



Deep-sea soft-bottom macroinfaunal communities from SE Pacific: Composition, abundance, distribution, and their relationship with environmental forcing

Eulogio H. Soto^{a,*}, Carlos Sanchis^a, Eduardo J. Quiroga^b

^a Centro de Observación y Análisis del Océano Costero (COSTAR). Facultad de Ciencias del Mar y de Recursos Naturales, Universidad de Valparaíso, Viña Del Mar, Chile

^b Escuela de Ciencias Del Mar, Pontificia Universidad Católica de Valparaíso, Chile

ARTICLE INFO

Keywords:

Macrobenthos
Seamounts
Organic content
Copepoda
Polychaeta
Abyssal
Hadal

ABSTRACT

Abyssal and hadal macroinfaunal communities (>300 µm) were studied across a longitudinal geographic transect in the Southeast Pacific region (71°–109°W). Composition, structure, and distribution were analyzed in relation to the seafloor organic content associated with surface productivity. Sediment samples were collected at each study site with a multicore containing eight cores of 7.5 cm internal diameter, covering associated seamounts, oceanic islands, and trench environments. Faunal composition was dominated by Crustacea, Mollusca, and Annelida, with Crustacea as the most diverse. Polychaeta and Copepoda were always the most common and abundant in all sites recording a relative abundance of 38% and 33%, respectively. Vertical distribution showed that 73% of fauna inhabit the first centimeter of sediment. The number of individuals was low and mean density per site was 710 ind. m⁻², however the high number of species recorded only once would indicate a high diversity of species in the study zone. Ecological indices showed higher values in eutrophic and mesotrophic areas coinciding with the record of the highest concentrations of parameters related to sediment organic content. Differences between habitats were observed, recording higher abundance and diversity on Trench and Seamount sites from eutrophic and mesotrophic zones, while lower values of these descriptors on Seamount and Oceanic Island sites associated with less productive zones. Statistical analysis and correlations showed that Chloroplast Pigment Equivalent and Chlorophyll-*a* may explain the observed patterns for the benthic community. The macroinfaunal communities described are typical of abyssal and hadal sediment environments and they appear to respond to organic inputs according to recorded spatial distribution patterns.

1. Introduction

The deep sea is considered one of the most extensive and remote ecosystems in the planet hosting 85% of the Earth surface (Harris et al., 2014). A large part of the seafloor is composed of soft sediments, however the study of this ecosystem has been a demanding challenge and historically it was thought to be azoic (Anderson and Rice, 2006). Currently, this assumption has changed by many subsequent investigations recording higher levels of benthic species richness than in the past at small spatial scales (Heip et al., 1985; Grassle and Maciolek, 1992) and highlighting the importance of deep-sea sediment ecosystems. Deep sea sediment ecosystems host a wide variety of organisms and habitats, and they are key in the provision of important services and goods (Thurber et al., 2013). The study of deep macrobenthic

communities remains a pending topic due to limited knowledge about the deep ocean. However, Rex et al. (2006) described a global pattern where abundance and biomass decrease with depth. Additionally, these communities are generally dominated by typical taxa such as polychaetes, crustaceans, bivalves, nematodes, and sipunculans (Brandt et al., 2019; Nomaki et al., 2021a,b).

According to Smith et al. (2008) the main energy source in the deep sea comes from the surface by means of vertical fluxes of particulate organic carbon (POC). POC fluxes decrease with depth, and at three thousand meters depth just 1% of total surface primary production is estimated to reach the seabed (Poulton et al., 2006). Lampitt (1985) and Billett et al. (2010) have also observed that seasonal pulses determine large concentrations of phytodetritus reaching the abyssal seafloor. These food inputs may determine different responses on deep-sea

* Corresponding author.

E-mail address: eulogio.soto@uv.cl (E.H. Soto).

<https://doi.org/10.1016/j.marenvres.2026.108190>

Received 4 December 2025; Received in revised form 7 June 2026; Accepted 8 June 2026

Available online 9 June 2026

0141-1136/© 2026 Elsevier Ltd. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

benthic biota, observing important shifts in composition, standing stock and function (Billett et al., 2010; Nomaki et al., 2021b; Gaurisas et al., 2025). This confirms that surface energy supply dynamics are key for deep benthic communities (Smith et al., 2008; Fernández-Urruzola et al., 2021).

Surface productivity and POC fluxes have been linked to the distribution of macrobenthic communities in the deep sea (Glover et al., 2002; Smith et al., 2008; Wei et al., 2010; Nomaki et al., 2021a,b). Several authors have found that an increase in these factors would explain increases in density, biomass, and composition of the macroinfauna (Levin et al., 2001; Smith et al., 2008; Wei and Rowe, 2019; Washburn et al., 2021). These findings are particularly important in the Southeast Pacific where an extreme productivity gradient has been recorded (0.017 mg m^{-3} to 10 mg m^{-3} chlorophyll-*a*) between the continent and the basin center (Von Dassow and Collado-Fabriz, 2014; Espinosa-Leal et al., 2021) associated with the presence of several seamounts. However, it has also been seen that productivity regimes in other seamount areas do not always lead to high abundances on macrobenthic communities (Bongiorni et al., 2013). For example, studies carried out on Condor seamount (NE Atlantic) showed macrofaunal diversity does not always reflect that seamounts slope and rise are more biodiverse than the surrounding seafloor areas (Rowden et al., 2010). The macrofauna community on the Condor summit recorded high abundance and dominance but low biodiversity, while low dominance and high biodiversity at the flank (Bongiorni et al., 2013).

Seamounts are marine elevations higher than one hundred meters that do not reach the ocean surface (Staudigel and Clague, 2010; Yesson et al., 2011). Studies estimate the total number of seamounts in the oceans to be between 35,000 and 150,000, and half of these would be in the Pacific Ocean (Kim and Wessel, 2011; Yesson et al., 2011).

Seamounts exhibit a complex oceanography; the interactions between currents and bathymetry cause several processes that determine the increase of local productivity, explaining in some cases the aggregations of pelagic and benthic species (Morato et al., 2010; Rogers, 2018), a phenomenon known as “the seamount effect” (Djurhuus et al., 2017; Frederick et al., 2018).

Several investigations consider seamounts as “hotspots” of productivity, diversity, and endemism (Koslow et al., 2001; Clark et al., 2010). Due to their varied topography (summit, terrace, flanks, and base) combined with soft and hard substrates, habitat heterogeneity allows the development of highly diverse benthic communities (Henry et al., 2014; De la Torre et al., 2019; 2020). However, there is still limited knowledge about their biology and ecology because only about 4% of all seamounts have been scientifically surveyed (Kvile et al., 2014). This lack of information questions the main paradigms (e.g., endemism, productivity) related to seamounts (Rowden et al., 2010).

This lack of knowledge is even more clear in the Southeast Pacific (SEP), where the few studies on benthic communities have focused on bathyal epifauna (Parin and Mironov, 1997; Mecho et al., 2021; Tapia et al., 2021). In the SEP there are two main seamount chains: Nazca and Salas y Gómez. These two chains are composed of over 110 seamounts formed from the Easter “hotspot” and measure approximately 2900 km. These seamount chains stand out for presenting high productivity and biological diversity (pelagic and benthic) as well as prominent levels of endemism (Parin and Mironov, 1997; Mironov et al., 2006; Gálvez-Larach, 2009; Friedlander et al., 2021; Wagner et al., 2021). Nevertheless, the exploration of these seamounts is limited and just 3% has been scientifically studied (Wagner et al., 2021); therefore, the SEP is still one of the least explored areas in the world.

The Salas y Gómez and Nazca seamount chains were declared as Ecologically and Biologically Significant Areas (EBSA) in 2014 (CBD, 2014). This confirms that these ecosystems are key zones for functioning of the global ocean. Several initiatives from the Chilean government have promoted the conservation of these seamounts and their waters, establishing the Motu Motiro Hiva (in 2010) and Nazca-Desventuradas (in 2016) Marine Parks in the areas of Salas y

Gómez and Nazca, respectively. The need for biological knowledge of benthic communities on these seamount chains is urgent considering that many of these seamounts are in international waters where important anthropogenic pressures and activities take place.

At present in this area, except for only one study on meiobenthic communities (Horacek et al., 2022), there is no biological-ecological information on the seamount bases or adjacent abyssal plains. Because most research efforts have focused on the study of mesophotic communities at less than five hundred meters depth (Mecho et al., 2021; Tapia-Guerra et al., 2021), studies below one thousand meters are very scarce (Parin and Mironov, 1997; Friedlander et al., 2021). This research seeks to cover this essential information gap for deep-sea macroinfaunal benthic communities.

The current study aimed to describe the soft-bottom macroinfaunal communities inhabiting abyssal and hadal environments, (abyssal sites on this study are associated to seamount and oceanic island bases), and characterize their response to distinct sediment parameters related to organic content. Because there is a close relationship between deep benthos and surface productivity (benthic-pelagic coupling), we hypothesized the longitudinal productivity gradient in the SE Pacific Ocean influencing deep-sea macroinfaunal communities, while the effect of local seamount productivity on benthos is less. Therefore, changes in macroinfaunal composition and a decrease in the abundance and taxa richness should be expected as we approach more oligotrophic conditions in the center of the South Pacific Subtropical Gyre (SPSG).

2. Methods

2.1. Study area

Between January 27th and March 2nd, 2019, the oceanographic cruise MR18-06 Leg 3 “East/Central Pacific International Campaign” (EPIC-II) was conducted onboard the vessel R/V *Mirai* of the Japan Agency for Marine-Earth Science and Technology (JAMSTEC). Seven sampling stations were established along a longitudinal transect (East to West), including one sampling station in the hadal environment at the Atacama Trench (SPG1), located approximately 160 km off the Chilean coast. Six abyssal sites were located at seamount bases (SPG2 to SPG7) between 4114 and 2999 m depth and the last abyssal site, around Rapa Nui Island, was located at 2895 m depth. Two stations (SPG2-SPG3) were isolated seamounts between the Salas y Gómez Ridge and the Atacama Trench. SPG4 and SPG5 were located at the intersection of the Salas-y-Gómez Ridge (SYG) and the Nazca Ridge (NR), and the last seamount (SPG6) was in the middle of SYG. Finally, the westernmost station was located near the base of Rapa Nui Island, one of the two points that rise above sea level from these chains, located 3700 km off the coast in the center of the SPSG (Newman and Foster, 1983). It should be noted that all stations except SPG2 and SPG5 are within Chile's Exclusive Economic Zone (Table 1, Fig. 1).

2.2. Oceanographic background

The SE Pacific Ocean has a clear productivity gradient between the coastal waters, influenced by the Humboldt Current, and the center of the basin, which is influenced by the SPSG, one of the least productive areas on the planet (Morel et al., 2010; Von Dassow and Collado-Fabriz, 2014). Thus, four zones have been identified on this gradient concerning chlorophyll concentration: eutrophic coastal waters (chlorophyll $>0.5 \text{ mg}^{-3}$), mesotrophic coastal transition zone ($0.5 - 0.1 \text{ mg}^{-3}$), oligotrophic oceanic waters ($0.1-0.05 \text{ mg}^{-3}$), and ultra-oligotrophic conditions ($<0.05 \text{ mg}^{-3}$) in the center of the SPSG (González et al., 2019; Espinosa-Leal et al., 2021).

In surface waters, an increase in temperature and surface salinity has also been recorded (Fuenzalida et al., 2007), along with a decrease in the availability of nutrients and Colored Dissolved Organic Matter (CDOM) from east to west (Morel et al., 2010). At depth, the conditions are

Table 1

Geographic position and information for the sampled stations. Categorization of surface productivity is according to [González et al. \(2019\)](#).

