

ARTICLE

Distribution and abundance of planktonic mollusks along a longitudinal gradient in the Southeastern Pacific off Chile

Distribución y abundancia de moluscos planctónicos en un gradiente longitudinal en el Pacífico suroriental frente a Chile

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Resumen.- Los objetivos de esta investigación fueron estimar la abundancia de los principales grupos de moluscos planctónicos (larvas meroplancónicas, gasterópodos holoplancónicos y paralarvas de cefalópodos) y relacionarla con las propiedades fisicoquímicas del agua, a lo largo de un gradiente longitudinal entre Caldera en la costa continental de Chile y la ecorregión de Isla de Pascua (Isla de Rapa Nui e Isla Salas y Gómez), en el sureste del océano Pacífico. Se recolectaron muestras de plancton durante el Crucero CIMAR 21-Islas, en octubre y noviembre de 2015, en 33 estaciones oceanográficas con una red WP2 (180 µm de abertura de malla) en lances verticales entre los 300 m de profundidad y la superficie del mar. Los moluscos se clasificaron, contaron y asignaron inicialmente a nivel de Clase, para su posterior identificación en niveles taxonómicos inferiores. Se obtuvieron moluscos planctónicos en todas las estaciones, con 92,7% de Gastropoda y 7,3% de Bivalvia. La abundancia total de moluscos varió entre 55 y 4.922 individuos 100 m⁻³. Los gasterópodos Euthecosomata exhibieron la mayor ocurrencia en el área oceánica. No se obtuvieron paralarvas. Las diferencias en la composición de los moluscos planctónicos entre las zonas continental y oceánica se hicieron evidentes. Las larvas de bivalvos aumentaron su abundancia en aguas más cálidas, saladas y verticalmente mezcladas. Estos resultados son el primer registro de moluscos meroplancónicos en aguas cercanas a las islas oceánicas chilenas. Los moluscos planctónicos presentan una variación espacial a escala de la cuenca del Pacífico Sur, relacionada con las condiciones hidrográficas y la estructura de la columna de agua.

Palabras clave: Meroplancton, holoplancton, ecología larval, Rapa Nui, islas oceánicas

Abstract.- The objectives of this research were to estimate the abundance of the main groups of planktonic mollusks (meroplanktonic larvae, holoplanktonic gastropods and cephalopod paralarvae), and relate these groups to the physical-chemical water properties along a longitudinal gradient between Caldera, on the coast of mainland Chile, and the Easter Island ecoregion (Rapa Nui Island and Salas y Gómez Island), in the Southeast Pacific Ocean. Plankton samples were collected over the course of the CIMAR 21-Islas Cruise, from October to November 2015, at 33 oceanographic stations via vertical hauls of a WP2 net (180-µm mesh size) from a maximum depth of 300 m to the sea surface. Mollusks were sorted, counted and initially assigned to Class rank, later being identified to lower taxonomic ranks. Planktonic mollusks were obtained at all stations, and were composed of 92.7% of Gastropoda and 7.3% of Bivalvia. The total abundance of mollusks varied between 55 and 4,922 individuals 100 m⁻³. Euthecosomate gastropods exhibited the highest occurrence within the oceanic area. Meanwhile, no paralarvae were captured. Differences in the composition of planktonic mollusks between the continental and oceanic zones were evident. Bivalve larvae increased their abundance in warmer, salty and vertically mixed waters. These results are the first record of meroplanktonic mollusks in waters near the Chilean oceanic islands, and suggest that planktonic mollusks display spatial variation at the scale of the South Pacific Basin, which could be related to the hydrographic conditions and the water column structure.

Key words: Meroplankton, holoplankton, larval ecology, Rapa Nui, oceanic islands

INTRODUCTION

The Southeast Pacific region is characterized by a remarkable zonal gradient in both productivity and oceanographic conditions, from the highly productive and cold Humboldt Current ecosystem ($>20 \text{ mg m}^{-3}$ Chl-*a*) in the coastal zone to the oligotrophic/ultra-oligotrophic South Pacific central gyre ($<0.02 \text{ mg m}^{-3}$ Chl-*a*) (von Dassow & Collado-Fabbri 2014, Meerhoff *et al.* 2018, Espinosa-Leal *et al.* 2021). These contrasting water mass properties across the zonal gradient may exert a strong influence on the distributional patterns of planktonic organisms (Espinosa-Leal *et al.* 2021).

Planktonic mollusks play an important role in ocean trophic dynamics, by supporting secondary consumers which also inhabit the water column (Young & Chia 1987), as well as in the biodiversity conservation, since their absence, presence or abundance in a given place can be used as indicators of environmental change (Shelton 2014). In addition, the geographic dispersion of adult populations may reflect characteristics of the life history of the species (Botsford *et al.* 2001, Shanks 2001, Young 2002, Trakhtenbrot *et al.* 2005).

Most benthic mollusks develop larvae in the water column as components of meroplankton, remaining as part of the planktonic community for a few hours up to months, or even years, depending on the species, environmental conditions and food availability (Scheltema 1986a, Pechenik 1987, Strathmann & Strathmann 2007). Most of the mollusk larvae are either actaeplanic or teleplanic (Strathmann & Strathmann 2007), the latter having the ability to be transported long distances (Shanks 1995). On the other hand, gastropod mollusks of the Order Pteropoda and the Superfamily Pterotracheoidea (=Heteropoda) develop their whole life cycle (larva, juvenile and adult) in the water column, forming part of the holoplankton. These gastropod groups are of particular importance because some species act as sensitive indicators of water masses (Chen & Hillman 1970) and climate change (Hughes 2000), as well as playing an important role in the marine food web (Wall-Palmer *et al.* 2016). Cephalopod paralarvae and juveniles also form part of the planktonic mollusk community. Along with the other planktonic mollusks, they play a key role in marine food webs and have been considered potential indicators of environmental change (García-Guillén *et al.* 2018).

