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Socioenvironmental and Spatial Criteria as Tools for the Management and Conservation of Hydrozoans in Protected and Unprotected Areas

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Abstract: The cnidarians of the class Hydrozoa comprise 3720 species, are globally distributed, and can have complex life cycles. In the Espíritu Santo Archipelago (ESA), Mexico, hydrozoans are understudied, and, for this reason, the present work describes the taxocene of hydrozoans and their oceanographic preferences in the area. Hydrozoans were collected at 12 sampling stations in the archipelago during the temperate season; these organisms were morphologically identified and a systematic list including socioenvironmental attributes (SEA) was created. Species richness was used to assess the representativeness of the sampling and identify the distribution of species assemblages in relation to their SEA and environmental factors. In total, 31 species were described, representing 70% of the area's potential diversity, and 97% of observations described species that had not yet been recorded in the area. Native, cryptogenic, and exotic species were found, including stinging and harvestable species. Groups with low, medium and high species richness were distributed heterogeneously, forming a spatial aggregation pattern. The results of this work suggest that the ESA has a highly diverse taxocene, with SEA and spatial aggregate structure relevant for integrative management and conservation of hydrozoans in natural protected areas.

Keywords: biocompounds; biological monitoring; Medusozoa; spatial analysis



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1. Introduction

Biological inventories constitute mandatory and basic work for the reliable management and conservation of biodiversity [1]. They should provide a comprehensive understanding of the usefulness criteria by assessing the ecological properties relevant to ecosystems [2]. In addition, these inventories should provide a socioenvironmental perspective of the biota, such as a description of ecosystem services that could benefit humans (*sensu* [3]). Likewise, these properties can be integrated into a spatial analysis as part of a community-ecosystem approach to identify possible patterns in community structure from different geographical scales [1,4,5].

The class Hydrozoa is the most diverse member of the subphylum Medusozoa, with 3762 species (91.75%) recorded on the World Register of Marine Species (WoRMS) [6]. Hydrozoans can have different life cycle stages, which can exist exclusively in the water column (holoplanktonic cycle), fixed to a substrate (benthic cycle) or in both environments (metagenetic cycle or alternation of generations) [7,8]. These life stages are medusa, polyp and siphonophore, though they may be reduced or absent in some evolutionary lineages [9,10]. Nonetheless, these stages should be considered for a more complete understanding of their diversity.

The social and economic relevance of hydrozoans comes from their being a source of biocompounds [11,12], relevant to the construction of military vehicles and environmental sensors [13], classified as potential stingers for humans [14,15], and sometimes used for environmental education in aquariums and ecotourism [16]. In the environment, hydrozoans contribute to benthic-pelagic energy transfer [17,18] and establish numerous ecological interactions with marine flora and fauna [19–21]. In addition, some species are non-native in certain areas [22–24]. However, despite the importance of hydrozoans, in the management plans for natural protected areas in Mexico, they have been addressed only superficially, as in the case of Revillagigedo National Park [25], or omitted, as in the case of Islas Marietas National Park [26] and Espíritu Santo Archipelago (ESA) Marine Area National Park [27].

The ESA has been designated a Natural Protected Area (NPA) since 10 May 2010 [28], and within the Gulf of California, it is recognized for its tourism-based economic output [27], its marine biodiversity, and the ever-increasing anthropogenic pressure [29]. Currently, activities are carried out based on the principles of conservation and sustainability, fishing, ecotourism, biological monitoring and environmental education [27]. Still, there is a need to monitor the biodiversity and heterogeneity of these ecosystems, to achieve the integrative management of this NPA [30].

At present, scientific understanding of hydrozoan diversity in the ESA comprises three publications from the 20th century, in which five species of benthic hydroids were recorded [31–33]; these species were not considered in the management plan [27], and the pelagic phase of hydrozoans remains undescribed. Thus, this work focuses on describing the socioenvironmental components of three life stages of the hydrozoan taxocene from the benthic and pelagic zones of the ESA for the first time. To accomplish this goal, this study integrated components such a diversity, life cycles, geographic and environmental distribution, and potential anthropogenic value of the species to generate useful information for the future conservation and management of this fauna.

2. Materials and Methods

2.1. Study Area and Sampling

Espíritu Santo Archipelago is situated in the southwestern Gulf of California, Mexico (Figure 1A). This archipelago conforms mainly to the emerged lands of Espíritu Santo (83.79 km²), La Partida (0.94 km²) and Los Islotes (0.03 km²) [34]. The shoreline is characterized by rocky (75%) and sandy (11%) substrates, with a minor contribution of coral deposits and macroalgae [35,36]. The area has a semi-desert climate due to low cloud coverage and mean evaporation (300 mm) that is greater than the mean precipitation (180 mm). In addition, negligible freshwater is provided by rivers or arroyos, as they are dry most of the year, creating hyperhaline conditions [37].

