Zooplankton distribution in a mesophotic corals reef habitat at Bajo Frijol seamount, Colombian Caribbean

Laura Contreras-Vega*1, Alejandro Henao-Castro1, Gabriel R. Navas-S2

Abstract
Mesophotic coral ecosystems (MCEs) shelter unique communities. Coral zooxanthellae in these environments feature a low photosynthesis rate; therefore, zooplankton becomes MCEs’ primary food source. These MCEs have not been studied enough due to the high cost of current assessment technologies, so these endeavors remain a challenge. The purpose of this work was to study the zooplankton community associated to the MCEs on seamount Bajo Frijol, within the Corales de Profundidad National Natural Park (off the Colombian Caribbean coast) and to compare its composition with that from shallower parts of the water column. Three samples were taken, filtering 24 L of seawater (via a mesh of size 45 µm) at each station with a device designed to collect zooplankton right on top of the reef substrate. Taxonomic composition, density and relative abundance were obtained. A resemblance analysis was performed, complemented with a cluster, an MDS and a modified Kandooor test. The analysis showed clear differences between the water column samples from those taken close to the reef. It also showed the separation of the community into two large groups: north and center-south, both with unique species.

Keywords: deep-sea corals; deep-sea protected areas; mesophotic corals; mesophotic ecosystems; zooplankton community; zooplankton distribution.

1. Introduction

Mesophotic coral ecosystems (MCEs) consist of light-dependent corals, usually found at depths of 30 m –at the euphotic zone limit– where light incidence is < 1%. These ecosystems are a direct extension of shallow reefs, harboring a high richness and biodiversity in their benthic habitat; furthermore, MCE communities reveal unique structures (Kahng et al., 2010, 2014; Laverick et al., 2017; Enrichetti et al., 2019).

MCEs are research and conservation hotspots because of their role as potential refuges. Along with deep coral reefs, MCEs act as source and receptors of fish larvae from shallow zones during or after a perturbation, protect a high number of species, and play an important role in the physical and biological interactions of the trophic structure (Semmler et al., 2017; Shlesinger et al., 2018; Sánchez et al., 2019).

Due to the scarce light, MCEs species have adapted to low photosynthetically active radiation (PAR). Lesser et al. (2009); Bessell-Browne et al. (2014), and Nir et al. (2014) suggested that some mesophotic corals change their trophic strategy to counteract the reduction in calcification, resulting from zooxanthellae’s low photosynthetic rate, by increasing heterotrophy and, in some cases, feeding only on zooplankton. In such cases, the latter have been regarded as key organisms
Zooplankton distribution at Bajo Frijol MCEs

Therefore, it is necessary to understand the ecological processes that allow the existence of such unique environments.

Zooplankton consists of a large assemblage of heterotrophic organisms, mostly microscopic and with limited motion capability. These organisms are widely distributed across world’s oceans, and are essential for the maintenance of reef ecosystems. Zooplankton constitutes a link between primary production and higher trophic levels, participating in biogeochemical cycles and in benthic and pelagic recruitment (Baéz-Polo, 2013; Carrillo-Baltodano and Morales-Ramírez, 2016; Nakajima et al., 2017; Lorda et al., 2019; MacKenzie et al., 2019).

Research conducted on MCEs has mainly focused on sessile organisms, like scleractinian corals, octocorals, and sponges, as well as on mobile organisms like fishes (Kahng et al., 2014; Scott and Pawlik, 2019); only few authors have addressed zooplankton organisms. Andradi-Brown et al. (2016) recently reported the first comparison between zooplankton communities associated with mesophotic and shallow reefs, concluding that further investigation is necessary to understand the distribution pattern of zooplankton communities in MCEs.

Corales de Profundidad National Natural Park (PNNCPR) is the first marine protected area of deep zones in Colombia (Alonso et al., 2015). Given the ecological importance of zooplankton and its use as a biological indicator, PNNCPR has prioritized zooplankton study, within a monitoring program. The purpose of this work was to analyze the distribution of the zooplankton community associated with MCEs on the seamount Bajo Frijol, located in PNNCPR’s protected area, comparing its composition with the zooplankton community from shallower parts of the water column.

