

The Influence of Climate Variability on Holoplanktonic Polychaetes Populations of Ocean Sector of the Colombian Pacific Basin

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Abstract

Studies of holoplanktonic polychaetes in the Tropical Eastern Pacific have focused on their systematics and distribution however, population responses related to climate variability are non-existent. Therefore, the present work described for the first time the influence of the climatic variability 2004-2012 on the holoplanktonic polychaetes populations, as well as their relationship to environmental variables. Species of the Alciopidae, Lopadorrhynchidae and Iospilidae families were identified from 85 samples collected in the Pacific Basin of Colombia, contrasting them with the presence of ENSO, and correlating them with the environmental variables of temperature, salinity and chlorophyll-*a* concentration. Of the 14 species identified, only *Lopadorrhynchus cf. henseni* and *L. cf. brevis* increased their densities under El Niño and correlated positively with temperature. *Rhynchonereella cf. petersii* correlated negatively with temperature; while *R. cf. gracilis* and *Pelagobia cf. longicirrata* were positively correlated with chlorophyll-*a* concentration and salinity, respectively. Additionally, with the first description of the environmental ranges of the 14 species identified for the Colombian Pacific basin, it was found that the most common species presented broader environmental ranges. The results from the current research are consistent with previous studies in other regions of the Pacific and latitudes. The responses of the organisms suggest trophic and mobility trends that were not known for tropical holoplanktonic polychaete species.

Keywords

Temperature, Chlorophyll, Oceanic Province, Tropical Region, El Niño Southern Oscillation—ENOS

1. Introduction

The marine zooplankton is composed by many organisms that together help to modulate the life of the planet [1]. In this community are found the holoplanktonic polychaetes; organisms that come from their benthic congeners [2]. They have evolved to fully live their entire life cycle in the water column [3] [4]. The holoplanktonic polychaetes are taxonomically represented by nine families that group about 100 species distributed in all oceans [2] [5], particularly in subtropical and tropical regions [6] [7].

Although holoplanktonic polychaetes are not abundant or diverse in the different oceanic planktonic assemblages, they are frequent [3] [7]. Studies have found that the protein content of holoplanktonic polychaetes is of excellent quality [3] [8]. In addition, it has been shown that they have many feeding strategies, as well as different types of food [2] [9]. These characteristics allow them to be considered as an ecological group of great importance in the planktonic community because they help in the mineralization processes of organic matter and in the transfer of energy to higher trophic levels such as fish larvae [10] [11]. They are also considered by some authors as indicators of water masses, being found in greater abundance with waters from upwelling [4] [12].

Despite these considerations, studies of holoplanktonic polychaetes are scarce compared to other zooplankton groups such as copepod, chaetognaths, and euphausiids [3] [9] [13] [14]. These studies have been carried out based on transoceanic campaigns of the last century e.g. [15] [16], mainly describing species and their geographical distributions to macroscale [17]. In the Pacific Ocean, the most information of this group has been obtained in the Eastern Tropical Pacific Ocean—ETP from the work by Fernández-Álamo [18], who identified 44 species from five families, with Alciopidae and Lopadorrhynchidae as the most frequent and diverse.

In the Colombian Pacific basin (CPB), which is part of the ETP, few studies have been carried out on holoplanktonic polychaetes. In addition to the three taxonomic works carried out by Fernández-Álamo [18] [19] [20], only one ecological study has been found in the neritic province of the CPB that describes the relationship of the group with the concentration of chlorophyll- α , temperature and salinity during 1996 and 1997 [21]. However, the analyses were not performed at the species level. With these four studies, [22] species of holoplanktonic polychaetes have been recorded in the CPB for the Colombian Pacific basin, all extracted from stations located in the Neritic province.

It has become imperative to carry out ecological studies on various biological

groups to know the different population responses to climate variability and thus complement and improve the understanding of life on the planet, providing new knowledge, as well as data for the predictive models created to understand the effect of climate change [22] [23] [24] [25]. Studies have shown that organisms can have different responses to similar environmental conditions when contrasted between regions [26]. An example of this can be evidenced by the responses of population densities. When the climate variability increases the temperature, salinity or quantity and quality of the available food from the water, population increases of some species have been found [27]. The same response, in the same species, has also been observed when the values of the environmental variables are inversed or have combinations [28] [29].

In the ETP region, one of the main modulators of climate variability is the El Niño Southern Oscillation—ENSO [30] [31] [32]. This event changes environmental conditions by increasing or decreasing sea temperatures, as well as stratifying or mixing the water column [33] [34]. Marine communities have been found to adapt to changes caused by ENSO [35] [36] [37]. In the case of the Colombian Pacific basin, as in the ETP, the studies have focused on the effect and response of warming waters (e.g. El Niño). These studies have found that populations in the Neritic province and coastal region decrease their densities due to the decrease in the quality and quantity of food [21] [38].

However, no works have been found in the literature that attempt to study the response at the population level of the different holoplanktonic polychaetes to climate variability. This has caused gaps in knowledge and a lack of necessary supplies to better understand the dynamics of our ecosystems. Therefore, and considering that described above, the aims of this study were 1) described the influence of climate variability on the populations of some species of holoplanktonic polychaetes present in the oceanic province of the Pacific Basin of Colombia; and 2) described the relation between the presence of the species and their population densities with the environmental variables of temperature and salinity, as well as chlorophyll- α concentration.

2. Methods

2.1. Study Area

The Region I of the central ETP is located within the Colombian Pacific Basin—CPB [39]. It has an approximate area of 49,000 km² (14% of the CPB) (**Figure 1**) and depths greater than 3000 m. The water column is stable and has no direct influence on coastal environmental factors, making it a sector of purely oceanic water mass [33] [40]. The annual pattern of water temperature and salinity, as well as rainfalls, are modelled by the Tropical Northeast Pacific warm pool, the Inter Tropical Convergence Zone—ITCZ and the ENSO [31] [41].

2.2. Environmental Variables and Climate Variability

Monthly time series of temperature, salinity and chlorophyll- α concentration of

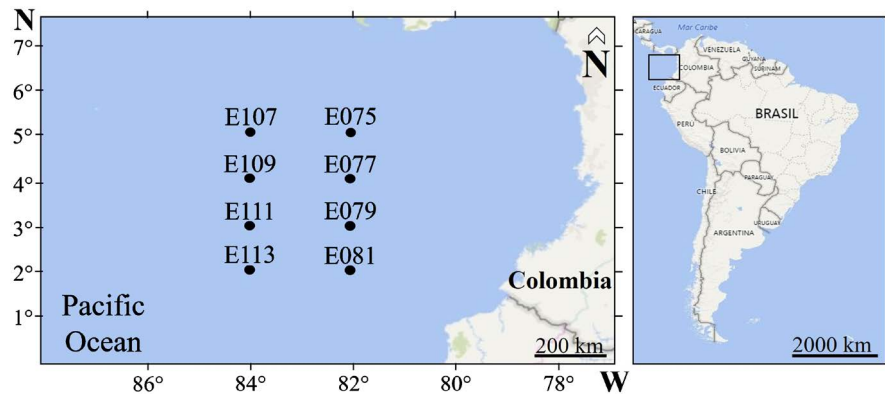


Figure 1. Geographic location of sampling stations in the Colombian Pacific Basin.

the sea surface were used from the works carried out by Cabarcas-Mier [39] and O'Brien *et al.* [42], who obtained the information from satellite images. The Southern Oscillation Index—SOI [43] was used to identify climate variability caused by El Niño or La Niña events (**Appendix—Table A1**).

2.3. Field Sampling

The ERFEN program established eight stations in the study area (**Figure 1**). Samples between 2004 and 2012 were annual between September and October. Additional samples were also obtained between the months of February and March of the 2007–2009 period (**Appendix—Table A2**). To simplify the analyzes, the samples obtained between February and March are considered as the first half of the year (I); while the samples obtained between September and October are the second half of the year (II). Sampling time depended on the arrival of the vessel at each station. All samples could be used because no significant differences were found between population density values obtained at day and night (Mann-Whitney test p -value > 0.05).