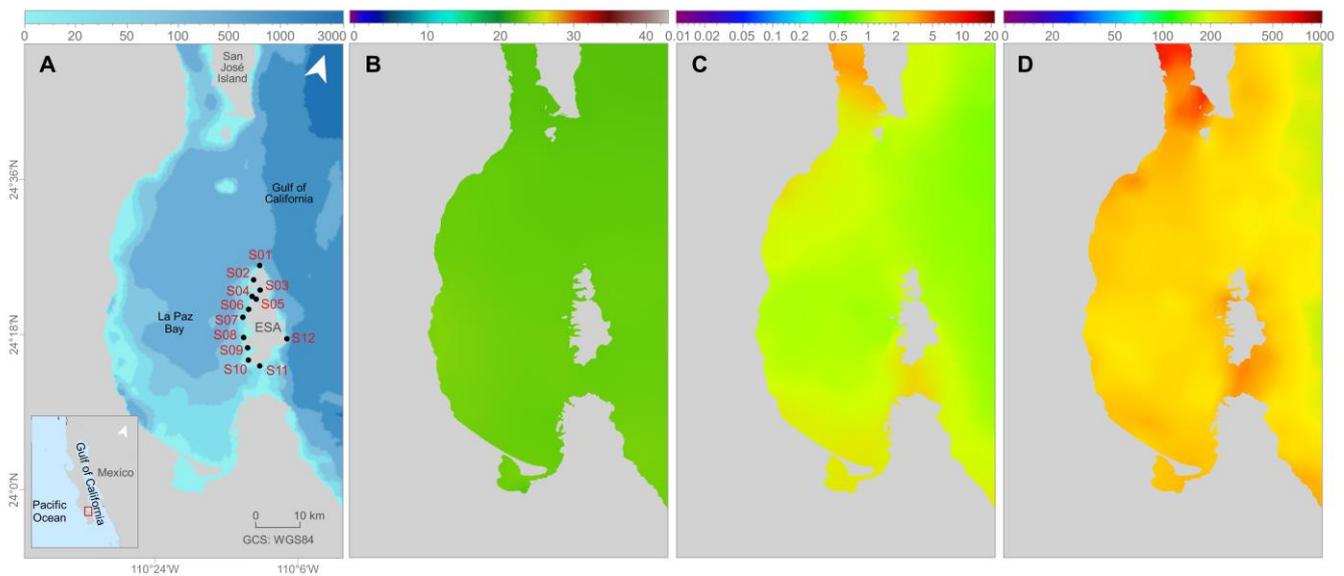


Figure 1. Study area map of Espiritu Santo Archipelago showing bathymetry data from the GEBCO Compilation Group [38] and physical environmental factors during the temperate phase (November–May) of 2002–2020 obtained from the NASA Ocean Biology Processing Group [38]. Sampling sites are represented by the twelve black points (S01–S12). (A) Bathymetry (m); (B) Sea surface temperature ($^{\circ}\text{C}$); (C) Chlorophyll-a (mg m^{-3}); (D) Particulate organic carbon (mg m^{-3}).

On an annual basis, the ESA regime is characterized by an anticyclonic surface marine circulation, with the main current flow directed southward along the east coast of the Gulf of California and northward along the west coast [39,40]; in addition, in this area of the gulf, there is semiannual variation in which no oceanic gyres are recorded during the months of January–March, although the main flow is maintained in a southerly direction [40]. Our sampling program carried out on 27 April 2019 was under a typical temperate regime (November–May) [41,42].

Inside this area, hydrozoans were collected at 12 coastal sampling sites (Figure 1A). Samples were taken from 11 sites in the pelagic zone and four sites in the benthic zone (Table 1), and salinity and sea surface temperature were measured in situ using a portable refractometer and a standard mercury thermometer.

Table 1. Characteristics of the sampling sites in the Espiritu Santo Archipelago. ND: no data.

ID	Sampling Site	Latitude (N)	Longitude (W)	Environment	Depth (m)
S01	Los Islotes	24°35'50"	110°35'50"	Pelagic	0–0.3
S02	Ensenada Grande	24°33'55"	110°24'13"	Pelagic	0–0.3
S03	El Cardonal	24°33'00"	110°22'55"	Pelagic	0–0.3
S04	Anegada de la Partida	24°31'56"	110°23'39"	Pelagic	0–0.3
		24°31'56"	110°23'39"	Benthic	0–2
S05	Caleta la Partida	24°31'47"	110°23'00"	Pelagic	0–0.3
S06	El Candelero	24°30'17"	110°23'30"	Pelagic	0–0.3
		24°29'07"	110°23'41"	Pelagic	0–0.3
S07	Isla Ballena	24°29'07"	110°23'52"	Benthic	0–2
		24°28'43"	110°23'51"	Benthic	18
S08	Barco Fang-Ming	24°26'48"	110°22'51"	Pelagic	0–0.3
		24°25'46"	110°21'52"	Pelagic	0–0.3
S09	Bahía San Gabriel	24°25'46"	110°21'52"	Benthic	0–2
		24°25'00"	110°22'00"	Benthic	ND
		24°24'22"	110°21'13"	Pelagic	0–0.3
S10	Punta Dispensa	24°24'22"	110°21'13"	Pelagic	0–0.3
S11	Punta Lupon	24°24'10"	110°19'31"	Pelagic	0–0.3
		24°28'27"	110°17'19"	Pelagic	0–0.3
S12	Bahía Salinita	24°28'27"	110°17'19"	Benthic	11.4–14.8

2.2. Data Analysis

Hydrozoan taxonomy was done following specialized literature for the life stages of medusa (e.g., [43–46]), polyp (e.g., [46–49]) and siphonophore (e.g., [50–52]). Subsequently, the systematic list of species was complemented with the species' taxonomic status according to WoRMS [6] and specialized literature for *Ventromma halecioides* [49]. Systematic classification at the family level was conducted following Maronna et al. [9]. For each species, the observed phase and life stage, as well as the type of substrate for the benthic phase, were recorded. Additionally, to identify the species' biogeographic status, a search was conducted on taxa with species-level identifications in the online Global Invasive Species Database for internationally distributed species [53] and in CONABIO for species distributed in Mexico [54]. New records of species were assembled at the spatial level of ESA, the Gulf of California, and the Mexican Pacific following Estrada-González et al. [55], and species attributes were assessed in the cultural, medical and tourism sectors according to Santhanam [15] and Marambio et al. [56]. These ecological and socioeconomic characteristics were grouped by the sampling station and geo-represented using Quantum GIS (QGIS) version 3.16.16 [57].

The completeness of the species richness sampling effort was explored through the construction of a rarefaction curve based on the frequency incidence of species presence-absence data per sampling station with the iNEXT library [58] in the R programming environment, version 4.0.4 [59]. This rarefaction curve constitutes a statistical approach to resampling and was estimated from the complete data set [60]. The asymptote or undetected species richness of this biological inventory [61,62] was estimated based on the Chao 2 nonparametric estimator using the SpadeR library [63] and its respective confidence interval (95%) [64–66].

The hydrozoan data in each sampling station were organized in a Jaccard similarity matrix [67]. This data matrix was used to generate a cluster analysis with the stats library [59] and its statistical support was corroborated in PRIMER-E version 6.0 through the SIMPROF test (999 permutations, $\alpha = 0.05$) [68,69].

Additionally, the R vegan library [70] was used to perform a non-metric multidimensional scaling (NMDS) analysis and to generate the ordination of the taxocene by sampling station [71] using 9999 permutations; we used the stress value as a proxy for the goodness of fit of the ordination, with values <0.05 indicating an excellent graphical representation, values <0.1 reflecting a good ordination, values <0.2 suggesting a functional representation, and values >0.2 being a poor interpretation [71]. In PRIMER-E, we corroborated statistically significant differences through the one-way similarity analysis (ANOSIM) and its respective pairwise test, both of which used 35 permutations, $\alpha = 0.05$ and an R-value between 0 (no differences) and 1 (with differences). Reported differences were analyzed with the percentage of average similarity (SIMPER), which uses the Bray–Curtis similarity index and detects the significant contribution of species when the similarity or dissimilarity and standard deviation ratio presented values >1 [71,72].

