

Article

Taxonomic Diversity, Community Structure, and Ecological Recovery of Soft-Bottom Fish Assemblages in La Paz Lagoon (Gulf of California, Mexico)

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Abstract

La Paz Lagoon is a semi-enclosed coastal ecosystem in the southwestern Gulf of California that was historically affected by wastewater discharges and other anthropogenic disturbances. This study evaluated the taxonomic diversity and community structure of soft-bottom fish assemblages across two climatic periods (Neutral, 2016–2017, and La Niña, 2022–2023) using alpha (α), beta (β), and gamma (γ) diversity metrics together with taxonomic distinctness indices (Δ , Δ^* , $\Delta+$, and $\Delta+$). Six bimonthly surveys were conducted during each climatic period at seven sampling stations. A total of 93 fish species, representing 65 genera, 33 families, and 17 orders, were recorded across the two climatic periods. Species richness exhibited marked temporal variation, reaching its highest value in April and its lowest value in March. Periods of reduced richness were associated with increased species turnover among stations. Taxonomic distinctness indices remained within the expected confidence limits, indicating a stable taxonomic structure despite historical anthropogenic impacts. Dominant species included *Paralabrax maculatofasciatus*, *Diapterus brevirostris*, *Eucinostomus gracilis*, *Urobatis halleri*, and *Synodus scituliceps*. Overall, the results indicate that the soft-bottom fish assemblage of La Paz Lagoon exhibits characteristics consistent with a stable and well-structured community. Multivariate analyses further identified water temperature as the principal environmental variable associated with community variation. Collectively, these findings support the hypothesis that La Paz Lagoon is undergoing ecological recovery and provide a robust ecological baseline for long-term monitoring, conservation, and ecosystem management.

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1. Introduction

Coastal lagoons are among the most productive and ecologically important ecosystems worldwide, functioning as transitional environments between terrestrial, freshwater, and marine systems. Their high habitat heterogeneity, environmental variability, and connectivity with adjacent coastal areas support diverse biological communities and provide essential ecosystem services by functioning as nursery, feeding, refuge, and reproductive habitats for numerous fish species [1,2].

Fish assemblages are particularly useful indicators of ecological condition because they respond rapidly to environmental changes and integrate the effects of multiple ecological processes operating across spatial and temporal scales. Variations in species richness, abundance, and community composition are frequently associated with fluctuations in environmental conditions, habitat complexity, and anthropogenic disturbance [3,4]. Consequently, analyses of fish assemblages have become fundamental tools for evaluating ecosystem condition and biodiversity patterns in coastal ecosystems.

The Gulf of California supports one of the most diverse fish faunas of the eastern Pacific, with numerous species utilizing coastal lagoons during different stages of their life cycles [5]. Previous studies conducted in coastal and reef ecosystems of the region have demonstrated that fish assemblages exhibit marked spatial and seasonal variation associated with environmental gradients and habitat characteristics [6,7]. These studies highlight the importance of local environmental conditions and connectivity in shaping fish community structure.

Traditionally, ecological assessments of fish assemblages have relied on species richness, abundance, and diversity indices. However, these metrics may not fully capture changes in community structure because they do not incorporate the hierarchical taxonomic relationships among species. Taxonomic distinctness indices, including Taxonomic Diversity (Δ), Taxonomic Distinctness (Δ^*), Average Taxonomic Distinctness (Δ^+), and Variation in Taxonomic Distinctness (Δ^+), provide complementary ecological information by incorporating taxonomic relatedness into biodiversity assessments [8,9]. These metrics have proven particularly useful for evaluating ecological integrity because they are relatively insensitive to sampling effort and capable of detecting structural changes associated with environmental stress.

La Paz Lagoon is one of the most important coastal lagoon systems in the southwestern Gulf of California. Historically, portions of the lagoon were affected by wastewater discharges, hydrological alterations, and increasing urban development, raising concerns about ecosystem integrity and biodiversity conservation. Previous evaluations based on taxonomic distinctness suggested that the lagoon maintained a relatively healthy ecological condition despite these historical anthropogenic impacts [10].

However, those assessments were conducted several years ago, and updated information is needed to determine whether current fish assemblages continue to exhibit community patterns consistent with ecological recovery.

The present study evaluated the fish assemblage of La Paz Lagoon through analyses of species composition, diversity patterns, taxonomic distinctness, and community structure. Specifically, we assessed spatial and temporal variation in fish diversity and examined whether taxonomic distinctness indices remained within the expected limits derived from the regional species pool.

We hypothesized that if ecological conditions within La Paz Lagoon have improved following the reduction of historical anthropogenic impacts, the fish assemblage should exhibit a taxonomically representative structure, with Average Taxonomic Distinctness (Δ^+) and Variation in Taxonomic Distinctness (Δ^+) values remaining within the expected confidence limits, together with diversity and community patterns characteristic of a functionally structured coastal lagoon ecosystem.

2. Materials and Methods

2.1. Study Area

La Paz Lagoon is located on the southwestern coast of the Gulf of California, Baja California Sur, Mexico, and constitutes one of the most important coastal lagoon systems in the region (Figure 1). The lagoon is characterized by shallow depths, extensive soft-bottom habitats dominated by sandy, muddy, and mixed sand–mud substrates, tidal influence, and permanent connectivity with adjacent marine environments. These environmental characteristics support diverse benthic and demersal fish assemblages and provide nursery, feeding, and refuge habitats for numerous coastal and marine species.

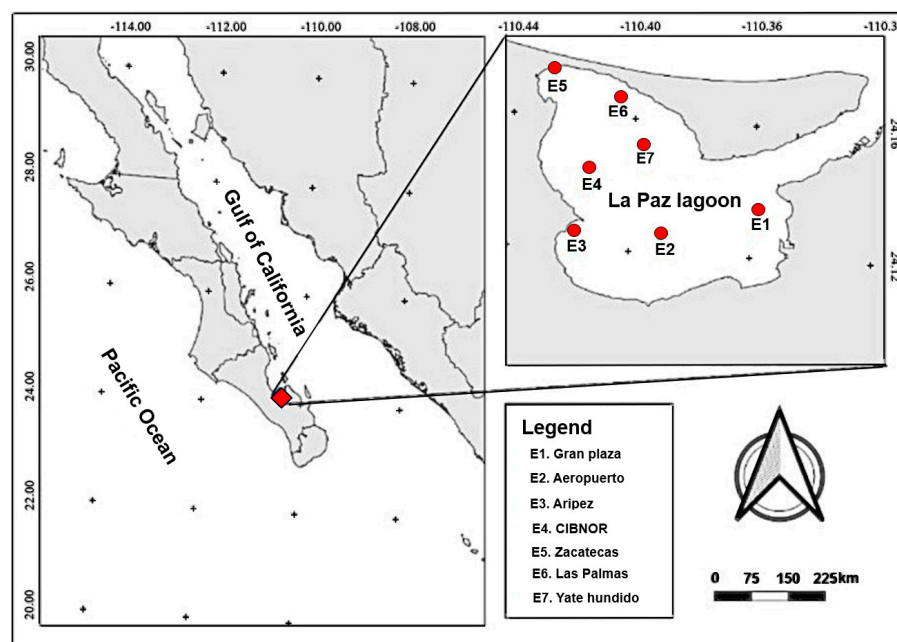


Figure 1. Location of La Paz Lagoon in the southwestern Gulf of California, Mexico, showing the seven sampling stations (E1–E7) surveyed between April 2022 and March 2023.

Historically, portions of the lagoon were influenced by urban development, wastewater discharges, and hydrological modifications associated with the expansion of La Paz City. In recent decades, improvements in wastewater management and environmental regulations have reduced some of these anthropogenic pressures, making the lagoon an appropriate system for evaluating contemporary patterns of fish diversity and community structure.