The samples were obtained with oblique trawls in the first 200 m depth using a bongo system with 60 cm diameter rings, 250 μ m mesh pore nets and General Oceanic mechanical flowmeter to measure the filtered volume. The samples were fixed and preserved in formalin at 5% final concentration, following the basic suggestions for handling and storage [44]. More detailed procedures are recorded in Uribe-Palomino *et al.* [27] and CPPS [45].

2.4. Laboratory

A total of 85 samples were used. The analyzes were made with a fraction that corresponded to 25% of each sample. To do this, each sample had to be divided twice with a Folsom splitter. Polychaetes were removed entirely from each fraction using a stereoscope. Preliminarily, polychaetes were separated at the family level. Only the organisms of the families Alciopidae, Iospilidae and Lopadorrhynchidae were identified and quantified to species level. The Tomoteridae and Typhloscolecidae families, as well as the larvae, were not identified due to

deterioration of the specimens or the difficulty of identification. The taxonomic identifications were based on the keys of Dales [15], Orensanz and Ramírez [46], Støp-Bowitz [16], Suárez-Morales *et al.* [12] and de León-González *et al.* [47]. Identities and the validation of species were verified in the World Registry of Marine Species [48]. The identified material will be deposited in the biological collections of the Museum of Marine Natural History of Colombia (MHNMC)—Makuriwa. The population density was expressed in individuals per 100 cubic meters (ind/100m³).

2.5. Analysis of Data

An environmental description of the study area was made before determining the influence given by both, spatial and temporal environmental conditions on the population densities of holoplanktonic polychaetes, as well as the relation with environmental variables.

To establish if the study area was homogeneous, we carry out a hierarchical agglomerative analysis of weighted average similarity—CLUSTER and non-metric multidimensional scaling—NMDS. These analyses were performed from the databases of temperature, salinity, and chlorophyll- α , using a triangular similarity matrix from the Euclidean distance algorithm. The analyses were realized using the statistical program Primer-e V.7 [49].

Climate variability was described by plotting monthly Southern Oscillation Index—SOI values between 2004 and 2012, as well as the average SOI values corresponding to the sampling times (*i.e.*, three months before the sampling month, and the sampling month). This sampling time is due to the ecological time of renewal of the zooplankton community [50] [51]. The neutral period was considered when the SOI values were between -0.25 and 0.25 , the presence of El Niño when the values were <-0.25 , and the presence of La Niña with values > 0.25 . Additionally, anomalies of the environmental variables were calculated for each sampling moment using the analysis of transform Z (E.1) [39]. The general average per month and its standard deviation were calculated from each data set until 2003.

$$T_z = \frac{(x - \bar{X})}{S.D.} \quad (\text{E.1})$$

With:

- T_z = Transform Z
- x = Individual value
- \bar{X} = Mean
- $S.D.$ = Standard deviation

To determine the influence by both spatial and temporal environmental conditions on the population densities of holoplanktonic polychaetes, graphic descriptions of the distribution and population density of the species were made considering the environmentally formed sectors and the climate variability of the study period. The population density is expressed in individuals per 100 cu-

bic meters (ind/100m³). To obtain the population density of each species, the following formula was used (E.2):

$$Pd = \frac{(Oc * P)}{F.V.} * 100 \quad (E.2)$$

With:

- *Pd* = Population density
- *Oc* = Organism count
- *P* = Proportion of the revised sample
- *F.V.* = Filtered volume

Additionally, non-parametric Kruskal-Wallis tests were carried out with the six most frequent species since they met the minimum statistical requirements of the test. The spatial factors were equivalent to the sectors formed and the temporal factors to the ENSO conditions at the time of sampling. The significant tests were complemented with the Dunn test, which establishes the factor that generated the difference.

Finally, to describe the relation between the presence of the species and their population densities with the environmental variables of temperature, salinity, and chlorophyll- α , the environmental ranges of all species were calculated from the presence data. Additionally, environmental variables were correlated with population densities using the Pearson and Spearman tests. Both, the Kruskal-Wallis and Dunn tests and the Spearman and Pearson correlation tests were performed with the statistical package for Excel Real-Statistics v5.4 [52].

3. Results and Discussion

The Cluster and NMDS justified divide the study area into three sectors (**Figure 2**). **Figure 3** shows the spatial differences. The northern sector was the warmest and less saline (\bar{X} : 27.5°C ± 1.0°C and 32.4°C ± 0.7°C), while the southern sector was the less warm and most saline (\bar{X} : 26.1°C ± 0.8°C and 33.3°C ± 0.7°C). The central sector presented intermediate values (\bar{X} : 26.8 ± 0.9°C and 32.8°C ± 0.7°C). The chlorophyll- α concentration, showed similar values among the three sectors (\bar{X} : north 228.4 ± 84.4 µg/m³; central 270.7 ± 135.3 µg/m³; south 270.1 ± 102.1 µg/m³). However, the central sector presented the most extreme peaks and valleys, while the northern sector had the less time variations.

The condition of La Niña predominated between 2004 and 2012, increasing durations and intensities annually. The period of 2010-2011 was the La Niña strongest. The condition of El Niño appeared at the beginning of the period study and at the end of 2009. The neutral periods presented were short, the most prominent being that of 2012 (**Figure 4(a)**). Sampling time reflected the general annual pattern of ENSO (**Figure 4(b)**).

The environmental variables allowed sectorizing the study area latitudinally. The highest values were measured in the northern sector and gradually decreased towards the southern sector, which allowed inferring that it was the dominant variable in this spatial delimitation. Additionally, it coincides with the temperature

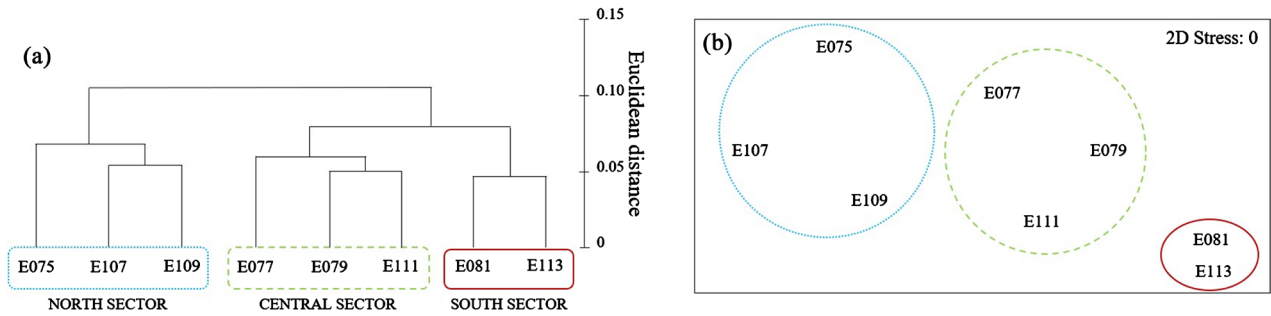


Figure 2. Graphical representation of multivariate non-parametric analyses based on data from environmental variables. (a) Cluster; (b) nMDS.

