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Ichthyoplankton Diversity and Spatial Turnover in the Neritic Zone of the Colombian Pacific (Eastern Tropical Pacific)

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Abstract

Larval fish assemblages provide critical insights into reproductive dynamics, biodiversity baselines, and ecosystem resilience, yet remain poorly documented in the Colombian Pacific. This study analyzed ichthyoplankton diversity and spatial turnover across six neritic localities sampled between 2008 and 2022. Standardized plankton tows yielded 43,277 larvae representing 291 morphospecies, 150 genera, 66 families, and 38 orders. The richness observed accounts for ~34% of fish species listed for the Eastern Tropical Pacific and 15% of adult bony fishes reported for the Colombian Pacific, exceeding previous records. Diversity patterns revealed pronounced spatial heterogeneity: Cupica emerged as a biodiversity hotspot, Pizarro and Tortugas were dominated by few taxa, and Sanquianga exhibited high evenness despite moderate richness. Beta diversity analyses indicated turnover exceeding 60% and dissimilarity surpassing 70%, underscoring strong locality identity shaped by oceanographic gradients, geomorphology, and estuarine dynamics. Dominance patterns highlighted contrasting ecological strategies, with cosmopolitan taxa such as *Cetengraulis mysticetus* coexisting alongside habitat-restricted species of *Labrisomus*. These findings establish the Colombian Pacific neritic zone as a reservoir of genetic and functional diversity, with high richness and turnover reinforcing its role in sustaining ecosystem functioning and fisheries productivity. Methodological handicaps—including reliance on morphology-based identification, formalin preservation limiting molecular analyses, and uneven temporal coverage—constrain taxonomic resolution, yet the ecological patterns observed provide a robust foundation for conservation planning. Future research integrating molecular tools, trait-based approaches, and long-term monitoring will be essential to refine diversity estimates and strengthen adaptive management under scenarios of climate variability and increasing anthropogenic pressures in the Eastern Tropical Pacific.

Keywords: larval fish assemblages; biodiversity hotspot; biodiversity monitoring; species turnover; conservation

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1. Introduction

Ichthyoplankton, characterized by pronounced spatial variability, represents one of the most extensively studied components of the zooplankton due to its ecological relevance and socioeconomic importance [1]. Analyses of larval assemblages provide critical insights into species richness, spawning dynamics, the spatial distribution of fishing grounds, and recruitment levels of fish stocks, thereby complementing estimates derived from fisheries gear and visual censuses [2,3]. Such information is indispensable for fisheries science

and management, as it underpins the formulation of policies aimed at the sustainable exploitation of marine resources [4,5].

In the Colombian Pacific, larval assemblage composition is shaped by strong oceanographic gradients—including Panama upwelling, river discharge, and the Intertropical Convergence Zone (ITCZ), a near-equatorial region where the Northern and Southern Hemisphere trade winds converge—which interact with geomorphological diversity to generate latitudinal contrasts and spatial heterogeneity in community structure [6]. Upwelling enhances primary productivity and zooplankton abundance, increasing prey availability for larvae, while river discharge modifies salinity, turbidity, and nutrient concentrations, creating estuarine conditions that stimulate plankton blooms and reduce predation risk [7–12]. ITCZ variability alters rainfall and wind regimes, reshaping stratification and circulation patterns that influence larval retention and dispersal pathways [13–18]. Together, these drivers establish the environmental gradients that underpin ichthyoplankton diversity in the region.

Recent studies have highlighted the ecological complexity of ichthyoplankton assemblages in the Colombian Eastern Pacific, underscoring the influence of environmental variability on larval distribution. In southern Colombia, salinity and dissolved oxygen have been shown to regulate larval abundance in estuarine systems, with high species turnover in transitional zones reflecting the nursery functions of mangrove–estuary complexes [19]. Along the northern Colombian Pacific, chlorophyll *a* concentration, mesozooplankton biomass, and hydrographic variability shape larval assemblage composition, revealing pronounced spatiotemporal heterogeneity and shifts in taxonomic dominance [6]. Seasonal turnover and high taxonomic richness documented in the Gulf of Tribugá further emphasize the dynamic nature of ichthyoplankton diversity in this region [20]. Collectively, these studies demonstrate that ichthyoplankton diversity is not merely a measure of species richness but a dynamic indicator of ecosystem functioning, driven by environmental variability across the neritic zone of the Colombian Pacific coast.

Understanding these interacting mechanisms is essential not only for advancing ecological theory but also for informing fisheries management and marine spatial planning, as the protection of nursery habitats and recognition of turnover-driven localities are critical for sustaining biodiversity and ecosystem services [21–23]. Documenting ichthyoplankton assemblages therefore represents a direct contribution to biodiversity science. Yet, despite the exceptional biological richness and endemism of the Colombian Pacific, this region remains underrepresented in global assessments of marine diversity [24]. Early life stages of fishes are rarely incorporated into biodiversity inventories, even though they are crucial for identifying spawning grounds, detecting recruitment bottlenecks, and revealing ecological processes that sustain population persistence [25,26]. Long-term datasets documenting larval fish diversity and distribution in this region remain scarce, constraining our ability to evaluate spatial heterogeneity at regional scales and to integrate early life stages into conservation frameworks. Addressing this gap, the present study provides the first systematic assessment of ichthyoplankton assemblages across the Colombian Pacific, thereby advancing understanding of larval diversity patterns and their implications for conservation planning in the Eastern Tropical Pacific.

By integrating ecological theory with applied conservation needs, this study establishes a baseline of ichthyoplankton diversity in the Colombian Pacific and evaluates spatial heterogeneity across the neritic zone. We advance two central hypotheses: first, that larval fish assemblages are structured by the combined influence of regional oceanographic gradients and local habitat conditions; and second, that locality identity plays a decisive role in driving diversity and turnover. Together, these hypotheses provide a coherent framework for interpreting biodiversity patterns and generate insights directly applicable to fisheries

management, marine spatial planning, and the protection of coastal ecosystems in this region of the Eastern Tropical Pacific.

2. Materials and Methods

The neritic zone of the Colombian Pacific extends ~1495 km along a coastline shaped by cliffs, deltaic plains, and extensive mangrove marshes under a macrotidal regime (Figure 1). Rainfall regimes vary regionally: unimodal in the northern and southern sectors, bimodal in the central zone [27]. Annual precipitation ranges from 730 to 13,000 mm, with mean temperatures between 23–27 °C [28]. Climatic dynamics are driven by the latitudinal displacement of the Intertropical Convergence Zone (ITCZ) and modulated by Panama upwelling and El Niño–La Niña events [6,29,30].

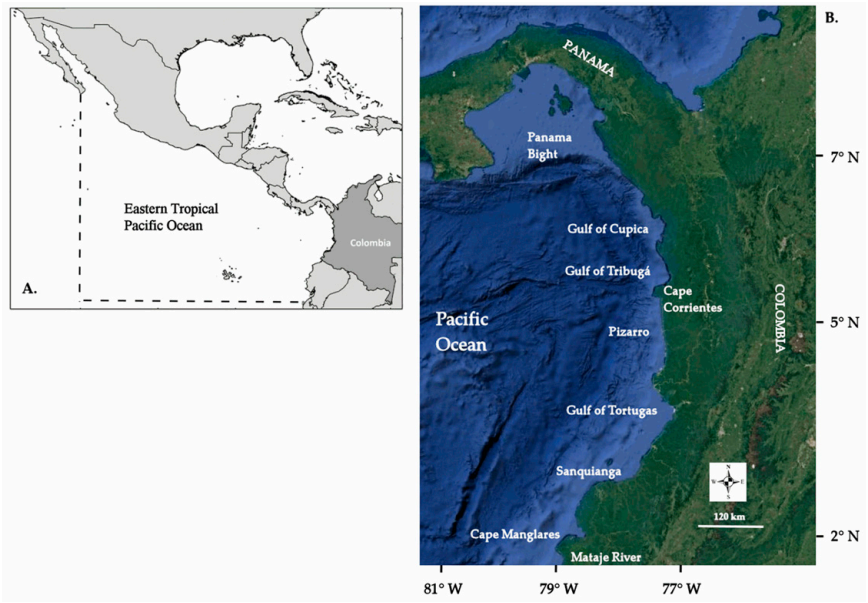

Figure 1. Study area in the Colombian Pacific (Eastern Tropical Pacific). (**A**) Location of Colombian Pacific within the Eastern Tropical Pacific, indicated by the dashed line. (**B**) Neritic zone along the Pacific coast of Colombia, highlighting the sampling localities: Gulf of Cupica, Gulf of Tribugá, Pizarro, Gulf of Tortugas, Sanquianga, and Cape Manglares. Sampling effort was restricted to areas shallower than the 100 m isobath. Because of scale limitations, bathymetric contours are not represented in detail. Image source: Google Earth®, Landsat/Copernicus, SIO, NOAA, U.S. Navy, NGA, GEBCO. 12/31/2020, altitude 1300 km.

