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The metazoan parasite infracommunities of flounders as indicators of environmental impact in the southern Gulf of Mexico: taxonomic and functional approaches

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Abstract

The performance of taxonomical and functional traits, together with functional diversity indices of metazoan parasites of flounders, as bioindicators of environmental impact, was evaluated along the continental shelf of the Southern Gulf of Mexico (SGoM). Metazoan parasites were collected from the flounders *Syacium gunteri* and *Syacium papillosum*, together with hydrocarbons, heavy metals, and physicochemical variables from water and sediments during 13 oceanographic cruises. We compared a region without oil extraction, the Yucatán Shelf (YS), one with high oil extraction activity, the Campeche Sound (CS), and one with oil seeps and exposure to polluted runoff of the Río Grande, Tamaulipas–Veracruz (TV). Statistical associations among parasite taxonomy, functional traits, and three functional diversity indices with environmental variables, hydrocarbons, and heavy metals were evaluated using redundancy analysis (RDA) at infracommunity level, accounting for potential spatial and temporal autocorrelation. The amount of explained variance for the statistical association between taxonomical and functional parasite community metrics and environmental factors and pollutants was higher in the region with oil extraction (CS) activity than in the regions with oil seeps and runoff pollution (TV). The YS appears to be an ecologically healthy region with rich metazoan parasite communities, a high number of species and individuals, and heavily influenced by oceanographic currents. For environmental studies at the infracommunity level, it is recommended to use both taxonomic and functional indices. Taxonomical diversity indices, such as core, intermediate, and satellite species, can also serve as functional indicators when a proper morphospecies characterization is applied.

Introduction

Currently, marine and freshwater ecosystems are under enormous pressure such as global warming, decreasing oxygen levels, acidification, and human activities, including the discharge of pollutants into the environment (Sures et al., 2023). In marine ecosystems, the use of fertilizers for agriculture contaminates coastal waters when nutrients or pesticides are transported from agricultural fields into the sea through rainfall (Mateo-Sagasta et al., 2017). Nutrients are also implicated in a potential increase in sargassum biomass in the Atlantic Ocean (Wang et al., 2019; Johnson et al., 2020). Other pollutants, such as plastics, polychlorobiphenyls, heavy metals, hormones, sewage, antibiotics, and processed hydrocarbons, are also transported from the continents into the sea by wind or rivers (Sericano et al., 2019; Bashir et al., 2020). The consequences of exposure to these pollutants include changes in the health status of plant and animal communities (Bashir et al., 2020). The direct consequence of these changes in species composition of the communities or biodiversity is the loss of environmental services, with dramatic consequences at ecological and economic levels (Holt and Miller, 2010; Sures et al., 2023; Smit and Sures, 2025).

If we are to control and remediate these ecological disasters, we first need tools to diagnose and establish the prognosis. One of these tools is the bioindicators, which are organisms, species, or communities sensitive to the stressors affecting those ecosystems (Holt and Miller, 2010; Guerrero-Aguilar et al., 2022). In marine environments, benthic invertebrates, periphyton, and fish have traditionally been considered as bioindicators of environmental impact (Chovanec et al., 2003; Guerrero-Aguilar et al., 2022). However, as Pietrock et al. (2003), Marcogliese (2023), and Sures et al. (2025) expressed, marine parasites are just as exposed to environmental impact and anthropogenic pollution as free-living marine organisms. Parasites indeed can influence important ecosystem processes such as biogeochemical cycles, ecosystem energy flow, and temporal ecosystem dynamics, and certainly can help us to determine environmental health and its changes through time (Kuris et al., 2008; Louvard et al., 2025). In fact, there are many examples showing that parasites are robust indicators of environmental impact in marine environments (Lafferty, 1997; Vidal-Martínez et al., 2010; Sures et al., 2023, Sures et al., 2025, and references therein). For example, it has been shown that the removal of top predators by fishing negatively affects the completion of marine parasites' life cycles due to the interference in marine food webs (Sasal et al., 1996; Wood et al., 2014; Marcogliese, 2023). It has been also demonstrated that marine parasites are good pollutants bioaccumulation indicators (Nachev et al., 2016; Sures et al,. 2017; Soler-Jiménez et al., 2020; Brazova et al., 2021; Marcogliese 2023; Sures et al., 2025), and effect bioindicators with changes in their numbers under different pollution levels (Lafferty 1997; Blanar et al., 2009; Vidal-Martínez et al., 2010; Sures et al., 2017; Vidal-Martínez et al., 2019; García-Teh et al., 2022; Germán-Gómez, 2024).

The environmental impact in one place becomes evident as changes in the taxonomic species composition and relative abundance of the parasite populations or communities of marine organisms compared to nearby sites (a few dozen to hundreds of kilometers) where such an impact is not occurring (Marcogliese et al., 2009; Centeno-Chale et al., 2015). However, the effect of geographical distance among sampling sites has proven to have a contrasting influence on the composition of the parasite communities of aquatic organisms, as in some cases it leads to a decay of faunal similarity in the parasite communities of freshwater fishes (Poulin and Morand 1999; Poulin, 2007). In contrast, in some marine fish species, geographical distance has no effect on parasite faunal similarity, for example, *Sebastes capensis* from Chile (González and Poulin, 2005) and *Boops boops* in the Iberian Peninsula (Pérez del Olmo et al., 2009). However, it is important to note that these fish species are pelagic, not benthic, which is an important difference because the vagility of pelagic fishes could increase the likelihood of parasite spread within a geographical region.

In the specific case of benthic flatfishes of the Campeche Sound (CS) and Yucatan shelf (YS) Southern Gulf of Mexico (sGOM), Ocaña et al. (2021) and Vidal-Martínez et al. (2022) found that, with an increase in geographical distance between sites, the usefulness of the parasite communities as indicators of environmental impact decreased, especially when using a taxonomic diversity approach, with community metrics such as species composition or relative abundance. As shown by these authors, the practical problem for parasite ecologists is that decision makers across fields (e.g., fisheries, biodiversity conservation, and oil companies) require information at large spatial scales from sites or regions located thousands of km apart. In addition, there were unexplored regions for metazoan parasites of flounders in the southern Gulf of Mexico (sGOM), including the Tamaulipas region near the US maritime border. However, in 2015, a major research project was conducted to establish a baseline of the environmental and biological conditions in the pelagic and benthic zones of the Tamaulipas region prior to oil extraction activities (Suárez-Mozo et al., 2021; Soler-Jiménez et al., 2022). As part of this effort, we obtained data on the metazoan parasite communities of the flounders *Syacium gunteri* and *Syacium papillosum* for Tamaulipas. This information allowed us to compare the parasite communities of these two host species across the entire southern Gulf of Mexico (sGoM; Fig. 1).

As suggested by Ocaña et al. (2021) and Vidal-Martínez et al. (2022), a faster and cheaper alternative to overcome the difficulty of comparing parasite communities across distant areas or regions is to use functional traits. These traits can be biological (e.g., weight, total length, or the presence of hard body parts) or ecological (e.g., invasion strategy, feeding habits, direct or indirect life cycles) (Chevenet et al., 1994; Beauchard et al., 2017; Llopis-Belenguer et al., 2019). These biological and ecological traits are expected to be at least as informative as classical taxonomic traits because the species forming communities in a region, independent of their phylogenetic relatedness, should be responding to the same environmental selective forces in that region (Beauchard et al., 2017). Then, it would be expected that the species in a specific region would develop similar strategies, such as hard shells, attaching structures, or active infection capacities, to cope with specific selective forces. In fact, Ocaña et al. (2021) and Vidal-Martínez et al. (2022) found that the variance explained by the taxonomic and functional metrics of metazoan parasite communities at the component community level of the dusky flounder (*Syacium papillosum*) and the shoal flounder (*Syacium gunteri*) as indicators of chemical pollution in the southern Gulf of Mexico (sGOM) was similar (~ 50%) when comparing temporal and spatial data from two contiguous regions in the sGOM, the Yucatan Shelf (YS) and the Campeche Sound (CS). To count on enough individual fishes for comparisons, we will follow the suggestion of Vidal-Martinez et al (2019) that, since *S. papillosum* and *S. gunteri* are sympatric and their feeding habits and parasite fauna overlap (Fraser, 1971; García-Abad et al, 1992), their parasite infracommunities are comparable. Also, to ensure a sound statistical analysis, we conducted our study at the infracommunity level, which enabled us to use parasitological data at the individual-fish level. Additionally, the usefulness of functional diversity indices (*sensu* Ahmed et al, 2019) as bioindicators of environmental impact in environmental parasitology has not been explored. These indices have been useful for understanding the relationship between biodiversity, ecosystem functioning, and environmental forcings (Mouchet et al., 2010; Casanoves et al., 2011).

Now, with the recently obtained parasitological and environmental information from Tamaulipas we can determine if there are also statistical associations between the taxonomic and functional traits and functional diversity indices of metazoan parasite communities with environmental data in this new region, as well as the amount of variance explained by these associations in a region with oil extraction activity (CS), one with oil seeps and runoff pollution (TV), and one without this activity (YS). Indeed, only the CS produces an annual release of 250,000 to 1.4 million barrels of oil per year (MacDonald et al., 2015; Árcega-Cabrera and Dótor-Álmazan, 2021). In addition, there is a release of processed hydrocarbons, other organic pollutants (e.g., pesticides and polychlorinated biphenyls or PCBs), and sewage from coastal cities (Vidal-Martínez et al., 2006). In contrast, aside from the natural hydrocarbon releases from seeps along the border of the continental platform of the YS (Love, 2013), there are no other oil extraction activities in this region (Árcega-Cabrera and Dótor-Álmazan, 2021). Thus, due to the deleterious effects of pollutants such as hydrocarbons and heavy metals on both hosts and their metazoan parasites (e.g. Vidal-Martínez et al., 2006; Marcogliese and Pietrock, 2011; Quintanilla-Mena et al., 2020; Soler-Jiménez et al., 2020), it would be reasonable to expect a stronger influence of the environmental variables (including pollutants) on both taxonomical and functional parasite metrics in the region with oil extraction activities compared with the regions without these activities. Thus, our hypothesis was that we would have higher values on the amount of explained variance on the effect of environmental variables (including hydrocarbons and heavy metals) on the taxonomical and functional traits and functional indices of the metazoan parasites of both host species for the region with oil extraction activity than those without such activity. Thus, the objective of this study was to determine whether there were higher values on the amount of explained variance on the effect of environmental variables (including hydrocarbons and heavy metals) on the taxonomical, functional traits, and functional indices of the metazoan parasites of two flounder species in the region with oil extraction activity compared with those without such activity.

Methods

Sampling

Shoal flounder (*S. gunteri*) specimens were collected from 19 sampling stations from the Campeche Sound (CS), eight sampling stations in the Yucatan Shelf (YS), and 16 sampling stations from Tamaulipas and north Veracruz (TV). The dusky flounder (*S. papillosum)* specimens were collected from 26 sampling sites in CS, 33 in YS, and eight in TV. Fish were collected along 13 oceanographic cruises performed between 2015 and 2018 onboard shrimp fishing boats and oceanographic vessels. The sampling sites in which the fish (*S. gunteri* and *S. papillosum*) were captured, were grouped into three regions following Soler-Jiménez et al. (2024): 1) Yucatan Shelf ([YS] Gomex 1–6 cruises); 2) Campeche Sound [CS] cruises: CO2015, KAB121-1, KAB121-2, LBA-AC08, LBA-AC18, and LBA0509); and 3) from Coatzacoalcos, Veracruz to Tamaulipas ([TV] cruises: LBA-AC02, LBA-AC32 and PERDIDO 01-04). All the sampling stations were located along the continental shelf of the southern Gulf of Mexico (Fig. 1). At each station, fish were collected during 0.5 h trawls using two 20 m commercial shrimp nets at a speed of 2.0–2.3 knots.

The physicochemical data and environmental variables, including the presence of heavy metals and hydrocarbons in sediments, were obtained on board *Justo Sierra*, *Riviera Maya* and *Alpha Helix* oceanographic vessels (OVs), using a 0.25 m^2 Hessler Sandia MK-III box corer. Additionally, water samples from a Niskin bottle closed nearest to the sea bottom were collected. These samples were obtained at depths of 15–250 m (Fig. 1) using 20 L plastic Niskin bottles arranged in a rosette. These bottles were closed electronically underwater to prevent contamination with surface mixtures. A total of 32 environmental variables were measured in all these oceanographic cruises, including physicochemical variables (e.g., oxygen (mg/L), salinity (UPS), pH, nitrate (μm)), hydrocarbons and heavy metals from water and sediment (Vidal-Martinez et al., 2014; Centeno-Chalé, 2015; Vidal-Martínez et al., 2019; Sánchez-Soto et al., 2021). Sediment samples were placed in high-density polythene bags and maintained at 4°C for transportation to CINVESTAV-IPN-Mérida. Hydrocarbon sampling procedures are described elsewhere (Vidal-Martínez et al., 2006). The physicochemical characteristics and the hydrocarbon and heavy metal concentrations of the sediment were determined at the Laboratory of Geochemistry (CINVESTAV-IPN-Mérida) following standard protocols by Sericano (1990) and Wade (1993).

