



<https://doi.org/10.15517/pvx7p780>

## Effects of environmental changes on total length of three Copepod species (Crustacea: Copepoda) on Gorgona Island, Colombia, 2013-2022

Manuela Gutiérrez-Ospina<sup>1\*</sup>; <https://orcid.org/0009-0007-9894-8682>

Mauricio Jerez-Guerrero<sup>2</sup>; <https://orcid.org/0000-0002-2408-4849>

Alan Giraldo<sup>1,3</sup>; <https://orcid.org/0000-0001-9182-888X>

1. Grupo de Investigación en Ciencias Oceanográficas, Departamento de Biología, Facultad de Ciencias Naturales y Exactas, Universidad del Valle, Cali, Colombia; [manuela.gutierrez@correounivalle.edu.co](mailto:manuela.gutierrez@correounivalle.edu.co)
2. Departamento de Biología, Facultad de Ciencias Naturales y Exactas, Universidad del Valle, Cali, Colombia; [mauricio.jerez@correounivalle.edu.co](mailto:mauricio.jerez@correounivalle.edu.co)
3. Grupo de Investigación en Ecología Animal, Departamento de Biología, Facultad de Ciencias Naturales y Exactas, Universidad del Valle, Cali, Colombia; [alan.giraldo@correounivalle.edu.co](mailto:alan.giraldo@correounivalle.edu.co) (\*Correspondence).

Received 18-VII-2024. Corrected 05-V-2025. Accepted 26-XI-2025.

### ABSTRACT

**Introduction:** Copepods are influenced by various climatic and oceanographic changes, including global warming, which increases the frequency of the warm phase of ENSO (El Niño-Southern Oscillation) and contributes to reductions in their mean population body size.

**Objectives:** To evaluate the effects of temperature, salinity, and dissolved oxygen concentration, measured at standard depths, on the mean total length of three copepod species: *Ditrichocorycaeus andrewsi*, *Centropages furcatus* and *Subeucalanus pileatus*, within the pelagic environment of Gorgona Island over a nine-year period.

**Methods:** Each year, 25 healthy female and male specimens per copepod species were selected during the cold-water season from 2013 to 2022. Vertical variability in temperature, salinity, and dissolved oxygen was analyzed. A mixed linear model was used to assess the independent effects of mean total length by sex, species, and year, while Spearman correlation confirmed associations with environmental variables. ANOVA followed by Tukey's test identified significant differences in total length among years for each species.

**Results:** A weak positive correlation was detected between temperature and the total length of the three species studied. A linear mixed model confirmed a significant species-sex-year interaction effect. Copepods *D. andrewsi* and *S. pileatus* exhibited smaller sizes during warm periods, while *C. furcatus* displayed considerable variation with no clear association to thermal conditions.

**Conclusions:** This study establishes a baseline for future research on the effects of climate change on copepod body size in the Colombian Pacific and the Eastern Tropical Pacific and offers valuable insights into how inter-annual climatic variability shapes copepod populations in tropical environments and contributes to a broader understanding of climate change impacts on marine ecosystems.

**Key words:** body size; ENSO; global warming; zooplankton.



## RESUMEN

### Efectos de los cambios ambientales en la longitud total de tres especies de copépodos (Crustacea: Copepoda) en la Isla Gorgona, Colombia, 2013-2022

**Introducción:** Los copépodos son afectados por diversos cambios climáticos y oceanográficos, incluido el calentamiento global que ha aumentado la frecuencia de la fase cálida del ENSO (El Niño-Oscilación del Sur) y estaría contribuyendo a la reducción del tamaño corporal promedio de sus poblaciones.

**Objetivos:** Evaluar los efectos de la temperatura, la salinidad y la concentración de oxígeno disuelto, medidos a profundidades estándar, en la longitud total promedio de tres especies de copépodos: *Ditrichocorycaeus andrewsi*, *Centropages furcatus* y *Subeucalanus pileatus*, en el ambiente pelágico de la Isla Gorgona durante un periodo de nueve años.