Two biogeographic subregions were distinguished. The northern sector, extending from Cabo Corrientes to the Panamá border, is characterized by cliffs, rocky shores, sandy beaches, and occasional coral reef formations, whereas the southern sector, from Cabo Corrientes to the Mataje River at the Ecuador border, features sandy–muddy beaches, barrier islands, and extensive mangrove forests [31,32] (Figure 1). These contrasts guided a stratified sampling design that integrated regional gradients and local habitat heterogeneity in ichthyoplankton assemblages. Stations were distributed across latitudinal sectors and representative coastal habitats, strategically positioned to capture variations in continental shelf width, mangrove extent, sandy–muddy beaches, and the presence of rocky and coral reef systems. This design provided a robust framework for comparing assemblage composition and spatial turnover across the study area. Samples were collected by the Oceanographic Sciences Research Group at Universidad del Valle between 2010 and 2022 in six localities, spanning northern (Cupica, Tribugá, Pizarro), central (Tortugas), and southern (Sanquianga, Cape Manglares) sectors (Figure 1). A detailed breakdown of sampling effort is provided in Table S1, expanded to include both the total number of

samples per individual field survey (n) and the cumulative number of samples per locality across all surveys (N). All sampling stations followed a fixed design; no opportunistic sampling was conducted.

Ichthyoplankton sampling followed standardized protocols [33]. Zooplankton was collected using surface tows conducted consistently from 15 m depth to the surface across all localities. This depth stratum corresponds to the upper mixed layer where ichthyoplankton are most abundant and was selected to capture variability in larval distribution while ensuring methodological comparability among sites. Sampling employed a bongo net (30 cm mouth opening, 300 µm mesh, 180 cm length) towed for 5 min at a speed of 2 knots, with Hydrobios® flowmeters (Altenholz, Germany) used to quantify the volume of water filtered. This gear proved suitable for shallow bays and estuaries, effectively capturing both pre-flexion and post-flexion larvae while minimizing clogging under turbid conditions. Zooplankton samples were preserved in 4% buffered formalin and subsequently transported to the Oceanographic Sciences Laboratory at Universidad del Valle for processing.

Fish larvae were sorted, counted, and identified to the lowest possible taxonomic level following regional ichthyoplankton identification guides [34,35], comparative reference collections, and published morphological descriptions. For families with notoriously challenging larval stages, such as Gobiidae and Labrisomidae, diagnostic criteria included pigmentation patterns along the body and head, myomere counts, jaw and head morphology, and fin ray development. These traits were cross-checked against reference specimens and the available literature to minimize misidentification. When species-level identification was not possible, individuals were assigned to morphospecies based on consistent and distinguishable morphological traits (e.g., pigmentation patterns, meristic counts, body proportions), following standardized ichthyoplankton identification protocols to ensure reproducibility and taxonomic coherence. A detailed account of the identification confidence assigned to each taxon is presented in Table S2, indicating the lowest taxonomic resolution achieved (species, genus, or family). Abundance was standardized to individuals per 100 m^3 of filtered seawater.

For analytical purposes, samples collected in different years were pooled by locality, such that all samples from a given site, regardless of year, were combined to increase taxonomic coverage and strengthen the representativeness of assemblage composition. Alpha diversity was quantified using the Shannon index (H′) [36], with evenness evaluated by Pielou's index (J′). A jackknife correction reduced bias in similarity estimates [37]. Pairwise differences in H′ and J′ among stations were tested using permutation procedures (999 iterations), suitable for small sample sizes [38]. Beta diversity was calculated using Whittaker's index ($\beta = \gamma/\alpha - 1$), highlighting compositional turnover among sites [37,39]. All analyses were performed in PAST® v4.03 [40].

Assemblage structure was analyzed using the Bray–Curtis similarity index, calculated from species abundance matrices. To minimize the influence of rare taxa and reduce noise in multivariate analyses while retaining ecologically meaningful patterns, only taxa with an occurrence frequency greater than 5% across the dataset were included [38]. Data were log-transformed [$\log(x + 1)$] to reduce dominance effects and skewness. Group-average clustering was applied to construct similarity dendrograms, with SIMPROF routines used to test cluster significance, incorporating geographic and oceanographic factors described by Zapata et al. [41]. Species contributions to similarity groups were determined using SIMPER in PRIMER v6.0®. Differences in assemblage composition among localities were evaluated using a one-way Analysis of Similarities (ANOSIM), performed with 999 permutation iterations to provide robust estimates of significance. Assemblages were considered completely distinct when R values approached 0.75–1.0 [42].

3. Results

A total of 43,277 fish larvae were recorded, representing 291 morphospecies. Of these, 107 were identified to species level (36.8%), 159 to genus (54.6%), and 25 to family (8.6%) (Table S2). Overall, larvae were grouped into 150 genera, 66 families, and 38 orders. The families Labrisomidae (39.1%), Engraulidae (25.7%), and Sciaenidae (6.5%) accounted for the highest relative abundances in the neritic zone of the Colombian Pacific (Figure 2A). In terms of richness, Sciaenidae was the most diverse family, followed by Gobiidae and Carangidae (Figure 2B).

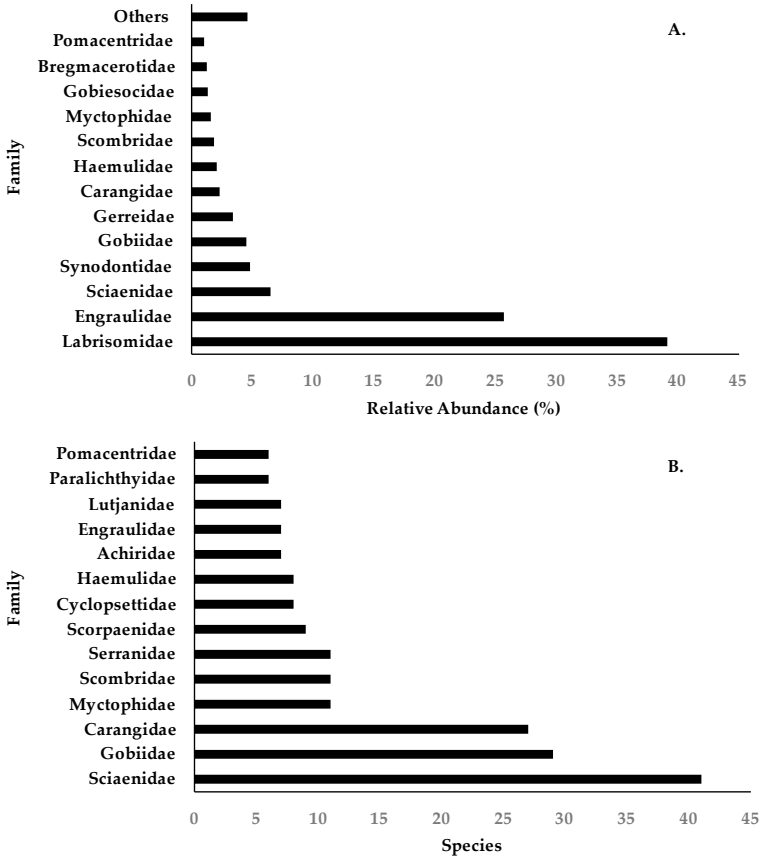

Figure 2. Relative abundance and taxonomic richness of fish larvae by family in the neritic zone of the Colombian Pacific (Eastern Tropical Pacific). (**A**) Relative abundance (%) of families based on morphospecies composition. (**B**) Taxonomic richness, expressed as the total number of morphospecies recorded per family. Locality-specific composition is provided in Table S2.