Sampling procedures for flatfishes and helminth parasites

The total length, standard length, maximum height (cm ± 0.1 cm), and weight (g ± 0.1 g) of each individual fish collected were recorded. Each individual was subsequently examined externally for gross pathologies (e.g., tumors, ulcers and rotten fins, among others) before undergoing dissection to obtain samples

of the gills, spleen, liver, kidney, and muscle for histology (Aquatic Pathology Laboratory at Cinvestav, Mérida). The remaining tissues of each individual fish were tagged, maintained in isolated plastic bags at −20°C on board the vessel, and transported to the Cinvestav, Mérida Unit for parasitological examination. The *S. papillosum* and *S. gunteri* collected were identified by ichthyologists of the Necton Laboratory (Cinvestav, Mérida). The body surface, cavities, and internal organs were examined individually for parasites using a dissection microscope following the procedures described by Vidal-Martinez et al. (2001). All metazoan parasites (monogeneans, digeneans, cestodes, nematodes, and parasitic crustaceans) from each individual host were counted *in situ,* and a sample of up to 30 individuals of each preliminarily identified parasite species was preserved in 4% formalin or 96% alcohol in labeled vials for subsequent morphological or molecular taxonomic identification. Digeneans, cestodes and acanthocephalans were stained using Mayer's paracarmine technique, and nematodes were cleared using increasing concentrations of glycerin (Vidal-Martinez et al., 2001) for morphological identification. Voucher specimens have been deposited in the National Helminthological Collection, Universidad Nacional Autónoma de México (see Vidal-Martínez et al., 2014 and Vidal-Martínez et al., 2019 for collection numbers). The prevalence and mean abundance of each parasitic species were determined following Bush et al. (1997). Host-specialist metazoan parasite species were those previously reported in fish species of the same genus or family, whereas generalist species were those previously reported in fish species from different families.

Metrics of the parasite infracommunities of both host species used as dependent variables

Core, intermediate and satellite species were defined following Bush and Holmes (1986) and Holmes (1990). Briefly, core species are the most frequent and abundant species, with a prevalence above 30%; intermediate species are those with a prevalence 10%-29%. Satellite species were those with a prevalence of less than 10%. The infracommunity was defined as all metazoan parasites infecting an individual fish. At the infracommunity level, the mean ± SD (standard deviation) of the number of species and individual metazoan parasites per fish were calculated for each host species in each of the three regions. The Brillouin diversity index was also calculated. It is important to note that the number of individual *S. gunteri* in the YS was low (n = 11), reflecting that this species is relatively rare in this region. Despite this, we decided to keep these samples in the analysis because they are extremely difficult (= costly) to obtain and because the data at the infracommunity level are useful for comparison at this specific hierarchical level.

Biological traits and trait approach

For each of the species in Table 1, we determined the state of each of the seven trait categories proposed by Ocaña et al. (2021): body tegument, life cycle, transmission, feeding mode, life stage, host specificity, and attachment organs. We did this because most of the metazoan parasites of both flatfish species (*S. gunteri* and *S. papillosum*) were already classified into functional groups based on these trait categories for the CS and the YS (see Ocaña et al. 2021 and Vidal-Martínez et al. 2022), but not for the TV region. As an example, we illustrate the selection process with some of these trait categories for the adult digenean *Helicometrina nimia*. The two categories of body tegument in Ocaña et al. (2021) classification were soft or hard. Since adult digeneans such as *H. nimia* have a soft tegument, that was the chosen trait category. In the case of the life cycle, this could be direct or indirect, but *H. nimia* has several intermediate hosts. Thus, the selection was an indirect life cycle. In the case of transmission, this could be active or passive. Since adult digeneans develop in the intestine of vertebrates after the ingestion of infected intermediate hosts, the transmission process is passive. The classification of each metazoan parasite species in Table 1 into the seven categories mentioned above is presented in Table 3. Ascribing a parasite species to a particular trait category was based on microscopy observations (e.g., attachment organs), a literature review of the species or closely related taxa (i.e., genus or family) and expert consulting.

Functional diversity indices

To capture the impacts on functional diversity, we used a combination of three functional diversity indices following Ahmed et al. (2019) and their definitions. 1) Functional richness (FR) was the amount of niche space filled by all the species in the community. In this case, we used the Functional dendrogram suggested by Petchey and Gaston (2006); 2) Functional evenness (FEve) was defined as the evenness of abundance distribution in the filled niche space; 3) Functional divergence was the degree to which the distribution of species abundances in niche space maximises total community variation. All these indices were produced at the infracommunity level and used as dependent variables in a Canonical Ordination Redundancy Analysis (RDA) (see below).

Data analysis

Randomization of fish along each fishing haul

Since flatfish were obtained by a fishing boat using commercial fishing nets, it is impossible to know what was the geographical position at which each fish was obtained. This is necessary to apply spatial analyses. To solve this problem, we obtained the geographic position of each individual fish as follows. The starting point of the fishing haul was taken as the center of the trawl path. A buffer zone with a radius of 2 nautical miles (4 nm in diameter or 7.41 km) was established around the center of the trawl path. Subsequently, the orientation of the depth contour (isobath) was calculated and measured in degrees with respect to the north, increasing clockwise from 0 degrees representing north to 360 degrees completing a full circle. The pixel values within the circle of each fishing haul were extracted, and the average was calculated. With this average value and the orientation of the depth contour we projected the potential path of the trawl. Then, based on the number of flatfish individuals retrieved from each haul, the same number of points were randomly placed along the potential path. This procedure allowed us to obtain geographic positions for each individual fish within each trawl.

Canonical Ordination Redundancy Analysis (RDA) considering spatial and temporal autocorrelation

We determined possible multivariate statistical associations between dependent and independent variables using redundancy analysis (RDA). To considering the potential influence of spatial autocorrelation between sampling points, we used the methods proposed by Bauman et al. (2018). We also included the dates of the oceanographic cruises as covariates, considering potential temporal autocorrelation. Our dependent variables were the abundance of core, intermediate, and satellite species, the number of individuals of each species presenting the functional traits presented in Table 2 and the values of the three

functional diversity indices as dependent variables. Our independent variables were all the 18 environmental variables that were measured in all these oceanographic cruises, including the length (cm) and weight (g) of each individual fish, the physicochemical variables [e.g., oxygen (mg/L), salinity (UPS), pH, nitrate (μm)], hydrocarbons and heavy metals from water and sediments (Online Resource 1). First, we built a spatial neighborhood using Gabriel´s graph as a frame. Second, we determined the potential presence of spatial autocorrelation in the independent variables, using Moran's index random test (Thioulouse et al. 2018). If spatial autocorrelation was present, then spatial weighting matrices constituted by spatial predictors called Moran Eigenvector Maps (MEMs) were produced. MEMs allow the separation of the variance explained by spatial autocorrelation from that explained by the environmental variability. Finally, redundancy analysis (RDA) and variance partitioning (Perez-Neto et al. 2006) were used to determine the amount of explained variance by spatial autocorrelation and environmental variables with respect to the statistical associations between these independent variables and the parasite metrics (number of individuals of each parasite species, and number of parasite species and individuals). All the environmental and dependent variables were transformed to Hellinger distance. Temporal autocorrelation was accounted for including a qualitative independent variable containing a sequential number for each oceanographic cruise (C1, C2..C13). All Brillouin diversity indices, functional diversity indices as well as spatial and multivariate analyses were performed in R programming language (R Core Team, 2026) using the packages ade4, adespatial, ape, adegraphics, dplyr, EcoUtils, entropart, FD, fundiv, fundiversity, ggplot2, spdep, maptools, tabula and vegan, modifying the scripts proposed by Dray and Dufour (2007), Dray et al (2025), Frerebeau (2019), Grenié and Gruson (2023, 2025), Laliberte and Legendre (2010), Marcon and Herault (2015), Oksanen et al (2025), Paradis and Schliep (2019), Pebesma and Bivand (2023), Siberchicot et al (1017), Wickham (2016). The significance level for all statistical analyses was set at $\alpha = 0.05$ unless otherwise stated.

Results

Table 1 lists 57 metazoan parasites recovered from 398 flatfishes [*S. gunteri* (n = 137) and *S. papillosum* (n = 261)] from the three regions: TV, CS and YS. The proportion of species in the larval stage was 67.22%, compared with 32.78% in adults. The proportion of generalists, specialists and unknown status species was 91.81%, 3.27% and 4.9%, respectively. The proportion of the most frequent and abundant species was 47.45% of which 89.28% were larval stages and 10.71% were adults. Table 1 also shows the status of core, intermediate and satellite for each species of metazoan parasite per host species and region. Clearly, there were metazoan parasite species that for one host/locality combination were core, but for another locality were intermediate or even satellite.

The descriptive data at sampling site level on the metazoan parasite communities of *S. gunteri* and *S. papillosum* for the YS and CS have been published elsewhere (Vidal-Martínez et al., 2014; Vidal-Martínez et al., 2019). However, the descriptive data of the metazoan parasite communities of *S. gunteri* and *S. papillosum* for TV are presented for the first time. The data on the parasite infracommunities of these host species together with data on the infracommunities of the same host species for the CS and YS regions are provided in Table 2.

Table 1. Metazoan parasites of the shoal flounder *Syacium gunteri* (Sg) and the dusky flounder *Syacium papillosum* (Sp) for each of three regions of the southern Gulf of Mexico. C = Core species, I = Intermediate species and S = Satellite species. The raw data on the number of individuals per fish for each metazoan parasite species for the three regions are presented in Online Resource 1.

Metazoan parasites	Regions					
	Veracruz - Tamaulipas (TV)		Campeche Sound (CS)		Yucatan Shelf (YS)	
	Sg (60)	Sp (21)	Sg (69)	Sp (71)	Sg (8)	Sp (169)
Monogenea						
Microcotyle sp.[A, G, Ge]						S
Neoheterobotrium papillosum[A, G, Spe]						S
Digenea						
Bucephalidae gen. sp. 1[L, G, M, Ge]					I	S
Bulbocirrus sp.[L, DT, U]				S		S
Cryptogonimidae gen. sp. 1[L, G, M, Ge]	I		I	C	I	I
Cryptogonimidae gen. sp. 2[L, G, M, Ge]	S	I	S	S	I	S
Didymozoidae (*Neotorticaecum*-like)[L, DT, Ge]	S	I	S	I	I	I
Diplomonorchis caballeroi[A, DT, U]			S			S
Dollfustrema sp.[L, G, Ge]			S			S
Gonocerca crassa[A, S, Ge]						S
Helicometrina nimia[A, In, Ge]					I	C
Lecithochirium floridense[A, In, Ge]	I	C	I	C	C	C
Opecoelidae gen. sp. [A, In, U]				S		S
Prosorhynchus sp.[L, F, Ge]					I	S
Rhiphidocotyle sp.[L, F, Ge]				S		S
Stephanostomum sp. 1[L, A, Ge]	C	C	C	C	C	C
Stephanostomum sp. 2[L, G, F, Ge]	I	C	I	C	C	C
Stephanostumum sp. 3[L, F, Ge]			S	I		I
Stephanostomum sp. 4[L, G, F, Ge]	I	C		I	C	C
Stephanostomum sp. 5[L, F, M, Ge]		S	S	I	C	I
Stephanostomum sp. 6[L, G, M, Ge]	S	S		S		S
Stephanostomum minankisi[A, In, U]				S	I	I
Cestoda						
Dasyrhynchus sp. [L, G, M, DT, Ge]	S					S
Lecanicephalum sp.[L, F, Ge]	I	I	I	C	C	C
Tetraphyllidea gen. sp. [L, In, Ge]	C	C	S	I	I	I
Kotorella pronosoma[L, DT, Ge]	C	I	I	C	C	C
Kotorelliella sp. [L, DT, Ge]	I	C	S			S
Nybelinia sp. 1[L, G, DT, Ge]	I	S		S	I	I
Nybelinia sp. 2[L, G, M, DT, Ge]	S	S	S	I		I
Nybelinia sp. 3[L, G, DT, Ge]	I	S	S	I	C	C

Nybelinia sp. 4[L, G, Ge]	I	S		S	I	S
Nybelinia sp. 5[L, G, S, Ge]				S		S
Onchoprotocephaloidea gen. sp. [L, In, Ge]	S	S				
Oncomegas wageneri[L, DT, Ge]	S		S	S		S
Trypanorhyncha gen. sp. [L, In, Ge]	S	I	C			S
Pterobothridae gen. sp.[L, In, Ge]	S	S		S		S
Nematoda						
Anisakidae gen. sp.[L, In, Ge]	S	S	S	I	I	S
Anisakis sp.[L, In, Ge]						S
Capillaridae gen. sp.[A, In, Ge]				S	I	
Ascarophis sp. [L, Me, Ge]		S			I	
Contracaecum sp. [L, Me, Ge]			C			
Cucullanus sp.[A, I, Ge]	I	S		I		I
Echinocephalus sp. [L, In, Ge]		C				S
Hysterothylacium fortalezae[L, DT, Ge]	S	I	S	S	C	S
Hysterothylacium deardoffoverstreetorum[L, DT, Ge]	I	C		S		S
Hysterothylacium reliquens[L, DT, Ge]		I	C	C	C	I
Hysterothylacium sp.[L, DT, Ge]	S	S	C	I	I	I
Pseudoterranova sp. [L, Me, Ge]	S			S		S
Spirocamallanus chetumalensis[A, I, Ge]		I	I	I	C	I
Acanthocephala						
Serrasentis sagittifer[A, In, Ge]	I	S	S	I	C	S
Gorgorynchus clavatus[A, In, Ge]	S	I		S		S
Acanthocephaloides plagiusae[A, In, Ge]			S			S
Acanthocephala gen. sp. (acanthella) [L, In, Ge]	S	S				S
Arthropoda						
Caligus sp. [A, G, Ge]	S			S		S
Cresseyus confusus[A, G, Ge]	S	I	S	S	I	I
Gnathia sp.[L, G, Ge]				S		S
Hirudinea						
Trachellobdella lubrica[A, G, Ge]				S		S

Notes: [A]adult parasite, [L]larval parasite, [F]fins, [G]gills, [In]intestine, [Me]mesenteries, [M]muscle, [DT]digestive tract, [Ge]generalist parasite, [U]unknown status.