2. Methods

2.1. Studied area

PNNCPR is located in the Colombian Caribbean, across from the Archipelago of San Bernardo. It has an extension of 142 192 km² and its depth ranges from 31 m to 1240 m (Morales et al., 2017). Within this marine protected area, the seamount Bajo Frijol was chosen as study area (Figure 1).

Bajo Frijol is located at the edge of the Colombian Caribbean continental shelf and has a mostly flat bottom at a depth of 36 m and mainly covered by calcareous rhodoliths. At Bajo Frijol’s shallowest point, around 32 m deep, some coral colonies and hard coralline landforms are present. Said landforms adjoin with flat zones a little deeper (down to 40 m) with isolated coral and sponge promontories. This zone boasts fish richness and abundance (Chasqui and Gonzalez, 2019).

As for zooplankton, Gutiérrez (2010) has reported around Islas del Rosario—an oceanic zone close to Bajo Frijol– dominance of copepods (68 %), followed by appendicularians (23 %). On deeper zones, copepods are still dominant (75 %) and are followed by ostracods (15 %). Chaetognates and other groups account for 3 % of the zooplankton. Medellín-Mora and Martínez-Ramírez (2010) also reported at a station close to PNNCPR a dominance of copepods (82 793 individuals/100 m³), followed by appendicularians (10 738 individuals/100 m³), and echinoderm larvae (4677 individuals/100 m³). A net with mesh size of 200 µm was used on both studies.
2.2. Sample collection and analysis

Five sites were chosen for sample collection, with depths between 35 m and 70 m, trying to cover most of the seamount area (Figure 1). Diurnal samplings took place in the five stations in August (E1, E5, and E7) and December (E2 and E4) 2016. Three samples were taken at each station using a device (Figure 2) designed to collect zooplankton samples right on top the mesophotic reef substrate (Contreras-Vega et al., 2020). The sampling device filters 24 dm$^3$ of sea water with a mesh size of 45 µm, and recovers an extract of 250 cm$^3$ into plastic bottles. Zooplankton samples were preserved with 4% formalin neutralized with borax (Baéz-Polo, 2013). Two additional samples were collected to assess the zooplankton community in the upper zones of the water column and serve as references in the study; R1 at station E1, and R2 at station E2, at 15 m and 5 m depth, respectively.

Following Boltovskoy (1981), each sample was sedimented for 72 h. A 50 cm$^3$ extract was used for specimen observation under an optical microscope with 100× magnification. Each entire sample was assessed through aliquots on a Bogorov plate. Taxonomic identification of zooplankton was conducted with the following guides: Boltovskoy (1981); Zheng (1989); Fernandes (2004a,b); Johnson and Allen (2005); Figueroa et al. (2005); Costa (2006); Riviera (2006), the online data bases Dolven and Skjerpen (2007) and the World Register of Marine Species WORMS (2017).
2.3. Data analysis

An abundance matrix was built by taxon for each station to describe the composition and ecological attributes of the community. These matrices were used to estimate the percentage abundance and overall and station-wise species richness. An ecological attribute analysis (Shannon-Wiener diversity, Pielou’s uniformity and Simpson’s predominance) was run for each station. The following equation was used to calculate zooplankton density (individuals/m³):

\[ \text{Density} = \frac{N}{V}, \]

where \( N = \text{Abundance} \) and \( V = \text{Filtered volume (m}^3\)).

To study the distribution of zooplanktonic assemblages in Bajo Frijol, a similarity test ANOSIM was run to determine if there were significant differences between sampling stations (Clarke et al., 2014). Additionally, a resemblance matrix between samples was calculated using the Bray-Curtis similarity index, data were fourth root transformed to guarantee that the program showed the composition similarities of the entire community, given that most of the identified taxa had very low abundances while others were too high (Clarke et al., 2014). The resemblance matrix was complemented with a classification analysis (cluster), using a SIMPROF test and a multidimensional scaling analysis (MDS) to observe the aggrupation and ordination of the samples.