Site	Location	Productivity	Latitude (S)	Longitude (O)	Depth (m)
SPG 1	Atacama Trench	Eutrophic	25°38.47	71°32.85	7742
SPG 2	Off San Ambrosio	Mesotrophic	26°04.84	75°57.33	3982
SPG 3	Off San Ambrosio	Mesotrophic	26°31.63	79°38.36	3447
SPG 4	SE of Stockman guyot	Mesotrophic	25°25.51	81°38.87	2999
SPG 5	Pearl Seamount	Oligotrophic	25°41.87	88°55.25	4114
SPG 6	Seamount N° 30	Ultraoligotrophic	26°04.58	102°49.85	3214
SPG 7	Off Easter Island	Ultraoligotrophic	26°57.41	109°08.23	2895

relatively homogeneous, dominated by Pacific Deep Water (PDW), which has low oxygen concentration and high nutrients ([Peters et al., 2018](#)).

2.3. Sampling design and sediment processing

The selection of each sampling station prioritized the presence of flat bottoms with soft sediments on each study area. The search for these conditions was performed by a multibeam and sub-bottom profiler from the R/V *Mirai*. The surface sediment was obtained using a multicorer

(JAMSTEC). The instrument consisted of the body (600 kg) and eight acrylic cores, each measuring 60 cm in length and 7.5 cm in diameter (Material supplementary 6a, b). Of the eight available cores, five were chosen for macrofauna analysis and one for the analysis of biogeochemical variables of the sediment. The remaining two cores were used for meiofauna analysis (see [Horacek et al., 2022](#)). Box-core devices (0.25 m²) are commonly used for abyssal macroinfaunal communities, however for this study a multicore was used since box-core was not available on the ship.

Sediment redox potential (EhNHE) was measured for the 0–2 cm surface sediment layer using a platinum standard combination electrode with a calomel internal reference (SG™, Mettler Toledo). The pH of the 0–2 cm surface sediment and water was measured using a LE 438 IP67 Sensor (Five Go™, Mettler Toledo). Both measurements were done onboard directly on the one intact core before slicing and at once after samples were collected. Due to equipment malfunctioning, the pH could not be recorded for the sediment from stations SPG4, SPG5, SPG6 and SPG7.

For macroinfauna analysis, most cores were separated into layers up to 20 cm (0–1, 1–3, 3–5, 5–10, 10–15, and 15–20), preserved in 26% formalin for 24 h, then emptied and filled with 80% alcohol. However, the results presented on this study correspond to first three layers (0–1, 1–3 and 3–5 cms), since no macroinfauna was recorded below 5 cm. For the first three layers macroinfauna was manually sorted in the Benthology laboratory of the University of Valparaíso using a stereoscopic microscope (Nikon SZX7). Starting from the fourth layer (5–10 cms) samples were sieved using a 300 µm mesh sieve. Identification was conducted to the highest taxonomic level possible (family, genus or species/morphotypes, depending on the case) based on the condition of

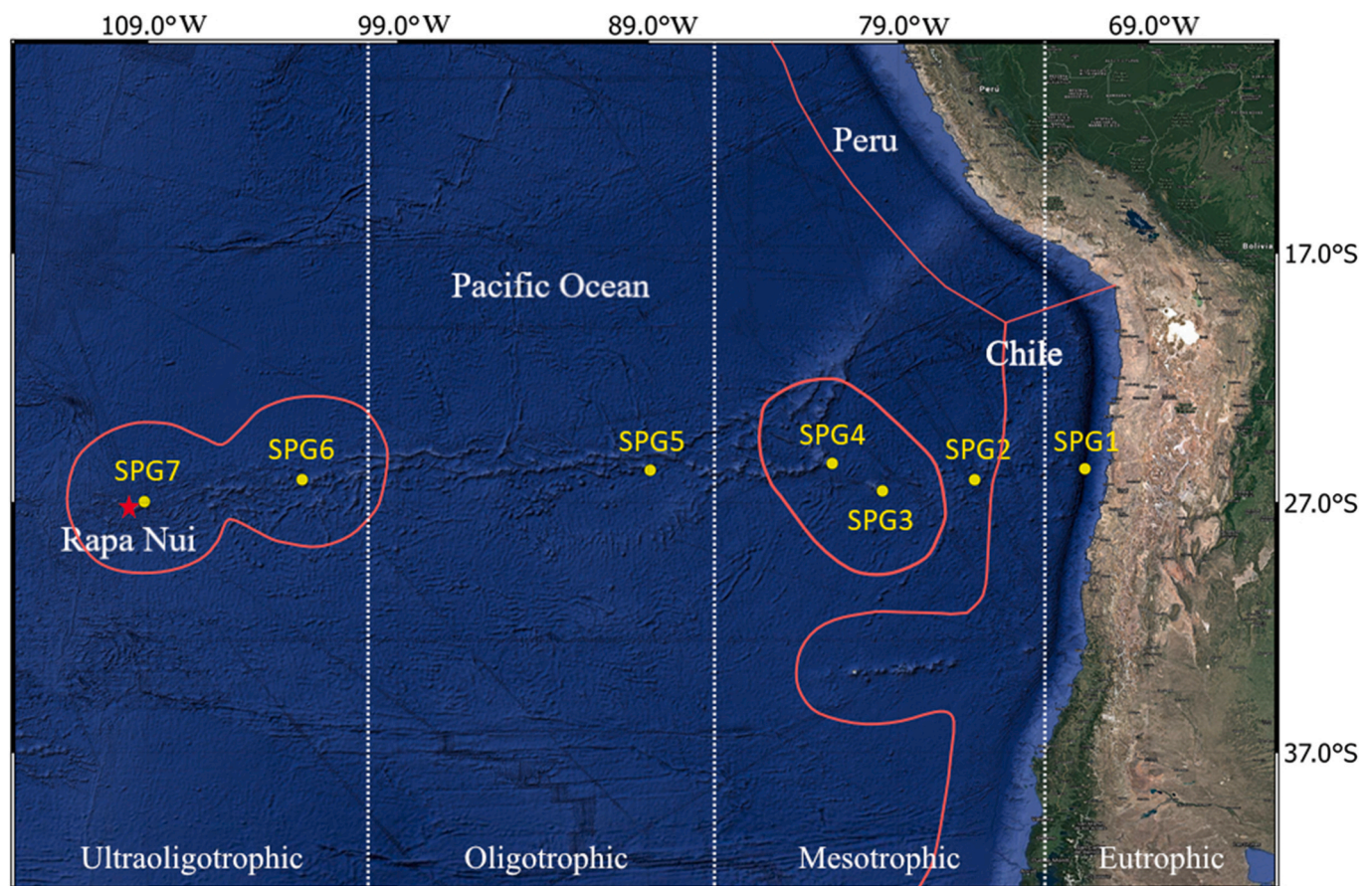


Fig. 1. Study area in the Southeast Pacific showing the sampling sites. SPG: South Pacific Gyre. Red lines indicate the Chile Exclusive Economic Zone and productivity zones (dotted white lines) according with [Espinosa-Leal et al. \(2021\)](#). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the organisms using the microscope. Two cores per station were used for live sorting of macroinfauna: the 0–5 cm layer was resuspended in cold seawater, sieved over a 300 μm mesh sieve, and examined using a Leica S8Apo stereomicroscope. This 0–5 cm layer was not separated into smaller layers. Live-sorted specimens were preserved in 95% ethanol or subsampled into 95% ethanol with morphological vouchers fixed in 10% formalin and deposited in the Scripps Institution of Oceanography Benthic Invertebrate Collection (SIO-BIC) in La Jolla, California, USA (Material supplementary 7). For biogeochemical variables, the core was separated into 1 cm layers, and the samples were frozen (-20°C) before carbon and nitrogen isotope analysis for organic matter analysis.

2.4. Biogeochemical analysis of the sediment

Total organic carbon (TOC), total nitrogen (TN), carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes in surface sediments (0–2 cm) were analyzed by mass spectrometry (Thermo Scientific Delta V Advantage IRMS with EA-2000 Flash Elemental analyzer). In sediment the $\delta^{13}\text{C}$ (‰) values were compared to the Vienna Pee Dee Belemnite (VPDB), and the nitrogen isotope values were relative to the air. Analyses were performed at the Laboratory of Biogeochemistry and Applied Stable Isotopes (LABASI, Pontificia Universidad Católica), Chile.

The calcium carbonate contents (CaCO_3) of the sediment in the cores (0–1 cm) were determined with the use of dried homogenized sediment (0.1 g, accurately weighed) in centrifuge tubes; 2 mL hydrochloric acid (10%) was then added. Once the effervescence ceased, concentrated HCl (~ 5 drops) was added to samples for the total dissolution of the carbonate. Afterwards, the solution was diluted with Milli-Q water, centrifuged (3000 rpm for 10 min), and then the supernatant was removed. The decarbonated sediment was dried to 60°C by 24 h and weighed, after which carbonate content was calculated using the difference between the weight before and after carbonate removal. Analyses were performed at the Laboratory of Oceanography and Benthos (LOBOS, Pontificia Universidad Católica de Valparaíso), Chile.

Sediment-bound chlorophyll (Chla.) and phaeopigments (Phaeo.) (0–1 cm) were extracted from duplicate subsamples of wet sediment (ca. 1 g) using 90% acetone. After 24 h of darkness at 4°C , the samples were sonicated for 5 min, centrifuged at 3000 rpm ($1000\times g$) for 10 min, and extracts were analyzed fluorometrically for Chla. and Phaeo. Content in quadruplicate. The values for photosynthetic pigment were obtained before and after acidification with 1 N HCl (Lorenzen, 1967; Parsons et al., 1984), substituting the dry weight (DW) of the sediment in grams per volume of water. After drying duplicate sediment subsamples (ca. 1 g) at 105°C for 20 h, values were expressed as $\mu\text{g Chla g}^{-1}\text{ DW}$ after correcting for porosity obtained from the water content. The sum of Chla and Phaeo, referred to as the chloroplast pigment equivalent (CPE), provides an indicator of phytodetrital input to sediments (Quiroga et al., 2016).

2.5. Data processing

Abundance was analyzed as the total number of individuals per core due to the high difference between the area captured by the core (0.0043 m^2) compared to a 0.25 m^2 box corer, which is the more common sampling device used on these environments. Therefore, we avoided the results being potentially overestimated. However, abundance data was also standardized to individuals $\bullet\text{ m}^{-2}$ for comparisons with other studies (Table 2b).

Species richness (S) was considered as taxa richness and calculated as the number of distinct morphotypes (species) in a sample. Since taxonomic identification at species level was often not possible the category of morphotype sp1, sp2, etc. was mainly assigned. Diversity indices such as Shannon diversity and Pielou evenness (H' ($\log_e$) and J' , respectively) were calculated using the statistical software Primer-e v6 and excluding the abundance of “Copepoda incertae sedis”, as this taxon corresponds to various copepods that could not be identified due to their degree of

degradation. Higher values of H' show a more diverse macrobenthic community, while that J' values close to 1 show a more uniform community in terms of abundance. Anyway, the diversity estimates should be considered with caution due to limitations on species-level taxonomic resolution. For the non-metric multidimensional scaling (nMDS) (Clarke and Gorley, 2006) and dendrogram (Cluster) (Warwick and Clarke, 1993) analysis, the average abundance of major taxonomic groups per station was used (see major groups on Tables 2a and 2b for more details), transformed to square root, due to the high number of taxa recorded only once and dissimilarity between stations.

Principal Component Analysis (PCA) was performed using a Euclidean distance matrix, based on the normalized values of the biogeochemical variables. Normalization was done to avoid different measurement scales. Chla and Phaeo values were excluded from the analysis as they were correlated with CPE. To calculate the correlation between biological diversity variables (abundance, taxa richness, Shannon diversity and major faunal groups) and environmental variables (Chl-a, CPE, Longitude, CaCO_3 and d13%) Spearman rank correlation was analyzed (Zar, 2005).

Statistical analyses were performed using the softwares Primer-e v6 (Clarke and Gorley, 2006) (www.primer-e.com) and PAST v4.12 b (Hammer et al., 2001) (<https://www.nhm.uio.no/english/research/resources/past/>).

3. Results

3.1. Macrofaunal communities

3.1.1. Composition, abundance and diversity

A total number of 106 macrobenthic individuals were recorded, and 77 different morphotypes (species) were identified. The organisms were assigned to 15 major taxonomic groups among Phylum, Order, and Class (Tables 2a and 2b). Approximately 90% of all species (69 morphotypes) were recorded only once. Hence, our results would indicate that there is a direct relationship between abundance and taxa richness (number of species) in the study area.