Patterns of the parasite infracommunities of S. gunteri and S. papillosum

The most relevant pattern in Table 2 was that the YS remains the region with the largest number of metazoan parasite species and individuals for both *S. gunteri* and *S. papillosum*. In fact, by grouping the infracommunity data of *S. gunteri* and *S. papillosum,* there were significant differences in the mean number of species between regions (ONE-WAY ANOVA; $F_{2, 395} = 75.98$; $P < 0.0001$). A Tukey post-hoc test revealed that TV had a significantly lower number of species per fish than CS ($P < 0.05$) and YS ($P < 0.05$), but there was no significant difference between CS and YS ($P > 0.05$). For the number of individuals per fish, there were also significant differences among regions (ONE-WAY ANOVA; $F_{2, 395} = 25.38$; $P < 0.0001$). A Tukey post-hoc test showed that YS had a significantly larger number of individuals per fish than CS ($P < 0.05$) and TV ($P < 0.05$) respectively. The largest value of the Brillouin´s diversity index was for *S. papillosum* in TV. In fact, we found significant differences among regions in the values of the Brillouin diversity index for *S. gunteri* and *S. papillosum* (ONE-

WAY ANOVA; $F_{5, 407} = 79.97$; $P < 0.0001$). Even when the sample size for *S. gunteri* (n = 8) in YS was low compared to that of *S. papillosum* (n = 169), both host species had a similar number of species and individuals in this region, suggesting that both were exposed to the same pool of parasites and that the comparison of their infracommunities was possible using mean values for these community metrics. Grouping the infracommunity data of *S. gunteri* and *S. papillosum* there were significant differences in the mean values of the Brillouin diversity index between regions (ONE-WAY ANOVA; $F_{2, 410} = 4.55$; $P < 0.01$). A Tukey post-hoc test revealed that CS had a significantly lower mean value of the Brillouin diversity index per fish than YS and TV ($P < 0.05$), but there was no significant difference between these two last regions ($P > 0.05$). For functional richness, the largest mean values were found in YS for both host species. These values were significantly higher for YS (ONE-WAY ANOVA; $F_{2, 398} = 62.12$; $P < 0.0001$) than those of the other two regions. In the case of functional evenness, for *S. gunteri*, the largest value was found in YS, while for *S. papillosum*, the largest values were found in CS and YS. Again, grouping the infracommunity data of *S. gunteri* and *S. papillosum* the functional evenness values for YS were significantly higher (ONE-WAY ANOVA; $F_{2, 398} = 17.32$; $P < 0.0001$) than those of the other two regions. For functional divergence, TV had a significantly lower value for *S. papillosum* (ONE-WAY ANOVA; $F_{2, 398} = 9.16$; $P < 0.0001$) than the two other regions.

Table 3 shows the trait profiles of the 57 metazoan parasite taxa recovered from *S. papillosum* and *S. gunteri* for the southern Gulf of Mexico. Since the usefulness of these trait profiles was already discussed by Vidal-Martínez et al 2021 and Ocaña et al (2022), here we will use them only as dependent variables for testing our original hypotheses. Therefore, all these variables (core species, intermediate species, satellite species, the three functional diversity indices and the functional traits of each metazoan parasite species) at infracommunity level were used as dependent variables in redundancy analysis (Table 4), using as independent variables all the physicochemical variables and contaminants mentioned in Table 5.

Redundancy analyses (RDA)

The RDA, with all the flatfish from the three regions (TV, CS and YS) was performed with all the available dependent and independent variables including fish total length, standard length (cm) and weight (g). This analysis was significant ($p < 0.001$), explained 44.50% of variance, eliminated these three fish morphometric variables and kept only the independent variables presented in Table 5. Therefore, from now on, for the following redundancy analyses, the dependent and independent variables for sediment and water across all 56 sampling sites in the 3 regions are those in Tables 4 and 5. Table 6 shows the percentage of variance explained by the statistical association of core, intermediate and satellite species (taxonomic diversity) as dependent variables at the infracommunity level with environmental, spatial and temporal independent variables.

The percentage of variance explained by the global statistical association including all the regions in one analysis was 54.20%, with a high contribution of the combination of environment and temporal variables (27.20%), and a low contribution of the spatial variables (MEMs = 1.80%). Therefore, the contribution of the spatial autocorrelation was negligible. Figure 2A shows the biplot with the statistical associations between the dependent and independent variables in Tables 4 and 5 explaining the greatest amount of variance at infracommunity level for taxonomic diversity. The most relevant patterns in Figure 2A were the negative association between the core species and the concentrations of heavy metals such as lead and nickel, as well as their positive associations with particulate organic carbon (cop), nitrites and nitrates (NO_2-NO_3), ammonium (NH_4) and polyaromatic hydrocarbons (PAHs). The intermediate species had strong associations with spatial (MEM4) and temporal variables (oceanographic cruises 7 and 8). Another interesting pattern was the positive association between the satellite species, phosphates and the oceanographic cruise 10 (C10).

Table 2. The infracommunities of the metazoan parasites of *Syacium gunteri* and *Syacium papillosum* for three regions of the southern Gulf of Mexico. Error values are standard deviations in all cases.

	S. gunteri			*S. papillosum*		
Community characteristics	Tamaulipas - Veracruz (TV)	Campeche Sound (CS)	Yucatan Shelf (YS)	Tamaulipas - Veracruz - (TV)	Campeche Sound (CS)	Yucatan Shelf (YS)
Sample size	60	69	8	21	71	169
Mean number of species	4.17 ± 1.92	3.57 ± 1.90	8.75 ± 2.43	6.09 ± 2.79	6.72 ± 2.63	8.75 ± 3.53
Mean number of individuals	51.11 ± 43.17	108.90 ± 218.62	218.75 ± 132.30	66.04 ± 52.63	230.31± 303.62	225.79 ± 234.22
Mean value of Brillouin´s diversity index	0.98 ± 0.29	0.84 ± 0.28	1.05 ± 0.36	1.27 ± 0.46	1.10 ± 0.33	1.10 ± 0.39
Mean value of functional richness	1.14 ± 0.43	0.92 ± 0.47	1.88 ± 0.26	1.31 ± 0.40	1.65 ± 0.34	1.78 ± 0.45
Mean value of functional evenness	0.42 ± 0.27	0.35 ± 0.31	0.62 ± 0.11	0.53 ± 0.20	0.60 ± 0.18	0.60 ± 0.15
Mean value of functional divergence	0.87 ± 0.10	0.87 ± 0.19	0.90 ± 0.07	0.70 ± 0.13	0.87 ± 0.10	0.84 ± 0.13

The results for each region were very specific. In the case of Campeche Sound, the association between the dependent and independent variables was stronger (61.30%) than that of the global analysis. In this case, the contribution of the association between environment and MEMs was the highest (24.30%)

(Table 6). Figure 2B shows the statistical associations between the dependent and independent variables in Tables 4 and 5 at infracommunity level of taxonomic diversity for CS. The most relevant patterns in Figure 2B were the negative associations between the core species and the concentrations of lead, oxygen and temperature. The intermediate species had strong negative associations with depth and MEMs 10 and 11. In the case of the satellite species, the positive associations with phosphates, pH and Cruise 2 were relevant. For the Yucatan Shelf the association between dependent and independent variables was also significant, but weak with 22.80% of variance explained. (Table 6). In this case, the combination of variables that contributed the most to the variance was that of the environmental, temporal and spatial variables.

Figure 2C shows the statistical associations between the dependent and independent variables in Tables 4 and 5 at infracommunity level of taxonomic diversity for YS. In Figure 2C there were significant positive associations of the core species and environmental variables such as phosphates, nitrites and nitrates, particulate organic carbon, ammonium, among others, as well as the negative associations with PAHs and MEM2. The intermediate species had strong positive associations with MEM1 and Cruise 8, which suggests spatial and temporal influences. Satellite species had a negative association with MEM1 and Cruise 8.

In the case of Tamaulipas-Veracruz, we had a significant association with 46.10% of variance explained. In this case, the separate contributions of the environmental and spatial variables were the most important ones for the association (Table 6). Figure 2D shows the statistical associations between the dependent and independent variables in Tables 4 and 5 at infracommunity level of taxonomic diversity for TV. The most relevant patterns in Figure 2D were the positive associations between the core species and environmental variables such as pH, redox potential, ammonium and temperature. The intermediate species had a strong positive association with MEM1 and phosphates. Satellite species were not significant dependent variables in this analysis and by this reason their patterns are not described. Note that even when aliphatic hydrocarbons appeared in Table 5, their contribution as independent variables was irrelevant.

In the case of the percentage of variance explained by the statistical association of functional diversity indices (functional richness, functional evenness, functional divergence) with environmental (Env), spatial and temporal variables (independent variables), the results are presented in Table 6.

Table 3. Trait profiles of the 57 metazoan parasite taxa recovered from *Syacium papillosum* and *Syacium gunteri* from the southern Gulf of Mexico.

Species	Body tegument		Life cycle		Transmission		Feeding mode		Life stage		Specificity	
	Soft	Hard	Direct	Indirect	Active	Passive	Absorption	Predation	Adult	Larvae	Specialist	Generalist
Neoheterobotrium papillosum	1	0	1	0	1	0	0	1	1	0	1	0
Microcotyle sp.	1	0	1	0	1	0	0	1	1	0	1	0
Bucephalidae gen. sp.	1	0	0	1	1	0	1	0	0	1	0	1
Bulbocirrus sp.	1	0	0	1	1	0	1	0	0	1	0	1
Cryptogonimidae gen. sp.1	1	0	0	1	1	0	1	0	0	1	0	1
Cryptogonimidae gen. sp.2	1	0	0	1	1	0	1	0	0	1	0	1
Didymozoidae (Neotorticaecum-like)	1	0	0	1	0	1	1	0	0	1	0	1
Diplomonorchis caballeroi	1	0	0	1	0	1	1	0	1	0	0	1
Dollfustrema sp.	1	0	0	1	1	0	1	0	0	1	0	1
Gonocerca crassa	1	0	0	1	0	1	1	0		0	0	1
Helicometrina nimia	1	0	0	1	0	1	1	0	1	0	0	1
Lecithochirium floridense	1	0	0	1	0	1	1	0	1	0	0	1
Opecoelidae gen. sp.	1	0	0	1	0	1	1	0	1	0	0	1
Prosorhynchus sp.	1	0	0	1	1	0	1	0	0	1	0	1
Rhiphidocotyle sp.	1	0	0	1	1	0	1	0	0	1	0	1
Stephanostomum sp.1	1	0	0	1	1	0	1	0	0	1	0	1
Stephanostomum sp.2	1	0	0	1	1	0	1	0	0	1	0	1
Stephanostomum sp.3	1	0	0	1	1	0	1	0	0	1	0	1
Stephanostomum sp.4	1	0	0	1	1	0	1	0	0	1	0	1
Stephanostomum sp.5	1	0	0	1	1	0	1	0	0	1	0	1
Stephanostomum sp.6	1	0	0	1	1	0	1	0	0	1	0	1
Stephanostomum minankisi	1	0	0	1	1	0	1	0	0	1	0	1
Dasyrhynchus sp.	1	0	0	1	0	1	1	0	0	1	0	1
Kotorella pronosoma	1	0	0	1	0	1	1	0	0	1	0	1
Kotorelliella sp.	1	0	0	1	0	1	1	0	0	1	0	1
Lecanicephalum sp.	1	0	0	1	1	0	1	0	0	1	0	1
Nybelinia sp.1	1	0	0	1	0	1	1	0	0	1	0	1
Nybelinia sp.2	1	0	0	1	0	1	1	0	0	1	0	1
Nybelinia sp.3	1	0	0	1	0	1	1	0	0	1	0	1
Nybelinia sp.4	1	0	0	1	0	1	1	0	0	1	0	1
Nybelinia sp.5	1	0	0	1	0	1	1	0	0	1	0	1
Onchoprotocephaloidea gen. sp.	1	0	0	1	0	1	1	0	0	1	0	1
Oncomegas wageneri	1	0	0	1	0	1	1	0	0	1	0	1
Pterobothridae gen. sp.	1	0	0	1	0	1	1	0	0	1	0	1
Tetraphyllidea gen. sp.	1	0	0	1	0	1	1	0	0	1	0	1
Trypanorhyncha gen. sp.	1	0	0	1	0	1	1	0	0	1	0	1