At the locality scale, Gulf of Tribugá exhibited the highest richness (144 morphospecies), followed by Pizarro (128) and Cupica (117), whereas Sanquianga recorded the lowest richness with 22 morphospecies (Table 1). The most abundant taxa were *Labrisomus* sp.1 (38.9%), *Cetengraulis mysticetus* (23.9%), and *Synodus* sp. (4.7%) (Table S2). *Labrisomus* sp. 1, despite being the most abundant morphotype, could not be confidently assigned to a species due to the absence of diagnostic traits at the larval stage. Although congeners such as *Labrisomus multiporosus* occur in the region, molecular confirmation would be required. Adult *Labrisomus* species, while not commercially important, are relatively common in reef and rocky habitats of the Colombian Pacific. In contrast, *C. mysticetus* dominated overall abundance and is a species of high fisheries relevance. Additionally, the presence of larvae from commercially valuable taxa such as *Caranx caballus*, *Caranx sexfasciatus*, *Lutjanus guttatus*, and *Thunnus albacares* (Table S2, Figure 3) highlights the coexistence of abundant resident species with key fisheries resources in the neritic zone of the Colombian Pacific.

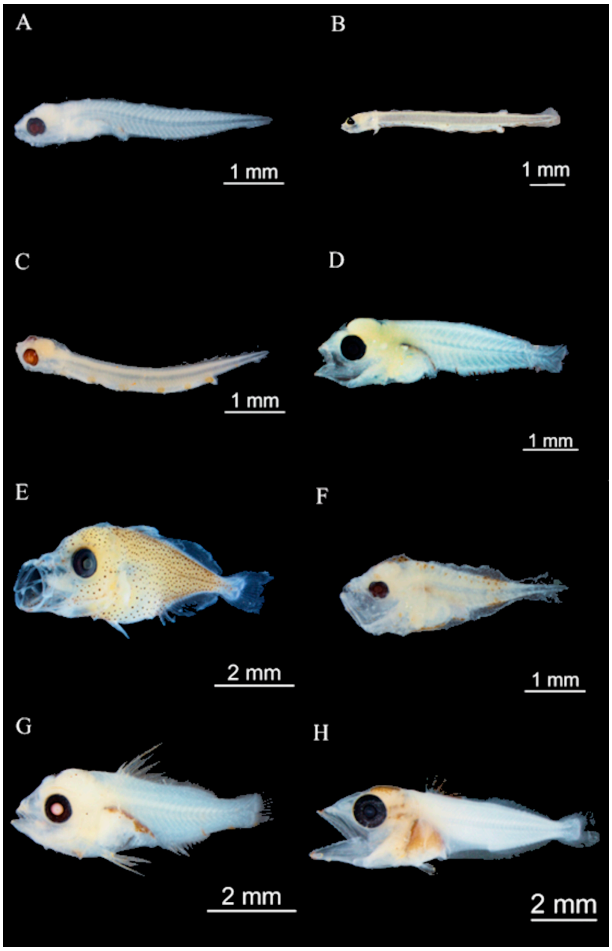

Figure 3. Most abundant fish larvae and highlighted commercial species in the neritic zone of the Colombian Pacific (Eastern Tropical Pacific). (**A**) *Labrisomus* sp.—the most abundant morphospecies. (**B**) *Cetengraulis mysticetus*—dominant in overall abundance and of high fisheries relevance. (**C**) *Synodus* sp.—representative of demersal assemblages. (**D**) *Eucinostomus* sp.—common estuarine-associated species. (**E**) *Caranx caballus*—a commercially important carangid. (**F**) *Caranx sexfasciatus*—another carangid of fisheries relevance. (**G**) *Lutjanus guttatus*—a key snapper species targeted by artisanal fisheries. (**H**) *Thunnus albacares*—yellowfin tuna, of major commercial importance in regional fisheries.

Table 1. Relative abundance and taxonomic richness of fish larvae by family in the neritic zone of the Colombian Pacific (Eastern Tropical Pacific): A: Relative abundance (%); R: Taxonomic richness by family (number of taxa); GC: Gulf of Cupica; GT: Gulf of Tribugá; P: Pizarro; GTo: Gulf of Tortugas; S: Sanquianga; CM: Cape Manglares.

Family	A	R	Taxonomic Richness per Locality (Number of Taxa)					
			GC	GT	P	GTo	S	CM
Achiridae	0.4829	7		6	3	4	1	3
Albulidae	0.0046	1		1				
Alepisauridae	0.0023	1	1					
Alosidae	0.0901	2	1				1	2
Antennariidae	0.0069	1	1					
Apogonidae	0.0023	1	1					
Aulopidae	0.0023	1						1
Balistidae	0.0023	1	1					
Bathylagidae	0.0601	5						5

Table 1. *Cont.*

Family	A	R	Taxonomic Richness per Locality (Number of Taxa)					
			GC	GT	P	GTo	S	CM
Belonidae	0.0023	1						1
Blenniidae	0.3351	5	5	3	3	1		
Bothidae	0.0092	2						2
Bramidae	0.0023	1				1		
Bregmacerotidae	1.2547	2	2	2	1	1		2
Carangidae	2.3130	27	16	17	14	13	4	11
Centropomidae	0.1571	3	3	1	1	1		
Ceratiidae	0.0023	1						1
Congridae	0.0023	1						1
Coryphaenidae	0.2103	4	3	2	4	1		2
Cyclopsettidae	0.1664	8	1	2	1			7
Diodontidae	0.0023	1	1					
Eleotridae	0.0069	3				1		2
Elopidae	0.0023	1						1
Engraulidae	25.6695	7	4	4	3	4	2	6
Ephippidae	0.0323	2	1	2		1	1	
Exocoetidae	0.0300	2	2	1	1			
Fistulariidae	0.0693	3	1	1	1	1		2
Gerreidae	3.3944	5	4	3	2	2		1
Gobiidae	4.5012	29	7	12	16	18	5	3
Gobiesocidae	1.3310	4	2	2	3	4	1	
Gonostomatidae	0.0023	1				1		
Haemulidae	2.0796	8	4	5	6	4	1	2
Hemiramphidae	0.0601	3	1	1	2		1	
Holocentridae	0.0069	1	1					
Labridae	0.1641	5	1	4	5			1
Labrisomidae	39.0993	4	3	3	2	1		1
Lobotidae	0.1895	2	2	2	1	1		1
Lutjanidae	0.3951	7	2	3	3	2		5
Microdesmidae	0.0670	2	2	2	1	1		1
Mugilidae	0.1849	3	2	2	1	2		1
Mullidae	0.0277	1		1	1			
Muraenidae	0.0046	1		1	1			
Myctophidae	1.5851	11	3	2	4	2		7
Nemichthyidae	0.0023	1		1				
Nomeidae	0.0485	1	1	1				
Oneirodidae	0.0046	1	1					
Ophichthidae	0.0046	2						2
Ophidiidae	0.0855	4	1	2		1		3
Opistognathidae	0.0208	1				1		
Ostraciidae	0.0023	1	1					
Paralichthyidae	0.0970	6		2	1	1		4
Phosichthyidae	0.1964	1				1		1
Polynemidae	0.0092	2				1		1
Pomacentridae	1.0213	6	5	6	4	2	2	1