Planktonic mollusks from the Southeast Ocean off north-central Chile have mainly been the subject of general zooplankton studies or the identification of selected species (Fagetti 1958, 1968; Fagetti & Fischer 1964, Palma *et al.* 1976, Prado 1983, Campos & Ramorino 1984, Palma & Rosales 1995, Vega *et al.* 1999, Poulin *et al.* 2002a, b; Romero & Valdebenito 2002, Labrín *et al.* 2015, Torreblanca *et al.* 2016, Carrasco *et al.* 2019). However, the knowledge concerning the distribution and abundance of these groups is

very scarce especially in oceanic areas. It was hypothesized that the main groups of planktonic mollusks would exhibit distribution and abundance patterns along the longitudinal gradient between Caldera and the Easter Island ecoregion (Rapa Nui Island and Salas y Gómez Island) according to the environmental conditions of the water column (*i.e.* groups related to coastal/productive waters, oceanic/oligotrophic waters, and around islands). The objectives of this study were to determine the abundance of main planktonic mollusks groups along a longitudinal transect between Caldera and the Easter Island ecoregion, and to relate their distribution with the physical-chemical characteristics of the water column.

MATERIALS AND METHODS

This study was carried out along a longitudinal transect between Caldera (~27°S-70.1°W), on the continental coast, and the Easter Island ecoregion (Rapa Nui Island, 27°S-109°22'W and Salas y Gómez Island, 26°28'S, 105°21'W), Chile (Fig. 1), during the oceanographic cruise CIMAR 21-Islas, from October 13th to November 4th (austral spring) 2015, onboard the Chilean Navy research vessel AGS "Cabo de Hornos".

The continental coast of Caldera is influenced by Equatorial Subsurface Water and upwelling processes, generating a system high in nutrients. While towards Rapa Nui, the mesotrophic transition and oligotrophic zones are composed by Sub Antarctic Water and Subtropical Water, respectively, with lower nutrient concentrations compared to the coastal zone (González *et al.* 2020). The sea surface water temperatures and salinities, from the coast to the open ocean, range from 14.9 to 21.4 °C and from 34.7 to 35.9, respectively. A well-oxygenated surface layer ($>5 \text{ mL L}^{-1}$) has been recorded all along the latitudinal gradient, however its depth ranges from ~35 m, near the coast, to ~215 m, in the open ocean (Espinosa-Leal *et al.* 2021).

Mollusks were obtained from 60 plankton samples collected at 33 sampling stations (Fig. 1). At each station, samples were obtained by means of vertical tows of a WP2 net (180-μm mesh size), equipped with a TSK flowmeter, down to a maximum depth of 300 m. The collected samples were preserved onboard with 96% ethanol. Once in the laboratory, this fixative was replaced with a solution of 96% ethanol with sodium glycerophosphate (pH> 8.5). Each mollusk was manually removed from the sample under a Leica MZ8 stereo microscope and preserved in 96% ethanol with sodium glycerophosphate. Every specimen was first assigned to one of the following Classes: Bivalvia or Gastropoda. Since gastropods have both holoplanktonic and meroplanktonic representatives, specimens of this Class were classified into three groups: 1. Meroplanktonic larvae (from benthic species), 2. Order Pteropoda and 3. Superfamily Pterotracheoidea (=Heteropoda), based on Bouchet *et al.* (2017).

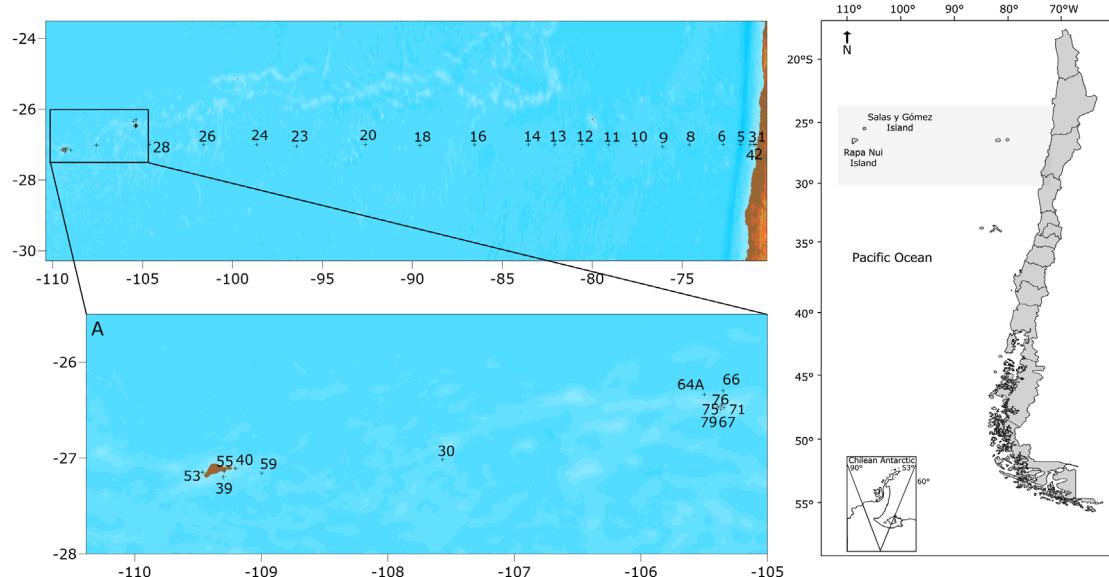


Figure 1. Location of the oceanographic stations of the CIMAR 21-Islands cruise, from October 13th to November 4th, 2015. A) Rapa Nui (left) and Salas y Gómez (right) island stations / Ubicación de las estaciones oceanográficas del crucero CIMAR 21-Islands, desde el 13 de octubre al 4 de noviembre, 2015. A) estaciones en las islas Rapa Nui (izquierda) y Salas y Gómez (derecha)