**Métodos:** Cada año, durante la temporada de agua fría entre 2013 y 2022, se seleccionaron 25 especímenes sanos, tanto hembras como machos, de cada especie de copépodo. Se analizó la variabilidad vertical de la temperatura, salinidad y oxígeno disuelto. Se utilizó un modelo lineal mixto para evaluar los efectos independientes de la longitud total promedio según el sexo, especie y año, y una correlación de Spearman para confirmar las asociaciones con las variables ambientales. Finalmente, se utilizó una prueba de ANOVA seguido de la prueba de Tukey para identificar diferencias significativas en la longitud total entre años para cada especie.

**Resultados:** Se detectó una correlación positiva débil entre la temperatura y la longitud total de las tres especies estudiadas. El modelo lineal mixto confirmó un efecto significativo de interacción entre especie, sexo y año. Los copépodos *D. andrewsi* y *S. pileatus* presentaron menores tamaños en los periodos cálidos, mientras que *C. furcatus* mostró una variabilidad considerable sin una clara asociación con las condiciones térmicas.

**Conclusiones:** Este estudio establece una línea base para futuras investigaciones sobre los efectos del cambio climático en el tamaño corporal de los copépodos en el Pacífico colombiano y el Pacífico Tropical Oriental. Además, proporciona información valiosa sobre cómo la variabilidad climática interanual influye en las poblaciones de copépodos en ambientes tropicales, contribuyendo a una comprensión más amplia del impacto del cambio climático en los ecosistemas marinos.

**Palabras clave:** tamaño corporal; ENSO; calentamiento global; zooplancton.

## INTRODUCTION

The reduction in mean body size is a widespread response among multiple species to global warming. This phenomenon is supported by Bergmann's rule for endotherms (Gardner et al., 2011) and extended to ectotherms through the Temperature-Size Rule (TSR) (Forster et al., 2011), which states that individuals reared in lower-temperature environments exhibit slower growth but attain larger adult body sizes than those raised in warmer conditions. This pattern has been confirmed across various taxa, including insects, crustaceans, fish, amphibians, birds, and mammals (Campbell et al., 2021; Daufresne et al., 2009; Garzke et al., 2015; Reading, 2007; Sheridan & Bickford, 2011). Specifically, aquatic species tend to experience body mass reductions in response to warming at a rate approximately ten times greater than terrestrial species, possibly driven by changes in

dissolved oxygen concentrations (Forster et al., 2011; Garzke et al., 2016).

Aquatic organisms are also influenced by temporal variations in climatic and oceanographic conditions. In the Eastern Tropical Pacific, where the Colombian Pacific is situated, the Intertropical Convergence Zone (ITCZ) dictates two distinct oceanographic seasons: a cold-water season (December to April), characterized by low precipitation, cold and saline surface waters, and a shallow thermocline; and a warm-water season (May to November), marked by high precipitation, warm and lower-salinity surface waters, and a deeper thermocline (Jerez-Guerrero et al., 2022; Valencia et al., 2013). However, the seasonal variability of oceanographic characteristics in the Colombian Pacific is further modulated by the El Niño-Southern Oscillation (ENSO). Positive sea surface temperature (SST) anomalies occur during the warm phase (El Niño), whereas

negative SST anomalies are observed during the cold phase (La Niña) (Valencia et al., 2013; Wang & Fiedler, 2006). Both ENSO phases significantly alter oceanographic conditions in the pelagic environment, modifying copepods distribution, abundance, and phenology in response to changes in their optimal thermal habitat (Edwards & Richardson, 2004; McGinty et al., 2021; Poloczanska et al., 2013).