2.3. Spatial Analysis

For the first time, a spatial analysis was run to provide an environmental interpretation of the axes of the NMDS analysis for the hydrozoan taxocene. To do so, the vector representation envfit of the vegan library was used [70]. The environmental variables were two in situ factors of salinity (SA) and sea surface temperature (SST) and five satellite factors estimated with the minimum spatial resolution available: chlorophyll-*a* (Chlo), dissolved oxygen (DO), particulate organic carbon (POC), SA and SST.

The variables Chlo, DO, pH, SA and SST were chosen according to the known biological requirements of hydrozoans [18], and they were obtained from the Landsat 8 Level-1 scene (LC08_L1TP_034043) with a 30 m pixel resolution. These pixels were radiometrically and geodetically calibrated to physical units through atmospheric correction [73], and accomplished through the analysis with the R programming language packages [59] such as raster [74], RCP [75], RStoolbox [76], rgdal [77] and nightmares [78]. From these data,

environmental factors were estimated with a linear model fitted for La Paz Bay (LPB) [79]. POC had not previously been considered in hydrozoan studies, but was now obtained from MODIS-Aqua Level-3 products, with a spatial resolution of 4 km and pixels calibrated as geophysical variables in a spatial grid [38].

Finally, the environmental factors that had a significant effect in explaining the taxocene structure were selected to represent the environmental preferences of the hydrozoans across a three-dimensional environmental space, as well as to indicate which of these preferences contributed to the structure of the taxocene. The values of selected environmental factors were represented as isolines in QGIS. Based on the obtained results, trends regarding environmental factors that influence the structure of the taxocene were identified. These variables were selected to create the environmental space of the hydrozoans within the framework of the taxocene structure, which shows the environmental conditions of the area and where the species were recorded. This environmental space was built from 10,000 random points in a polygon that represented the study area in QGIS (where each cell corresponded to a unique set of environmental conditions) [80]. Using a value extraction analysis in R, the values for each of the Landsat-processed variables were obtained, and three-dimensional graphs were created.

3. Results

A total of 4254 solitary and colonial hydrozoan organisms were identified in the coastal zone of the ESA, and these organisms were grouped into, 25 families, 30 genera and 31 species (Table 2). At the subclass taxonomic level, for Hydroidolina and Trachylinae, 26 and four species were found, respectively. At the superorder level, Leptothecata presented 15 species, while “Anthoathecata” was represented by five species and Siphonophorae was represented by seven species. In categorizations by life stage, there was a greater representation of polyps with 14 species, followed by jellyfish with 11 species and, finally, siphonophores with seven species.

The pelagic hydrozoan species *Muggiaea atlantica*, *Nanomia bijuga* and *Rhopalonema velatum* were the most recorded species at sampling stations with six of twelve locations. The rarefaction curve (Figure 2) did not exhibit asymptotic behavior; nevertheless, this study recorded a sound baseline representation of the Hydrozoa taxocene in the ESA with 71.49% of the expected species richness estimated by Chao 2 (43.36 ± 10.56 species).

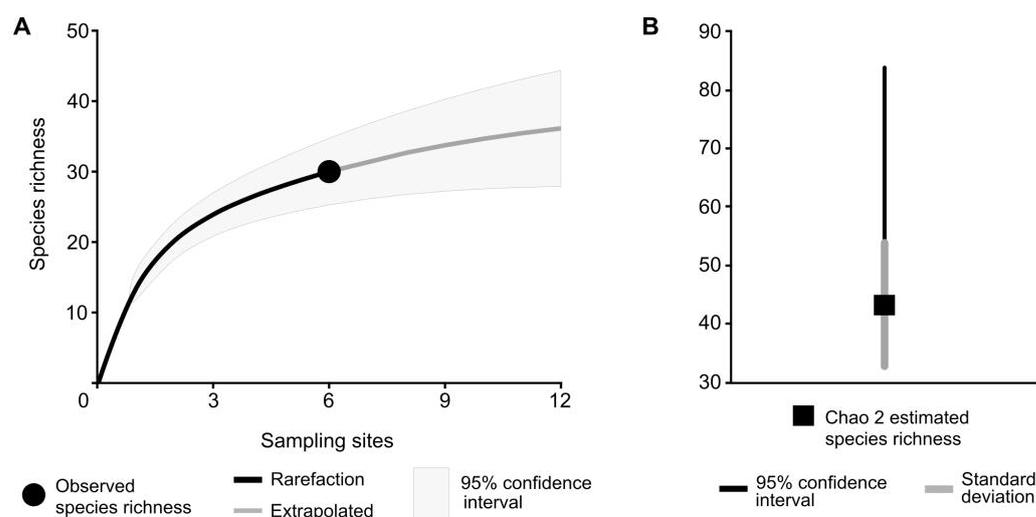


Figure 2. Representativeness of simplified hydrozoan sampling in the Espíritu Santo Archipelago. (A) Sample-based rarefaction and extrapolated analysis; (B) Chao 2 estimated species richness.

Table 2. Systematic annotated list of Hydrozoa in the Espiritu Santo Archipelago. NA: not applicable, ND: no data.