In addition, a modified inverse analysis (Kaandorp, 1986; Navas et al., 2010) was performed. This consisted of a new abundance matrix by taxon for each group obtained in the Bray-Curtis cluster, which was used to estimate the percentage abundance, species richness, density and frequency,
as well as the generalist and exclusive species for each assemblage. An ecological-attribute analysis (including Shannon-Wiener diversity Mean, Pielou’s uniformity Mean and Simpson’s predominance Mean) was run first for each group obtained in the Bray-Curtis cluster, this time including the reference samples. All ecological tests were performed using the statistical software PRIMER-E V7.

3. Results and Discussion

3.1. Community composition and density

A total of 123 taxa (114 species, 9 larvae) were identified, grouped in 19 zooplankton groups: Amphipoda, Appendicularia, Bryozoa, Cnidarian larvae, Copepoda, Doliolida, Echinoderm larvae, Foraminifera, Hydrozoa, Nauplii, Ostracoda, Polychaeta, Protozoa, Pteropoda, Radiolaria, Rotifer, Siphonophora, Tintinida, and Veliger of Mollusca.

Tintinnids revealed the greatest richness (33 species), followed by radiolarians with 32 species. These groups are the most diverse in tropical zones, having high richness and low abundance. The latter, however, tends to increase with depth (Anderson, 1994; Armstrong and Brasier, 2005). Copepods had 24 species (Table 1), mostly calanoids, similar to those reported by Gutiérrez (2010) and Medellín-Mora and Martínez-Ramírez (2010) in an area close to that assessed in the present study.

Table 1. Total richness ($S$), density (individuals/m$^3$) and abundance of each identified zooplankton group.

<table>
<thead>
<tr>
<th>Zooplankton group</th>
<th>$S$</th>
<th>Density</th>
<th>Abundance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphipoda</td>
<td>1</td>
<td>111</td>
<td>0.19</td>
</tr>
<tr>
<td>Appendicularia</td>
<td>2</td>
<td>2611</td>
<td>4.46</td>
</tr>
<tr>
<td>Bryozoa</td>
<td>1</td>
<td>97</td>
<td>0.17</td>
</tr>
<tr>
<td>Cnidarian larvae</td>
<td>2</td>
<td>361</td>
<td>0.62</td>
</tr>
<tr>
<td>Copepoda</td>
<td>24</td>
<td>6361</td>
<td>10.87</td>
</tr>
<tr>
<td>Decapod larvae</td>
<td>1</td>
<td>28</td>
<td>0.05</td>
</tr>
<tr>
<td>Doliolida</td>
<td>1</td>
<td>14</td>
<td>0.02</td>
</tr>
<tr>
<td>Echinoderm larvae</td>
<td>3</td>
<td>153</td>
<td>0.26</td>
</tr>
<tr>
<td>Foraminifera</td>
<td>14</td>
<td>8875</td>
<td>15.16</td>
</tr>
<tr>
<td>Hydrozoa</td>
<td>1</td>
<td>194</td>
<td>0.33</td>
</tr>
<tr>
<td>Nauplii</td>
<td>1</td>
<td>23 028</td>
<td>39.34</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>1</td>
<td>1014</td>
<td>1.73</td>
</tr>
<tr>
<td>Polychaeta</td>
<td>1</td>
<td>181</td>
<td>0.31</td>
</tr>
<tr>
<td>Pteropoda</td>
<td>1</td>
<td>125</td>
<td>0.21</td>
</tr>
<tr>
<td>Radiolaria</td>
<td>32</td>
<td>3889</td>
<td>6.64</td>
</tr>
<tr>
<td>Rotifer</td>
<td>1</td>
<td>292</td>
<td>0.50</td>
</tr>
<tr>
<td>Siphonophora</td>
<td>1</td>
<td>28</td>
<td>0.05</td>
</tr>
<tr>
<td>Tintinida</td>
<td>33</td>
<td>9653</td>
<td>16.49</td>
</tr>
<tr>
<td>Veliger of Mollusca</td>
<td>2</td>
<td>1528</td>
<td>2.61</td>
</tr>
</tbody>
</table>

As to density, a total of 58 543 individuals/m$^3$ were identified. Nauplii had the major abundance with 39.34% (23 028 individuals/m$^3$, showing continuous reproductive cycles, typical for tropical species (Boltovskoy, 1981). These organisms can exceed copepodites and some adult
copepods in number (Thompson, 2001; Thompson et al., 2013) just as observed in Bajo Frijol (Table 1). Tintinnids had a share of 16.49 \% (9653 individuals/m$^3$), being one of the main groups of microzooplankton. Tintinnids are central to secondary production in all seas (Boltovskoy, 1981; Pierce and Turner, 1993; Thompson et al., 1999; Thompson, 2001). Foraminiferans and copepods also had a significant abundance with 15.16 \% and 10.87 \% (8875 individuals/m$^3$ and 6361 individuals/m$^3$), respectively (Table 1).

