Regional Studies in Marine Science 52 (2022) 102280

Contents lists available at ScienceDirect

Regional Studies in Marine Science

journal homepage: www.elsevier.com/locate/rsma

Temporal changes in the epipelagic copepod assemblage at Gorgona Island, Colombian Eastern Tropical Pacific ocean

Mauricio Jerez-Guerrero [a,b,*], Alan Giraldo [b,c], María I. Criales-Hernández [d]

[a] *Universidad del Valle, Facultad de Ciencias Naturales y Exactas, Programa de Postgrado en Ciencias Biología, Cali, Colombia*
[b] *Universidad del Valle, Facultad de Ciencias Naturales y Exactas, Departamento de Biología, Grupo de Investigación en Ciencias Oceanográficas, Cali, Colombia*
[c] *Universidad del Valle, Facultad de Ciencias Naturales y Exactas, Instituto de Ciencias del Mar y Limnología - INCIMAR, Cali, Colombia*
[d] *Universidad Industrial de Santander, Facultad de Ciencias Básicas, Escuela de Biología, Laboratorio de Hidrobiología, Bucaramanga, Colombia*

ARTICLE INFO

Article history:
Received 3 May 2021
Received in revised form 18 February 2022
Accepted 2 March 2022
Available online 8 March 2022

Keywords:
Intertropical Convergence Zone
Panama bight
Colombian pacific
Zooplankton

ABSTRACT

Temporal variations in the hydrographic conditions of the Eastern Tropical Pacific (ETP) can modulate the assemblage structure of marine organisms, including copepods. While this taxonomic group has been widely recognized as important in the energy flow of the pelagic environment, fundamental ecological aspects are still unknown particularly possible relationships with oceanographic variations that have been described for ETP. In this paper, we evaluated the intra-annual and interannual variation of structure, richness, diversity, and similarity of the epipelagic copepod assemblage of Gorgona Island (Colombian ETP) based on samples collected during six oceanographic campaigns carried out between 2010 and 2016. We found significant changes in the oceanographic conditions and abundance of copepods between periods and years. Seven significant clusters were identified: five for each sampled period and two for the period of October 2010. *Ditrichocorycaeus andrewsi*, *Oncaea clevei*, *Paracalanus parvus*, and *Subeucalanus pileatus* were the species with the greatest contribution to group formation. Our results suggest that the intra-annual changes in the assemblage of epipelagic copepods recorded in Gorgona Island are a consequence of the displacement of the Intertropical Convergence Zone throughout the ETP during the year. This is due to the fact that during the periods of March they respond to the entry of subsurface waters from the Ensenada de Panama, and during the periods of October respond to the increase of the continental runoff on the pelagic environment of Colombian ETP.

1. Introduction

Copepods constitute one of the most abundant groups within zooplankton. They play a key role in the energy flow and dynamics of the pelagic environment and have been widely studied to understand how the marine ecosystem works (Selander et al., 2019; Campos et al., 2017; Jackson and Lenz, 2016; McKinnon and Duggan, 2014; Sampey et al., 2007). One of the main factors affecting the distribution and diversity of marine species within the Eastern Tropical Pacific (ETP) is the movement between 5°N and 10°N of the Intertropical Convergence Zone (ITCZ) (Amador et al., 2006; Kessler, 2006; Lavín et al., 2006). The effect of this atmospheric process has been detected in the eastern region of ETP, associated with the Panama Bight and Colombian Pacific Basin (CPB) zone (Rodríguez-Rubio et al., 2003; Devis-Morales et al., 2008; Rodríguez-Rubio and Giraldo, 2011; Corredor-Acosta et al., 2020), and even in continental insular locations such as Gorgona Island, which is located in the southern CPB (Giraldo et al., 2008, 2011, 2014a; Lozano-Cortés et al., 2014; Osorio et al., 2014; Sampson and Giraldo, 2014). When the ITCZ is located at its most southern position during the boreal winter, a shallower thermocline (up to 7.5 m depth) has been recorded in the pelagic area of Gorgona Island while when the ITCZ is located at its most northern position during the boreal summer a deeper thermocline (up to 47 m depth) has been recorded in this region (Giraldo et al., 2008, 2011, 2014a; Lozano-Cortés et al., 2014; Osorio et al., 2014; Sampson and Giraldo, 2014). Furthermore, during this latter period, there is significant freshwater input to the pelagic system associated with Colombian ETP due to Guapi, Patía, and Sanquianga rivers runoff, located approximately 50 km from the island (Zapata, 2001; Restrepo-López, 2006; Giraldo et al., 2008; Blanco, 2009).

The variations in marine hydrographic conditions could influence the zooplankton community and in tropical pelagic ecosystems, copepods make up between 50 and 90% of zooplankton

---

[*] Corresponding author at: Universidad del Valle, Facultad de Ciencias Naturales y Exactas, Programa de Postgrado en Ciencias Biología, Cali, Colombia.
E-mail address: mauricio.jerez@correounivalle.edu.co (M. Jerez-Guerrero).

https://doi.org/10.1016/j.rsma.2022.102280

abundance (Fernández-Álamo and Färber-Lorda, 2006; Giraldo and Gutiérrez, 2007; Murcia and Giraldo, 2007; Morales-Ramírez, 2008; Márquez-Rojas et al., 2009; Yang et al., 2017; Srichandan et al., 2018). Due to their abundance and to the fact that they respond rapidly to variations in oceanographic conditions (Cajaraville et al., 2016; Araujo et al., 2017; Jerez-Guerrero et al., 2017; Miyamoto et al., 2017), copepods are used as a model to understand spatial and temporal changes in mesozooplankton assemblages (Gusmão and McKinnon, 2009; Garzke et al., 2015; Rice et al., 2015; Medellín-Mora et al., 2016; Miyamoto et al., 2017). Moreover, these organisms play an important role in energy transfer in marine trophic webs and represent the largest component of secondary production in tropical marine ecosystems (López-Ibarra et al., 2014; Burd and Thomson, 2015; Dias et al., 2015; Kozak et al., 2017).

According to McKinnon and Duggan (2014), copepods in tropical environments find warm temperature conditions with low chlorophyll concentrations. These conditions favor small-sized copepods and short life cycles in diversity and abundance because they can better exploit the microbial trophic web and suspended particulate matter in the water column. However, other studies have reported that the structure of this assemblage could vary as a function of other factors, such as seasonal changes in phytoplankton biomass and salinity (Jagadeesan et al., 2013; Medellín-Mora et al., 2016; Venkataramana et al., 2017), or even by the influence of continental runoff and upwelling events that increase food availability favoring mainly large-sized copepods (López-Ibarra et al., 2014; Escribano et al., 2016; Fontana et al., 2016; Márquez-Rojas et al., 2016).

Based on this information, this study sought to expand the knowledge on the dynamics of the epipelagic copepod assemblage associated to an insular location in the southeastern ETP, Gorgona Island, Colombia. The following research questions were raised. Did the taxonomic composition of the copepod assemblage around Gorgona Island change temporally as a response to the variations in the local oceanographic conditions? and was the abundance and assemblage structure of epipelagic copepods related to the temporal variability in the local oceanographic conditions around Gorgona Island?

2. Materials and methods

2.1. Study area

Gorgona Island (2°58′N–78°11′W) is located 36 km from the continent in the southern Colombian Pacific (Fig. 1), with maximum depths of 90 m. The insular area (26 km^2) and 617 km^2 of surrounding marine area are part of the national system of marine protected areas under the category National Natural Park of Colombia (UAESPNN, 2005; PNN, 2018). The oceanographic circulation in the area is influenced by the Panama Current and the Colombia Current, creating a coastal surface circulation towards the northwest of Gorgona Island, with approximate speeds between 14 and 90 cm min^{-1} (Díaz et al., 2001; Giraldo et al., 2008; Osorio et al., 2014; Calle-Bonilla et al., 2017). In this area, the annual average precipitation ranges between 4000 and 8000 mm, resulting in at least 25 creeks (on average 0.06 m^3 s^{-1}) flowing into the ocean during the low precipitation season (December–February) and another 70 creeks (on average 0.33 m^3 s^{-1}) during the season of greater precipitation (May–October) (Díaz et al., 2001; Blanco, 2009; Giraldo, 2012; PNN, 2018).

The general oceanographic conditions at this location are under the influence of a characteristic intra-annual variation. From February to April the thermocline is found at depths between 8 and 24 m, superficial temperatures range from 26 to 28 °C, and salinity ranges from 29 to 34.8. From May to January, the thermocline is found at depths between 36 and 47 m, the superficial temperature is about 28 °C, and salinity ranges from 28 to 32.2 (Giraldo, 2008; Giraldo et al., 2008, 2014b; Sampson and Giraldo, 2014).

2.2. Sampling

Since 2005, the pelagic environment around Gorgona Island has been sampled twice a year following a sampling grid of 24 equidistant stations around the island. To carried out the present study, the outermost stations in the sampling grid were selected (Fig. 1). These stations are located 6 km from the island and were selected in order to reduce the effect of water runoff from the island on the copepod species present in the pelagic environment. Stations were sampled in October 2010, March 2011, March 2013, October 2013, October 2015, and March 2016.

At each station, the water column transparency was assessed with a Secchi disk and a continuous record of temperature and salinity was obtained with a SeaBird-19 CTD profiler. Water samples were obtained at four standard depths (1 m, 10 m, 30 m, 50 m) using a 5-L Niskin bottle to quantify dissolved oxygen concentration using a YSI85 multiparametric probe. The superficial chlorophyll-*a* concentration was estimated from MODIS AQUA satellite data (weekly averages of spatial resolution of 4 km) available on the NASA Giovanni portal (http://giovanni.gsfc.nasa.gov/). Zooplankton samples were collected by performing 10-min oblique tows down to an approximate 40 m depth, using a 30 cm diameter bongo net with 300 μm mesh size and a General Oceanic flowmeter to quantify the volume of filtered water. Samples were fixed in a formalin–seawater solution at a final 4% concentration and transported to the laboratory for processing.

2.3. Laboratory work

Zooplankton samples were fractionated in the laboratory using a Motoda sample splitter (Motoda, 1959). The identification and quantification of copepod species were performed only on adult individuals, using keys and taxonomic reference sheets by Boltovskoy (1981, 1999), Bradford-Grieve (1994), Palomares-García et al. (1998), Boxshall and Halsey (2004), and the Razouls et al. (2021) database. Postel et al. (2000) recommendations were followed to perform the counts, using a Discovery V12 stereoscope–microscope and Axiolab triocular microscope to identify individuals. Taxonomic nomenclature used in the study followed the WoRMS Editorial Board (2021) database. The abundance of the observed copepod species was standardized to individuals per 100 m^3 (ind. 100 m^3) as a function of filtered water volume.

2.4. Data analysis

To describe the temporal variation in oceanographic conditions at Gorgona Island, the following organization scheme was used: March 2011 and October 2010 was considered as year 1; March 2013 and October 2013 as year 2; and October 2015 and March 2016 as year 3. Intra-annual comparative analyses (March vs. October of each year) and interannual analyses (March year 1 vs. March year 2 vs. March year 3, October year 1 vs. October year 2 vs. October year 3) were undertaken to evaluate the temperature and salinity at four depths (1 m, 10 m, 30 m, 50 m), the dissolved oxygen concentration at three depths (1 m, 10 m, 30 m), the chlorophyll-*a* concentration (0 m), and water column transparency at one depth. Mann–Whitney tests were used for intra-annual comparisons and Kruskal–Wallis tests for interannual comparisons, with post-hoc Tukey tests to identify the source of variation. A Mann–Whitney test was used

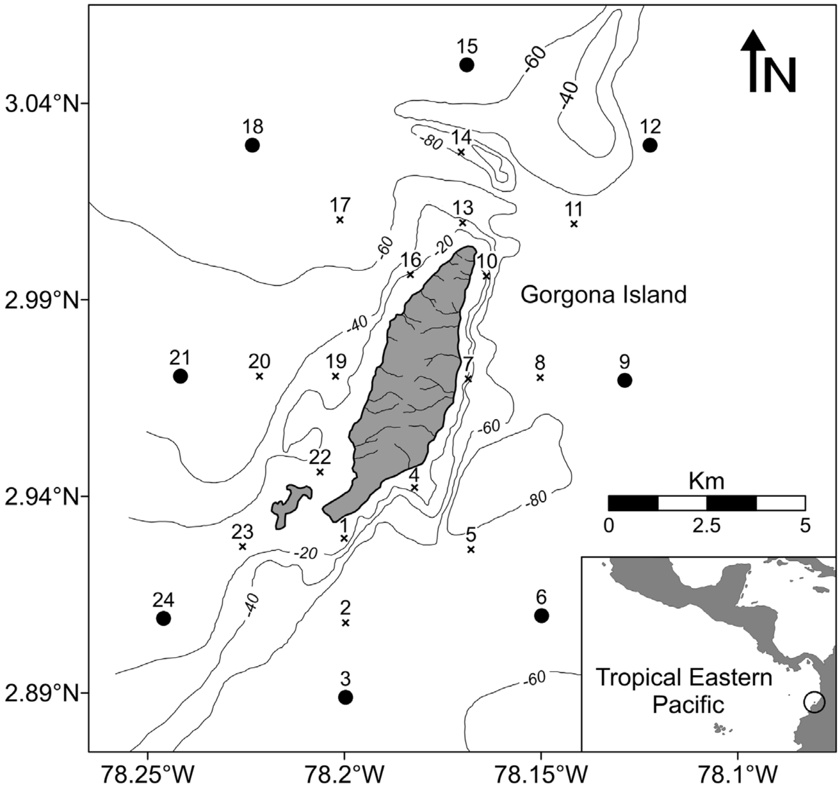

Fig. 1. Geographic location of sampling stations around Gorgona Island. Black dots show the eight sampling stations used in the present study. The hydrography of the island and the surrounding bathigraphy are observed. The circle shows the location of the island in the eastern sector of the ETP.

to compare copepod abundance intra-annually, and a Kruskal–Wallis test with an additional post-hoc Tukey test was used for inter-annual comparison.