About abundance (total number of individuals), Arthropoda (mostly Copepoda) was the dominant Phylum, representing 44.3% of the total macroinfauna (47 individuals), and was the only group present at all stations. The class Copepoda, represented by the order Harpacticoida, recorded a total of 33 individuals, corresponding to 31.1% of the total abundance. The Phylum Annelida, represented widely by the class Polychaeta, was second with 36.8% of the total macroinfaunal community (39 individuals) and was not recorded at SPG5. Nematoda and Mollusca represented 5% and 4.7% of the abundance, respectively, while Nemertea, Porifera, and Sipuncula recorded abundances less than 5%. (Fig. 2a; 2 b).

The highest values of total abundance and taxa richness were recorded in the sampling station associated with the Atacama Trench (SPG1 site), with 29 individuals and 21 taxa, respectively (Fig. 3a; 3 b). On this environment such polychaetes, harpacticoid copepods, and nematodes were the dominant faunal groups (Fig. 2b). Besides, in sampling sites associated with the base of seamounts, the highest abundances were recorded in the seamounts closest to the Desventuradas and the Nazca Ridge areas, reaching the highest values in SPG3 and SPG4 sites with 22 individuals. By contrast, the lowest abundance was recorded at SPG5 and SPG6 sites, both found in Salas y Gómez Ridge, with 3 and 2 individuals, respectively.

Mean density (individuals $\bullet\text{ m}^{-2}$) varied from 93 individuals $\bullet\text{ m}^{-2}$ at SPG6 (Salas y Gómez Ridge) to 1349 individuals $\bullet\text{ m}^{-2}$ at SPG1 (Atacama Trench). The average per sampling site was 710 individuals $\bullet\text{ m}^{-2}$ (Table 2b). In terms of major taxonomic groups, the lower densities per site were recorded in the groups such Sipuncula, Gastropoda, Bivalvia, Monoplacophora, Cumacea and Annelida (Polychaeta excluded) with mean densities of 47 individuals $\bullet\text{ m}^{-2}$. While that the higher densities per site corresponded to Polychaeta and Copepoda with mean values of

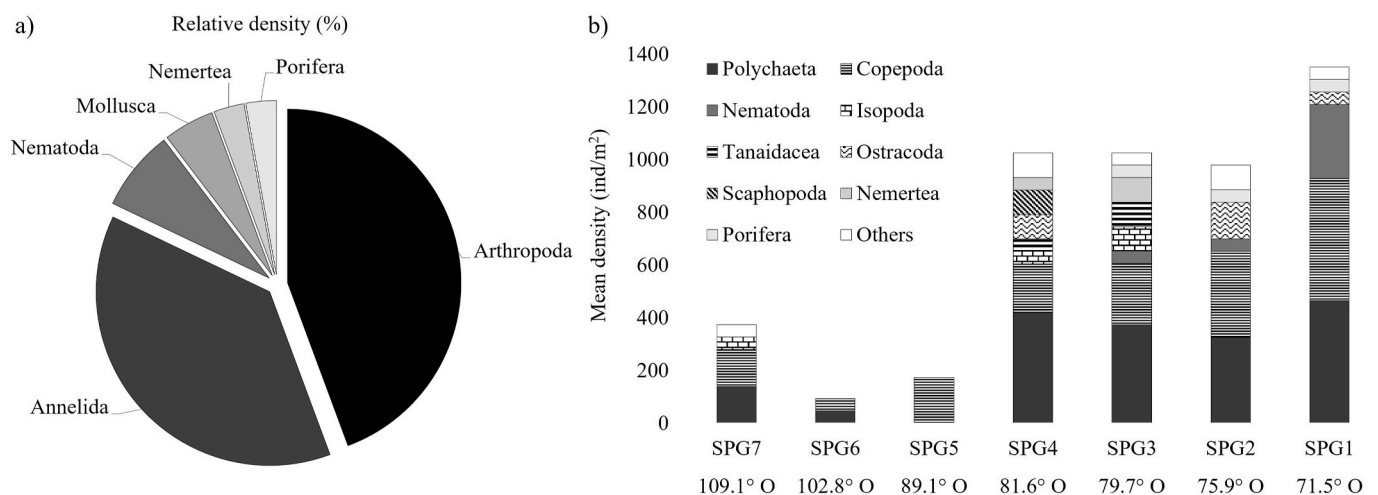
Table 2a

Total abundance by major taxonomic groups per station.

Phylum	Major groups	SPG1	SPG2	SPG3	SPG4	SPG5	SPG6	SPG7	Total abundance
Annelida	Annelida	1	0	0	0	0	0	0	1 (0,9%)
	Sipuncula	0	0	0	1	0	0	0	1 (0,9%)
	Polychaeta	10	7	8	9	0	1	3	38 (35,8%)
Arthropoda	Cumacea	0	0	1	0	0	0	0	1 (0,9%)
	Isopoda	0	0	2	1	0	0	1	4 (3,8%)
	Tanaidacea	0	0	2	1	0	0	0	3 (2,8%)
	Copepoda	10	7	5	4	3	1	3	33 (31,1%)
	Ostracoda	1	3	0	2	0	0	0	6 (5,7%)
	Mollusca	0	1	0	0	0	0	0	1 (0,9%)
Mollusca	Gastropoda	0	0	0	0	0	0	1	1 (0,9%)
	Monoplacophora	0	0	0	1	0	0	0	1 (0,9%)
	Scaphopoda	0	0	0	2	0	0	0	2 (1,9%)
	Nematoda	6	1	1	0	0	0	0	8 (7,5%)
Nemertea	Nemertea	0	0	2	1	0	0	0	3 (2,8%)
Porifera	Porifera	1	1	1	0	0	0	0	3 (2,8%)
Total abundance		29	20	22	22	3	2	8	106

Table 2bMean density (individuals m^{-2}) by major taxonomic groups for each sampling site.

Phylum	Major groups	SPG1	SPG2	SPG3	SPG4	SPG5	SPG6	SPG7	Total
Annelida	Annelida	47							47
Annelida	Polychaeta	465	326	373	419		47	140	1768
Annelida	Sipuncula				47				47
Arthropoda	Copepoda	465	326	233	186	174	47	140	1570
Arthropoda	Cumacea			47					47
Arthropoda	Isopoda			93	47			47	186
Arthropoda	Ostracoda	47	140		93				279
Arthropoda	Tanaidacea			93	47				140
Mollusca	Bivalvia		47						47
Mollusca	Gastropoda							47	47
Mollusca	Monoplacophora				47				47
Mollusca	Scaphopoda				93				93
Nematoda	Nematoda	280	47	47					373
Nemertea	Nemertea			93	47				140
Porifera	Porifera	47	47	47					141
Total		1349	931	1025	1024	174	93	372	

**Fig. 2.** a) Relative density (%) of the major taxonomic groups and, b) Mean density (ind/ m^2) of the major taxonomic groups per sampling site.

465 individuals m^{-2} (Table 2b). The spatial analyses of this variable clearly proved the higher densities of macrofaunal individuals are in mesotrophic areas.

The highest values of taxa richness in abyssal-seamount associated ecosystems were also recorded on SPG3 and SPG4 sites with 20 morphotypes (species). However, SPG5 and SPG6 sites, in the center of

SPSG, showed the lowest taxa richness, with 2 morphotypes each one. Clearly these results show there were more species in mesotrophic areas, however these spatial patterns may be influenced by the taxonomic resolution that was not always at species level.

The macrofaunal communities described in the eastern area (SPG1 to SPG4) presented a greater number of higher taxonomic groups

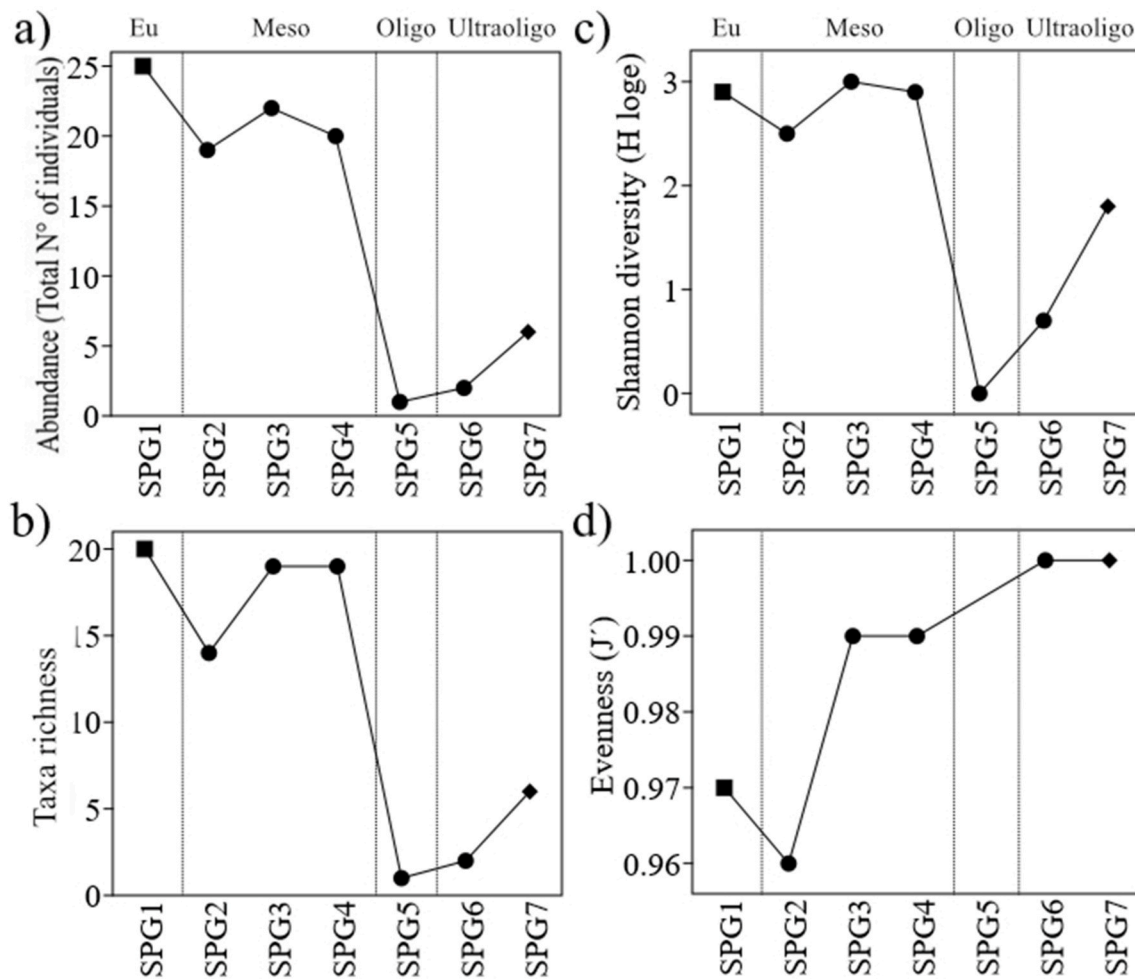


Fig. 3. Ecological parameters per sampling site. a) Abundance, b) Taxa richness, c) Shannon diversity and d) Pielou evenness. The dotted vertical lines separate the distinct productivity zone according with [Espinosa-Leal et al. \(2021\)](#). Eu (eutrophic), Meso (mesotrophic), Oligo (oligotrophic) and Ultraoligo (Ultraoligo trophic).

(Fig. 2b), which is also related to higher diversity values (H'). The highest value was 2.97 recorded in SPG3 (Fig. 3c). In contrast, the communities recorded to the west, within the Salas and Gómez Ridge and Rapa Nui area, were characterized by lower diversity values, composed exclusively of Polychaeta, Copepoda, and Isopoda organisms,

including the lowest value at SPG6 site with 0.69. The value of 0 reported for SPG5 was due to the deteriorated condition of the organisms and taxonomic difficulties that reduced the data matrix used for the index. Evenness (J') values between sampling sites were relatively homogeneous (Fig. 3d), varying from 0.95 (SPG2) to 1 (SPG6 and SPG7).

