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Herbivorous Reef Fish Interaction with the Habitat and Physicochemical Variables in Coral Ecosystems in the Mexican Tropical Pacific

Diana Morales-de-Anda [1,2], Amílcar Leví Cupul-Magaña [2,*], Consuelo María Aguilar-Betancourt [3], Gaspar González-Sansón [3], Fabián Alejandro Rodríguez-Zaragoza [4] and Alma Paola Rodríguez-Troncoso [2]

[1] Laboratorio de Ecología de Ecosistemas de Arrecifes Coralinos (LEEAC), Departamento de Recursos del Mar, Cinvestav, Unidad Mérida, Mérida 97205, Mexico; dianamorales9009@gmail.com
[2] Laboratorio de Ecología Marina (LEMAC), Departamento de Ciencias Biológicas, CUCosta Universidad de Guadalajara, Puerto Vallarta 48280, Mexico; alma.rtroncoso@academicos.udg.mx
[3] Departamento de Estudios para el Desarrollo Sustentable de la Zona Costera, CUCSur Universidad de Guadalajara, Cihuatlán 48980, Mexico; coquiaguilar06@yahoo.es (C.M.A.-B.)
[4] Laboratorio de Ecología Molecular, Microbiología y Taxonomía (LEMITAX), Departamento de Ecología, CUCBA, Universidad de Guadalajara, Zapopan 45200, Mexico
* Correspondence: amilcar.cupul@gmail.com; Tel.: +52-3221184764

Abstract: Herbivorous fish can mediate spatial competition between algae and corals, which is crucial for coral ecosystems. However, in areas with limited coral coverage like the Mexican tropical Pacific (MTP), this dynamic is not fully understood. This study, using a functional trait approach and ordination analysis, explores whether herbivorous reef fish assemblage influences the benthic habitat components or if physicochemical factors define the habitat variability in the MTP's Cleofas and Marietas insular systems. We analyzed if this relationship persisted across systems and over time, and identified species traits tied to habitat variability. Island comparison analyses between Cleofas and Marietas reveal that both herbivorous reef fish and physicochemical variables shape the habitat. Cleofas had larger mobile herbivorous fish that formed groups related mostly to macroalgae cover. In contrast, temporal analysis of Marietas shows that the habitat is primarily shaped by physicochemical variables with herbivorous fish being mainly small farmer species related to branching corals. Notably, these closely situated insular systems present varied ecosystem mediators, influenced by diverse drivers including fish traits and environmental factors. This study underscores the potential of employing a framework of ecological species traits combined with ordination methods to unravel the distinct site dynamics that contribute to the persistence of coral ecosystems within the MTP.

Keywords: traits; functional ecology; RLQ; reefs

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1. Introduction

Grazing by herbivorous fish and other organisms helps control macroalgae overgrowth, thereby facilitating the recruitment and sustaining the coverage of corals and other benthic groups [1,2]. However, fish grazing effects on coral reefs depend on the species' functional traits (i.e., size, feeding mode) and their biomass [3,4]. In herbivorous fish, size is related to effective grazing: larger herbivores are more efficient at macroalgae control than smaller individuals, which require an increased number of bites to remove the same amounts of algae [5,6]. Furthermore, herbivore fish biomass is often related to the functionality and maintenance of the ecological state and its recovery through positive feedback [7,8].

The structure and composition of herbivorous reef fish assemblages, including their traits, are shaped by direct influences such as the intensity of fishing pressure [2,9]. Additionally, physicochemical alterations in their habitats, such as changes in water temperature, salinity, and nutrient availability, often resulting from broader environmental shifts like climate change, indirectly affect these assemblages by modifying habitat characteristics [10]. The impact on the habitat of coral reefs can be particularly pronounced during intense environmental events such as the El Niño–Southern Oscillation (ENSO) [11] with thermal positive and negative anomalies, which exacerbates stresses on corals and can lead to shifts from habitats dominated by coral reefs to alternate states dominated by other benthic components such as fleshy macroalgae [12]. This pressure can selectively impact fish assemblages and can lead to a decline in those species that play critical roles within the reef ecosystem [13,14]. The loss of species with specific functional traits that are vital to the ecosystem can precipitate a cascade effect potentially compromising the maintenance of coral reef ecosystems [7].

Herbivory has been considered a critical function in coral reefs that, in combination with a high diversity of corals and associated organisms, can provide the ecosystem with the ability to cope with disturbance (resistance) or to recover from disturbances (resilience) [2,15]. While herbivory is crucial for coral reef resistance and resilience, the survival of these ecosystems often hinges more on natural factors like storms and temperature fluctuations, which can be exacerbated by human-induced changes such as global warming and eutrophication [16–18]. Particularly in lower-latitude reefs, often referred to as marginal reefs, these ecosystems are exposed to environmental conditions that inhibit optimal coral reef development and exhibit a diminished abundance of herbivores [19,20].

Coral reef ecosystems have suffered extensive loss of live coral cover, and most are currently in critical condition or threatened [21,22]. The degradation of coral reef ecosystems can compromise vital ecosystem services, such as fisheries and coastal protection, which are integral to human well-being. The loss of these services can lead to economic hardships, increased vulnerability to natural disasters, and a decline in the cultural and recreational benefits that contribute to the social and mental well-being of coastal populations [23]. Therefore, it is imperative to comprehend the drivers and functional roles of species within these processes, such as herbivory, which are pivotal for reef ecosystem maintenance [24,25]. While herbivorous interactions and their ecological impacts have been well-documented in the Indo-Pacific and Caribbean coral reefs [2,26,27], such studies remain limited within the Mexican tropical Pacific (MTP). Thus, studying coral ecosystems and their ecological processes becomes critical, particularly due to the characteristics of MTP coral communities that experience greater environmental variability and typically exhibit lower reef fish diversity [28–30].

MTP coral communities are found over rocky structures with patches of coral from the genera *Pocillopora*, *Porites*, and *Pavona* [31]. They experience ocean–atmosphere transitional characteristics and ENSO, which are not as suitable for coral reef development as more stable, tropical marine conditions [30]. Fishing in the area is a widespread activity even observed within the reserve's non-fishing areas [32–34]. Additionally, MTP herbivorous fish assemblages have lower diversity, and the abundance of herbivorous fish with specific traits, e.g., larger scraper fish or excavating herbivorous fish, such as those from the genus *Scarus*, [3] which are characterized by traits such as farming strategies and restricted mobility range, including damselfish (i.e., fish from the genus *Stegastes*), that do not effectively remove algae limits the effective algae removal [3,35].