We used the Bray–Curtis similarity index to analyze the temporal variations in the copepod community structure at Gorgona Island, based on abundance data transformed to log10 (n + 1) to reduce the importance of species found at very high abundances and increase the weight of rare species (Clarke and Warwick, 2001). Only species found at over 15% frequency of occurrence during any of the study periods were used to create the similarity matrix (Valencia et al., 2013). A grouping analysis was then performed using the group-average linkage method, and the significance of the formed groups was assessed using a SIMPROF test. Based on the defined groups, a similarity percentage analysis (SIMPER) was carried out to determine which species contributed to the similarity of each group and the dissimilarity between groups.

The relationship between oceanographic variables and copepod community structure was evaluated using the BEST Bio-Env analysis (Clarke and Warwick, 2001). This multivariate analysis uses a biological matrix created with the Bray–Curtis similarity index and a matrix with oceanographic conditions created with Euclidean distances to find the maximum correlation between matrices, calculating the Spearman correlation coefficient (ρs). All multivariate analyses were carried out with Primer v7 software (Clarke and Gorley, 2015).

3. Results

3.1. Oceanographic conditions

The temperature around Gorgona Island showed an intra-annual trend. In March 2011 and 2013, the thermocline was located around 20 m depth (Fig. 2). For March 2016, temperature data at standard depths are shown, as no records were obtained with a profiler (CTD) during that time (Fig. 2). In October 2010, 2013, and 2015, the water column temperature was homogeneous around 30 m depth, where the thermocline was located (Fig. 2). In March 2011 and 2013, the halocline was located between 10 and 20 m depth (Fig. 3). Salinity at standard depths is shown for March 2016 (Fig. 3). In October 2010, 2013, and 2015, the halocline was located between 30 and 40 m depth (Fig. 3).

Based on records at standard depths, the average temperature (±standard deviation) in the water column (0–50 m) in March was 22.45 °C (±2.08 °C) and in October it was 25.16 °C (±1.42 °C), while the average salinity (±standard deviation) of the water column (0–50 m) during the March samplings was 31.22 (±0.86), and during October samplings it was 29.21 (±0.78) (Table 1). The surface chlorophyll-*a* concentration showed an intra-annual trend. There were greater chlorophyll-*a* values during March samplings, with average values (±standard deviation) of 3.41 mg m^{-3} (±2.16 mg m^{-3}), and lower values during October samplings, with average values of 0.97 mg m^{-3} (±0.7 mg m^{-3}). The oxygen sensor during the campaigns of October 2015 and March 2016 malfunctioned, which is why these records were not included in the analyzed data set. However, it was established that the average dissolved oxygen in the water column (0–30 m) presented with lower values during March samplings (2011–2013), with average values (±standard deviation) of 4.9 mg L^{-1} (±0.7 mg L^{-1}), and higher values during October samplings (2010–2013), with average values of 6.6 mg L^{-1} (±0.19 mg L^{-1}) (Table 1). Water column transparency did not show an evident trend, with the highest average transparency values (±standard deviation) in March 2011 with 10.76 m (±2.61 m), October 2013 with 11.38 m (±2.26 m) and October 2015 with 10 m (±3.42 m), and the lowest values in March 2016 with 4.69 m (±2.55 m) (Table 1).

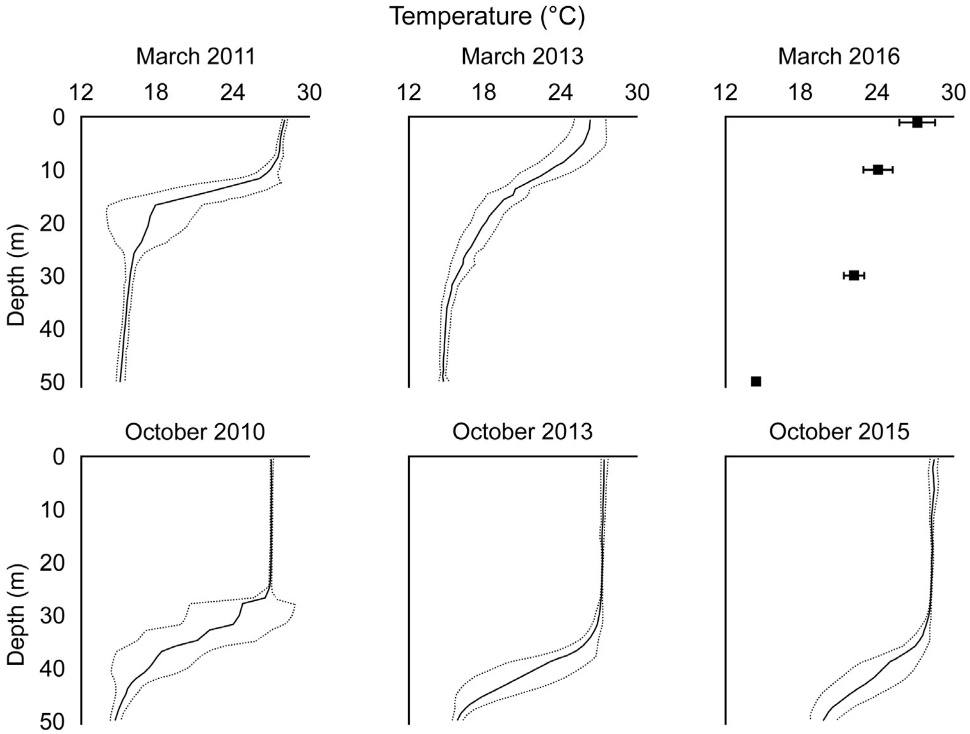

Fig. 2. Vertical variation of temperature around Gorgona Island during the periods of March 2010 and 2013, October 2010, 2013 and 2015, and vertical variation at standard depths during March 2016. The solid line is the mean and the dotted line is the standard deviation. For March 2016, the black dots represent the mean and the bars the standard deviation.

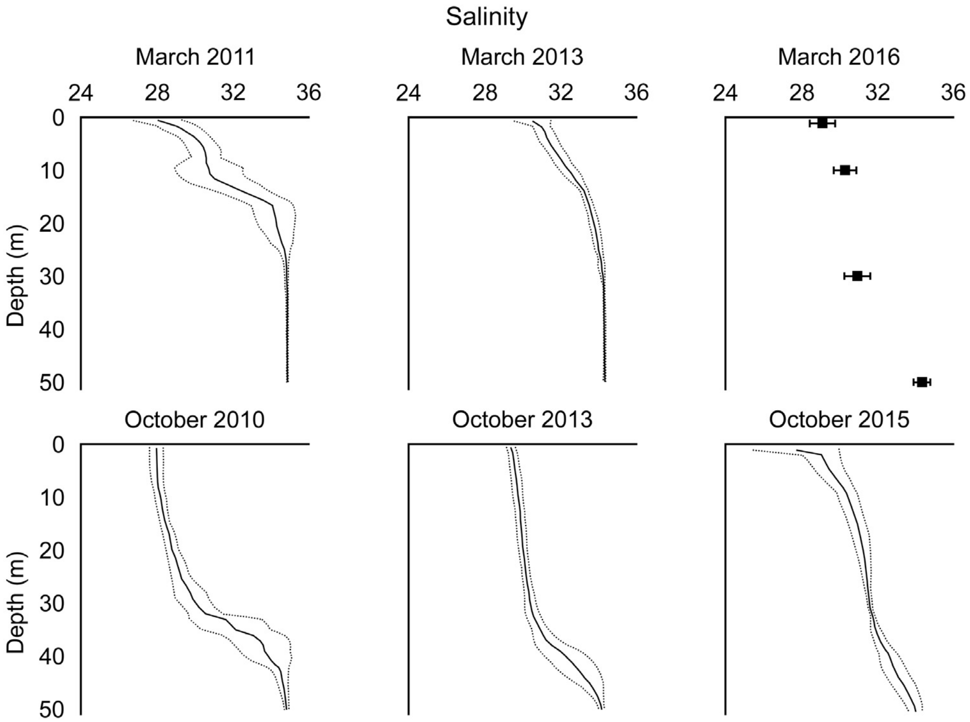

Fig. 3. Vertical variation of salinity around Gorgona Island during the periods of March 2010 and 2013, October 2010, 2013 and 2015, and vertical variation at standard depths during March 2016. The solid line is the mean and the dotted line is the standard deviation. For March 2016, the black dots represent the mean and the bars the standard deviation.

The intra-annual (March vs. October) comparison of the water column showed significant differences in sea surface temperature (SST) and average temperature (0–50 m) for all years (Mann–Whitney, $p < 0.01$), except for the SST in year 3, which did not differ significantly between periods (Mann–Whitney, $p > 0.05$) (Fig. 4). Moreover, there were significant differences in surface salinity of year 3 between periods (Mann–Whitney, $p < 0.01$), as well as in average salinity (0–50 m) between periods during

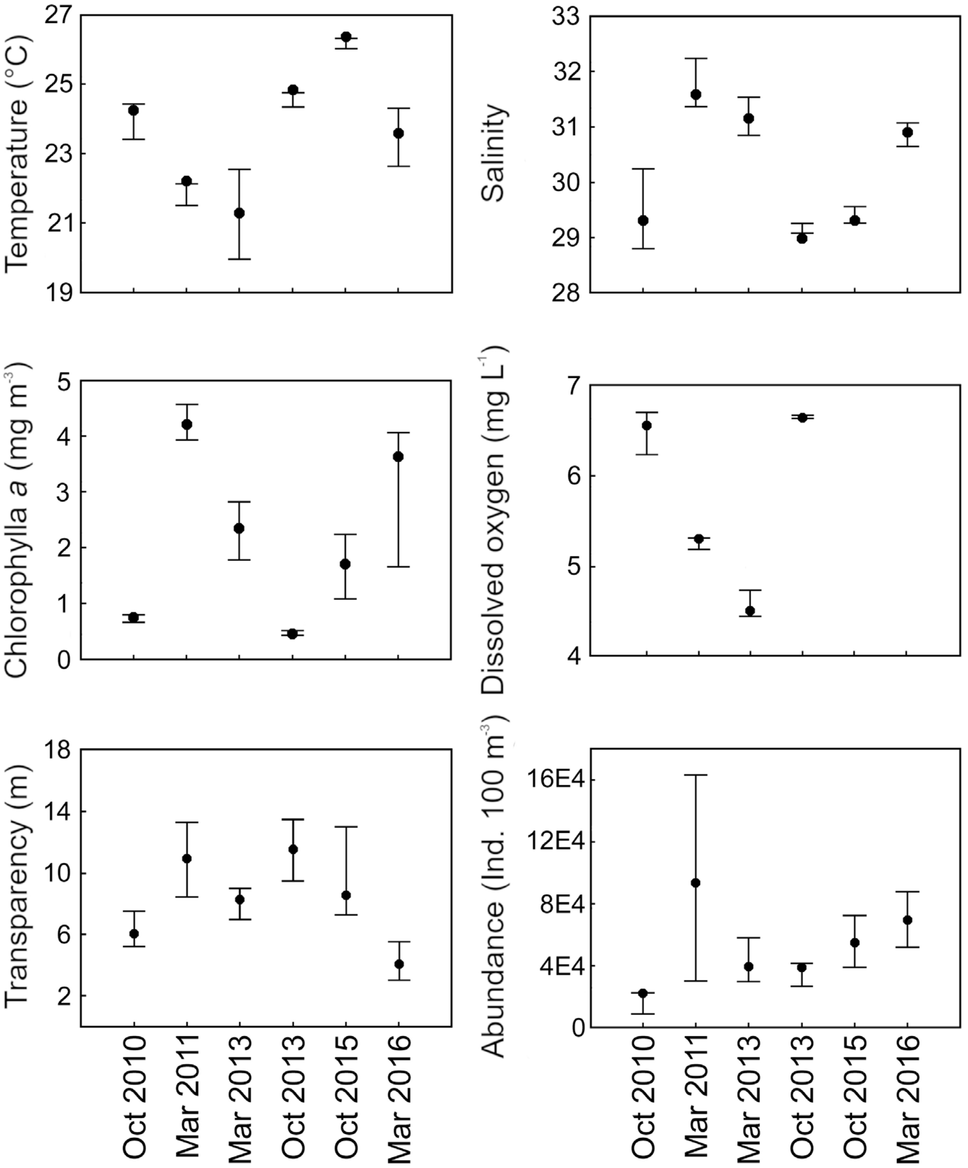

Fig. 4. Comparison of the average values of temperature (0–50 m), salinity (0–50 m), surface chlorophyll-a, dissolved oxygen (0–30 m), transparency of the water column, and total abundance of copepods around Gorgona Island during the study period. The black dot in each graph shows the average and the lines show the 25% and 75% ranges. Mar: March, Oct: October.

the three years (Mann–Whitney, $p < 0.01$) (Fig. 4). There were significant differences in surface and average (0–30 m) dissolved oxygen between March and October in years 1 and 2 (Mann–Whitney, $p < 0.01$) (Fig. 4). There were significant differences between March and October in terms of surface chlorophyll-*a* in years 1 and 2 (Mann–Whitney, $p < 0.01$), and significant differences in water column transparency between the two periods during the three study years (Mann–Whitney, $p < 0.01$) (Fig. 4).

