simultaneous with sampling and with surface Chl a taken 4 months before sampling (i.e., in late winter). The peak of f in the water column near Amanay-El Banquete ($f = 0.7$ – 1.4) was located deeper (ca. 55–90 m) than the summits of these banks. By contrast, near-bottom peaks of f were at 43 m ($f = 0.19$) at Amanay and 71 m ($f = 0.05$) at El Banquete (at ca. 20–50 m of banks summits) located clearly above the subsurface chlorophyll (fluorescence) maximum (SCM) found at 80 (Amanay) and 110 m (El Banquete, Fig. 2). Although the larval increase over these banks could be a consequence of surface increase of phytoplankton biomass, another possible cause is the advection of waters with high fluorescence, in the form of algae from the SCM (in the water column) ascending up bank walls close to the summits.

Advected particles have been considered as a more likely source of production than near-surface production over shallow seamounts (Cobb Seamount, Dower and Mackas, 1996). On Ampère and Senghor seamounts, horizontal current-driven advection of planktonic prey was the most important factor sustaining the benthopelagic fish food web (Denda et al., 2017). Such advection of fluorescence could be a consequence of topographically induced upwelling (Boehlert and Genin, 1987) or resuspension that entrains nutrients into the photic zone in

oligotrophic areas like Canary waters (Davenport et al., 2002). This same trend in fluorescence (f) was not found near the bottom at Concepción, with highest near-bottom $f = 0.06$ – 0.07 (at 194 and 274 m), well below the SCM (ca. at 50 m). Over Concepción, Taylor caps develop as hydrographic structures that can generate upwelling. Such structures are more sporadic and weaker over Amanay-El Banquete (Martín-Sosa, 2013a, b). Also, coastal upwelling filaments from Cape Yubi on the Moroccan coast can reach the E of eastern Canary Islands, enhancing an SCM at depths of ca. 60–80 m (Neuer et al., 2002). So, a number of hydrographic structures that have not been evaluated in this study (deep-reaching eddies, internal waves, upwelling filaments, etc.) can act as mixing agents enhancing particle resuspension and availability. Rivera et al. (2016) recently suggested that particle resuspension can be induced locally by internal waves generated at depths of the NACW-AAIW confluence. This is fully consistent with the local increase of zooplankton: total biomass and copepod, cnidarian, or chaetognath biomass in our results at the NACW-AAIW confluence near 700 m (Fig. 6). Also, internal waves are mainly generated to the SW of the bank (Rivera et al., 2016), due to optimal inclination of the seamount flanks. This area coincided with the location of NACW-AAIW hauls at Concepción Bank (Figs. 6 and 8). This increase of near-bottom zooplankton biomass could favour the development of coral reefs on Concepción's SW slope due to greater food availability.

Neuer et al. (2002) also found an increase of particle flux on the east side of Lanzarote at 700 m in summer, influenced by the NW African

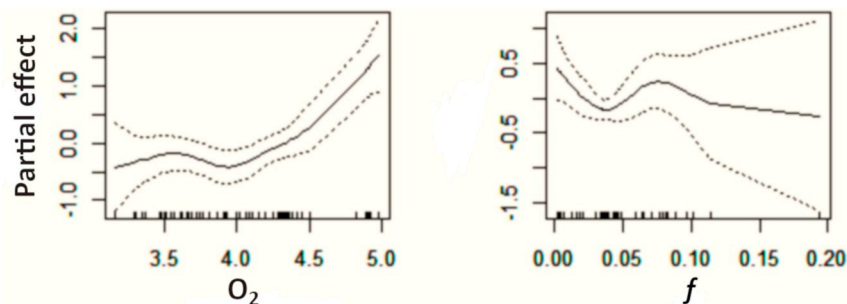


Fig. 9. GAM results: smoothed fit of covariates (O_2 and fluorescence- f) modelling total zooplankton biomass (total) for data from the 3 Banks (All Banks) studied in the eastern Canary Islands. Tick marks on the abscissa are the observed data points.

upwelling system. Unfortunately, and due to technical limitations of the near-bottom sampling (very steep walls on the E-SE side of Concepción), it was not possible to perform any hauls in this sector and depth range to check for a possible local increase of near-bottom zooplankton. In addition, plumes and filaments can arrive in summer linked to trade winds, with increasing upwelling in July–August (Aristegui et al., 1997), though with high local variability. However, it does not seem, in view of the rather moderate values of Chl *a* found, that plumes related to coastal, northwest African upwelling (Barton et al., 2004; Brochier et al., 2008) are the main factor related to Amanay-El Banquete eco-dynamics in the sampling period. Zooplankton biomass decreased close to Canary waters (St 26°14'N, St 31°12'N in Vereshchaka et al., 2016), as expected in an oligotrophic (Davenport et al., 2002), subtropical region like the Canary Islands (Clark et al., 2001). As expected, also, carnivorous taxa (e.g. chaetognaths, cnidarians) were among the most abundant groups in the BBL zooplankton of the eastern Canary Islands. Exceptions would be crustacean larvae, of lower trophic levels, relatively abundant at Amanay-El Banquete.