Although herbivory is often related to the maintenance or recovery of coral reef ecosystems, the unique oceanographic and habitat characteristics of the Mexican tropical Pacific (MTP), combined with the relatively low diversity of herbivorous reef fish, could limit herbivory's effectiveness to such an extent that herbivory alone may be insufficient to address ecosystem challenges [36]. Therefore, in this work, the main goal was to evaluate, under a functional trait approach, whether herbivorous reef fish assemblages of the MTP shape the habitat's benthic components or if physicochemical characteristics dominate habitat variability. We aim to (1) analyze temporal and island comparison changes in herbivorous fish composition and structure; (2) evaluate if herbivorous fish assemblage composition is significantly related to habitat or if physicochemical variables define habitat variability; and (3) identify, with ordination methods, the traits of herbivorous fish assemblage composition that are related to habitat variability. Assessments across the Cleofas and Marietas marine protected areas, along with temporal analyses within Marietas over successive years and hydroclimatic periods, were conducted. The objective was to discern whether the interrelationships among herbivorous fish assemblages, habitat benthic components, and physicochemical parameters are sustained within the coral communities of the Mexican tropical Pacific.

Through a functional trait approach, this work aims to assess the ecological characteristics of herbivorous reef fish assemblages. The application of functional trait analyses is emerging as an insightful method for unraveling the complex influence of environmental variables on reef assemblages [37–39], shedding light on their role in ecosystem dynamics and services [40,41]. These can be approached through various quantitative tools, including functional metrics [42], functional diversity indices [39,43,44], and multi-dimensional ordination techniques [45–48]. This approach underscores the unique aspects of our study, adding to the growing body of studies on functional traits and their implications for ecosystem management and conservation in the MTP.

2. Materials and Methods

2.1. Study Area

Two insular coral ecosystems in the MTP were assessed: Islas Marietas National Park and Isla María Cleofas of Islas Marias Biosphere Reserve (Figure 1). The circulation and water masses' dynamics characterize the MTP area as possessing two hydroclimatic periods: cold (approximately January–May) and warm (approximately July–November), with their associated seasonal transitions [49]. These insular systems are also influenced by thermal anomalies and other variables derived from ENSO events [50].

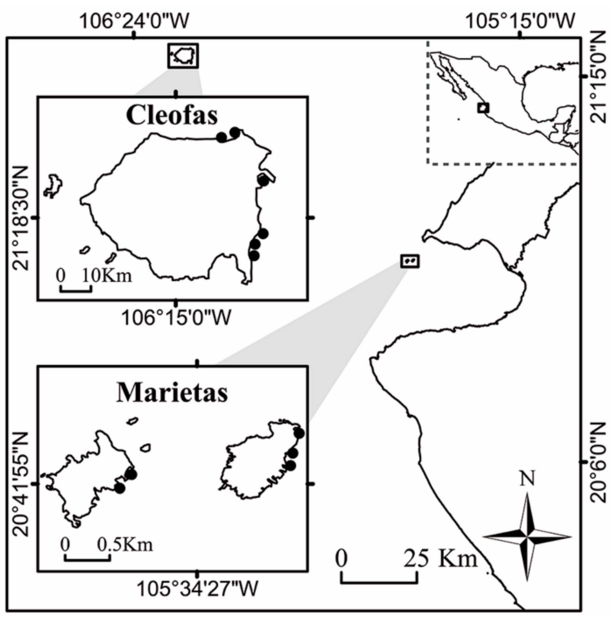


Figure 1. Study area and survey sites. Monitoring sites (black dots) of the insular systems in Mexican Tropical Pacific Isla María Cleofas part of the Islas Marías Biosphere Reserve, Islas Marietas National Park.

Although both insular systems are exposed to the ocean–atmosphere interactions previously mentioned, they have specific environmental conditions and differ in their habitat characteristics (Table S1) and history of management strategies. Islas Marietas, hereafter referred as Marietas, has been protected since 2005 and has experienced increased tourism activities in the last 10 years, mainly on "Playa del Amor", a site included within the MPA monitoring and subject to reinforced restrictions by the authorities since 2017. Marietas' closeness to the mainland (~4 km offshore) has allowed daily surveillance over the past years [33]. In comparison, Isla María Cleofas, hereafter referred to as Cleofas, forms part of the Biosphere Reserve Islas Marías, which has been a protected area since 2000 [34]. Located approximately 54 km off the mainland, this reserve was under the jurisdiction of a Mexican Federal Penitentiary until 2019, with the Mexican Navy ensuring its protection. Given these conditions, the capacity for ongoing monitoring efforts in Cleofas is limited compared to the more accessible Marietas National Park, where consistent studies have been conducted for more than a decade. During the study period, the intense ENSO event of 2015–2016 impacted the insular complexes, resulting in a decrease in live coral cover from previously recorded levels. Recovery in coral cover was observed in Marietas, while Cleofas experienced an increase in macroalgae cover instead [51,52].

2.2. Data

Biological data were obtained through the monitoring of the insular systems with underwater visual censuses. Temporal variability in Marietas was represented by data from 12 surveys conducted through six years (2013–2018), including the cold (April/May) and warm (September/October) hydroclimatic periods. Insular system comparison (between Marietas and Cleofas) was represented by data from six surveys carried out solely in the cold period (April) of three years (2016–2018). Comparisons between Marietas and Cleofas were limited to the cold period due to the lack of data from Cleofas for other periods. Surveys consisted of underwater visual censuses in six fixed sites per island (Figure 1). Within sites, five semi-fixed belt transects (visual census of 25 m length and 4 m wide, 100 m^2) were placed parallel to the coast to record data concerning herbivorous fish and habitat variables (benthic components). Each belt transect was considered as a replicate. Our semi-fixed transect method involves establishing transects at consistent locations while avoiding the use of permanent markers to minimize site disturbance by visitors. The underwater visual censuses through transects used across numerous reef sites are crucial for characterizing a range of ecological groups, including fish, benthic organisms, and echinoderms [52–54]. Distance between the transects within each site was, on average, 8 m with recorded depths between 3 and 13 m. The sites and transects were selected to represent the island's heterogeneity in marine habitat benthic components and have been part of the monitoring from the MPAs. Data for physicochemical variables were obtained from NOAA repositories (described in more detail below and in Table S2).