The interannual comparison between March periods showed significant differences in the SST between years 1 and 2 (Kruskal–Wallis, $p < 0.01$, Tukey, $p < 0.01$), and average temperature (0–50 m); with year 3 being the source of variation (Kruskal–Wallis, $p < 0.05$, Tukey, $p < 0.05$) (Fig. 4). The surface salinity presented differences between years 1 and 3 (Kruskal–Wallis, $p < 0.05$, Tukey, $p < 0.05$), but the average salinity (0–50 m) did not present significant differences between March periods (Kruskal–Wallis, $p > 0.05$) (Fig. 4). The surface and average (0–30 m) dissolved oxygen presented significant differences between years 1 and 2 (Mann–Whitney, $p < 0.01$) (Fig. 4). Surface chlorophyll-*a* showed significant differences between the three March periods, with year 1 being the source of variation (Kruskal–Wallis, $p < 0.01$, Tukey, $p < 0.05$) (Fig. 4). The water column transparency presented significant differences, being year 3 the source of variation (Kruskal–Wallis, $p < 0.01$, Tukey, $p < 0.01$) (Fig. 4).

The interannual comparison between October periods showed significant differences in the SST and average temperature (0–50 m) between the three years, with year 3 being the source of variation (Kruskal–Wallis, $p < 0.05$, Tukey, $p < 0.05$) (Fig. 4). There were no significant differences in surface salinity and average salinity (0–50 m) (Kruskal–Wallis, $p > 0.05$) (Fig. 4). The surface and average (0–30 m) dissolved oxygen not presented significant differences between October periods of years 1 and 2 (Mann–Whitney, $p > 0.05$) (Fig. 4). Surface chlorophyll-*a* showed significant differences, with year 3 being the source of variation (Kruskal–Wallis, $p < 0.01$, Tukey, $p < 0.01$) (Fig. 4). The water column transparency presented significant differences, being year 1 the source of variation (Kruskal–Wallis, $p < 0.01$, Tukey, $p < 0.05$) (Fig. 4).

Table 1
Average values of the oceanographic parameters recorded at standard depths during the study periods around Gorgona Island, Colombian Pacific. **A.:** average, **S.D.:** standard deviation.

Parameter	Year 1				Year 2				Year 3			
	October 2010		March 2011		March 2013		October 2013		October 2015		March 2016	
	A.	S.D.	A.	S.D.	A.	S.D.	A.	S.D.	A.	S.D.	A.	S.D.
Temperature 0 m (°C)	26.69	0.18	28.10	0.26	26.01	1.23	27.54	0.32	28.46	0.37	27.23	1.36
Temperature 10 m (°C)	26.68	0.13	26.83	0.75	23.89	2.04	27.38	0.20	28.33	0.21	24.14	1.11
Temperature 30 m (°C)	25.93	1.18	16.53	0.40	16.35	0.57	27.17	0.13	27.97	0.21	22.23	0.75
Temperature 50 m (°C)	14.72	0.49	15.10	0.31	14.63	0.18	15.81	0.42	19.69	1.00	14.50	0.08
Temperature 0–50 m (°C)	24.27	1.53	22.40	2.26	21.33	2.13	24.83	1.00	26.38	0.73	23.62	1.24
Salinity 0 m	27.51	0.39	27.96	0.63	28.66	1.34	27.16	0.19	26.93	0.94	29.11	0.63
Salinity 10 m	27.73	0.40	30.73	1.47	30.36	0.54	27.53	0.29	27.98	0.51	30.33	0.57
Salinity 30 m	29.40	1.57	34.17	0.30	32.22	0.24	27.99	0.19	29.30	0.29	30.97	0.64
Salinity 50 m	34.82	0.11	34.87	0.04	34.31	0.06	34.15	0.15	33.99	0.34	34.35	0.42
Salinity 0–50 m	29.33	1.09	31.59	1.16	31.16	0.73	28.99	0.59	29.33	0.61	30.91	0.54
Superficial chlorophyll-*a* (mg m^{-3})	0.74	0.08	4.25	0.74	2.33	0.61	0.46	0.07	1.70	0.81	3.64	3.50
Dissolved oxygen 0 m (mg L^{-1})	6.67	0.33	6.31	0.28	5.60	0.26	6.73	0.12	[a]	[a]	[a]	[a]
Dissolved oxygen 10 m (mg L^{-1})	6.70	0.35	5.97	0.57	5.09	0.50	6.65	0.13	[a]	[a]	[a]	[a]
Dissolved oxygen 30 m (mg L^{-1})	6.01	0.43	3.19	0.12	2.47	1.25	6.52	0.15	[a]	[a]	[a]	[a]
Dissolved oxygen 0–30 m (mg L^{-1})	6.55	0.26	5.30	0.58	4.50	0.61	6.64	0.08	[a]	[a]	[a]	[a]
Transparency (m)	6.18	1.44	10.76	2.61	8.19	2.07	11.38	2.26	10.00	3.42	4.69	2.55

[a] Dissolved oxygen value was not recorded due to sensor malfunction during the sampling campaign.

3.2. Copepod richness and abundance

A total of 73 copepod species were identified. Twenty species were found only in March samples and 4 species only in October samples (Table 2). The most abundant species during the entire study were *Ditrichocorycaeus andrewsi* (Farran, 1911), *Oncea clevei* Früchtl, 1923, and *Paracalanus parvus* (Claus, 1863) (Fig. 5). These species were also the most abundant in October, whereas the most abundant species in March samples were *O. clevei*, *P. parvus*, and *Subeucalanus pileatus* (Giesbrecht, 1888) (Table 2, Fig. 5).

There was an intra-annual variation in the abundances of copepod species from years 1 and 3, with greater values in March compared with October for each year studied (Table 2). The intra-annual comparison of abundance values showed significant differences between March and October of year 1 (Mann–Whitney, $p < 0.01$), but not between March and October of years 2 and 3 (Mann–Whitney, $p > 0.05$) (Fig. 4). The interannual comparison of the copepod abundance between March periods did not show significant differences (Kruskal–Wallis, $p > 0.05$), while significant differences were found between October periods, with year 1 being the source of variation (Kruskal–Wallis, $p < 0.01$, Tukey, $p < 0.01$) (Fig. 4). Nearly 70% of the abundance was represented by four to seven species in March 2011, 2013, and 2016, whereas about 70% of abundance was represented by four to five species in October 2010, 2013, and 2015 (Fig. 6).

3.3. Copepod community structure

The grouping analysis (Fig. 7) highlighted the temporal community structure of copepods around Gorgona Island. There were seven significant groups, considering the SIMPROF analysis ($p < 0.05$) and the cophenetic correlation coefficient ($r_c = 0.8$) as indicators of group significance. Three of the formed groups corresponded to each of the March periods, with similarity percentages between 70.96% and 74.1%, and the other four formed groups corresponded to each of the October periods, with similarity percentages between 65.68% and 77.71% (Table 3). *D. andrewsi*, *O. clevei*, and *P. parvus* contributed the most to all formed groups, and *S. pileatus* contributed only to March groups (Table 3).

The dissimilarity between periods was characterized by the presence and/or absence of some species, as well as changes in abundance. The comparison of March 2011 and October 2010 showed that every species contributing over 5% to dissimilarity was present in March 2011 and not in October 2010 (Table 4). The presence–absence of some species, such as *Euterpina acutifrons* (Dana, 1847) (Fig. 5) and *Farranula concinna* (Dana, 1849), was observed between March and October 2013, whereas *S. pileatus* was recorded during the two periods and presented greater abundances in March 2013 (Table 4). In March 2016 and October 2015, there was presence–absence of some species (*e.g. Acartia (Odontacartia) lilljeborgi* Giesbrecht, 1889 and *F. concinna*) during the two periods, with greatest abundances of *S. pileatus* in March 2016, which contributed to the dissimilarity (4.16%) between the two periods (Table 4). March 2011 presented the greatest dissimilarity from the other March samples, due to the presence or greater abundance of some species, such as *Acartia (Acartia) danae* Giesbrecht, 1889, *Calocalanus pavo* (Dana, 1852), *Clausocalanus jobei* Frost & Fleminger, 1968, and *Oncaea mediterranea* (Claus, 1863) (Table 4). October 2015 was the most dissimilar from the other October samples because it presented greater abundances of some species such as *Acrocalanus gibber* (Giesbrecht, 1888), *Bestiolina* cf. *similis* (Sewell, 1914), *Clausocalanus furcatus* (Brady, 1883), and *E. acutifrons* (Table 4).

The five best results of the BEST Bio-Env analysis that identify the oceanographic variables which most influenced the copepod community structure during each of the sampled years are presented in Table 5. During year 1 (October 2010–March 2011) and year 3 (October 2015–March 2016), the variables that explained variation the most were temperature, salinity, and water column transparency (Table 5). During year 2 (March 2013–October 2013) the variables that explained most variation were temperature, salinity, surface chlorophyll-a, and water column transparency (Table 5).

4. Discussion

4.1. Intra-annual and interannual changes in oceanographic conditions

The intra-annual variations in the oceanographic conditions of the Gorgona pelagic environment observed in this study have been previously described by other authors (Giraldo, 2008; Giraldo et al., 2008, 2014a), and are attributed mainly to the effect of the ITCZ moving over the ETP. This movement modulates the climate of the region and contributes to create an upwelling process in the Panama Bight during the first part of the year (Rodríguez-Rubio et al., 2003; Amador et al., 2006; Devis-Morales et al., 2008; Valencia et al., 2019; Corredor-Acosta et al., 2020),

Table 2
Average abundance of copepod species recorded and total abundance for each sampled month. The abundance values are shown as individuals per 100 m^3. **A.A.:** average abundance, **S.E.:** standard error.