Copepods are holoplanktonic crustaceans that constitute between 50 and 90 % of total zooplankton abundance, playing a fundamental role in energy transfer within marine ecosystems (Jerez-Guerrero et al., 2020; Richardson, 2008; Walter & Boxshall, 2025). Given their high biomass in pelagic food webs, it is crucial to assess whether their mean population body size decreases as SST increases, as such reductions could ultimately affect food availability and biomass accumulation at primary and higher trophic levels (Garzke et al., 2015; Hoegh-Guldberg & Bruno, 2010).

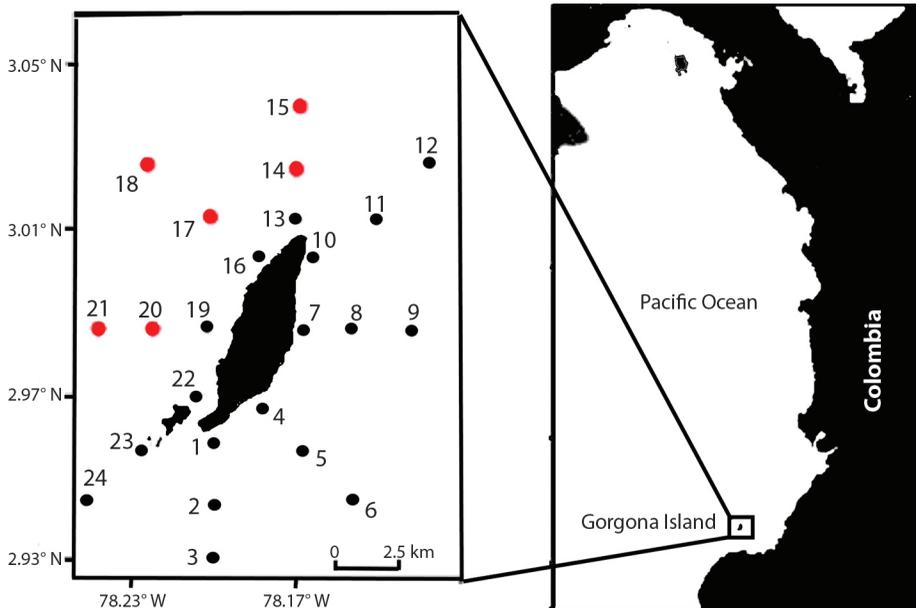
This study evaluated the effects of temperature, salinity, and dissolved oxygen variability on the pelagic environment of the Southern Colombian Pacific, based on a morphometric analysis of three copepod species collected over a nine-year period in the marine protected area of Gorgona Island. Specifically, the study addressed the following research questions: (1) Does interannual variation in temperature, salinity, and dissolved oxygen affect the body size of three copepod species representative of Gorgona Island's pelagic environment? (2) Is Temperature-Size Rule applicable to these copepod species inhabiting this region? and (3) Does the body sizes of male and female copepods in Gorgona Island respond differentially to oceanographic variability associated with ENSO? We hypothesize that oceanographic changes in the Colombian Pacific, driven by warm phase of ENSO, result in a reduction in mean body size among the most abundant copepod species in Gorgona Island's pelagic environment. Specifically, we expect that individuals developing under warmer conditions tend to be smaller than those developing in cooler environments.

## MATERIALS AND METHODS

Gorgona Island, located South of the Colombian Pacific continental shelf, has been part of the national system of protected areas since 1984. It encompasses both insular and maritime zones covering 617 km<sup>2</sup>, recognized for their high biological diversity (Giraldo, Diazgranados & Gutiérrez-Landázuri, 2014; Jerez-Guerrero et al., 2022; Sampson & Giraldo, 2014). The island is subject to climatic and oceanographic variations, including intra-annual shifts driven by the displacement of the Intertropical Convergence Zone (ITCZ), which alternates between phases of lower and higher precipitation (Giraldo et al., 2008; Jerez-Guerrero et al., 2022). On an interannual scale, the island is influenced by phenomena such as ENSO, which consists of a warm phase (El Niño) and a cold phase (La Niña) (Brainard et al., 2018; Valencia et al., 2013).