2.2.1. Herbivorous Fish Species and Traits

The reef fish considered in our study were those that consume either some or solely algae in coral ecosystems. We included 13 species from four families: Acanthuridae, Kyphosidae, Pomacentridae, and Scaridae (Figure S1). The selected functional traits mainly aimed to represent different functions of reef fish (i.e., mobility, nutrient budget, and defense against predation). We particularly focused on those traits that allow us to discriminate between feeding strategies among herbivores, focusing on food acquisition. We selected seven ecological traits: size, aggregation type, mobility, feeding mode, position in the water column, trophic level, and consumption/biomass ratio (Q/B) (Table S3). Feeding mode, position in the water column, aggregation type, and size have been used in ecological studies of herbivorous reef fish (i.e., [55,56]). Additionally, we used the combination of trophic level and Q/B consumption as a proxy of grazing rate or feeding rates. Q/B ratio is a population-based food consumption estimate that considers the amount of food ingested (Q) by a population relative to its biomass (B) [57]. The traits' information was obtained from multiple sources, including our own data, web search, field experience, and the scientific literature (detailed information on Table S3).

2.2.2. Habitat Benthic Components

To characterize the habitat's benthic components, we selected four benthic components involved in the relationship between herbivorous fish assemblages and physicochemical variables: fleshy macroalgae, turf algae, branching coral, and submassive coral cover. The percentage of coverages were visually recorded in the field with six quadrants (1 m^2) per transect that were placed every 5 m along each 25 m belt transect. Each 1 m^2 frame was subdivided into 100 smaller quadrants (10 cm^2 each) to facilitate the visual estimation of benthic component coverage [52,53].

2.2.3. Physicochemical Variables

Five physicochemical variables that commonly drive habitat benthic components (primarily live coral cover) were selected [48–53]. The physicochemical variables were sea surface temperature (SST), multivariate ENSO index (MEI), degree heating weeks (DHWs), photosynthetically available radiation (PAR), diffuse attenuation coefficient (Kd490), and chlorophyll a (Chl a) (Table S2). Values were obtained from 14 day or monthly composite databases available from the data server of Environmental Research Division's Data Access Program (ERDAAP) (SST, DHW, PAR, Kd490, and Chl a) and monthly MEI values from NOAA-ESRL (details in Table S2).

2.3. Statistical Analyses

2.3.1. Differences between Insular Systems and Temporal Variability of Herbivorous Reef Fish

Two permutational multivariate analyses of variance (PERMANOVAs) were performed on the herbivorous fish assemblage composition and abundance to detect differences in the assemblage structure with transects considered as a replicate. The first model was designed to compare only the variation between Marietas and Cleofas. The second model had a two-way crossed factors (year $\times$ period) temporal design exclusive to Marietas, with two fixed factors: years (six: 2013–2018) and hydroclimatic periods (two: cold and warm). PERMANOVAs were performed based on a Bray–Curtis similarity matrix and data with previous fourth-root transformation. Statistical significance was tested using a sum of squares type III and 10,000 permutations of residuals under a reduced model for the first design and unrestricted permutations of raw data for the second design. The test of homogeneity of dispersions (PERMDISP) was used for assessing the multivariate dispersion among the levels of the terms of the mentioned experimental designs. A similarity percentage analysis (SIMPER) was used to estimate species contributions to average dissimilarities among each factor's levels. Non-metric multidimensional scaling (NMDS) was carried out to visualize the multivariate dispersions of the models.

PERMDISP, SIMPER, and NMDS analyses were conducted with the same resemblance coefficient and data pre-treatment as PERMANOVA. The PERMANOVA, PERMDISP, SIMPER, and NMDS analyses were performed in PRIMER+PERMANOVA [58].

2.3.2. Link between Herbivorous Fish–Habitat–Physicochemical Variables

For the two models described above (between insular systems and temporal), we applied two ordination methods as an extension of co-inertia analyses; here, the transects were aggregated into the level analyzed (between insular systems: insular system/year; temporal: hydroclimatic period/year;). First, we aimed to explore if the combination of herbivorous fish was correlated with habitat or if physicochemical variables were linked to habitat variability. For this objective, we used multiple factor analysis (MFA) [59] to identify an initial link among three subsets of variables (herbivorous fish, habitat benthic components, and physicochemical). Although it is not commonly used in ecological studies, multiple authors have demonstrated MFA's high potential, stemming from its capacity to simultaneously link subsets of variables [60,61]. We used only quantitative data; thus, in our case, MFA is mainly a principal component analysis for all sets of variables that weight each subset. We performed MFA with Hellinger-transformed fish abundance data. The correlation between each subset of variables was represented by the RV coefficient [62] and tested with 10,000 permutations [63]. To visualize MFA results, the correlation circles of the significant subsets with the quality of each variable's contribution (cos2) to the two first dimensions were plotted.

2.3.3. Relationship between Herbivorous Reef Fish Traits and Habitat

We then used RLQ analysis to identify the herbivorous fish traits that were associated with the benthic components. RLQ analysis allowed the simultaneous analysis of species abundance, species traits, and habitat benthic components [45,46,64]. This method includes three matrices: the L table of species × samples (abundance of species at each island or period/year), the Q table of species × traits (trait values for each herbivorous fish species), and the R table of environment × samples (habitat for each factor). The analysis links the three matrices based on R and Q tables' ordination method in a correspondence analysis of the L table. Due to our variables' nature (mixed qualitative and quantitative), the R and Q tables were analyzed with Hill–Smith principal component analysis [65]. We used the approach described in [47], which combines RLQ analysis and the fourth corner method to evaluate the response of traits to variables. For the fourth corner analysis, we used the statistic D2, which selects the significant association and provides a correlation coefficient indicating the strength of association based on 50,000 permutations. Both methods consider the fourth-corner matrix, which is a combination of the three tables (R, L, and Q) used to describe the relationship and environment association. MFA, RLQ, and fourth corner analysis were performed with the ade4 package in R [64,66].