Anisakidae gen. sp.	0	1	0	1	0	1	0	1	0	1	0	1
Anisakis sp.	0	1	0	1	0	1	0	1	0	1	0	1
Ascarophis sp.	0	1	0	1	0	1	0	1	0	1	0	1
Capillaridae gen. sp.	1	0	0	1	0	1	0	1	1	0	1	0
Contracaecum sp.	0	1	0	1	0	1	0	1	0	1	0	1
Cucullanus sp.	0	1	0	1	0	1	0	1	1	0	0	1
Echinocephalus sp.	0	1	0	1	0	1	0	1	0	1	0	1
Hysterothylacium deardoffoverstreetorum	0	1	0	1	0	1	0	1	0	1	0	1
Hysterothylacium fortalezae	0	1	0	1	0	1	0	1	0	1	0	1
Hysterothylacium reliquens	0	1	0	1	0	1	0	1	0	1	0	1
Hysterothylacium sp.	0	1	0	1	0	1	0	1	0	1	0	1
Pseudoterranova sp.	0	1	0	1	0	1	0	1	0	1	0	1
Spirocamallanus chetumalensis	0	1	0	1	0	1	0	1	1	0	0	1
Acanthocephaloides plagiusae	1	0	0	1	0	1	1	0	1	0	0	1
Acanthocephala gen. sp.	1	0	0	1	0	1	1	0	1	0	0	1
Gorgorynchus clavatus	1	0	0	1	0	1	1	0	1	0	0	1
Serrasentis sagittifer	1	0	0	1	0	1	1	0	1	0	0	1
Caligus sp.	0	1	1	0	1	0	0	1	1	0	0	1
Cresseyus confusus	0	1	1	0	1	0	0	1	1	0	0	1
Gnathia sp.	0	1	1	0	1	0	0	1	1	0	0	1
Trachellobdella lubrica	1	0	1	0	1	0	0	1	1	0	0	1

Table 4: Significant dependent variables larger than the median length of the vectors in the Redundancy Analysis are indicated by 1, non-significant by 0. The results are shown for the whole Gulf of Mexico (GOM) and for each region (Campeche Sound (CS), Yucatan Shelf (YS) and Tamaulipas-Veracruz (TV)). Acronyms are as follows: Core = core species, Int = intermediate species, Sat = Satellite species, Me = median of species, FDiv = functional divergence, FE = functional evenness, FRic = functional richness. The categories soft, hard, absorption, etc. are the functional traits of the metazoan parasite species. Yucatan and Tamaulipas do not appear in the functional traits category because their RDA analyses were not significant.

	Taxonomic Diversity				Functional Diversity				Functional Traits	
	Whole GOM	Campeche Sound	Yucatan shelf	Tamaulipas	Whole GOM	Campeche Sound	Yucatan shelf	Tamaulipas	Whole GOM	Campeche Sound
Variable										
Core	1	1	1	1	0	0	0	0	0	0
Int	1	1	1	1	0	0	0	0	0	0
Sat	1	1	0	1	0	0	0	0	0	0
Me	0	0	1	0	0	0	0	0	0	0
FDiv	0	0	0	0	0	1	0	1	0	0
FE	0	0	0	0	1	1	1	1	0	0
FRic	0	0	0	0	0	0	1	0	0	**0**
soft	0	0	0	0	0	0	0	0	1	1
hard	0	0	0	0	0	0	0	0	1	1
absorption	0	0	0	0	0	0	0	0	1	1
predation	0	0	0	0	0	0	0	0	1	1
adult	0	0	0	0	0	0	0	0	1	1
larvae	0	0	0	0	0	0	0	0	1	1
specialist	0	0	0	0	0	0	0	0	0	1
generalist	0	0	0	0	0	0	0	0	0	1

Table 5: Significant independent variables larger than the median length of the vectors in the Redundancy Analysis are indicated by 1, non-significant by 0. The results are shown for the whole Gulf of Mexico (GOM) and for each region (Campeche Sound (CS), Yucatan Shelf (YS) and Tamaulipas-Veracruz (TV)). Acronyms are as follows: MEM = Moran's eigenvector maps, Taxonomic = Taxonomic diversity Cruises C1-C13 = the oceanographic cruises. Yucatan and Tamaulipas do not appear in the functional traits category because their RDA analyses were not significant.

	Taxonomic diversity				Functional diversity				Functional traits	
	Whole GOM	Campeche Sound	Yucatan shelf	Tamaulipas	Whole GOM	Campeche Sound	Yucatan shelf	Tamaulipas	Whole GOM	Campeche Sound
Variable										
MEM1	1	0	1	1	0	0	0	1	1	1
MEM2	1	1	1	1	1	1	0	0	0	1
MEM3	0	1	1	1	1	0	0	0	0	0
MEM4	1	0	0	1	0	0	0	0	0	0
MEM5	0	1	1	1	1	1	1	0	1	0
MEM6	1	1	1	0	1	0	0	0	0	0
MEM7	1	0	0	1	0	0	0	0	1	0
MEM9	0	0	0	1	0	0	0	0	0	0
MEM10	0	1	0	0	0	0	0	0	0	0
MEM11	0	1	0	0	0	0	0	0	0	0
MEM13	0	0	0	1	0	0	0	0	0	0
MEM14	0	0	0	1	0	0	0	0	0	0
MEM18	0	0	0	1	0	0	0	0	0	0
MEM19	0	0	0	1	0	0	0	0	0	0
MEM28	0	0	0	1	0	0	0	0	0	0
MEM38	0	0	0	1	0	0	0	0	0	0
MEM45	0	0	0	1	0	0	0	0	0	0
Host species	0	0	0	0	0	1	0	0	0	0
Ammonium	1	0	0	0	0	0	1	1	1	1
Depth	0	0	1	1	1	1	1	1	0	0
Temperature	0	0	1	1	1	1	1	1	0	1
Salinity	1	1	1	1	1	0	1	0	0	1
Oxygen	1	0	1	1	1	1	1	1	1	1
pH	1	0	1	1	0	1	1	1	1	0
Phosphates	1	1	1	1	1	1	1	1	0	1
Silicates	0	1	1	1	0	0	0	0	1	0
Nitrites/nitrates	1	0	1	1	0	0	0	0	0	1
Particulate organic carbon	1	1	1	1	1	0	1	0	1	0
Chloropyll a	1	0	1	1	1	0	1	0	1	0
Redox potential	1	1	1	1	1	1	1	0	1	0
Aliphatic hydrocarbons	0	0	1	1	0	1	0	1	0	1
Polyaromatic hydrocarbons	1	0	0	0	0	1	0	1	0	0
Total hydrocarbons	0	0	0	0	0	1	0	0	0	1
Cd		1	0	1		0	0	0	0	
Ni	1	1	0	1	1	0	0	0	1	1
Pb	1	0	0	0	1	1	0	0	1	1

V	0	0	0	0	1	1	0	0	1	0
Cruise C2	1	1	0	1	1	1	0	0	1	1
Cruise C3	1	1	0	1	1	0	0	0	1	1
Cruise C4	1	1	0	1	0	0	0	0	0	1
Cruise C5	1	0	0	0	1	0	1	0	1	0
Cruise C6	1	1	1	0	1	1	1	0	1	1
Cruise C7	1	0	0	0	1	0	0	0	1	0
Cruise C8	1	0	0	0	1	0	0	1	1	0
Cruise C10	1	0	0	0	1	0	0	0	0	0
Cruise C13	1	1	0	0	1	1	0	0	1	1

Table 6. Percentage of variance explained (%) by the statistical association of taxonomical (core, intermediate and satellite species) and functional (functional diversity indices and functional traits) community metrics as dependent variables at infracommunity level with environmental (Env), spatial and temporal variables as independent variables. Spatial variables were generated with Moran´s Eigenvector Maps (MEM) analyses. Temporal variables (Tem) were included as dummy variables in the analysis.

Taxonomic diversity indices (core, intermediate and satellite species)										
Group	Variance explained by the association	P value	Env	Tem	MEM	Env/tem	Env/MEM	Tem/MEM	Env/Tem/MEM	Residuals
Global	54.20	0.001	3.30	10.80	1.80	27.20	1.10	2.50	7.40	45.80
Yucatan Peninsula (YS)	22.80	0.001	5.70	0.20	5.20	0.60	5.30	1.10	4.20	77.60
Campeche Sound (CS)	61.30	0.001	10.90	0.10	7.70	5.50	24.30	0.10	9.00	42.90
Tamaulipas-Veracruz (TV)	46.10	0.001	1.30	0.10	0.10	3.00	19.50	0.80	22.60	55.40
Functional diversity indices (functional diversity, functional evenness, functional divergence)										
	Variance explained	P value	Env	Tem	MEM	Env/tem	Env/MEM	Tem/MEM	Env/Tem/ MEM	Residuals
Global	29.70	0.001	0.10	4.30	0.90	20.30	0.60	0.30	3.40	70.30
Campeche Sound (CS)	39.50	0.001	9.00	0.10	0.40	9.20	13.20	0.10	7.40	61.20
Yucatan Shelf (YS)	17.69	0.001	3.80	4.00	0.70	1.40	1.60	1.70	1.90	84.90
Tamaulipas-Veracruz (TV)	5.30	0.362	2.3	0.10	3.80	2.30	2.50	2.50	0.10	91.70
Functional traits (body tegument, life cycle, transmission, feeding mode, life stage, specificity and attachment organs)										
	Variance explained	P value	Env	Tem	MEM	Env/tem	Env/MEM	Tem/MEM	Env/Tem/ MEM	Residuals
Global	40.30	0.001	1.40	10.7	<0	26.00	0.30	0.50	1.60	59.70
Campeche Sound (CS)	47.60	0.001	25.40	<0	0.30	0.072	0.056	<0	<0	62.70
Yucatan shelf (YS)	0.90	0.218	0.70	<0	<0	<0	<0	<0	0.1	99.70
Tamaulipas-Veracruz (TV)	-	-	-	-	-	-	-	-	-	-

The percentage of variance explained by the global statistical association, including all regions, was 29.70%, with a high contribution from the combination of environment and temporal variables (20.30%) and a low contribution from the spatial variables (MEMs = 0.90%). As in the previous analysis, the contribution of the spatial autocorrelation was negligible. Figure 3A shows the statistical associations between the dependent and independent variables in Tables 4 and

5 for the functional diversity indices across the entire southern Gulf of Mexico. The only significant dependent variable in this analysis was functional evenness (Table 4). This variable had strong negative associations with phosphates, lead, nickel, temperature, oxygen, redox potential and Cruise 2.

For Campeche Sound, the statistical association between functional diversity and the independent variables was stronger (39.50%) than that of the global analysis. In this case the contribution of the environmental and spatial variables was the most important one for the association (13.20%), followed by the contribution of the environmental and temporal variables (9.20%) (Table 6). Figure 3B shows the statistical associations between the dependent and independent variables in Tables 4 and 5 for the functional diversity indices of the Campeche Sound (CS). In this case, the only significant dependent variables were functional evenness (FE) and functional divergence (FDiv) (Table 4). Figure 3B shows strong negative associations between functional evenness (FE) and lead, temperature, oxygen, MEM 2 and 3 and Cruise 2. In the case of functional divergence (FDiv), there were positive associations with lead, temperature, oxygen, MEM 2 and 3 and Cruise 2. For the Yucatan Shelf the statistical association between dependent and independent variables (Tables 4 and 5) was significant, but the percentage of variance explained was low (17.69%; Table 6). In this case the separate contribution of the environmental and temporal variables was the most important one for the association (Table 6). In this case, the only significant dependent variables were functional evenness (FE) and functional richness (FRic) (Table 4). In Figure 3C, in the case of FE, there were associations with MEM16, C6, and nitrates and nitrates. For FDiv, there were positive associations with MEM8 and MEM23. For FDiv, there were negative associations with PAHs, aliphatic hydrocarbons and temperature. FDiv, had also positive associations with phosphates, ammonium, depth, pH, COP and Cruise 6.

In the case of Tamaulipas-Veracruz, the whole RDA analysis was not significant (Table 6). However, the patterns in the RDA analysis indicate potential statistical associations (Fig. 3D). In Figure 3D there were positive associations between the FRic and pH, redox potential, ammonium, temperature, depth and particulate organic carbon. There were also negative associations of this dependent variable with phosphates, chlorophyll a and Cruise 6. In the case of Functional Evenness (FEv), there were only relevant negative associations with particulate organic carbon, salinity and MEM17.

For functional traits, the percentage of variance explained by the statistical association of these dependent variables with environmental (Env), spatial and temporal variables (independent variables) is shown in Table 6. The percentage of variance explained by the global association including all regions was 40.30%, with a high contribution (26.20%) of the combination of environmental and temporal variables, and a negligible contribution of the spatial variables (MEMs < 0%).