### 3.2. Composition and density per sampling site

Station E1, located at the center of the seamount, was the richest of all stations with 85 taxa. This station basted the highest richness of radiolarians (23 species). Tintinnids, copepods and foraminifers also had a high richness (16, 15, and 12 species, respectively). E7, located at the south of the seamount, had the highest number of copepods (21 species), whereas E4, located at the north, had the most of tintinnids species (20 species). E2, located at the north, revealed the lowest total richness (70 species), preceded by E4 and E7 having similar richness (72 species each) (Table 2 and Table 3).

As to density, E1 had the highest overall abundance (14000 individuals/m$^3$), followed by E5 and E7 with 12819 individuals/m$^3$ and 12431 individuals/m$^3$, respectively. E7 had the highest abundance of copepods (1694 individuals/m$^3$), and foraminifers (2931 individuals/m$^3$) (Tables 2 and 3). E4 had the highest density of Appendicularians, with 1194 individuals/m$^3$, while E1 and E7 has the highest density of mollusc veliger. Nauplii dominated in all the stations. Tintinnids, radiolarians, foraminifers and copepods were identified abundantly on each station (Table 2).

### Table 2. Zooplankton group density ($N$) individuals/m$^3$ and richness ($S$) by station.

<table>
<thead>
<tr>
<th>Zooplankton group</th>
<th>E1</th>
<th>E2</th>
<th>E4</th>
<th>E5</th>
<th>E7</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$N$</td>
<td>$S$</td>
<td>$N$</td>
<td>$S$</td>
<td>$N$</td>
</tr>
<tr>
<td>Amphipoda</td>
<td>28</td>
<td>1</td>
<td>69</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Appendicularia</td>
<td>417</td>
<td>2</td>
<td>250</td>
<td>2</td>
<td>1194</td>
</tr>
<tr>
<td>Brioza</td>
<td>14</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cnidarian larvae</td>
<td>222</td>
<td>2</td>
<td>28</td>
<td>1</td>
<td>42</td>
</tr>
<tr>
<td>Copepoda</td>
<td>1000</td>
<td>15</td>
<td>1125</td>
<td>14</td>
<td>1292</td>
</tr>
<tr>
<td>Decapod larvae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>Doliolida</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Echinoderm larvae</td>
<td>28</td>
<td>2</td>
<td>14</td>
<td>1</td>
<td>28</td>
</tr>
<tr>
<td>Foraminifera</td>
<td>2403</td>
<td>12</td>
<td>944</td>
<td>9</td>
<td>944</td>
</tr>
<tr>
<td>Hydrozoa</td>
<td>28</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nauplii</td>
<td>4917</td>
<td>1</td>
<td>3639</td>
<td>1</td>
<td>3750</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>278</td>
<td>1</td>
<td>236</td>
<td>1</td>
<td>125</td>
</tr>
<tr>
<td>Polychaeta</td>
<td>42</td>
<td>1</td>
<td>28</td>
<td>1</td>
<td>111</td>
</tr>
<tr>
<td>Pteropoda</td>
<td>42</td>
<td>1</td>
<td>28</td>
<td>1</td>
<td>14</td>
</tr>
<tr>
<td>Radiolaria</td>
<td>1319</td>
<td>23</td>
<td>806</td>
<td>19</td>
<td>806</td>
</tr>
<tr>
<td>Rotifer</td>
<td>167</td>
<td>1</td>
<td>42</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Siphonophora</td>
<td>14</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tintinida</td>
<td>2653</td>
<td>16</td>
<td>1722</td>
<td>16</td>
<td>1778</td>
</tr>
<tr>
<td>Veliger of Mollusca</td>
<td>431</td>
<td>2</td>
<td>83</td>
<td>2</td>
<td>208</td>
</tr>
</tbody>
</table>
Reports on radiolarians and tintinnids in the Colombian Caribbean are scarce. This is because the net size used in most studies (> 100 µm) does not allow the retention of those groups (Thompson, 2001; Vanegas and Arregocés, 2015). This could also explain nauplii dominance, since nets with mesh sizes larger than 45 µm (as used in the current research), would not retain early-stage individuals (Thompson, 2001), as observed in Gutiérrez (2010) and Medellín-Mora and Martínez-Ramírez (2010), who used a mesh size of 200 µm, revealing copepods, appendicularians, and decapods as the dominant groups. On the other hand, foraminifers, are organisms with a great preference for clean waters, without suspended organic matter and with salinity between 32 ppt and 42 ppt (Boltovskoy, 1981), as is usually found on coral reef habitats.