3. Results

3.1. Island Comparison (Marietas vs. Cleofas)

From the surveys through 2016–2018, we registered 6762 individuals (Marietas = 3538 and Cleofas = 3224) from 13 species (Marietas = 9, Cleofas = 13). The herbivorous fish assemblage significantly varied in composition and abundance (dispersion) between the insular systems (Table 1), which can be observed in the NMDS output (Figure S1).

Table 1. PERMANOVAs and PERMDISP results of the temporal (Marietas) and island comparisons (Cleofas vs. Marietas) variation in herbivorous fish assemblage composition in insular systems from the Mexican tropical Pacific. Codes: CV is the coefficient of variation. Bold numbers correspond to $p \leq 0.05$.

PERMANOVA Overall Test Source	Pseudo-F	pPerm	CV (%)	PERMDISP Test F	pPerm
Insular systems - df					
Island (Is) - 1	100.880	**<0.001**	52.601	24.789	**<0.001**
Residual - 178			47.399		
Temporal differences - df					
Year (Yr) - 5	2.459	**0.009**	2.264	0.500	0.819
Period (Pr) - 1	8.020	**0.001**	3.632	1.030	0.329
Yr × Pr - 5	1.316	0.228	0.981	0.643	0.877
Residual – 348			93.124		

		Pairwise among years (pPerm)					
		2013	2014	2015	2016	2017	2018
Pairwise among years (t)	2013		0.114	0.220	0.344	**0.008**	**0.007**
	2014	1.44		0.167	0.466	**0.019**	**0.029**
	2015	1.24	1.35		0.460	0.115	0.241
	2016	1.04	0.90	0.90		0.063	0.099
	2017	2.17	1.99	1.51	1.70		0.130
	2018	2.32	1.94	1.22	1.54	1.49	

The species responsible for these differences were the family Acanthuridae: *Acanthurus nigricans*, *A. troistegus*, and *A. xanthopterus*, mostly present in Cleofas. Notably, *Scarus rubroviolaceus* was absent in Marietas (Figure 2a).

The MFA that explored the correlation between the three groups of variables shows that habitat benthic components are strongly linked to herbivorous fish assemblage composition (RV = 0.850, $p = 0.019$), which, in turn, is delimited by physicochemical variables (RV = 0.683, $p = 0.043$; Figure 3a). However, we found no correlation between the herbivorous fish assemblages' composition and physicochemical variables (RV = 0.643, p= 0.067). The first two axes in the island comparison MFA represent 83.8% of the variation, whereby the most abundant species in Cleofas, such as *A. xanthopterus* and *S. rubroviolaceus*, are positively correlated with macroalgae that, in turn, are related to SST (Figure 3a). Conversely, branching coral and submassive coral cover are negatively correlated with SST and positively with Chl a, Kd490, and PAR (Figure 3a).

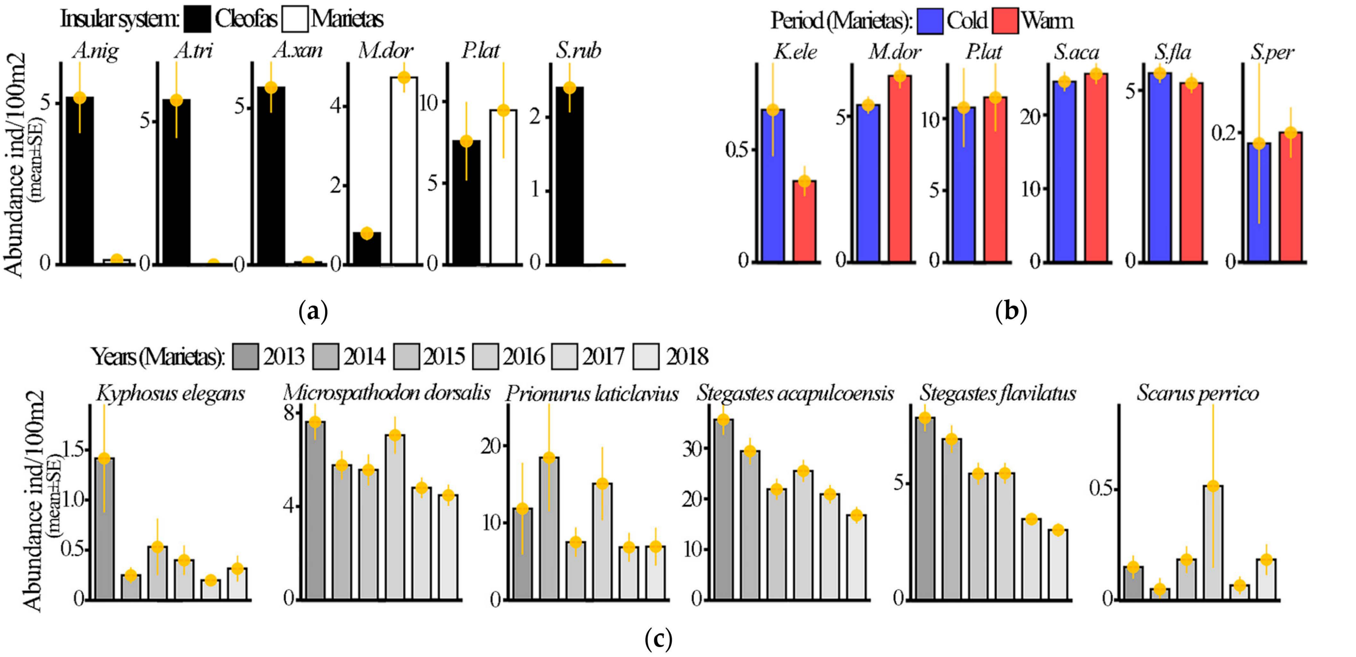


Figure 2. Average abundances (±SE) of herbivorous fish per transect (ind/100 m^2) responsible for the dissimilarity between (**a**) insular systems (Cleofas and Marietas), (**b**) hydroclimatic periods (cold and warm), and (**c**) years (2013–2018). Species from the families: Acanthuridae (*Acanthurus triostegus*, *A. xanthopterus*, *A. nigricans*, *Prionurus laticlavius*), Kyphosidae (*Kyphosus elegans*, *K. vaigiensis*), Pomacentridae (*Microspathodon dorsalis*, *Stegastes acapulcoensis*, *S. flavilatus*), and Scaridae (*Nicholsina denticulata*, *Scarus ghobban*, *S. perrico*, *S. rubroviolaceus*).

