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Research article

Spatial distribution of zooplanktonic acoustic biomass and its relationship with oceanographic variables under different upwelling regimes in La Guajira, Colombian Caribbean

Distribución espacial de la biomasa acústica zooplanctónica y su relación con variables oceanográficas bajo distintos regímenes de surgencia en La Guajira, Caribe Colombiano

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ABSTRACT

We evaluated the distribution of zooplankton biomass in the Guajira Upwelling System (Caribbean Sea) using more than 800 km of acoustic transects collected during two field campaigns in 2018: one in May (weak upwelling) and another in December (intense upwelling). Spatial variability of zooplankton acoustic biomass was modeled with geostatistical methods, and its relationships with environmental variables were assessed using generalized additive models. The results revealed marked seasonal differences in zooplankton distribution. In May, biomass was concentrated along the continental shelf edge, whereas in December it was associated with upwelling centers influenced by fluvial inputs from the Magdalena River (Gulf of Salamanca). During weak upwelling, zooplankton biomass was higher and linked to elevated dissolved oxygen concentrations and low chlorophyll-a levels. Overall, seasonal variability in zooplankton biomass did not show a linear relationship with upwelling intensity, likely reflecting complex air–ocean–river interactions in the region.

Keywords: Chlorophyll-a, echosounder, plankton, productivity, temperature.

RESUMEN

La distribución de la biomasa de zooplancton en el sistema de surgencia de La Guajira (Mar Caribe) se evaluó utilizando más de 800 km lineales de datos acústicos obtenidos de dos muestreos realizados en 2018 durante un período de surgencia débil (mayo) e intensa (diciembre). La modelación de la variabilidad espacial e interpolación de la biomasa acústica del zooplancton se realizó con un método geoestadístico, y se analizó su relación con variables ambientales a través de modelos aditivos generalizados. Se encontró que la distribución espacial de la biomasa acústica del zooplancton fue diferente en los dos períodos evaluados. Para mayo se concentró en el borde de la plataforma continental, y en diciembre se asoció con focos de surgencias o zonas con altos aportes fluviales del río Magdalena (Golfo de Salamanca). En el período de afloramiento débil, la biomasa de zooplancton fue mayor y se asoció con altas concentraciones de oxígeno disuelto y niveles bajos de clorofila-a. La variabilidad estacional de la biomasa de zooplancton no mostró una relación lineal con la intensidad de los afloramientos, probablemente como consecuencia de procesos de interacción aire-océano-río que afectan la región.

Palabras clave: Clorofila-a, ecosonda, plancton, productividad, temperatura.

INTRODUCTION

In some coastal regions, wind-driven upwelling brings cold subsurface waters enriched in nutrients to the surface, stimulating biological productivity (Sverdrup and Kudela, 2020; Behrenfeld *et al.,* 2006). Such coastal upwelling zones are particularly intense and extensive along subtropical eastern boundary systems (Chavez and Messié, 2009), where zooplankton play a key role as the primary link between phytoplankton and fishery resources (Ballón *et al.,* 2011). In the southern Caribbean, off northern Colombia and Venezuela (10°00'00"–12°30'00" N; 63°00'00"–75°30'00" W), an intense coastal upwelling also occurs, although with lower productivity compared with subtropical systems (Rueda-Roa and Muller-Karger, 2013). This South Caribbean Coastal Upwelling System (SCUS hereinafter) comprises two regions with distinct dynamics. The eastern region, off Venezuela and Trinidad and Tobago (10°07'00"–11°06'00" N; 62°00'00"–66°06'00" W), is influenced by moderate but year-round trade winds. In contrast, the western region, off northern Colombia (74°00'00"–71°00'00" W), experiences intense trade winds during specific months (December–April and June; Correa-Ramírez *et al.,* 2020) and is commonly referred to as the Guajira Upwelling System.

In the Guajira Upwelling System, a mismatch between planktonic community maxima and periods of intense upwelling has been reported (García-Hoyos, 2008), along with abrupt declines in plankton biomass during peak upwelling events (Parámo *et al.,* 2011). However, the limited and fragmented data available for phytoplankton and zooplankton in this system constrain ecosystem modeling efforts, hindering a more comprehensive understanding of productivity and biogeochemical processes in the region (Vásquez-Carrillo and Sullivan, 2021; Criales *et al.,* 2006).

Several aspects of zooplankton in the Guajira Upwelling System have been investigated, including community structure (Bernal and Zea, 2000), biomass (Silva-Trujillo *et al.,* 2017), and the influence of stratification on community composition (Medellín-Mora, 2016). Zooplankton biomass is a key metric, as it reflects the abundance of secondary producers and the transfer of energy to higher trophic levels (Miller and Wheeler, 2012). This information is essential for assessing food availability for commercially important pelagic fish (Parámo *et al.,* 2003).

Among the available approaches for quantifying zooplankton biomass, acoustic methods provide one of the most accurate estimates (Burd and Thomson, 2012). These techniques rely on the intensity of sound backscatter emitted and received by echosounders (Lezama-Ochoa *et al.,* 2011), offering high-resolution spatial information (Simmonds and MacLennan, 2005) and reducing the subsampling bias caused by macrozooplankton avoidance (Fleminger and Clutter, 1965).

Upwelling regions are global hotspots that sustain major fisheries (Barua, 2019). In Colombia, the Guajira Upwelling System is among the areas with the largest aggregations of small pelagic fish (Parámo *et al.,* 2003) and hydrobiological resources with high fishing potential (Zamora, 2012). Improving knowledge of the temporal variability and abundance of zooplankton biomass, as well as its relationship with upwelling intensity, is therefore highly relevant. In this context, the present study evaluates the spatial distribution of relative zooplankton acoustic biomass (ZAB) in the Guajira Upwelling System (GUS) under contrasting wind-driven upwelling conditions (moderate winds in May and strong winds in December), and examines its relationships with oceanographic variables on the continental shelf.