Table 1. *Cont.*

Family	A	R	Taxonomic Richness per Locality (Number of Taxa)					
			GC	GT	P	GTo	S	CM
Sciaenidae	6.4931	41	6	27	20	18	3	8
Sparidae	0.0046	1		1				
Sphyraenidae	0.4252	3	2	2	3	2		2
Syngnathidae	0.0069	1			1	1		
Synodontidae	4.8039	3		1	2	3		3
Tetraodontidae	0.5592	4	3	3	3	2		2
Total			117	144	128	111	22	106

Diversity and evenness varied markedly among localities, reflecting pronounced spatial heterogeneity in larval assemblages. The Gulf of Cupica exhibited the highest diversity and evenness ($H' = 3.73$ nats/ind, $J' = 0.78$), indicating balanced species distribution and low dominance ($D = 0.04$). In contrast, Pizarro showed the lowest values ($H' = 1.17$, $J' = 0.24$) with high dominance ($D = 0.65$), suggesting that a few species accounted for most individuals. Intermediate values were observed in the Gulf of Tribugá ($H' = 3.48$, $J' = 0.70$) and Cape Manglares ($H' = 3.00$, $J' = 0.64$). Sanquianga displayed relatively high evenness ($J' = 0.81$) despite moderate diversity ($H' = 2.47$), pointing to a more equitable distribution among fewer taxa. The Gulf of Tortugas presented moderate diversity ($H' = 1.73$) and low evenness ($J' = 0.39$), with dominance ($D = 0.43$) indicating assemblages skewed toward a few abundant species (Table 2). Collectively, these alpha diversity patterns highlight Cupica as a biodiversity hotspot with balanced assemblages, Pizarro and Tortugas as dominance-driven systems with reduced evenness, and Sanquianga as a locality characterized by equitable but moderate diversity. Tribugá and Cape Manglares occupy intermediate positions, underscoring the mosaic-like structure of larval fish communities along the Colombian Pacific.

Beta diversity analysis further emphasized the mosaic structure of larval assemblages. Whittaker's index revealed substantial species turnover among localities, with values exceeding 59% in most pair-wise comparisons (Table 2). This high turnover underscores strong spatial differentiation of larval assemblages, likely driven by oceanographic gradients, coastal geomorphology, and estuarine inputs. Within the northern region (Gulf of Cupica, Gulf of Tribugá, and Pizarro), turnover values were comparatively lower (34–45%), reflecting greater similarity among geographically proximate sites. In contrast, comparisons involving southern localities (Sanquianga, Cape Manglares, and Gulf of Tortugas) consistently showed higher dissimilarity (>70%), highlighting the distinctiveness of larval communities in these areas.

Overall, the combined alpha and beta diversity results reveal a complex ecological mosaic in which northern sites share a core assemblage, while southern and central localities harbor unique species compositions. These findings suggest that larval fish diversity in the Colombian Pacific is structured by both localized dominance and regional heterogeneity, reinforcing the need for conservation strategies that account for biodiversity hotspots as well as turnover-driven assemblages.

For similarity analysis, *Cetengraulis mysticetus* was excluded due to its widespread occurrence (present in 65.1% of stations). To reduce the influence of rare taxa, only morphospecies with >5% occurrence were retained, narrowing the dataset from 291 to 73 morphospecies. Cluster analysis (SIMPROF, $p < 0.05$) identified five significant groups, with dissimilarity among groups exceeding 70% (Figure 3). Group E was the only cluster comprising two localities—Gulf of Tribugá and Pizarro—driven primarily by *Stelifer* sp.1, *Eucinostomus*

sp., *Gobiesox* sp.1, *Anchoa* sp., and *Anisotremus* sp.2 (SIMPER, 57.9% similarity). All other groups consisted of single localities, underscoring the strong identity and distinctiveness of assemblage structures at the site level (Figure 4).

Table 2. Alpha and beta diversity indices of larval fish assemblages in the neritic zone of the Colombian Pacific (Eastern Tropical Pacific). Alpha diversity metrics include the Simpson dominance index (D), Shannon diversity (H′, nats/ind), and Pielou's evenness (J′), calculated for each locality: Gulf of Cupica (GC), Gulf of Tribugá (GT), Pizarro (P), Gulf of Tortugas (GTo), Sanquianga (S), and Cape Manglares (CM). Pairwise beta diversity (Whittaker index) among Colombian Pacific localities. Values are presented in a color-coded matrix to improve readability, with red indicating higher dissimilarity, green indicating medium dissimilarity, and blue indicating lower dissimilarity.

Diversity Index	**Locality**					
	GC	**GT**	**P**	**GTo**	**S**	**CM**
Alpha:						
Simpson (D)	0.04	0.09	0.64	0.43	0.11	0.11
Shannon (H′)	3.73	3.48	1.17	1.73	2.47	3
Pielou (J′)	0.78	0.70	0.24	0.39	0.81	0.64
Beta:						
Whittaker	GC	GT	P	GTo	S	CM
GC	0	0.408	0.445	0.618	0.768	0.658
GT		0	0.343	0.591	0.829	0.653
P			0	0.648	0.812	0.717
GTo				0	0.709	0.701
S					0	0.857
CM						0

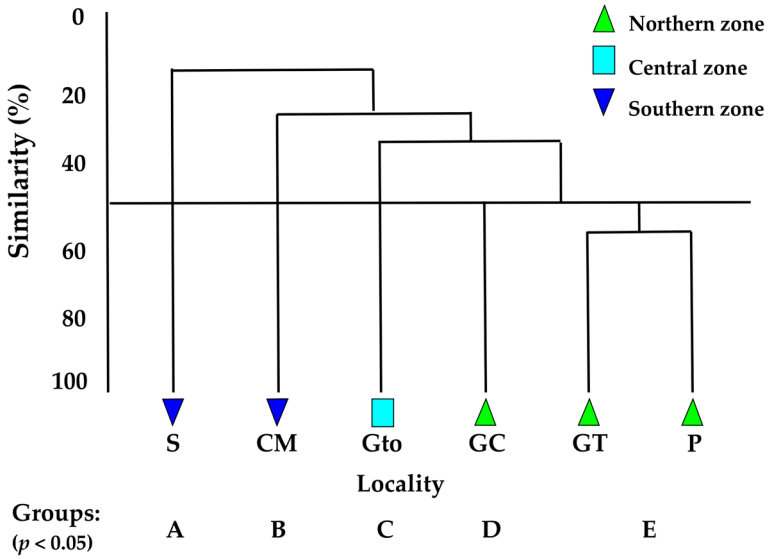

Figure 4. SIMPROF dendrogram of larval fish assemblages in the neritic zone of the Colombian Pacific (Eastern Tropical Pacific). Analyses excluded *Cetengraulis mysticetus* and retained morphospecies with >5% occurrence (73 taxa). Five significant groups were identified ($p < 0.05$), with Gulf of Tribugá and Pizarro forming the only multi-locality cluster. Assemblages also clustered by geographic sector, with dissimilarity among sectors exceeding 66%.