Taxa	March 2011 A.A. ± S.E.	March 2013 A.A. ± S.E.	March 2016 A.A. ± S.E.	October 2010 A.A. ± S.E.	October 2013 A.A. ± S.E.	October 2015 A.A. ± S.E.
CALANOIDA						
Acartiidae						
Acartia (Acartia) danae	2320.83 ± 2111.35	0	192 ± 0	0	0	425 ± 0
Acartia (Acartia) negligens	158 ± 4.24	68 ± 0	0	55 ± 0	62 ± 15.56	193.33 ± 107.52
Acartia (Odontacartia) lilljeborgi	0	79 ± 48.08	1551.57 ± 1690.96	1007 ± 0	0	0
Calanidae						
Canthocalanus pauper	1353.25 ± 1789.54	283.4 ± 223.78	328 ± 106.9	1364.71 ± 2133.41	1096.75 ± 1272.87	2053.67 ± 2199.43
Nannocalanus minor[a]	5193.83 ± 9349.86	57 ± 0	684.17 ± 647.71	0	0	0
Undinula vulgaris	682 ± 0	0	0	80.67 ± 99.12	169.6 ± 145.24	158.5 ± 51.62
Candaciidae						
Candacia catula	252 ± 118.79	0	0	148.83 ± 215.98	273.5 ± 200.9	116 ± 16.54
Candacia curta	0	91.5 ± 48.79	179.75 ± 44.38	0	163 ± 0	0
Candacia pachydactyla[b]	0	0	0	0	76.5 ± 7.78	0
Candacia truncata[a]	0	0	282 ± 127.28	0	0	0
Centropagidae						
Centropages furcatus	5608.38 ± 7461.3	1209 ± 848.54	8915.38 ± 3722.96	649.57 ± 246.38	613.63 ± 819.49	497.67 ± 181.27
Clausocalanidae						
Clausocalanus furcatus	938 ± 531.42	63 ± 0	0	0	4746.5 ± 5318.15	2142 ± 1579
Clausocalanus jobei	1714.17 ± 1875.81	0	0	0	0	1114 ± 1176.63
Clausocalanus mastigophorus[b]	0	0	0	0	0	493 ± 98.99
Clausocalanus minor	1475 ± 0	0	0	28 ± 0	0	296 ± 268.7
Eucalanidae						
Pareucalanus attenuatus[a]	1193 ± 716.5	0	502 ± 334.73	0	0	0
Pareucalanus langae[a]	523.33 ± 255.77	135 ± 75.45	0	0	0	0
Subeucalanus crassus[a]	0	97.67 ± 46.92	0	0	0	0
Subeucalanus pileatus	7508.38 ± 12,075.93	2140.13 ± 965.05	13,220 ± 8388.15	100.17 ± 48.38	151.33 ± 100.83	269.33 ± 22.81
Subeucalanus subtenuis[a]	2012 ± 0	89 ± 0	0	0	0	0
Euchaetidae						
Euchaeta indica	449.5 ± 313.25	0	0	74 ± 0	109.5 ± 94.83	0
Euchaeta longicornis[a]	0	0	214 ± 0	0	0	0
Euchaeta marina	0	80	0	37 ± 0	117 ± 0	0
Euchaeta rimana[b]	0	0	0	0	51 ± 0	0
Lucicutiidae						
Lucicutia flavicornis	622.5 ± 405.17	0	478.5 ± 375.47	95.75 ± 11.15	0	141 ± 0
Paracalanidae						
Acrocalanus gibber	0	269 ± 218.35	1142.83 ± 1064.58	175.5 ± 170.41	921 ± 973.59	4133.67 ± 4357.65
Acrocalanus longicornis	1542.38 ± 1215.71	498.17 ± 458.49	1410.75 ± 608.96	1320.43 ± 1881.41	1880.25 ± 2101.99	0
Bestiolina cf *similis*	751 ± 644.88	0	656 ± 377.62	548.17 ± 571.21	0	127 ± 19.8
Calocalanus contractus[a]	0	0	299 ± 179.61	0	0	0
Calocalanus curtus	418.5 ± 372.65	0	0	37.33 ± 5.51	0	0
Calocalanus pavo	1147.13 ± 1112.88	206.75 ± 145.21	0	161.5 ± 136.75	280.17 ± 206.94	273.5 ± 155.63
Calocalanus styliremis	2790.5 ± 3003.52	0	1357 ± 709.94	0	0	141 ± 0
Mecynocera clausi[a]	778 ± 151.32	0	679 ± 52.33	0	0	0
Paracalanus aculeatus	0	80	744 ± 292.65	28 ± 0	0	0
Paracalanus parvus	13,281.13 ± 7033.95	14,910.25 ± 11,798.28	7518.5 ± 4960.05	5095.14 ± 6415.45	9929.13 ± 6582.06	3936.17 ± 2537
Parvocalanus crassirostris	322 ± 0	0	213 ± 0	89 ± 70.87	0	142 ± 0
Phaennidae						
Phaenna spinifera	228 ± 0	0	146 ± 36.77	0	111 ± 73.54	0
Pontellidae						
Calanopia minor	922.29 ± 644.23	218.8 ± 291.19	213 ± 0	160.8 ± 111.76	84.33 ± 23.35	131.5 ± 13.44
Labidocera acuta	81 ± 0	68 ± 0	225.67 ± 112.54	69 ± 40.14	166.43 ± 210.57	0
Labidocera detruncata[b]	0	0	0	0	59 ± 0	0
Pontellina sobrina	671 ± 0	80	0	0	0	113 ± 0
Rhincalanidae						
Rhincalanus nasutus[a]	671 ± 0	147 ± 80.25	214 ± 0	0	0	0
Temoridae						
Temora discaudata	399.67 ± 237.02	512.75 ± 495.47	851.2 ± 807	165.6 ± 120.25	752.14 ± 869.95	378.5 ± 269.16
CYCLOPOIDA						
Corycaeidae						
Corycaeus crassiusculus	0	0	365.33 ± 377	0	101 ± 0	0
Corycaeus speciosus	671 ± 0	0	0	37.5 ± 7.78	155.4 ± 156.64	282 ± 0
Ditrichocorycaeus andrewsi	7949.13 ± 8656.16	3187.63 ± 2496.25	6126 ± 3258.24	2647.43 ± 2377.08	5422 ± 5467.92	10,865.67 ± 10,042.81
Ditrichocorycaeus erythraeus	4666.13 ± 4387.94	1149.57 ± 744.79	1172.63 ± 792.51	1094.29 ± 501.48	888.5 ± 543.92	1480.6 ± 1605.41
Onychocorycaeus agilis	330.33 ± 306.21	0	845.83 ± 478.37	478 ± 496.89	639 ± 690.14	2143 ± 1460.69
Onychocorycaeus pacificus	702.75 ± 453.07	0	319 ± 139.19	104.25 ± 50.37	104 ± 48.01	272.5 ± 212.84
Farranula carinata[a]	0	0	428 ± 0	0	0	0
Farranula concinna	605.2 ± 799.17	0	0	675.43 ± 568.8	2119.25 ± 2233.58	914.83 ± 796.15
Lubbockiidae						
Lubbockia marukawai[a]	0	73 ± 0	120	0	0	0
Lubbockia squillimana[a]	228 ± 0	73 ± 0	120	0	0	0
Oithonidae						
Oithona cf. *brevicornis*	1532.33 ± 1789.32	4757.25 ± 6255.58	1620.75 ± 1106.44	135 ± 108.92	392.29 ± 480.51	2312.67 ± 1960.59
Oithona oswaldocruzi[a]	0	0	1152 ± 0	0	0	0
Oithona plumifera	4509 ± 2999.49	512.38 ± 624.47	972 ± 855.23	480 ± 330.67	718.63 ± 841.12	593.5 ± 653.13
Oithona setigera[a]	463 ± 179.61	0	0	0	0	0
Oithona simplex	2515 ± 3081.57	808.5 ± 908.81	678.57 ± 652.28	83.6 ± 91.26	70.5 ± 16.26	464.5 ± 456.08
Oncaeidae						
Oncaea clevei	21,329.88 ± 26,612.5	4653.75 ± 4556.42	3715 ± 2214.32	6083.86 ± 11,617.94	10,683.13 ± 13,489.85	21,346.83 ± 24,834.73
Oncaea mediterranea[a]	6363.71 ± 5189.47	497.5 ± 17.68	1044.25 ± 783.17	0	0	0
Oncaea scottodicarloi	1327.2 ± 944.73	554.43 ± 573.68	1129 ± 816.59	85 ± 0	240.67 ± 245.13	272 ± 212.13
Oncaea venusta	1907.75 ± 1742.54	566.25 ± 509.08	2183.75 ± 1749.53	365.5 ± 437.73	1589.43 ± 1138.63	346.33 ± 264.72
Sapphirinidae						
Copilia mirabilis	0	107.83 ± 46.13	235 ± 127.43	0	0	122 ± 0
Sapphirina auronitens[a]	0	0	195.75 ± 124.07	0	0	0
Sapphirina metallina[a]	0	0	186 ± 44.68	0	0	0
Sapphirina nigromaculata	233 ± 0	83.67 ± 37.07	598 ± 457.81	0	117 ± 0	0
Sapphirina opalina[a]	0	0	372 ± 0	0	0	0
Sapphirina sinuicauda[a]	0	89.67 ± 32.59	99 ± 0	0	0	0

(*continued on next page*)

which affects not only the coastal CP (Jerez-Guerrero et al., 2017; Valencia et al., 2019) but also modulates the oceanographic conditions around Gorgona Island (Giraldo, 2008; Giraldo et al., 2008, 2011, 2014a). The effect of the ITCZ moving towards the south in March promotes the intrusion of subsurface waters from the Panama Bight around Gorgona island; this led to a shallower thermocline and halocline and the presence of low dissolved oxygen concentrations. On the contrary, the movement of the ITCZ towards the north in October intensifies precipitation in the area (Giraldo et al., 2008, 2011, 2014a; Blanco, 2009), and its effect was

Table 2 (*continued*).

Taxa	March 2011 A.A. ± S.E.	March 2013 A.A. ± S.E.	March 2016 A.A. ± S.E.	October 2010 A.A. ± S.E.	October 2013 A.A. ± S.E.	October 2015 A.A. ± S.E.
HARPACTICOIDA						
Clytemnestridae						
Clytemnestra scutellata	449.5 ± 313.25	136 ± 14.14	309.4 ± 165.14	43.33 ± 11.5	0	0
Ectinosomatidae						
Microsetella norvegica	0	146 ± 0	0	0	0	194.5 ± 125.16
Microsetella rosea	0	89 ± 0	0	0	30	0
Euterpinidae						
Euterpina acutifrons	1375.71 ± 1369.61	3446.75 ± 3328.88	13,567.88 ± 12,051.08	256.83 ± 146.65	60	991.4 ± 1004.89
Miraciidae						
Macrosetella gracilis	419.5 ± 355.67	73 ± 0	172 ± 0	49 ± 8.49	0	117.5 ± 6.36
Total abundance	93,509	39,625	69,657	21,986	38,733	54,862

[a] Unique copepod species during March periods.

[b] Unique copepod species during October periods.

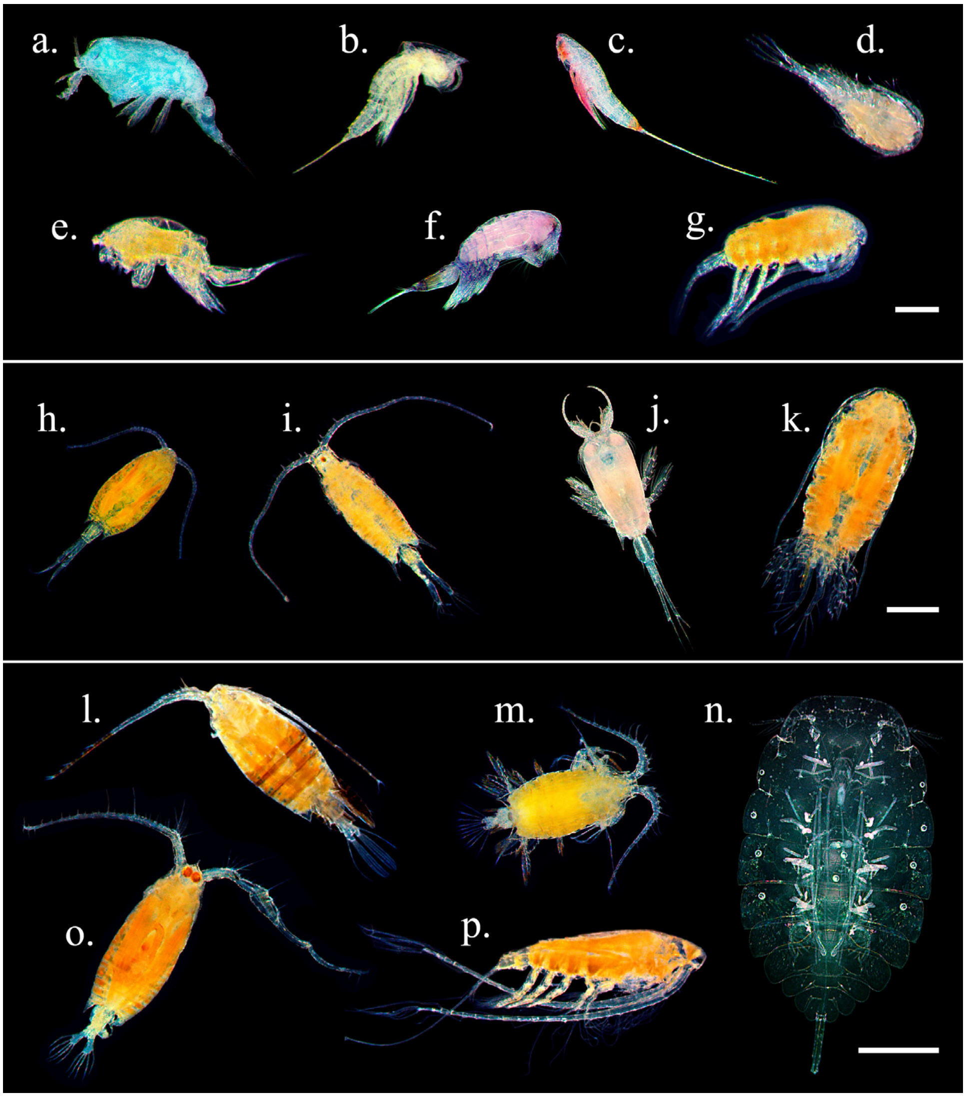

Fig. 5. Photographs of some species of female (F) and male (M) copepods found around Gorgona Island during the study periods. **a.** *Ditrichocorycaeus andrewsi* (H), **b.** *Euterpina acutifrons* (H), **c.** *Microsetella norvegica* (H), **d.** *Oithona* cf. *brevicornis* (H), **e.** *Oncaea clevei* (H), **f.** *O. scottodicarloi* (H), **g.** *Paracalanus parvus* (H), **h.** *Calanopia minor* (H), **i.** *Centropages furcatus* (H), **j.** *Corycaeus speciosus* (M), **k.** *Temora discaudata* (H), **l.** *Candacia pachydactyla* (H), **m.** *C. curta* (H), **n.** *Copilia mirabilis* (M), **o.** *Labidocera acuta* (M), **p.** *Subeucalanus pileatus* (H). Scale photographs to the right; **a–g**: 200 µm, **h–k**: 400 µm, **l–p**: 1000 µm. Photographs taken by Mauricio Jerez Guerrero.