Seven sampling stations (E1–E7) were established throughout the lagoon to encompass the principal environmental conditions and habitat types present within the system. Geographic coordinates and station characteristics are presented in Table 1. Sampling stations were selected to represent the spatial heterogeneity of the lagoon and to allow the evaluation of temporal and spatial variation in fish assemblages.

Table 1. Geographic coordinates of the seven sampling stations established in La Paz Lagoon, Gulf of California, Mexico, during the study period (April 2022–March 2023).

EST. 1 Grand Plaza	24 07.816	110 21.480
EST. 2 Aeropuerto	24 07.264	110 23.354
EST. 3 Aripez	24 07.243	110 25.081
EST. 4 Cibnor	24 08.368	110 24.859
EST. 5 Zacatecas	24 10.152	110 25.627

EST. 6 Las Palmas	24 09.697	110 24.338
EST. 7 Yate Hundido	24 08.851	110 23.779

2.2. Fish Sampling

Fish sampling was conducted at seven stations (E1–E7) distributed throughout La Paz Lagoon (Figure 1; Table 1). Sampling was conducted during six bimonthly surveys carried out in April, June, August, October, and December 2022, and March 2023, resulting in a total of 42 sampling events. The sampling protocol was identical to that previously applied in La Paz Lagoon [10], thereby allowing direct methodological comparisons among studies conducted within the system.

Sampling stations were selected to encompass the principal environmental conditions and habitat types present within the lagoon, allowing the evaluation of spatial and temporal variation in fish assemblage composition.

Fish were collected using an experimental bottom trawl net 9 m in length, with a vertical opening of 4.5 m and a mesh size of 1.5 inches. Trawling operations were conducted from a 22-ft vessel equipped with a 75 HP four-stroke outboard engine. Each trawl lasted 20 min at an average speed of 3.5 km h^{−1} and was carried out at an average depth of approximately 5 m. All captured specimens were transported to the Fish Ecology Laboratory of the Universidad Autónoma de Baja California Sur (UABCS), where they were processed for subsequent identification and analysis.

Environmental variables, including water temperature and salinity, were measured to characterize the environmental conditions prevailing during each sampling survey.

2.3. Species Identification

All fish specimens collected during the study were transported to the Fish Ecology Laboratory of the Universidad Autónoma de Baja California Sur (UABCS) for processing and identification. Each specimen was identified to the lowest possible taxonomic level, generally species, using the specialized taxonomic literature and regional identification guides.

Species identification was based on standard regional ichthyological guides, including [5,11,12]. Current scientific names, taxonomic validity, and nomenclature were verified using FishBase [13] to ensure taxonomic consistency throughout the manuscript.

For each specimen, total length (TL, mm) and wet weight (g) were recorded. Subsequently, specimens were grouped by species and organized into a hierarchical taxonomic classification including species, genus, family, order, and class. This classification was used to calculate taxonomic distinctness indices and perform community structure analyses.

The final taxonomic inventory was used to generate presence–absence and abundance matrices, which served as the basis for diversity, taxonomic distinctness, and multivariate analyses.

2.4. Diversity Analyses

Fish diversity was evaluated using alpha (α), beta (β), and gamma (γ) diversity metrics in order to describe temporal and spatial patterns of biodiversity within La Paz Lagoon.

Alpha diversity (α) was defined as the average number of species recorded per sampling unit and was used as a measure of local species richness. Temporal and spatial variation in alpha diversity was evaluated among sampling periods and sampling stations.

Gamma diversity (γ) was defined as the total number of species recorded within a given sampling period or station and represented the overall richness of the assemblage at a broader spatial or temporal scale.

Beta diversity (β) was used as a measure of species turnover and was calculated according to [14]:

$$\beta = \gamma/\alpha$$

where γ represents total species richness and α corresponds to average local richness. Higher beta diversity values indicate greater species replacement among sampling units, whereas lower values indicate greater similarity in species composition.

Temporal diversity analyses were performed to evaluate seasonal variation among sampling periods, whereas spatial analyses were conducted to assess differences among sampling stations. The combined use of alpha, beta, and gamma diversity metrics allowed the characterization of local richness, total richness, and species turnover within the lagoon ecosystem.

2.5. Taxonomic Distinctness Analyses

Taxonomic structure of the fish assemblage was evaluated using four complementary indices: Taxonomic Diversity (Δ), Taxonomic Distinctness (Δ^*), Average Taxonomic Distinctness (Δ^+), and Variation in Taxonomic Distinctness (Δ^+), following the methodology proposed by [8].

Taxonomic Diversity (Δ) incorporates information on species abundance and taxonomic relatedness among species, providing a measure of biodiversity that accounts for both taxonomic composition and relative abundance. Taxonomic Distinctness (Δ^*) evaluates the average taxonomic distance among individuals belonging to different species and is considered less sensitive to sample size than traditional diversity metrics.

Average Taxonomic Distinctness (Δ^+) was calculated using presence–absence data and represents the mean taxonomic distance among all possible pairs of species within the assemblage. Variation in Taxonomic Distinctness (Δ^+) measures the variability of taxonomic distances among species and reflects the consistency of the taxonomic structure within the community.

To evaluate whether observed taxonomic distinctness values differed from those expected under random assembly processes, funnel plots were generated for both Δ^+ and Δ^+ using 95% confidence limits derived from repeated randomizations of the regional species pool. Assemblages with values located within the confidence funnels were considered consistent with the expected taxonomic structure of the regional fauna, whereas values falling outside the confidence limits were interpreted as deviations from the expected taxonomic structure.

All taxonomic distinctness analyses were performed using the taxonomic diversity routines implemented in PRIMER 8 (PRIMER-E Ltd., Plymouth, UK).

2.6. Community Structure Analyses

Species dominance was evaluated using the Biological Value Index (BVI), calculated according to the modified methodology of Loya-Salinas and Escofet [15], which integrates species abundance and frequency of occurrence to identify the ecologically most representative species within the assemblage. The BVI was used to characterize species dominance prior to the multivariate community analyses.

Spatial and temporal patterns in fish assemblage composition were evaluated using multivariate analyses based on species abundance data. A species-by-sample matrix was constructed using the abundance of each species recorded at every sampling station and sampling period. Prior to similarity analyses, species abundance data were fourth-root transformed to reduce the influence of highly abundant species while preserving the contributions of less abundant taxa to community structure.

Similarity among samples was calculated using the Bray-Curtis similarity coefficient, one of the most widely used measures for ecological community analyses because of its effectiveness in handling species abundance data and its low sensitivity to joint absences.

Patterns of community structure were visualized using non-metric multidimensional scaling (nMDS). This ordination technique represents multivariate relationships among samples in a reduced number of dimensions while preserving the rank order of similarities among sampling units. Samples with similar species composition are positioned closer together in the ordination space, whereas samples with distinct assemblages are located farther apart.

The goodness-of-fit of the ordination was evaluated using the stress statistic. Stress values lower than 0.05 were considered indicative of an excellent representation of multivariate relationships, whereas values below 0.10 were considered highly reliable for ecological interpretation.

The nMDS analysis was used to identify patterns of similarity and differentiation among sampling stations and sampling periods and to evaluate the overall structure of the fish assemblage within La Paz Lagoon.

2.7. Statistical Analyses

Descriptive statistics were used to summarize environmental variables, species richness, abundance, biomass, and diversity metrics. Temporal and spatial patterns in fish assemblages were evaluated using both univariate and multivariate approaches.

Alpha (α), beta (β), and gamma (γ) diversity metrics were calculated to characterize biodiversity patterns at local, regional, and turnover levels. Taxonomic diversity indices (Δ , Δ^* , Δ^+ , and Δ^+) were used to assess the taxonomic structure of the assemblage and its relationship to the regional species pool.