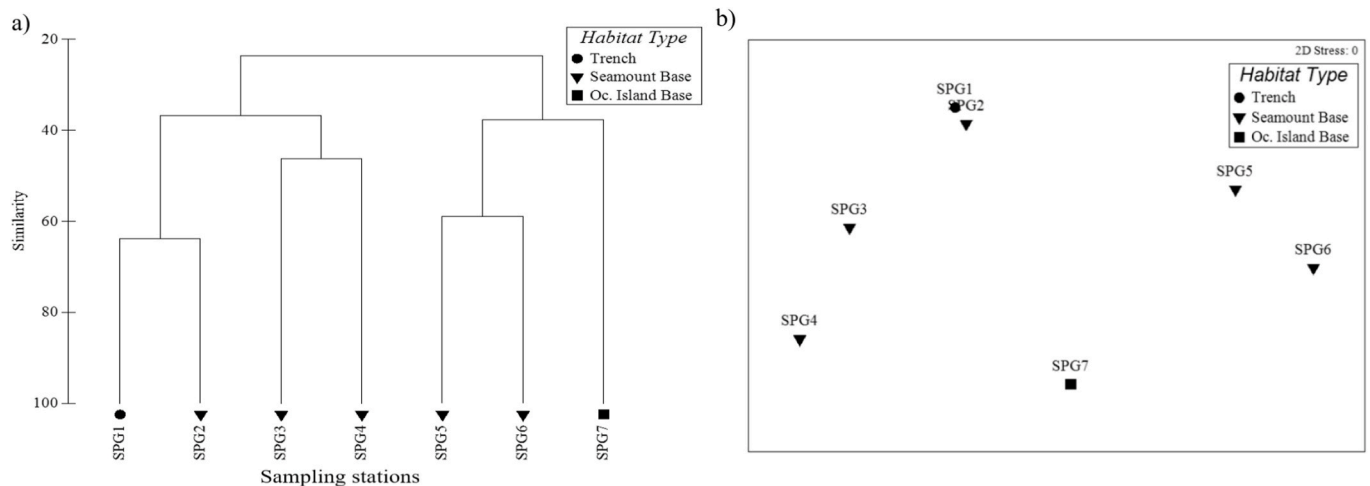


Fig. 4. a) Cluster analysis and b) Non-metric multidimensional scaling (NMDS) ordination plot based on average abundance of major taxonomic groups by habitat type.

Similarly, nMDS and Cluster ordination analyses (Fig. 4) at higher taxonomic group levels demonstrated a clear differentiation between the composition and abundance of the macroinfaunal communities located in the Salas y Gómez Ridge area (SPG5, SPG6, and SPG7) and those sites to the east of this area (SPG1, SPG2, SPG3, and SPG4). These distribution patterns suggest a benthic community response to different productivity regimes.

3.1.2. Macrobenthos vertical distribution

Most of the macroinfaunal abundance (73%) was concentrated at the first centimeter of the sediment column, followed by 1–3 cm (21%) and 3–5 cm (6%) sediment layers (Fig. 5). Below five centimeters of depth, no organisms were recorded, and only calcareous remains such as bivalve and ostracod shells were seen. Like abundance, the diversity of higher faunal groups decreased with depth. All taxonomic groups were recorded in the first centimeter, while only 6 groups (Copepoda, Monoplacophora, Nematoda, Ostracoda, Polychaeta, and Tanaidacea) were recorded between 1 and 3 cm and only 3 groups (Copepoda, Polychaeta, and Porifera) were found between 3 and 5 cm (Fig. 5 and Material supplementary 5).

3.2. Environmental variables and its relationships with macroinfaunal communities

Environmental parameters mean values are shown on Table 3. The highest values of redox potential in the first 2 cm sediment layer were recorded at SPG6 (372 mV) and the lowest at SPG1 (209 mV). The highest concentrations of chloroplast pigment equivalents (CPE) were recorded at the Atacama Trench site SPG1 (20.61 ± 3.06), while the lowest values were recorded at SPG6 (0.04 ± 0), associated with ultra-oligotrophic conditions. The carbon isotopic signal ($\delta^{13}\text{C}$) varied from $-23.17 (\pm 0.08)$ at SPG7 to $-25.4 (\pm 0.02)$ at SPG1, while the nitrogen isotopic signal ($\delta^{15}\text{N}$) showed values from $12.59 (\pm 1.53)$ at SP2 to $7.5 (\pm 0.9)$ at SPG7, the westernmost site. Overall percentages of nitrogen and carbon less than 0.5% were recorded, with the maximum values at SPG5 (0.07 ± 0.03 and 0.46 ± 0.21 , respectively) and minimum values at SPG6 (0.01 ± 0.01 and 0.15 ± 0.01 , respectively) in the middle of Subtropical Gyre. The highest C/N ratio values were recorded at SPG7 (13.07 ± 0.42) and the lowest at SPG5 (6.46 ± 0.52). Finally, the CaCO_3 concentration was highest at SPG4 (1.42 ± 0.11) and lowest at SPG1 (0.16 ± 0.11) (Material supplementary 1). Differences across sites were clear mostly between SPG1 and the rest of the sampling sites. The influence of high productivity on hadal environment (SPG1) were mirrored in the organic content of this site, while oligotrophic conditions in the center of Subtropical Gyre explain lower values of organic content at the base of the studied seamounts.

The variability of the biogeochemical variables was examined using Principal Component Analysis (PCA, Fig. 6). This allowed us to distinguish station SPG1 from the other stations due to its high concentration

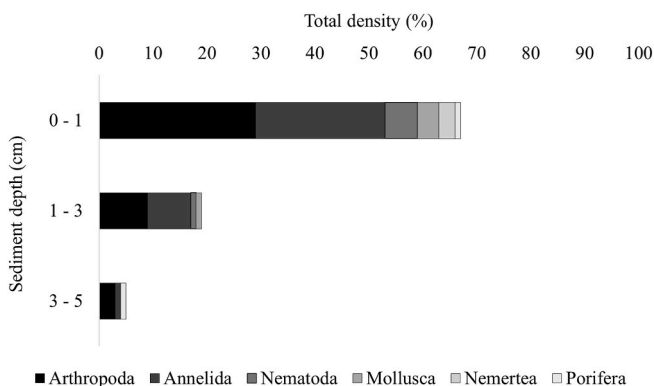


Fig. 5. Total density (%) per sediment depth of the major taxonomic groups.

Table 3
Environmental variables for the first 0–2 cm of sediment, including the following: pH, redox potential normalized to hydrogen potential ($\text{Redox}_{\text{NHE}}$), chlorophyll a-bounded sediment (Chla), phaeopigment (Phaeop), chloroplastic pigment equivalent (CPE), d^{15}N , d^{13}C , nitrogen (%), organic carbon (Corg), carbon and nitrogen ratio (C/N) and calcium carbonate contents (CaCO_3). Data are means and standard deviations (SD). (–) denotes no data was obtained.

analyses no data was obtained.

Site	Location	Depth (m)	pH	Redox _{NHE} (mV)	Chla (ug/g)		Phaeop (ug/g)		CPE (ug/g)		d ¹⁵ N (‰)		d ¹³ C (‰)		N (%)		Corg (%)		C/N (molar)		CaCO ₃ (%)	
					0-1 cm	Mean	SD	0-1 cm	Mean	SD	0-2 cm	Mean	SD	0-2 cm	Mean	SD	0-2 cm	Mean	SD	0-2 cm	Mean	SD
SPG1	Chile trench	7742	7.43	209	3.56	0.75	17.04	3.00	20.61	3.06	8.42	0.81	-25.42	0.02	0.05	0.01	0.41	0.07	8.25	0.12	0.16	0.01
SPG2	Off San Ambrosio	3982	7.23-7.39	262-237	0.07	0.01	0.41	0.03	0.49	0.02	12.59	1.53	-23.39	0.18	0.06	0.01	0.43	0.10	6.83	0.60	1.07	0.10
SPG3	Off San Ambrosio	3447	7.35-7.20	236-246	0.08	0.02	0.29	0.13	0.37	0.13	12.03	1.01	-23.21	0.30	0.02	0.01	0.21	0.02	9.22	0.66	1.42	0.01
SPG4	SE of Stock man guyot	2999	-	235	0.15	0.05	0.83	0.05	0.98	0.10	8.88	1.28	-23.27	0.22	0.02	0.01	0.23	0.12	10.34	3.01	1.42	0.11
SPG5	Pearl Seamount	4114	-	267	0.04	0.01	0.07	0.01	0.11	0.00	11.53	1.69	-23.61	0.56	0.07	0.03	0.46	0.21	6.46	0.52	0.54	0.09
SPG6	Seamount No.30	3214	-	372-270	0.02	0.01	0.02	0.01	0.04	0.00	9.07	0.99	-23.36	0.19	0.01	0.01	0.15	0.01	10.82	1.08	1.16	0.11
SPG7	Off Easter Islands	2895	-	259-161	0.04	0.01	0.12	0.01	0.16	0.01	7.53	0.90	-23.17	0.08	0.02	0.01	0.32	0.03	13.07	0.42	1.42	0.01

of photosynthetic pigments in the sediment (CPE), with an average value of $20.61 \pm 3.06 \mu\text{g/g}$, compared to the other stations which had average values below $0.98 \pm 0.1 \mu\text{g/g}$.

The PC-axis 1 represented the highest percentage of variance and showed a clear gradient in Corg%, N%, and the state of organic matter (C/N). This showed a decrease in the concentration and quality of organic content from left to right, proving that SPG5 and SPG2 have the highest concentrations, which decrease through SPG3, SPG4, SPG6, and SPG7. This is associated with the approach to the center of the SPSG, where surface productivity and carbon flux are significantly lower. Therefore, this lower concentration and bioavailability of food sources affected macroinfaunal communities as observed in this study.

Spearman correlations found that CPE in the sediments (specifically Chl-*a*) was important in the distribution of benthic macroinfauna (Table 4) and community parameters (abundance, taxa richness, and diversity). CPE decreased from east to west along the study transect and this pattern was related to the decrease in the abundance of copepods and polychaetes. Carbonates (CaCO_3) and the carbon isotopic signal ($\delta^{13}\text{C}$) positively correlated with isopoda, instead longitude showed a negative correlation with Copepoda and Nematoda. The rest of major taxonomic groups and environmental variables did not showed correlations.

4. Discussion

4.1. Composition, abundance and ecological patterns

This study provides the first approaches to understanding the composition and structure of abyssal and hadal macroinfaunal communities inhabiting mostly the bases of seamounts in the southeastern Pacific Ocean. The results showed that Annelida and Arthropoda dominated the composition of the benthic macroinfauna, particularly by Polychaeta and Copepoda, followed in third and fourth place by Nematoda and Ostracoda. Meanwhile, other taxonomic groups represented significantly lower abundance in these communities, being considered occasional groups during the study (Material supplementary 4). The dominance of Polychaeta is like recorded by Glover et al. (2002) in the

north and central Pacific; however, in terms of Crustacea, studies have found Isopoda to be dominant rather than Copepoda (Brix et al., 2020; Pasotti et al., 2021).

Faunal composition decreased towards oligotrophic areas; Crustacea, Mollusca, Nematoda and other groups showed a decreasing trend to the ultraoligotrophic areas and only Copepoda was present in all sites. Horacek et al. (2022) recorded a similar pattern for meiofauna at the same study zone, while that similar responses have also been observed in other areas, for example the Gulf of Mexico (Wei and Rowe, 2019) and Madeira Abyssal plain (Glover et al., 2001), confirming that productivity can determine changes in benthic community composition. On this study the sampling sites associated with seamounts that recorded a higher diversity of major taxonomic groups were SPG4 and SPG3. According with the González et al. (2019) these sites are located under mesotrophic conditions; therefore, the higher diversity seen on them (also recorded in the Shannon index and Taxa richness) may also be related to local seamount productivity.