evident around Gorgona Island, where temperature, salinity, and dissolved oxygen concentrations in the water column were more homogeneous. The higher values of dissolved oxygen concentration detected in October could be attributed to the increase in primary production, as has been reported by some authors for the island (Soto et al., 2001; Giraldo et al., 2014a) along with presence of small-celled organisms such as cyanophytes, pennate diatoms, and dinoflagellates, due to the input of allochthonous nutrients from continental runoff (Jack et al., 2009; Herfort et al., 2012; Cloern et al., 2014; Corredor-Acosta et al., 2020).

The observation of interannual differences showed that year 3, corresponding to October 2015–March 2016, presented significantly different temperature values compared with the other two years. This suggests that during this period the pelagic

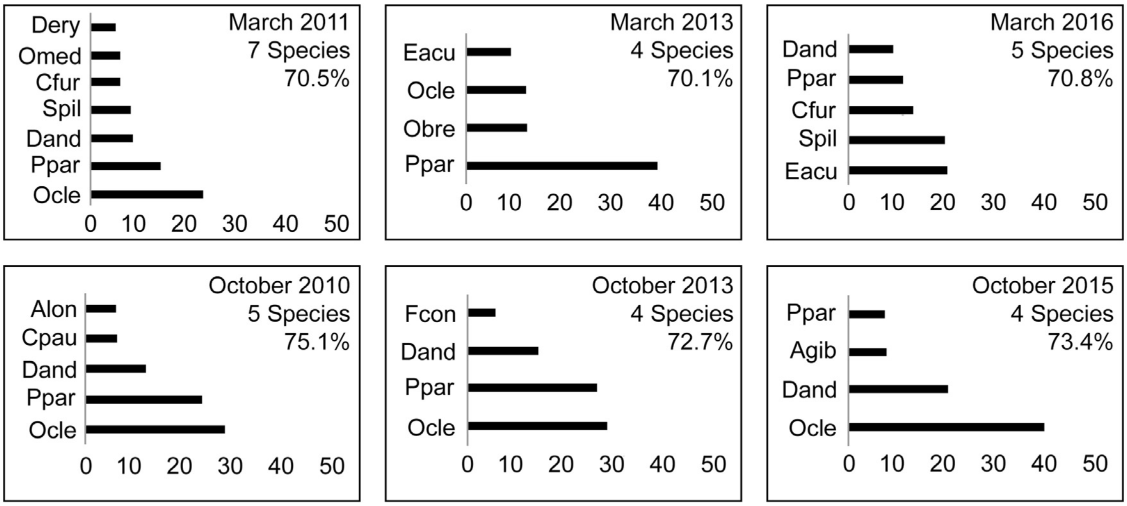

Fig. 6. Relative abundance of the dominant epipelagic copepods recorded around Gorgona Island during the study period. Only species contributing around 70% of the total abundance for each period are shown. **Agib**: *Acrocalanus gibber*, **Alon**: *Acrocalanus longicornis*, **Cfur**: *Centropages furcatus*, **Cpau**: *Canthocalanus pauper*, **Dand**: *Ditrichocorycaeus andrewsi*, **Dery**: *Ditrichocorycaeus erythraeus*, **Eacu**: *Euterpina acutifrons*, **Fcon**: *Farranula concinna*, **Obre**: *Oithona* cf. *brevicornis*, **Ocle**: *Oncaea clevei*, **Omed**: *Oncaea mediterránea*, **Ppar**: *Paracalanus parvus*, **Spil**: *Subeucalanus pileatus*.

Table 3
Copepod species that contributed to the similarity between stations of the clusters generated (SIMPER analysis) for the study periods on Gorgona Island. Only the species that contributed 40% of the total similarity of each grouping are shown.

Cluster (similarity percentage, %)	March 2011 (71.88)	March 2013 (74.10)	March 2016 (70.96)	October 2010a (77.71)	October 2010b (65.68)	October 2013 (73.35)	October 2015 (68.08)
Morphospecies	Contribution percentage (%)						
Acrocalanus gibber	–	–	–	–	–	–	7.55
Acrocalanus longicornis	–	–	–	6.5	–	6.85	–
Bestiolina cf. *similis*	–	–	–	–	8.04	–	–
Centropages furcatus	–	–	7.02	–	–	–	–
Ditrichocorycaeus andrewsi	5.68	7.83	6.71	7.31	8.62	8.18	8.83
Ditrichocorycaeus erythraeus	5.75	–	–	6.65	8.29	–	–
Euterpina acutifrons	–	7.70	7.18	–	–	–	–
Farranula concinna	–	–	–	5.92	–	7.5	–
Oithona plumifera	6.12	–	–	–	7.56	–	–
Oncaea clevei	6.53	8.13	6.25	7.29	–	8.76	9.69
Oncaea mediterranea	6.02	–	–	–	–	–	–
Onychocorycaeus agilis	–	–	–	–	–	–	7,51
Paracalanus parvus	6.77	9.65	6.74	7.84	9.74	9.35	8.15
Subeucalanus pileatus	5.35	7.67	7.15	–	–	–	–

environment of Gorgona Island could have been influenced by conditions associated with the warm phase of the El Niño-Southern Oscillation, which was reported for 2015–2016 for the oceanic ETP by Brainard et al. (2018), L'Heureux et al. (2017), and Newman et al. (2018), as well as for other coastal regions of the ETP by Sánchez-Velasco et al. (2017) and Alvarado et al. (2020). However, in this study it is not possible to assess whether the pelagic environment of Gorgona Island is directly influenced by ENSO because a longer time series is required.

4.2. Abundance of copepods on Gorgona island

The abundance of copepods recorded in the pelagic area of Gorgona Island in March was higher than the abundances recorded in other studies undertaken in the CP. Martínez-Aguilar et al. (2007) recorded a total of 863 ind. 100^{-3} at station 8 (3°N, 78°W), close to Gorgona Island, during a study undertaken along the CP coast in March 2006. Giraldo et al. (2014a) recorded a median number of 29,395 ind. 100 m^{-3} in March 2011. These values were below those found in March samplings in this study, although Giraldo et al. (2014a) included abundance records obtained in areas closer to the coast of Gorgona Island. Similarly, other studies found lower abundance values in October samples compared with our results. Giraldo et al. (2014a) found a median value of 17,656 ind. 100 m^{-3} copepods around Gorgona Island in October 2010; low values were also reported in studies undertaken using the El Niño Phenomenon Regional Study (ERFEN) grid in the CP. López (2012) reported an average value of 25,422 ind. 100 m^{-3} copepods for September–October 2004, Murcia and Giraldo (2007) reported 29,992 ind. 100 m^{-3} copepods for the same period, and Jaimes and López (2014) reported 14,933 ind. 100 m^{-3} copepods for September 2007.

The difference in the abundances reported by previous authors compared with our results could be explained by the fact that previous authors analyzed samples to the level of the subclass Copepoda, thus decreasing the abundance that each species can contribute to the sample. It was, however, evident that the greatest abundance values occurred in March, and other authors (Giraldo et al., 2008, 2014a; Jerez-Guerrero et al., 2017; Valencia et al., 2019) similarly attributed this to the effect of the entrance of subsurface waters from the upwelling event that occurs in the Panama Bight because of the ITCZ moving along the CPC.

4.3. Copepod community structure

The temporal changes found in copepod abundance were reflected in the grouping analysis of community structure. Each sampled period formed a group; the division of the March and

Table 4
Copepod species that contributed to the dissimilarity between clusters generated (SIMPER analysis) on Gorgona Island. Only the species that contributed 20% of total dissimilarity between the groups are shown.

Clusters (similarity percentage, %)	March 2011 vs. October 2010a (42.90)	March 2011 vs. October 2010b (50.26)	March 2013 vs. October 2013 (44.19)	March 2016 vs. October 2015 (51.24)	March 2011 vs. March 2013 (44.01)	March 2011 vs. March 2016 (45.42)	March 2013 vs. March 2016 (37.70)
Morphospecies	Contribution percentage (%)						
Acartia (Acartia) danae	5.34	4.74	–	–	5.26	4.02	–
Acartia (Odontacartia) lilljeborgi	–	–	–	3.9	–	3.7	4.71
Acrocalanus gibber	–	–	–	–	–	–	–
Acrocalanus longicornis	–	–	–	–	–	–	–
Bestiolina cf. *similis*	–	–	–	–	–	–	4.91
Calanopia minor	–	4.41	–	–	–	3.74	–
Calocalanus pavo	–	–	–	–	–	4.23	–
Calocalanus styliremis	5.46	4.84	–	–	5.37	3.61	–
Centropages furcatus	–	–	–	3.82	–	–	–
Clausocalanus furcatus	–	–	–	3.84	–	–	–
Corycaeus crassiusculus	–	–	–	–	–	–	3.61
Euterpina acutifrons	–	–	7.01	–	–	–	–
Farranula concinna	–	–	6.66	4.09	–	–	–
Nannocalanus minor	4.67	–	–	–	4.36	–	3.65
Oithona cf. *brevicornis*	–	–	–	–	–	–	–
Oncaea mediterranea	6.3	4.54	–	–	5.06	–	–
Oncaea venusta	–	–	–	–	–	–	–
Onychocorycaeus agilis	–	–	–	–	–	–	4.3
Onychocorycaeus pacificus	–	–	–	–	–	–	–
Subeucalanus pileatus	–	3.1	5.72	4.16	–	–	–
Temora discaudata	–	–	–	–	–	–	–

Clusters (similarity percentage, %)	October 2010a vs. October 2010b (34.37)	October 2010a vs. October 2013 (31.23)	October 2010b vs. October 2013 (41.96)	October 2010a vs. October 2015 (38.13)	October 2010b vs. October 2015 (43.32)	October 2013 vs. October 2015 (39.29)
Morphospecies	Contribution percentage (%)					
Acartia (Acartia) danae	–	–	–	–	–	–
Acartia (Odontacartia) lilljeborgi	–	–	–	–	–	–
Acrocalanus gibber	–	–	–	6.77	5.87	4.95
Acrocalanus longicornis	–	–	–	7.04	–	6.90
Bestiolina cf. *similis*	4.02	–	6.45	–	4.6	–
Calanopia minor	5.63	4.59	–	–	–	–
Calocalanus pavo	–	–	–	–	–	–
Calocalanus styliremis	–	–	–	–	–	–
Centropages furcatus	–	–	–	–	–	–
Clausocalanus furcatus	–	–	–	5.98	5.52	–
Corycaeus crassiusculus	–	–	–	–	–	–
Euterpina acutifrons	–	6.39	5.75	–	–	5.03
Farranula concinna	–	–	–	–	–	–
Nannocalanus minor	–	–	–	–	–	–
Oithona cf. *brevicornis*	4.33	–	3.92	–	5.70	–
Oncaea mediterranea	–	–	–	–	–	–
Oncaea venusta	–	–	3.94	–	–	–
Onychocorycaeus agilis	–	4.99	–	–	–	5.59
Onychocorycaeus pacificus	4.34	–	–	–	–	–
Subeucalanus pileatus	–	4.88	–	–	–	–
Temora discaudata	3.96	–	–	–	–	–

October periods was evidenced by the presence/absence and difference in the abundances of species among the groups. There were higher chlorophyll-*a* values in March than in October. As some authors have suggested (Rodríguez-Rubio et al., 2003; Giraldo et al., 2008, 2014a; Jerez-Guerrero et al., 2017; Valencia et al., 2019; Corredor-Acosta et al., 2020), the ITCZ moves to the south during this time of year which creates an upwelling process in the Panama Bight that can extend to the waters surrounding Gorgona Island, and can cause subsequent increases in phytoplankton growth (Soto et al., 2001; Giraldo et al., 2014a) which in turn could promote a surge in the abundance of copepods. This situation could favor an increase in the abundance of copepods such as *Subeucalanus pileatus* in March, as well as the presence of other members of the family Eucalanidae, such as *Pareucalanus attenuatus* (Dana, 1849), *P. langae* (Fleminger, 1973), *S. crassus* (Giesbrecht, 1888), and *S. subtenuis* (Giesbrecht, 1888). This is in relation to October, when their abundance decreased or when they were absent. In particular, *S. pileatus* is characteristic of coastal tropical areas and is commonly found after phytoplankton blooms from which it benefits (Jiménez-Pérez and Lavaniegos, 2004; Tutasi et al., 2011), as it is a large coarse filter-feeding herbivore like other members of the family Eucalanidae (Timonin, 1971; Benedetti et al., 2018).