Since 2005, the pelagic environment of Gorgona Island has been sampled twice a year as part of the protected area's oceanographic monitoring program, which consists of sampling a 24 oceanographic stations grid equidistantly separated around the island (Jerez-Guerrero et al., 2020). Samples from 2013 to 2022 were used for the present study, covering only the cold-water season selecting stations 14, 15, 17, 18, 20, and 21 corresponding to the outer and middle stations on the West side of the Gorgona island, avoiding the influence of island and continental runoff (Fig. 1).

At each station, continuous records of temperature and salinity were obtained using a CastAway® CTD multiparameter sonde. Likewise, water samples were obtained at four standard depths (1, 10, 30, and 50 m) using a 5l Niskin bottle to measure dissolved oxygen concentration, temperature, and salinity using the YSI85 multiparameter sonde. Zooplankton samples were collected by performing oblique trawls from approximately 40 m depth to the surface with a 30 cm wide Bongo net with a mesh size of 300 µm, equipped with flowmeters (Hydro-Bios) calibrated to quantify the volume of filtered water. The samples were fixed in a



**Fig. 1.** Geographic location of Gorgona island in the Colombian Pacific Ocean. Red dots show the selected sampling stations.

4 % formalin-seawater solution and transported to the oceanographic sciences laboratory at Universidad del Valle, Cali, Colombia.

The most abundant species in the periods of study were identified using previous publications (Jerez-Guerrero et al., 2020; Jerez-Guerrero et al., 2022). Based on this information, three target species, *Ditrichocorycaeus andrewsi* (Faran, 1911), *Subeucalanus pileatus* (Giesbrecht, 1888), and *Centropages furcatus* (Dana, 1849), were selected considering that: a) they were present in all selected samples, b) they were highly abundance and frequent, and c) there was the presence of adult males and females in healthy condition. A Bogorov counting chamber was used to count the organisms based on the analysis of aliquots obtained from the total sample using a Folsom fractionator, following the methodology proposed by Jerez-Guerrero et al. (2020). Taxonomic identity was confirmed following Bradford-Grieve (1994), Bradford-Grieve (1999), Palomares et al. (1998), Boxshall and Halsey (2004), Razouls et al. (2025) database. Subsequently, up to 25 adult females and 25 males were separated from each total

zooplankton sample in good body condition for total body length measurement (Fig. 2) (Garzke et al., 2015; Hidalgo et al., 2012; Jerez-Guerrero et al., 2020). Digital photographs were taken using a NIKON SMZ-1 500 stereoscope equipped with a NIKON DS-Ri1 U3 camera, and measurements were made using NIS-Elements Br software. According to Pöhlupüü (2007), there is no statistically significant difference in the body length of preserved adult copepods. Therefore, this measurement can be used as an unbiased indicator of copepod length at any time.

Vertical temperature profiles were generated using data from the CastAway® CTD multiparameter sonde. Descriptive graphs were constructed for temperature, salinity, and dissolved oxygen concentration at each standard depth, as well as for total body length measurements of the three copepod species. Shapiro-Wilk tests were applied to biological and environmental data to determine whether parametric or non-parametric analyses were appropriate. Based on these results, ANOVA ( $\alpha = 0.05$ ) was performed to assess variations in