Multivariate analyses were conducted using Bray-Curtis similarity matrices and non-metric multidimensional scaling (nMDS) ordination. The quality of ordination results was assessed using the stress statistic.

Differences in fish assemblage composition among sampling periods and stations were evaluated using permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis similarity matrices calculated from fourth-root transformed abundance data. The analysis employed 999 permutations under a reduced model, and statistical significance was assessed at $p < 0.05$ [16,17].

All ecological analyses were performed using PRIMER-E software (PRIMER-E Ltd., Plymouth, UK). Taxonomic distinctness analyses and funnel plots were generated using the taxonomic diversity routines available within the software package. Additional statistical calculations, data organization, and graphical processing were performed using Microsoft Excel and other standard statistical software when required.

Statistical significance was evaluated at $\alpha = 0.05$ whenever hypothesis testing was applied.

3. Results

3.1. Fish Assemblage Composition

A total of 4285 individuals representing 93 fish species, 65 genera, 33 families, and 17 orders were recorded across the two climatic periods (Table 2). The Neutral period (2016–2017) comprised 72 species, whereas 53 species were recorded during the La Niña period (2022–2023). Of the total inventory, 31 species were shared between climatic periods, whereas 41 and 22 species were exclusive to the Neutral and La Niña periods, respectively.

Table 2. Taxonomic composition and total abundance (*N* (number of individuals) of the soft-bottom fish assemblage recorded during the Neutral (2016–2017) and La Niña (2022–2023) climatic periods in La Paz Lagoon, Gulf of California. The inventory comprised 93 species belonging to 65 genera, 33 families, and 17 orders, with a total of 4285 individuals.

Order	Family	Species	<i>N</i>
Acanthuriformes	Ephippidae	Chaetodipterus zonatus (Girard, 1858)	2
Anguilliformes	Ophichthidae	Ophichthus triserialis (Kaup, 1856)	3
Aulopiformes	Synodontidae	Synodus scituliceps Jordan & Gilbert, 1882	114
Blenniiformes	Labrisomidae	Paraclinus ditrichus Rosenblatt & Parr, 1969	2
Blenniiformes	Labrisomidae	Paraclinus mexicanus (Gilbert, 1890)	2
Blenniiformes	Labrisomidae	Paraclinus sini Rosenblatt & Parr, 1969	1
Carangiformes	Carangidae	Caranx caballus Günther, 1868	15
Carangiformes	Carangidae	Gnathanodon speciosus (Forsskal, 1775)	33
Carangiformes	Carangidae	Oligoplites saurus (Bloch & Schneider, 1801)	2
Carangiformes	Carangidae	Trachinotus kennedyi Steindachner, 1876	9
Carangiformes	Nematistiidae	Nematistius pectoralis Gill, 1862	1
	Dorosoma-		
Clupeiformes	tidae	Opisthonema libertate (Günther, 1867)	80
Clupeiformes	Engraulidae	Anchoa ischana (Jordan & Gilbert, 1882)	34
Eupercaria	Gerreidae	Diapterus brevirostris (Sauvage, 1879)	199
Eupercaria	Gerreidae	Diapterus peruvianus (Cuvier, 1830)	683
Eupercaria	Gerreidae	Eucinostomus argenteus Baird & Girard, 1855	272
Eupercaria	Gerreidae	Eucinostomus currani Zahuranec, 1980	112
Eupercaria	Gerreidae	Eucinostomus dowii (Gill, 1863)	56
Eupercaria	Gerreidae	Eucinostomus entomelas Gilbert, 1892	22
Eupercaria	Gerreidae	Eucinostomus gracilis (Gill, 1862)	186
Eupercaria	Gerreidae	Eugerres axillaris (Günther, 1864)	52
Eupercaria	Gerreidae	Eugerres lineatus (Humboldt, 1821)	26
Eupercaria	Gerreidae	Gerres cinereus (Walbaum, 1792)	163
Eupercaria	Haemulidae	Anisotremus interruptus (Gill, 1862)	22
Eupercaria	Haemulidae	Brachygenys californiensis (Steindachner, 1876)	28
Eupercaria	Haemulidae	Haemulon flaviguttatum Gill, 1862	1
Eupercaria	Haemulidae	Haemulon maculicauda (Gill, 1862)	32
Eupercaria	Haemulidae	Haemulon scudderii Gill, 1862	91
Eupercaria	Haemulidae	Haemulon sexfasciatum Gill, 1862	231
Eupercaria	Haemulidae	Haemulon steindachneri (Jordan & Gilbert, 1882)	3
Eupercaria	Haemulidae	Haemulopsis axillaris (Steindachner, 1869)	44
Eupercaria	Haemulidae	Haemulopsis leuciscus (Günther, 1864)	17
Eupercaria	Haemulidae	Orthopristis chalceus (Günther, 1864)	84
Eupercaria	Haemulidae	Orthopristis reddingi (Jordan & Richardson, 1895)	16
Eupercaria	Haemulidae	Rhencus macracanthus (Günther, 1864)	3
Eupercaria	Haemulidae	Rhencus panamensis (Steindachner, 1876)	5

Eupercaria	Haemulidae	Xenichthys xanti Gill, 1863	1
Eupercaria	Lutjanidae	Hoplopagrus guentherii Gill, 1862	2
Eupercaria	Lutjanidae	Lutjanus argentiventris (Peters, 1869)	8
Eupercaria	Lutjanidae	Lutjanus novemfasciatus Gill, 1862	3
Eupercaria	Sciaenidae	Atractoscion nobilis (Ayres, 1860)	1
Eupercaria	Sciaenidae	Bairdiella icistia (Jordan & Gilbert, 1882)	13
Eupercaria	Sciaenidae	Cheilotrema saturnum (Girard, 1858)	4
Eupercaria	Sciaenidae	Cynoscion othonopterus Jordan & Gilbert, 1882	7
Eupercaria	Sciaenidae	Cynoscion parvipinnis Ayres, 1861	5
Eupercaria	Sciaenidae	Cynoscion reticulatus (Günther, 1864)	2
Eupercaria	Sciaenidae	Cynoscion squamipinnis (Günther, 1867)	1
Eupercaria	Sciaenidae	Larimus pacificus Jordan & Bollman, 1890	101
Eupercaria	Sciaenidae	Microlepidotus brevipinnis (Steindachner, 1869)	16
Eupercaria	Sciaenidae	Micropogonias altipinnis Günther, 1864	7
Eupercaria	Sciaenidae	Micropogonias megalops (Gilbert, 1890)	74
Eupercaria	Sciaenidae	Ophioscion strabo Gilbert, 1898	1
Eupercaria	Sciaenidae	Stellifer illecebrosus (Jordan & Gilbert, 1882)	30
Eupercaria	Sciaenidae	Umbrina xanti Gill, 1862	3
Eupercaria	Sparidae	Calamus brachysomus (Lockington, 1880)	24
Mugiliformes	Mugilidae	Mugil cephalus Linnaeus, 1758	1
Mulliformes	Mullidae	Pseudupeneus grandisquamis (Gill, 1863)	3
Myliobatiformes	Dasyatidae	Dasyatis brevis (Garman, 1880)	5
Myliobatiformes	Dasyatidae	Hypanus dipterurus (Jordan & Gilbert, 1880)	5
Myliobatiformes	Urotrygoni- dae	Urobatis concentricus Osburn & Nichols, 1916	1
Myliobatiformes	Urotrygoni- dae	Urobatis halleri (Cooper, 1863)	125
Myliobatiformes	Urotrygoni- dae	Urobatis maculatus Garman, 1913	44
Myliobatiformes	Urotrygoni- dae	Urotrygon chilensis (Günther, 1872)	1
Perciformes	Serranidae	Diplectrum labarum Rosenblatt & Johnson, 1974	2
Perciformes	Serranidae	Diplectrum pacificum Meek & Hildebrand, 1925	101
Perciformes	Serranidae	Paralabrax maculatofasciatus (Steindachner, 1868)	595
Perciformes	Serranidae	Paralabrax nebulifer (Girard, 1854)	1
Perciformes	Serranidae	Rypticus nigripinnis Gill, 1861	1
Perciformes	Serranidae	Serranus psittacinus Valenciennes, 1846	10
Perciformes	Triglidae	Prionotus birostratus Richardson, 1844	1
Perciformes	Triglidae	Prionotus horrens Richardson, 1844	1
Perciformes	Triglidae	Prionotus ruscarius Gilbert & Starks, 1904	40
Pleuronectifor- mes	Achiridae	Achirus mazatlanus (Steindachner, 1869)	209