The highest near-bottom zooplankton biomass was over the summits of the three banks studied. Over seamounts within the depth range of strong vertical migrations (a few hundred meters, in general, Angel, 1985), this biomass accumulation must be a consequence of the bottom trapping of zooplankton migrating downward by day (Genin and Dower, 2007).

As deduced from the GLM-GAM results for all three banks, increased dissolved oxygen (O_2) in the near-bottom water column was, together with near-bottom fluorescence, the main variable having a positive correlation with near-bottom zooplankton biomass in our sampling. Accordingly, lower O_2 coincided with minimum zooplankton biomass, especially at Amanay-El Banquete (Fig. 5). The O_2 concentration decreased at depths occupied by NACW (especially over Amanay-El Banquete) and AAIW, the latter with the minimum O_2 levels in the area (Schmitz, 1996; Fraile-Nuez et al., 2010; Bashmachnikov et al., 2015). AAIW does, however, undergo seasonal changes in the area, and its main mass transport into Canary waters occurs later than June, the time of our sampling (Fraile-Nuez et al., 2010). By contrast, NACW mass transport increases in our sampling period (Fraile-Nuez et al., 2010). Whatever the cause, low near-bottom O_2 coincided with low zooplankton biomass, especially among copepods and euphausiids. These minima of zooplankton biomass and oxygen were not totally in parallel, and at depths where NACW and AAIW converged, we found more biomass of a number of taxa: chaetognaths, fish, cnidarians and copepods. So, the (daytime) minimum of biomass was in general situated immediately above the depth of minimum O_2 concentration, and the increase of zooplankton biomass at the “NACW-AAIW boundary” was primarily carnivorous zooplankton (e.g., chaetognaths), situated at middle and higher trophic levels (Fanelli et al., 2013) and likely with lower metabolic rates than the larvae found in SF. A similar tendency for O_2 concentration to decrease at intermediate depths was also found in the water column (not at the BBL) over Senghor Seamount north of Cape Verde by Denda and Christiansen (2013). It is also possible (as discussed above) that aggregation of particles at water mass (NACW-AAIW) confluences (as discussed by McManus and Woodson, 2012; Rivera et al., 2016) and micro-upwelling phenomena enhance zooplankton biomass.

Biomass increased in general at MW levels below ca. 1000 m, where O_2 also increased downward from its vertical minimum. Relationships between zooplankton biomass in the BBL and O_2 are evident in other areas along continental margins. In the deep Balearic Basin (Cartes et al., 2013) zooplankton biomass increased at ca. 1000–1200 m, coinciding with an increase of near-bottom O_2 below the Levantine Intermediate Water (LIW). There was a parallel increase of turbidity (suspended particles) at that interface of Mediterranean water masses. At Galicia Bank, minimum biomass of near-bottom zooplankton was found at levels of MOW (MW) influence (Papiol et al., 2014), where O_2 decreased. In general, there seems to be a direct relationship between

near-bottom zooplankton and near-bottom O_2 .

The advective collision of water masses with seamount slopes is one of the mechanisms proposed to explain zooplankton aggregations adjacent to seamounts (Genin and Dower, 2007). We hypothesize, in light of the results reported here, that the attraction of organisms to stationary physical substrates could be related (over Canary banks, especially those with summits in the epipelagic layer) with increases of near-bottom fluorescence and of near-bottom O_2 that enhance zooplankton aggregations. Other processes like internal breaking waves could also explain local increases of zooplankton biomass, as seems to occur over Concepción, likely due to an increase of resuspended particles. Since near-bottom zooplankton supports the diet of diverse bottom living organisms in open sea areas, knowledge of the distributions of zooplankton biomass near the bottom, together with their possible causes could help explain the occurrence and distribution of diverse ecosystems, such as deep - cold - coral reefs and associated fauna over seamounts.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.dsr.2019.04.003>.

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