The insular system comparison RLQ analysis summarizes the main relationships between species composition and their traits. The first axis (RLQ1) explains 96.7% of the co-variance among the three tables. The global test indicates an association between herbivorous fish assemblage composition and habitat benthic components (model 4; p = 0.010), with no association between a specific trait and the components of the habitat (model 2; p = 0.060), except for the position in the water column and branching corals (Figure 4a).

RLQ results highlight the island differences observed in the previous analyses: Marietas was characterized by *Microspathodon dorsalis*, *Stegastes acapulcoensis*, and *Stegastes flavilatus*, herbivorous fish species with short-range mobility and a low trophic level, generally solitary and found on the bottom, with their prevalence, thus, generally related to turf, branching coral, and submassive coral (Figure 4a). Despite the absence of larger herbivorous fish and with the composition almost defined by small farming herbivorous fish, the mean percentage of macroalgae in Marietas was less than 1% (Figure 5a). On the other hand, Cleofas herbivorous fish assemblage was characterized by two groups: the first, *Kyphosus elegans*, *Acanthurus xanthopterus*, and *A. triostegus*, all have substantial mobility, larger size, and prefer the upper water column, while the second, *Prionurus laticlavius*, is usually observed in large schools (Figure 4a). All of these species' presence was associated with the high macroalgae coverage present in Cleofas from up to 24% in 2017. The fourth-corner analysis shows that the only significant trait is the water column position in the first axis, which is positively related to macroalgae and negatively to branching coral

(Figures 4a and 5a). In combination, the RLQ and fourth-corner results with the habitat benthic components and herbivorous fish assemblages' composition suggest that the high values of macroalgae and low coral cover in Cleofas define the presence of these mobile species, contrary to those found primarily in Marietas, with low values of macroalgae (Figures 4a and 5a; Table S1).

The spatial RLQ analysis summarizes the main relationships between species composition and their traits; the first axis (RLQ1) explains 96.7% of the co-variance among the three tables. The global test indicates an association between herbivorous fish assemblage composition and habitat benthic components (model 4; p = 0.010), with no association between a specific trait and the components of the habitat (model 2; p = 0.060) except for the position in the water column and branching corals (Figure 4a).

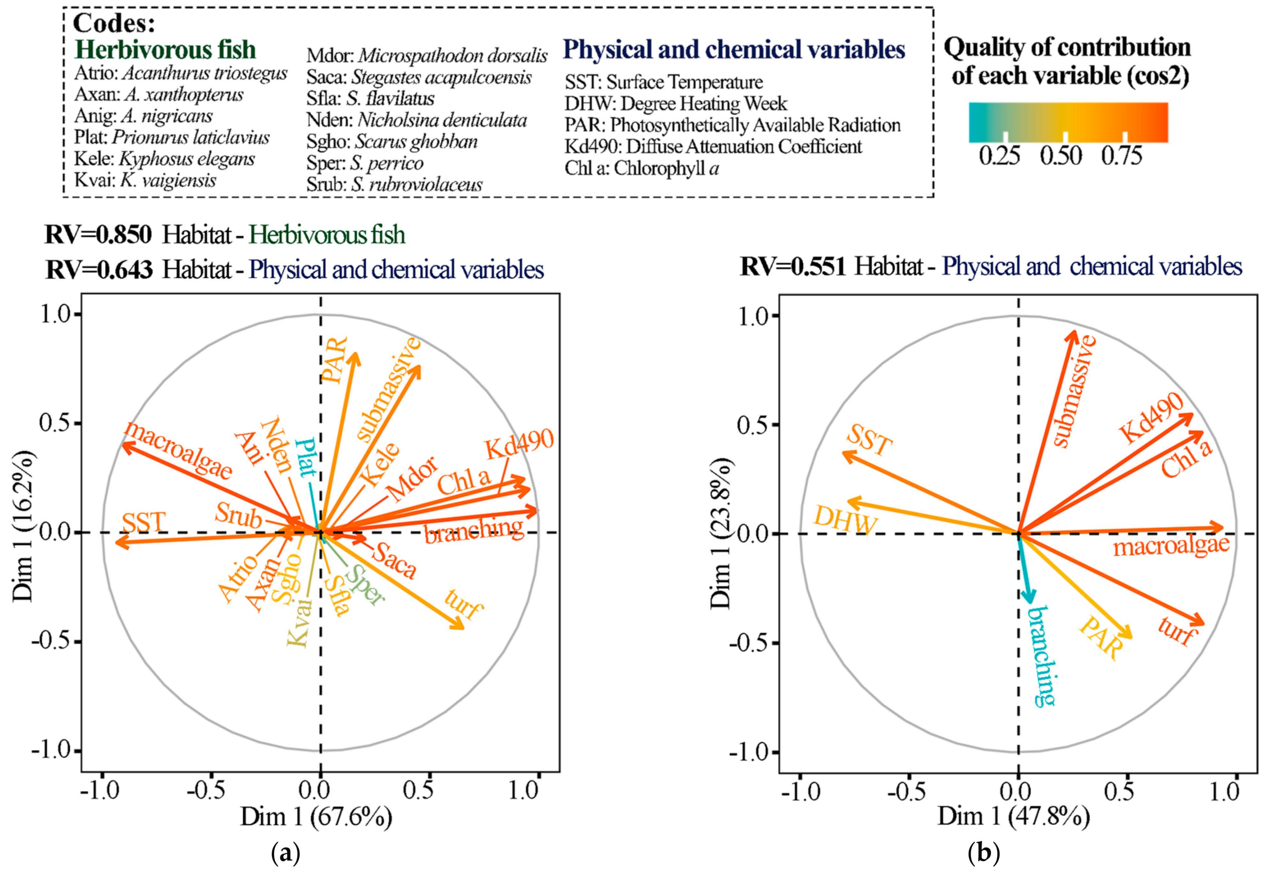
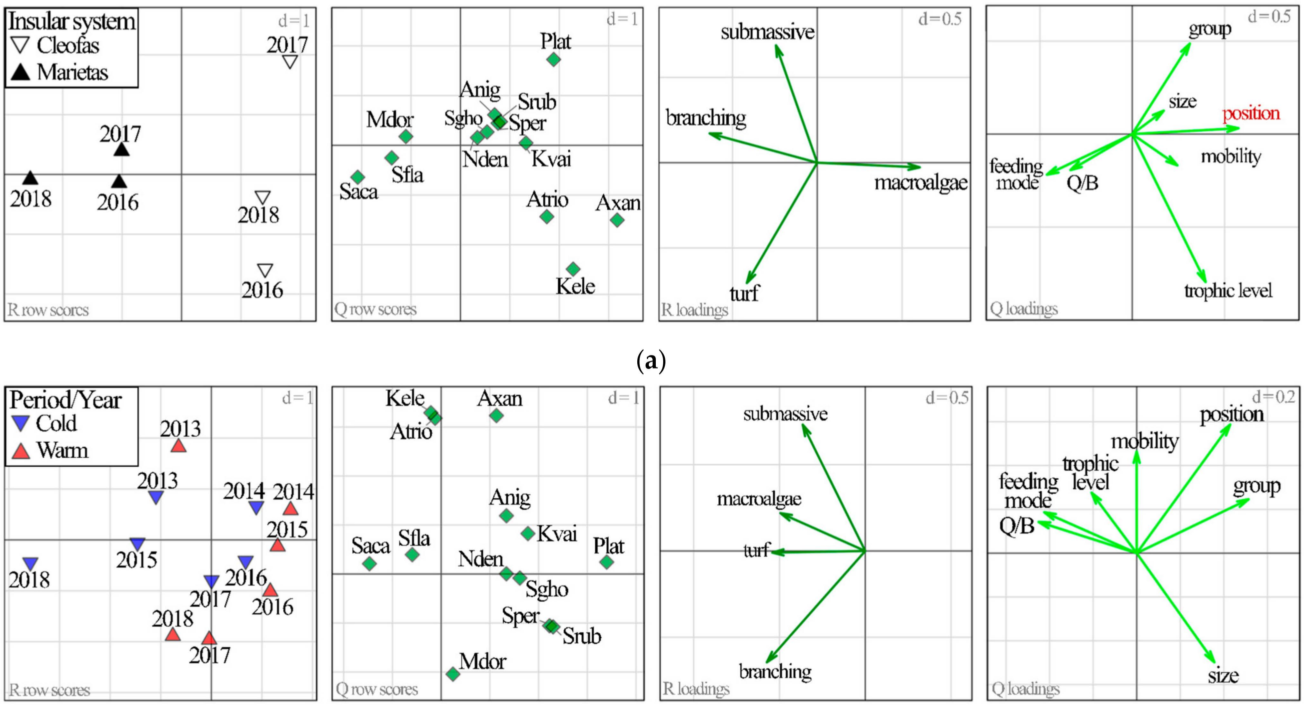