Figure 4A shows the statistical associations between the dependent and independent variables in Tables 4 and 5 for the Functional Traits of the southern Gulf of Mexico. In this case, the significant dependent variables were parasites with hard and soft body tegument, absorbers, predators, adults and larvae (Table 4). Thus, adult parasites with soft body tegument and absorber feeding mode (such as adult digeneans) had a strong negative association with heavy metals such as vanadium, nickel, and lead, and with environmental variables such as temperature, redox potential and Cruises 2, 7 and 8. This group of dependent variables also had positive associations with particulate organic carbon, pH, ammonium and Cruises 3, 5 and 6. In contrast, for parasites with hard body tegument and predation feeding mode (such as nematodes), and for larval parasites, there were positive associations with vanadium, nickel, and lead, and with environmental variables such as temperature and redox potential and Cruises 2, 7 and 8. There were also negative associations with pH, ammonium and Cruises 3, 5 and 6.

In the case of Campeche Sound (CS), the statistical association between dependent and independent variables was stronger (47.60%) than that of the global analysis. In this case, the contribution of the environmental variables was the highest (25.40%) (Table 6). Figure 4B shows the statistical association between the dependent and independent variables in Tables 4 and 5 for the functional traits of CS. In Figure 4B, very strong positive associations between parasites with predator feeding mode and hard body tegument parasites with Cruise 2, phosphates, lead, temperature and oxygen can be observed. There were also negative associations between these parasites with aliphatic hydrocarbons, ammonium, silicates, vanadium, cadmium and Cruise 6. In the case of adults with absorber feeding mode and soft body tegument, there were positive associations with aliphatic hydrocarbons, ammonium, silicates, vanadium, cadmium and Cruise 6. For the Yucatan Shelf and the Tamaulipas-Veracruz regions, none of the associations were significant and there were no biplots.

Discussion

The main hypothesis of this paper was that there would be higher values of explained variance for the effects of environmental variables (including hydrocarbons and heavy metals) on the taxonomic, functional traits and functional indices of the metazoan parasites of flounders for region with oil extraction activities in southern Gulf of Mexico compared with regions without this activity. This hypothesis was partially accepted because there was no complete dichotomy in the kind of statistical associations observed across different regions and indices. In regions with strong oil extraction activities, as expected, there were strong and significant association between the dependent variables and combinations of pollutants and environmental variables. However, in the region that was supposed to be free of the oil extraction activities, there were weak but still significant associations with heavy metals and hydrocarbons. Also, there were different results depending on the kind of indices used (i.e. taxonomic, functional diversity indices or functional traits). All these differences are explained below, after a brief account of the differences in the pool of parasites and the metrics of the parasite communities among the regions compared.

Pool of parasites

The information in Table 1 shows that both host species are exposed to the same pool of parasites in the whole sGOM. Clearly, the most frequent and abundant species of metazoan parasites in both host species (e.g. *Stephanostomum* sp. 1, *Lecanicephalum* sp., *K. pronosoma* and *Lecithochirium floridense*) were present in all regions.

It is important to note that two of this species were larval stages of cestodes with elasmobranchs as definitive hosts and are very frequent in sGOM (see Vidal-Martínez et al., 2014; Vidal-Martínez et al., 2019). In the case of *L. floridense*, it is a generalist digenean that is widely distributed in the sGOM across

several fish families. This repeatability of the composition of the dominant species across regions suggests nestedness, since the most frequent and abundant metazoan parasite species of *S. gunteri* are a subset of the parasite fauna of *S. papillosum* (Table 1). This means that both host species are exposed to the same pool of parasites in the sGOM, but they become differentially infected by these metazoan parasites in the three regions, probably due to slight biological differences in their feeding habits or specific habitat conditions. Certainly, a formal study of nestedness in the metazoan parasite communities of *S. gunteri* and *S. papillosum* will be necessary. Therefore, this is enough reason to pool them for further statistical analyses such as the redundancy analysis (see below). Our results concur with those of González and Poulin (2005) for the parasite component communities of the rockfish *Sebastes capensis* from the Pacific coast of South America. These authors found the presence of nestedness in the parasite communities of this fish consistently along the coast of Chile for endoparasites and attributed its variability to the feeding habits and characteristics of the habitat of the rockfish along its geographical distribution. Similar results were also found by Aparicio-Rizzo and González (2015) for five intertidal fish species from Chile. These authors found that those fish species with the highest numbers of metazoan parasite species and individuals presented a nested pattern. This was certainly the case for the parasite communities of the two flounder species in the present study.

Metrics of the parasite communities

The mean number of metazoan parasite species per fish of the shoal flounder *S. gunteri* (Table 2) for the three regions (TV, CS and YS) was higher than that previously described for the Mexican flounder *C. chittendeni* (1.19 ± 1.17 to 3.27 ± 1.64 species per fish; Centeno-Chalé et al., 2005), for the tonguefish *S. plagiusa* (2.00 ± 0.55 to 3.00 ± 0.66; Santa-Piñeros et al., 2012), and even higher than those of *S. papillosum* from TV and CS (Table 2). In the specific case of the Yucatan shelf, both *S. gunteri* and *S. papillosum* had very similar mean number of metazoan parasites species. These results suggest that both the shoal flounder and the dusky flounder individuals are acquiring similar numbers of metazoan parasite species because they are exposed to the same regional pool of parasites.

In the case of the mean number of individual parasites per fish (Table 2), the shoal flounder and the dusky flounder from TV were within the range found for *S. plagiusa* in the Campeche Sound (47.00 ± 31.81) (Vidal-Martínez et al., 2014). However, *S. gunteri* for the Campeche Sound had twice the mean number of individuals than those from TV. In the Yucatan shelf both *S. gunteri* and *S. papillosum* had the largest values for the mean number of individuals for the entire southern Gulf of Mexico. Those values are within the range reported for other marine fishes in the region. This is the case of Florida pompano *Trachinotus carolinus* which had maximum values of 218 ± 297 individuals from Celestun, Yucatán (Sanchez-Ramírez and Vidal-Martínez, 2002). However, the mean number of individual parasites of the flounders was almost twice the maximum mean number of individuals for the red grouper *Epinephelus morio* of Campeche (140.67 ± 238.70) (Vidal-Martínez et al., 1998). These results suggest that a large number of individuals are parasitizing fish on the Yucatan shelf. This finding may indicate a healthy environment, given the high transmission levels of both parasite species and individuals on the Yucatán shelf compared to CS and TV. This is consistent with the previous pattern reported by Vidal-Martínez et al (2019) regarding the good environmental conditions of the Yucatan shelf and in agreement with Hudson et al (2006) who assumed that a healthy ecosystem is one with a large number of parasite species and individuals.

The Brillouin's diversity values for the parasite infracommunities of *S. gunteri* and *S. papillosum* (Table 2) were higher than those of the Mexican flounder *C. chittendeni* from the Campeche Sound (range: 0.110 ± 0.170- 0.640 ± 0.350 (Centeno-Chalé et al., 2005)). This was also the case for these index values for the parasite communities of the Florida pompano *T. carolinus* (range: 0.60 ± 60.39- 0.93 ± 60.38 (Sánchez-Ramírez and Vidal-Martínez, 2002)), and the red grouper *Epinephelus morio* (range: 0.13 ± 0.18- 0.87 ± 0.34) (Vidal-Martínez et al., 1998) both from the Yucatan shelf, and both pelagic fishes. In the case of *C. chittendeni* individuals, they came from a region impacted by oil spills (Centeno-Chalé et al., 2005), which in turn could explain the low values of the Brillouin´s index with respect to those of *S. gunteri* and *S. papillosum.* In the case of the Brillouin´s values for the pelagic fishes, the most probable explanation is that the benthic environment offers higher probabilities of infection, especially for flounders with limited mobility compared to the vagility of the pelagic fishes in the water column.

The functional richness and evenness values of YS for both host species were significantly higher than those for the other two regions. This result concurs with the higher species richness and number of individuals in YS compared with the other two regions. Since we concur with the notion that a healthy ecosystem has a larger number of parasite species and individuals (Hudson et al, 2006) than an impacted one, the high YS values for both functional indices support the notion of a healthy marine ecosystem in this zone. A similar argument but with different ecological indicators was proposed by Vidal-Martínez et al. (2019). The divergence index did not show a clear trend in either the impacted or non-impacted regions. In the case of the functional diversity indices obtained for the shoal flounder and the dusky flounder, we could not find values for other fish species in the extant literature to compare. Since both host species are benthic fishes, it seems reasonable to compare their functional diversity values with those obtained for benthic free-living animals. In this case, the values of functional richness of both shoal flounder and the dusky flounder (Table 4) were low compared to those of benthic communities from the Bohai Sea (China), which were between 1.94 and 3744.67 in summer and 42.04 to 10442.76 for winter (Wang et al., 2022). This seems to be logical, since benthic communities of free-living organisms are richer in number of species and individuals. However, an advantage of the parasite communities of marine fishes is that they have well defined physical limits established by the body of the hosts, and then an infracommunity can be treated as a whole parasite community and all the added fishes in a sample as replicates of that community, providing a very strong way to account for the variability of the parasite community for a specific sampling point. Similar interpretations of the usefulness of infracommunity data have been provided by Holmes (1990) and references therein.

Redundancy analyses

The redundancy analysis including the flatfish from the three regions (TV, CS and YS) was performed at global level, with all the available dependent and independent variables including fish total length, standard length (cm) and weight (g). This analysis removed these three fish morphometric co-variables and kept only the independent variables presented in Table 5. The most probable reason for this removal was the lack of variability in these morphometric variables, due to a selectivity of a specific fish size for the obtention of sample for histopathology and other physiological and molecular biology studies by the technicians on-board. This is because most of the fish selected for environmental studies are the largest available in each trawl to maximize the amount of tissue obtained. However, instead of a drawback, this could be considered as an advantage since most of the fish compared among sampling sites would

be in the same size and weight range, and then variables such as age or size could not be considered confounding factors in this analysis, but constants and by that reason were removed by the analysis. Thus, the effect of the remaining independent variables could be explored safely. The most recent literature on the evaluation of functional traits of parasites has been performed at compound community level (Krasnov et al., 2024; Krasnov and Khokhlova, 2025) and at biogeographical level (Poulin, 2021), and host size has resulted in an important variable. Thus, in the future, the fish infracommunity data obtained from oceanographic cruises should consider all the host size ranges obtained during the trawls.

The performance of core, intermediate and satellite species (taxonomic diversity) as dependent variables for determining the statistical association with environmental, spatial and temporal variables was the best in the study at both the whole southern Mexico and for each one of the regions (Table 6). The amount of explained variance for this association based on taxonomic diversity was the highest in the global analysis and in each region (Table 6). Certainly, the contribution of the combination of environmental, spatial and temporal variables depended on the spatial scale and region. However, it is remarkable that the Campeche Sound had the highest amount of explained variance (61.30%), followed by the Tamaulipas region (TV) (46.10%; Table 6). We attribute this to the stronger influence of environmental variables (including hydrocarbons and heavy metals) on the parasites life cycles in CS, as suggested by the percentages of explained variance for the environmental variables alone or for the combination of the environmental and spatial variables (Table 6). In the case of TV, there are no oil extraction activities, but there is the presence of a large number of oil seeps (Love et al., 2013) and the influence of the release of a large amount of chemicals from the Rio Grande in the border between the United States and Mexico (Bilbe, 2006). This could also influence the response of the parasites infecting flounders in TV.

In contrast, the lowest explained variance was on the Yucatan Shelf (22.80%; Table 6). This could probably be attributed to strong influence of oceanographic currents along the Yucatan Shelf, which would produce uniformity in the values environmental variables diminishing their variability, as well as the lower influence of the natural release of hydrocarbons by oil seeps (Love et al. 2013) in comparison with regions with oil extraction activities such as CS. Similar patterns in the influence of oceanographic currents on the statistical association between parasite metrics and environmental variables have been reported for the tomtate grunt, *Haemulon aurolineatum,* along the Yucatan Shelf (Garcia-Teh et al., 2022). With respect to the temporal autocorrelation, except in the global analysis, the percentage of explained variance attributable to this variable was rather low across all regions (0.20-10.8%; Table 6). In any case, the methodology proposed by Bauman et al. (2018) allowed us not only to control but to quantify the influence of the spatial and temporal autocorrelation. The statistical association between parasites and environmental variables, including pollutants, has been reported before for parasite communities of flounders for different regions of the southern Gulf of Mexico by Centeno-Chale et al (2005), Vidal-Martínez et al. (2014), Vidal-Martínez et al. (2015) and Vidal-Martínez et al. (2019). This certainly reinforces the view that parasites can act as bioindicators of environmental impact, especially in regions with oil extraction activities such as CS. In addition, for communities of benthic organisms, the Campeche Sound, as an oil extraction region, has the most deteriorated sediment condition in the southern Gulf of Mexico, especially compared with the sediments of the Yucatan Shelf (Santibañez-Aguascalientes et al., 2020, Santibañez-Aguascalientes et al., 2021; Santibañez-Aguascalientes et al., 2023).