When geographic sector was incorporated into the similarity dendrogram, larval assemblages clustered by sector, with dissimilarity among sectors exceeding 66%. This pattern indicates greater similarity within sectors, reflecting broader regional influences, while maintaining distinct community structures at the locality scale. The exception was Gulf of Tribugá and Pizarro, which grouped together despite belonging to different sectors, possibly due to shared ecological drivers or hydrographic connectivity overriding sectoral boundaries. The highest dissimilarity was observed between Sanquianga and Cape Manglares (90.87%), driven primarily by *Gobiidae* sp.4, *Bairdiella* sp., *Gobiidae* sp.1, *Caranx* sp., and *Menticirrhus* sp.2 (Table S3). Other comparisons involving Sanquianga also showed strong differentiation (82–84%), with contributions from taxa such as *Achirus* sp. and *C. orqueta.* Substantial dissimilarity was also evident between Cape Manglares and Gulf of Cupica (72.87%) and Cape Manglares and northern localities (72–77%), largely explained by *B. panamense, Stelifer* sp., *Anisotremus* spp., and *Labrisomus* sp. Moderate values were recorded for Gulf of Tortugas vs. Gulf of Cupica (69.91%) and Gulf of Tortugas vs. Gulf of Tribugá–Pizarro (63.87%), with differentiation driven by *Synodus* sp., *Auxis* sp., *Anisotremus* spp., and *Eucinostomus* spp. The lowest dissimilarity occurred between Gulf of Cupica and Gulf of Tribugá–Pizarro (50.05%), reflecting greater similarity, with shared contributions from *Labrisomus* sp., *Caranx sexfasciatus*, *Stelifer* sp.1, *Gobiidae* sp.9, and *Auxis* sp.

The one-way ANOSIM indicated complete separation among assemblages (R = 1.0), suggesting strong differences between groups. The associated *p*-value (0.067), derived from 999 permutation iterations, reflects borderline statistical support and therefore requires careful interpretation. Consistently high dissimilarity values and distinct taxa contributions point to pronounced spatial heterogeneity in larval fish communities of the Colombian Pacific, shaped by regional gradients and local habitat conditions. Low replication in certain localities (e.g., Sanquianga) may have influenced the reliability of *p*-values, particularly when R values suggest strong group separation but statistical support remains marginal.

4. Discussion

This study documented 291 morphospecies of fish larvae in the neritic zone of the Colombian Pacific, representing higher richness than previously reported for the region. Earlier surveys recorded fewer species—199 in the northern Colombian Pacific [6], 89 in the Gulf of Tribugá [20], and 153 at Cape Manglares [43]. The richness observed here accounts for 34% of fish species listed for the Eastern Tropical Pacific [44] and 15% of adult bony fishes reported by Tavera et al. [45], underscoring the importance of larval surveys in strengthening biodiversity baselines. Assemblage composition revealed notable differences compared with earlier studies. Families such as Phosichthyidae, Gobiidae, and Myctophidae have frequently dominated ichthyoplankton in the Colombian Pacific [6,41–49]. In contrast, our findings showed stronger dominance of Sciaenidae, Labrisomidae, and Synodontidae, which together accounted for nearly half of total abundance. This shift suggests that larval assemblages are dynamic, responding to local ecological conditions, spawning strategies, and habitat heterogeneity [11,50,51].

The marked dominance of *Cetengraulis mysticetus*, consistently reported in earlier studies [6,47], was again confirmed, representing 23.9% of relative abundance and occurring in 65% of sampling stations. Its broad distribution appears linked to continuous reproduction, multiple spawning peaks, and tolerance to environmental variability [52]. This supports the hypothesis that cosmopolitan taxa with flexible life histories sustain wide distributions across sectors. Conversely, *Labrisomus* sp. 1 emerged as the most abundant morphospecies (38.9%) but was restricted to Cupica, Tribugá, Pizarro, and Tortugas, consistent with the expectation that habitat-restricted taxa exhibit strong site identity. Diversity and evenness analyses revealed pronounced spatial heterogeneity. The Gulf of Cupica emerged as a biodi-

versity hotspot with high diversity and balanced assemblages, while Pizarro and the Gulf of Tortugas were characterized by low diversity and strong dominance. Sanquianga displayed high evenness despite moderate diversity, reflecting equitable distribution among fewer taxa. Gulf of Tribugá and Cape Manglares occupied intermediate positions. These patterns emphasize that larval assemblages are structured by localized dominance and regional heterogeneity, reinforcing the mosaic-like nature of ichthyoplankton communities [53,54].

Beta diversity analyses further highlighted strong spatial differentiation. Whittaker's index revealed turnover exceeding 59% among most localities, underscoring the role of oceanographic gradients, geomorphology, and estuarine inputs in shaping assemblage identity [55–57]. Lower turnover within northern sites (Cupica, Tribugá, and Pizarro) suggests a shared core assemblage, while higher dissimilarity in Sanquianga, Cape Manglares, and Tortugas points to distinct southern and central communities. These results support the hypothesis that habitat heterogeneity generates strong locality identity. Multivariate analyses confirmed that larval assemblages clustered by sector, with dissimilarity among sectors exceeding 66%. Gulf of Tribugá and Pizarro grouped together despite belonging to different sectors, likely reflecting shared ecological drivers or hydrographic connectivity. High dissimilarity values were driven by taxa such as *Gobiidae* sp., *Bairdiella* sp., and *Menticirrhus* sp. 2, whereas lower values reflected shared contributions from *Labrisomus* sp., *Caranx sexfasciatus*, and *Auxis* sp. Although ANOSIM indicated complete separation among assemblages (R = 1.0), the associated *p*-value (0.067) suggests limited statistical support, likely influenced by low replication in certain localities. These outcomes highlight robust ecological patterns but also the need for cautious interpretation.

Comparisons with ichthyoplankton studies from other Eastern Tropical Pacific regions (Costa Rica, Mexico, and Ecuador) suggest both convergent and divergent patterns. In several areas, clupeids and engraulids tend to dominate coastal larval assemblages [58], yet Colombian localities appear to show a stronger representation of estuarine taxa than the offshore assemblages reported for the Costa Rica Dome [59] or the neritic–oceanic contrasts described in the Gulf of Nicoya and Golfo Dulce [60]. Along the central Pacific coast of Mexico, surveys documented an overwhelming prevalence of *Bregmaceros bathymaster*, with seasonal peaks linked to the California Current influence [61], while in the Gulf of Tehuantepec, larval assemblages combined coastal-pelagic forms with unexpectedly high diversity of shallow demersal species even at oceanic stations [62]. In Ecuador, the Gulf of Guayaquil has been characterized by high abundances of anchovies and sciaenids, particularly during transitional months, reflecting strong estuarine influence on larval composition [58]. Taken together, these regional contrasts point to the possibility that riverine inputs, coastal geomorphology, and local hydrographic regimes interact in complex ways to shape larval community structure, and that the Colombian Pacific may be distinguished by the relative prominence of estuarine taxa within its assemblages

Methodological constraints must be acknowledged. Reliance on morphology-based identification limited taxonomic resolution, with only 36.8% of taxa resolved to species level. Cryptic species and overlapping larval traits may influence diversity and turnover estimates, particularly when morphospecies represent aggregated lineages [63]. Formalin preservation further restricted the application of molecular techniques. Future integration of DNA barcoding and embryological approaches will be essential to refine species-level resolution, reduce uncertainty, and improve comparability across ichthyoplankton studies in the Eastern Tropical Pacific [64–66]. Further, temporal pooling also represents a handicap. While pooling samples across years increased taxonomic coverage and reduced stochastic effects, it may have inflated diversity estimates or obscured seasonal and interannual dynamics. Climatic processes such as El Niño, La Niña, Panama upwelling, and ITCZ-driven rainfall variability can substantially affect larval abundance and dispersal,

reshaping diversity at local scales [67–71]. Unequal sampling effort among localities further complicates comparisons, as northern and central sites were surveyed more intensively than southern ones. Future research should adopt standardized sampling designs, expand spatial and temporal coverage, and incorporate trait-based and ecosystem modeling frameworks [64,72–74]. These advances will refine diversity estimates, strengthen biodiversity baselines, and enhance the capacity of ichthyoplankton studies to inform adaptive management and conservation planning in the Colombian Pacific.