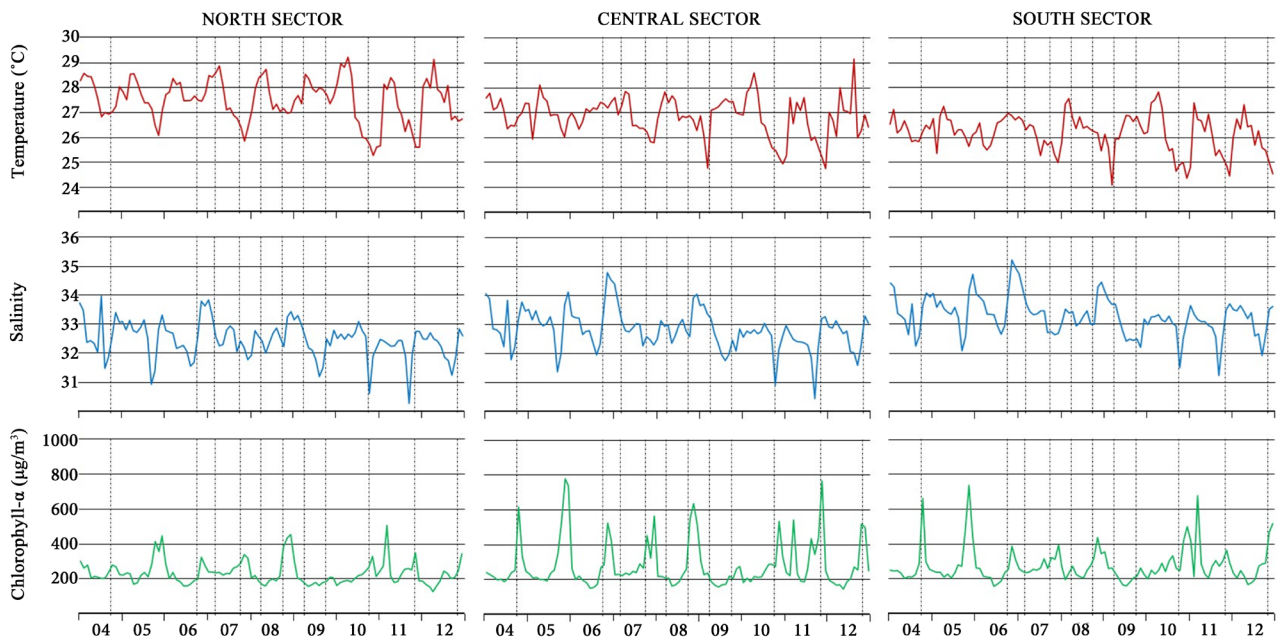


Figure 3. Time series between 2004 and 2012 of environmental values by sector formed in the study area. Vertical lines: sampling month.

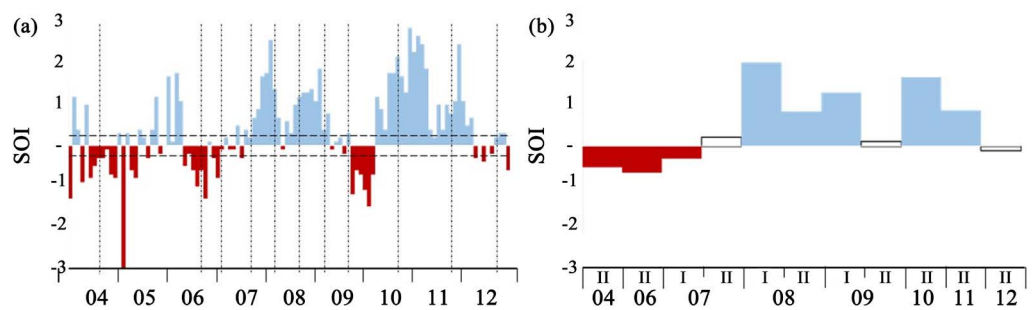


Figure 4. Southern Oscillation Index (SOI) during the 2004-2012 period. (a) SOI monthly. (b) SOI during the sampling time (three months before and the sampling month). Vertical lines: sampling month; horizontal lines: limit chosen for the ENSO influence. I: First semester; II: Second semester (see Methods).

patterns modulated by the Tropical Northeast Pacific warm pool [31], as well as the circulation at the mesoscale level of the region [53]. Previous studies had

classified the study area as homogeneous [39] [40]. However, these previous studies classified the area from a purely physical perspective and not consider the biological communities. It has been shown that the change in a Celsius degree is enough to modify the behaviour of many of the marine species [54]. Therefore, from an ecological perspective, it was necessary to consider the oceanic province of the Colombian Pacific Basin as a heterogeneous area.

The distribution of surface salinity was inverse to temperature, but with its main axis coming from the north coast of Colombia. Coastal rainfall is what modulates the distribution of salinity in the Colombian Pacific Basin—CPB [40] and the North Pacific coast of Colombia is the place of greatest precipitation in the Tropic [55]. This could cause the E079 station to end up belonging more to the central sector, while the E109 to the north sector.

The distribution of the chlorophyll-*a* concentration is according to expectations. The Central sector has factors that generate higher productivity and more changes during the year. In this sector is Malpelo Island [56], which generates local conditions such as upwelling areas [57], benefiting phytoplankton. Furthermore, due to the movement of nutation of the earth, the ITCZ in the Central sector generates contrasting seasons during the year. In the Northern sector the ITCZ influence is more constant, so rainfall occurs throughout most of the year; different from the Southern sector, where the influence of the ITCZ is less, causing a prolonged drought during the year [31]. Productivity in the North and South sectors reflects this condition, with a lower concentration of chlorophyll-*a* and fewer changes during the year with respect to the Central sector.

In general, the behaviour of the environmental variables during the sampling time was influenced by climate variability similarly between the sectors and response patterns were evidenced according to ENSO conditions (Figure 5). Temperature, salinity and chlorophyll-*a* were more influenced in periods of La Niña. For the first variable there was a decrease in the values, while for the other two, the values increased.

The climate variability moderately changed the normal conditions during the study period, increasing or decreasing the values of the environmental variables analysed as described in other studies [58]. It was also determined that for the sampling periods no differentiation was observed in the impact according to the

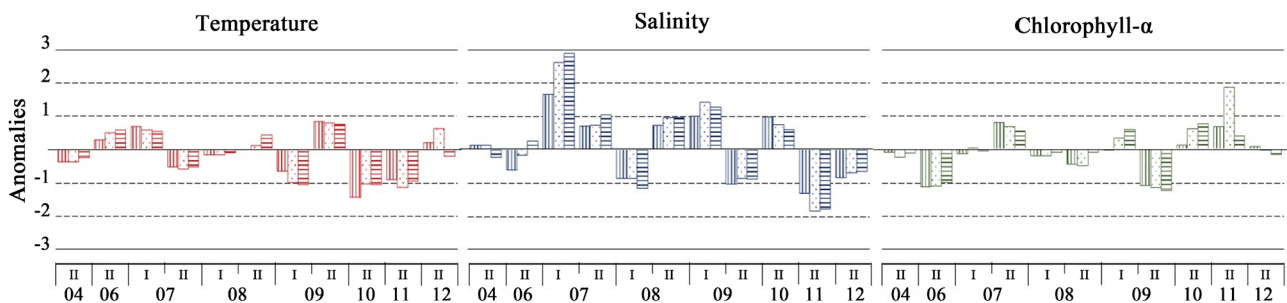


Figure 5. Anomalies of the environmental variables during the sampling moments (three months before and the sampling month). Vertical lines: northern sector; Dots: central sector; Horizontal lines: southern sector.

sector. ENSO progressively impacts the different coastal regions of the Pacific, with the equatorial sector being the first to receive it. For the study area, the southern sector receives the impact two months after it occurs, while for the northern sector it can take up to four months [39]. The short time of involvement between sectors is reflected in the anomalies since only four months were considered.

The 14 identified species of holoplanktonic polychaetes belonged mostly to the Alciopidae and Lopadorrhynchidae families; only one species belonging to the family Iospilidae appeared. The frequency of occurrence of the species did not exceed 50% of the samples reviewed. *Lopadorrhynchus* cf. *henseni*, *L.* cf. *brevis* and *Pelagobia* cf. *longicirrata* (Lopadorrhynchidae); and *Plotohelmis* cf. *capitata*, *Rhynchonereella* cf. *petersii* and *R.* cf. *gracilis* (Alciopidae) were the species that had occurrence frequencies greater than 10% and represented 85% of the total population density (**Appendix—Figure A1**).

The low frequency of occurrence and population density of holoplanktonic polychaetes was consistent with that registered in various studies conducted in open water of the Pacific Ocean [3] [4] [18] [59], contrary to what some authors have mentioned for studies done in coastal areas in other oceans [7] [60]. This difference in the ecological system can cause patterns to change [61]: low productivity areas similar to ocean province, have greater competition for the resource, while areas with external contributions (*i.e.* river plume or upwelling) as coastal sectors, allow all organisms to increase their densities more easily [62].