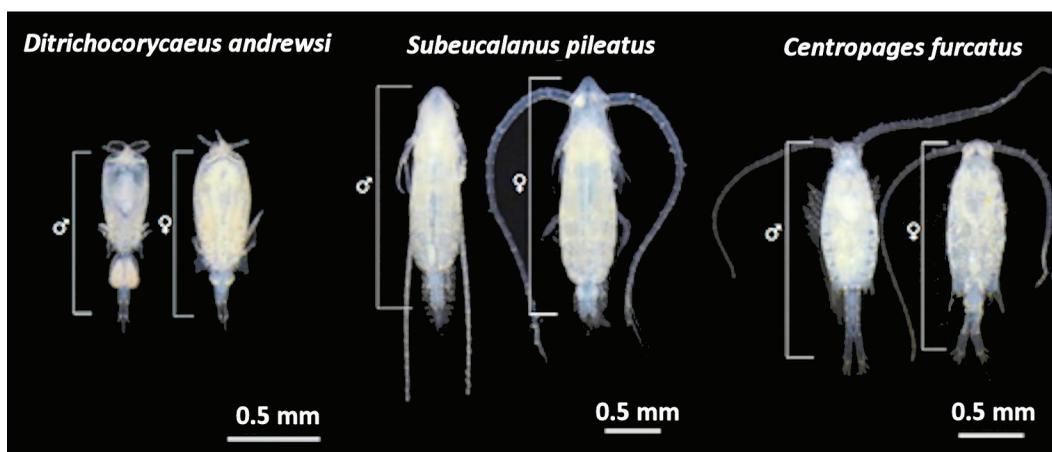


Fig. 2. Digital photographs of *Ditrichocorycaeus andrewsi*, *Subeucalanus pileatus*, and *Centropages furcatus*, captured on Gorgona Island. The male is on the left, the female on the right.

temperature, salinity, and oxygen across depths, followed by Tukey's multiple comparison test. To evaluate interannual variation in copepod body size, mixed linear models with factorial structures were implemented, analyzing the independent effects of sex, species, and year, as well as interactions between these factors. Depending on the model, homogeneous or heterogeneous variance was assumed. Model selection was based on the Akaike Information Criterion, Bayesian Information Criterion, and log-likelihood values. Finally, ANOVA and Tukey's multiple comparison tests were conducted to determine significant differences in total length across study years for each species. The data analysis was performed using RStudio (Posit team, 2025).