The abundance of mollusks was standardized in number of individuals · 100 m⁻³ (indiv. 100 m⁻³). Salinity, water temperature and dissolved oxygen data were recorded using a Seabird SB-19 CTD (conductivity/temperature/depth profiler) at each sampling station. The environmental conditions were also characterized by vertical temperature, salinity and oxygen gradients, $\Delta V = V_{\text{sup}} - V_{200m}$, where V_{sup} is the surface value and V_{200m} is the value measured at 200 m depth for each of the corresponding variables. Prior to the correlation analyses between environmental variables and standardized mollusk abundances, the normality of the data was checked by means of the Shapiro-Wilk test. Since most of the analyzed variables did not fulfill the normality assumption ($P < 0.05$), the Spearman rank correlation was applied.

Adobe® Photoshop CS6 13.0 was used for editing the digital images of the mollusks. Global Mapper (Blue Marble Geographics)¹ and Surfer® 10 Golden Software, Llc; USA) software programs were used for graphics.

Comparisons were made between groups of stations, which were divided into oceanic waters (O), Rapa Nui Island

(RN) and Salas y Gómez Island (SG). The standardized abundances of heteropods, pteropods and gastropod larvae were utilized for comparisons. A Principal Component Analysis (PCA) was applied to compare the mollusk composition among locations and was tested via a one-way PERMANOVA (Anderson 2001), using Bray-Curtis similarity index. All statistical analyses were carried out using Past 3.26 software (Hammer *et.al* 2001).

RESULTS

Planktonic mollusks were represented by larvae and juvenile Pteropoda Euthecosomata, Gymnosomata and Pterotracheoidea gastropods (holoplankton) as well as by larvae of benthic bivalves and gastropods (meroplankton), (Fig. 2). Cephalopod paralarvae were not captured.

The holoplanktonic Euthecosomata gastropods were represented by larvae and juveniles of the families Cavoliniidae (*Cavolinia* spp., *Diacria* spp.), Cliidae (*Clio* spp.), Creseidae (*Creseis* spp., *Hyalocylis striata*), Cuvierinidae (*Cuvierina* sp.) and Limacinidae (*Limacina* spp.). While, the Pseudothecosomata were represented by juveniles and adults of the families Desmopteridae (*Desmopterus pacificus*) and Peraclidae (*Peraclae* spp.), and the Gymnosomata were only represented by larvae of the family Clionidae. The Pterotracheoidea were represented by larvae and juveniles of the family Atlantidae (*Atlanta* spp.).