Taxa	Life Phase	Life Stage	Biogeographic Status	Sting Level	Ecosystem Services
Class Hydrozoa Owen, 1843					
Subclass Hydroidolina Collins, 2000					
Superorder “Anthoathecata” Cornelius, 1992					
“Anthoathecata” sp. Indet.	Medusa	Pelagic	NA	NA	NA
<i>Bougainvillia muscus</i> (Allman, 1863)	Medusa	Pelagic	Native	ND	ND
Capitata sp. Indet.	Medusa	Pelagic	NA	NA	NA
<i>Corydendrium parasiticum</i> (Linnaeus, 1767)	Polyp	Benthic	Native	ND	ND
<i>Corymorpha nutans</i> M. Sars, 1835	Medusa	Pelagic	Cryptogenic	ND	ND
Corynidae sp. Indet.	Polyp	Benthic	NA	NA	NA
<i>Pennaria disticha</i> Goldfuss, 1820	Polyp	Benthic	Cryptogenic	Very stinging	ND
<i>Turritopsis</i> sp.	Polyp	Benthic	NA	NA	NA
<i>Sphaerocoryne</i> sp.	Polyp	Benthic	NA	NA	NA
<i>Stauridiosarsia ophiogaster</i> (Haeckel, 1879)	Medusa	Pelagic	Native	ND	ND
Superorder Leptothecata Cornelius, 1992					
<i>Aglaophenia pinguis</i> Fraser, 1938	Polyp	Benthic	Cryptogenic	Stinging	ND
<i>Antennella secundaria</i> (Gmelin, 1791)	Polyp	Benthic	Native	ND	ND
<i>Clytia hemisphaerica</i> (Linnaeus, 1767)	Medusa	Pelagic	Cryptogenic	ND	Yes ¹
<i>Clytia linearis</i> (Thornely, 1900)	Polyp	Benthic	Cryptogenic	ND	ND
<i>Clytia simplex</i> (Browne, 1902)	Medusa	Pelagic	Cryptogenic	ND	ND
<i>Dynamena disticha</i> (Bosc, 1802)	Polyp	Benthic	Native	ND	ND
<i>Dynamena quadridentata</i> (Ellis and Solander, 1786)	Polyp	Benthic	Native	ND	ND
<i>Eucoilota comata</i> (Bigelow, 1909)	Medusa	Pelagic	Native	ND	ND
<i>Eucoilota paradoxica</i> Mayer, 1900	Medusa	Pelagic	Cryptogenic	ND	ND
<i>Halopteris violae</i> Calder, Mallinson, Collins and Hickman, 2003	Polyp	Benthic	Cryptogenic	ND	ND
Hebellidae sp. Indet.	Polyp	Benthic	NA	NA	NA
<i>Hydrodendron mirabile</i> (Hincks, 1866)	Polyp	Benthic	NA	NA	NA
<i>Laodicea</i> sp.	Medusa	Pelagic	NA	NA	NA
Leptothecata sp. Indet.	Medusa	Belagic	NA	NA	NA
<i>Macrorhynchia philippina</i> Kirchenpauer, 1872	Polyp	Benthic	Native	Very stinging	Yes ²
<i>Obelia dichotoma</i> (Linnaeus, 1758)	Polyp	Benthic	Exotic	ND	ND
<i>Obelia</i> spp.	Medusa	Pelagic	NA	NA	NA
<i>Plumularia floridana</i> Nutting, 1900	Polyp	Benthic	Cryptogenic	ND	ND
<i>Ventromma halecioides</i> (Alder, 1859)	Polyp	Benthic	Cryptogenic	ND	ND
Superorder Siphonophorae Eschscholtz, 1829					
<i>Abylopsis eschscholtzii</i> (Huxley, 1859)	Siphonophora	Pelagic	Native	ND	Yes ³
Agalmatidae sp. Indet.	Siphonophora	Pelagic	NA	ND	NA
<i>Diphyes bojani</i> (Eschscholtz, 1825)	Siphonophora	Pelagic	Native	ND	ND
Diphyidae sp. Indet.	Siphonophora	Pelagic	NA	ND	NA
<i>Enneagonum hyalinum</i> Quoy and Gaimard, 1827	Siphonophora	Pelagic	Native	ND	ND
<i>Eudoxoides mitra</i> (Huxley, 1859)	Siphonophora	Pelagic	Native	ND	ND
<i>Halistemma rubrum</i> (Vogt, 1852)	Siphonophora	Pelagic	Native	ND	ND
<i>Muggiaea atlantica</i> Cunningham, 1892	Siphonophora	Pelagic	Native	ND	ND
<i>Nanomia bijuga</i> (Delle Chiaje, 1844)	Siphonophora	Pelagic	Native	ND	ND
Subclass Trachylinae Haeckel, 1879					
<i>Aglaura hemistoma</i> Péron and Lesueur, 1810	Medusa	Pelagic	Native	ND	ND
<i>Liriope tetraphylla</i> (Chamisso and Eysenhardt, 1821)	Medusa	Pelagic	Native	Very stinging	Yes ⁴
<i>Rhopalonema velatum</i> Gegenbaur, 1857	Medusa	Pelagic	Native	ND	ND
<i>Solmundella bitentaculata</i> (Quoy and Gaimard, 1833)	Medusa	Pelagic	Native	ND	ND

¹ Model species; ² Anticarcinogenic and antiparasitic; ³ Ember protein; ⁴ General fluorescent activity.

The spatial distribution of the hydrozoan taxocene showed a trend of increasing species richness toward the south of the archipelago (Figure 3A), where S10 (10 species), S11 (18 species) and S12 (21 species) were located. In the central-western region of the archipelago, the second-highest diversity zone was found in S04 (nine species) and S07 (nine species). The five types of Hydrozoa life cycles within the ESA were represented, mainly within the high-diversity group in the ESA's southern area (Figure 3B); siphonophores constituted the most common life cycle (10 stations). Regarding meroplanktonic life cycles, complementary phases were potentially recorded for six jellyfish (*Bougainvillia muscus*,

Clytia simplex, *Corymorpha nutans*, *Eucheilota comata*, *Eucheilota paradoxica* and *Stauridiosarsia ophiogaster*), as well as six polyps (*Clytia linearis*, *Dynemena quadridentata*, *Macrorhynchia philippina*, *Obelia dichotoma*, *Pennaria disticha* and *V. halecioides*). Only in the species *C. linearis* were polyp and medusa stages recorded.