Regardless of the technical reasons related to capture and analysis methods [44], it was hypothesized that low frequencies of occurrence and population densities due to aspects such as the great mobility of holoplanktonic polychaetes [63], the rapid reaction of movement to water disturbances [44], the capacity that allows them to fractionate and regenerate again [47], and natural migrations to mesopelagic depths [3]. These factors would facilitate evasion to be captured. It could also be considered that, compared to copepods, holoplanktonic polychaetes are less adapted to the environment [64] and their presence in the zooplanktonic community is more recent than most other groups [65], which would give them disadvantages of colonization of niches.

The distribution and population density by sector and sampled period were different for all species (**Figure 6**) (**Appendix—Table A3**). The species of Alciopidae appeared in more sampling periods and were better distributed in the three sectors contrasting for to Lopadorrhynchidae species. In general, the species increased population densities at the end of the period studied, with a decrease in densities during 2009, as observed more clearly with *Plotohelmis* cf. *capitata* and *Pelagobia* cf. *longicirrata* (**Figure 6(g)**, **Figure 6(m)**).

Of the Alciopidae, *Rhynchonereella* cf. *moebii* and *Krohnia* cf. *lepidota* appeared in two periods with averages of population density below 6 ind/100m³. The first species appeared during 2007 in the northern and central sectors, while the second was between the second semester of 2007 and the first of 2008 in the

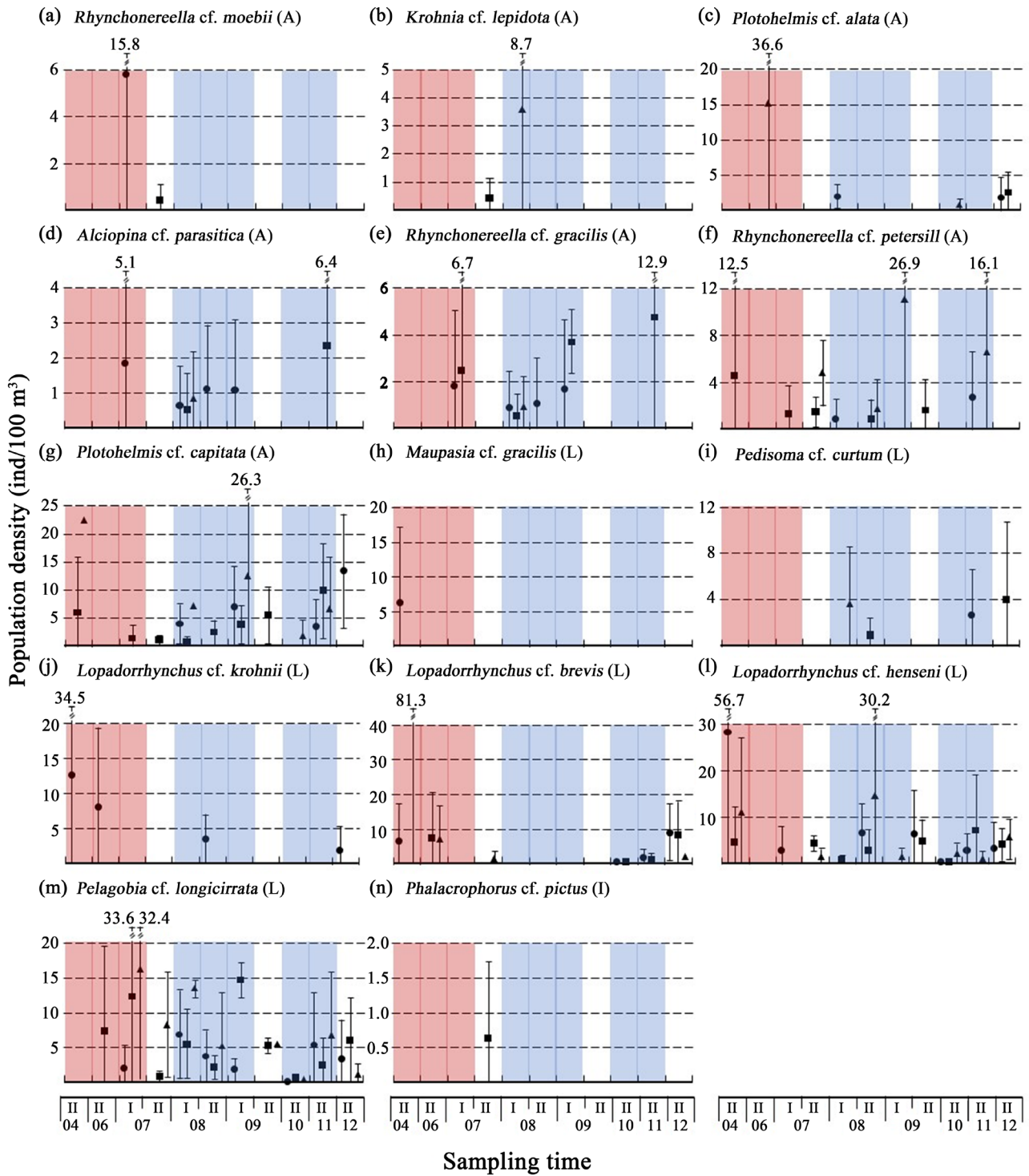


Figure 6. Mean population density and its standard deviations by sector of quantified holoplankton polychaete species during the 2004-2012 period. Square: northern sector; Circle: central sector; Triangle: southern sector. Red: El Niño condition; Blue: La Niña condition; No color: Neutral condition.

central and southern sectors (**Figure 6(a)**, **Figure 6(b)**). *Plotohelms cf. alata* and *Alciopina cf. parasitica* were collected in four and five sampling periods respectively, with 2008 being the best spatially represented for the second species.

The average population densities were less than 5 ind/100m³. Both species were collected in the three sectors, although for *A.cf. parasitica* it was more predominant in the northern sector, representing more than 50% of appearance and density population (**Figure 6(c), Figure 6(d)**). *Rhynconereella cf. gracilis* was collected in five sampled periods and, like *A. cf. parasitica*, 2008 was the year in which it was best represented spatially, but with average population densities less than 2 ind/100m³. This species appeared in the three sectors, with the south being the least present (**Figure 6(e)**).

Rhynconereella cf. petersii and *Plotohelms cf. capitata*, were those that occurred in the greatest number of sampled periods, with eight and ten times, respectively. Both species were not collected in 2006, and the case of *R. cf. petersii*, they did not appear in 2010 and 2012. The average population densities of *R. cf. petersii* were mostly below 5 ind/100m³; while for *P. cf. capitata* the average population densities were divided equally below and above the 5 ind/100m³. Like *Alciopina cf. parasitica*, for *R. cf. petersii* and *P. cf. capitata* there was a decrease in population density during 2008. Both *R. cf. petersii* and *P. cf. capitata* were presented in the three sectors, the central one being the one with the highest frequency of appearance and the south with the highest population densities (**Figure 6(f), Figure 6(g)**).

As for the species of the Lopadorrhynchidae, specimens of *Maupasias cf. gracilis* were collected only during 2004 with an average density above 5 ind/100m³ (**Figure 6(h)**). *Pedinosoma cf. curtum* and *Lopadorrhynchus cf. krohnii* were presented during four sampled periods, the first species in the middle and end of the sampling period, while the second was distributed throughout the study period. The average population density of *P. cf. curtum* was close to 4 ind/100m³, while for *L. cf. krohnii* it started above 10 ind/100m³ and was decreasing over time to a value less than 5 ind/100m³. *Pediosoma cf. curtum* was collected in all three sectors, while *L. cf. krohnii* only in the north (**Figure 6(i), Figure 6(j)**).

Lopadorrhynchus cf. brevis was collected at the beginning and end of the study period for a total of six of the sampled periods. It presented average population densities variable in time, being the highest at the beginning and end of the study (2004 and 2012), showing a similar pattern to some of the species of the Alciopidae with a decrease in densities towards the middle of the period. This species was present in all three sectors, being predominant in the south in the first sampling periods, and in the north and central the last sampled periods (**Figure 6(k)**).