¹<<https://www.bluemarblegeo.com/>>

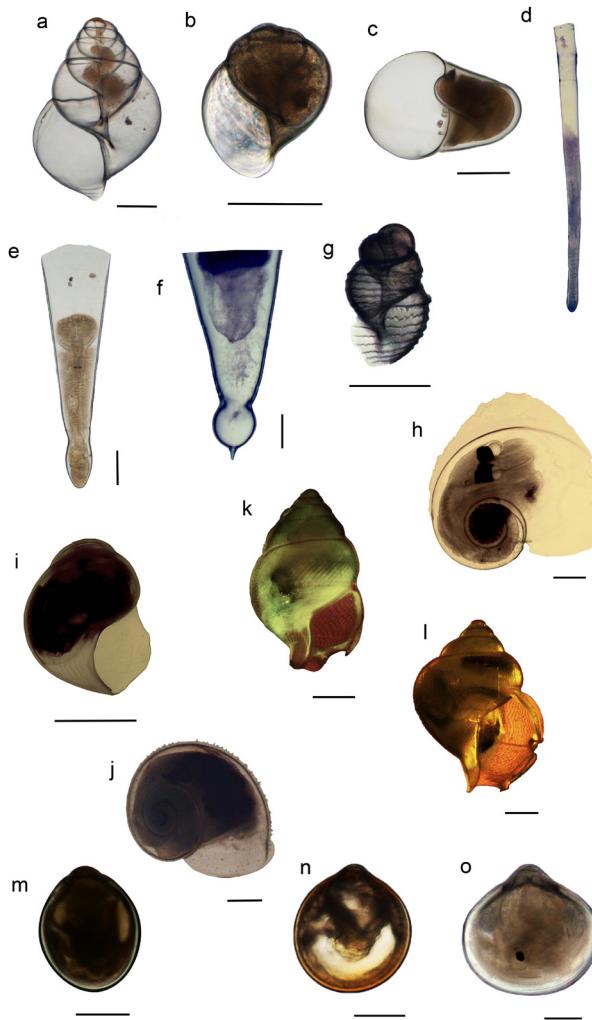


Figure 2. Selection of planktonic mollusks collected during the CIMAR-21 Cruise: a= *Limacina bulimoides*, b= *Limacina* sp., c= *Heliconoides inflatus*, d= *Creseis acicula*; e= *Diacria quadridentata*, f= *Clio cuspidata*; g= larva of *Atlanta* sp., h= adult *Atlanta* sp.; i-l= unidentified meroplanktonic gastropod larvae; m= larva of Teredinidae bivalve, n, o= unidentified bivalve larvae. Scale bars: a-l= 200 µm; m-o= 100 µm/ Selección de moluscos planctónicos recolectados durante el crucero Cimar-21: *Limacina bulimoides*, b= *Limacina* sp., c= *Heliconoides inflatus*, d= *Creseis acicula*; e= *Diacria quadridentata*, f= *Clio cuspidata*; g= larva de *Atlanta* sp., h= adulto de *Atlanta* sp.; i-l= larvas meropláncticas no identificadas de gasterópodos; m= larva de bivalvo Teredinidae, n, o= larvas no identificadas de bivalvos. Barras de escala: a-l= 200 µm; m-o= 100 µm

Over 40 morphotypes of gastropod larvae were collected. They were tentatively assigned to the families Neolepetopsidae, Seguenzidae, Trochidae, Cerithiidae, Turritellidae, Capulidae, Epitonidae, Littorinidae, Naticidae, Triphoridae, Rissoidae, Eulimidae, Cymathiidae, Buccinidae, Columbellidae, Nassariidae, Muricidae, Mitridae, Siphonariidae, and to the order Nudibranchia. It was not possible to assign at least 15 morphotypes to their corresponding families. Nineteen morphotypes of bivalve larvae were collected. Fifteen morphotypes were tentatively assigned to the families Mytilidae, Arcidae, Gryphaeidae, Pectinidae, Anomiidae, Cardiidae, Teredinidae, Pholadidae, Lyonsiidae and Hiatellidae, whereas it was not possible to allocate 4 morphotypes to any families. Morphotype description of both benthic bivalve and gastropod larvae is still under way and will be published elsewhere.

DISTRIBUTION AND ABUNDANCE

Planktonic mollusks were collected at all the stations, adding to a total of 12,761 individuals.

The total standardized abundances of planktonic mollusks varied from 55 indiv. 100 m^{-3} (St. 24) in the oceanic area to 4,922 indiv. 100 m^{-3} (St. 4) over the shelf-break off Caldera (Fig. 3). Gastropods constituted 92.7% of the total mollusks collected, while bivalves only represented 7.3%. The percentage of these two Classes varied among stations (Fig. 4), with gastropods dominating over 80% of 27 of the 33 sampled stations. The station (St.) 75, in waters bordering SG, was the only station with a greater abundance of bivalves (59%) than gastropods.

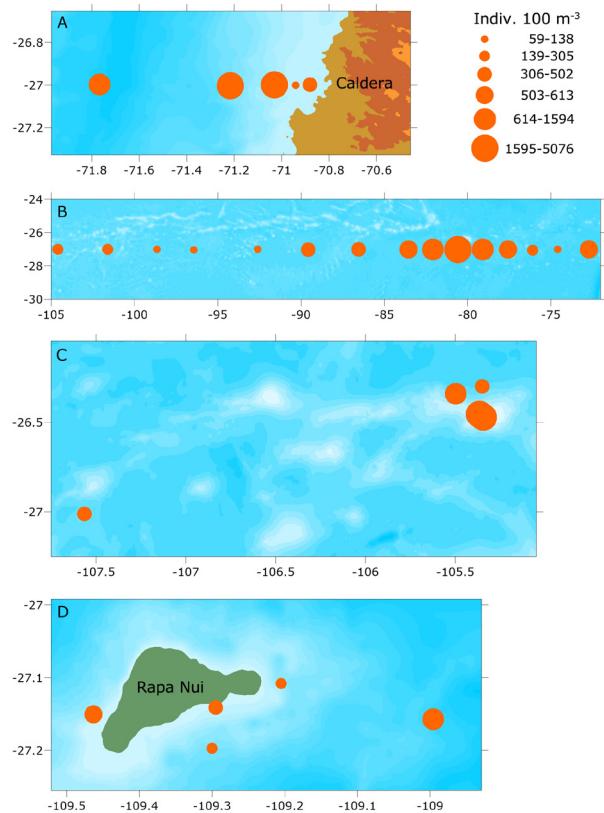


Figure 3. Standardized total abundance (indiv. 100 m³) of planktonic mollusks collected during the CIMAR 21-Islands cruise, from October 13th to November 4th, 2015. A) stations 1-5, B) stations 6-28, C) stations 30 and Salas y Gómez Island, D) stations Rapa Nui Island / Abundancia total estandarizada (indiv. 100 m³) de moluscos planctónicos recolectados durante el crucero CIMAR 21-Islas, desde el 13 de octubre al 4 de noviembre, 2015. A) estaciones 1-5, B) estaciones 6-28, C) estaciones 30 e isla Salas y Gómez, D) estaciones Isla Rapa Nui