Spatial patterns in larval assemblages are also shaped by coastal habitat heterogeneity, which provides critical nursery functions and reinforces locality identity. Mangroves, coral reefs, estuaries, and variable continental shelf morphologies create environments that function as nurseries or dispersal corridors, reinforcing localized dominance and regional heterogeneity [75–78]. Structurally complex habitats enhance food availability and provide refuge from predation, generating distinctive assemblages that can serve as indicators of spawning grounds and nursery functions [73,74,79]. Recent studies emphasize that habitat complexity underpins biodiversity maintenance and larval recruitment, highlighting the ecological significance of coastal mosaics in sustaining ichthyoplankton diversity [50,80]. Within the context of our findings, these habitat features interact with oceanographic gradients to strengthen locality identity, reinforcing the interpretation of spatial heterogeneity in larval assemblage composition. Together, the combined influence of oceanographic variability and coastal habitat heterogeneity highlights the ecological processes that sustain ichthyoplankton diversity, providing a foundation for biodiversity conservation strategies in the Eastern Tropical Pacific.

In summary, the patterns observed in this study suggest that ichthyoplankton assemblages in the Colombian Pacific are shaped by the combined influence of oceanographic variability, geomorphological gradients, and habitat complexity. Nonetheless, methodological handicaps—including reliance on morphology-based identification, formalin preservation limiting molecular analyses, uneven sampling effort, and temporal pooling—constrain taxonomic resolution and comparability. These limitations indicate that the ecological interpretations presented here should be viewed as indicative rather than definitive. Future research incorporating standardized sampling designs, long-term monitoring, and integrative approaches that combine molecular tools, trait-based analyses, and ecosystem modeling may help refine diversity estimates and strengthen biodiversity baselines. Such efforts could enhance the capacity of ichthyoplankton studies to inform adaptive fisheries management and conservation planning under changing oceanographic conditions in the Eastern Tropical Pacific.

5. Conclusions

This study provides the most comprehensive assessment of larval fish assemblages in the Colombian Pacific, documenting 291 morphospecies and adding 67 new records to regional baselines. Richness and diversity patterns revealed a mosaic-like structure, with the Gulf of Cupica emerging as a biodiversity hotspot, Pizarro and the Gulf of Tortugas dominated by a few taxa, and Sanquianga showing high evenness despite moderate diversity. Beta diversity analyses underscored strong spatial differentiation, with northern sites characterized by lower turnover and a shared core assemblage, while southern and central localities displayed distinct community identities shaped by estuarine dynamics, geomorphology, and nutrient variability. By linking these spatial differences to subregional drivers, the study provides an ecological foundation for conservation planning, highlighting the need to integrate nursery functions, turnover-driven localities, and climatic variability into marine spatial strategies and protected area design.

Despite its strengths, the study faced handicaps related to taxonomic uncertainty, uneven spatial coverage, and the use of formalin preservation, which limited the application of molecular techniques. Future efforts incorporating DNA barcoding and complementary approaches will be essential to resolve hidden diversity and strengthen taxonomic baselines. Moreover, pooling samples across years may obscure seasonal and interannual dynamics; thus, long-term monitoring programs, trait-based approaches, and ecosystem modeling are needed to refine diversity estimates, link larval dynamics with ecological processes, and strengthen the evidence base for adaptive fisheries management and conservation planning under changing oceanographic conditions in the Eastern Tropical Pacific.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d18090505/s1; Table S1: Sampling campaigns conducted between 2008 and 2022 in the neritic zone of the Colombian Pacific (Eastern Tropical Pacific); Table S2: Taxonomic richness and relative abundance of fish larvae in the neritic zone of the Colombian Pacific (Eastern Tropical Pacific); Table S3: Pairwise comparisons of larval fish assemblages across the neritic zone of the Colombian Pacific (Eastern Tropical Pacific), showing percentage dissimilarity and the dominant taxa contributing to differences among sectors.

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Data Availability Statement: The data supporting the findings of this study are available from the corresponding author upon reasonable request. Raw ichthyoplankton records and processed datasets generated under Permit Res-1070 (issued by the National Authority of Environmental Licenses, ANLA) are archived by the Oceanographic Sciences Research Group at Universidad del Valle. Vouchers of fish larvae collected during the study were deposited in the Zoological Practices Collection of Universidad del Valle. Summary tables are provided within the article and its Supplementary Materials.

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References

1. Zhang, H.; Li, Y.; Jiang, C. Biological and ecological studies on marine ichthyoplankton. *Front. Mar. Sci.* **2022**, *9*, 948521. [CrossRef]
2. Primo, A.L. Ecology of Marine Fish Larvae. In *Life Below Water*; Encyclopedia of the UN Sustainable Development Goals; Leal Filho, W., Azul, A.M., Brandli, L., Lange Salvia, A., Wall, T., Eds.; Springer: Cham, Switzerland, 2002; pp. 323–332. [CrossRef]
3. Houde, E.D. Fish larvae. In *Encyclopedia of Ocean Sciences*, 3rd ed.; Cochran, J.K., Bokuniewicz, H.J., Yager, P.L., Eds.; Academic Press: Burlington, VT, USA, 2009; pp. 286–292. [CrossRef]
4. Aburto-Oropeza, O.; Erisman, B.; Galland, G.R.; Mascareñas-Osorio, I.; Sala, E.; Ezcurra, E. Large recovery of fish biomass in a no-take marine reserve. *PLoS ONE* **2011**, *6*, e23601. [CrossRef] [PubMed]
5. Guerchon, J.; Morov, A.R.; Tagar, A.; Rubin-Blum, M.; Tikochinski, Y.; Berenshtein, I.; Rilov, G.; Stern, N. Marine top secrets: Ichthyoplankton in surface water uncover hidden knowledge on fish diversity and distribution. *Estuar. Coast. Shelf Sci.* **2023**, *282*, 108226. [CrossRef]
6. Valencia, B.; Rivera-Gómez, M.; Jerez-Guerrero, M.; Rondón-Ramos, M.; Giraldo, A. Temporal and spatial variability of ichthyoplankton assemblages in the Eastern Tropical Pacific off Colombia. *Cont. Shelf Res.* **2024**, *275*, 105228. [CrossRef]
7. Jacox, M.G.; Bograd, S.J.; Fiechter, J.; Pozo Buil, M.; Alexander, M.; Amaya, D.; Quiros, N.C.; Ding, H.; Rykaczewski, R.R. Linking upwelling dynamics and subsurface nutrients to projected productivity changes in the California Current System. *Geophys. Res. Lett.* **2024**, *51*, e2023GL108096. [CrossRef]
8. Arteaga, M.; Vásquez, S.I.; Neira, S.; Cubillos, L. Effect of wind variability on the recruitment of anchovy *Engraulis ringens* in the southern Humboldt upwelling ecosystem. *Fish. Oceanogr.* **2024**, *33*, e12677. [CrossRef]
9. Goldenberg, S.U.; Sswat, M.; Thielecke, A.; Ofelio, C.; Aguirre-Velarde, A.; Rioual, F.; Dorssers, S.; Daussmann, V.; Spisla, C.; Riebesell, U. Nutrient and light availability control food webs and fish larvae in the Peruvian upwelling system. *Limnol. Oceanogr.* **2026**, *71*, e70349. [CrossRef]
10. Sarma, V.V.S.S.; Krishna, M.S.; Srinivas, T.N.R. Long-term changes in nutrient concentration and fluxes from the Godavari estuary: Role of river discharge and fertilizer inputs. *Estuaries Coast* **2023**, *46*, 959–973. [CrossRef]
11. Whitfield, A.K.; Houde, E.D.; Neira, F.J.; Potter, I.C. Importance of marine-estuarine-riverine connectivity to larvae and early juveniles of estuary-associated fish taxa. *Environ. Biol. Fishes* **2023**, *106*, 1983–2009. [CrossRef]
12. Whitfield, A.K.; Blaber, S.J.; Elliott, M.; Harrison, T.D. Trophic ecology of fishes in estuaries. *Rev. Fish Biol. Fish.* **2024**, *34*, 1371–1405. [CrossRef]
13. Torres, R.R.; Giraldo, E.; Muñoz, C.; Caicedo, A.; Hernández-Carrasco, I.; Orfila, A. Seasonal and El Niño–Southern oscillation-related ocean variability in the Panama bight. *Ocean Sci.* **2023**, *19*, 685–701. [CrossRef]
14. Herrera-Carmona, J.C.; Selvaraj, J.J.; Giraldo, A. Dynamic regionalization of the Panama Bight, Eastern Tropical Pacific, using remote sensing data. *Int. J. Remote Sens.* **2022**, *43*, 3131–3151. [CrossRef]
15. Amador, J.A.; Alfaro, E.J.; Lizano, O.G.; Magaña, V.O. Atmospheric forcing of the eastern tropical Pacific: A review. *Prog. Oceanogr.* **2006**, *69*, 101–142. [CrossRef]
16. Fiedler, P.C.; Talley, L.D. Hydrography of the eastern tropical Pacific: A review. *Prog. Oceanogr.* **2006**, *69*, 143–180. [CrossRef]
17. Kessler, W.S. The circulation of the eastern tropical Pacific: A review. *Prog. Oceanogr.* **2006**, *69*, 181–217. [CrossRef]
18. Fernández-Álamo, M.A.; Färber–Lorda, J. Zooplankton and the oceanography of the eastern tropical Pacific: A review. *Prog. Oceanogr.* **2006**, *69*, 318–359. [CrossRef]
19. Gallego-Zerrato, J.J.; Cuellar, A.; Giraldo, A. Ichthyoplankton composition and environmental drivers in the Sanquianga Tapaje Estuarine System, Eastern Tropical Pacific. *Diversity* **2025**, *17*, 649. [CrossRef]
20. Rondon, M.; Giraldo, A. Taxonomic richness, diversity, temporal variation, and ecological aspects of fish larvae in the Gulf of Tribuga, Colombia. *Rev. Biol. Trop.* **2025**, *73*, e56289. [CrossRef]
21. Wanek, E.; Esteban-Cantillo, O.J.; Bourgeois-Gironde, S. Valuing marine plankton: A review of ecosystem services and disservices and an expert assessment of the potential of area-based protection. *Front. Mar. Sci.* **2025**, *12*, 1607996. [CrossRef]
22. Abinaya, R.; Addamo, A.M.; Principe, S.C.; Stephenson, F.; Sajeevan, M.; Costello, M.J. Identifying priority areas for marine protection in Europe to support fisheries. *npj Ocean Sustain.* **2026**, *5*, 6. [CrossRef]
23. Russo, L.; Bellardini, D.; Casotti, R.; Licandro, P.; Mazzocchi, M.G.; Murillas, A.; Percopo, I.; Sarno, D.; D'Alelio, D. The Spatiotemporal Variability of Marine Plankton Ecosystem Services at the Regional Scale: A Combined Approach Using a Systematic Review and Network Analysis. *Sustainability* **2025**, *17*, 1182. [CrossRef]