MATERIALS AND METHODS

Study area and acoustic sampling design

Coastal upwelling near the La Guajira Peninsula, the northernmost tip of South America, is primarily driven by the seasonality of the northeast trade winds (Andrade and Barton, 2005; Torres and Tsimplis, 2012). To quantify zooplankton biomass, oceanographic and acoustic sampling was conducted on the continental shelf of the Guajira Upwelling System (11°00'00"–11°31'12" N; 72°41'00"–74°21'36" W), covering the area from the Magdalena River mouth (MGR; 12°07'12" N, 74°51'00" W) to Cabo de la Vela (12°07'12" N, 72°54'00" W). Data were collected in 2018 during two field campaigns: the first from May 5 to July 6 (~480 km) and the second from December 3 to 13 (~330 km) (Fig. 1).

The scientific echosounder used was a SIMRAD EK80 operating at 38 kHz (250 W) and 200 kHz (750 W) with a pulse duration of 1024 ms. Acoustic data quality control and noise reduction were carried out following the recommendations of Perrot *et al*. (2018), IRD (2018), and Ballón *et al*. (2011). Raw acoustic files were first converted to HAC format (ICES, 2003) using HERMES v1.69 (IFREMER, 2021), and subsequently to HDF5 format with Matecho v6 (Perrot *et al.,* 2018) for further processing. To distinguish planktonic organisms, we applied the bi-frequency method described by Ballón *et al*. (2011). The Nautical Area Scattering Coefficient (NASC) was obtained through echo-integration at a vertical resolution of 1 m and horizontal

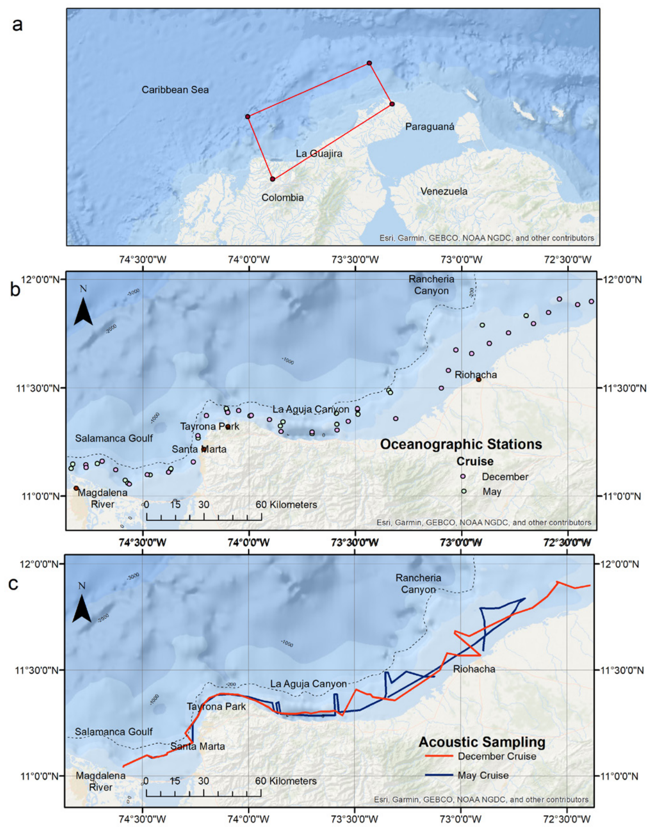

Figure 1. Sampling of information in the area of La Guajira. a) General location of the study The Guajira Upwelling System (GUS), the red line represents the polygon of the evaluated monthly means, b) Oceanographic stations with CTD launch in the two surveys in 2018 evaluated, c) Acoustic sampling lines.

resolution of 0.5 nmi (Jech *et al.,* 2018; Foote and Stanton, 2000), from 10 m below the surface to minimize vessel pitch and roll noise to a maximum depth of 150 m.

The spatial distribution of zooplankton acoustic biomass (ZAB) was modeled geostatistically following Cressie (2015). Spatial variogram models were fitted to the ZAB data using weighted least squares, and the optimal weights for each station were determined. Kriging interpolation was then applied to estimate ZAB at unsampled locations using R v3.6 (R Core Team, 2020) with the packages geoR v1.8 (Ribeiro *et al.,* 2020) and sp v1.4 (Pebesma *et al.,* 2021). The normality of ZAB samples was tested with the Kolmogorov–Smirnov test, and differences between May and December were assessed using the Wilcoxon rank-sum test for independent samples, with a 95% confidence level.

Oceanographic information

MODIS-Aqua Level-3 satellite data of monthly sea surface temperature (SST) at ~4 km resolution were obtained from OceanColor Web (https://oceancolor.gsfc.nasa.gov/). Monthly chlorophyll-a concentrations were derived from the Visible Infrared Imaging Radiometer Suite (VIIRS) at ~4 km resolution (https://data.nodc.noaa.gov/cgi-bin/iso?id=gov.noaa.ncdc:C01415). A mask was applied to exclude chlorophyll-a data at depths <10 m using ETOPO-1 bathymetry (https://www.ngdc.noaa.gov/mgg/global/), since values in shallow coastal waters are less reliable unless verified with in situ measurements. Monthly averages of wind speed and direction at 10 m height were obtained from daily ERA5 reanalysis fields, the fifth-generation ECMWF global atmospheric dataset (Hersbach *et al.,* 2020; https://climate.copernicus.eu/climate-reanalysis).

Oceanographic data were processed in R v3.6. Monthly SST, chlorophyll-a, and wind fields were spatially averaged to construct regional time series, using all grid nodes within a polygon defined by four vertices (10°33′36″ N, 73°28′48″ W; 12°12′36″ N, 71°18′00″ W; 13°42′00″ N, 71°33′36″ W; 12°42′00″ N, 74°09′36″ W). This polygon was selected to encompass the four most intense upwelling centers in the Guajira Upwelling Region, as identified by Rueda-Roa *et al.* (2013).