Copepods represent one of the largest and most important groups within zooplankton communities (due to its high richness and abundance), distributed in a cosmopolitan manner, and present in various vertical strata (Boltovskoy, 1981; Bernal and Zea, 1993; Thompson, 2001; Gutiérrez, 2010; Hernandez-Trujillo et al., 2010), which explains its presence in each of the sampled stations, with some fluctuations per station, probably due to availability of the resource or possible vertical migrations (Boltovskoy, 1981; Bernal and Zea, 1993).

Ecologic attribute analyses showed high evenness values on each station ($J'$ between 0.62 and 0.70) (Table 3). E1 had the highest diversity, followed by E4 ($H' = 3.07$ and $H' = 3.01$; respectively), meanwhile E5 had the lowest diversity value ($H' = 2.63$) (Table 3). E2 and E7 had comparable diversity values (2.86 and 2.91, respectively).

### 3.3. Zooplankton community distribution

The ANOSIM showed differences between stations. However, this analysis also revealed similarities between the stations located at the center and south of the seamount (E1-E5; $R = 0.11$; $p < 0.3$), those located at the south (E5-E7; $R = 0.22$; $p < 0.3$), and the stations located at the north (E2-E4; $R = 0.22$; $p < 0.1$) (Table 4).

Additionally, the Bray-Curtis resemblance cluster, complemented with a SIMPROF (cophenetic index of 0.88 and an MDS (stress 0.06) showed data clustering into four groups: A (R1), B (R2), C (E1, E5 and E7) and D (E2 and E4) (Figure 3).

**Group A.** This group consists of the reference sample (R1) collected at E2 at 5 m depth, which does not correspond to a mesophotic zone. This assemblage presented the greatest abundance with 45 750 individuals/m³ and richness of 79 species, three of them exclusive (the crustaceans *Evadne* sp., *Pontellina* sp., and the radiolarian *Lamprocyclas* sp.) (Figure 4).

<table>
<thead>
<tr>
<th>Station</th>
<th>$S$</th>
<th>$N$</th>
<th>$J'$</th>
<th>$H'$</th>
<th>$\lambda$</th>
</tr>
</thead>
<tbody>
<tr>
<td>E1</td>
<td>85</td>
<td>14 000</td>
<td>0.69</td>
<td>3.07</td>
<td>0.14</td>
</tr>
<tr>
<td>E2</td>
<td>70</td>
<td>9 139</td>
<td>0.68</td>
<td>2.91</td>
<td>0.17</td>
</tr>
<tr>
<td>E4</td>
<td>72</td>
<td>10 361</td>
<td>0.70</td>
<td>3.01</td>
<td>0.15</td>
</tr>
<tr>
<td>E5</td>
<td>71</td>
<td>12 819</td>
<td>0.62</td>
<td>2.63</td>
<td>0.23</td>
</tr>
<tr>
<td>E7</td>
<td>72</td>
<td>12 431</td>
<td>0.67</td>
<td>2.86</td>
<td>0.16</td>
</tr>
</tbody>
</table>

Table 3. Ecological attributes per sampling site: Richness ($S$), Density ($N$), Pielou evenness ($J'$), Shannon-Wienner diversity ($H'$), and Simpson dominance ($\lambda$).
Group B. This group consists of the reference sample (R2) from E1 collected at 15 m depth, which does not correspond to a mesophotic zone. This assemblage had a density of 12,250 individuals/m³ and a richness of 57 species, and it featured only two exclusive species, the tintinnid Coxliela sp. and the radiolarian Cladoscenium sp. (Figure 4).