In the case of the percentage of variance explained by the association of functional diversity indices and functional traits with environmental, spatial and temporal variables, there were several interesting patterns. First, the global analysis for both sets of dependent variables was significant. Second, for both functional indices and traits, the percentage of explained variance for CS was higher than that of the global analysis. These results reinforce the view that the influence of the environmental and spatial variables on the parasite infracommunity metrics is stronger in that region, and that with an increase in the values of the taxonomical diversity indices, there is also an increase in the values of these functional indices. Third, the amount of explained variance between functional indices and traits, and environmental, spatial and temporal variables was lower or non-significant at YS and TV compared with those of CS (Table 6). This last pattern suggests that, depending on the region in which the environmental studies are conducted, the performance of these functional metrics can vary. This is to say that, for a region with high environmental impact such as CS, the two sets of dependent variables (taxonomical and functional) could be useful. But, for a region with strong influence of oceanographic currents such as YS, the performance of these functional variables could be rather weak. In the specific case of Tamaulipas, we consider that the fish sample size was not large enough to obtain a reliable result. This is because for this kind of analysis, a sample size of at least 100 sampling sites (in this case individual fishes) would be recommended (Bauman et al., 2018). So, at this point, the best option for using functional indices and functional traits of fish parasites in environmental studies is to combine them with taxonomic diversity indices. It is also important to bear in mind that the present study was performed at infracommunity level, and that previous work has been developed at component community level (e.g. Ocaña et al., 2021; Vidal-Martínez et al., 2022). In fact, these authors found that the variance explained by the taxonomic and functional metrics of metazoan parasite communities of the flounders *S. papillosum* and *S. gunteri* as indicators of chemical pollution in the southern Gulf of Mexico (sGOM) was similar (~50%) when comparing temporal and spatial data from two contiguous regions in the sGOM, the Yucatan Peninsula (YP) and the Campeche Sound (CS). This is an important result for parasite ecologists working on environmental impact studies because they can use these functional traits at component community level instead of detailed taxonomical identifications at the species level for rapid environmental assessments. Similar usefulness of functional traits of fishes, benthic organisms and ciliates as bioindicators of environmental impact have been published elsewhere (Xu et al., 2018; Aguilar-Medrano and Vega-Cendejas, 2020; González-Gandara 2020; Santibañez-Aguascalientes et al., 2021). Additionally, we do not need to spend as much time and resources on identifying functional traits for bioassessments as we do on identifying species at the species level. In this sense, using functional traits will save time and money.

The level of explained variance reached with the taxonomic diversity indices (61.30%; Table 6) was within the range of those found for other fish species in the southern Gulf of Mexico. This is the case for the association between parasite metrics and environmental and pollutant variables of *H. aurolineatum* of the YS with 44% of explained variance (Garcia-Teh et al., 2022), for *Cyclopsetta chittendeni* which was 47% (Centeno-Chalé et al., 2015) and for *S. gunteri* from the Campeche Sound which was between 23 and 68% (Vidal-Martínez et al., 2014). Here, it is important to note that none of the papers mentioned above included spatial or temporal variables in the RDA analysis. In fact, when these variables are considered, there is an increase in the percentage of explained variance of the association between parasite metrics at infracommunity level and environmental and pollutant variables, as it has been shown by Santana-Piñeros et al (2012) for the tonguefish *Symphurus plagiusa* from the Campeche coast, southern Mexico. These authors found values between 49% and 83.3 of explained variance within a year for the metazoan parasites of coastal tonguefish. Thus, considering these spatial and temporal variables can help to

improve the percentage of explained variance for this association. From this, it is evident that the use of core, intermediate and rare species as dependent variables was very informative about the effect of the environmental, spatial and temporal variables at both global and regional levels (Table 6). However, these three parasite categories can also be seen as functional expressions of the parasite life cycles. In this case, core species are the most frequent (widely distributed species among fish hosts, i.e. with high prevalence) and locally abundant species. In both cases these are expressions of the capacity of the parasite to distribute widely in the host population, being able to reach high local abundance in the fish. This would be the case of larval species such as *Stephanostomum* sp. 1, *Lecanicephalum* sp., Trypanorhyncha gen. sp., or adult species such as *Lecithochirium floridense* (Table 1*)*. Thus, by different ways, both larval or adult species can reach both high prevalence and abundance in the fish hosts, or low prevalence and abundance as in the case of satellite species. These characteristics can be considered as functional traits characteristic of each group of species, and certainly can be easily calculated without the need for a formal taxonomical identification, but simply by making a morphospecies identification and characterizing them as core, intermediate or satellite species based on the prevalence and abundance values. In this way, core and satellite metazoan parasite species can be interpreted as Hanski (1982) proposed, without the intervention of a proper taxonomic identification.

Conclusions

The amount of explained variance for the statistical association between environmental factors and pollutants (independent variables) and the taxonomical and functional parasite community metrics (dependent variables) of flounders was higher in the region with oil extraction (CS) activity than in the regions without this activity (YS and TV). This association seems to be stronger in regions with high oil extraction activities such as the CS, or those in which there is a natural release of hydrocarbons and anthropogenic release of chemicals as in TV. In contrast, YS appears to be an ecologically healthy region with rich metazoan parasite communities with a high number of species and individuals, and heavily influenced by oceanographic currents. For this kind of environmental studies at infracommunity level, it is recommended to use taxonomical, functional diversity indices and functional traits together. Taxonomical diversity indices such as core, intermediate and satellite species can also be seen as functional indicators based on a proper morphospecies characterization.

Declarations

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

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Authors contributions: VMVM conceived the study, analyzed data, and drafted the manuscript. All authors read and approved the final manuscript. FAO, JMM, IVA, ZPAP, JRVZ, and MVO contributed to the methodology, conducted the statistical analyses, and reviewed and edited the manuscript. LCSJ participated in the study design and data curation. ALMT and JGGT conducted data curation and analysis and helped review and edit the manuscript. OACC data curation and performed the maps. MLAM contributed to funding acquisition and project administration, participated in the study design, and reviewed the original draft of the manuscript.

References

1. Aguilar-Medrano R, Vega-Cendejas ME (2019) Implications of the environmental heterogeneity on the distribution of the fish functional diversity of the Campeche Bank, Gulf of Mexico. Mar Biodivers 49:1913–1929. https://doi.org/10.1007/s12526-019-00954-y
2. Ahmed DA, van Bodegom PM, Tukker A (2018) Evaluation and selection of functional diversity metrics with recommendations for their use in life cycle assessments. Int J Life Cycle Assess 23:2415–2428
3. Aparicio-Rizzo P, Muñoz G (2015) Nestedness of parasite communities of intertidal fish in central Chile: how influential is the body length of the host? Rev Biol Trop 63:995–1005

4. Árcega-Cabrera F, Dótor-Almazán A (2021) Hidrocarburos. In: Herzka SZ, Zaragoza Álvarez RA, Peters EM, Hernández Cárdenas G (eds) Atlas de línea base ambiental del golfo de México, tomo IV. Consorcio de Investigación del Golfo de México, México
5. Bauman D, Drouet T et al (2018) Disentangling the drivers of spatial variation in community composition. Ecography 41:1645–1656. https://doi.org/10.1111/ecog.03380
6. Beauchard O, Veríssimo H, Queirós AM, Herman PMJ (2017) The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. Ecol Indic 76:81–96. https://doi.org/10.1016/j.ecolind.2017.01.011
7. Bilbe L (2006) Anthropomorphic effects on the Rio Grande: a biogeographic assessment. River Systems Institute, Texas State University, Texas
8. Blanar CA, Munkittrick KR, Houlahan J, MacLatchy DL, Marcogliese DJ (2009) Pollution and parasitism in aquatic animals: a meta-analysis of effect size. Aquat Toxicol 93:18–28. https://doi.org/10.1016/j.aquatox.2009.03.002
9. Brázová T, Miklisová D, Barčák D et al (2021) Hazardous pollutants in the environment: fish host-parasite interactions and bioaccumulation of polychlorinated biphenyls. Environ Pollut 291:118175
10. Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al revisited. J Parasitol 83:575–583
11. Bush AO, Holmes JC (1986) Intestinal helminths of lesser scaup ducks: patterns of association. Can J Zool 64:132–141
12. Casanoves F, Pla L, Di Rienzo JA, Díaz S (2010) FDiversity: a software package for the integrated analysis of functional diversity. Methods Ecol Evol 1:233–237
13. Centeno-Chalé OA, Aguirre-Macedo ML, Gold-Bouchot G, Vidal-Martínez VM (2015) Effects of oil spill related chemical pollution on helminth parasites in Mexican flounder *Cyclopsetta chittendeni* from the Campeche Sound, Gulf of Mexico. Ecotoxicol Environ Saf 119:162–169
14. Chevenet F, Dolédec S, Chessel D (1994) A fuzzy coding approach for the analysis of long-term ecological data. Freshw Biol 31:295–309
15. Chovanec A, Hofer R, Schiemer F (2003) Fish as bioindicators. In: Markert AM, Breure H, Zechmeister H (eds) Bioindicators and biomonitors. Elsevier, Amsterdam, pp 639–676
16. Dray S, Dufour A (2007) The ade4 package: implementing the duality diagram for ecologists. J Stat Softw 22:1–20
17. Dray S, Bauman D, Blanchet G et al (2025) adespatial: multivariate multiscale spatial analysis. R package version 0.3-28
18. Fraser TH (1971) Notes on the biology and systematics of the flatfish genus *Syacium* (Bothidae) in the Straits of Florida. Bull Mar Sci 21:491–509
19. Frerebeau N (2019) tabula: an R package for analysis, seriation, and visualization of archaeological count data. J Open Source Softw 4:1821
20. García-Abad MC, Yáñez-Arancibia A, Sánchez-Gil P, Tapia-García M (1992) Distribución, reproducción y alimentación de *Syacium gunteri* en el Golfo de México. Rev Biol Trop 39:27–34
21. García-Teh JG, Vidal-Martínez VM, Mariño-Tapia I et al (2022) Metazoan parasite infracommunities of the tomtate grunt (*Haemulon aurolineatum*) as potential bioindicators of environmental conditions in the Yucatan continental shelf, Mexico. Bull Environ Contam Toxicol 108:49–54
22. González MT, Poulin R (2005) Spatial and temporal predictability of parasite community structure of a benthic marine fish. Int J Parasitol 35:1369–1377
23. González-Gándara C (2020a) La comunidad de peces del arrecife Palo Seco, Veracruz, golfo de México y su relación con los grupos morfofuncionales. CienciaUAT 14:34–50. https://doi.org/10.29059/cienciauat.v14i2
24. Grenié M, Gruson H (2023) fundiversity: a modular R package to compute functional diversity indices. Ecography 2023:e06585
25. Grenié M, Gruson H (2025) fundiversity: easy computation of functional diversity indices. R package version 1.1.1. https://doi.org/10.5281/zenodo.4761754
26. Guerrero-Aguilar A, Rodríguez-Castrejón UE, Serafín-Muñoz AH et al (2022) Bioindicators and biomonitoring: review of methodologies applied in water bodies. Acta Univ 32:e3388
27. Holt E, Miller S (2010) Bioindicators: using organisms to measure environmental impacts. Nat Educ Knowl 3:10
28. Holmes JC (1990) Helminth communities in marine fishes. In: Esch GW, Bush AO, Aho JM (eds) Parasite communities: patterns and processes. Chapman and Hall, London, pp 101–130
29. Hudson PJ, Dobson AP, Lafferty KD (2006) Is a healthy ecosystem one that is rich in parasites? Trends Ecol Evol 21:381–385
30. Johnson DR, Franks JS, Oxenford HA, Cox SL (2020) Pelagic sargassum prediction and marine connectivity in the tropical Atlantic. Gulf Caribb Res 31: GCFI20–GCFI30. https://aquila.usm.edu/gcr/vol31/iss1/15
31. Krasnov BR, Khokhlova IS, López Berrizbeitia MF et al (2024) Relationships between functional alpha and beta diversities of flea parasites. Parasitology 151:449–460
32. Krasnov BR, Khokhlova IS (2025) Decomposition of functional beta, but not alpha, diversity detects deviations from the "host-diversity-begets-parasite-diversity" rule in flea-mammal associations. Parasitol Res 124:80. https://doi.org/10.1007/s00436-025-08527-8
33. Kuris AM, Hechinger RF, Shaw JC et al (2008) Ecosystem energetic implications of parasite and free-living biomass. Nature 454:515–518
34. Lafferty KD (1997) Environmental parasitology: what can parasites tell us about human impacts? Parasitol Today 13:251–255
35. Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity. Ecology 91:299–305
36. Llopis-Belenguer C, Balbuena JA, Lange K, de Bello F, Blasco-Costa I (2019) Towards a Unified Functional Trait Framework for Parasites. Trends Parasitol 35: 972-982. https://doi.org/10.1016/j.pt.2019.09.003.
37. Louvard C, Hadfield KA, Vanhove MPM, Sures B, Smit NJ (2025) Unveiling the hidden players: exploring the intricate dance of aquatic parasites, host biodiversity and ecosystem health. In: Smit NJ, Sures B (eds) Aquatic parasitology: ecological and environmental concepts and implications of marine and freshwater parasites. Springer, pp 167–198