Pleuronectiformes	Bothidae	Bothus leopardinus (Günther, 1862)	12
Pleuronectiformes	Bothidae	Engyophrys sanctilaurentii Jordan & Bollman, 1890	1
Pleuronectiformes	Cyclopsettidae	Cyclopsetta panamensis (Steindachner, 1876)	2
Pleuronectiformes	Cyclopsettidae	Etropus crossotus Jordan & Gilbert, 1882	2
Pleuronectiformes	Cyclopsettidae	Syacium ovale (Günther, 1864)	15
Pleuronectiformes	Cynoglossidae	Symphurus chabanaudi Mahadeva & Munroe, 1990	1
Pleuronectiformes	Paralichthyidae	Paralichthys aestuarius Gilbert & Scofield, 1898	11
Pleuronectiformes	Paralichthyidae	Paralichthys woolmani Jordan & Williams, 1897	7
Rhinopristiformes	Rhinobatidae	Pseudobatos leucorhynchus (Günther, 1867)	1
Rhinopristiformes	Rhinobatidae	Pseudobatos productus (Ayres, 1854)	7
Siluriformes	Ariidae	Bagre panamensis (Gill, 1863)	7
Siluriformes	Ariidae	Occidentarius platypogon (Günther, 1864)	27
Syngnathiformes	Syngnathidae	Hippocampus ingens Girard, 1858	34
Syngnathiformes	Syngnathidae	Syngnathus leptorhynchus Girard, 1854	1
Tetraodontiformes	Diodontidae	Diodon holocanthus Linnaeus, 1758	13
Tetraodontiformes	Diodontidae	Diodon hystrix Linnaeus, 1758	1
Tetraodontiformes	Tetraodontidae	Arothron hispidus (Linnaeus, 1758)	13
Tetraodontiformes	Tetraodontidae	Sphoeroides annulatus (Jenyns, 1842)	16
Tetraodontiformes	Tetraodontidae	Sphoeroides lobatus (Steindachner, 1870)	14
Tetraodontiformes	Tetraodontidae	Sphoeroides sechurae Hildebrand, 1946	2

The families Gerreidae, Haemulidae, Serranidae, Synodontidae, Urotrygonidae, and Achiridae were among the most representative groups in terms of species richness and abundance. Several species, including *Paralabrax maculatofasciatus*, *Synodus scituliceps*, *Urobatis halleri*, and *Achirus mazatlanus*, were recorded during both climatic periods, whereas others were restricted to either the Neutral or La Niña period, reflecting species turnover between climatic conditions. The Biological Value Index (BVI) identified *Paralabrax maculatofasciatus*, *Diapterus brevirostris*, and *Eucinostomus gracilis* as the dominant species within

the assemblage, reflecting their consistently high abundance and frequency of occurrence throughout the study (Figure 2).

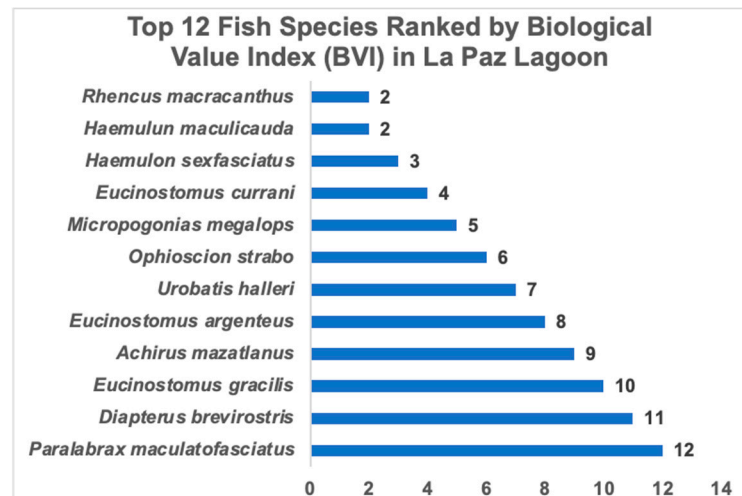


Figure 2. Biological Value Index (BVI) of the 12 most ecologically important fish species recorded in La Paz Lagoon, Gulf of California, during the study period (April 2022–March 2023). Higher BVI values indicate greater ecological importance based on species occurrence, abundance, and persistence throughout the sampling period.

The most abundant species were *Paralabrax maculatofasciatus*, *Diapterus brevirostris*, *Eucinostomus gracilis*, *Achirus mazatlanus*, *Eucinostomus argenteus*, and *Urobatis halleri*. Together, these species represented a large proportion of the total individuals collected during the study period.

Biomass patterns differed slightly from numerical abundance (Figure 3). *Paralabrax maculatofasciatus* contributed the largest proportion of total biomass, followed by *Diapterus brevirostris*, *Synodus scituliceps*, *Urobatis halleri*, and *Haemulon sexfasciatum*. These species collectively accounted for a substantial proportion of the biomass recorded in the lagoon, highlighting the importance of demersal predators and benthic-associated fishes within the assemblage.

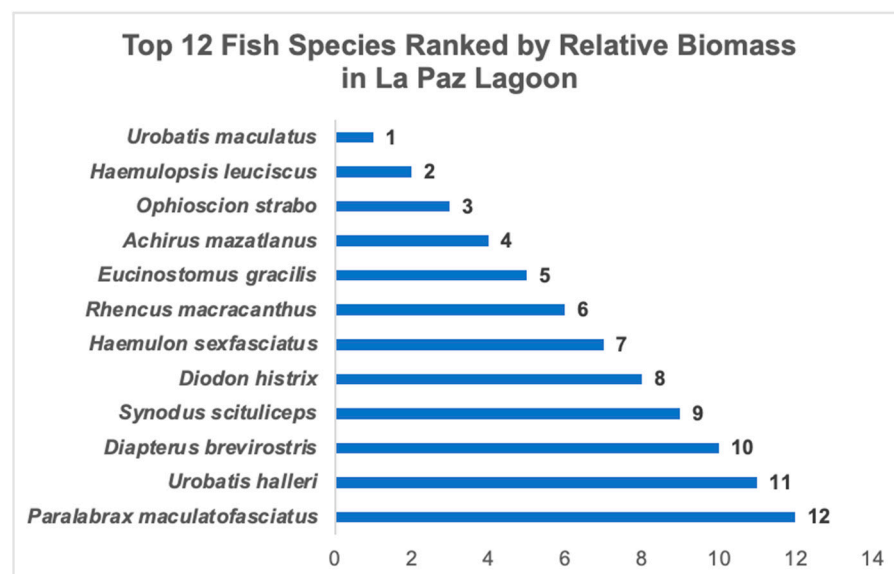


Figure 3. Relative biomass contribution of the 12 dominant fish species recorded in La Paz Lagoon, Gulf of California, during the study period (April 2022–March 2023).

The fish community was composed of resident lagoon species together with transient coastal marine species, resulting in a taxonomically diverse assemblage associated primarily with sandy and muddy bottom habitats. The presence of both benthic and demersal taxa contributed to the overall structural complexity of the community (Table 1).