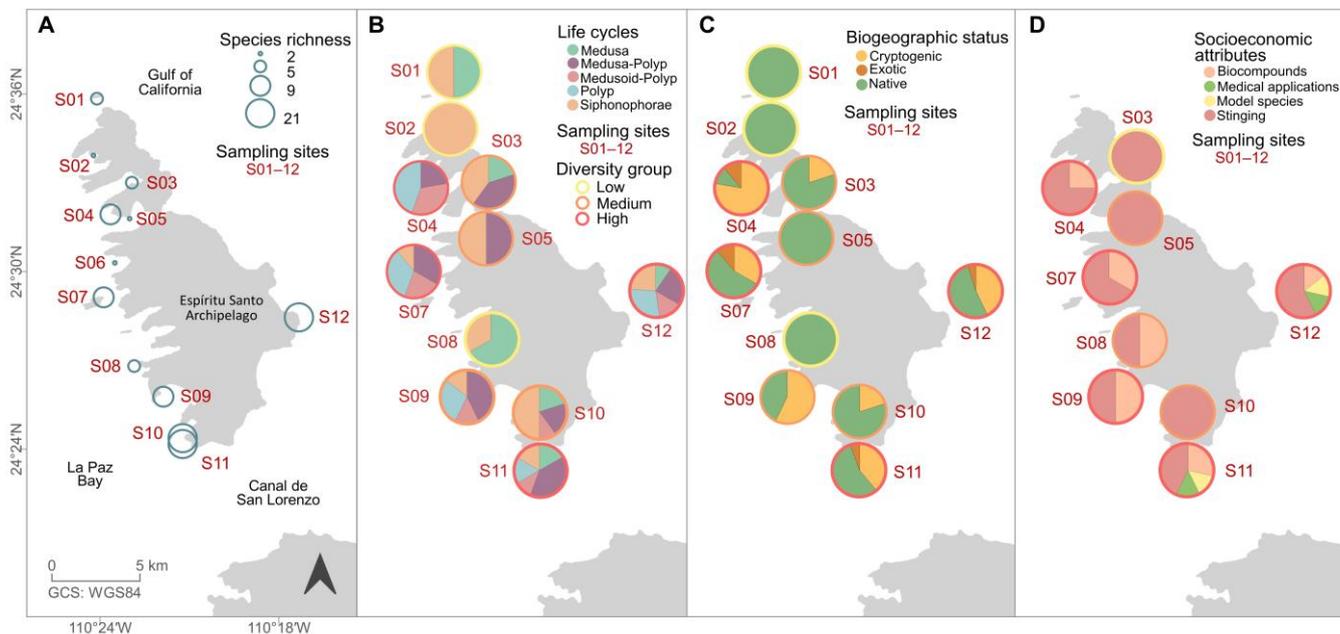


Figure 3. Distribution of ecological and socioeconomic attributes of the Hydrozoa taxocene in the Espíritu Santo Archipelago (ESA). (A) Species richness; (B) Life cycle; (C) Biogeographic status; (D) Socioeconomic attributes.

Regarding the biogeographic status of Hydrozoa, no species was considered to be invasive or exotic according to the Global Invasive Species Database, while CONABIO considered 19 species native, 11 cryptogenic and one exotic (*O. dichotoma*) in Mexico. The ESA zones with the highest concentration of cryptogenic species were the central (S04 and S07, both eight species and S11, 10 species) and southern zones (S10, eight species and S11, 10 species) and one exotic species was found in S04, S07, S11 and S12 (Figure 3C). The newly recorded species were present in S04, S07 and S10–S12, and were comprised of 30 species for the ESA, four species for the Gulf of California and two species at the Mexican Pacific level. The socioeconomic attributes of biocompounds, medical applications, model species and stinging capability were gathered with main distribution in S11 and S12 (Figure 3D); four species found in six stations (S04, S07–S09, S11 and S12) were reported with a potentially dangerous capacity to sting, while four species had the potential to be used for biocompounds (fluorescent orange protein or ember and fluorescent activity), as model species for genetic and embryological studies and in medicinal applications (anticarcinogenic activity and antiparasitic activity against Chagas disease) (Table 2).

Hierarchical clustering analysis showed statistically significant differences ($p < 0.05$) for groups that were geographically discordant, but associated with a species richness gradient, as follows: low (S01, S02 and S08), medium (S03, S05 and S10) and high diversity (S04, S07, S11 and S12) (Figure 4A). In the NMDS, a two-dimensional solution was observed for the clusters and a good ordination (stress = 0.053) was present (Figure 4B). The statistically significant differences of these three groups ($R = 0.75$, $p < 0.05$) were corroborated with ANOSIM (Supplementary Material Table S1).

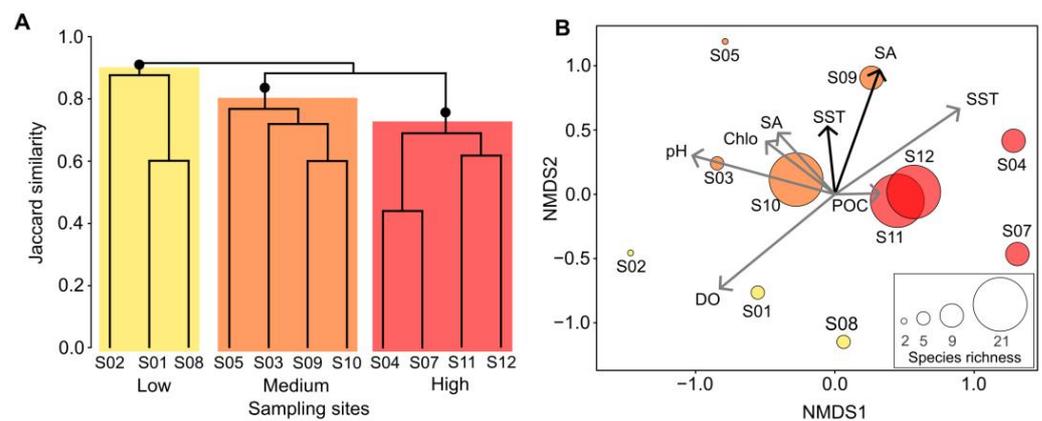


Figure 4. Structure of the hydrozoan taxocene in the Espíritu Santo Archipelago. **(A)** Hierarchical clustering analysis. Significant differences ($p < 0.001$) are denoted at the nodes; **(B)** Non-metric multi-dimensional scaling analysis showing in situ (black arrows) and satellite (gray arrows) environmental factors. Circle size reflects the species richness at each sampling site (S01–S12). Chlo: chlorophyll-*a*, DO: dissolved oxygen, POC: particulate organic carbon, SA: salinity, SST: sea surface temperature. The diversity groups correspond to the colors of the cluster.

The relationship between the spatial configuration of the taxocene and environmental factors was not statistically significant ($R^2 < 0.50$, $p > 0.05$) (Supplementary Material Table S2). However, the environmental vectors SST, DO and POC tended to be directed and explain the diverse groups of sampling sites (Figure 5B). In addition to this, as the diversity per group increased, in situ SST and DO tended to decrease, while POC and satellite SST tended to increase (Table 3). The two data sources, in situ and satellite data for SA and SST variables, did not overlap in the graphical ordination; it was observed that the satellite estimation tended to present lower TSS values and higher ES values compared to the field measurements (Figure 5B).