38. Love MS, Baldera A, Yeung C, Robbins C (2013) The Gulf of Mexico ecosystem: a coastal and marine atlas. Ocean Conservancy, Gulf Restoration Center, 232 pp
39. MacDonald IR, García-Pineda O, Beet A, Daneshgar AS, Feng L, Graettinger G, French-McCay D, Holmes J, Hu C, Huffer F, Leifer I, Muller-Karger F, Solow A, Silva M, Swayze G (2015) Natural and unnatural oil slicks in the Gulf of Mexico. J Geophys Res Oceans 120:8364–8380. https://doi.org/10.1002/2015JC011062
40. Marcogliese DJ, Gendron AD, Cone DK (2009) Impact of municipal effluents and hydrological regime on myxozoan parasite communities of fish. Int J Parasitol 39:1345–1351
41. Marcogliese DJ, Pietrock M (2011) Combined effects of parasites and contaminants on animal health: parasites do matter. Trends Parasitol 27:123–13Marcogliese DJ (2023) Major drivers of biodiversity loss and their impacts on helminth parasite populations. J Helminthol 97:e34
42. Marcon E, Herault B (2015) entropart: an R package to measure and partition diversity. J Stat Softw 67:1–26
43. Mateo-Sagasta J, Zadeh SM, Turral H (2017) Water pollution from agriculture: a global review – executive summary. FAO, Rome
44. Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures. Funct Ecol 24:867–876
45. Nachev M, Sures B (2016) Environmental parasitology: parasites as accumulation bioindicators. J Sea Res 113:45–50
46. Ocaña FA, Soler-Jiménez LC, Aguirre-Macedo ML, Vidal-Martínez VM (2021) Performance of taxonomic and trait-based approaches in parasite communities. Environ Pollut 287:117622
47. Oksanen J, Simpson G, Blanchet F et al (2025) vegan: community ecology package. R package version 2.8-0
48. Paradis E, Schliep K (2019) ape 5.0: an environment for phylogenetics. Bioinformatics 35:526–528
49. Pebesma E, Bivand R (2023) Spatial data science with applications in R. Chapman and Hall, Boca Raton. https://r-spatial.org/book/
50. Pérez-del-Olmo A, Fernández M, Raga JA, Kostadinova A, Morand S (2009) Follow-up trends of parasite community alteration in a marine fish after the Prestige oil-spill: shifting baselines? Environ Pollut 157:221–228
51. Peres-Neto PR, Legendre P, Dray S, Borcard D (2006) Variation partitioning of species data matrices. Ecology 87:2614–2625
52. Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9:741–758
53. Pietrock M, Marcogliese DJ (2003) Free-living endohelminth stages. Trends Parasitol 19:293–299
54. Poulin R (2007) Are there general laws in parasite ecology? Parasitology 134:763–776
55. Poulin R (2021) Functional biogeography of parasite traits: hypotheses and evidence. Philos Trans R Soc B 376:20200365. https://doi.org/10.1098/rstb.2020.0365
56. Quintanilla-Mena M, Gold-Bouchot G, Zapata-Pérez O, Rubio-Piña J, Quiroz-Moreno A, Vidal-Martínez VM, Puch-Hau CA (2020) Biological responses of shoal flounder (*Syacium gunteri*) to toxic environmental pollutants from the southern Gulf of Mexico. Environ Pollut 258:113669. https://doi.org/10.1016/j.envpol.2019.113669
57. R Core Team (2026) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.r-project.org/
58. Sánchez-Soto MF, Cerqueda-García D, Alcántara-Hernández RJ, Falcón LI, Pech D, Árcega-Cabrera F, Aguirre-Macedo ML, García-Maldonado JQ (2021) Assessing the diversity of benthic sulfate-reducing microorganisms in northwestern Gulf of Mexico by Illumina sequencing of dsrB gene. Microb Ecol 81:908–921. https://doi.org/10.1007/s00248-020-01631-5
59. Sánchez-Ramírez C, Vidal-Martínez VM (2002) Metazoan parasite infracommunities of Florida pompano (*Trachinotus carolinus*) from the coast of the Yucatan Peninsula, Mexico. J Parasitol 88:1087–1094
60. Santana-Piñeros AM, Pech D, Vidal-Martínez VM (2012) Spatial structure of the helminth parasite communities of the tonguefish, *Symphurus plagiusa*, from the Campeche coast, southern Mexico. Int J Parasitol 42:911–920
61. Santibañez-Aguascalientes NA, Borja Á, Montero-Muñoz JL, Herrera-Dorantes MT, Ardisson PL (2020) Setting reference conditions to assess the ecological status of the sublittoral and bathyal benthic communities of the southern Gulf of Mexico. Ecol Indic 111:105964. https://doi.org/10.1016/j.ecolind.2019.105964.
62. Santibañez-Aguascalientes NA, Borja Á, Ardisson PL (2021) Sustainability situations for the southern Gulf of Mexico seafloor, based on environmental, benthic, and socioeconomic indicators. Sci Total Environ 787:147726. https://doi.org/10.1016/j.scitotenv.2021.147726.
63. Santibañez-Aguascalientes NA, Borja Á, Ardisson PL (2023) Assessing the large-scale and long-term changes in the southern Gulf of Mexico benthic ecological status under natural and human-induced disturbances. Estuar Coast Shelf Sci 283:108282. https://doi.org/10.1016/j.ecss.2023.108282.
64. Sasal P, Morand S, Guégan JF (1996) Determinants of parasite species richness in Mediterranean marine fishes. Mar Ecol Prog Ser 142:117–123
65. Sericano JL, Wade TL, Vidal-Martínez VM, Gold-Bouchot G, Knap AH (2019) Organic chemical pollutants and contamination in the Gulf of Mexico. In: Bianchi TS, Morrison E, Robinson DM, Rosenheim BE, He R, Warrillow J (eds) Gulf of Mexico origin, waters, and biota: volume 5, chemical oceanography. Texas A&M University Press, College Station, pp 234–272
66. Sericano JL, Atlas EL, Wade TL, Brooks JM (1990) NOAA's status and trends mussel watch program: chlorinated pesticides and PCBs in oysters (Crassostrea virginica) and sediments from the Gulf of Mexico, 1986–1987. Mar Environ Res 29:161–203. https://doi.org/10.1016/0141-1136(90)90033-K
67. Siberchicot A, Julien-Laferrière A, Dufour AB, Thioulouse J, Dray S (2017) adegraphics: an S4 lattice-based package for the representation of multivariate data. R J 9:198–212. https://journal.r-project.org/archive/2017/RJ-2017-042/index.html
68. Smit NJ, Sures B (eds) (2025) Aquatic parasitology: ecological and environmental concepts and implications of marine and freshwater parasites. Springer, Cham. https://doi.org/10.1007/978-3-031-83903-0

69. Soler-Jiménez LC, Hernández-Núñez E, Velázquez-Abunader I, Centeno-Chalé OA, Vidal-Martínez VM (2020) Polycyclic aromatic hydrocarbons in the cestode *Oncomegas wageneri* parasite of Mexican flounder *Cyclopsetta chittendeni*. Parasitol Res 119:903–913. https://doi.org/10.1007/s00436-019-06597-z
70. Soler-Jiménez LC, Aguirre-Macedo ML, Vega-Cendejas ME, García-Teh JG, Enríquez-Ortiz CE, Vidal-Martínez VM (2022) Metazoan parasites of some meso- and bathypelagic fish from the Perdido region, southern Gulf of Mexico. J Mar Biol Assoc UK 102:391–401. https://doi.org/10.1017/S0025315422000649
71. Soler-Jiménez LC, Ocaña FA, Hernández-Mena DI, Centeno-Chalé OA, Aguirre-Macedo ML, Vidal-Martínez VM (2024) Ecological and phylogenetic components of flatfish ectoparasites (Pleuronectiformes: Paralichthyidae) from the southern Gulf of Mexico. PLoS One 19:e0309818
72. Suárez-Mozo NY, Vidal-Martínez VM, Aguirre-Macedo ML, Pech D, Guerra-Castro E, Simões N (2021) Bivalve diversity on the continental shelf and deep sea of the Perdido fold belt, northwest Gulf of Mexico, Mexico. Diversity 13:166. https://doi.org/10.3390/d13040166
73. Sures B, Nachev M, Selbach C, Marcogliese DJ (2017) Parasite responses to pollution. Parasit Vectors 10:1–19
74. Sures B, Nachev M, Schwelm J, Grabner D, Selbach C (2023) Environmental parasitology: stressor effects on aquatic parasites. Trends Parasitol 39:461–474. https://doi.org/10.1016/j.pt.2023.03.005
75. Sures B, Nachev M, Grabner D, Wepener V, Zimmermann S (2025) Environmental parasitology: interactions between parasites and pollutants. In: Smit NJ, Sures B (eds) Aquatic parasitology: ecological and environmental concepts and implications of marine and freshwater parasites. Springer, pp 445–470. https://doi.org/10.1007/978-3-031-83903-0_20
76. Thioulouse J, Dray S, Dufour AB, Siberchicot A, Jombart T, Pavoine S (2018) Multivariate analysis of ecological data with ade4. Springer, New York. https://doi.org/10.1007/978-1-4939-8850-1
77. Valtonen T, Holmes J, Aronen J, Rautalahti I (2003) Parasite communities as indicators of recovery from pollution. Parasitology 126:S43–S52
78. Vidal-Martínez VM, Aguirre-Macedo ML, Vivas-Rodríguez CM et al (1998) Las comunidades de macroparásitos del mero *Epinephelus morio* (Pisces: Serranidae) en la península de Yucatán, México. In: Proceedings of the 50th Gulf and Caribbean Fisheries Institute, Fort Pierce, Florida, pp 764–769
79. Vidal-Martínez VM, Aguirre-Macedo ML, Del Rio-Rodríguez R, Gold-Bouchot G, Rendón-von Osten J, Miranda-Rosas GA (2006) The pink shrimp *Farfantepenaeus duorarum*, its symbionts and helminths as bioindicators of chemical pollution in Campeche Sound, Mexico. J Helminthol 80:159–174. https://doi.org/10.1079/joh2006358
80. Vidal-Martínez VM, Pech D, Sures B, Purucker ST, Poulin R (2010) Can parasites really reveal environmental impact? Trends Parasitol 26:44–51
81. Vidal-Martínez VM, Centeno-Chalé OA, Torres-Irineo E, Sánchez-Ávila J, Gold-Bouchot G, Aguirre-Macedo ML (2014) The metazoan parasite communities of the shoal flounder (*Syacium gunteri*) as bioindicators of chemical contamination in the southern Gulf of Mexico. Parasit Vectors 7:1–14. https://doi.org/10.1186/s13071-014-0541-3
82. Vidal-Martínez VM, Torres-Irineo E, Romero D, Gold-Bouchot G, Martínez-Meyer E, Valdés-Lozano D, Aguirre-Macedo ML (2015) Environmental and anthropogenic factors affecting the probability of occurrence of *Oncomegas wageneri* (Cestoda: Trypanorhyncha) in the southern Gulf of Mexico. Parasit Vectors 8:609
83. Vidal-Martínez VM, Velázquez-Abunader I, Centeno-Chalé OA, May-Tec AL, Soler-Jiménez LC, Pech D, Aguirre-Macedo ML (2019) Metazoan parasite infracommunities of the dusky flounder (*Syacium papillosum*) as bioindicators of environmental conditions in the continental shelf of the Yucatan Peninsula, Mexico. Parasit Vectors 12:1–18. https://doi.org/10.1186/s13071-019-3524-6
84. Vidal-Martínez VM, Ocaña FA, Soler-Jiménez LC, García-Teh JG, Aguirre-Macedo ML, May-Tec AL, Árcega-Cabrera F, Herrera-Silveira JA (2022) Functional groups of metazoan parasites of the dusky flounder (*Syacium papillosum*) as bioindicators of environmental health of the Yucatan shelf. Bull Environ Contam Toxicol 108:24–29. https://doi.org/10.1007/s00128-021-03177-9
85. Wade TL, Brooks JL, Kennicutt MC II, McDonald TJ, Sericano JL, Jackson TJ (1993) GERG trace organic contaminant analytical techniques. In: Sampling and analytical methods of the National Status and Trends Program, National Benthic Surveillance and Mussel Watch projects 1984–1992, vol IV. NOAA Technical Memorandum NOS ORCA 71, pp 121–139
86. Wang M, Hu C, Barnes BB et al (2019) The great Atlantic Sargassum belt. Science 365:83–87
87. Wang Q, Shi S, Liu X (2022) Functional diversity of macrofaunal assemblages as indicators to assess heavy metal pollution in the Bohai Sea, China. Mar Pollut Bull 184:11414
88. Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer, New York. https://ggplot2.tidyverse.or
89. Wood CL, Sandin SA, Zgliczynski B et al (2014) Fishing drives declines in fish parasite diversity. Ecology 95:1929–1946
90. Xu Y, Stoeck T, Forster D, Ma Z, Zhang L, Fan X (2018) Environmental status assessment using biological traits analyses and functional diversity indices of benthic ciliate communities. Mar Pollut Bull 131:646–654. https://doi.org/10.1016/j.marpolbul.2018.04.051