Three of the most abundant groups recorded in this study (Copepoda, Nematoda, and Ostracoda) are generally considered meiofauna components (Hessler and Jumars, 1974; Dinert et al., 1985), although it is common for the macrofauna size class to contain large nematode and copepod species (Gunton et al., 2017). The presence of these taxa in our samples was due to the use of $300 \mu\text{m}$ size mesh during the sorting process, which is a standard size limit for abyssal studies (Leduc et al., 2020; Lins et al., 2021). These faunal groups formed approximately 25% of the total taxa richness and 45% of abundance. Considering exclusively the macroinfauna, the communities described for the seamount-associated sites (SPG2 and SPG6) and near the base of Rapa Nui Island (SPG7), were characterized by polychaetes and peracarid crustaceans. These compositions showed a similar pattern to those recorded in other studies conducted in abyssal environments of the Pacific Ocean (De la Torriente et al., 2019; Wilson, 2017; Chuar et al., 2020; Brandt et al., 2019; Kamenev et al., 2022; Nomaki et al., 2021a, b). The same occurred at SPG1 (Atacama Trench site), where faunal composition was similar to that recorded in other trenches of the Pacific such as the Aleutian Trench (Jumars and Hessler, 1976) and Kuril-Kamchatka Trench (Fischer and Brandt, 2015; Kamenev et al.,

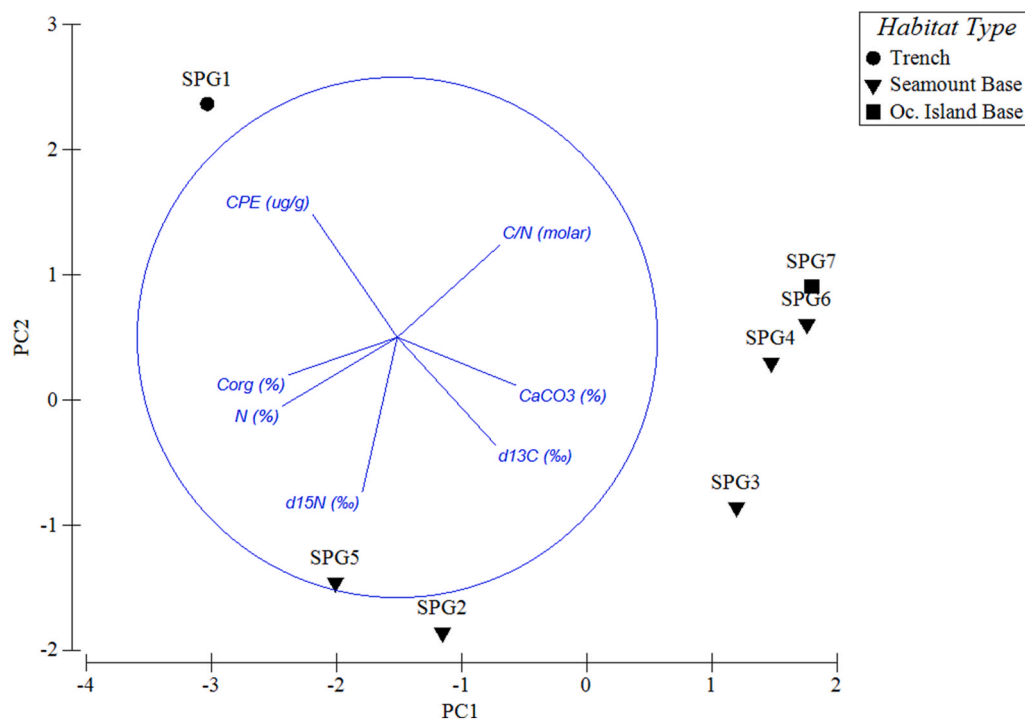


Fig. 6. Principal Component Analysis (PCA) ordination plot of sediment biogeochemical variables by sampling sites and habitat type.

Table 4

Spearman correlations between environmental sediment variables and macroinfauna according to major taxonomic groups. Bold values = p (<0.05), N = abundance, S = taxa richness, H' = Shannon diversity index.

Variables	N	S	H'	Polychaeta	Copepoda	Nematoda	Isopoda
CPE	0,93	0,92	0,73	0,93	0,88	0,65	0,11
Chl- α	0,98	0,96	0,82	0,94	0,85	0,66	0,24
Longitude	-0,77	-0,76	-0,63	-0,71	-0,94	-0,90	0,18
CaCO ₃	-0,03	0	0,32	0,03	-0,33	-0,43	0,87
d13%	-0,12	-0,09	0,22	-0,07	-0,37	-0,41	0,84

2022). Earlier studies on infaunal communities at the Atacama Trench have only addressed meiofaunal components (Danovaro et al., 2002; Shimabukuro et al., 2022; Horacek et al., 2022).

The recorded abundance in the study area, in terms of total number of individuals, was low, with only 106 individuals in 35 cores. These results were likely due to the size of the sampling device used (Material supplementary 6). The comparison of abundance with other studies was challenging because multicore is not the most common sampling gear for deep-sea quantitative studies of macrofauna. Several authors recommend a box core (typically 0.25 m²) for these purposes (Montagna et al., 2017; Lins et al., 2021). Therefore, standardizing abundance from the 7.5 cm corer to density (m²) could result in an overestimation of our data. This is relevant to consider in future expeditions for making comparisons with other studies, especially considering the complexity of sampling in these remote areas.

There are no studies on deep sea abyssal macroinfaunal communities' ecology in the SE Pacific associated with seamounts, therefore, the following discussion compares our results with studies from Atlantic and North and Central Pacific. Bongiorno et al. (2013) sampled different areas associated with Condor Seamount (Azores, NE Atlantic), and on those areas far from the summit (1900-m depth) recorded mean abundances in a range from 150 to 533 ind. m⁻². For our study, these values are more similar to those observed in oligotrophic sites, but they are lower in relation to mesotrophic sites. Lourido et al. (2024) recorded an average of 1033 ind. m⁻² for a group of eight sites found between 1477 and 2274 m depth in the Galicia Bank seamount (NE Atlantic). These values are like those recorded in our sites associated with mesotrophic conditions (SPG2, SPG3 and SPG4). At abyssal depths (4558-4629) studies made by Pasotti et al. (2021) in the Clarion-Clipperton Fracture area (NE Pacific) record 176 ind. m⁻² at the nodule-free site, coinciding with the second lowest value obtained at SPG5. Studies made by Levin and Thomas (1989) in the Magellan Rise Plateau (Horizon Guyot, Central Pacific) at 3150 m depth recorded densities 388 ind. m⁻², being similar to density recorded in SPG7 (372 ind. m⁻²). This similarity could be explained by both sites are in geographic areas where the oligotrophic conditions are dominant, therefore lower food supply to the benthos determines lower macroinfaunal abundances.

In relation to Atacama Trench site, mean density is compared with studies from other trenches because there are no previous studies on macroinfaunal communities on this trench. Preickschardt et al. (2025) recorded mean density of 561 ind. m⁻² between 7139 and 7287 m depth at Aleutian trench, NE Pacific. In the same trench Jumars and Hessler (1976) recorded a slightly lower value (1272 ind. m⁻²) at 7298 m. Schmidt et al. (2019) recorded mean densities between 196 and 1124 ind. m⁻², but in the Kuril-Kamchatka Trench (NW Pacific) at 5144-9540 m depth. The higher macroinfaunal density recorded in the Atacama Trench (1349 ind. m⁻²) is related to the high surface productivity where it is located. Deep sea trenches tend to accumulate organic matter promoting elevated abundances of the hadal biota (Schmidt and Arbizu, 2015).

Although the abundance was low, a high percentage of taxa was recorded only once (89,6%) (Material supplementary 4). According to Grassle and Maciolek (1992) the presence of a high number of species recorded only once (the concept is commonly called "singletons" by this and other authors) is characteristic in the deep-sea at all sampling scales,

suggesting that to correctly determine the species richness an increased sampling effort is necessary. A similar conclusion was highlighted by Pasotti et al. (2021), who, studying the macroinfauna of abyssal sediments influenced by manganese nodules in the Clarion-Clipperton Fracture Zone, also found a high number of singletons which is also the case for this study. These authors concluded that the sampling effort was insufficient to characterize the diversity of dominant taxa at the morphospecies level.

In this study we believe that taxa richness was high because 77 different morphotypes were recorded from a total of 106 individuals. In this sense Polychaeta recorded the higher number of taxa (38) separated into 14 families, all these species being unique. However, we think that this taxa' richness estimate should be taken with caution due to the high number of taxa recorded only once, taxonomic resolution and the sampling gear used. Pasotti et al. (2021) have also concluded that a high number of singletons and low densities may lead to an underestimation of species diversity.

The comparison between sampling sites indicates SPG1 recorded higher number of taxa of polychaetes (10) followed by SPG4 (9), then SPG3 (8) and finally SPG2 (7). Another faunal groups that also recorded a higher number of taxa were Copepoda and Nematoda with 7 taxa and Ostracoda with five taxa.

Considering the low number of individuals per sample, in many cases equal to zero and therefore the low abundances recorded per sampling site, diversity estimates based on Shannon (H') and Pielou (J') indices may be biased. In this study Shannon diversity index (H') showed high values always associated with eutrophic-mesotrophic areas and low values in oligotrophic areas. This decrease in the Shannon index related to productivity was also described in abyssal polychaete communities in the central Pacific (Glover et al., 2002). Besides, the analysis of evenness (J') results is also complex due to the high number of taxa recorded only once. Therefore, it is not accurate to analyze and compare evenness in this situation.

Despite the differences in the number of individuals, similar trends in diversity indices were detected for meiofaunal communities in the same study area. Horacek et al. (2022) found that various diversity indices (e. g. H'_{log_e} , Margalef, Shannon-Wiener and Hill and others) show a decreasing pattern moving into oligotrophic areas. These authors suggest that productivity and food supply are determinative for nematode diversity and evenness. The spatial patterns seen for abundance, taxa richness and Shannon diversity index in this study for macroinfaunal communities also show a decrease in values possibly explained by conditions more oligotrophic-ultraoligotrophic on these areas.

Therefore, our hypothesis that looks to test whether the transition to oligotrophic conditions produces changes in composition and decreases in abundance in macroinfaunal communities may be accepted. Our results proved these variations but also recorded lower diversity values in oligotrophic conditions.

4.2. Biogeochemistry of abyssal-seamount sediments in the Southeast Pacific ocean

The measured environmental parameters associated with the sediment organic content showed spatial variability possibly mirrored by the distinct productive regimes influencing the study sites. In the same

way, some biogeochemical parameters showed correlations with some ecological descriptors, which may explain the observed patterns on macroinfaunal community.

In general, the %C, %N, and Redox values demonstrated that these samples were typical of sediments from oligotrophic abyssal environments (Whelan, 1977; Müller, 1977), probably with low sedimentation rates (Jumars and Hessler, 1976; Pedrosa-Pamies et al., 2015), which is consistent with the low surface productivity of this area influenced by the SPSG. Meanwhile, the isotopic signal of organic matter ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), in combination with the C/N ratio, reflected that the organic material in the sediments was possibly of marine origin (Meyers, 1994; Rumolo et al., 2011), which is consistent with the great distance between the stations and the continent.

The concentrations of CPE in the sediments were generally low ($<1 \mu\text{g/g}$) except for those recorded in SPG1 ($20.61 \pm 3.06 \mu\text{g/g}$). This is probably because the Atacama Trench is located beneath one of the most productive marine ecosystems on the planet (Tapia et al., 2021), coupled with the dynamics that accumulate organic material at the bottom of the trenches due to horizontal transport, sediment sliding, and animal carcasses (Ichino et al., 2015; Jamieson, 2015). Furthermore, the decrease in this parameter as the stations approached the SPSG is consistent with chlorophyll-a concentrations observed in the column water (Material supplementary 3), and with the reduction of carbon flux recorded in this area at depths greater than 1000 m by Pavia et al. (2019) and the biogeographic gradient proposed by Watling et al. (2013).