Group C. This group assembles the stations located at the center and south of the Bajo Frijol seamount (E1, E5, and E7), as supported by the ANOSIM results. This assemblage had 76 (± 4.70) species and an abundance of 13,065 individuals/m³ (± 453.91). This group had the highest number of exclusive species (20); the most frequent were the tintinnid Codonella sp. with 56% and the radiolarian Clathromitra sp. with 44% (Figure 4).

Group D. This group entails the northern stations of Bajo Frijol (E2 and E4), as revealed by the ANOSIM. This assemblage had an abundance of 9,757 individuals/m³ and a richness of 71 species. Eight exclusive species were found in this group, the most frequent of them were the tintinnid Undella globosa with 67% and Protorhabdonella simplex with 33% (Figure 4).

The upper zone of the water column, called Superficial Tropical Water Mass (AST), presents an amplitude of 35 m depth, and its physicochemical parameters have low variation; most of their variation occurs in the superficial layers. Following this mass of water, is the Superficial Subtropical Water Mass (ASS), starting from the AST lowest limit to the photic zone limit (150 m to 200 m) (Longhurst, 1985). Gutiérrez (2010) found that even though the oceanic mesozooplankton community, close to Bajo Frijol, may be just one, its structure varies, firstly due to these water masses that compose the water column, and secondly, due to local outside factors specific for each area. Submarine current patterns could account for one of these factors, which may have caused a segregation of oceanic and typically neritic species to the north (group D), and oceanic and warm-water species to the center-south (group C). Given that the seamount is located at the edge of the continental shelf, as reported by Neumann-Leitão et al. (2008), the narrowness of the continental shelf and the effects of the currents and winds from the coast led communities to mix. A depth difference could have also influenced the division, because the northern assemblage is located in a shallower zone (35 m to 36 m). In addition, the center-south assemblage presents deeper zones (37 m, 45 m and 70 m).

The complete isolation of Groups A and B, shows that MCEs also form unique communities for zooplankton, different from communities in upper zones of the water column, possibly influenced by water masses, depth and light limitations. Andradi-Brown et al. (2016) reported significant differences between the zooplankton community at an MCE and a shallow reef community in Honduras, mainly in abundance, being higher in mesophotic zones, whereas richness was fairly equal. However, in the current research, the water column’s zooplankton community showed a greater abundance than the mesophotic community. This particular difference from the study made in Honduras, could be explained because coral reefs are highly biodiverse and most of its associated

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**Table 4.** Similarity analysis ANOSIM. Global $R$ of 0.681 ($p < 0.001$).

<table>
<thead>
<tr>
<th></th>
<th>E7</th>
<th>E5</th>
<th>E1</th>
<th>E4</th>
<th>E2</th>
</tr>
</thead>
<tbody>
<tr>
<td>E7</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E5</td>
<td>0.22</td>
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</tr>
<tr>
<td>E4</td>
<td>0.96</td>
<td>0.89</td>
<td>0.85</td>
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<td></td>
</tr>
<tr>
<td>E2</td>
<td>1</td>
<td>1</td>
<td>0.85</td>
<td>0.22</td>
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</tbody>
</table>
Figure 3. Classification and multidimensional scaling analysis. (a) Bray-Curtis similarity cluster complemented with a SIMPROF (Coph index 0.88). (b) MDS (stress 0.06), this figure shows samples clustering into four groups: R1, R2, E2-E4, and E1-E5-E7. The first two groups were separated due to their depth; the third and fourth group separated by their location on the seamount.