24. Dorado-Roncancio, E.F.; Montoya-Cadavid, E.; Rodríguez-Toscano, A.J.; Lopez de Mesa, L.A.; Chasqui, L.; Londoño-Cruz, E.; Bechara-Escudero, R.M.; Cedeño-Posso, M.C.; Barrios-Vásquez, E.; Atencia-Galindo, M.; et al. Open-access marine biodiversity records from the Colombia BIO Juradó-Cupica Expedition, Northern Colombian Pacific. *Biodivers. Data J.* **2026**, *14*, e189764. [CrossRef] [PubMed]
25. Puentes, V.; Murillo, J.D.; Pardo, R. A Review of Marine Protected Areas and Fisheries in Colombia: Past, Present and Alternatives. *Sust. Aqua. Res.* **2025**, *4*, 331–357. [CrossRef]
26. Li, H.; Chen, Y.; Li, X.; Zhou, P.; Xiong, X. Assessing larval fish diversity and conservation needs in the Luzon strait using DNA barcoding. *Front. Mar. Sci.* **2023**, *10*, 1268399. [CrossRef]
27. León, G.; Zea, J.; Eslava, J. Circulación general del trópico y la zona de confluencia intertropical en Colombia. *Meteorol. Colomb.* **2000**, *1*, 31–38.
28. Álvarez-Villa, O.D.; Vélez, J.I.; Poveda, G. Improved long-term mean annual rainfall fields for Colombia. *Int. J. Climatol.* **2010**, *31*, 2194–2212. [CrossRef]
29. Corredor-Acosta, A.; Cortés-Chong, N.; Acosta, A.; Pizarro-Koch, M.; Vargas, A.; Medellín-Mora, J.; Saldías, G.S.; Echeverry-Guerra, V.; Gutiérrez-Fuentes, J.; Betancur-Turizo, S. Spatio-Temporal Variability of Chlorophyll-A and Environmental Variables in the Panama Bight. *Remote Sens.* **2020**, *12*, 2150. [CrossRef]
30. Moreno-Rincón, J.L.; Pabón-Caicedo, J.D. Fluctuaciones de la temperatura superficial del mar del Pacífico tropical nororiental extremo no asociadas a ENSO. *Earth Sci. Res. J.* **2025**, *29*, 387–398. [CrossRef]
31. Posada, B.O.; Henao, W.; Guzmán, G. *Diagnóstico de la Erosión y Sedimentación en la Zona Costera del Pacífico Colombiano*; Instituto de Investigaciones Marinas y Costeras (INVEMAR): Santa Marta, Colombia, 2009; pp. 1–148.
32. Correa, I.; Morton, R. Pacific Coast of Colombia. In *Encyclopedia of the World's Coastal Landforms*; Bird, E., Ed.; Springer Science Business Media: Heidelberg, Germany, 2010; pp. 193–198. [CrossRef]
33. Giraldo, A.; Valencia, B.; Acevedo, J.D.; Rivera, M. Protocolo para la obtención de datos oceanográficos y de plancton. In *Protocolos de Investigación en Ecosistemas Terrestres, Intermareales, Submareales y Pelágicos Para el Parque Nacional Natural Gorgona*; Giraldo, A., Moreno, X., Eds.; Departamento de Biología, Facultad de Ciencias Naturales y Exactas, Universidad del Valle: Cali, Colombia, 2011; pp. 85–97.
34. Moser, H.G. (Ed.) *The Early Stages of Fishes in the California Current Region*; California Cooperative Oceanic Fisheries Investigations Atlas No. 33; Allen Press: Lawrence, KS, USA, 1996; 1505p.
35. Beltrán-León, B.S.; Ríos, R. *Estadios Tempranos de Peces del Pacífico Colombiano*; Instituto Nacional de Pesca y Acuicultura (INPA): Buenaventura, Colombia, 2000; 727p.
36. Magurran, A.E. *Measuring Biological Diversity*; Blackwell Publishing: Malden, MA, USA, 2004; 256p.
37. Chuang, C.J. Estimation of similarity indices via two-sample jackknife procedure. *J. Appl. Sci. Eng.* **2012**, *15*, 301–310. Available online: https://www.airitilibrary.com/Article/Detail/15606686-201209-201302050014-201302050014-301-310 (accessed on 20 August 2026). [CrossRef]
38. Zar, J.H. *Biostatistical Analysis*, 5th ed.; Pearson Education: Hoboken, NJ, USA, 2010; 944p.
39. Whittaker, R.H. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* **1960**, *30*, 279–338. [CrossRef]
40. Hammer, Ø.; Harper, D.A.T.; Ryan, P.D. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* **2001**, *4*, 9.
41. Zapata, L.A.; Rodríguez, G.; Gómez, G.; Angulo, W.; Gómez, A.; Beltrán, B.; Morales, Y. *Prospección de los Principales Bancos de Pesca en el Pacífico Colombiano*; Informe Técnico Final INPA/COLCIENCIAS/VECEP/DIMAR BAN 9805; Instituto Nacional de Pesca y Acuicultura (INPA): Buenaventura, Colombia, 1998.
42. Clarke, K.R.; Warwick, R.M. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd ed.; PRIMER-E Ltd.: Plymouth, UK, 2001; 176p.
43. Giraldo, A. Ictioplancton de Cabo Manglares (Distrito Nacional de Manejo Integrado Cabo Manglares, Bajo Mira y Frontera), Nariño, Colombia. *Bol. Cient. Mus. Hist. Nat.* **2020**, *24*, 135–149. [CrossRef]
44. Robertson, D.R.; Allen, G.R. *Shorefishes of the Tropical Eastern Pacific: Online Information System, Version 3.0*; Smithsonian Tropical Research Institute: Panama, CA, USA, 2024; Available online: https://biogeodb.stri.si.edu/sftep/en/pages (accessed on 30 May 2026).
45. Tavera, J.; Beltrán-León, B.S.; Polanco, A.; Zapata, L.A.; Zapata, F.A.; Acero, A. Voucher-verified checklist of Colombian Pacific marine fishes with emphasis on material deposited in Colombian museums. *ZooKeys* **2026**, *1272*, 337. [CrossRef] [PubMed]
46. Martínez-Aguilar, T.I.; Giraldo, A.; Rodríguez-Rubio, E. Ictioplancton en la zona costera del Pacífico colombiano durante la fase terminal de El Niño 2006–2007. *Lat. Am. J. Aquat. Res.* **2010**, *38*, 151–166. [CrossRef]
47. Beltrán-León, B.S.; Morales-Osorio, Y.A. Distribución, composición y abundancia del ictioplancton en tres áreas marinas protegidas del Pacífico colombiano. *Bol. Investig. Mar. Cost.* **2021**, *50*, 31–52. [CrossRef]
48. Gallego-Zerrato, J.J.; Córdoba-Rojas, D.F.; Giraldo, A. Composición taxonómica de las larvas de peces en el arrecife coralino de La Azufrada, Pacífico colombiano, entre 2017 y 2019. *Bol. Cient. Cent. Mus. Mus. Hist. Nat.* **2023**, *27*, 245–261. [CrossRef]