Figures

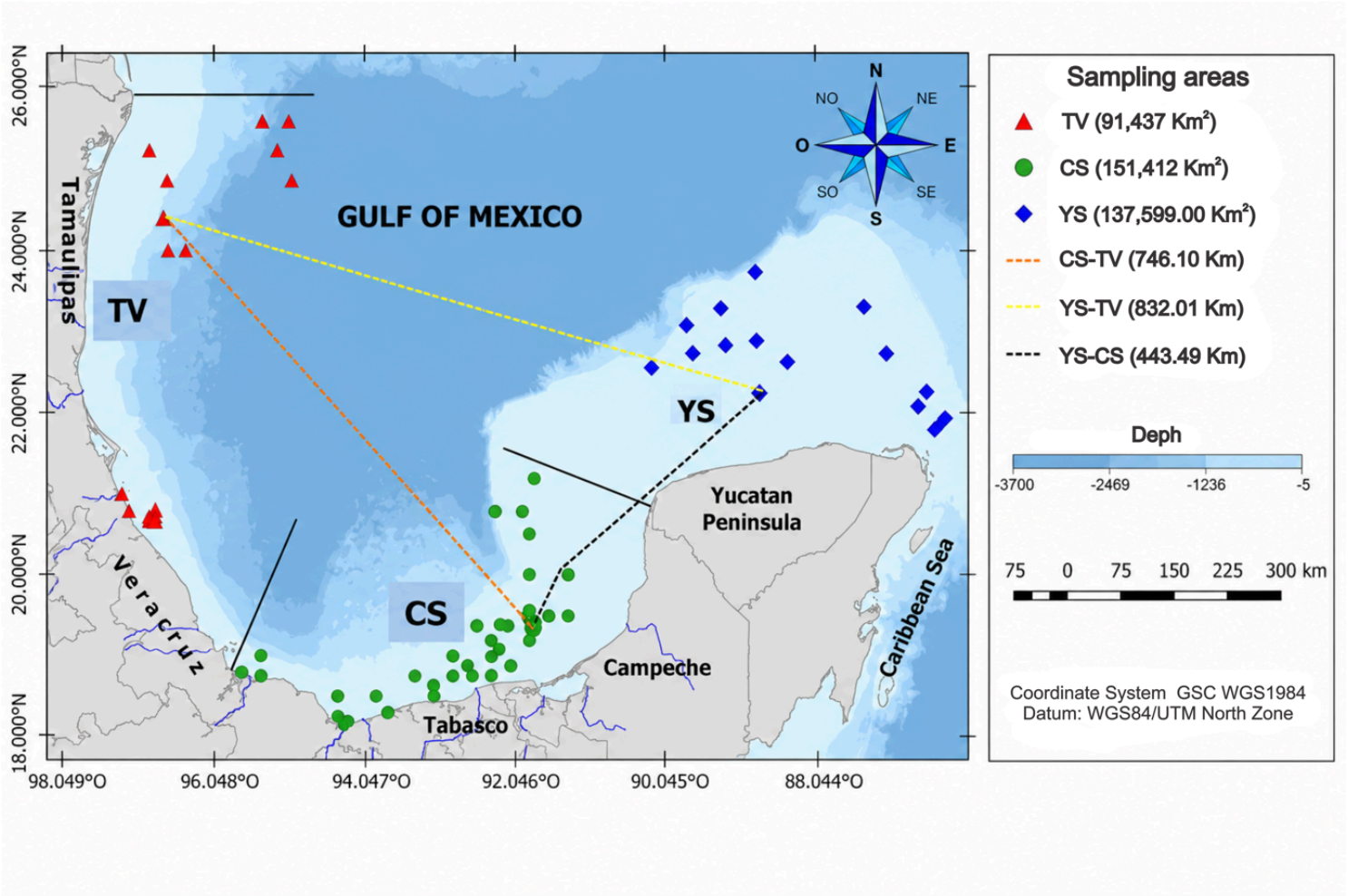


Figure 1

The three regions in which the whole southern Gulf of Mexico was divided: Campeche Sound (CS), Tamaulipas-Veracruz (TV) and Yucatan shelf (YS). The marks in different colors represent the geographical positions of the sampling sites.

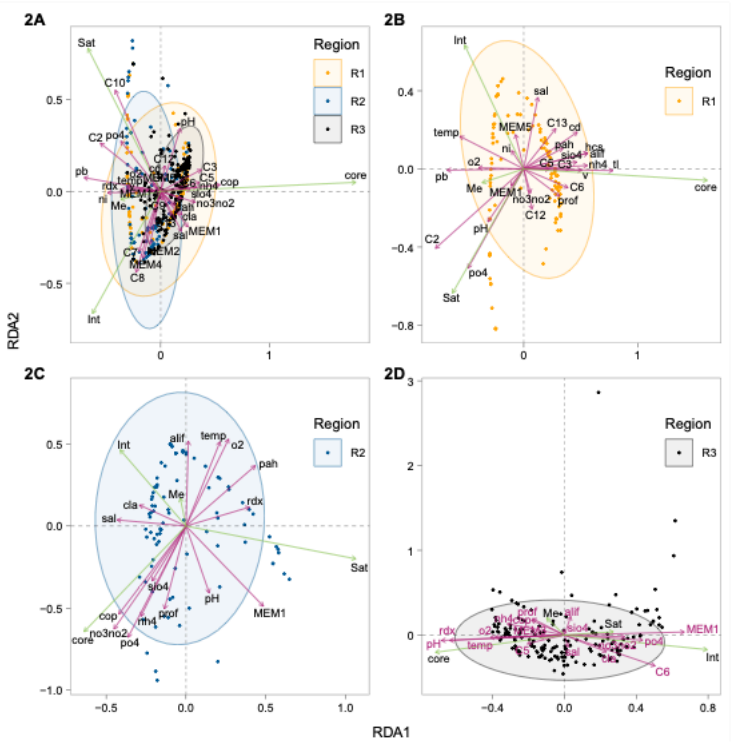


Figure 2

Redundancy analysis (RDA) describing the statistical associations between the taxonomical diversity indicators core species, intermediate species, median of all species and satellite species of the metazoan parasite infracommunities of *Syacium gunteri* and *Syacium papillosum* for three regions of the Southern Gulf of Mexico: Campeche Sound (CS), Tamaulipas-Veracruz (TV) and Yucatan Shelf (YS) (Table 5) and the environmental variables of Table 6. All RDA analyses were significant at $p < 0.001$, and details of the explained variance for each analysis are presented in Table 6. 2A: RDA for all regions; 2B: RDA for CS; 2C: RDA for TV; 2D: RDA for YS. Acronyms were as follows: Dependent variables: Core = core species, Int = intermediate species, Sat = satellite species, Me = median values of all the species; Independent variables: MEM1-14, = Moran´s eigenvalue maps 1-14; hospp = host species (*S. gunteri* and *S. papillosum*), nh4 =ammonium, prof = depth, temp = temperature, sal = salinity, o2 = oxygen, po4 =phosphates, si04 =silicates, no3no2 = nitrites/nitrates, cop = particulate organic carbon, cla = chloropyll a, rdx = redox potential, alif = aliphatic hydrocarbons, pah = polyaromatic hydrocarbons, cd = cadmium, ni = nickel, pb = lead, v = vanadium, C2-C13 = oceanographic cruises C2-C13. The squares in each figure (Regions 1-3) refer to CS, YS and TV respectively.

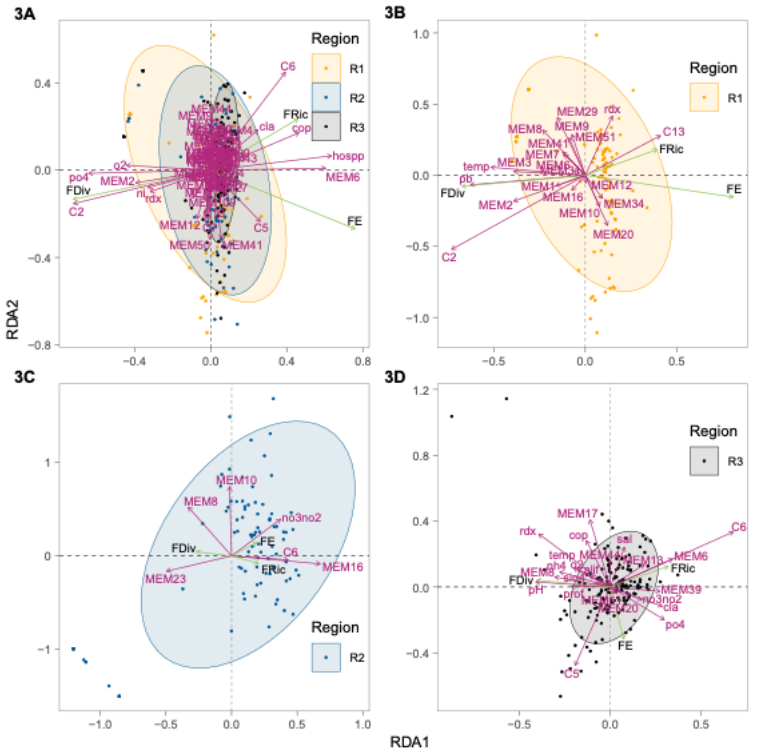


Figure 3

Redundancy analysis (RDA) describing the statistical associations between functional richness, functional evenness and functional divergence of the metazoan parasite infracommunities of *Syacium gunteri* and *Syacium papillosum* for three regions of the Southern Gulf of Mexico: Campeche Sound (CS), Tamaulipas-Veracruz (TV) and Yucatan Shelf (YS) (Table 5) and the environmental variables of Table 6. With exception of the RDA for TV (Fig. 3D), which was included only for descriptive purposes, all other RDA analyses were significant at $p < 0.001$. The details about the explained variance values for each RDA analysis are presented in Table 6. 3A: RDA for all regions, 3B: RDA for CS; 3C: RDA for YS; 3D: RDA for TV (non-significant). Acronyms were as follows: Dependent variables: FRic = Functional richness, FE = Functional evenness, FDiv = Functional divergence; Independent variables: MEM1-MEM51 = Moran´s eigenvalue maps 1-51; hospp = host species (S. gunteri and S. papillosum), nh4 =ammonium, prof = depth, temp = temperature, sal = salinity, o2 = oxygen, po4 =phosphates, si04 =silicates, no3no2 = nitrites/nitrates, cop = particulate organic carbon, cla = chloropyll a, rdx = redox potential, alif = aliphatic hydrocarbons, pah = polyaromatic hydrocarbons, cd = cadmium, ni = nickel, pb = lead, v = vanadium, C2-C13 = oceanographic cruises C2-C13. The squares in each figure (Regions 1-3) refer to CS, YS and TV respectively.

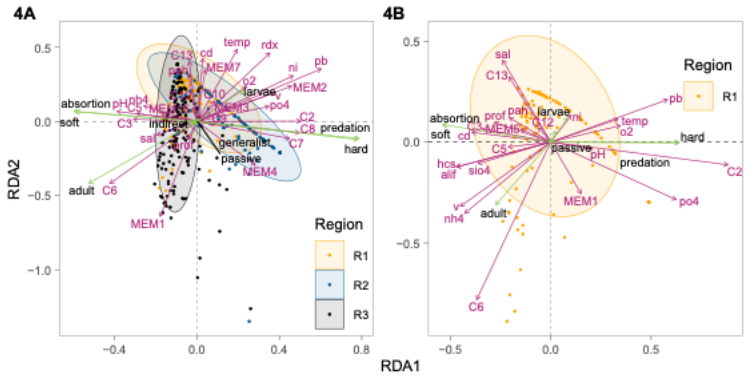


Figure 4

Redundancy analysis (RDA) describing the statistical associations between functional traits of the metazoan parasite infracommunities of *Syacium gunteri* and *Syacium papillosum* for three regions of the Southern Gulf of Mexico: Campeche Sound (CS), Tamaulipas-Veracruz (TV) and Yucatan Shelf (YS) (Table 5) and the environmental variables of Table 6. The RDA analyses for all the three regions together and for the Campeche Sound (CS) were significant at $p < 0.001$. The RDA for the Tamaulipas-Veracruz region and for the Yucatan Shelf (YS) were not significant. The details about the explained variance values for each RDA analysis are presented in Table 6. 4A: RDA for all regions, 4B: RDA for CS. Acronyms were as follows: Dependent variables: absorption, adult, generalists, hard, larvae, predation, soft, specialists; Independent variables: MEM1-MEM15 = Moran´s eigenvalue maps 1-15; hospp = host species (*S. gunteri* and *S. papillosum*), nh4 =ammonium, prof = depth, temp = temperature, sal = salinity, o2 = oxygen, po4 =phosphates, si04 =silicates, no3no2 = nitrites/nitrates, cop = particulate organic carbon, cla = chloropyll a, rdx = redox potential, alif = aliphatic hydrocarbons, pah = polyaromatic hydrocarbons, cd = cadmium, ni = nickel, pb = lead, v = vanadium, C2-C13 = oceanographic cruises C2-C13. The squares in each figure (Regions 1-3) refer to CS, YS and TV respectively.

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