During the acoustic surveys, 61 vertical profiles of temperature, salinity, and dissolved oxygen were obtained with a CTDO (YSI EXO2) from the surface to a maximum depth of 200 m. Of these, 29 casts were collected in May and 32 in December 2018 (Fig. 1). From the profiles, T–S diagrams were constructed to identify water masses by calculating potential temperature and potential salinity (IOC *et al.,* 2010), using Ocean Data View v5.0 (https://odv.awi.de/) and R software.

Relationships between oceanographic conditions and ZAB

Generalized Additive Models (GAMs) were applied to analyze the relationships between ZAB and a set of environmental and spatial variables. Satellite-derived SST and chlorophyll-a, as well as in situ temperature, salinity, and dissolved oxygen (averaged over the upper 5 m from CTDO profiles), were included as predictors. Location variables (latitude, longitude, and depth) were also considered. Prior to modeling, ZAB and in situ data were interpolated onto a 4 km spatial grid using Kriging. GAM analyses were conducted in R with the packages *mgcv* v1.8 (Wood, 2021) and *nlme* v3.1 (Pinheiro *et al.,* 2021). Model selection was based on the lowest Akaike Information Criterion (AIC) value (Wang and Liu, 2006).

RESULTS

Oceanographic conditions on the continental shelf of the GUS

During 2018, spatially averaged winds were intense from January to March and from June to August, with a maximum monthly mean speed of 8.9 m s^{-1} observed in February and July (Fig. 2a-2d). Lower wind speeds occurred in two periods: April–May (mean 7.4 m s⁻¹) and September–November, with October exhibiting the lowest values (mean 5.0 m s⁻¹). In February, a small core of cold surface water was observed off Santa Marta (12°00’00”–12°18’00’ N, 71°18’00”–72°18’00” W; Fig. 2b-2d). In February, spatially averaged cold waters reached the lowest seasonal SST (24.1°C). From March to May, SST increased, and in June–July the spatially averaged SST decreased. Between August

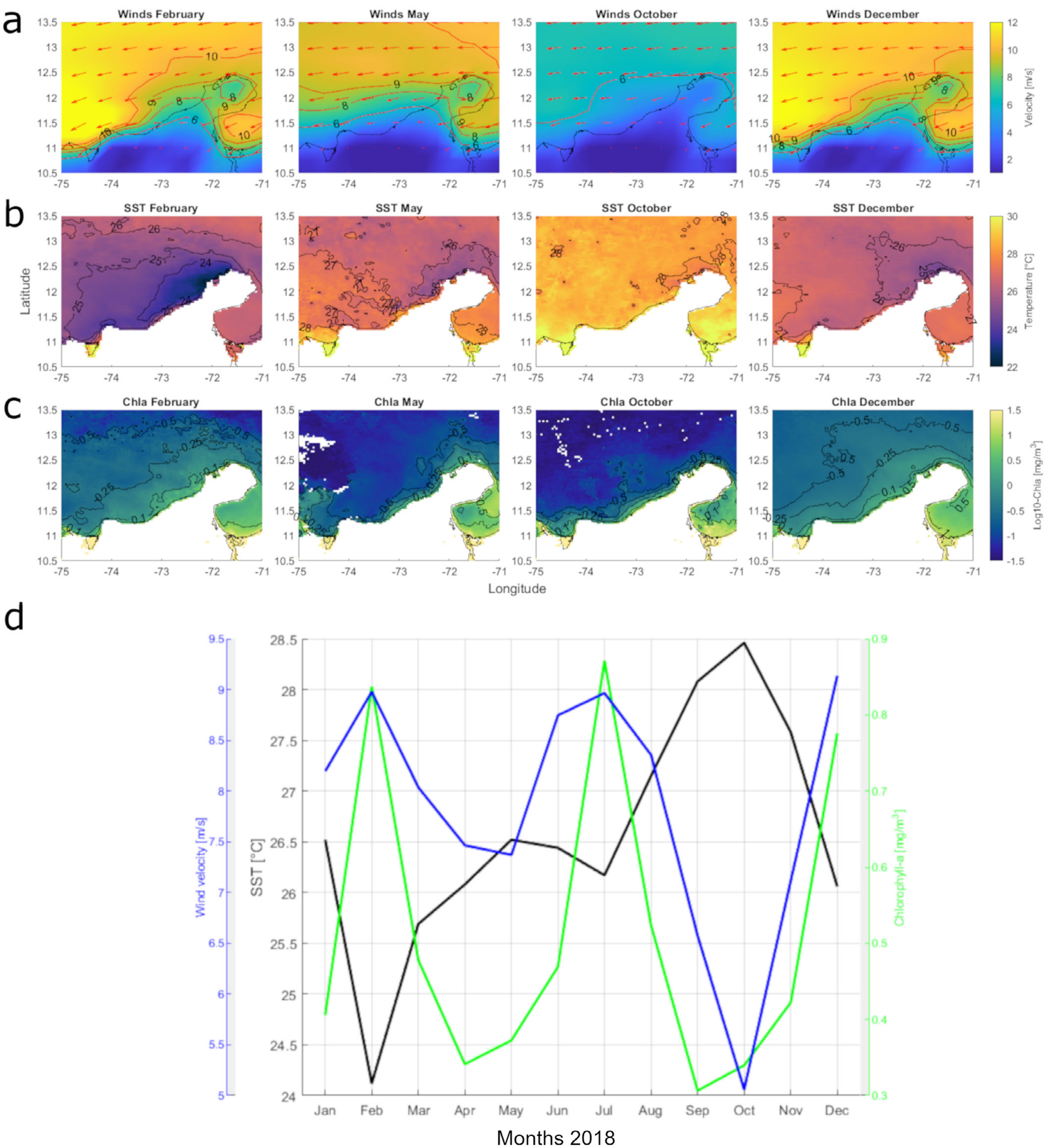

Figure 2. Oceanographic conditions in GUS, year 2018. a) Monthly averages of wind. b) Monthly sea surface temperature (SST). c) Monthly satellite chlorophyll-a. d). Time series of the monthly averages in the reference polygon.