species, like fishes, corals, among others, feed on plankton (Lesser et al., 2009; Bejarano et al., 2014; Kahng et al., 2014), likely leading to a decrease in the zooplankton abundance. Besides, plankton associated with reefs had exclusive species and some species that modify their behaviour to live in these ecosystems (Heidelberg et al., 2004). Pelagic zooplankton, on the other hand, tends to be more abundant in shallow layers (Marín et al., 2004; Gutiérrez, 2010) because some species migrate vertically to avoid predators and get food (Zaret and Suffern, 1976; Stich and Lampert, 1981; Bernal and Zea, 1993), which could also be influencing the high abundances observed in shallower zones on Bajo Frijol seamount.
Zooplankton distribution at Bajo Frijol MCEs

Figure 4. Exclusive species within: Group A: (a) Evadne sp., (b) Pontellina sp., (c) Lamprocyclas sp.; Group B: (d) Coxiela sp., (e) Cladoscenium sp.; Group C: (f) Codonella sp., (g) Clathromitra sp.; and Group D: (h) Undella globosa, (i) Protorhabdonella simplex.

Additionally, nine exclusive taxa for the MCE zone were identified, which means, they were present only in the assemblages C and D (Figure 5), mostly tintinnids and radiolarians. 36 generalist taxa (Table 5) were also identified, mostly copepods (9), tintinnids (8) and radiolarians (6), nine of them with an average frequency of 100%. The larvae nauplii had the greatest abundance in every assemblage (46%, 40%, 41% and 38%).

The mesophotic community, northern and south assemblages, and the mesophotic zone in general, had tintinnids and radiolarians as exclusive species. Tintinnids are abundant organisms and can be found at depths of up to 100 m, inhabiting various environments (Pierce and Turner, 1993; Thompson et al., 1999; Thompson, 2001); whereas, radiolarians become more frequent as depth increases, and different species appear according to the forming vertical barriers (between depths of 50 m and 100 m). Therefore, it was expected that most of the exclusive species were among those groups (Anderson, 1994; Boltovskoy, 1981; Thompson et al., 1999; Thompson, 2001; Armstrong and Brasier, 2005).

The tintinnid Undella hyalina was identified as exclusive within assemblage C, which has been reported between 15 m and 30 m depth (Thompson, 2001), however its distribution range appears to be broader, provided that all of the U. hyalina samples from assemblage C were found in a depth range of 37 m to 70 m.
As for generalist species, most of them were crustaceans. Crustaceans constitute the largest zooplanktonic group, with representatives of almost all of its classes and orders (Barnacles, copepods, cladocerans, ostracods, amphipods, euphausiids, among others), both as larvae and adults and in different sizes and trophic groups (Boltovskoy, 1981; Gasca and Castellanos, 1993; Thompson, 2001; Gutiérrez, 2010; Hernandez-Trujillo et al., 2010). This explains their observed frequency in all the assemblages obtained for both environments.

The ecologic attributes analysis showed high uniformity values in each assemblage ($J'$ between 0.62 and 0.71), after transformation. The highest diversity was observed in group D ($H' = 2.96$), whereas that the rest of the assemblages did not show conspicuous differences between this attribute (from 2.72 to 2.88). The highest value of predominance was for group A ($\lambda = 0.22$), while the rest of the groups had similar values (0.16 to 0.18), low in general (Table 6).
4. Conclusions

The studied zooplankton community on seamount Bajo Frijol (PNNCPR - Colombian Caribbean) presented unique species that distinguished this community from others in upper zones. This particular might be influenced by depth and light limitations.

The mesophotic zooplankton community of Bajo Frijol is divided in two large assemblages, which presented exclusive species and different abundance and taxonomic composition. All of these are likely shaped by submarine current patterns that may have caused segregation of oceanic and typically neritic species at the north (group D), and the presence of oceanic and warm water
Table 6. Mean ecological attributes by assemblage. Richness (S), Density (N), Pielou evenness (J'), Shannon-Wiener diversity (H'), Simpson dominance (λ ± S.E).