The differential response observed in sediment biogeochemistry of each seafloor environment is a clear demonstration of the benthic-pelagic coupling processes that have place in the ocean. The distinct regimes of surface productivity observed in the SPSG characterized by distinct drivers such upwelling, seamounts or oceanic islands, are linked to seabed and therefore determined the quality and amount of organic content in the sediments, influencing finally the changes and patterns of the macroinfaunal communities.

4.3. Relationship between environmental variables and macroinfauna

Univariate and multivariate analyses showed that CPE was positively related to the distribution of macroinfauna in the study area. This relationship has been widely described in benthic environments (Witte, 2000; Pilditch et al., 2015; Vedenin et al., 2018), as it provides an estimate of the organic matter derived from surface productivity and the concentration of bioavailable content (Chl-*a*) for macrofauna consumption (Berkenbusch et al., 2011). CPE was directly correlated with total abundance and taxa richness, while more labile content (Chl-*a*) showed a positive correlation with diversity (H') that was not the case for CPE (Table 4), as it also has less reactive elements (Pilditch et al., 2015). It is also possible to see that there was a direct relationship between CPE and ecological variables. At stations SPG2, SPG3 and SPG4 the highest CPE values coincided with the highest values for total number of individuals, taxa richness and Shannon diversity index. Studies made by Glover et al. (2002) in the central Atlantic with polychaete assemblages have also shown the close relationships between species diversity and productivity, specifically with particulate organic carbon fluxes.

Vertical distribution could be associated with the availability of oxygen and food in the uppermost layers of the sediment column, as in oligotrophic environments with low sedimentation rates, most of the organic matter is degraded at the surface and does not get buried in the lower levels (Witte, 2000; Nomaki et al., 2021a,b). The results presented in this study correspond to the first 2 cm of sediment or only the 0-1 cm layer for some parameters; therefore, it is not possible to know if some organic content indicators were distributed in the deepest layers (Material supplementary 5).

The results showed that the decrease in carbon flux, using CPE as a proxy, between the sampling station closest to the coast and the center of the SPSG was directly correlated with the loss of abundance, richness,

and diversity of benthic communities. Polychaetes and copepods were the most sensitive groups to these changes. This type of gradient has been widely investigated in the northeast Pacific Ocean (CCFZ), concluding with similar patterns to those presented in this study. Additionally, several authors have also found Polychaeta as one of the groups that best describes changes in carbon flux in abyssal environments (Wilson, 2017; Bonifacio et al., 2020; Chuar et al., 2020; Washburn et al., 2021).

This pattern may influence the greater abundance, richness, and diversity recorded between the seamounts SPG2 and SPG4, which are located under an area considered to be a mesotrophic transition zone (González et al., 2019), compared to what was recorded between SPG5 and SPG7, located within the SPSG, in low-productivity waters (Von Dassow and Collado-Fabri, 2014), where the lowest values were recorded for ecological descriptors previously mentioned.

About the SPG1 site located at the Atacama Trench, any comparison with the rest of sampling sites should consider that this sampling station is in a distinct environment. This site corresponds to a hadal system regularly receiving the food inputs from one of the most productive areas in the planet and therefore may be considered an outlier for our analysis. This condition is confirmed by Principal component analyses (Fig. 6) and Cluster analyses (Fig. 4a). At the SPG1 site the highest concentrations of organic content were recorded, explaining why the maximum abundance and number of species were also observed. The high productivity of this environment is also thought to determine the high abundance and diversity recorded for meiofaunal communities as observed by Danovaro et al. (2002) and Shimabukuro et al. (2022).

In addition to sediment biogeochemistry and water productivity there are other factors that may explain the observed changes on macroinfaunal communities. It is important to mention that a couple of manganese nodules were found in the sediment of the sampling stations SPG2 and SPG5. According to numerous studies, manganese nodules promote benthic diversity because these minerals support habitat heterogeneity in the seafloor by providing additional hard substrates to the soft-bottom environments (Smith et al., 2008; Gollner et al., 2017; Yu et al., 2018). In this sense, our results did not support this theory for both cases because SPG2 recorded higher values of abundance and diversity indices in comparison to SPG5 where the lowest values for all study were recorded. These differences may indicate that the influence of manganese nodules on the ecology of the macroinfaunal communities studied is not as relevant as food availability. However, it is not possible to say if in both sampling sites the number of manganese nodules was high or low. Studies made by Pasotti et al. (2021) in the Northeast Pacific show that there are no significant differences between nodule-rich and the nodule-free sites in terms of biotic factors, suggesting that macrofauna are represented by comparable densities and higher-taxon diversity across sites. Further and comprehensive studies will allow a better understanding of the response of benthic communities to different environmental forcing.

5. Conclusions

This study stands for the first records of composition, abundance, diversity and distribution on soft-bottom macroinfaunal communities in hadal and seamount-abyssal environments in the Southeast Pacific. Faunal composition was characterized by the higher presence of Annelida, Crustacea and Mollusca, with Polychaeta and Copepoda being the most diverse and abundant. A low number of individuals (per core) was recorded in each sampling station, while mean density (ind. m^{-2}) in some sites was similar to other studies; however, the number of species was high (77) in relation to the total number of individuals recorded (106).

The benthic community showed a response to organic inputs associated with the distinct productive regimes. Geographically, the sampling sites associated with Atacama trench and those seamount bases influenced by mesotrophic conditions recorded the highest values of

abundance and diversity, while sites under oligotrophic conditions towards the center of the Subtropical Pacific Gyre (associated with seamount bases and oceanic islands) recorded the lowest values.

The presence of this longitudinal pattern allows support our first hypothesis, although it would be interesting to review it considering a larger sample volume, and more sampling sites just considering abyssal-seamount environments. The overall spatial trend also showed that several parameters related to sediment organic content decreased in oligotrophic areas, although the statistical analyses performed did not always show clear or direct relationships.

Although most study sites were associated with seamounts, the influence of these ecosystems supporting higher abundance and diversity due to local food supply was not clear. We recommend sampling the flanks and summits in future surveys to better characterize the typical benthic fauna of a seamount.

The Southeast Pacific is one of the most unknown ocean areas and the information about deep-sea benthos, biogeochemistry and ecosystem functioning is just developing. It is urgent to keep moving forward in the study of these environments with higher sampling efforts and devices that allow a better understanding about their biology and ecology. The generation of biological information for this area is also especially important to support the creation of the first Marine Protected Area in the high seas, even more considering that some anthropogenic pressures like deep-sea mining, fisheries and climate change are well established.

CRedit authorship contribution statement

Eulogio H. Soto: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Carlos Sanchis:** Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Writing – original draft, Writing – review & editing. **Eduardo J. Quiroga:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors are thankful for the support of the R/V *Mirai* crew who helped with each multicorer deployment and operations onboard. At the same time, we thank the Japanese Agency for Marine-Earth Science and Technology (JAMSTEC, Japan) for the wonderful opportunity to develop this research on these remote areas. Also, we want to express our gratitude to Dr. Dhugal Lindsay (JAMSTEC), who was the chief scientist during the East-Pacific International Campaign Cruise (EPIC-II). Charlotte Seid and Greg Rouse (Scripps Institution of Oceanography Benthic Invertebrate Collection at the University of California San Diego) performed live-sorting and further identification of live-sorted specimens, respectively. Finally, many thanks to Instituto Milenio de Oceanografía and Universidad de Valparaíso for the financial support provided. This publication is dedicated to the memory of our friend, colleague and teacher Dr. Eduardo Quiroga Jamett.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2026.108190>.

Data availability

Data will be made available on request.

References

- Anderson, T.R., Rice, T., 2006. Deserts on the seafloor: Edward forbes and his azoic hypothesis for a lifeless deep ocean. *Endeavour* (Camb.) 30, 131–137. <https://doi.org/10.1016/j.endeavour.2006.10.003>.
- Berkenbusch, K., Probert, P., Nodder, S., 2011. Comparative bio-mass of sediment benthos across a depth transect, chatham rise, southwest Pacific Ocean. *Mar. Ecol. Prog. Ser.* 425, 79–90. <https://doi.org/10.3354/meps09014>.
- Billett, D.S.M., Bett, B.J., Reid, W.D.K., Boorman, B., Priede, I.G., 2010. Long-term change in the abyssal NE Atlantic: the 'Amperima Event' revisited. *deep-sea res. Part II: Topical stud. Oceanography* (Wash. D. C.) 57, 1406–1417. <https://doi.org/10.1016/j.dsr2.2009.02.001>.
- Bongiorni, L., Ravara, A., Paretti, P., Santos, R., Rodrigues, C., Amaro, T., Cunha, M., 2013. Organic matter composition and macrofaunal diversity in sediments of the condor seamount (azores, NE Atlantic). *Deep Sea Res. Part II* 98 (A), 75–86. <https://doi.org/10.1016/j.dsr2.2013.08.006>.
- Bonifacio, P., Martínez-Arbizu, P., Menot, L., 2020. Alpha and beta diversity patterns of polychaete assemblages across the nodule province of the eastern clarion-clipperton fracture zone (Equatorial Pacific). *Biogeosciences* 17, 865–886. <https://doi.org/10.5194/bg-17-865-2020>.
- Brandt, A., Alalykina, I., Brix, S., Brenke, N., Błażewicz, M., Golovan, A., Johannsen, N., Hrinko, A., Jazdzewska, M., Jeskulke, K., Kamenev, Gennady, Lavrenteva, V., Malyutina, M., Riehl, T., Lins, L., 2019. Depth zonation of northwest Pacific deep-sea macrofauna. *Prog. Oceanogr.* 176. <https://doi.org/10.1016/j.pocean.2019.102131>.
- Brix, S., Osborn, K.J., Kaiser, S., Truskey, S.B., Schnurr, S.M., Brenke, N., Malyutina, M., Martínez Arbizu, P., 2020. Adult life strategy affects distribution patterns in abyssal isopods – implications for conservation in Pacific nodule areas. *Biogeosciences* 17, 6163–6184. <https://doi.org/10.5194/bg-2019-358>.
- CBD, 2014. Decision adopted by the conference of the parties to the convention on biological diversity. In: *Conference of the Parties to the Convention on Biological Diversity Twelfth Meeting*.
- Chuar, C., Tong, S., Chim, C., Wong, H., Tan, K., 2020. Abyssal macrofaunal community structure in the polymetallic nodule exploration area at the easternmost region of the clarion-clipperton fracture zone. *Pacific Ocean Deep Sea Res. Part I* 161, 103284. <https://doi.org/10.1016/j.dsr.2020.103284>.
- Clark, M., Rowden, A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K., Rogers, A., O'Hara, T., White, T., Shank, T., 2010. The ecology of seamounts: structure, function, and human impacts. *Ann. Rev. Mar. Sci.* 2, 253–278. <https://doi.org/10.1146/annurev-marine-120308-081109>.
- Clarke, K., Gorley, R., 2006. *PRIMER v6: User Manual/tutorial*. PRIMER-E Ltd. Plymouth Marine Laboratory, U. K, p. 190.
- Danovaro, R., Gambi, C., Della, N., 2002. Meiofauna hotspot in the atacama trench (southern Pacific Ocean). *Deep-Sea Res., Part A* 49 (5), 843–857.
- De la Torre, A., Aguilar, R., González-Irusta, J., Blanco, M., Serrano, A., 2020. Habitat forming species explain taxonomic and functional diversities in a mediterranean seamount. *Ecol. Indic.* 118, 106747. <https://doi.org/10.1016/j.ecolind.2020.106747>.
- De la Torre, A., González-Irusta, J., Aguilar, R., Fernández, S., Punzón, A., Serrano, A., 2019. Benthic habitat modelling and mapping as a conservation tool for marine protected areas: a seamount in the Western mediterranean. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 29 (5), 732–750. <https://doi.org/10.1002/aqc.3075>.
- Dinet, A., Desbruyères, D., Khripounoff, A., 1985. Abondance des peuplement macroet meiobenthiques: repartition et strategie dechantillonnage. In: *En Laubier, L., Monniot, C. (Eds.), Peuplements Profonds Du Golfe De Gascogne: Campagnes Biogas. Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), pp. 121–142.*
- Djurhuus, A., Read, J., Rogers, A., 2017. The spatial distribution of particulate organic carbon and microorganisms on seamounts of the south west Indian ridge. *Deep Sea Res. Part II* 136, 73–84. <https://doi.org/10.1016/j.dsr2.2015.11.015>.
- Espinosa-Leal, L., Escobano, R., Riquelme-Bugueño, R., Corredor-Acosta, A., 2021. Distribution and biodiversity patterns of Hyperiid amphipods across the coastal-offshore gradient of the sub-tropical southeast Pacific. *Mar. Biodivers.* 51, 13. <https://doi.org/10.1007/s12526-020-01152-x>.
- Fernández-Urruzola, I., Ulloa, O., Glud, R., Pinkerton, M., Schneider, W., Wenzhöfer, F., Escobano, R., 2021. Plankton respiration in the atacama trench region: implications for particulate organic carbon flux into the hadal realm. *Limnol. Oceanogr.* 66 (8), 1–15. <https://doi.org/10.1002/lno.11866>.
- Fischer, V., Brandt, A., 2015. Composition of the abyssal infauna of the kuril-kamchatka area (NW Pacific) collected with a box corer. *Deep Sea Res. II* 111, 26–33. <https://doi.org/10.1016/j.dsr2.2014.10.002>.
- Friedlander, A., Goodell, W., Giddens, J., Easton, E., Wagner, D., 2021. Deep-sea biodiversity at the extremes of the salas y gómez and nazca ridges with implications for conservation. *PLoS One* 16 (6), e0253213. <https://doi.org/10.1371/journal.pone.0253213>.
- Fuenzalida, R., Schneider, W., Blanco, J., Garcés-Vargas, J., Bravo, L., 2007. Sistema de corrientes Chile-Perú y masas de agua entre Caldera e Isla de Pascua. *Revista Ciencia y Tecnología del Mar* 30 (2), 5–16.
- Gaurisais, D.Y., de Jonge, D.S.W., Alves, F.M.M., Smith, A.J., Sweetman, A.K., Bernardino, A.F., 2025. Short-term response of an abyssal macrofaunal community to a simulated phytodetrital pulse in the Cabo Verde abyssal basin, northeast tropical