(mean 27.1 °C) and October (mean 28.5 °C), surface waters warmed. In December, upwelling foci developed again, lowering the SST. Satellite chlorophyll-a concentrations were higher near the coast (Fig. 2c–2d), with intra-annual variability evident in the spatially averaged time series. Three mean peaks were recorded: July (mean 0.87 mg m^{-3}), February (0.84 mg m^{-3}), and December (0.77 mg m^{-3}). In the remaining months, chlorophyll-a concentrations were generally low, with occasional high values in the monthly time series (>2 mg m^{-3}) in the GUS and near the Magdalena River (MGR) mouth.

CTDO profiles in May 2018 showed cold surface waters (26–27 °C) and a well-mixed water column in the northeastern zone (72°00′00″–73°07′12″ W), and warmer waters (≥28 °C) in the GUS. In December, surface waters were colder (~26 °C) than in May between 73°18′00″ W and 74°36′00″ W and within the GUS (74°07′12″–74°25′12″ W). In May, surface salinity (PSU) was higher (~37) in the NE zone (<73° W) and decreased southwestward from 37 to 28.6. In the GUS and near the MGR, surface salinity was low (<30). In December, higher salinity prevailed west of 73°18′00″ W, indicating limited continental influence; only within the GUS up to the MGR (74°36′00″–74°28′48″ W) was lower surface salinity observed. Surface dissolved oxygen (DO) was slightly higher in May (6.0 ± 0.4 mg L^{-1}) than in December (5.8 ± 0.4 mg L^{-1}).

The isopycnals in May evidenced the dominance of surface water conditions, in contrast to those found in December (Fig. 3). Caribbean Surface Water (CSW) was identified in May above ~70 m depth at NE stations and to ~100 m at SW stations; salinity ranged 35.3–37.3, temperature from 25–29 °C, and potential density anomaly from 22–25 kg m^{-3}. In December, temperatures were similar (25–29 °C), but CSW salinity decreased southeast of the shelf (34.6–37.3). Subtropical Underwater (SUW) was the second water mass observed, characterized by its higher salinity and lower temperature relative to CSW. In May, SUW was observed at ~80–100 m at the SW stations, with salinity 37.4–37.5, temperature of 19–24 °C, and potential density anomaly of 26.0–26.5 kg m^{-3}. Beneath SUW, North Atlantic Central Water (NACW) was observed at ~150–200 m only in December, as deeper casts were available. This water mass was the coldest (17–19 °C) and densest (potential density anomaly 26.7–27.0 kg m^{-3}) recorded in the study, with slightly lower salinity than SUW (36.9–37.3).

Distribution of zooplankton biomass on the continental shelf of the GUS

The spatial structure of zooplankton acoustic biomass (ZAB) was modeled using variograms. The mean squared error (MSE) was lower for the exponential model (May: 1345.8, December: 1086.8). In May, the variogram showed a 21.4% nugget (nugget = 109.8, sill = 511.2, range = 12,032.1 m). In December, the nugget was 22.3% (nugget = 275.8, sill = 1233.7, range = 13,481 m).

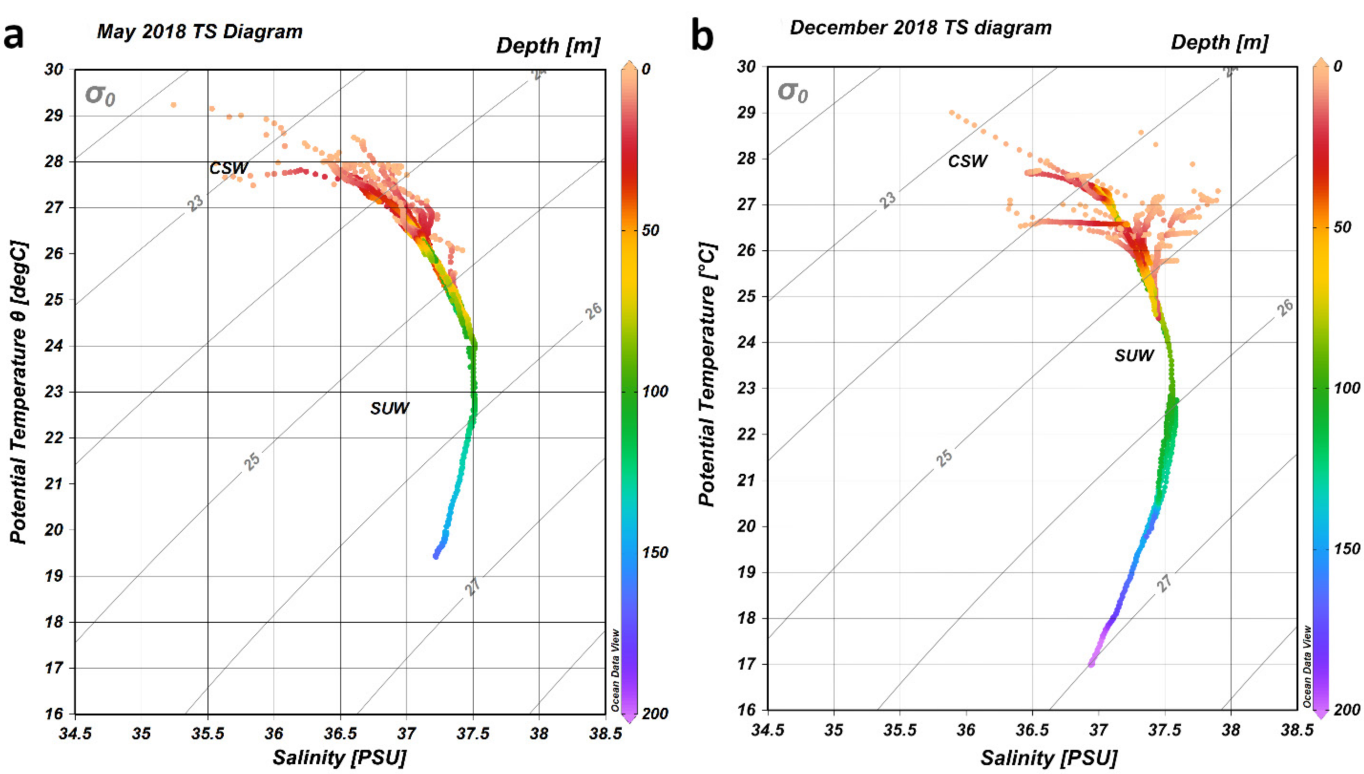

Figure 3. TS diagrams and identification of the water masses in GUS. The colors represent the depth and the gray lines the isopycnals.