3.2. Temporal Patterns of Diversity

Marked seasonal variation was observed in fish diversity throughout the study period (Table 3; Figure 4). Total species richness (γ -diversity) reached its highest value in April, when 38 species were recorded, followed by October (26 species) and December (22 species). In contrast, the lowest richness was observed in March, with only seventeen species recorded.

Table 3. Temporal variation in gamma diversity (γ), mean alpha diversity ($\bar{\alpha}$), and Whittaker beta diversity (β) recorded during the six sampling surveys conducted in La Paz Lagoon, Gulf of California.

Survey	γ Diversity	Mean $\bar{\alpha}$ Diversity	β Diversity
April 2022	38	10	3.8
June 2022	21	7.86	2.67
August 2022	20	6.71	2.98
October 2022	26	7.29	3.57
December 2022	22	5.71	3.85
March 2023	17	1.57	10.82

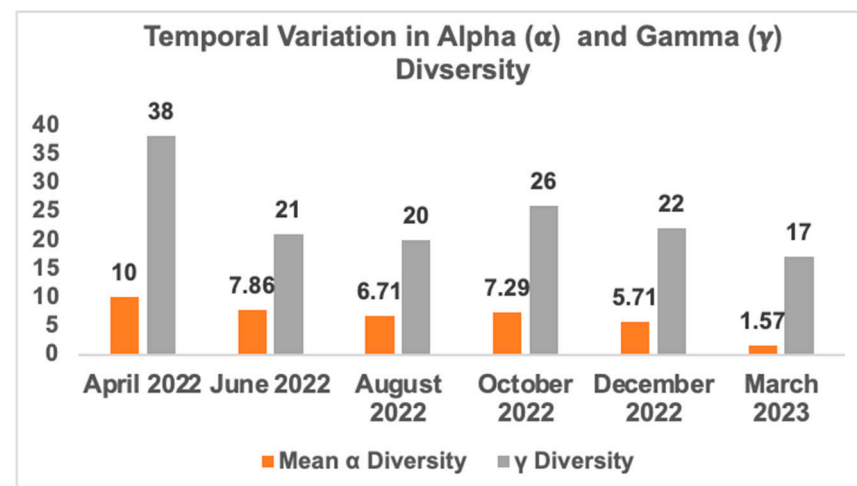


Figure 4. Temporal variation in mean alpha diversity ($\bar{\alpha}$) and gamma diversity (γ) of the fish assemblage recorded during six seasonal sampling surveys conducted in La Paz Lagoon, Gulf of California, between April 2022 and March 2023.

Average alpha diversity ($\bar{\alpha}$) exhibited a similar seasonal pattern (Table 3; Figure 5). The highest value was recorded in April ($\bar{\alpha}$ = 10.3 species per station), whereas the lowest values occurred in December and March ($\bar{\alpha}$ = 1.57 species per station). Intermediate values were observed during June ($\bar{\alpha}$ = 7.0), August ($\bar{\alpha}$ = 5.3), and October ($\bar{\alpha}$ = 4.7).

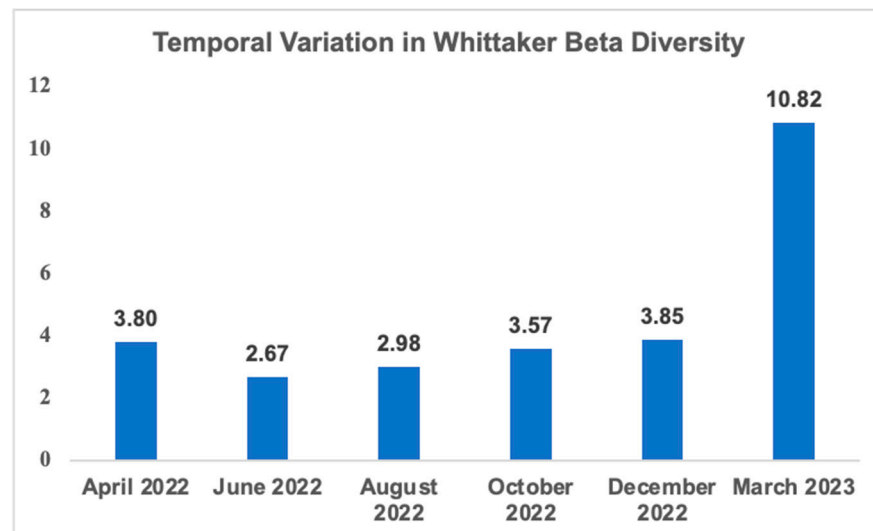


Figure 5. Temporal variation in Whittaker beta diversity (β) during the six sampling surveys conducted in La Paz Lagoon, Gulf of California.

Beta diversity (β), which reflects species turnover among sampling stations, showed a pattern opposite to that of species richness (Table 3; Figure 5). The highest β -diversity values were recorded during March ($\beta = 10.82$), December ($\beta = 3.85$), and April ($\beta = 3.80$), indicating greater differences in species composition among stations during these sampling periods. In contrast, lower β -diversity values were observed during June ($\beta = 2.67$), August ($\beta = 2.98$), and October ($\beta = 3.57$), indicating a more homogeneous species composition among sampling stations.

The seasonal relationship between richness and turnover was particularly evident during periods of reduced diversity. Months characterized by lower γ -diversity generally exhibited higher β -diversity values, whereas periods of elevated richness showed lower levels of species turnover among stations (Figures 4 and 5).

Overall, seasonal fluctuations in diversity metrics revealed substantial temporal variation in fish diversity throughout the lagoon during the study period (Table 3; Figures 4 and 5).

3.3. Spatial Patterns of Diversity

Spatial variation in fish diversity was evident among the seven sampling stations throughout La Paz Lagoon (Table 2). Overall species richness (γ -diversity) ranged from 17 to 23 species among stations. The highest richness values were recorded at stations E1, E3, and E5, with 23, 21, and 22 species, respectively, whereas station E6 exhibited the lowest richness, with only eight species recorded during the study period.

Average alpha diversity ($\bar{\alpha}$) showed a pattern similar to that observed for species richness. Station E1 presented the highest average local richness ($\bar{\alpha} = 7.5$ species per sampling event), followed by E3 and E5. In contrast, station E6 displayed the lowest average alpha diversity ($\bar{\alpha} = 3.8$ species per sampling event), indicating reduced local richness relative to the remaining stations.

The spatial distribution of diversity metrics revealed that stations characterized by higher species richness generally also supported higher local diversity. In contrast, stations with lower richness tended to exhibit reduced alpha diversity, reflecting differences in fish assemblage structure among sampling locations within La Paz Lagoon.

Overall, the observed spatial patterns indicate substantial variation in fish diversity and species turnover among stations within La Paz Lagoon, reflecting differences in assemblage composition across the study area.

3.4. Taxonomic Distinctness

Taxonomic distinctness indices exhibited relatively consistent values among sampling stations throughout La Paz Lagoon (Table 4). Taxonomic Diversity (Δ) ranged from 68.38 at station E1 to 77.22 at station E4, whereas Taxonomic Distinctness (Δ^*) ranged from 72.25 at station E3 to 81.09 at station E4.

Table 4. Species richness (S), taxonomic diversity (Δ), taxonomic distinctness (Δ^*), average taxonomic distinctness (Δ^+), and variation in taxonomic distinctness (Δ^+) calculated for the seven sampling stations in La Paz Lagoon, Gulf of California.