- Atlantic Ocean. *Limnol. Oceanogr.* 70, 521–535. <https://doi.org/10.1002/lno.12775>.
- Glover, A., Paterson, Gordon, Bett, Brian, Gage, John, Sibuet, Myriam, Sheader, Martin, Hawkins, Lawrence, 2001. Patterns in polychaete abundance and diversity from the madeira abyssal plain, northeast Atlantic. *Deep Sea Res. Oceanogr. Res. Pap.* 48 (1), 217–236. [https://doi.org/10.1016/S0967-0637\(00\)00053-4](https://doi.org/10.1016/S0967-0637(00)00053-4).
- Glover, A.G., Smith, C.R., Paterson, G.L.J., Wilson, G.D.F., Hawkins, L., Sheader, M., 2002. Polychaete species diversity in the central Pacific abyss: local and regional patterns, and relationships with productivity. *Mar. Ecol. Prog. Ser.* 240, 157–170. <https://doi.org/10.3354/meps240157>.
- Gálvez-Larach, M., 2009. Seamounts of nazca and salas y gómez: a review for management and conservation purposes. *Lat. Am. J. Aquat. Res.* 37 (3), 479–500. <https://doi.org/10.3856/vol37-issue3-fulltext-16>.
- Gollner, S., Kaiser, S., Menzel, L., Jones, D.O.B., Brown, A., et al., 2017. Resilience of benthic deep-sea fauna to mining activities. *Mar. Environ. Res.* 129, 76–101. <https://doi.org/10.1016/j.marenvres.2017.04.010>.
- González, C., Escribano, R., Bode, A., Schneider, W., 2019. Zooplankton taxonomic and trophic community structure across biogeochemical regions in the eastern south Pacific. *Front. Mar. Sci.* 5, 498. <https://doi.org/10.3389/fmars.2018.00498>.
- Grassle, J., Maciolek, N., 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *Am. Nat.* 139 (2), 313–341. <https://doi.org/10.1086/285329>.
- Hammer, O., Harper, D., Ryan, P., 2001. PAST: paleontological statistics software package for education and data analysis. *Paleontol. Electron.* 4 (1), 9. <https://folk.uio.no/ohammer/past/>.
- Harris, P., Macmillan-Lawler, M., Rupp, J., Baker, E., 2014. Geomorphology of the oceans. *Mar. Geol.* 352 (1), 4–24. <https://doi.org/10.1016/j.margeo.2014.01.011>.
- Heip, C., Vincx, M., Vranken, G., 1985. The ecology of marine nematodes. *Oceanogr. Mar. Biol. Annu. Rev.* 23, 399–489.
- Henry, L.A., Vad, J., Findlay, H., Murillo, J., Milligan, R., Roberts, J., 2014. Environmental variability and biodiversity of megabenthos on the hebrides terrace seamount (northeast Atlantic). *Nature* 5589. <https://doi.org/10.1038/srep05589>.
- Hessler, R., Jumars, P., 1974. Abyssal community analysis from replicate box cores in the central north Pacific. *Deep-Sea Res.* 21, 185–209. [https://doi.org/10.1016/0011-7471\(74\)90058-8](https://doi.org/10.1016/0011-7471(74)90058-8).
- Horacek, I.I.H., Soto, E., Quiroga, E., Ingels, J., 2022. Meiofaunal nematode abundance, composition, and diversity at bathyal to hadal depths in the southeast Pacific Ocean. *Deep-Sea Res., Part A* 188, 103837. <https://doi.org/10.1016/j.dsr.2022.103837>.
- Ichino, M., Clark, M., Drzen, J., Jamieson, A., Jones, D., Martin, A., Rowden, A., Shank, T., Yancey, P., Ruhl, H., 2015. The distribution of benthic biomass in hadal trenches: a modelling approach to investigate the effect of vertical and lateral organic matter transport to the seafloor. *Deep. Sea. Res. Part. I* 100, 21–33. <https://doi.org/10.1016/j.dsr.2015.01.010>.
- Jamieson, A.J., 2015. *The Hadal Zone: Life in the Deepest Oceans*. Cambridge University Press. <https://doi.org/10.1017/CBO9781139061384>.
- Jumars, P., Hessler, R., 1976. Hadal community structure: implications from the aleutian trench. Reprint from. *J. Mar. Res.* 34 (4).
- Kamenev, G., Mordukhovich, V., Alalyskina, I., Chernyshev, G., Maiorova, A., 2022. Macrofauna and nematode abundance in the abyssal and hadal zones of interconnected deep-sea ecosystems in the kuril basin (sea of okhotsk) and the kuril-kamchatka trench (pacific ocean). *Front. Mar. Sci.* 9, 812464. <https://doi.org/10.3389/fmars.2022.812464>.
- Kim, S., Wessel, P., 2011. New global seamount census from altimetry-derived gravity data. *Geophys. J. Int.* 186, 615–631. <https://doi.org/10.1111/j.1365-246X.2011.05076.x>.
- Koslow, J., Gowllett-Holmes, K., Lowry, J., O'Hara, T., Poore, G., Williams, A., 2001. Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Mar. Ecol. Prog. Ser.* 213, 111–125. <https://doi.org/10.3354/meps213111>.
- Kvile, K., Taranto, G., Pitcher, T., Morato, T., 2014. A global assessment of seamount ecosystems knowledge using an ecosystem evaluation framework. *Biol. Conserv.* 173, 108–120. <https://doi.org/10.1016/j.biocon.2013.10.002>.
- Lampitt, R., 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. *Deep-Sea Res. Part A-Oceanogr. Res. Papers* 32, 885–897. [https://doi.org/10.1016/0198-0149\(85\)90034-2](https://doi.org/10.1016/0198-0149(85)90034-2).
- Leduc, D., Nodder, S.D., Rowden, A.A., Gibbs, M., Berkenbusch, K., Wood, A., De Leo, F., Smith, C., Brown, J., Bury, S.J., Pallentin, A., 2020. Structure of infaunal communities in New Zealand submarine canyons is linked to origins of sediment organic matter. *Limnol. Oceanogr.* 1–25. <https://doi.org/10.1002/lno.11454>.
- Levin, L., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. *Annual Review of Ecology and Systems* 32, 51–93. <https://doi.org/10.1146/annurev.ecolsys.32.081501.114002>.
- Levin, L.A., Thomas, C.L., 1989. The influence of hydrodynamic regime on infaunal assemblages inhabiting carbonate sediments on central Pacific seamounts. *Deep-Sea Res., Part A* 36, 1897–1915. [https://doi.org/10.1016/0198-0149\(89\)90117-9](https://doi.org/10.1016/0198-0149(89)90117-9).
- Lins, L., Zeppilli, D., Menot, L., Michel, L.N., Bonifacio, P., Brandt, M., Pape, E., Rossel, S., Uhlenkott, K., Macheriotou, L., Bezerra, T., Sanchez, N., Alfaro-Lucas, J. M., Martínez Arbizu, P., Kaiser, S., Murakami, C., Vanreusel, Ann, 2021. Toward a reliable assessment of potential ecological impacts of deep-sea polymetallic nodule mining on abyssal infauna. *Limnol. Oceanogr. Methods* 19, 626–665. <https://doi.org/10.1002/lom3.10448>.
- Lorenzen, C., 1967. Determination of chlorophyll and Pheo-pigments: spectrophotometric equations. *Limnol. Oceanogr.* 12 (2), 343–346. <https://doi.org/10.4319/lno.1967.12.2.0343>.
- Lourido, A., Parra, S., Serrano, A., 2024. Bathyal infaunal communities from a deep seamount (galicia bank, northeast Atlantic). *Sci. Mar.* 88 (3), e088. <https://doi.org/10.3989/scimar.05514.088>.
- Mecho, A., Dewitte, B., Sellanes, J., van Genrip, S., Easton, E., Gusmao, J., 2021. Environmental drivers of mesophotic echinoderm assemblages of the southeastern Pacific Ocean. *Deep-Sea Environments and Ecology* 8, 574780. <https://doi.org/10.3389/fmars.2021.574780>.
- Meyers, P., 1994. Preservation of elemental and isotopic source identification of sedimentary organic matter. *Chem. Geol.* 114 (3–4), 289–302. [https://doi.org/10.1016/0009-2541\(94\)90059-0](https://doi.org/10.1016/0009-2541(94)90059-0).
- Mironov, A.N., Molodtsova, T.N., Parin, N., 2006. *Soviet and Russian Studies on Seamount Biology*.
- Müller, P., 1977. CN ratios in Pacific deep-sea sediments: effect of inorganic ammonium and organic nitrogen compounds sorbed by clays. *Geochem. Cosmochim. Acta* 41 (6), 765–776. [https://doi.org/10.1016/0016-7037\(77\)90047-3](https://doi.org/10.1016/0016-7037(77)90047-3).
- Montagna, P.A., Baguley, J.G., Hsiang, C.Y., Reuscher, M.G., 2017. Comparison of sampling methods for deep-sea infauna. *Limnol. Oceanogr. Methods* 15, 166–183. <https://doi.org/10.1002/lom3.10150>.
- Morato, T., Hoyle, S., Allain, V., Nicol, S., 2010. Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proc. Natl. Acad. Sci. USA* 107 (21), 9707–9711. <https://doi.org/10.1073/pnas.0910290107>.
- Morel, A., Claustre, H., Gentili, B., 2010. The most oligotrophic subtropical zones of the global ocean: similarities and differences in terms of chlorophyll and yellow substance. *Biogeosciences* 7, 3139–3151. <https://doi.org/10.5194/bg-7-3139-2010>.
- Newman, W., Foster, B., 1983. The Rapaunian faunal district (easter and salas y gómez), in search of ancient archipelagos. *Bull. Mar. Sci.* 33 (3), 633–644.
- Nomaki, H., Rastelli, E., Alves, A., Suga, H., Ramos, S., Kitahashi, T., Tsuchiya, M., Ogawa, N., Matsui, Y., Seike, K., Miyamoto, N., Corinaldesi, C., Manea, E., Ohkouchi, N., Danovaro, R., Nunoura, T., Amaro, T., 2021a. Abyssal fauna, benthic microbes, and organic matter quality across a range of trophic conditions in the Western Pacific Ocean. *Prog. Oceanogr.* 195, 102591. <https://doi.org/10.1016/j.pocean.2021.102591>.
- Nomaki, H., Rastelli, E., Ogawa, N.O., Matsui, Y., Tsuchiya, M., Manea, E., Corinaldesi, C., Hirai, M., Ohkouchi, N., Danovaro, R., Nunoura, T., Amaro, T., 2021b. In situ experimental evidences for responses of abyssal benthic biota to shifts in phytodetritus compositions linked to global climate change. *Glob. Change Biol.* 27, 6139–6155. <https://doi.org/10.1111/gcb.15882>.
- Parin, N., Mironov, K. Nesis, 1997. Biology of the nazca and sala y gomez submarine ridges, an outpost of the indo-west Pacific fauna in the eastern Pacific Ocean: composition and distribution of the fauna, its communities and history. *Adv. Mar. Biol.* 32, 145–242. [https://doi.org/10.1016/S0065-2881\(08\)60017-6](https://doi.org/10.1016/S0065-2881(08)60017-6).
- Parsons, T., Maita, Y., Lalli, C., 1984. *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, Oxford, p. 173. <https://doi.org/10.25607/OBP-1830>.
- Pasotti, F., Mevenkamp, Lisa, Pape, Ellen, Błażewicz, Magdalena, Bonifácio, Paulo, Riehl, Torben, De Smet, Bart, Lefaible, Nene, Lins, Lidia, Ann, Vanreusel, 2021. A local scale analysis of manganese nodules influence on the clarion-clipperton fracture zone macrobenthos. *Deep Sea Res. Oceanogr. Res. Pap.* 168, 103449. <https://doi.org/10.1016/j.dsr.2020.103449>.
- Pedrosa-Pamies, R., Parinos, C., Sánchez-Vidal, A., Gogou, A., Calafat, A., Canals, M., Bouloubassi, I., Lampadariu, N., 2015. Composition and sources of sedimentary organic matter in the deep eastern Mediterranean Sea. *Biogeosciences* 12, 7379–7402. <https://doi.org/10.5194/bg-12-7379-2015>.
- Peters, B., Jenkins, W., Swift, J., German, C., Moffert, J., Cutter, G., Brzenzinski, M., Casciotti, K., 2018. Water mass analysis of the 2013 US GEOTRACES eastern Pacific zonal transect (GP16). *Mar. Chem.* 201, 6–19. <https://doi.org/10.1016/j.marchem.2017.09.007>.
- Pilditch, C., Leduc, D., Nodder, S., Probert, P., Bowden, D., 2015. Spatial patterns and environmental drivers of benthic infaunal community structure and ecosystem function on the New Zealand Continental margin. *N. Z. J. Mar. Freshwater Res.* 37–41. <https://doi.org/10.1080/00288330.2014.995678>.
- Poulton, A.J., Sanders, R., Holligan, P.M., Stinchcombe, M.C., Adey, T.R., et al., 2006. Phytoplankton mineralization in the tropical and subtropical Atlantic Ocean. *Global Biogeochem. Cycles* 20, GB4002. <https://doi.org/10.1029/2006GB002712>.
- Preikschart, M., Di Franco, D., Kelch, A., Meißner, Karin, Brandt, A., Kaiser, S., 2025. Abyssal and hadal macroinfaunal assemblages in the eastern aleutian trench (NE Pacific). *Prog. Oceanogr.* 237, 103508. <https://doi.org/10.1016/j.pocean.2025.103508>.
- Quiroga, E., Ortiz, P., González-Saldías, R., Reid, B., Tapia, F., Pérez-Santos, I., Rebolledo, L., Mansilla, R., Pineda, C., Cari, I., Salinas, N., Montiel, A., Gerdes, D., 2016. Seasonal benthic patterns in a glacial Patagonian fjord: the role of suspended sediment and terrestrial organic matter. *Mar. Ecol. Prog. Ser.* 561, 31–50. <https://doi.org/10.3354/meps11903>.
- Rex, M., Etter, R., Morris, J., Crouse, J., McClain, G., Johnson, N., Stuart, C., Deming, J., Thies, R., Avery, R., 2006. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Mar. Ecol. Prog. Ser.* 317, 1–8. <https://doi.org/10.3354/meps317001>.
- Rogers, A., 2018. The biology of seamounts: 25 years on. *Adv. Mar. Biol.* 79, 137–224. <https://doi.org/10.1016/bs.amb.2018.06.001>.
- Rowden, A., Schlacher, T., Williams, A., Clark, M., Stewart, R., Althaus, F., Bowden, D., Consalvey, M., Robinson, W., Dowdney, J., 2010. A test of the seamount oasis hypothesis: seamounts support higher epibenthic megafaunal biomass than adjacent slopes. *Mar. Ecol. Prog. Ser.* 317, 95–106. <https://doi.org/10.1111/j.1439-0485.2010.00369.x>.