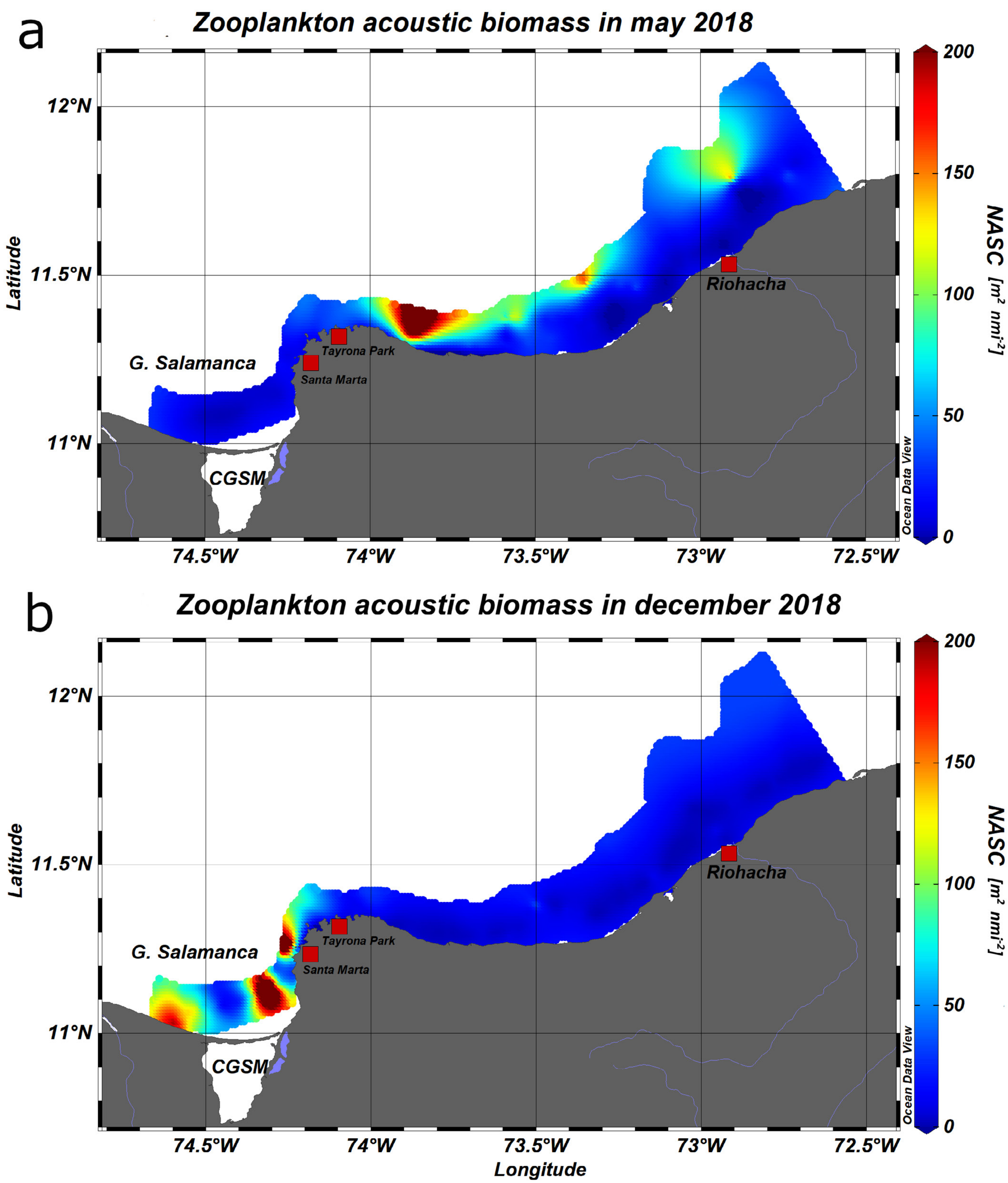

Figure 4. Spatial distribution of the acoustic biomass of zooplankton in the La Guajira area in ab) May and) December 2018. The NASC (Nautical Area Scattering Coefficient) in $m^2 \cdot nmi^{-2}$ represents the units of zooplankton acoustic biomass referenced to the bar colored to the right.