Some copepods, such as *D. andrewsi*, *O. clevei*, and *P. parvus*, were found during all evaluated periods, and were more abundant in October samples; added to the decrease in abundance of *S. pileatus*, they formed the October groups. These copepods are considered small (total length under 1,500 μm) (Turner, 2004; Rakhesh et al., 2013; Jerez-Guerrero et al., 2017); *D. andrewsi* is an ambush carnivore, *O. clevei* a detritivore, and *P. parvus* a fine filter-feeding herbivore (Timonin, 1971; Benedetti et al., 2018). They can exploit different food sources, including the microbial loop, and ingest small particles without competing with each other. In October, the movement of the ITCZ to the north increases precipitation and nutrient input from continental runoff (Giraldo et al., 2008, 2011, 2014a; Blanco, 2009), which could create a change in food availability, increasing organic matter and the abundance of small organisms such as cyanophytes, pennate diatoms, and dinoflagellates, as has been reported by some authors

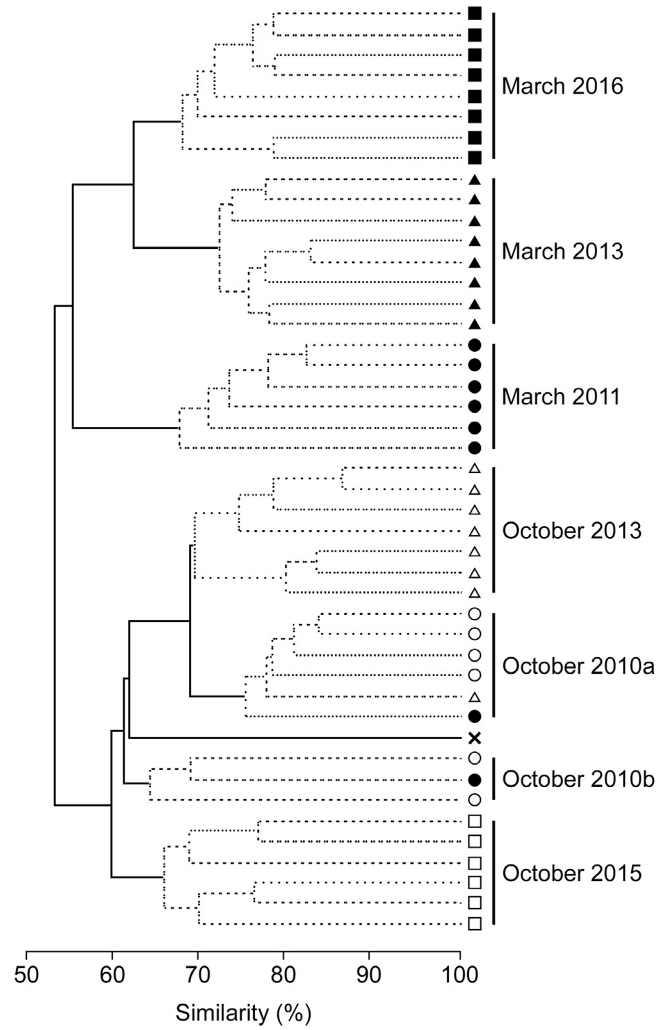

Fig. 7. Grouping analysis of the copepod community recorded around Gorgona Island during the study period. The dotted line represents the significance of the groups created (SIMPROF, $p < 0{,}05$). The sampling stations are represented as follows; circle: year 1, triangle: year 2, square: year 3. The filled figures represent the periods of March, and the empty figures represent the periods of October.

Table 5
BEST Bio-Env analysis results for each year of study. Only the best five results are shown. **ρs:** Spearman's correlation coefficient, **$T_{1\ m}$:** temperature at 1 m, **$T_{30\ m}$:** temperature at 30 m, **$T_{50\ m}$:** temperature at 50 m, **$S_{10\ m}$:** salinity 10 m, **$S_{30\ m}$:** salinity at 30 m, **$S_{50\ m}$:** salinity at 50 m, **Chl:** superficial chlorophyll-*a*, **Twc:** transparency of the water column.

Year 1 (October 2010–March 2011)		
No. of variables	ρs	Best variables
2	0.755	S_{10m}, Twc
3	0.733	T_{30m}, S_{10m}, Twc
3	0.732	S_{10m}, S_{30m}, Twc
2	0.725	S_{30m}, Twc
2	0.718	T_{30m}, Twc
Year 2 (March 2013–October 2013)		
No. of variables	ρs	Best variables
5	0.832	T_{1m}, T_{50m}, S_{10m}, Chl, Twc
5	0.83	T_{10m}, T_{30m}, T_{50m}, S_{10m}, Twc
5	0.83	T_{10m}, T_{30m}, T_{50m}, Chl, Twc
5	0.827	T_{10m}, T_{30m}, S_{50m}, Chl, Twc
5	0.827	T_{10m}, T_{50m}, S_{10m}, S_{30m}, Twc
Year 3 (October 2015–March 2016)		
No. of variables	ρs	Best variables
2	0.868	T_{30m}, Twc
3	0.866	T_{10m}, T_{30m}, Twc
3	0.865	T_{30m}, S_{10m}, Twc
4	0.858	T_{10m}, T_{30m}, S_{10m}, Twc
6	0.847	T_{10m}, T_{30m}, S_{10m}, S_{30m}, S_{50m}, Twc

for the area (Soto et al., 2001; Valencia and Giraldo, 2012; Giraldo et al., 2014a). This would benefit small-sized copepods during October periods, although these organisms were found during all periods evaluated in this study. Similarly, this process could explain the significant increase recorded in copepod abundance in March 2011, but this could also be attributed to the impact of the cold phase of the El Niño-Southern Oscillation phenomenon 2010–2011 (standardized SOI index October 2015: −1.7, March 2016: −0.1, NOAA, 2021, ONI index, October 2015: 2.4, March 2016: 1.6, Climate Prediction Center Internet Team, 2021). During this phenomenon, there was an increase in precipitation in the CP region (IDEAM, 2011; Hoyos et al., 2013; Vargas et al., 2018), coinciding with the greatest values of surface chlorophyll-*a* recorded in this study. ENSO could be an important driver of copepod community structure in the pelagic environment of Gorgona Island, but it was not possible to assess because the time scale is not sufficient to corroborate it.

The Bio-Env analysis revealed that the copepod community structure was influenced not only by trophic preferences and nutrient availability (chlorophyll-*a* and water column transparency) but also by temperature and salinity. This was particularly evident in years 1 (October 2010–March 2011) and 3 (October 2015–March 2016), which presented the greatest differences and during which an increase in copepod abundance was also observed. Studies undertaken in areas close to the coast (Santhanam and Perumal, 2012; Yoshida et al., 2012; Boersma et al., 2016; Chew and Chong, 2016; Jerez-Guerrero et al., 2017) have shown how temperature and salinity affect the copepod community, particularly in terms of distribution, metabolic processes, reproduction, growth, and community structure. In this study, the parameters that most influenced the community structure were temperature and salinity, especially in March, when 20 exclusive species were found, including *Lubbockia squillimana* Claus, 1863, *Mecynocera clausi* Thompson I.C., 1888, *P. attenuatus*, and *Rhincalanus nasutus* Giesbrecht, 1888. These species could present preferences for the cold and salty conditions recorded around Gorgona Island in March, compared with October. Some authors (Björnberg, 1963; Ehrhardt, 1967; Xu and Gao, 2011; Razouls et al., 2021) have reported a similar trend in temperature and salinity preferences for these species, which are also considered oceanic water species (Bradford-Grieve et al., 1999; Razouls et al., 2021). These results demonstrate the entrance of oceanic cold and salty subsurface waters into the pelagic environment of Gorgona Island; these waters are the result of the upwelling process that occurs in the Panama Bight as a consequence of the ITCZ movement over the ETP, which has been reported by other authors for different regions of the CP (Giraldo, 2008; Giraldo et al., 2008, 2014a; Jerez-Guerrero et al., 2017; Valencia et al., 2019; Corredor-Acosta et al., 2020).

5. Conclusion

This study is the first to document the intra-annual and interannual changes in abundance, composition, and community structure of the epipelagic copepods around Gorgona Island, a location of particular interest due to its high diversity levels and its location in the easternmost region of the ETP. Changes to the copepod community structure are a consequence of the movement of the ITCZ over the ETP, which modulates the entrance of subsurface waters coming from the Panama Bight in March and the increase in continental runoff in October. The abundance of copepod species is affected mainly by temperature, salinity, chlorophyll-*a,* and water column transparency. The most important copepods were *S. pileatus* in March and *D. andrewsi*, *O. clevei*, and *P. parvus* in October, which shows that the copepod community in the pelagic environment of Gorgona Island has a dynamic structure and composition.

The identification of temporal variability effects on energy flows in the pelagic system of the marine protected area associated with Gorgona Island is one of the medium-term research challenges that this study leaves open. Finally, a temporal series analysis is necessary to determine the response of the copepod community in the study area to the effect of large-scale processes such as ENSO, considering differences in the oceanographic parameters and changes in the abundances of copepods recorded during the present study.

CRediT authorship contribution statement

Mauricio Jerez-Guerrero: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Alan Giraldo:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **María I. Criales-Hernández:** Conceptualization, Validation, Resources, Writing – review & editing, Supervision, Funding acquisition.

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.

Data availability

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Acknowledgments

We thank Andrés Cuellar, Andrés Ortiz, Bellineth Valencia, Diego Córdoba, Gustavo Ramírez, Isabel Calle, Juan David Acevedo, Juan José Gallego, Katherine Mejía, Luis David Lizcano, Luis Piñeros, Marisol Rivera, Natalia Rivera, Natalia Uribe, and Natasha Valencia for their help during oceanographic sampling trips to Gorgona Island. We thank the Gorgona National Natural Park (NNP) and Henry von Prahl Scientific Station employees for their contribution to the implementation of the oceanographic monitoring program at Gorgona NNP. This study was co-financed by the Universidad del Valle, Gorgona NNP, and the Universidad Industrial de Santander, and is part of the one author's (M.J.G.) research thesis to obtain the title of Master of Science from the Universidad del Valle. This is the publication number 018 of the Instituto de Ciencias del Mar y Limnilogía (INCIMAR), Universidad del Valle.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

References

Alvarado, J.J., Sánchez-Noguera, C., Arias-Godínez, G., Araya, T., Fernández-García, C., Guzmán, A.G., 2020. Impact of El Niño 2015–2016 on the coral reefs of the Pacific of costa rica: the potential role of marine protection. Rev. Biol. Trop. 68, S271–S282. http://dx.doi.org/10.15517/rbt.v68is1.41190.

Amador, J., Alfaro, E., Lizano, O., Magaña, V., 2006. Atmospheric forcing of the eastern tropical Pacific: A review. Prog. Oceanogr. 69, 101–142. http://dx.doi.org/10.1016/j.pocean.2006.03.007.

Araujo, A.V., Dias, C.O., Bonecker, S.L.C., 2017. Differences in the structure of copepod assemblages in four tropical estuaries: Importance of pollution and the estuary hydrodynamics. Mar. Pollut. Bull. 115, 412–420. http://dx.doi.org/10.1016/j.marpolbul.2016.12.047.

Benedetti, F., Vogt, M., Righetti, D., Guilhaumon, F., Ayata, S.D., 2018. Do functional groups of planktonic copepods differ in their ecological niches? J. Biogeogr. 45, 604–616. http://dx.doi.org/10.1111/jbi.13166.

Björnberg, T.K., 1963. On the marine free-living copepods off Brazil. Bol. Inst. Oceanogr. Sao Paulo 13, 3–142. http://dx.doi.org/10.1590/S0373-55241963000100001.

Blanco, J.F., 2009. The hidroclimatology of Gorgona island: seasonal and ENSO-related patterns. Actual. Biol. 31, 111–121.