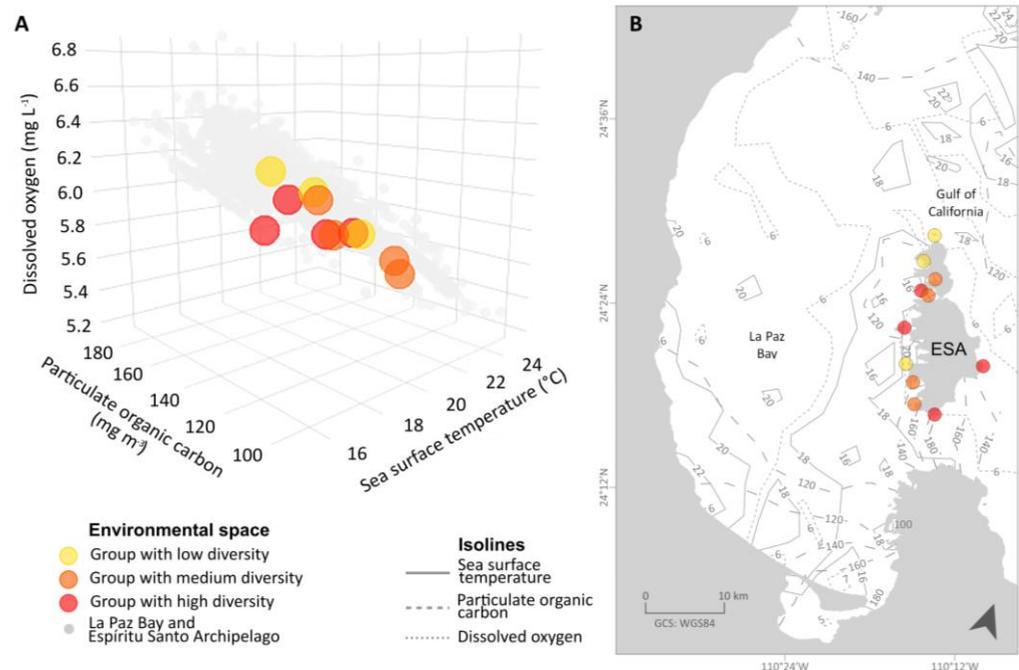


Figure 5. Environmental factors of particulate organic carbon, dissolved oxygen and sea surface temperature in the La Paz Bay and Espíritu Santo Archipelago. **(A)** Three-dimensional environmental space; **(B)** Isoline map.

Table 3. Environmental range for each diversity group in the Espiritu Santo Archipelago.

Data Origin	Environmental Factor	Low Diversity	Medium Diversity	High Diversity
In situ	Salinity	32.63 (± 1.19)	33.25 (± 0.34)	33.70 (± 0.87)
	Sea surface temperature ($^{\circ}\text{C}$)	23.21 (± 0.40)	24.04 (± 0.92)	22.97 (± 1.11)
Satellite	Chlorophyll- <i>a</i> ($\mu\text{g L}^{-1}$)	3.07 (± 0.13)	3.08 (± 0.07)	3.04 (± 0.06)
	Dissolved oxygen (mg L^{-1})	6.09 (± 0.14)	5.80 (± 0.19)	5.73 (± 0.10)
	Particulate organic carbon (mg m^{-3})	123.40 (± 3.80)	126.67 (± 8.69)	138.05 (± 31.04)
	pH	8.07 (± 0.19)	8.06 (± 0.04)	7.98 (± 0.02)
	Salinity	34.03 (± 2.08)	36.22 (± 3.20)	34.04 (± 2.13)
	Sea surface temperature ($^{\circ}\text{C}$)	17.94 (± 1.39)	20.05 (± 1.50)	20.63 (± 0.79)

The three diversity groups were geographically discontinuous, but they overlapped in the environmental space generated for the LPB and the ESA; specifically, the low-diversity group tended to be oriented towards increasing DO, while the medium-diversity group was oriented toward increasing SST and the high-diversity group was oriented toward increasing POC and SST (Figure 5A). The sampling sites of the low- and medium-diversity groups were characterized by abiotic conditions that were also present in most of the LPB and the ESA, while the sampling sites of the high-diversity group were represented by conditions that occurred in limited areas, such as the south of San Jose Island, the San Lorenzo Channel and from Pichilingue Peninsula to the Channel of Ensenada de La Paz (Figure 5B).

The global ANOSIM test showed statistically significant differences between diversity groups ($p < 0.05$, $R = 0.748$). SIMPER analysis highlighted that 12 of the 31 species contributed significantly to the hydrozoan taxocene in the ESA (Supplementary Material Tables S3 and S4). This analysis also reflected that the average dissimilarity of hydrozoan species composition in the spatial groups tended to increase as their diversity increased, with the following results for the diversity groups: low \times medium, 83.78% dissimilarity; medium \times high, 80.78% dissimilarity; and low \times high, 86.96% dissimilarity. Three species made significant contributions in the low \times medium combination, with an accumulated contribution of 24.18%, while 11 species did so in the medium \times high combination, with a contribution of 58.61%. Nine species made significant contributions in the low \times high combination, with a contribution of 55.66% (Table 4).

Within groups, pairwise ANOSIM tests exhibited significant differences ($p < 0.05$) and a gradient of similarity in species composition from low to medium ($R = 0.657$), medium to high ($R = 0.708$) and low to high ($R = 0.815$) diversity. SIMPER analysis also revealed a trend of higher average similarity of species composition per sampling station, corresponding with increasing species diversity for the low-diversity, 32.38% similarity; medium-diversity, 42.81% similarity; and high-diversity, 52.58% similarity groups. The medium- and high-diversity groups both contained species that made significant contributions; in the medium-diversity group, two pelagic species, *Abylopsis eschscholtzii* and *S. ophiogaster*, made a cumulative contribution of 85.04%, while in the high-diversity group, three benthic species, *C. linearis*, *M. philippina* and *O. dichotoma*, made a cumulative contribution of 42.21% (Table 4).

Hydrozoan species in the pelagic phase, *A. eschscholtzii*, *M. atlantica* and *S. ophiogaster*, showed a wider range of environmental preferences of satelital DO (5.56–6.08 mg L^{-1}), POC (116.20–182.40 mg m^{-3}) and SST (18.31–21.92 $^{\circ}\text{C}$) than their benthic counterparts with narrow values of DO (5.63–6.02 mg L^{-1}), POC (116.20–182.40 mg m^{-3}) and SST (18.31–21.32 $^{\circ}\text{C}$) (Figure 6), which was reflected in the extent of their distribution in the sampling sites. In the benthic phase, *V. halecioides* was the only species with a wide ecological

valence of DO (5.63–6.02 mg L⁻¹), POC (117.00–182.40 mg m⁻³) and SST (18.31–21.32 °C), which also showed a wide distribution in the ESA.