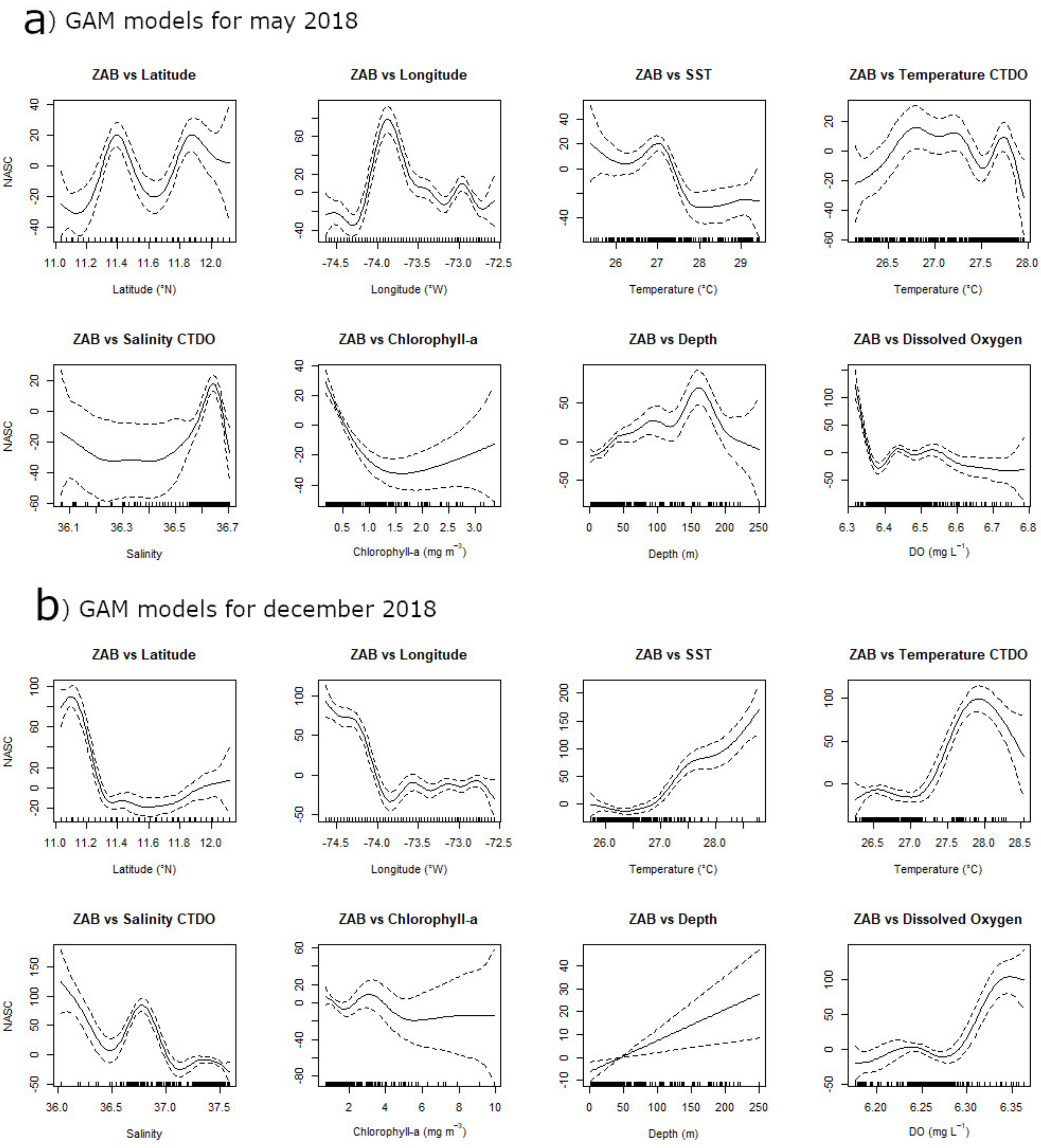

Figure 5. Results of the GAM modeling a) May and b) December, of the relationships between ZAB (NASC m^2 nmi^{-2}) and the predictors latitude (°N), longitude (°W), SST (°C), CTDO temperature (°C), chlorophyll-a VIIRS (mg m^{-3}), depth (m) and OD (mg L^{-1}) for the May 2018 survey over the GUS continental shelf. The dotted lines represent the 95 % confidence intervals of the estimates.

Table 1. Zooplankton biomass values in the GUS area and reviews from the literature.

Survey area	Biomass value (g m^{-2})	Reference
Coast of the department of Magdalena (Colombian Caribbean)	0.06 - 1.04	Silva-Trujillo *et al.* (2017)
Coast in front of Magdalena (Colombian Caribbean)	mean biomass 0.75	Bernal *et al.* (2004)
Perú-Chile upwelling	~100	Ballón *et al.* (2011)
Perú-Chile upwelling	17.8 – 61.5	Aronés *et al.* (2019)
Benguela upwelling (Africa)	4 - 9	Timonin *et al.* (1992)
Ocean of the South (Antarctica)	103.8	Ballón *et al.* (2011)
Eastern Canada	3.5	Ballón *et al.* (2011)
The Guajira Upwelling System	May mean 36.35 NASC and December mean 26.68 NASC	This study

In May, ZAB was highly heterogeneous (Fig. 4a): low values occurred nearshore (0–20 m² nmi^{-2}) and increased offshore (20–40 m² nmi^{-2}) between La Guajira (72°21′36″–73°14′24″ W) and the Gulf of Salamanca (GoS; 74°06′00″–74°21′00″ W). Three high-biomass aggregations (>100 m² nmi^{-2}) were identified: (i) between 73°18′00″ W and Tayrona National Natural Park (~74°00′00″ W), extending from nearshore across the shelf to 150–200 m depths; (ii) between 73°09′00″ and 73°08′24″ W at the shelf edge; and (iii) on the shelf near the Rancheria Canyon (~72°33′36″ W; ~11°30′00″ N), where high ZAB (>70 m² nmi^{-2}) occurred at depths >50 m.

In December (Fig. 4b), ZAB concentrations were lower in the northern sector. Three high-biomass nuclei were evident: (i) off Santa Marta (~74°06′36″ W); (ii) in the mid-GoS (~74°10′48″ W), where the maximum concentration of 289 m² nmi^{-2} was recorded; and (iii) between GoS and the MGR mouth (~74°21′36″ W). Mean and median ZAB were higher in May (mean: 36.3; median: 23.4 m² nmi^{-2}) than in December (mean: 26.6; median 11.7 m² nmi^{-2}). According to the Kolmogorov–Smirnov test, distributions were non-normal (May: $D = 0.19$, $p < 2.2 \times 10^{-16}$; December: $D = 0.31$, $p < 2.2 \times 10^{-16}$). The Wilcoxon test indicated that ZAB differed significantly between the two seasonal surveys ($W = 11,087,712$, $p < 2.2 \times 10^{-16}$).