Station	S	Δ	Δ^*	Δ^+	Δ^+
Station 1	23	68.38	72.36	73.52	340.59
Station 2	23	76.16	79.66	78.42	237.82
Station 3	33	69.9	72.25	75.19	189.74
Station 4	12	77.22	81.09	82.73	228.93
Station 5	35	70.68	73.39	76.77	306.9
Station 6	19	74.21	79.07	77.19	305.57
Station 7	20	71.2	75.46	79.58	206.14

Overall, taxonomic distinctness indices revealed a relatively stable taxonomic structure among sampling stations throughout La Paz Lagoon (Table 4; Figure 6A,B).

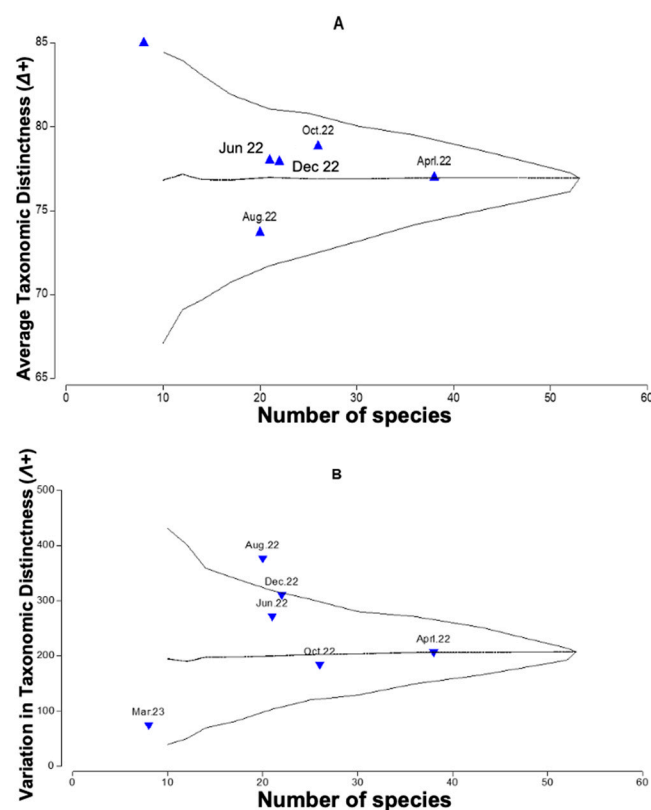


Figure 6. Funnel plots of taxonomic distinctness indices for the seven sampling stations in La Paz Lagoon, Gulf of California. (A) Average Taxonomic Distinctness (Δ^+) and (B) Variation in Taxonomic Distinctness (Δ^+) plotted against species richness (S). Solid lines represent the 95% confidence limits generated from randomization procedures based on the regional species pool.

Similarly, all sampling periods fell within the expected confidence intervals for both Δ^+ and Δ^+ , indicating that temporal fluctuations in species richness did not produce

significant changes in the overall taxonomic structure of the fish assemblage (Table 4; Figure 7A,B).

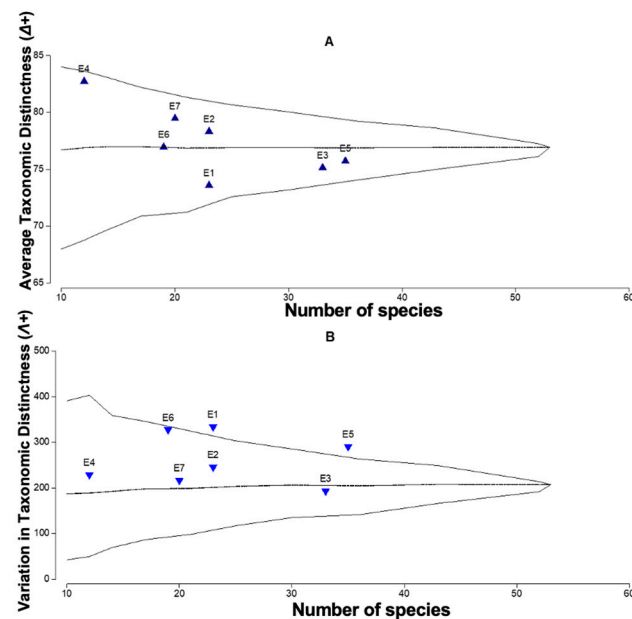


Figure 7. Funnel plots of taxonomic distinctness indices for the six seasonal sampling surveys conducted in La Paz Lagoon, Gulf of California. (A) Average Taxonomic Distinctness ($\Delta+$) and (B) Variation in Taxonomic Distinctness ($\Delta+$) plotted against species richness (S). Solid lines represent the 95% confidence limits generated from randomization procedures based on the regional species pool. All sampling periods remained within the expected confidence limits.

3.5. Community Structure and Multivariate Patterns

Permutational multivariate analysis of variance (PERMANOVA) revealed significant differences in fish assemblage composition between climatic periods (Pseudo-F = 3.76, $p = 0.004$) and among sampling stations (Pseudo-F = 4.00, $p = 0.001$). In contrast, the interaction between climatic period and station was not significant (Pseudo-F = 0.77, $p = 0.910$), indicating that although temporal and spatial differences in assemblage composition were evident, the spatial patterns remained generally consistent between climatic periods.

Non-metric multidimensional scaling (nMDS) ordination supported the PERMANOVA results by showing partial separation between samples from the Neutral and La Niña periods (Figure 8). Although the relatively high stress value (0.26) indicates that the ordination should be interpreted with caution, Neutral samples tended to form a more compact cluster, whereas La Niña samples were more dispersed, suggesting greater variability in fish assemblage composition during the La Niña period.

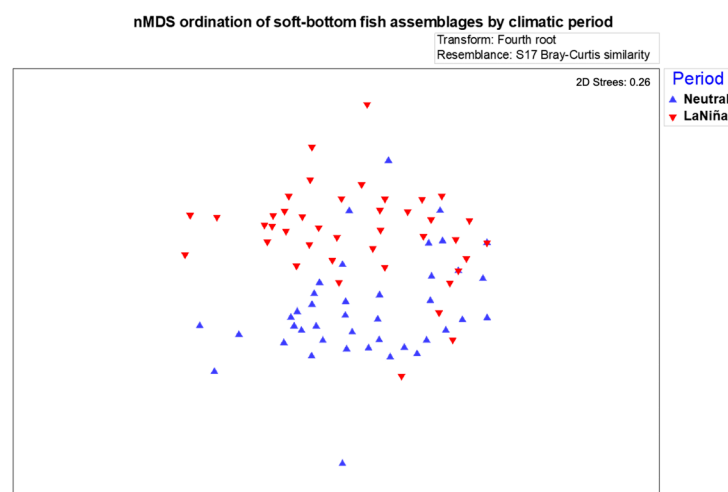


Figure 8. Non-metric multidimensional scaling (nMDS) ordination of fish assemblages from La Paz Lagoon, Gulf of California, Mexico, grouped according to climatic period (Neutral and La Niña). The ordination was based on fourth-root transformed species abundance data using Bray-Curtis similarity. The stress value (0.261) indicates that the ordination provides a general representation of multivariate relationships among samples.

SIMPER analysis indicated an average Bray-Curtis dissimilarity of 80.48% between Neutral and La Niña periods. The species contributing most to this dissimilarity were *Paralabrax maculatofasciatus*, *Eucinostomus currani*, *Achirus mazatlanus*, *Diodon holocanthus*, *Haemulon sexfasciatum*, *Urotrygon chilensis*, *Diapterus peruvianus*, *Eucinostomus dowii*, *Umbriina xanti*, and *Synodus scituliceps*, indicating that differences between climatic periods were primarily associated with changes in the abundance of these taxa.