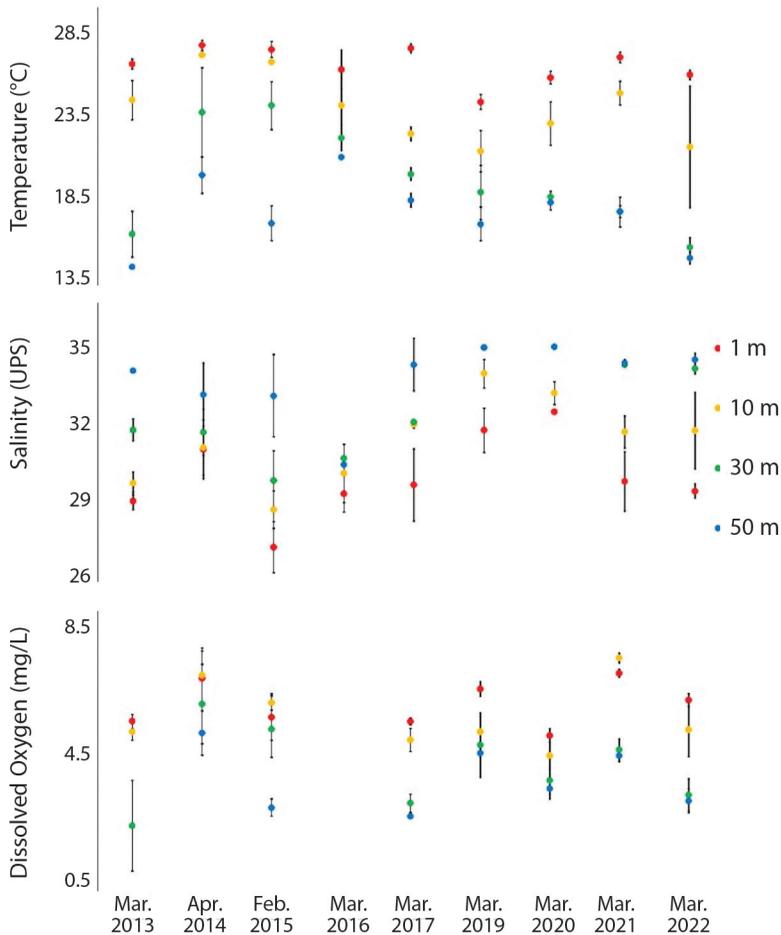
## RESULTS

Temperature, salinity, and dissolved oxygen records at standard depths varied significantly across study periods, despite all measurements being taken during the cold-water season (Tukey,  $p < 0.05$ , Fig. 3). In April 2014, February 2015, March 2021, and March 2022, the surface layer of the water column in the study area was warm, with lower salinity and higher dissolved oxygen concentrations,

with the 21° C isotherm and the 33 PSU isohaline located at depths greater than 30 m. In contrast, during March 2013, March 2016, March 2017, and March 2020, the surface layer of the water column was cold, exhibiting higher salinity and lower dissolved oxygen concentrations, with the 21° C isotherm and the 33 PSU isohaline positioned at depths of less than 10 m (Fig. 3, Fig. 4).

The oceanographic conditions observed during these periods aligned with descriptions of the study area under the influence of the warm and cold phases of ENSO. Consequently, based on these findings, the copepod assemblage in the upper water column of the pelagic environment surrounding Gorgona Island experienced contrasting oceanographic conditions on an interannual scale throughout the study period.

The mean total length of *D. andrewsi*, *S. pileatus*, and *C. furcatus* varied across study period (Fig. 5). The best-fitting linear mixed model, according to the applied criteria, was the one that assessed the combined effects of species, sex, and year on individual total length, identifying a significant species-sex-year interaction effect (ANOVA,  $p = 0.0001$ ). Female *D. andrewsi* exhibited the smallest total length in March 2022 ( $p < 0.05$ , Fig. 5), a period when



**Fig. 3.** Comparison of the mean temperature, salinity, and dissolved oxygen concentrations measured at standard depths between 2013 and 2022.

the surface layer of the water column was warm. Conversely, male *D. andrewsi* exhibited the greatest total length in February 2015 ( $p < 0.05$ , Fig. 5), when the upper water column was cold (Fig. 2). Meanwhile, both male and female *S. pileatus* showed a similar trend in size variation, with smaller sizes observed during warm surface temperature periods, particularly in March 2022 ( $p < 0.05$ , Fig. 5). Finally, male and female *C. furcatus* exhibited considerable variation in size throughout the study period, with no discernible temporal relationship to the local thermal conditions of the water column ( $p < 0.05$ , Fig. 5).

## DISCUSSION

The three copepod species examined in this study—*S. pileatus*, *C. furcatus*, and *D. andrewsi*—were representative of the cold-water copepod assemblage at Gorgona Island (Jerez-Guerrero et al., 2020; Jerez-Guerrero et al., 2022). These species have been recorded with significantly higher average abundances compared to other species reported for the region (Jerez-Guerrero et al., 2020). Specifically, *D. andrewsi* is considered a small copepod species, whereas *C. furcatus* is classified as medium-sized, and *S. pileatus* as large (Jerez-Guerrero et al., 2020). The size measurements