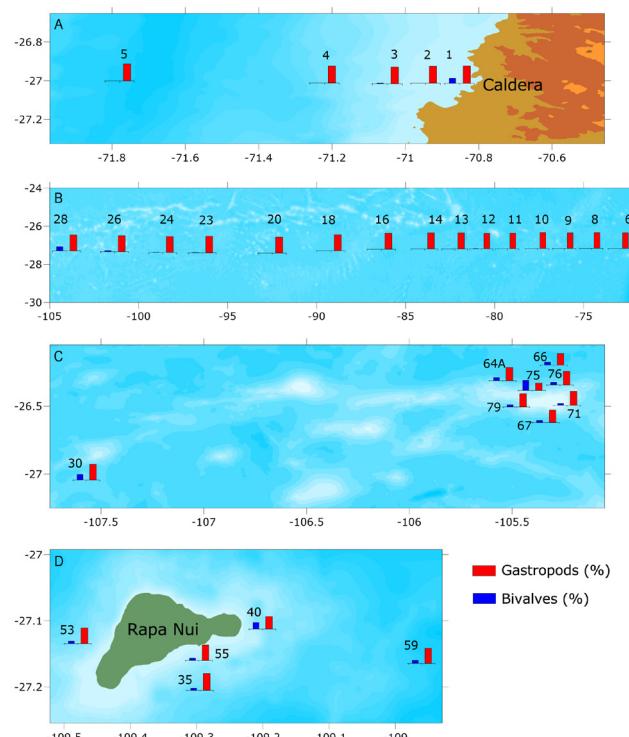


Figure 4. Percentage (%) of gastropods (in red) and bivalves (in blue) collected during the CIMAR 21-Islands cruise, from October 13th to November 4th, 2015. A) stations 1-5, B) stations 6-28, C) stations 30 and Salas y Gómez Island, D) stations Rapa Nui Island / Porcentaje de gasterópodos (en rojo) y bivalvos (en azul) recolectados durante el crucero CIMAR 21-Islas, desde el 13 de octubre al 4 de noviembre, 2015. A) estaciones 1-5, B) estaciones 6-28, C) estaciones 30 e isla Salas y Gómez, D) estaciones Isla Rapa Nui

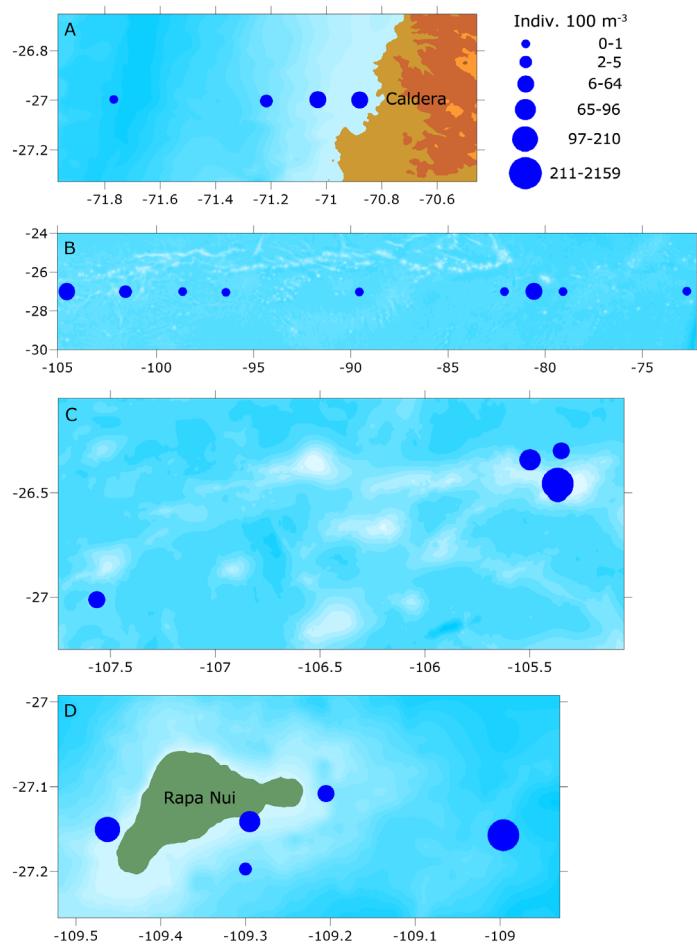


Figure 5. Standardized total abundance (indiv. 100 m⁻³) of bivalve larvae collected during the CIMAR 21-Islas cruise, from October 13th to November 4th, 2015. A) stations 1-5, B) stations 6-28, C) stations 30 and Salas y Gómez Island, D) stations Rapa Nui Island / Abundancia total estandarizada (indiv. 100 m⁻³) de larvas de bivalvos recolectadas durante el crucero CIMAR 21-Islas, desde el 13 de octubre al 4 de noviembre, 2015. A) estaciones 1-5, B) estaciones 6-28, C) estaciones 30 e isla Salas y Gómez, D) estaciones Isla Rapa Nui

Abundance of bivalve larvae was highly variable along the longitudinal transect, ranging from 0 indiv. 100 m⁻³ (St. 2, 8, 9, 10, 14, 16 and 20) to 2,159 indiv. 100 m⁻³ (St. 75) (Fig. 5). Gastropods abundance also varied along the transect, spanning from 57 indiv. 100 m⁻³ (St. 24) to 5,037 indiv. 100 m⁻³ (St. 4) (Fig. 6).

Among the planktonic gastropods, the standardized abundance of heteropods varied between 1 indiv. 100 m⁻³ (St. 9) and 1,171 indiv. 100 m⁻³ (St. 71), with larger abundances around SG (Fig. 7). The standardized abundance of pteropods differed between 4 indiv. 100 m⁻³ (St. 8) and 2,601 indiv. 100 m⁻³ (St. 12). While the

standardized abundance of meroplanktonic gastropod larvae ranged between 4 indiv. 100 m⁻³ (St. 24) and 2,831 indiv. 100 m⁻³ (St. 4), with larger abundances near the continental coast and around SG. Proportions of relative abundances of planktonic gastropods showed clear variations in dominance throughout the studied area. Larvae were dominant in coastal waters over the shelf and in the open ocean, while around Rapa Nui ratios were similar, though heteropods dominated the waters adjacent to Salas y Gómez Island (Fig. 7).