3.6. Environmental Drivers of Community Structure

Distance-based linear modelling (DistLM) indicated that water temperature, salinity, and dissolved oxygen were all significantly associated with variation in fish assemblage composition in the marginal tests (Temperature: Pseudo-F = 2.40, $p = 0.007$; Salinity: Pseudo-F = 1.91, $p = 0.021$; Dissolved oxygen: Pseudo-F = 1.79, $p = 0.038$). In the sequential tests, temperature remained the principal explanatory variable (Pseudo-F = 2.40, $p = 0.011$), followed by salinity (Pseudo-F = 1.89, $p = 0.035$), whereas dissolved oxygen did not contribute significantly after accounting for the other variables (Pseudo-F = 1.37, $p = 0.150$). The final model explained 6.82% of the total variation in fish assemblage composition.

Distance-based redundancy analysis (dbRDA) showed that the first two canonical axes explained 87.82% of the fitted variation (Axis 1 = 57.63%; Axis 2 = 30.19%). Temperature was primarily associated with the first canonical axis, whereas salinity and dissolved oxygen contributed to the second axis. Although these environmental variables explained only a modest proportion of the total variation (6.82%), the dbRDA ordination supported the DistLM results by highlighting temperature as the principal environmental gradient associated with differences in fish assemblage composition (Figure 9).

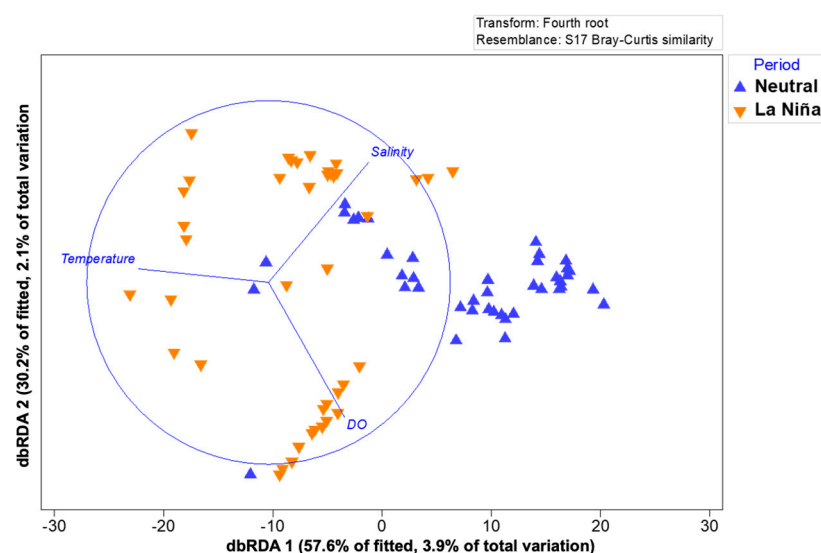


Figure 9. Distance-based redundancy analysis (dbRDA) ordination showing the relationship between fish assemblage structure and environmental variables (water temperature, salinity, and dissolved oxygen) in La Paz Lagoon. The ordination is based on Bray-Curtis similarities calculated from fourth-root transformed species abundance data. Samples are grouped according to climatic period (Neutral and La Niña). The first two dbRDA axes explained 57.6% and 30.2% of the fitted variation, respectively.

4. Discussion

4.1. Fish Assemblage Composition and Ecological Implications

The fish assemblage recorded in La Paz Lagoon was composed of 93 species belonging to 65 genera, 33 families, and 17 orders, confirming the ecological importance of this coastal lagoon as a biodiversity reservoir within the southwestern Gulf of California. The observed richness is comparable to that reported for other subtropical lagoon systems of northwestern Mexico. For example, Moreno-Pérez et al. [7] documented 95 fish species in the Navachiste coastal lagoon, emphasizing the importance of coastal lagoons as habitats that support diverse fish assemblages through the combined influence of environmental variability, habitat heterogeneity, and marine connectivity.

The taxonomic composition of the assemblage was dominated by representatives of Gerreidae, Haemulidae, Serranidae, Achiridae, and Urotrygonidae. According to Whitfield [2], these families are among the most characteristic components of subtropical and tropical lagoon ecosystems because they include species capable of exploiting a broad spectrum of environmental conditions and trophic resources. Their presence is frequently associated with nursery functions, feeding grounds, and habitat connectivity between coastal and marine environments.

The dominance of species such as *Paralabrax maculatofasciatus*, *Diapterus brevirostris*, *Eucinostomus gracilis*, *Achirus mazatlanus*, and *Urobatis halleri* reflects the coexistence of benthic, demersal, and transient marine fishes within the lagoon. Nagelkerken et al. [3] highlighted that habitat mosaics composed of shallow soft bottoms, adjacent coastal habitats, and nursery areas enhance species coexistence and contribute significantly to ecosystem functioning through trophic connectivity and energy transfer.

Overall, the observed taxonomic composition agrees with patterns previously documented for coastal lagoon ecosystems of the Gulf of California and confirms the ecological relevance of La Paz Lagoon as a habitat supporting multiple ecological guilds.

4.2. Seasonal Patterns of Diversity

The pronounced seasonal variation observed in fish diversity reflects the dynamic environmental conditions that characterize subtropical coastal lagoons. Species richness reached its highest value during April and progressively declined toward the end of the study period, with the lowest richness recorded in March. Similar seasonal patterns have been documented in subtropical coastal lagoons of the Gulf of California, where fish assemblages respond to seasonal fluctuations in environmental conditions and habitat availability.

Moreno-Pérez et al. [7] also reported marked changes in fish abundance, life stages, and habitat use associated with seasonal environmental variability in a subtropical lagoon of the Gulf of California.

Seasonal increases in richness may be associated with enhanced biological productivity and the coexistence of resident and transient species. Sheaves et al. [4] emphasized that seasonal shifts in productivity and habitat connectivity strongly influence fish assemblages in estuarine and lagoon systems by facilitating recruitment, feeding opportunities, and species movements. Likewise, Whitfield [2] recognized seasonal environmental variability as one of the principal drivers of fish community dynamics in coastal lagoons worldwide.

An important finding of the present study was the inverse relationship between species richness and beta diversity. Periods characterized by lower richness exhibited higher species turnover among stations, whereas periods of elevated richness showed lower turnover. Elliott et al. [1] proposed that estuarine fish assemblages respond to environmental variability through shifts in habitat occupancy and community composition, generating spatially heterogeneous assemblages under certain environmental conditions. Similar mechanisms may explain the patterns observed in La Paz Lagoon. The exceptionally high β -diversity observed during March suggests that species were distributed more heterogeneously among sampling stations, resulting in greater compositional differentiation across the lagoon despite the reduced overall richness.

These results highlight the importance of incorporating temporal variability into biodiversity assessments and support the notion that seasonal environmental processes play a fundamental role in structuring fish assemblages in coastal lagoons.

4.3. Spatial Patterns of Diversity and Ecological Implications

The spatial distribution of diversity metrics demonstrated that fish richness and turnover were not homogeneous throughout La Paz Lagoon. Stations E1, E3, and E5 consistently supported higher richness and greater temporal turnover, whereas E6 exhibited lower richness and reduced species replacement through time.

Habitat heterogeneity is widely recognized as one of the principal drivers of biodiversity in coastal ecosystems. Nagelkerken et al. [3] demonstrated that structurally complex habitats provide refuge, feeding opportunities, and nursery functions that promote species coexistence and increase local diversity. Similarly, Whitfield [2] highlighted that differences in habitat complexity frequently explain spatial variation in fish assemblages within coastal lagoons.

The spatial patterns documented here are consistent with observations reported by Moreno-Pérez et al. [7], who found that fish species distribution within a subtropical coastal lagoon was strongly associated with habitat use, seasonal movements, and environmental gradients.

The elevated β -diversity observed at station E5 suggests substantial seasonal changes in species composition, potentially associated with recruitment dynamics and seasonal movements of transient species within the lagoon. According to Sheaves et al. [4], coastal lagoons function as transition zones between marine and estuarine environments, where fish communities respond rapidly to changing environmental conditions.