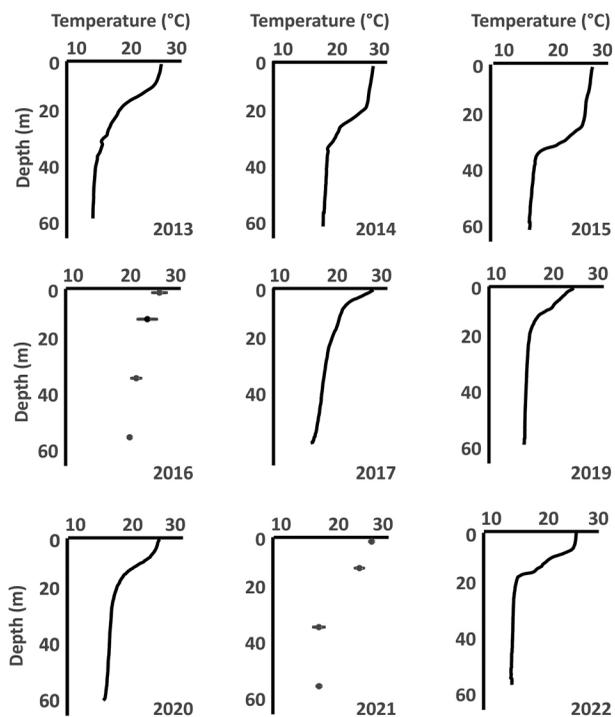


Fig. 4. Vertical variation of sea water temperature during cold-water period in Gorgona island between 2013 to 2022.

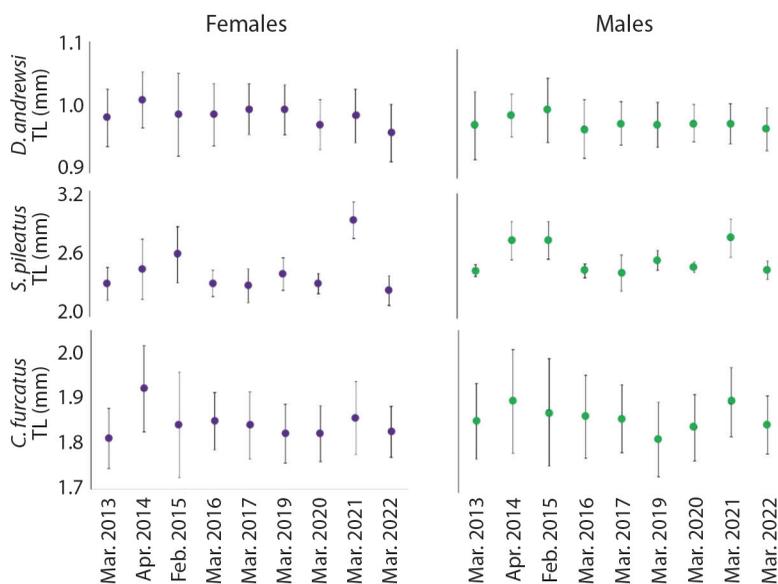


Fig. 5. Temporal variation of total length (TL) of *Ditrichocorycaeus andrewsi*, *Subeucalanus pileatus*, and *Centropages furcatus* in Gorgona island during cold-water period between 2013 to 2022.



obtained for these species during the study period fall within the range documented in the global database of marine copepods (Razouls et al., 2025). However, specific patterns of size variation were observed in association with interannual thermal variability in the study region. Individuals exhibited smaller sizes during periods influenced by the warm phase of ENSO, although this relationship was not always consistent.

Campbell et al. (2021) reported that marine copepods inhabiting polar and temperate zones generally follow Bergmann's rule, which states that organisms within the same clade tend to be larger in colder temperatures and smaller in warmer conditions. However, based on the findings of the present study, this pattern—well-documented for polar and temperate regions—does not appear to be dominant in this locality of the Eastern tropical Pacific. This discrepancy is likely due to the relatively small magnitude of thermal variation on a seasonal or interannual scale in tropical environments such as Gorgona Island. The temperature fluctuation reported by Campbell et al. (2021) exceeded 30 °C, whereas in the present study, the interannual variation in sea surface temperature was only 3 °C. Nevertheless, previous laboratory and field studies have indicated that higher rearing temperatures accelerate copepod hatching and development rates, leading to reduced adult body size and elemental composition (carbon, nitrogen, and phosphorus). These changes occur because of increased physiological rates, including ingestion, respiration, and reproduction (de Juan et al., 2023; de Juan et al., 2025; Doan et al., 2019; Garzke et al., 2015; Horne et al., 2016).