The last two species of the Lopadorrhynchidae, *Lopadorrhynchus cf. henseni* and *Pelagobia cf. longicirrata* were collected in ten of the eleven sampling periods. They differed in that *L. cf. henseni* specimens were not collected in 2006 and *P. cf. longicirrata* in 2004. The population densities of both species varied over time, showing a pattern of peaks and valleys. Both species were found in all three sectors, however, the highest densities for *L. cf. henseni* were in the northern sector, while for *P. cf. longicirrata* in the central and southern areas (**Figure**

6(l), Figure 6(m)). Finally, *Phalacrophorus* cf. *pictus*, of the Iospilidae family, appeared once during the second semester of 2007 in the central sector (Figure 6(n)).

Regarding the spatio-temporal distribution, *Phalacrophorus* cf. *pictus*, *Alciopina* cf. *parasitica*, *Rhynchonereella* cf. *moebii*, *Kronhia* cf. *lepidota*, *Plotohalmis* cf. *alata*, *Maupasia* cf. *gracilis*, *Pedisoma* cf. *curtum*, and *Lopadorrhynchus* cf. *krohnii* were considered rare species for CPB, as has been recorded in other regions such as North Pacific, ETP or Caribbean Sea [7] [14] [17]. Not knowing the environmental requirements of these species, it is difficult to find an answer to this result. However, it seems that in some species its appearance coincided with some environmental characteristics. For example, *L.* cf. *krohnii* only appeared in the northern sector, when climate variability allowed increases in water temperature; *P.* cf. *curtum* appeared when the intensity of La Niña began to decrease, and *A.* cf. *parasitica* had its greatest presence during La Niña from 2008-2009.

The other six species identified in the present study, *Rhynchonereella* cf. *gracilis*, *R.* cf. *petersii*, *Plotohalmis* cf. *capitata*, *Lopadorrhynchus* cf. *brevis*, *L.* cf. *henseni* and *Pelagobia* cf. *longicirrata* presented a wider geographical and temporal distribution. This same pattern has been described in other studies from Pacific Ocean [4] [9] [21], Atlantic Ocean and Caribbean Sea [63] [66] [67]. In all of them, *P.* cf. *longicirrata* was the most common species.

No statistical differences in population density between sectors were determined from the three most frequent species of both families, however, climate variability did influence the *Lopadorrhynchus* cf. *henseni* and *L.* cf. *brevis* (Kruskall-Wallis p-value < 0.05). In both cases, the population densities during the El Niño periods were significantly higher compared to the periods with La Niña and neutral for the first of the species, and with La Niña for the second (Dunn p-value < 0.02) (Appendix—Table A4, Figure A2).

The different sectors found from the environmental variables did not influence population densities in the six most common species. This could be due to the fact that the environmental differences were not marked enough to generate a natural barrier [68], and that the species have sufficient tolerance ranges to be able to live in other regions [3] [6] [69]. The latter fact could be verified with the environmental ranges of the species in the present study.

The holoplanktonic polychaetes presented different ranges of the environmental variables conditioned with the frequency of appearance (Figure 7). In the case of the species of the Alciopidae they tended to warmer temperatures, and higher salinities and chlorophyll-*a* concentrations, while the species of the Lopadorrhynchidae tended to colder temperatures and less salinity waters but with high chlorophyll-*a* concentrations. The most frequent species with the highest population densities (*Plotohalmis* cf. *capitata* and *Pelagobia* cf. *longicirrata*) were present in the entire range of temperature, salinity and chlorophyll-*a* concentration. The species with intermediate frequency and population density (*Rhynchonereella* cf. *petersii*, *R.* cf. *gracilis*, *Lopadorrhynchus* cf. *henseni*, and *L.* cf. *brevis*)

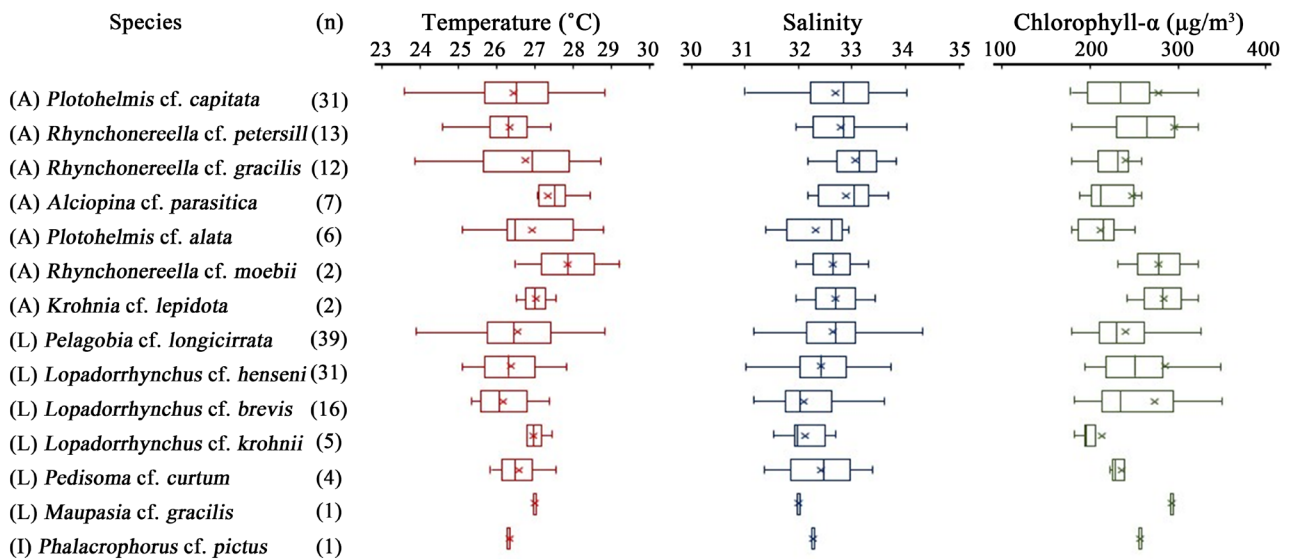


Figure 7. Ranges of environmental variables where holoplankton polychaete species appeared in the oceanic province of Colombian Pacific Basin during 2004-2012. (n): number of samples; (A): Alciopidae; (L): Lopadorrhynchidae; (I): Iospilidae.

coincided with the decrease in the range of at least one of the variables.

Less frequent species with low population densities (*Alciopina cf. parasitica*, *Plotohelmis cf. alata*, *Lopadorrhynchus cf. krohnii* and *Pedisoma cf. curtum*) coincided with a greater decrease in environmental ranges in general, with tendencies to warmer waters and medium salinities. They differ in chlorophyll-*a* concentrations, in which species of the Lopadorrhynchidae tended to appear with low concentrations. Finally, the species that were collected at two or fewer sampling times (*Rhynchonereella cf. moebii*, *Krohnia cf. lepidota*, *Maupasia cf. gracilis*, and *Phalacrophorus cf. pictus*) tended to appear with average values of each of the variables (Figure 7).

Regarding the correlations between population density of species and environmental variables, significant and positive statistical differences with temperature were found in *Lopadorrhynchus cf. henseni* (Pearson 0.32; p-value < 0.1) and *L. brevis* (Pearson 0.60; p-value < 0.05), with salinity in *Pelagobia cf. longicirrata* (Pearson 0.30; p-value < 0.1) and with chlorophyll-*a* concentration in *Rhynchonereella cf. gracilis* (Pearson 0.80; p-value < 0.05). *Rhynchonereella cf. petersii* was the only species to having a negative statistical significance with temperature (Pearson -0.58; p-value < 0.1) (Appendix—Table A5, Figure A3).

The population density of *Lopadorrhynchus cf. henseni* and *L. cf. brevis* showed a positive correlation with temperature and increased the population densities with El Niño compared to La Niña and Neutral condition. There are no data that support an explanation, but it was hypothesized that their densities are related to the fact that these species are considered omnivorous [2], added to the evidence that during El Niño the presence and abundance of omnivorous species increases [70] [71].

No evidence why *Rhynchonereella cf. petersii* showed negative correlation between population density and temperature. According to Jumars et al. [2], this

species is omnivorous with a tendency to herbivore. Continuing with the approach to the increase in omnivores due to the influence of El Niño, it can be hypothesized that this species is herbivorous in the study area; therefore it is affected with food decrease.