Boersma, M., Mathew, K.A., Niehoff, B., Schoo, K.L., Franco-Santos, R.M., Meunier, C.L., 2016. Temperature driven changes in the diet preference of omnivorous copepods: No more meat when it's hot? Ecol. Lett. 19, 45–53. http://dx.doi.org/10.1111/ele.12541.

Boltovskoy, D., 1981. Atlas del Zooplancton del Atlántico Sudoccidental y Métodos de Trabajo con el Zooplancton Marino. Publicación Especial del INIDEP, Mar del Plata.

Boltovskoy, D., 1999. South Atlantic Zooplankton, Vol. 1–2. Backhuys Publishers, Leiden.

Boxshall, G., Halsey, S., 2004. An Introduction to Copepod Diversity. The Ray Society, London.

Bradford-Grieve, J.M., 1994. The Marine Fauna of New Zealand: Pelagic Calanoid Copepoda: Megacalanidae, Calanidae, Paracalanidae, Mecynoceridae, Eucalanidae, Spinocalanidae, Clausocalanidae. New Zealand Oceanographic Institute Memoir, Wellington.

Bradford-Grieve, J.M., Markhaseva, E., Rocha, C., Abiahy, B., 1999. Copepoda. In: Boltovskoy, D. (Ed.), South Atlantic Zooplankton, Vol. 2. Backhuys Publishers, Leiden, pp. 869–1098.

Brainard, R.E., Oliver, T., McPhaden, M.J., Cohen, A., Venegas, R., Heenan, A., Vargas-Ángel, B., Rotjan, R., Mangubhai, S., Flint, E., Hunter, S.A., 2018. Ecological impacts of the 2015/16 El Niño in the central equatorial Pacific. Bull. Am. Meteorol. Soc. 99, S21–S26.

Burd, B., Thomson, R., 2015. The importance of hydrothermal venting to water-column secondary production in the northeast Pacific. Deep Sea Res. II Top. Stud. Oceanogr. 121, 85–94. http://dx.doi.org/10.1016/j.dsr2.2015.04.014.

Cajaraville, M.P., Orive, E., Villate, F., Laza-Martínez, A., Uriarte, I., Garmendia, L., Ortiz-Zarragoitia, M., Seoane, S., Iriarte, A., Marigómez, I., 2016. Health status of the Bilbao estuary: A review of data from a multidisciplinary approach. Estuar. Coast. Shelf Sci. 179, 124–134. http://dx.doi.org/10.1016/j.ecss.2016.01.013.

Calle-Bonilla, I.C., Giraldo, A., Cuéllar-Chacón, A., 2017. Variación espacio temporal del ensamble de larvas de peces coralinos en isla Gorgona, Pacífico colombiano. Bol. Invest. Mar. Costeras 46, 55–72. http://dx.doi.org/10.25268/bimc.invemar.2017.46.2.728.

Campos, C.C., Garcia, T.M., Neumann-Leitão, S., Soares, M.O., 2017. Ecological indicators and functional groups of copepod assemblages. Ecol. Indic. 83, 416–426. http://dx.doi.org/10.1016/j.ecolind.2017.08.018.

Chew, L.L., Chong, V.C., 2016. Response of marine copepods to a changing tropical environment: Winners, losers and implications. PeerJ 4, e2052. http://dx.doi.org/10.7717/peerj.2052.

Clarke, K., Gorley, R., 2015. PRIMER V7: User Manual/Tutorial. PRIMER-E Ltd, Plymouth.

Clarke, K., Warwick, R., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, second ed. PRIMER-E Ltd, Plymouth.

Climate Prediction Center Internet Team, 2021. Cold & warm episodes by season. Accessed at: https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php. Accessed April 2, 2021.

Cloern, J.E., Foster, S.Q., Kleckner, A.E., 2014. Phytoplankton primary production in the world's estuarine-coastal ecosystems. Biogeosciences 11, 2477–2501. http://dx.doi.org/10.5194/bg-11-2477-2014.

Corredor-Acosta, A., Cortés-Chong, N., Acosta, A., Pizarro-Koch, M., Vargas, A., Medellín-Mora, J., Saldías, G.S., Echeverry-Guerra, V., Gutiérrez-Fuentes, J., Betancur-Turizo, S., 2020. Spatio-temporal variability of chlorophyll-a and environmental variables in the Panama Bight. Remote Sens. 12 (2150), http://dx.doi.org/10.3390/rs12132150.

Devis-Morales, A., Schneider, W., Montoya-Sánchez, R.A., Rodríguez-Rubio, E., 2008. Monsoon-like winds reverse oceanic circulation in the Panama Bight. Geophys. Res. Lett. 35, 1–6. http://dx.doi.org/10.1029/2008GL035172.

Dias, C.O., Araujo, A.V., Vianna, S.C., Fernandes, L.L., Paranhos, R., Suzuki, M.S., Bonecker, S.L.C., 2015. Spatial and temporal changes in biomass, production and assemblage structure of mesozooplanktonic copepods in the tropical south-west Atlantic Ocean. J. Mar. Biol. Assoc. UK 95, 483–496. http://dx.doi.org/10.1017/S0025315414001866.

Díaz, J.M., Pinzón, J., Perdomo, A., Barrios, L.M., López-Victoria, M., 2001. Generalidades. In: Barrios, L.M., López-Victoria, M. (Eds.), Gorgona Marina: Contribución al Conocimiento de Una Isla Única. INVEMAR, Serie de Publicaciones especiales No 7, Santa Marta, Colombia, pp. 17–26.

Ehrhardt, J.P., 1967. Contribution à l, étude du plancton superficiel et subsuperficiel du canal de sardaigne et de la mer sud-thyrrénienne. Cah. Oceanogr. 19, 729–781.

Escribano, R., Bustos-Rios, E., Hidalgo, P., Morales, C.E., 2016. Non-limiting food conditions for growth and production of the copepod community in a highly productive upwelling zone. Cont. Shelf Res. 126, 1–14. http://dx.doi.org/10.1016/j.csr.2016.07.018.

Fernández-Álamo, M.A., Färber-Lorda, J., 2006. Zooplankton and the oceanography of the eastern tropical Pacific: a review. Prog. Oceanogr. 69, 318–359. http://dx.doi.org/10.1016/j.pocean.2006.03.003.

Fontana, R.E., Elliott, M.L., Largier, J.L., Jahncke, J., 2016. Temporal variation in copepod abundance and composition in a strong, persistent coastal upwelling zone. Prog. Oceanogr. 142, 1–16. http://dx.doi.org/10.1016/j.pocean.2016.01.004.

Garzke, J., Ismar, S.M.H., Sommer, U., 2015. Climate change affects low trophic level marine consumers: warming decreases copepod size and abundance. Oecologia 177, 849–860. http://dx.doi.org/10.1007/s00442-014-3130-4.

Giraldo, A., 2008. Variabilidad espacial de temperatura, salinidad y transparencia en el ambiente pelágico del PNN Gorgona durante septiembre 2007 y marzo 2008. Bol. Cient. CIOH 163, 157–163. http://dx.doi.org/10.26640/01200542.26.157_163.

Giraldo, A., 2012. Geomorfología e hidroclimatología de isla Gorgona. In: Valencia, B., Giraldo, A. (Eds.), Isla Gorgona: Paraíso de Biodiversidad y Ciencia. Universidad del Valle, Cali, Colombia, pp. 17–23.

Giraldo, A., Diazgranados, M.C., Gutiérez-Landázuri, C.F., 2014b. Isla Gorgona, enclave estratégico para los esfuerzos de conservación en el Pacífico oriental tropical. Rev. Biol. Trop. 62, 1–12. http://dx.doi.org/10.15517/rbt.v62i0.15975.

Giraldo, A., Gutiérrez, E., 2007. Composición taxonómica del zooplancton superficial en el Pacífico colombiano (septiembre 2003). Invest. Mar. 35, 117–122. http://dx.doi.org/10.4067/S0717-71782007000100012.

Giraldo, A., Rodríguez-Rubio, E., Zapata, F., 2008. Condiciones oceanográficas en isla Gorgona, Pacífico oriental tropical de Colombia. Lat. Am. J. Aquat. Res. 36, 121–128.

Giraldo, A., Valencia, B., Acevedo, J.D., Rivera, M., 2014a. Fitoplancton y zooplancton en el área marina protegida de Isla Gorgona, Colombia, y su relación con variables oceanográficas en estaciones lluviosa y seca. Rev. Biol. Trop. 62, 117–132. http://dx.doi.org/10.15517/rbt.v62i0.15982.

Giraldo, A., Valencia, B., Ramírez, D.G., 2011. Productividad planctónica y condiciones oceanográficas locales en Isla Gorgona durante Julio 2006. Bol. Invest. Mar. Costeras 40, 185–201. http://dx.doi.org/10.25268/bimc.invemar.2011.40.1.108.

Gusmão, L.F.M., McKinnon, A.D., 2009. Sex ratios, intersexuality and sex change in copepods. J. Plankton Res. 31, 1101–1117. http://dx.doi.org/10.1093/plankt/fbp059.

Herfort, L., Peterson, T.D., Prahl, F.G., McCue, L.A., Needoba, J.A., Crump, B.C., Roegner, G.C., Campbell, V., Zuber, P., 2012. Red waters of myrionecta rubra are biogeochemical hotspots for the Columbia River Estuary with impacts on primary/secondary productions and nutrient cycles. Estuar. Coasts 35, 878–891. http://dx.doi.org/10.1007/s12237-012-9485-z.

Hoyos, N., Escobar, J., Restrepo, J.C., Arango, A.M., Ortiz, J.C., 2013. Impact of the 2010–2011 La Niña phenomenon in Colombia, south America: the human toll of an extreme weather event. Appl. Geogr. 39, 16–25. http://dx.doi.org/10.1016/j.apgeog.2012.11.018.

IDEAM, 2011. Análisis del impacto del fenómeno La Niña 2010–2011 en la hidroclimatología del país. Accessed at: http://www.institucional.ideam.gov.co. Accessed April 2, 2021.

Jack, J.P., Abdsalam, A.T., Khalifa, N.S., 2009. Assessment of dissolved oxygen in coastal waters of Benghazi, Libya. J. Black Sea/Mediterr. Environ. 15, 135–156.

Jackson, J.M., Lenz, P.H., 2016. Predator-prey interactions in the plankton: Larval fish feeding on evasive copepods. Sci. Rep. UK 6, 1–11. http://dx.doi.org/10.1038/srep33585.

Jagadeesan, L., Jyothibabu, R., Anjusha, A., Mohan, A.P., Madhu, N.V., Muraleedharan, K.R., Sudheesh, K., 2013. Ocean currents structuring the mesozooplankton in the Gulf of Mannar and the Palk Bay, southeast coast of India. Prog. Oceanogr. 110, 27–48. http://dx.doi.org/10.1016/j.pocean.2012.12.002.

Jaimes, J.C., López, R.H., 2014. Biomasa y abundancia de copepoda (Crustacea) en aguas superficiales del océano Pacífico colombiano durante septiembre de 2007. Rev. Biol. Mar. Oceanogr. 49, 31–41. http://dx.doi.org/10.4067/S0718-19572014000100004.

Jerez-Guerrero, M., Criales-Hernández, M.I., Giraldo, A., 2017. Epipelagic copepods in Bahía Cupica, Colombian pacific: Species composition, distribution and temporal variation. Rev. Biol. Trop. 65, 1046–1061. http://dx.doi.org/10.15517/rbt.v65i3.29449.

Jiménez-Pérez, L.C., Lavaniegos, B.E., 2004. Changes in dominance of copepods off Baja California during the 1997–1999 El Niño and La Niña. Mar. Ecol. Prog. Ser. 277, 147–165. http://dx.doi.org/10.3354/meps277147.

Kessler, W.S., 2006. The circulation of the eastern tropical Pacific: a review. Prog. Oceanogr. 69, 181–217. http://dx.doi.org/10.1016/j.pocean.2006.03.009.

Kozak, E.R., Franco-Gordo, C., Palomares-García, R., Gómez-Gutiérrez, J., Suárez-Morales, E., 2017. Annual egg production rates of calanoid copepod species on the continental shelf of the eastern tropical Pacific off Mexico. Estuar. Coast. Shelf Sci. 184, 138–150. http://dx.doi.org/10.1016/j.ecss.2016.11.012.

Lavín, M.F.F., Fiedler, P.C.C., Amador, J.A.A., Ballance, L.T.T., Färber-Lorda, J., Mestas-Nuñez, A.M.M., 2006. A review of eastern tropical Pacific oceanography: Summary. Prog. Oceanogr. 69, 391–398. http://dx.doi.org/10.1016/j.pocean.2006.03.005.