Relationship between oceanographic conditions and ZAB in the GUS

GAM modeling showed statistically significant relationships for most predictors, except the December model that included chlorophyll-a (Deviance explained: 3.3%, AIC: 3385, $p = 0.2$). Longitude was the strongest predictor of ZAB (Fig. 5). In May (Deviance explained: 34.8%, AIC: 3250), maxima (~70 m² nmi^{-2}) occurred to the east, off Palomino and Buritaca (~73°25′12″ W). In December (Deviance explained: 53%, AIC: 3160), maxima (~50–100 m² nmi^{-2}) occurred to the west within GUS. Considering latitude, December maxima occurred toward the southern GUS (Deviance explained: 56.4%, AIC: 3183). In May, elevated ZAB appeared near 11°14′24″ N (Santa Marta) and 11°32′24″ N (off the Rancheria Canyon; Deviance explained: 18.6%, AIC: 3320).

Chlorophyll-a was the best environmental predictor in May (Deviance explained: 23.4%, AIC: 3113), with higher ZAB occurring at low chlorophyll-a concentrations (<0.5 mg m^{-3}). Satellite-derived SST was the second-best environmental predictor in December, with higher ZAB associated with cooler waters (25.5–27.0°C). In May, the variability explained by satellite SST (Deviance explained: 21.5%, AIC: 3298) exceeded that from CTDO profiles (Deviance explained: 4.4%, AIC: 3347). Higher ZAB was associated with cooler SST (~25.0–27.2°C), whereas at 27.3–29.5 °C ZAB values were low. In May, GAMs using in situ CTDO temperatures showed high dispersion and low explained variability, likely due to the small sample size.

With salinity as a predictor, explained variability in May was low (Deviance explained: 17.2%, AIC: 3307) with broad dispersion at salinities of 36.1–36.5; only near 36.6 were the highest ZAB values observed. In December (Deviance explained: 57.6%, AIC: 3123), salinity was a stronger predictor, with high biomass at higher salinities (~36.8) and a decline at intermediate values (~36.5).

Dissolved Oxygen (DO) was a good predictor in May (Deviance explained: 25.5%, AIC: 3251), with the highest ZAB at ~6.3 mg L^{-1}. In December, the largest ZAB aggregations occurred at 6.30–6.36 mg L^{-1} (Deviance explained: 23.5%, AIC: 3251). Regarding bottom depth, in May (Deviance explained: 22.5%, AIC: 3258) high biomass occurred at depths >70 m, although expected values showed high dispersion beyond ~100 m. In December, explained variability was low (Deviance explained: 2.5%, AIC: 3258), yet ZAB still increased with depth, with higher values at >60 m.

DISCUSSION

Hydroacoustic techniques are widely recognized as a reliable approach for estimating zooplankton biomass, often providing greater accuracy than traditional methods (Stanton *et al.,* 1994). Nevertheless, acoustic estimates are typically calibrated with zooplankton net samples to obtain values that approximate absolute biomass (Ballón *et al.,* 2011). In the present study, no concurrent net sampling was conducted in the Guajira Upwelling System (GUS), which prevented direct conversion of acoustic estimates into biological biomass. Therefore, analyses were based on relative zooplankton acoustic biomass (ZAB), used here as a proxy for biological biomass. Despite this limitation, ZAB provides valuable insights into spatial distribution patterns and their associations with environmental variables.

The spatial variability of ZAB was well represented by exponential variograms, which provided good fits for both the May and December 2018 surveys. Comparable results have been reported previously for the GUS, with Nautical Area Scattering Coefficient (NASC) values ranging from 1.10 to 3.98 m^2 nmi^{-2} in the Gulf of Salamanca (GoS) region (Silva-Trujillo *et al.,* 2017).

Previous studies have classified ZAB in the GUS as low compared with other upwelling systems (Silva-Trujillo *et al.,* 2017; Bernal *et al.,* 2004; Table 1). Our observations reveal clear spatial and seasonal differences in ZAB, likely linked to upwelling variability. May is typically characterized by milder alongshore winds and weaker upwelling (Torres Parra *et al.,* 2023). In 2018, trade winds and upwelling were weak, as reflected by relatively high SST and low chlorophyll-a concentrations (Fig. 2). Despite these conditions, localized peaks of high ZAB were observed. In December, when winds intensified and upwelling strengthened (Fig. 2), ZAB concentrations decreased in some areas but increased in others.

Upwelling of cold, nutrient-rich waters stimulates phytoplankton growth and provides trophic support for zooplankton through enhanced primary production (Miller & Wheeler, 2012). Although the GAM analysis detected a relationship between ZAB and the presence of cold water (an indicator of upwelling; Fig. 5), our findings suggest that ZAB seasonality may not align directly with upwelling intensity. During the weak-upwelling period, high ZAB values were concentrated at depths of ~150 m (Fig. 5), which may reflect reduced turbulence and offshore advection associated with Ekman transport (Cury & Roy, 1989).

In other upwelling systems, such as the Peru–Chile and Canary Current regions, fish larval recruitment is favored under conditions of optimal upwelling and turbulence intensity, consistent with the Optimal Environmental Window hypothesis (Cury & Roy, 1989). By analogy, it is plausible that in the GUS, low turbulence and reduced offshore advection during weak-upwelling periods promote higher zooplankton biomass.

Spatially, the highest ZAB in May coincided with upwelling foci off Santa Marta and the Rancheria Canyon (Rueda-Roa & Muller-Karger, 2013). However, elevated ZAB was also detected in areas influenced by continental runoff. In both May and December (representing weak and intense upwelling conditions, respectively), high ZAB was observed in the GoS, a region influenced by inputs from the Magdalena River (MGR), the largest river discharging directly into the Colombian Caribbean (Restrepo & Kjerfve, 2000), with a mean flow of ~7,079 m^3 s^{-1} (Beier *et al.,* 2017). In May, the greatest ZAB values occurred off Palomino and Buritaca, where local contributions come mainly from the Palomino River (~25 m^3 s^{-1}) and the Don Diego River (~39 m^3 s^{-1}) (Beier *et al.,* 2017). This shelf sector is also intersected by the upper segment of La Aguja Canyon (Rangel-Buitrago & Idárraga-García, 2010), which may facilitate nutrient fertilization through intrusions of deeper waters under moderate upwelling. This process, however, requires further investigation.