The decrease of population density by El Niño has also been described for the entire assembly of holoplanktonic polychaetes during the period with the El Niño of 1997, one of the strongest in history [21]. El Niño condition in the present study it can be considered weak due to its low intensity and duration. This reason allows us to infer that *R. cf. petersii* may be the only one that is at the limit of environmental tolerance with respect to the other holoplanktonic polychaetes.

Rhynchonereella cf. gracilis showed a contrary pattern to that found in coastal regions with respect to correlation between population density and chlorophyll-*a* concentration [3] [21]. It is a species considered carnivorous [2], so possibly its positive correlation is due to the presence of its prey. However, there is no evidence to support it.

Finally, the population density of *Pelagobia cf. longicirrata* showed a positive correlation with salinity. As has happened with the species analyzed above, there are no previous studies that have related these variables and attributed any reason. It is hypothesized for this case that its morphology, a depressed body, different from the other identified species [18] may allow it an advantage to move when water density increases due to salinity. This morphological advantage, in turn, would explain why it is the most frequent species of holoplankton polychaetes. It would have an advantage in capturing prey from the pico- and nanoplankton since these organisms, being smaller, would find it difficult to move to avoid being predated [72].

4. Conclusions

This study provides new ecological information on 14 species of holoplanktonic polychaetes with respect to environmental variables of temperature, salinity, and chlorophyll-*a* concentration, as well as climate variability in a tropical region.

In ecological terms, the Colombian Pacific basin during the 2004-2012 climate variability presented a spatial differentiation from north to south, with the greatest differences being found between the North and South sectors, while the central sector was the most fluctuating annually. Climate variability during the study period was dominated by La Niña and did not differentially influence the sectors.

The present study confirms that the planktonic assemblages of the oceanic province present a high frequency and low population densities of holoplanktonic polychaetes. The 14 species identified did not show a spatially or temporally differentiated distribution. Only the species *Lopadorrhynchus cf. henseni* and *L. cf. brevis* were influenced by climate variability, increasing their populations with the influence of El Niño.

Finally, five species showed correlations with the environmental variables. *L. cf. henseni* and *L. cf. brevis* had a positive correlation with temperature; *Rhynchonereella cf. petersii* had a negative correlation with temperature, and *R. cf. gracilis* and *Pelagobia. cf. longicirrata* had a positive correlation with chlorophyll-*a* concentration and salinity, respectively.

Contributors

J.M.G.-S. carried out the separation, quantification and taxonomic identification of organisms, data analysis and wrote the manuscript as part of his Ph.D. thesis. A.C.-O. carried out the taxonomic identification and validation of the organisms. N.H.C. guided the structuring, edited, and made the final revision of the manuscript. The authors declare that they have no conflict of interest

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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Appendix

Supplementary data from sampling stations and environmental data; results of population analyses; and data on population density by species.

Table A1. Oceanographic and climatic data sources used for the present study. SST: sea surface temperature; SSS: sea surface salinity; SSC: sea surface chlorophyll- α concentration; SOI: Southern Oscillation Index. (): no units.

Variable	Type	Time	Periodicity	Unit	Spatial resolution	Source	Availability
SST	Oceanographic	1981-2015	Monthly	°C	Sampling points	Avhrrsst y Modis	Cabarcas (2017) (Personal request)
SSS	Oceanographic	1950-2015	Monthly	()	Sampling points	Hadley-EN4	COPEPODITE (https://www.st.nmfs.noaa.gov/copepodite/)
SSC	Oceanographic	1998-2016	Monthly	mg/m ³	Sampling points	OCCCI-v3.1	COPEPODITE (https://www.st.nmfs.noaa.gov/copepodite/)
SOI	Climatic	1951-2016	Monthly	()	Sampling points	NOAA	NOAA (https://www.ncdc.noaa.gov/teleconnections/enso/indicators/soi/)

Table A2. Information stations sampled. The sample identifier (ID.) is the combination of the station number, the semester, and the sampled year.

Station	Sampling time				ID.
	Year	Semester	Date	Hour	
E075	2004	2	28/09/2004	05:30 a.m.	E075.2.4
	2006	2	No information.		E075.2.6
	2007	1	05/02/2007	10:28 a.m.	E075.1.7
	2007	2	15/09/2007	06:00 p.m.	E075.2.7
	2008	1	16/03/2008	02:53 a.m.	E075.1.8
	2008	2	15/09/2008	05:46 a.m.	E075.2.8
	2009	1	18/03/2009	04:55 p.m.	E075.1.9
	2009	2	02/10/2009	05:38 a.m.	E075.2.9
	2010	2	02/10/2010	12:00 p.m.	E075.2.10
	2011	2	01/11/2011	08:56 p.m.	E075.2.11
	2012	2	09/09/2012	07:38 p.m.	E075.2.12
E077	2004	2	26/09/2004	10:00 p.m.	E077.2.4
	2006	2	19/09/2006	02:43 p.m.	E077.2.6
	2007	1	06/02/2007	11:00 p.m.	E077.1.7
	2007	2	14/09/2007	03:17 p.m.	E077.2.7
	2008	1	17/03/2008	09:44 a.m.	E077.1.8
	2008	2	16/09/2008	07:58 p.m.	E077.2.8
	2009	1	17/03/2009	12:56 a.m.	E077.1.9

Continued

	2009	2	30/09/2009	03:11 p.m.	E077.2.9
	2010	2	30/9/2010	09:10 p.m.	E077.2.10
	2011	2	01/11/2011	02:37 p.m.	E077.2.11
	2012	2	10/09/2012	01:18 a.m.	E077.2.12
	2004	2	04/10/2004	10:30 p.m.	E079.2.4
	2006	2	19/09/2006	07:42 a.m.	E079.2.6
	2007	1	14/02/2007	12:49 p.m.	E079.1.7
	2007	2	25/09/2007	05:22 p.m.	E079.2.7
	2008	1	25/03/2008	10:38 a.m.	E079.1.8
E079	2008	2	23/09/2008	06:32 p.m.	E079.2.8
	2009	1	06/03/2009	11:42 a.m.	E079.1.9
	2009	2	20/09/2009	10:26 p.m.	E079.2.9
	2010	2	21/09/2010	07:20 a.m.	E079.2.10
	2011	2	24/10/2011	05:10 a.m.	E079.2.11
	2012	2	11/09/2012	06:20 a.m.	E079.2.12
	2004	2	7/10/2004	02:30 a.m.	E081.2.4
	2006	2	16/09/2006	05:46 p.m.	E081.2.6
	2007	1	16/02/2007	08:50 p.m.	E081.1.7
	2007	2	27/09/2007	09:47 a.m.	E081.2.7
	2008	1	27/03/2008	01:40 a.m.	E081.1.8
E081	2008	2	25/09/2008	05:44 p.m.	E081.2.8
	2009	1	04/03/2009	04:30 a.m.	E081.1.9
	2009	2	18/09/2009	09:11 a.m.	E081.2.9
	2010	2	19/09/2010	06:26 a.m.	E081.2.10
	2011	2	21/10/2011	08:51 a.m.	E081.2.11
	2012	2	6/09/2012	07:20 a.m.	E081.2.12
	2004	2	09/10/2004	06:30 p.m.	E107.2.4
	2006	2		There are no samples.	
	2007	1	06/02/2007	12:45 a.m.	E107.1.7
	2007	2		There are no samples.	
E107	2008	1	16/03/2008	03:23 p.m.	E107.1.8
	2008	2	15/09/2008	10:15 p.m.	E107.2.8
	2009	1	18/03/2009	12:33 a.m.	E107.1.9
	2009	2	01/10/2009	02:11 p.m.	E107.2.9
	2010	2	01/10/2010	08:50 p.m.	E107.2.10