L'Heureux, M.L., Takahashi, K., Watkins, A.B., Barnston, A.G., Becker, E.J., Di Liberto, T.E., Gamble, F., Gottschalck, J., Halpert, M.S., Huang, B., Mosquera-Vásquez, K., Wittenberg, A.T., 2017. Observing and predicting the 2015/16 El Niño. Bull. Am. Meteorol. Soc. 98, 1363–1382. http://dx.doi.org/10.1175/BAMS-D-16-0009.1.

López, R.H., 2012. Distribución y abundancia de copépodos pelágicos en el Pacífico Colombiano. Univ. Mil. Nueva Granada 8, 108–131.

López-Ibarra, G.A., Hernández-Trujillo, S., Bode, A., Zetina-Rejón, M.J., 2014. Community structure of pelagic copepods in the eastern tropical Pacific ocean during summer and autumn. Cah. Biol. Mar. 55, 453–462.

Lozano-Cortés, D.F., Giraldo, A., Izquierdo, V., 2014. Short-term assessment of the sediment deposition rate and water conditions during a rainy season on La Azufrada coral reef, Gorgona Island, Colombia. Rev. Biol. Trop. 62, 107–116. http://dx.doi.org/10.15517/rbt.v62i0.15981.

Márquez-Rojas, B.J., Benítez-Brito, M., Troccoli, L., 2016. Hidrografía y cambios estructurales del mesozooplancton en el golfo de Cariaco, en dos períodos contrastantes. Rev. Biodivers. Neotrop. 6, 135–146. http://dx.doi.org/10.18636/bioneotropical.v6i2.346.

Márquez-Rojas, B.J., Díaz-Ramos, J., Troccoli, L., Marín, B., Varela, R., 2009. Densidad, biomasa y composición del zooplancton, en el estrato superficial de la cuenca de Cariaco, Venezuela. Rev. Biol. Mar. Oceanogr. 44, 737–749. http://dx.doi.org/10.4067/S0718-19572009000300019.

Martínez-Aguilar, T.I., Giraldo, A., Rodríguez-Rubio, E., 2007. Zooplancton en la corriente Colombia, pacífico colombiano durante marzo de 2006. Bol. Cient. CCCP 14, 69–82. http://dx.doi.org/10.26640/01213423.14.69_82.

McKinnon, A.D.D., Duggan, S., 2014. Community ecology of pelagic copepods in tropical coastal waters. In: Seuront, L. (Ed.), Copepods: Diversity, Habitat and Behavior. Nova Scotia Publishers, New York, pp. 25–49.

Medellín-Mora, J., Escribano, R., Schneider, W., 2016. Community response of zooplankton to oceanographic changes (2002–2012) in the central/southern upwelling system of Chile. Prog. Oceanogr. 142, 17–29. http://dx.doi.org/10.1016/j.pocean.2016.01.005.

Miyamoto, H., Itoh, H., Okazaki, Y., 2017. Temporal and spatial changes in the copepod community during the 1974–1998 spring seasons in the Kuroshio region; a time period of profound changes in pelagic fish populations. Deep Sea Res. I Oceanogr. Res. Pap. 128, 131–140. http://dx.doi.org/10.1016/J.DSR.2017.07.007.

Morales-Ramírez, Á., 2008. Caracterización cualitativa del zooplancton del área de conservación marina isla del coco (ACMIC), océano Pacífico de Costa Rica. Rev. Biol. Trop. 56, 159–169. http://dx.doi.org/10.15517/RBT.V56I2.27014.

Motoda, S., 1959. Devices of simple plankton apparatus. Mem. Fac. Fish. Hokkaido Univ. 7, 73–94.

Murcia, M., Giraldo, A., 2007. Condiciones oceanográficas y composición del mesozooplancton en la zona oceánica del Pacífico colombiano durante septiembre-octubre 2004. Bol. Cient. CCCP 14, 83–94.

Newman, M., Wittenberg, A.T., Cheng, L., Compo, G.P., Smith, C.A., 2018. The extreme 2015/16 El Niño, in the context of historical climate variability and change. Bull. Am. Meteorol. Soc. 99, S16–S20.

NOAA, 2021. Southern oscillation index (SOI). Accessed at: https://www.ncdc.noaa.gov/teleconnections/enso/indicators/soi/. Accessed April 2, 2021.

Osorio, A.F.A., Peláez-Zapata, D.S., Guerrero-Gallego, J., Álvarez-Silva, O., Osorio-Cano, J.D., Toro, F.M., Giraldo, A., 2014. Hydrodynamics applied to the management and conservation of marine and coastal ecosystems: Gorgona island, Colombian Pacific ocean. Rev. Biol. Trop. 62, 133–147. http://dx.doi.org/10.15517/rbt.v62i0.15983.

Palomares-García, R., Suárez-Morales, E., Hernández-Trujillo, S., 1998. Catálogo de Los Copépodos (Crustacea) Pelágicos Del Pacífico Mexicano. CICIMAR/ECOSUR, México.

PNN – Parques Nacionales Naturales de Colombia, 2018. Plan de Manejo Del Parque Nacional Natural Gorgona 2018-2023. Ministerio de Ambiente y Desarrollo Sostenible, Bogotá, Colombia.

Postel, L., Fock, H., Hagen, W., 2000. Biomass and abundance. In: Harris, R., Wiebe, P., Lenz, J. (Eds.), ICES Zooplankton Methodology Manual. Academic Press, San Diego, pp. 83–174.

Rakhesh, M., Raman, A., Ganesh, T., Chandramohan, P., Dehairs, F., 2013. Small copepods structuring mesozooplankton community dynamics in a tropical estuary-coastal system. Estuar. Coast. Shelf Sci. 126, 7–22. http://dx.doi.org/10.1016/j.ecss.2013.03.025.

Razouls, C., de Bovée, F., Kouwenberg, J., Desreumaux, N., 2021. Diversity and geographic distribution of marine planktonic copepods. Accessed at: http://copepodes.obs-banyuls.fr/en. Accessed April 2, 2021.

Restrepo-López, J.C., 2006. Aporte de caudales de los ríos Baudó, San Juan, Patía y Mira a la cuenca pacífica colombiana. Bol. Cient. CCCP 13, 17–32. http://dx.doi.org/10.26640/01213423.13.17_32.

Rice, E., Dam, H.G., Stewart, G., 2015. Impact of climate change on estuarine zooplankton: Surface water warming in long island sound is associated with changes in copepod size and community structure. Estuar. Coasts 38, 13–23. http://dx.doi.org/10.1007/s12237-014-9770-0.

Rodríguez-Rubio, E., Giraldo, A., 2011. Características oceanográficas en la isla malpelo y su relación con la cuenca oceánica del pacífico colombiano. Bol. Invest. Mar. Costeras 40, 19–32.

Rodríguez-Rubio, E., Schneider, W., Abarca del Río, R., 2003. On the seasonal circulation within the Panama Bight derived from satellite observations of wind, altimetry and sea surface temperature. Geophys. Res. Lett. 30, 1410–1413. http://dx.doi.org/10.1029/2002GL016794.

Sampey, A., McKinnon, A.D., Meekan, M.G., McCormick, M.I., 2007. Glimpse into guts: overview of the feeding of larvae of tropical shorefishes. Mar. Ecol. Prog. Ser. 339, 243–257. http://dx.doi.org/10.3354/meps339243.

Sampson, L., Giraldo, A., 2014. Annual abundance of salps and doliolids (Tunicata) around Gorgona island (Colombian Pacific), and their importance as potential food for green sea turtles. Rev. Biol. Trop. 62, 149–159. http://dx.doi.org/10.15517/RBT.V62I0.15984.

Sánchez-Velasco, L., Beier, E., Godínez, V.M., Barton, E.D., Santamaría-del Angel, E., Jiménez-Rosemberg, S.P.A., Marinone, S.G., 2017. Hydrographic and fish larvae distribution during the 'Godzilla El Niño 2015–2016' in the northern end of the shallow oxygen minimum zone of the eastern tropical Pacific ocean. J. Geophys. Res. Oceans 122, 2156–2170. http://dx.doi.org/10.1002/2016JC012622.

Santhanam, P., Perumal, P., 2012. Effect of temperature, salinity and algal food concentration on population density, growth and survival of marine copepod Oithona rigida giesbrecht. Indian J. Mar. Sci. 41, 369–376.

Selander, E., Berglund, E.C., Engström, P., Berggren, F., Eklund, J., Harðardóttir, S., Lundholm, N., Grebner, W., Andersson, M.X., 2019. Copepods drive large-scale trait-mediated effects in marine plankton. Sci. Adv. 5, eaat5096. http://dx.doi.org/10.1126/sciadv.aat5096.

Soto, P.A., Sánchez, S.L., Fernández, C.E., 2001. Comunidades planctónicas marinas. In: Barrios, L.M., López-Victoria, M. (Eds.), Gorgona Marina: Contribución Al Conocimiento de Una Isla única. INVEMAR, Serie de Publicaciones especiales No 7, Santa Marta, Colombia, pp. 93–105.

Srichandan, S., Baliarsingh, S.K., Prakash, S., Panigrahy, R.C., Sahu, K.C., 2018. Zooplankton research in Indian seas: A review. J. Ocean Univ. China 17, 1149–1158.

Timonin, A., 1971. The structure of plankton communities of the Indian ocean. Mar. Biol. 9, 281–289. http://dx.doi.org/10.1007/BF00372822.

Turner, J., 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs. Zool. Stud. 43, 255–266.

Tutasi, P., Palma, S., Cáceres, M., 2011. Epipelagic copepod distributions in the eastern equatorial Pacific during the weak la Niña event of 2001. Sci. Mar. 75, 791–802. http://dx.doi.org/10.3989/scimar.2011.75n4791.

UAESPNN, 2005. Plan Básico de Manejo 2005-2009. Parque Nacional Natural Gorgona. Unidad Administrativa Especial del Sistema de Parques Nacionales, Cali, Colombia.

Valencia, B., Giraldo, A., 2012. Structure of hyperiid amphipod assemblages on Isla Gorgona, eastern tropical Pacific off Colombia. J. Mar. Biol. Assoc. UK 92, 1489–1499. http://dx.doi.org/10.1017/S0025315411001780.

Valencia, B., Giraldo, A., Rivera-Gómez, M., Izquierdo-Peña, V., Cuellar-Chacón, A., 2019. Effects of seasonal upwelling on hydrography and mesozooplankton communities in a Pacific tropical cove off Colombia. Rev. Biol. Trop. 67, 945–962. http://dx.doi.org/10.15517/rbt.v67i4.35489.

Valencia, B., Lavaniegos, B., Giraldo, A., Rodríguez-Rubio, E., 2013. Temporal and spatial variation of hyperiid amphipod assemblages in response to hydrographic processes in the Panama Bight, eastern tropical Pacific. Deep Sea Res. I Oceanogr. Res. Pap. 73, 46–61. http://dx.doi.org/10.1016/j.dsr.2012.11.009.

Vargas, G., Hernández, Y., Pabón, J.D., 2018. La Niña event 2010–2011: Hydroclimatic effects and socioeconomic impacts in Colombia. In: Mal, S., Singh, R., Huggel, C. (Eds.), Climate Change, Extreme Events and Disaster Risk Reduction. Springer, Cham, Switzerland, pp. 217–232.

Venkataramana, V., Sarma, V.V.S.S., Reddy, A.M., 2017. River discharge as a major driving force on spatial and temporal variations in zooplankton biomass and community structure in the Godavari estuary India. Environ. Monit. Assess http://dx.doi.org/10.1007/s10661-017-6170-5.

WoRMS Editorial Board, 2021. World register of marine species. Accessed at: http://www.marinespecies.org. Accessed April 2, 2021.

Xu, Z., Gao, Q., 2011. Optimal salinity for dominant copepods in the east China sea, determined using a yield density model. Chin. J. Oceanol. Limnol. 29, 514–523. http://dx.doi.org/10.1007/s00343-011-0090-y.

Yang, G., Li, C., Wang, Y., Wang, X., Dai, L., Tao, Z., Ji, P., 2017. Spatial variation of the zooplankton community in the western tropical Pacific ocean during the summer of 2014. Cont. Shelf Res. 135, 14–22. http://dx.doi.org/10.1016/j.csr.2017.01.009.

Yoshida, T., Liong, C., Majid, A.M., Toda, T., Ross, B.H., 2012. Temperature effects on the egg development time and hatching success of three *Acartia* species (Copepoda: Calanoida) from the Strait of Malacca Teruaki. Zool. Stud. 51, 644–654.

Zapata, F., 2001. Formaciones coralinas de isla Gorgona. In: Barrios, L.M., López, M. (Eds.), Gorgona Marina: Contribución Al Conocimiento de Una Isla única. In: Serie Publicaciones Especiales No. 7, INVEMAR, Santa Marta (Colombia), pp. 27–40.