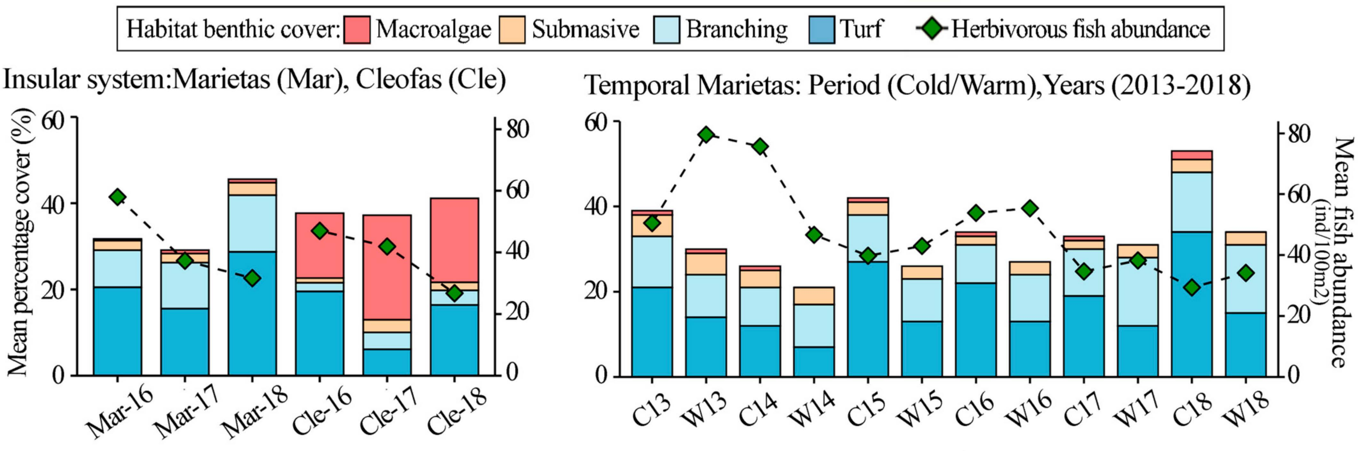
Figure 3. Two first axes of the MFA of the correlation circle with the group of variables with significant correlation in the multiple factor analysis (MFA) from the (**a**) insular system comparison: Marietas vs. Cleofas, demonstrating a significant link between herbivorous fish assemblages, habitat, and physicochemical variables and (**b**) temporal: Marietas 2013–2018, demonstrating a significant link between habitat and physicochemical factors. The color of the variables indicates the quality of contribution (cos2) of each variable to the insular system comparison and temporal model. A detailed list of variables is described in Table S2.



(**a**)

(**b**)

Figure 4. RLQ and fourth-corner analysis results of herbivorous fish assemblage abundances (L), traits (Q), and habitat benthic components (R) on insular systems from the Mexican tropical Pacific. (**a**) Insular systems RLQ plots from Marietas and Cleofas throughout 2016–2018 in the cold period and (**b**) temporal RLQ plots with from the two hydroclimatic periods throughout the five-year survey (2013–2016). Bold red trait indicates traits with significative relationship on the first axis according to fourth-corner analysis ($p < 0.05$) with 50,000 permutations. Herbivorous fish codes in Figure 3 and Table S2.



(**a**) (**b**)

Figure 5. Bar plot of the mean cover of habitat benthic components (submassive coral, branching coral, macroalgae, and turf) and mean abundance of herbivorous reef fish species from coral communities from the Mexican tropical Pacific. (**a**) Insular system comparison values from Marietas (Mar) and Cleofas (Cle) throughout the years 2016–2018; (**b**) temporal values from Marietas Island from 2013 to 2018 in cold (C) and warm (W) periods.