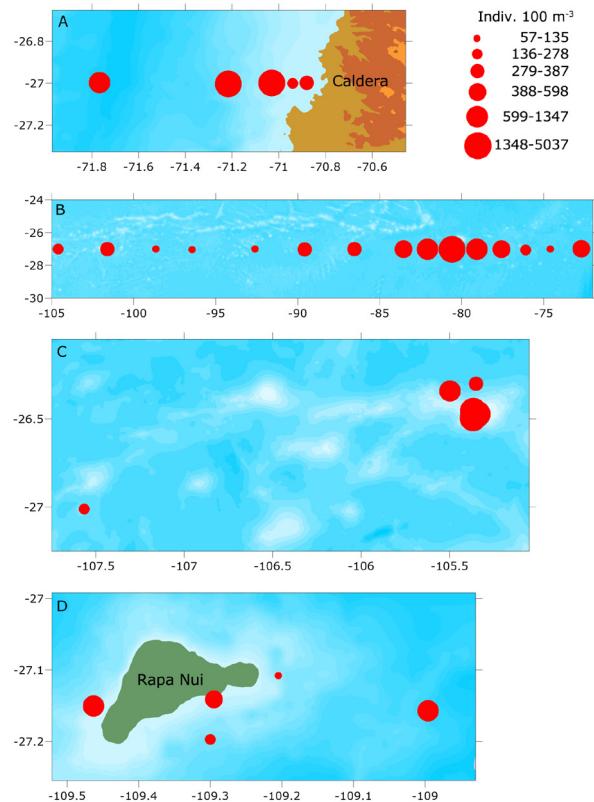


Figure 6. Standardized total abundance (indiv. 100 m³) of planktonic gastropods collected during the CIMAR 21-Islas cruise, from October 13th to November 4th, 2015. A) stations 1-5, B) stations 6-28, C) stations 30 and Salas y Gómez Island, D) stations Rapa Nui Island / Abundancia total estandarizada (indiv. 100 m³) de gasterópodos planctónicos recolectados durante el crucero CIMAR 21-Islas, desde el 13 de octubre al 4 de noviembre, 2015. A) estaciones 1-5, B) estaciones 6-28, C) estaciones 30 e isla Salas y Gómez, D) estaciones Isla Rapa Nui

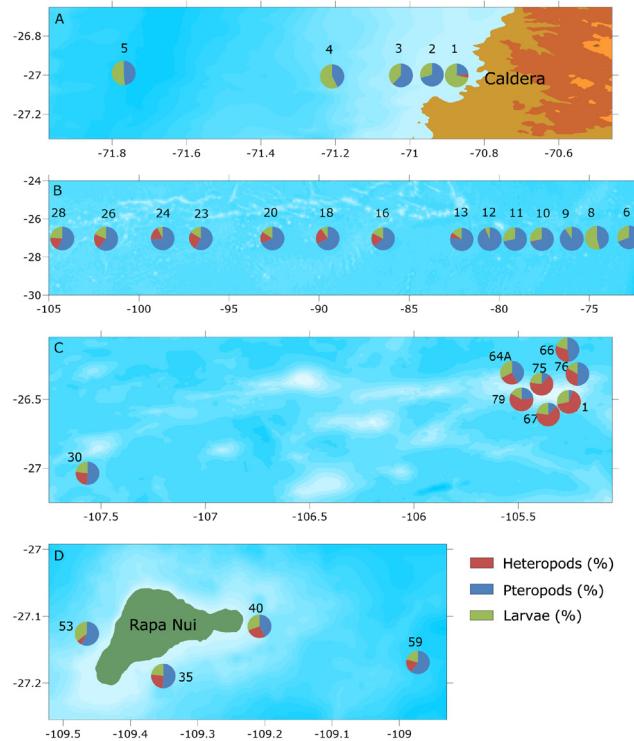


Figure 7. Percentage (%) of Pterotracheoid heteropods (in red), pteropods (in blue) and meroplanktonic gastropod larvae (in green) collected during the CIMAR 21-Islas cruise, from October 13th to November 4th, 2015. A) stations 1-5, B) stations 6-28, C) stations 30 and Salas y Gómez Island, D) stations Rapa Nui Island/ Porcentaje de heterópodos pterotracheoideos (en rojo), pterópodos (en azul) y larvas meropláncticas de gasterópodos (en verde), recolectados durante el crucero CIMAR 21-Islas, desde el 13 de octubre al 4 de noviembre, 2015. A) estaciones 1-5, B) estaciones 6-28, C) estaciones 30 e isla Salas y Gómez, D) estaciones Isla Rapa Nui

MULTIVARIATE ANALYSES

The PCA was explained by three components. PC1 described 74.4% of the variance; PC2 explained 16.3%, while PC3 illustrated only 9.3% (Fig. 8). PC1 was explained by the variability in the abundances of both pteropods (loading factor= 0.798) and gastropod larvae (loading factor= 0.601). PC2 showed variability in the stations around SG, and was positively correlated to larvae (loading factor= 0.661) and heteropods (loading factor= 0.580) (Fig. 8). All the stations executed around Rapa Nui (RN) showed similar compositions, e.g., all sampled stations occurred in a similar multivariate space in the PCA (Fig. 8). One-way PERMANOVA detected significant differences among locations (pseudo- F = 3.24, P = 0.005). Post-hoc analysis showed that, at a major taxonomic group scale, composition and abundance of planktonic mollusks were different between SG and O (Bonferroni-corrected P = 0.011), RN and SG (P = 0.040), but not between RN and O (P = 0.743). Therefore, the planktonic mollusk community along the longitudinal gradient was heterogeneous and differentially represented.