Salinity in the GUS is influenced by local river runoff (Beier *et al.,* 2017), seasonal advection of surface waters from the Orinoco River plume (Torres *et al.,* 2023), air–sea fluxes, and the input of upwelled waters, as the SUW that mixes with surface waters in the region typically has salinities >37.5 (Correa-Ramírez *et al.,* 2020). Consistent with this, the December GAM identified salinity as a strong predictor of ZAB under intense-upwelling conditions. The MGR follows a semiannual discharge cycle, with maxima in May–June and October–December, the latter being stronger (Beier *et al.,* 2017). In December, this pattern generated a pronounced surface salinity gradient: higher salinities in the northeastern GUS due to upwelled SUW, and lower salinities in the southwest due to freshwater inputs from the MGR, intensified by peak precipitation in October–November (Beier *et al.,* 2017). High ZAB was observed at both ends of this gradient (low and high salinity), suggesting that both upwelling fertilization and riverine inputs contribute to increased zooplankton biomass. However, the zooplankton community in the brackish GoS may differ substantially from that in the colder, saltier upwelling waters.

In upwelling systems, the role of continental inputs often lies in the supply of micronutrients (e.g., iron) to primary producers, which is essential for sustaining plankton biomass (Doney, 2006). For instance, in the California Current system (~25–50° N), outflows from the Columbia, Fraser, and Strait of Juan de Fuca rivers are associated with highly productive regions due to their nutrient inputs (Checkley & Barth, 2009; Hickey *et al.,* 2009). In the GUS, chlorophyll-a concentrations near the direct influence of the MGR reach 3.3 ± 1.4 mg m^{-3}, whereas outside that area values fall below 0.5 mg m^{-3}, indicating a positive relationship between chlorophyll-a, river discharge, and sediment load (Torregroza-Espinosa *et al.,* 2021).

Chlorophyll-a in the GUS exhibits strong seasonality associated with upwelling, with higher concentrations during December–April and June–July. As a proxy for phytoplankton biomass (i.e., food availability for zooplankton), chlorophyll-a might be expected to predict zooplankton biomass. However, it did not explain ZAB variability during the intense upwelling season off Santa Marta and in the GoS. Under strong upwelling, chlorophyll-a can decrease and become decoupled from upwelling dynamics (Paramo *et al.,* 2011; García-Hoyos, 2008). Relaxation events of trade-wind intensity lasting 3–7 days after an upwelling pulse favor phytoplankton growth and shelf-wide chlorophyll accumulation (Wilkerson *et al.,* 2006). In our results, although chlorophyll-a was the second-best predictor of ZAB during the weak upwelling season, the highest ZAB values were associated with low phytoplankton biomass (<0.3 mg m^{-3}), consistent with reduced chlorophyll concentrations due to zooplankton grazing. ZAB aggregations were only observed in areas directly influenced by MGR and GoS freshwater inputs, where warmer waters with elevated chlorophyll-a prevailed.

Overall, ZAB in the GUS was higher in May, when upwelling-favorable winds weakened and SST increased slightly; in contrast, December was not characterized by high satellite-derived chlorophyll-a. The inflow of continental waters with greater micronutrient availability better explains areas of elevated ZAB that were not associated with upwelling sources, particularly in the GoS and along the shelf between the Palomino and Don Diego rivers. In contrast, the high ZAB observed at the shelf edge and in the Rancheria Canyon is more consistent with the weak-upwelling conditions prevailing in May.

Regarding atmospheric forcing, trade-wind intensity off the Guajira Peninsula in 2018 exhibited a semiannual cycle that modulated coastal upwelling, driven by alongshore wind direction throughout the year, as previously reported for the GUS (Andrade & Barton, 2005). Annual wind variability is linked to the seasonal migration of the Intertropical Convergence Zone (ITCZ), which modulates the northeasterly (NE) trade winds and produces two periods of maximum intensity, one at the beginning and another in the middle of the year (Andrade & Barton, 2005). In the GUS, wind speeds up to 9.5 m s^{-1} have been reported (Paramo *et al.,* 2011), exceeding those observed in other upwelling systems such as Peru (5.9 m s^{-1}), NW Africa (6.8 m s^{-1}), Benguela (7.2 m s^{-1}), and California (7.8 m s^{-1}) (Chávez & Messié, 2009). Although high wind intensity enhances the upwelling of subsurface waters, it can also generate strong offshore advection of nutrients and plankton, potentially reducing phytoplankton and zooplankton biomass near the shoreline (Paramo *et al.,* 2011).

CONCLUSIONS

This study employed hydroacoustic techniques to estimate zooplankton biomass in the GUS, revealing marked spatial and seasonal variability associated with upwelling dynamics. Although acoustic estimates provide valuable insights into spatial distribution patterns and environmental relationships, the lack of concurrent biological sampling limited their conversion into absolute biomass values. Despite this limitation, our results show that higher relative zooplankton acoustic biomass (ZAB) in May coincided with weaker upwelling conditions, likely reflecting reduced turbulence and advection, contrary to expectations from classical upwelling theory. Spatial modeling using variogram analysis further revealed distinct ZAB patterns across the GUS, with concentrations linked both to upwelling centers and to areas influenced by continental river inputs, underscoring the combined influence of physical and continental drivers on biomass variability.

These findings underscore the complexity of zooplankton dynamics in the GUS, influenced not only by upwelling but also by freshwater inputs and possibly micronutrient availability, highlighting the need for further investigation of these ecological interactions.

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AUTHOR’S PARTICIPATION

J.S: Lead author, article writing, data curation, data analysis, formal research, article editing. J.P: Writing - review & editing, funding acquisition, conceptualization; Investigation. H.V: Review of eco-integration calculations. M.C: Manuscript review and editing. R.T: Review of physical oceanography component, Writing - review & editing.

CONFLICT OF INTEREST

The authors declare that there are no financial, personal, academic, or professional conflicts of interest that could have influenced the preparation, review, editorial decision, or publication of this manuscript.

This statement is made in compliance with the policies of Acta Biológica Colombiana, which guarantee transparency, objectivity, and integrity in the review and publication process of scientific articles.

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