3.2. Temporal Analyses

We registered a total of 17,431 individuals and 13 species of herbivorous fish from the six-year surveys in Marietas. Significant temporal differences in herbivorous fish assemblage composition were recorded; however, these yearly and seasonal differences partially explained the fish assemblage temporal variability (Table 1). Throughout the six-year survey, the composition was significantly different between years; with the fish assemblage in 2017 and 2018 dissimilar to the fish assemblage observed in 2013 and 2014 (Table 1). The species with the highest contribution to these dissimilarities were *K. elegans, M. dorsalis*, *P. laticlavius*, *S. acapulcoensis*, *S. flavilatus*, and *Scarus perrico* (Figure 2c; Table S4). All species decreased in abundance throughout the years except for *S. perrico*, with maximum abundance observed in 2016 (Figure 2c).

Seasonally, the herbivorous fish assemblage in Marietas also significantly differ in composition and abundance (Table 1). The species that contributed most to the dissimilarity were also those found to contribute strongly to yearly differences, with some species increasing in abundance during the warm period (*M. dorsalis, P. laticlavius*, and *S. perrico*) while others (*K. elegans*, *S. acapulcoensis*, and *S. flavilatus*) decreased (Figure 2b). The temporal MFA analysis in Marietas shows that herbivore abundance is not linked to habitat (RV = 0.306, p = 0.191) or physicochemical variables (RV = 0.103, p = 0.879). However, the physicochemical variables group is significantly linked to habitat (Figure 3b; RV = 0.551, p = 0.003). In the analysis, we only selected the physicochemical and habitat variables subsets, as the first two axes explained 71.6% of the variance (Figure 3b). The correlation circle shows that habitat benthic components are positively correlated to physicochemical variables related to water quality, Chl a (proxy of nutrients), Kd490 (a proxy of turbidity), and PAR (a proxy of solar radiation related to photosynthetic activity), especially the turf and macroalgae. However, the habitat benthic components branching coral and turf algae are also negatively correlated with SST and DHW, related to hydroclimatic periods (cold/warm) and ENSO events (Figure 3b).

The temporal RLQ analysis shows the main relationships between species and their traits and physicochemical variables; the first axis (RLQ1) explains 96.54% of the co-variance among the three tables (Figure 4b). However, the RLQ global test reveals no association between herbivorous fish assemblage and habitat (model 2; p= 0.236) or between individual traits and habitat (model 4; p= 0.086). Interestingly, despite the "El Niño" 2015–16 events, the mean macroalgae cover was low throughout the years and periods and was characterized by higher turf and branching coral in the five years surveyed (Figure 5b). Our results from the temporal RLQ and MFA in Marietas suggest that beyond the herbivorous fish assemblage (mostly formed by smaller farming species), other variables define habitat variability in Marietas (Figures 3b, 4b and 5b).

4. Discussion

Studies of reef fish in the MTP have usually focused on the evaluation of fish assemblages, functional diversity, and their relationship with habitat [28,67–70]. However, it remains less understood how herbivorous fish assemblages and their habitat interact and how these reef fish assemblages maintain their functions, processes, and services in the face of pronounced spatial and temporal variability. This is particularly critical in light of recent coral bleaching events and the recurrent ENSO thermal anomalies that impact the region [23,71].

MTP reefs share similarities with high-latitude marginal reefs that have limiting conditions for coral development and low herbivorous fish diversity [20,72]. This research employs a functional trait framework to investigate the roles of herbivorous reef fish across the MTP's marine protected areas (MPAs). Despite their geographic closeness, evidenced by less than a one-degree latitudinal separation, the study reveals markedly distinct herbivory patterns (Figure 1).

Specifically, in Marietas, we found that temporally, herbivorous reef fish assemblage was not related to the habitat benthic components, instead, it was explained by physicochemical variables that promote seasonal and interannual variability of the benthic components. This could evidence bottom–up processes. This has been observed in the Caribbean, with phase shifts that are not driven by the herbivorous fish composition [19]. This notion is supported by other studies that documented both top–down and bottom–up effects of herbivorous reef fish [73]. Further experimental and controlled analyses are required to delineate the interactions of herbivorous fish species and traits with benthic components in MTP coral communities [74,75].

Moreover, the composition of the herbivorous fish assemblage in Marietas was mostly dominated by farmer species, which, in some cases, under the absence of large foraging herbivores, shape the benthic components, mainly through succession [76]. Some damselfish species select specific areas for their territories and engage in behaviors that cultivate these spaces, thus, directing the successional trajectory of the benthic community. These territorial strategies can result in significant alterations to the composition and abundance of benthic species within their territories, emphasizing the critical role of farmer species in the succession process [77,78]. The predominance of small herbivorous fish in Marietas decreased through the study period, and in the absence of larger fish, such species can play a critical emergent role in controlling macroalgae composition [79]. The temporal decline observed in damselfish recorded in our results for Marietas may have multiple explanations, including predators feeding on these species in the early stages and enhanced territorial activity [80,81]. Habitat loss is among the most common drivers of site-attached species prevalence, as in the case of herbivorous fish species observed in Marietas on our study [79,80]. In Marietas, combined with the evidence of thermal resistance [82], successful sexual reproduction and recruitment of corals [83,84], as well as the recovery after disturbance events [52], could promote the persistence of habitat for reef fish, however, other drivers could compromise these characteristics.

Due to the predominance and decline of damselfish, further analyses in Marietas need to evaluate this herbivorous fish assemblage considering the physiological response and trophic interactions of damselfish to disentangle their ecological role in these coral ecosystems [9,85].

Additionally, Marieta's habitat benthic components did not change even after acute disturbance events that could have modified them, particularly the benthic components of a rapid life cycle, such as that of macroalgae. These components can reach their maximum cover within months, leading to the creation of exclusive feeding areas for herbivorous fish assemblages [72] and a lack of space to recruit other benthic groups. Studies show that once the habitat is permanently modified, changes are observed in the associated organisms of this ecosystem, and the effect on them depends on the relation of their traits to the habitat or environment [13]. These changes mostly influence resident species with small mobility ranges and are related to the coral reef habitat, compromising their functions in sites such as Marietas, predominated by small resident herbivores [9]. Nonetheless, corals in the area have revealed resistance to natural stressors [82] and recovered after a brief decrease in live coral cover following ENSO events [52]. However, it remains uncertain how the ecosystem will react if it crosses certain environmental thresholds. This could lead to an increase in macroalgae due to continuous favorable conditions for growth and the lack of larger herbivores, which are typically more effective at algae removal than smaller herbivores or farming species [35,86].