RELATIONSHIP WITH ENVIRONMENTAL VARIABLES

The standardized abundance of total mollusks did not significantly correlate with any of the environmental variables considered in this study ($P > 0.151$), nor did the gastropods ($P > 0.177$). However, the standardized abundance of bivalve larvae showed significant positive correlations with the mean water temperature ($rs= 0.584$, $P < 0.001$), the sea surface temperature ($rs= 0.568$, $P = 0.001$), the mean salinity ($rs= 0.704$, $P < 0.001$) and the sea surface salinity ($rs= 0.626$, $P < 0.001$). On the other hand, the standardized abundance of bivalve larvae showed a negative correlation with the vertical temperature gradient ($rs= -0.541$; $P = 0.002$) and the vertical dissolved oxygen gradient ($rs= -0.542$, $P = 0.002$). In summary, the standardized density of bivalve larvae increased in warmer, salty and vertically more mixed waters, while the hydrographic conditions and the water column structure did not have any significant effect on the abundance of total mollusks or gastropods.

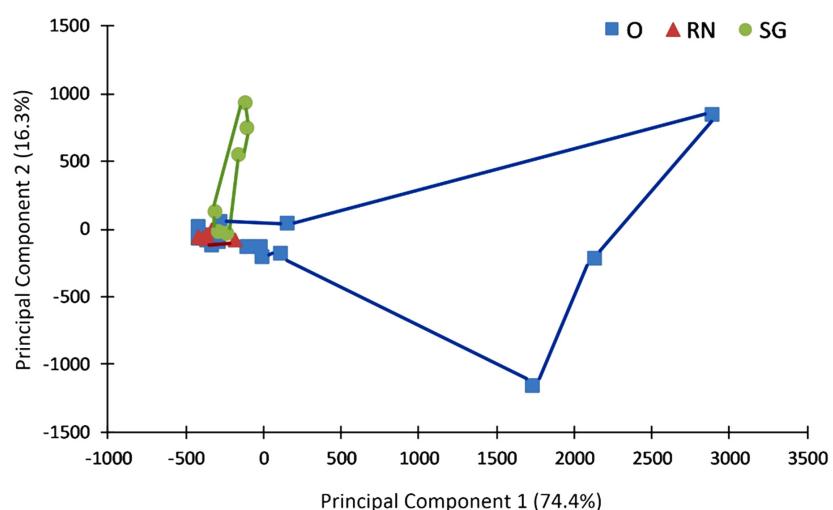


Figure 8. Principal Component Analysis (PCA) of composition and abundance of planktonic gastropods collected during austral spring 2015 in Southeast Pacific Ocean. O= oceanic, RN= Rapa Nui Island, SG= Salas y Gómez Island / Análisis de Componentes Principales (PCA) de la composición y abundancia de gasterópodos planctónicos recolectados durante la primavera austral 2015 en el océano Pacífico Sureste. O= oceánico, RN= isla Rapa Nui, SG= isla Salas y Gómez

DISCUSSION

DISTRIBUTION AND ABUNDANCE

The spatial distributional patterns of planktonic mollusks clearly exhibited a longitudinal gradient along the South Pacific, from continental coastal waters to oligotrophic oceanic waters, and around the oceanic islands, indicating that both adult and larvae are able to live in different oceanographic conditions across the basin.

The high abundance of holoplanktonic mollusks close to the continental coast could be the result of El Niño Godzilla 2015-2016, where warmer waters reached the Chilean coast (Sánchez-Velasco *et al.* 2017). A similar environmental condition was found by Labrín *et al.* (2015) during a previous survey in almost the same study area. On the other hand, the distribution and abundance of pteropods and heteropods, especially in the open ocean and near the oceanic islands, showed a similar pattern to those reported by Labrín *et al.* (2015) in their study of pteropods.

Meroplanktonic larval distribution could be explained by oceanographic and biological processes occurring in coastal waters, the open ocean and around the oceanic islands. Larvae could be transported off the coast by mesoscale activity in the mesotrophic coastal transition zone (CTZ), which is principally characterized by northwest travelling eddies (Hormazabal *et al.* 2004, González *et al.* 2021). On the contrary, the wind-influenced coastal circulation would prevent larval transport out to the open ocean via coastal retention processes (Marín & Moreno 2002, Aiken *et al.* 2011). The onshore-offshore temperature gradient could generate a physical barrier for more temperature-sensitive groups of planktonic mollusks, such as bivalve larvae which was the only group that showed a significant connection with the environmental conditions and structure of the water column.

Larvae found in the open ocean are more likely to be teleplanic, which have the ability to cross physical-chemical water barriers and survive even in oligotrophic waters (*e.g.*, Teredinidae bivalve larvae; Scheltema & Williams 1983). Scheltema (1986b) reported a 77.6% occurrence of teleplanic gastropod larvae in the surface waters of the Central Pacific Ocean, compared to the 47.1% of non-teleplanic larvae. Nevertheless, the occurrence of open ocean non-teleplanic gastropod and bivalve larvae, produced by demersal mollusks inhabiting seamounts and hydrothermal vents nearby the study area, cannot be discarded (see Yáñez *et al.* 2009, fig. 2 for seamounts location, and Fitzsimmons *et al.* 2014, fig. 1B for hydrothermal vents location). The absence of bivalve larvae in several oceanic stations could be explained by the short planktonic period (<4 weeks) of many coastal species (Shanks 2009), whose larvae would have completed their planktonic stage in less time than that required to be transported off the coast.