Therefore, the coexistence of stations exhibiting contrasting diversity patterns highlights the ecological heterogeneity of La Paz Lagoon and underscores the importance of preserving habitat variability as a mechanism for maintaining biodiversity.

4.4. Taxonomic Distinctness and Ecological Implications

Taxonomic distinctness analyses provided one of the strongest indicators of community structure within La Paz Lagoon. The funnel plots of average taxonomic distinctness ($\Delta+$) and variation in taxonomic distinctness ($\Lambda+$) indicated that most spatial and temporal assemblages remained within the 95% confidence limits generated from the regional species pool (Figures 6A,B and 7A,B). However, a few stations and sampling periods exhibited deviations in one or both indices, suggesting localized variation in taxonomic structure without altering the overall taxonomic integrity of the assemblage.

These results suggest that the fish community of La Paz Lagoon maintains a taxonomic structure consistent with regional expectations despite historical anthropogenic disturbances.

Notably, some stations and sampling periods exhibited relatively high values of $\Delta+$, particularly under conditions of reduced species richness, indicating that taxonomic breadth remained comparatively broad even when fewer species were present. This pattern highlights the importance of taxonomic distinctness metrics as complementary indicators to traditional measures of species richness and diversity and reinforces the value of taxonomic-based approaches for assessing ecological integrity.

Clarke and Warwick [8] proposed Average Taxonomic Distinctness ($\Delta+$) as a robust biodiversity metric capable of evaluating community structure independently of sampling effort. Later, Warwick and Clarke [9] demonstrated that reductions in taxonomic distinctness are frequently associated with environmental stress and biodiversity loss because sensitive lineages disappear while tolerant taxa become dominant. Consequently, taxonomic distinctness metrics have become widely recognized as effective tools for assessing ecosystem condition and detecting subtle changes in community organization that may not be evident from species richness alone.

These findings are consistent with Barjau-González et al. [6], who also reported stable taxonomic distinctness despite seasonal variation in fish assemblages from the southwestern Gulf of California.

Particularly noteworthy was the pattern observed during March 2023, when species richness reached its lowest value of the study, yet average taxonomic distinctness remained relatively high and within the expected confidence limits (Figure 7A). This result indicates that, although fewer species were present, they represented a comparatively broad range of taxonomic lineages. Such a pattern demonstrates that reductions in species richness do not necessarily imply a proportional loss of taxonomic diversity.

The absence of marked deviations in both $\Delta+$ and $\Lambda+$ suggests that the taxonomic framework of the assemblage remains intact. Consequently, taxonomic distinctness analyses indicate that seasonal fluctuations in richness and abundance have not resulted in substantial erosion of taxonomic diversity within the lagoon. Overall, the funnel plots support the view that La Paz Lagoon maintains a fish assemblage with a taxonomic structure consistent with regional expectations, reflecting a resilient community despite historical anthropogenic pressures.

Spatially, most sampling stations fell within the expected confidence limits, indicating a generally homogeneous taxonomic structure throughout the lagoon. Stations E1 and E5 exhibited deviations in one or both indices, suggesting localized differences in taxonomic composition that may reflect habitat heterogeneity rather than widespread taxonomic impoverishment. Station E4 exhibited comparatively high $\Delta+$ values and lower species richness; however, its position within the confidence funnel indicates that this pattern

reflects natural variation in species composition rather than taxonomic degradation. The consistency of these patterns suggests that E4 may represent a localized assemblage influenced by particular environmental or habitat conditions within the lagoon. Further studies incorporating habitat structure and environmental gradients would be useful to identify the mechanisms underlying this spatial differentiation, a pattern previously reported for fish and benthic assemblages exposed to natural spatial heterogeneity by Ellingsen et al. [18] and Somerfield et al. [19].

Similarly, most sampling periods remained within the expected confidence limits for both $\Delta+$ and $\Delta+$. However, August 2022 and March 2023 exhibited deviations in one or both taxonomic distinctness indices, indicating that seasonal variation influenced taxonomic structure during those surveys while the overall assemblage remained broadly consistent with regional expectations. Consequently, temporal fluctuations in species richness appear to reflect changes in species composition rather than a reduction in overall taxonomic breadth, which is consistent with previous interpretations of taxonomic distinctness patterns in marine assemblages proposed by Clarke and Warwick [8].

4.5. Community Structure and Ecological Recovery

The integration of diversity metrics, taxonomic distinctness indices, and multivariate analyses provided a comprehensive assessment of the ecological condition of La Paz Lagoon. Although the nMDS ordination revealed variation in species composition among sampling periods, the substantial overlap among samples suggests that the fish assemblage remained broadly coherent despite temporal variation.

The coexistence of resident lagoon species, benthic and demersal fishes, and transient marine visitors reflects the ecological connectivity characteristic of functional coastal lagoon ecosystems. Nagelkerken et al. [3] and Sheaves et al. [4] emphasized that connectivity among habitats is essential for sustaining fish biodiversity because it promotes trophic interactions, nursery functions, and species exchange across seascapes.

One of the most relevant findings of this study was that taxonomic distinctness values remained within expected confidence limits despite seasonal and spatial fluctuations in diversity. According to Warwick and Clarke [9], communities subjected to severe environmental degradation frequently exhibit reductions in taxonomic breadth and increased taxonomic clustering. Such patterns were not observed in La Paz Lagoon.

Historically, the lagoon experienced wastewater discharges and hydrological alterations that affected environmental quality and ecosystem functioning. Although the present study was not designed as a formal before-and-after comparison, the maintenance of broad taxonomic representation, together with the presence of a diverse and structured fish assemblage, suggests that important ecological processes remain functional.

The findings are therefore consistent with an ecosystem exhibiting characteristics associated with ecological recovery. The combination of species richness patterns, taxonomic distinctness indices, and multivariate community analyses indicates that La Paz Lagoon currently supports a diverse and taxonomically representative fish assemblage. Consequently, this study provides an updated ecological baseline for long-term monitoring, biodiversity conservation, and ecosystem management in the Gulf of California.

5. Conclusions

The fish assemblage of La Paz Lagoon was composed of 93 species belonging to 65 genera, 33 families, and 17 orders, confirming the ecological importance of this coastal lagoon as a reservoir of fish biodiversity within the southwestern Gulf of California. Species richness, alpha diversity, and beta diversity exhibited marked seasonal and spatial variation, highlighting the dynamic nature of fish assemblages in subtropical coastal lagoon ecosystems.

The taxonomic distinctness indices (Δ , Δ^* , $\Delta+$, and $\Delta+$) revealed a taxonomic structure consistent with that expected for the regional species pool. The fact that most $\Delta+$ and $\Delta+$ values remained within the expected confidence limits indicates that the assemblage maintains broad taxonomic representation and does not exhibit signs of severe taxonomic impoverishment. These findings demonstrate the value of taxonomic distinctness analyses as complementary tools for assessing biodiversity and ecological condition in coastal ecosystems.

Multivariate analyses further showed that, despite seasonal and spatial fluctuations in species composition, the fish community maintained a coherent assemblage structure across the study area. Together, the diversity metrics, taxonomic distinctness indices, and community analyses suggest that ecological processes supporting biodiversity remain functional within the lagoon.

Although historical wastewater discharges and hydrological alterations affected La Paz Lagoon in the past, the present results indicate that the system currently supports a diverse and taxonomically representative fish assemblage. The observed patterns are consistent with an ecosystem exhibiting important ecological functions and characteristics consistent with ecological recovery.

Consequently, this study provides an updated ecological baseline for long-term monitoring, conservation planning, and ecosystem management in one of the most important coastal lagoons of the Gulf of California and highlights the value of taxonomic distinctness metrics for evaluating ecological condition in coastal ecosystems.

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