In contrast, island comparison analyses highlight another dynamic within herbivory from an MTP island: the composition of herbivorous fish is related to the habitat benthic components, and, more specifically, to the cover of macroalgae and branching coral. Marietas was characterized by small farming herbivores and Cleofas by large herbivores. Marietas currently harbors a greater live coral cover (13%) and far smaller macroalgae cover, despite the previous decrease in live coral cover from 2010. In contrast, Cleofas currently has less than 1% live coral cover, while previous surveys in 2005 registered up to 49% [51]. In the three years surveyed (2015–2018), live coral cover decreased to ~5% compared to the average macroalgae cover of ~20% which was negatively related to SST and macroalgae benthic cover (this study). Coral ecosystem transitioning from coral to macroalgae dominance, as seen in our study, may change over a few months to several years, often influenced by factors like herbivore populations and disturbance severity [87]. Models indicate that in low (~5%) live coral cover ecosystems, reversing coral–algae shifts would require a significant increase in herbivorous fish [88]; thus, sites with a low abundance of herbivorous fish could remain fragile under these changes. Additionally, it would be necessary to eliminate the stressor and implement management strategies [89].

When considering herbivorous fish traits, we found that position in the water column was positively related to macroalgae and negatively related to live coral, suggesting that mobile herbivorous species could be moving from adjacent coral communities (i.e., larger islands from the Islas Marias Biosphere Reserve) to areas with greater food availability [90,91]. Herbivorous fish displacement ranges vary among species, and even with traits like large schooling aggregations improving displacement, overfishing on these schools can potentially compromise their range [92]. Some parrotfish schools can have an extensive potential home range (~24 km), although individual roving may be limited to less than 1 km (~200 m); thus, schooling can enhance range and even feeding rates [90]. In contrast, the herbivorous fish assemblage in Marietas was mostly defined by farmer damselfish, which are considered an ecosystem engineer species [78,93] that modify habitat through their feeding and territorial behavior but the large mobile herbivores that could be most effective in removing algae [6,94] were rare or absent. A trait-based analytical approach has been instrumental in detecting changes within herbivorous fish assemblages across coral ecosystems. Such methods have provided valuable insights in both tropical and temperate reef systems [56,95]. Additionally, investigating other fish traits, especially those related to nutrient cycling, could enhance our comprehension of the ecological functions of reef fish and the dynamics of coral reefs [96,97].

Overall, we found two scenarios in the insular MTP systems studied. Cleofas had higher macroalgae cover, providing feeding areas for the larger mobile herbivorous species, while Marietas had lower macroalgae cover and primarily small farmer herbivorous species. Marietas had few large herbivorous fish, even in the five-year survey. These changes in assembly structure could be due to a combination of multiple factors, including fishing pressure among these mobile herbivores or low food availability for Marietas [98]. Fishing and habitat loss have been established as drivers of fish assemblages [99,100] and, since they often impact fish with specific traits (i.e., larger piscivorous in fishing and herbivorous fish in habitat changes), they could further compromise the ecosystem functioning.

Although our study delineates two distinct scenarios, it is critical to conduct further research, especially for Cleofas. In particular, due to the increased abundance in herbivorous fish on Cleofas following coral cover reduction, physicochemical variables produced by "El Niño" (2015–16) indirectly shaped herbivorous fish composition through habitat changes [51,52]. The combination of recent benthic habitat changes in habitat benthic components and the diminished surveillance of illegal activities around the island (i.e., illegal fishing [32]) due to the changes of management and continued surveillance by federal authorities, constitutes a concern within the reserve. Thus, it is imperative to conduct additional analyses to understand the variations between the insular systems throughout the different hydroclimatic periods. Our current findings are specific to the patterns observed in Cleofas during the colder season. Despite these constraints, the contrast between Marietas and Cleofas during this period is apparent. This study lays the groundwork for future research that should investigate the full spectrum of hydroclimatic conditions to capture a more comprehensive picture of the ecological dynamics [49].

The role of fish assemblages in the maintenance of coral communities also depends on the array of species and their traits, which, once compromised, can negatively modify the ecosystem processes and services that they provide [23]. It is essential to understand the role that herbivory will have within coral ecosystems, particularly the influence of damselfish in Marietas and parrotfish in Cleofas. Therefore, experimental and observational studies are needed to clarify the complex herbivory dynamics in reef systems [101,102].

In summary, our investigation into temporal changes and inter-island differences, as well as the correlation between assemblage composition and habitat characteristics, has yielded new findings. We reveal two unique herbivory patterns, underscoring the urgent need for further study into the effects of fishing practices and habitat alterations on these assemblages. Our findings highlight the critical need for comprehensive assessments on these processes and functions to fully grasp and safeguard the intricate dynamics of coral ecosystems in the Mexican tropical Pacific, particularly under the current stressors due to climate change [73,96,102].

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/oceans5010002/s1, Figure S1: Nonmetric multidimensional scaling (NMDS) of herbivorous fish assembly in the insular systems (Marietas and Cleofas) in the Mexican tropical Pacific. Circles represent transects from the sites through time (2016–2018); Table S1: Average recorded values of the subsets of explanatory variables: habitat (branching coral, submassive coral, macroalgae, and turf) and physicochemical (temperature, MEI, DHW, Chl a, Kd490, and PAR) for Cleofas and Marietas; Table S2: Description of the physicochemical variables used for the multiple factor analysis (MFA) [75,103–106]; Table S3: Details of the herbivorous species functional traits used to differentiate between functions based on different feeding strategies amongst herbivorous reef fish from Natural Protected islands in Mexican Tropical Pacific [107–110]; Table S4: Temporal and island comparison SIMPER analysis summary. Total percentage of dissimilarity between pairs (in parenthesis) and percentage of contribution to the dissimilarity between levels per herbivorous fish in insular systems in the Mexican tropical Pacific. Blank spaces represent that in that between the pairs, the species did not contribute to the total percentage dissimilarity fish from natural protected insular systems in Mexican tropical Pacific.

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