The high variability in larval spatial abundances along the longitudinal gradient could be explained by the inherently patchy distribution, produced by the limited larval duration and episodic reproduction events exhibited by benthic mollusks (Shanks 2009), along with the water mass distribution. Although increases in larval abundances associated with higher temperatures have previously been recorded in closed coastal systems of Portugal and Tunisia (Chicharo & Chicharo 2000, 2001; Ziadi *et al.* 2015), to date this pattern had not been registered in the oceanic waters of the Pacific Ocean. The greater abundance of larvae found in waters around Rapa Nui could be due to an island-mass effect, which could cause an increase in local productivity as described by von Dassow & Collado-Fabbri (2014) and Meerhoff *et al.* (2018).

MOLLUSK GROUPS

Among the holoplanktonic mollusks, the occurrence of the pseudothecosomatous gastropod *Desmopterus pacificus* Essenberg, 1919 had previously been recorded in Chilean waters, at the beginning of the 20th century, according to Labrín *et al.* (2015). Campos & Ramorino (1984) recorded this species off Quintero (32°45'S), between the surface and 200 m depth, in December 1982 and January 1983, amid a recorded ENSO (El Niño-Southern Oscillation) event (Ramorino 1984). Cruz (2012) collected *D. papilio*, in surface equatorial water, also during an ENSO event, in April 1997, and Quesquén *et al.* (2016) recorded this species throughout the ENSO event of 2013 to 2015 off the coasts of Callao and Pisco, in Peru. These results confirm that this species acts as a good indicator of warmer waters arriving to the Chilean coast from the tropical Pacific throughout ENSO periods, in this case, during the arrival of the El Niño Godzilla 2015-2016 (Sánchez-Velasco *et al.* 2017).

The pterotracheoid gastropod genus *Atlanta*, which is mainly distributed in warm waters (Moreno-Alcántara *et al.* 2014, 2017, 2020; Wall-Palmer *et al.* 2016, Moreno-Alcántara 2019), and was collected at various stations during this cruise, had already been registered by Campos & Ramorino (1984) (*A. lesueuri*) almost all year-round at a principal depth of 75 m. Although Moreno-Alcántara *et al.* (2020) indicated the presence of 18 species of *Atlanta* in the Northeastern Pacific, Cruz (2012) only collected *A. gaudichaudi*, *A. lesueuri* and *A. peronii*, over the course of ENSO periods in Ecuador, while Quesquén *et al.* (2016) also recorded *A. heliconoidea* and *A. turriculata* in Peruvian waters. Of the pterotracheoids collected by Fagetti (1958, 1968) off the Chilean coast, only larvae of *Pterotrachea* sp. were captured with the WP2 net during this study.

In relation to meroplanktonic gastropod and bivalve larvae, this is almost their first record from the coast off Caldera as well as the waters adjacent to the Chilean oceanic islands. The closest record of gastropod larvae to our study area is from the coastal location 30°S, 71°21'W (Romero & Valdebenito 2002). Most of the families to which the larvae have been assigned so far in this study have previously been reported by Scheltema (1986b) for the Central Pacific islands, therefore representatives of these families seem to be common throughout the Pacific Ocean.

The absence of adult stages of some of the holoplanktonic gastropods in the samples as well as of paralarvae could have been largely due to a net effect. The WP2 net (180-200 µm mesh size) is suitable for capturing larval stages of mollusks but would not be as efficient in catching adult stages of thecosomatous gastropods, over 1 mm or cephalopod paralarvae because of their greater capacity to evade the net. Labrín *et al.* (2015) collected adults of several species of thecosomatous gastropods, using an IKMT net (10 mm mesh size), and Carrasco *et al.* (2019) captured paralarvae in waters of Rapa Nui Island using nets of 300 µm mesh size. In our research, mainly larval and juvenile stages of some of the genera collected by Labrín *et al.* (2015) were captured alongside a few adults of some of the species also recorded by these researchers.

The relative dominance of pteropods over the heteropods and meroplanktonic larvae in most stations should be interpreted with caution since the spatial distribution of the planktonic stages depends partly on, the developmental stage of the species, their capabilities to perform vertical migration and their kinetic behavior in response to oceanographic conditions (Young 1995, Kersten *et al.* 2019), as well as species-specific differences. These trends can also be affected by seasonality (*e.g.*, the sampling period encompassed only the austral spring), mesoscale oceanographic conditions (*e.g.*, shallow oxygen minimum zone near the continental shelf, ultra-oligotrophic conditions in the South Pacific Gyre, island-mass effect around oceanic islands) and interannual variability in environmental conditions (*e.g.*, the presence of the strong El Niño Godzilla during late 2015-early 2016).

In summary, the pelagic mollusk community display spatial variation at the scale of the South Pacific Basin, which can be related to both the hydrographic conditions and the water column structure. A more intense spatial and temporal sampling of planktonic mollusks could help to provide advances in our knowledge of not only their probable origin, but also their contribution to the colonization and connectivity of the oceanic islands and seamounts within the Easter Island ecoregion as well as in the shallower coastal zones.

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