Beyond temperature, copepod size variation has been linked to other environmental variables, such as dissolved oxygen concentration, chlorophyll-a concentration, and food availability (Hirst & Bunker, 2003; Horne et al., 2016; Lin et al., 2013). According to Roman and Pierson (2022), in marine environments where water temperature has increased, copepods' oxygen demand also rises due to the reduction in dissolved oxygen concentration, leading to higher metabolic expenditure.

This can promote the dominance of smaller copepod species and even drive a reduction in individual body size. Nawaz et al. (2024) reported a seasonal pattern in calanoid copepod size variation in the Bay of Benguela, with smaller calanoids observed during summer months when temperatures were high, whereas larger individuals were recorded during the monsoon season, when increased rainfall and nutrient availability prevailed. Negative correlations were observed between copepod size and temperature, while positive correlations were found with dissolved oxygen, pH, salinity, and chlorophyll-a concentration.

Similar to the findings of Nawaz et al. (2024), a significant positive relationship was established between the total length of *S. pileatus* and dissolved oxygen concentration at a depth of 30 m during the study period at Gorgona Island. It is important to highlight that the maximum rate of oxygen diffusion increases linearly with rising temperature, which heightens metabolic demand. However, elevated temperatures enhance oxygen diffusion through the copepods' surface tegument (Roman & Pierson, 2022), potentially facilitating increased final body size under such conditions. According to Campbell et al. (2021), in addition to oxygen availability, food supply represents a key driver of the Temperature-Size Rule (TSR). Greater resource abundance can enhance metabolic efficiency, leading to accelerated growth rates and increased body sizes in marine organisms (Blake & Marshall, 2023; Hopcroft & Roff, 1998; Huston & Wolverton, 2011; Lin et al., 2013; Sun et al., 2012; Lopes-da Rosa et al., 2023).

In the context of climate change, ocean warming appears to be irreversible (Bopp et al., 2013; Ruela et al., 2020) and is expected to drive a decline in phytoplankton biomass and copepod abundance (Behrenfeld et al., 2016; Stock et al., 2014; Woodworth-Jefcoats et al., 2017). The anticipated reduction in copepod size by thermal stress could further exacerbate negative effects on biomass availability for secondary consumers (Chew & Chong, 2016; Ledesma et al., 2021; Sheridan & Bickford, 2011). Although

previous studies had assessed the relationship between the copepod community and local oceanographic variables on Gorgona Island. (Giraldo, Valencia et al., 2014; Jerez-Guerrero et al., 2020; Jerez-Guerrero et al., 2022), this is the first study to assess size response of three dominant copepod from Gorgona Island to the effects of temperature, salinity, and dissolved oxygen. Although no definitive pattern was established between size variation and inter-annual temperature fluctuation, a tendency toward smaller sizes was observed when the study area was influenced by the warm phase of ENSO. Additionally, significant correlations were recorded between copepod size and other oceanographic factors, particularly dissolved oxygen which has been identified as potential driver of the Temperature-Dependent Response (TDR) and are closely linked to sea temperature dynamics. Our study offers valuable insight into how interannual climatic variability shapes copepod populations in tropical environments, contributing to a broader understanding of climate change impacts on marine ecosystems.

**Ethical statement:** The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

## ACKNOWLEDGMENTS

To Wilmar Torres for his support in the development of statistical analysis. To the image laboratory of the graduate program in Science-Biology at Universidad del Valle for providing the images of the studied species. To the members of the oceanographic sciences research group at Universidad del Valle for their support during the laboratory phase of this research. The samples used in this study were obtained within the framework of the oceanographic conditions monitoring program of PNN

Gorgona (Universidad del Valle and National Natural Parks, Pacific Territorial Division).

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