Continued

	2011	2	23/10/2011	07:00 a.m.	E107.2.11
	2012	2	09/09/2012	07:26 a.m.	E107.2.12
	2004	2	27/09/2004	11:30 a.m.	E109.2.4
	2006	2	17/09/2006	11:18 p.m.	E109.2.6
	2007	1	06/02/2007	08:29 a.m.	E109.1.7
	2007	2		There are no samples.	
	2008	1	16/03/2008	09:12 p.m.	E109.1.8
E109	2008	2	16/09/2008	06:16 a.m.	E109.2.8
	2009	1	17/03/2009	04:05 p.m.	E109.1.9
	2009	2	01/10/2009	06:24 a.m.	E109.2.9
	2010	2	01/10/2010	01:41 p.m.	E109.2.10
	2011	2	23/10/2011	01:01 a.m.	E109.2.11
	2012	2	09/09/2012	12:40 a.m.	E109.2.12
	2004	2	6/10/2004	01:30 a.m.	E111.2.4
	2006	2	17/09/2006	03:30 p.m.	E111.2.6
	2007	1	15/02/2007	01:35 p.m.	E111.1.7
	2007	2	26/09/2007	07:36 a.m.	E111.2.7
	2008	1	25/03/2008	09:30 a.m.	E111.1.8
E111	2008	2	29/09/2008	09:44 a.m.	E111.2.8
	2009	1	05/03/2009	02:40 p.m.	E111.1.9
	2009	2	20/09/2009	06:43 a.m.	E111.2.9
	2010	2	20/09/2010	05:45 p.m.	E111.2.10
	2011	2	22/10/2011	07:19 p.m.	E111.2.11
	2012	2	08/09/2012	04:17 a.m.	E111.2.12
	2004	2	06/10/2004	08:35 a.m.	E113.2.4
	2006	2	17/09/2006	08:11 a.m.	E113.2.6
	2007	1	15/02/2007	09:25 a.m.	E113.1.7
	2007	2	26/09/2007	01:53 a.m.	E113.2.7
	2008	1	26/03/2008	04:25 a.m.	E113.1.8
E113	2008	2	24/09/2008	11:41 p.m.	E113.2.8
	2009	1	05/03/2009	05:00 a.m.	E113.1.9
	2009	2	19/09/2009	11:06 p.m.	E113.2.9
	2010	2	20/09/2010	07:15 a.m.	E113.2.10
	2011	2	22/10/2011	01:42 p.m.	E113.2.11
	2012	2	07/09/2012	09:18 p.m.	E113.2.12

Table A3. Population density (ind/100m³) of holoplankton polychaetes found in the Pacific Ocean Basin of Colombia during the climate variability from 2004 to 2012.

Family	Species	Period	Sector								
			North			Central		South			
			E075	E107	E109	E077	E079	E111	E081	E113	
Alciopidae	<i>Alciopina</i> cf. <i>parasitica</i> Claparède & Panceri, 1867	2007-I			5.5						
		2008-I	1.9				1.6			1.8	
		2008-II	3.3								
		2009-I			3.3						
		2011-II					7.1				
	<i>Krohnia</i> cf. <i>lepidota</i> (Krohn, 1845)	2007-II				1.2					
		2008-I								7.2	
	<i>Plotohormis</i> cf. <i>alata</i> Chamberlin, 1919	2006-II								30.3	
		2008-I		3.1	2.7						
		2010-II							1.2		
		2012-II			5.6	5.9					
	<i>Plotohormis</i> cf. <i>capitata</i> (Greeff, 1876)	2004-II							17.4	22.0	22.4
		2007-I							4.0		
		2007-II				1.2			1.6		
		2008-I	5.8	6.2			1.6		7.2	7.2	
		2008-II					2.7	4.4			
		2009-I	14.2		6.7	6.4		4.9	2.7	22.3	
		2009-II				9.8		6.3			
		2010-II							3.7		
		2011-II		7.0			14.2	15.1	13.2		
		2012-II	9.6	24.7	5.6						
	<i>Rhynchonereella</i> cf. <i>gracilis</i> Costa, 1864	2007-I			5.5		7.4				
		2008-I			2.7		1.6			1.8	
		2008-II	3.3								
2009-I			5.1		2.1	4.0	4.9				
2009-II											
<i>Rhynchonereella</i> cf. <i>moebii</i> (Apstein, 1893)	2011-II					14.2					
	2007-I		17.4								
<i>Rhynchonereella</i> cf. <i>petersii</i> (Langerhans, 1880)	2007-II				1.2						
	2004-II					13.5					
	2007-I						4.0				
	2007-II				2.5	1.8		6.8	2.8		
	2008-I			2.7							
2008-II					2.7			3.5			

Continued

		2009-I							22.3
		2009-II				4.6			
		2011-II		5.4					13.3
		2004-II	18.9						67.3
		2006-II				22.1		14.1	
		2007-II							2.8
	<i>Lopadorrhynchus cf. brevis</i> Grube, 1855	2009-II							
		2010-II	1.2					0.6	
		2011-II		3.5				3.0	
		2012-II		9.9	16.8	6.0	18.8	1.7	2.2
		2004-II	56.7	28.5		13.5			22.4
		2007-I		8.7					
		2007-II				2.5	5.5	4.9	2.8
		2008-I					1.6		
	<i>Lopadorrhynchus cf. henseni</i> Reibisch, 1893	2008-II	13.2	6.7			8.0		25.6
		2009-I							2.7
		2009-II	13.0			4.9	9.3		
		2010-II		0.6			0.6		3.7
		2011-II			5.4			21.2	1.9
		2012-II	9.6			5.9		6.3	8.4
		2004-II	37.8						
Lopadorrhynchidae	<i>Lopadorrhynchus cf. krohnii</i> (Claparède, 1870)	2006-II			16.0				
		2008-II		6.7	3.9				
		2012-II			5.6				
	<i>Maupasia cf. gracilis</i> (Reibisch, 1893)	2004-II	18.9						
		2008-I							7.2
	<i>Pedinosoma cf. curtum</i> Reibisch, 1895	2008-II					2.7		
		2011-II			5.4				
		2012-II				11.8			
		2006-II				21.8			
		2007-I	5.9				36.9		27.6
		2007-II						1.6	13.7
		2008-I		12.5	8.1	9.6	6.6		14.5
	<i>Pelagobia cf. longicirrata</i> Greeff, 1879	2008-II	3.3		7.8	3.5	2.7		10.6
		2009-I	3.5	1.7		17.2	12.0	14.6	
		2009-II				4.9	4.6	6.3	5.5
		2010-II		0.6			1.2	0.6	0.6
		2011-II			10.8		7.1		13.3
		2012-II		9.9		5.9	11.9		2.2
Iospilidae	<i>Phalacrophorus cf. pictus</i> Greeff, 1879	2007-II					1.8		