Table 4. Similarity analysis (SIMPER) of low-, medium- and high-diversity groups of hydrozoans on the Espíritu Santo Archipelago. The breakdown of significant species contributions to the average similarity and dissimilarity (Sim/SD and Diss/SD > 1) are shown. Av.Sim: average similarity, Sim/SD: similarity to standard deviation ratio, Av.Diss: average dissimilarity, Diss/SD: dissimilarity to standard deviation ratio, Contr. %: percentage of contribution, in which (-) indicates species with no significant contribution.

Species	Medium			High			Low × Medium			Low × High			Medium × High		
	Av.Sim	Sim/SD	Contri.%	Av.Sim	Sim/SD	Contri.%	Av.Diss	Diss/SD	Contri.%	Av.Diss	Diss/SD	Contri.%	Av.Diss	Diss/SD	Contri.%
<i>Macrorhynchia philippina</i>	-	-	-	7.40	3.70	14.07	-	-	-	6.61	2.88	7.60	5.46	2.91	6.76
<i>Obelia dichotoma</i>	-	-	-	7.40	3.70	14.07	-	-	-	6.61	2.88	7.60	5.46	2.91	6.76
<i>Clytia linearis</i>	-	-	-	7.40	3.70	14.07	-	-	-	6.61	2.88	7.60	4.21	1.38	5.21
<i>Stauridiosarsia ophiogaster</i>	18.20	2.93	42.52	-	-	-	13.82	1.89	16.49	-	-	-	5.46	2.91	6.76
<i>Abylopsis eschscholtzii</i>	18.20	2.93	42.52	-	-	-	13.82	1.89	16.49	-	-	-	4.41	1.41	5.45
<i>Muggiaea atlantica</i>	-	-	-	-	-	-	7.37	1.02	8.80	-	-	-	3.3	1.11	4.09
<i>Hydrodendron mirabile</i>	-	-	-	-	-	-	-	-	-	5.40	1.41	6.21	4.41	1.41	5.45
<i>Pennaria disticha</i>	-	-	-	-	-	-	-	-	-	5.40	1.41	6.21	4.41	1.41	5.45
<i>Dynamena disticha</i>	-	-	-	-	-	-	-	-	-	4.44	1.36	5.11	3.73	1.39	4.62
<i>Aglaophenia pinguis</i>	-	-	-	-	-	-	-	-	-	4.44	1.36	5.11	3.26	1.10	4.03
<i>Plumularia floridana</i>	-	-	-	-	-	-	-	-	-	4.44	1.36	5.11	3.26	1.10	4.03
<i>Ventromma halecioides</i>	-	-	-	-	-	-	-	-	-	4.44	1.36	5.11	-	-	-

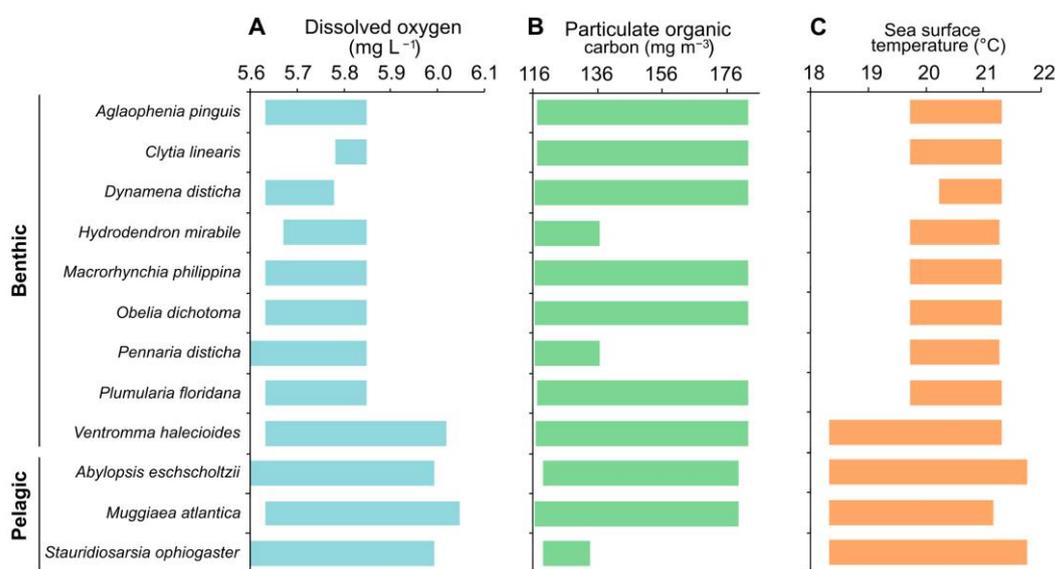


Figure 6. Environmental factors for potentially interpretation of composition species with a significant contribution to the hydrozoan taxocene in the Espíritu Santo Archipelago. (A) Dissolved oxygen (mg L⁻¹); (B) Particulate organic carbon (mg m⁻³); (C) Sea surface temperature (°C).

4. Discussion

The present work is the first study in Mexico that includes spatial and environmental analyses of the three life stages of the class Hydrozoa (medusa, polyp and siphonophore) in benthic and pelagic phases. It also includes an integrative description between species' taxonomy and spatial distribution among the sampling sites of the ESA. With this study,

known species richness in the ESA increased from five in 1938–1984 [31–33] to 34 species until now, such that 97% of observations were new records for the ESA. Thus, the ESA holds the record for the highest diversity of hydrozoans among NPA-designated archipelagos within the southern Gulf of California, supporting more recorded species than Islas Mariás (17 species) [81] or Islas Marietas (one species) [32,82]. It is worth mentioning that these other archipelagos have been examined by limited studies and are in the same subtropical/tropical transition zone exposed to the Gulf of California mouth dynamics, with sandy beaches, rocky substrate, and coral reefs [26,83]. This suggests that the first hydrozoan monitoring in these island complexes should be conducted under the socioenvironmental and spatial taxocene perspective. The diversity recorded in the ESA represented 15.19% and 7.82% of the diversity of the Gulf of California and the Mexican Pacific, respectively (cf. [55]).

Based on the species accumulation curve, the Hydrozoa taxocene recorded in the ESA proved to be sufficient to approximate the species richness under this simplified sampling procedure. It has been shown that a more complete approach to assessing Hydrozoa diversity involves increasing the sampling coverage in terms of space, seasons, circadian phenomena (nocturnal habits and cryptic species on substrates), depth, ecosystems [84]; additionally for hydrozoans such as *Obelia*, whose development is benefited by artificial structures of the coastal and offshore industry (e.g., aquaculture facilities, artificial reefs, boats, buoys, oil platforms, piers, etc.) [85–87]. Although this study has spatial and temporal limitations, the species richness of Hydrozoa in the ESA was approximately half of that recorded from the Insular system of the Gulf of California (68 species) [55]. This finding opens the way to new study opportunities to improve the management and conservation of this fauna.