- Rumolo, P., Barra, M., Gherardi, S., Marsella, E., Sprovieri, M., 2011. Stable isotopes and C/N ratios in marine sediments as a tool for discriminating anthropogenic impact. *J. Environ. Monit.* 13 (12), 3399–3408. <https://doi.org/10.1039/C1EM10568J>.
- Schmidt, C., Sattarova, V.V., Katrynski, L., Arbizu, P.M., 2019. New insights from the deep: meiofauna in the kuril-kamchatka trench and adjacent abyssal plain. *Prog. Oceanogr.* 173, 192–207.
- Schmidt, C., Arbizu, P.M., 2015. Unexpectedly higher metazoan meiofauna abundances in the kuril-kamchatka trench compared to the adjacent abyssal plains. *Deep Sea Res. Part II* 111, 60–75.
- Shimabukuro, M., Zeppilli, D., Leduc, D., Wenzhöfer, F., Berg, P., Rowden, A.A., Glud, R. N., 2022. Intra- and inter-spatial variability of meiofauna in hadal trenches is linked to microbial activity and food availability. *Sci. Rep.* 12, 4338. <https://doi.org/10.1038/s41598-022-08088-1>.
- Smith, C.R., De Leo, F., Bernardino, A., Sweetman, A., Arbizu, P., 2008. Abyssal food limitation, ecosystem structure and climate change. *Trends Ecol. Evol.* 23 (9), 518–528. <https://doi.org/10.1016/j.tree.2008.05.002>.
- Staudigel, H., Clague, D., 2010. The geological history of deep-sea volcanoes: biosphere, hydrosphere, and lithosphere interactions. *Oceanography (Wash. D. C.)* 23, 10–5670. <https://doi.org/10.1007/bf00347841>.
- Tapia, R., Ho, S., Núñez-Ricardo, S., Marchant, M., Lamy, F., Hebbeln, D., 2021. Increased marine productivity in the southern humboldt current system during MIS 2-4 and 10-11. *Paleoceanogr. Paleoclimatol.* 36. <https://doi.org/10.1029/2020PA004066> e2020PA004066.
- Tapia-Guerra, J., Mecho, A., Easton, E., De los Angeles, M., Gomy, M., Sellanes, J., 2021. First description of deep benthic habitats and communities of Oceanic islands and seamounts of the nazca desventuradas marine park, Chile. *Nature Sci. Rep.* 11, 6209. <https://doi.org/10.1038/s41598-021-85516-8>.
- Thurber, A.R., Sweetman, A.K., Narayanaswamy, B.E., Jones, D.O.B., Ingels, J., Hansman, R.L., 2013. Ecosystem function and services provided by the deep sea. *Biogeosci. Discuss.* 10 (11), 18193–18240. <https://doi.org/10.5194/bgd-10-18193-2013>.
- Von Dassow, P., Collado-Fabri, S., 2014. Biological oceanography, biogeochemical cycles, and pelagic ecosystem functioning of the east-central south Pacific gyre: focus on easter island and salas y gómez island. *Lat. Am. J. Aquat. Res.* 42 (4), 703–742. <https://doi.org/10.3856/vol42-issue4-fulltext-4>.
- Wagner, D., Van der Meer, L., Gorny, M., Sellanes, J., Gaymer, C., Soto, E., Easton, E., Friedlander, A., Lindsay, D., Molodtsova, T., Boteler, B., Durussel, C., Gjerde, K., Currie, D., Gianni, M., Brooks, C., Shipley, M., Willhelm, T., Quesada, M., Thomas, T., Dunstan, P., Clark, N., Villanueva, L., Pyle, R., Clark, M., Georgian, S., Morgan, L., 2021. The salas y gomez and nazca ridges: a review of the importance, opportunities and challenges for protecting a global diversity hotspot on the high seas. *Mar. Pol.* 126, 104377. <https://doi.org/10.1016/j.marpol.2020.104377>.
- Warwick, R., Clarke, K., 1993. Comparing the severity of disturbance: a meta-analysis of marine macrobenthic community data. *Mar. Ecol. Prog. Ser.* 92, 221–231, 0.3354/meps092221.
- Washburn, T., Menot, L., Bonifácio, P., Pape, E., Błażewicz, M., Bribiesca-Contreras, G., Dahlgren, T., Fukushima, T., Glover, A., Ju, S., Kaiser, S., Yu, O., Smith, C., 2021. Patterns of macrofaunal biodiversity across the clarion-clipperton zone: an area targeted for seabed mining. *Front. Mar. Sci.* 8, 626571. <https://doi.org/10.3389/fmars.2021.626571>.
- Watling, L., Guinotte, J., Clark, M., Smith, C., 2013. A proposed biogeography of the deep ocean floor. *Prog. Oceanogr.* 111, 91–112. <https://doi.org/10.1016/j.pocean.2012.11.003>.
- Wei, C.L., Rowe, G., Hubbard, G., Scheltema, A., Wilson, G., Petrescu, I., Foster, J., Wicksten, M., Chen, M., Davenport, R., Soliman, Y., Wang, Y., 2010. Bathymetric zonation of deep-sea macrofauna in relation to export of surface phytoplankton production. *Mar. Ecol. Prog. Ser.* 399, 1–14. <https://doi.org/10.3354/meps08388>.
- Wei, C.L., Rowe, G., 2019. Productivity controls macrofauna diversity in the deep northern Gulf of Mexico. *Deep Sea Res. Oceanogr. Res. Pap.* 143, 17–27. <https://doi.org/10.1016/j.dsr.2018.12.005>.
- Whelan, J., 1977. Amino acids in a surface sediment core of the Atlantic abyssal plain. *Geochem. Cosmochim. Acta* 41 (6), 803–810. [https://doi.org/10.1016/0016-7037\(77\)90050-3](https://doi.org/10.1016/0016-7037(77)90050-3).
- Wilson, G., 2017. Macrofauna abundance, species diversity and turnover at three sites in the clipperton-clarion fracture zone. *Mar. Biodivers.* 47, 323–347. <https://doi.org/10.1007/s12526-016-0609-8>.
- Witte, U., 2000. Vertical distribution of metazoan macrofauna within the sediment at four sites with contrasting food supply in the deep Arabian Sea. *Deep Sea Res. Part II* 47 (14), 2979. [https://doi.org/10.1016/S0967-0645\(00\)00055-2](https://doi.org/10.1016/S0967-0645(00)00055-2), 2997.
- Yesson, C., Clark, M., Taylor, M., Rogers, A., 2011. The global distribution of seamounts based on 30 arc seconds bathymetry data. *Deep-Sea Res., Part A* 58 (4), 442–453. <https://doi.org/10.1016/j.dsr.2011.02.004>.
- Yu, O., Lee, H., Kim, D., Hee, J., Kim, K., Yoo, C., 2018. Characterization of deep-sea macrofauna in the Korean exploration claim area in the clarion-clipperton fracture zone. *Northeastern Pacific Ocean. Ocean Sci. J.* 53 (2), 301–314. <https://doi.org/10.1007/s12601-018-0029-8>.
- Zar, J.H., 2005. Spearman Rank Correlation, vol. 7. *Encyclopedia of Biostatistics*. <https://doi.org/10.1136/bmj.g7327>.