<table>
<thead>
<tr>
<th>Group</th>
<th>S</th>
<th>N</th>
<th>J'</th>
<th>H'</th>
<th>λ</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>79</td>
<td>45 750</td>
<td>0.62</td>
<td>2.72</td>
<td>0.22</td>
</tr>
<tr>
<td>B</td>
<td>57</td>
<td>12 250</td>
<td>0.71</td>
<td>2.88</td>
<td>0.18</td>
</tr>
<tr>
<td>C</td>
<td>75.00 ± 4.70</td>
<td>13 065.00 ± 453.91</td>
<td>0.66 ± 0.02</td>
<td>2.85 ± 0.12</td>
<td>0.18 ± 0.03</td>
</tr>
<tr>
<td>D</td>
<td>71</td>
<td>9 757</td>
<td>0.69</td>
<td>2.96</td>
<td>0.16</td>
</tr>
</tbody>
</table>

species at the center-south (group C). In addition, the known vertical distribution range of the tintinnid *U. hyalina* could be broadened, because it was found 15 m to 30 m deeper than in most reports.

Given that this research was developed in a marine protected area, it is important to further study the dynamics of the zooplankton community on seamount Bajo Frijol, and to extend it to other areas within the park. For this reason, the results of this study were used to establish the monitoring and follow-up program for PNNCPR.

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6. Conflict of interest

Authors declare having no conflict of interest.

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Distribución de zooplankton en un hábitat de arrecifes coralinos mesofóticos en la montaña submarina Bajo Fríjol, Caribe Colombiano

Resumen: Los ecosistemas coralinos mesofóticos (MCEs) albergan comunidades únicas. Debido a que en estos ambientes las zooxantelas coralinas se caracterizan por una baja tasa fotosintética, el zooplancton es allí la principal fuente alimenticia. Estos MCEs no han sido suficientemente estudiados debido al alto costo de las tecnologías de investigación disponibles actualmente, por lo cual estos esfuerzos siguen siendo un desafío. El propósito de este trabajo fue estudiar la comunidad de zooplancton asociada a los MCEs en la montaña marina Bajo Fríjol dentro del Parque Nacional Natural Corales de Profundidad (frente a la costa caribe colombiana) y comparar su composición con la de partes más someras de la columna de agua. Se tomaron tres muestras, filtrando 24 L de agua de mar (por medio de una malla de 45 µm) en cada estación con un dispositivo diseñado para colectar zooplancton justo encima del sustrato arrecifal. Se obtuvieron la composición taxonómica, la densidad y la abundancia relativa. Se realizó un análisis de similitud, complementado con un cluster, un EMD y un test Kandoorp modificado. Los análisis mostraron claras diferencias entre las muestras de la columna de agua y las tomadas cerca del arrecife. También mostraron la separación de la comunidad en dos grandes grupos: norte y centro-sureste, ambos con especies únicas.

Palabras Clave: corales de aguas profundas; áreas protegidas de aguas profundas; corales mesofóticos; ecosistemas mesofóticos; comunidad de zooplancton; distribución de zooplancton.

Distribuição de zooplâncton num habitat de recifes de coral mesofótico no monte submarino Bajo Frijol no caribe colombiano

Resumo: Os ecossistemas de corais mesofóticos (ECMs) abrigam comunidades únicas. Dado que as zooxantelas coralinas nesses ambientes possuem baixa taxa fotosintética, o zooplâncton é o principal recurso alimentar dos ECMs. Estudar estes ecossistemas é um desafio por causa do alto custo das tecnologias de avaliação. O objetivo deste trabalho foi estudar a comunidade de zooplâncton associada aos ECMs do monte submarino Bajo Frijol, localizado no parque nacional natural “Corales de Profundidade”, ao largo da costa do Caribe colombiano e comparar sua composição com aquela de ecossistemas coralinos de partes mais rasas da coluna d’água. Foram coletadas três amostras filtrando 24 L de água de mar (através de uma malha de 45 µm) em cada estação usando um dispositivo desenhado para coletar zooplâncton em cima do substrato do recife. Obtivemos a composição taxonômica, densidade e abundância relativa. Foi feita uma análise de semelhança complementada com um cluster, um MDS e um teste de Kandoorp modificado. A análise mostrou diferenças claras entre as amostras da coluna d’água e as do recife. Também mostrou a separação da comunidade entre dois grandes grupos: norte e centro-sul, cada um com espécies únicas.

Palavras-chave: alto mar; áreas protegidas em alto mar; corais mesofóticos; ecossistemas mesofóticos; comunidade de zooplâncton; distribuição de zooplâncton.
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