It is also relevant to mention that further identification of three taxa at the family level (Corynidae, Diphyidae and Hebellidae) and four taxa at the genus level (*Laodicea*, *Obelia*, *Turritopsis* and *Sphaerocoryne*) could increase the diversity of the Hydrozoa community in the ESA with at least seven species. However, further identifying these taxa requires the use of integrative taxonomy, complemented by molecular and life history data, because current taxonomic information is insufficient to identify these lineages [88–92].

By integrating the socio-environmental attributes of Hydrozoa, such as their species richness, new records, valuable biocompounds and potentially dangerous capacity to sting, it was possible to elucidate that the ESA's central and southern zones could be especially important areas at which increased monitoring efforts might contribute to this fauna's management and conservation, according to the guidelines of the Natural Protected Areas [30]. The sampling sites used in this study do not match the restricted-use subzones relevant to the biodiversity conservation of this archipelago [27]; however, these sites could represent ecological entities that aggregate the biological diversity of Hydrozoa and its socioeconomic attributes such as a natural resource in the medical sector, as well as sting prevention and first aid in tourism activities [3]. In particular, tourism activities have been shown to have the potential to incorporate environmental education and citizen science approaches to enrich the knowledge of medusozoan records [93]. Increased exploration of ESA hydrozoans would allow us to discern whether their taxocene could have known applications in other marine areas, such as military use, environmental sensors and aquarium maintenance [13,16].

One exotic species and 11 cryptogenic species of Hydrozoa were registered in the ESA. Therefore, it is recommended that transdisciplinary monitoring be implemented to determine the impact of the introduced species *O. dichotoma*, which is native to the southwest coast of England [94], but is unknown at the national level [95], and determine the biogeographic status of cryptogenic species. Globally, it is increasingly common to find a high number of cryptogenic hydrozoan species—a consequence of insufficient data [85,96,97]. Delimiting their spatial distribution is complex, as they present cryptic speciation [98,99] and silently establish invasive populations in different marine regions [85,100,101], including islands [97,102]. In this sense, cryptogenic hydrozoans should be taken as a starting

point to discern native, introduced or invasive species, and identify the routes, susceptibility and success of biological invasions [103]. This situation is relevant in areas such as the ESA; throughout the area's historical use, causal agents of invasions have included overexploitation of marine resources and the physical and chemical modifications of the habitat [104] and maritime transport routes [104,105].

The benthic phase of eight hydrozoan species and the potential explanatory variables of DO, POC and SST contributed to spatial differences between the low-, medium- and high-diversity groups in the ESA. Among these environmental variables, SST has proven most important for supporting the biological requirements of benthic hydrozoans in other areas [18]. The species that most contributed to the taxocene of the ESA in this study exhibited a wide distribution, existing in both temperate and tropical waters [48,49,106], and are frequently observed within the LPB [107].

The high-diversity group had intermediate SST and DO, and higher POC values. Outside the ESA, the potential optimal zones for this group were found in Isla San José, the Pichilingue Peninsula, and south of the LPB. During the spring, these areas present an intrusion of warm water from the north mouth of the LPB that extends to the south of the ESA; at this time, these areas also present high values of chlorophyll-*a* [108], which could be a baseline indicator for species diversity and abundance of invertebrates in food webs [109,110]. In addition, the superficial circulation ensures nutritional requirements and prevents the accumulation of sediment in benthic hydrozoans [18]. For these reasons, the areas associated with channels, such as San José Island, Pichilingue Peninsula in the San Lorenzo Channel and the Ensenada de La Paz canal, could be high-diversity sites.

There are several lingering knowledge gaps in international literature regarding the environmental requirements of most hydrozoans. ESA species that were found within the SST intervals recorded in the literature included *A. eschscholtzii* (17.68–31.30 °C), *A. pinguis* (15–27 °C) [32,45], *D. disticha* (9–33 °C) [32,111,112], *M. atlantica* (17.86–31.30 °C) and *O. dichotoma* (15–30 °C) [18,32,82,111,113–116]. For the rest of the hydrozoans, the SST values recorded in the ESA were below the lower bound of previously reported SST intervals; specifically, SST was recorded as 19.71 °C for *C. linearis* (previously reported interval: 23–30 °C), *M. philippina* (28.50–29.80 °C), *P. disticha* (30–31.50 °C) and *P. floridana* (26.50–32 °C), and as 18.31 °C for *V. halecioides* (26.50–30 °C) [32,111,117,118]. For DO, ESA recorded value of 6.02 mg L⁻¹ was up the upper bound of previously reported interval for *A. eschscholtzii* (1.90–3.28 mg L⁻¹) and *M. atlantica* (1.90–6.05 mg L⁻¹) [115]. Finally, the knowledge of POC values compatible with hydrozoans is negligible at a global level; therefore, the POC values associated with hydrozoans obtained in this work are the first to be recorded.

5. Conclusions

The local scale of the ESA provides oceanographic conditions that support a phylogenetically and ecologically diverse and spatially heterogeneous planktonic-benthic hydrozoan taxocene. The community structure trends observed in this study suggest that the class Hydrozoa has the potential for systematic monitoring that could generate robust biological and socioeconomic knowledge; this knowledge could then be incorporated for the first time into the NPA in Mexico to strengthen the integrative management of the biota from NPAs and/or island complexes from the Gulf of California.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15020182/s1>. Table S1: ANOSIM results of global and pairwise comparison tests from the matrix of Jaccard's similarity for the Hydrozoa taxocene on the Espíritu Santo Archipelago; Table S2: Multiple regression results of supplementary environmental variables into the ordination of the Hydrozoa taxocene on the Espíritu Santo Archipelago; Table S3: Similarity analysis (SIMPER) between low, medium and high diversity groups of hydrozoans on the Espíritu Santo Archipelago. Av.Sim: average similarity, Sim/SD: similarity to standard deviation ratio, Contr. %: percentage of contribution, in which (-) indicates species with no significant contribution. Bolded items denote the species that made a significant contribution. Table S4. Similarity analysis

(SIMPER) with pairwise comparison within diversity groups of hydrozoans on the Espiritu Santo Archipelago. Av.Diss: average dissimilarity, Diss/SD: dissimilarity to standard deviation ratio, Contr.-%: percentage of contribution and (-) for species with no significant contribution. Bolded items denote the species that made a significant contribution.

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