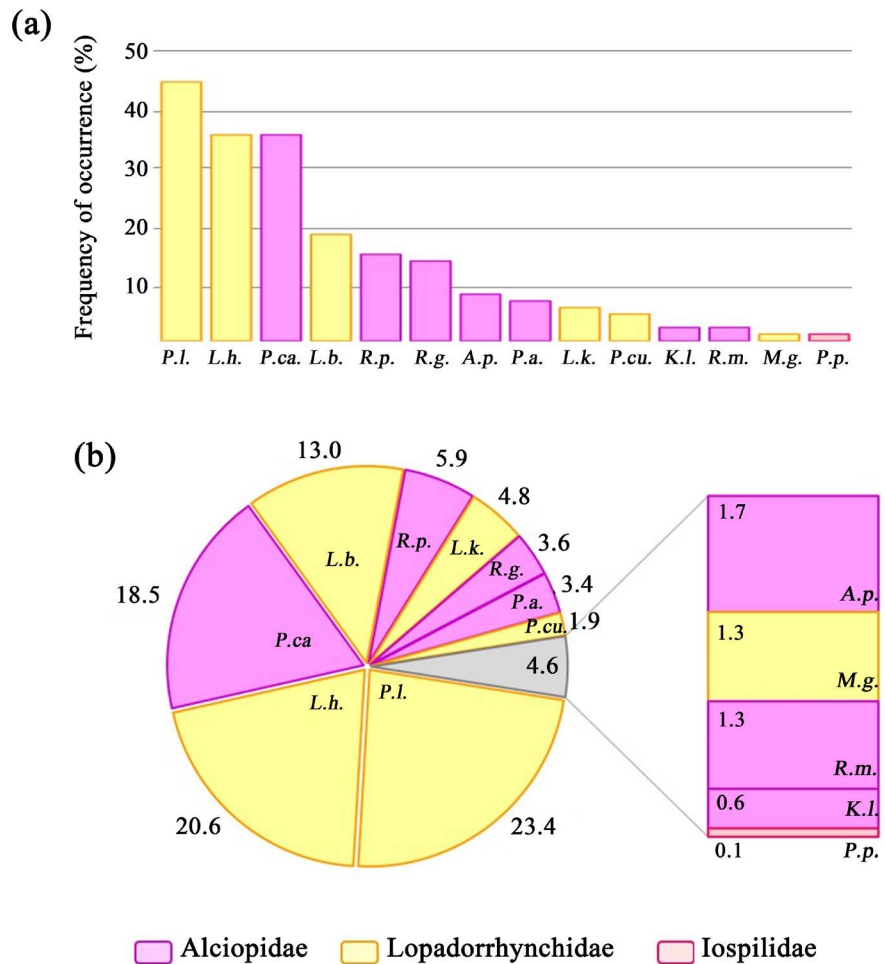


Figure A1. Proportion (%) of the biological attributes of quantified holoplanktonic polychaetes during the 2004–2012 period. A. Frequency of occurrence; B. Population density. A.p.: *Alciopina cf. parasitica*; K.l.: *Krohnia cf. lepidota*; P.a.: *Plotohelmis cf. alata*; P.ca.: *Plotohelmis cf. capitata*; R.g.: *Rhynchonereella cf. gracilis*; R.m.: *Rhynchonereella cf. moebii*; R.p.: *Rhynchonereella cf. petersii*; L.b.: *Lopadorrhynchus cf. brevis*; L.h.: *Lopadorrhynchus cf. henseni*; L.k.: *Lopadorrhynchus cf. krohni*; M.g.: *Maupasia cf. gracilis*; P.cu.: *Pedinosoma cf. curtum*; P.l.: *Pelagobia cf. longicirrata*; P.p.: *Phalacrophorus cf. pictus*.

Table A4. P-values of the Kruskal-Wallis test to determine if there are differences in the population densities of holoplankton polychaete species between sectors (North, Central and South) and by climate variability (El Niño—No, La Niña—Na and Neutral—N). *p-value < 0.05. **p-value < 0.017.

Species	Sector	Climate Variability	Dunn test
<i>Plotohelmis cf. capitata</i>	0.17	0.25	
<i>Rhynchonereella cf. petersii</i>	0.33	0.36	
<i>Rhynchonereella cf. gracilis</i>	0.45	-	
<i>Pelagobia cf. longicirrata</i>	0.63	0.13	
<i>Lopadorrhynchus cf. henseni</i>	0.18	0.01*	0.011** (No/N) - 0.003** (No/Na)
<i>Lopadorrhynchus cf. brevis</i>	0.93	0.02*	0.004** (No/Na)

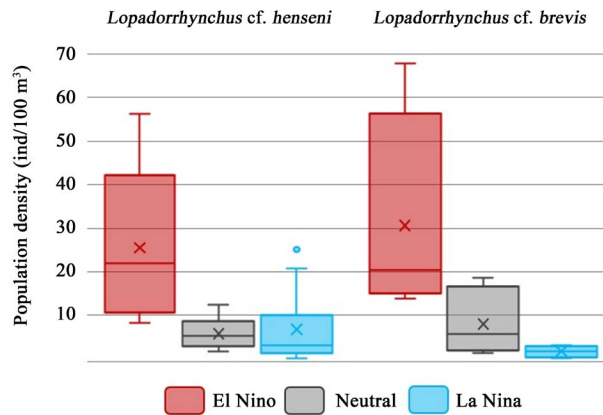


Figure A2. Graphical representation of the population density of two species of holoplanktonic polychaetes with statistical significance from the Kruskal-Wallis tests.

Table A5. Correlations between population density and environmental variables. n: number of data used; L: data transformed with logarithm base 10 to obtain normality; D: population density; T: temperature; S: salinity; C: chlorophyll-*a* concentration; P: Pearson test; S: Spearman test; **p* < 0.1; ***p* < 0.05.

Species	n	Data	Temperature	Salinity	Chlorophyll
<i>Pelagobia cf. longicirrata</i>	39	L(D); T; S; L(C)	(P) 0.14	(P) 0.30*	(P) 0.07
<i>Lopadorrhynchus cf. henseni</i>	31	L(D); T; S; C	(P) 0.32*	(P) 0.01	(S) -0.01
<i>Lopadorrhynchus cf. brevis</i>	16	L(D); T; S; C	(P) 0.60**	(P) 0.12	(S) -0.04
<i>Lopadorrhynchus cf. krohnii</i>	5	D; T; S; C	(S) 0.60	(S) -0.30	(S) 0.10
<i>Plotohelmis cf. capitata</i>	31	L(D); T; S; C	(P) -0.14	(P) -0.24	(P) 0.24
<i>Rhynchonereella cf. petersii</i>	13	L(D); T; S; C	(P) -0.58*	(P) 0.20	(S) 0.12
<i>Rhynchonereella cf. gracilis</i>	11	L(D); T; S; C	(P) -0.17	(P) -0.17	(P) 0.80**
<i>Alciopina cf. parasitica</i>	7	D; T; S; C	(S) -0.32	(S) -0.14	(S) 0.14
<i>Plotohelmis cf. alata</i>	6	D; T; S; C	(S) 0.09	(S) -0.09	(S) 0.09

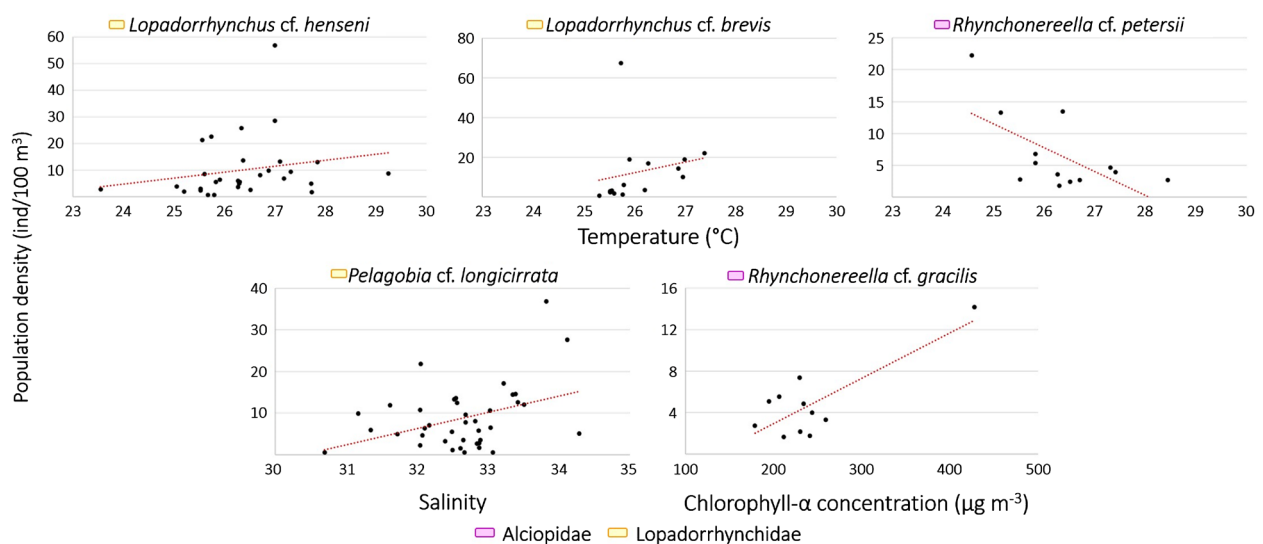


Figure A3. Relations between environmental variables and population density of holoplanktonic polychaete species with statistical significance based on correlation tests.