49. Gallego-Zerrato, J.J.; Córdoba-Rojas, D.F.; Giraldo, A. Fish larval assemblage associated with an Eastern Tropical Pacific coral reef: Seasonal and interannual variability. *Diversity* **2024**, *17*, 23. [CrossRef]
50. Buenafe, K.C.V.; Neubert, S.; Scales, K.L.; Dunn, D.C.; Everett, J.D.; Flower, J.; Suthers, I.M.; Granados-Dieseldorff, P.; Dabalà, A.; Jypson, K.; et al. Near-global spawning strategies of large pelagic fish. *Nat. Commun.* **2025**, *16*, 8146. [CrossRef] [PubMed]
51. Muenzel, D.; Critchell, K.; Treml, E.A.; Beger, M. Designing marine reserve networks to mitigate larval dispersal volatility with the connectivity portfolio effect. *Landsc. Ecol.* **2026**, *41*, 17. [CrossRef]
52. Raya, V.; Salat, J.; Sabatés, A. Recurrence of the Spatial Structure of Summer Larval Fish Assemblages Linked to Hydrodynamics in the NW Mediterranean. *Fish. Oceanogr.* **2025**, *34*, 99–120. [CrossRef]
53. Olivar, M.P.; Sabatés, A.; Raya, V.; Sarmiento-Lezcano, A.N.; Couret, M. Offshore larval fish assemblages in contrasting environmental zones around the Iberian Peninsula. *J. Mar. Syst.* **2026**, *255*, 104225. [CrossRef]
54. Zhao, P.; Jiang, R.; Li, Q.; Yin, R.; He, Y.; Han, Q.; Fang, G. Community Dynamics of Fish Larvae in Coastal Zhejiang: Seasonal Variations in Spatiotemporal Distribution and Environmental Driving Factors. *Fishes* **2025**, *10*, 24. [CrossRef]
55. Anderson, M.J.; Crist, T.O.; Chase, J.M.; Vellend, M.; Inouye, B.D.; Freestone, A.L.; Sanders, N.J.; Cornell, H.V.; Comita, L.S.; Davies, K.F.; et al. Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecol. Lett.* **2011**, *14*, 19–28. [CrossRef] [PubMed]
56. Legendre, P.; De Cáceres, M. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. *Ecol. Lett.* **2013**, *16*, 951–963. [CrossRef] [PubMed]
57. Bevilacqua, S.; Boero, F.; De Leo, F.; Guarnieri, G.; Mačić, V.; Benedetti-Cecchi, L.; Terlizzi, A.; Fraschetti, S. β-diversity reveals ecological connectivity patterns underlying marine community recovery: Implications for conservation. *Ecol. Appl.* **2023**, *33*, e2867. [CrossRef] [PubMed]
58. Calderón-Peralta, G.; Ayora-Macías, G.; Solís-Coello, P. Variación espacio-temporal de larvas de peces en el golfo de Guayaquil, Ecuador. *Bol. Invest. Mar. Cost.* **2020**, *49*, 135–156. [CrossRef]
59. Evseenko, S.A.; Shtaut, M.I. On the species composition and distribution of ichthyoplankton and micronekton in the Costa Rica Dome and adjacent areas of the tropical Eastern Pacific. *J. Ichthyol.* **2005**, *45*, 513–525.
60. Molina-Urena, H. Ichthyoplankton assemblages in the Gulf of Nicoya and Golfo Dulce embayments, Pacific coast of Costa Rica. *Rev. Biol. Trop.* **1996**, *44*, 173–182. [PubMed]
61. Franco-Gordo, C.; Suárez-Morales, E.; Godínez-Domínguez, E.; Flores-Vargas, R. A seasonal survey of the fish larvae community of the central Pacific coast of Mexico. *Bull. Mar. Sci.* **2001**, *68*, 383–396.
62. López-Chávez, O.; Aceves-Medina, G.; Saldierna-Martínez, R.J.; Jiménez-Rosenberg, S.P.; Murad-Serrano, J.P.; Marín-Gutiérrez, Á.; Hernández-Hernández, O. Cambios en la composición de especies y abundancia de larvas de peces en el Golfo de Tehuantepec, México. *CICIMAR Oceánides* **2012**, *27*, 1–11. [CrossRef]
63. Hernandez, F.J., Jr.; Carassou, L.; Graham, W.M.; Powers, S.P. Evaluation of the taxonomic sufficiency approach for ichthyoplankton community analysis. *Mar. Ecol. Prog. Ser.* **2013**, *491*, 77–90. [CrossRef]
64. Lira, N.L.; Tonello, S.; Lui, R.L.; Traldi, J.B.; Brandão, H.; Oliveira, C.; Blanco, D.R. Identifying fish eggs and larvae: From classic methodologies to DNA metabarcoding. *Mol. Biol. Rep.* **2023**, *50*, 1713–1726. [CrossRef] [PubMed]
65. Cowen, R.K.; Sponaugle, S. Larval dispersal and marine population connectivity. *Annu. Rev. Mar. Sci.* **2009**, *1*, 443–466. [CrossRef] [PubMed]
66. Green, A.L.; Fernandes, L.; Almany, G.; Abesamis, R.; McLeod, E.; Aliño, P.M.; White, A.T.; Salm, R.; Tanzer, J.; Pressey, R.L. Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. *Coast. Manag.* **2014**, *42*, 143–159. [CrossRef]
67. León-Chávez, C.A.; Sánchez-Velasco, L.; Beier, E.; Lavín, M.F.; Godínez, V.M.; Färber-Lorda, J. Larval fish assemblages and circulation in the Eastern Tropical Pacific in Autumn and Winter. *J. Plankton Res.* **2010**, *32*, 397–410. [CrossRef]
68. León-Chávez, C.A.; Beier, E.; Sánchez-Velasco, L.; Barton, E.D.; Godínez, V.M. Role of circulation scales and water mass distributions on larval fish habitats in the Eastern Tropical Pacific off Mexico. *Geophys. Res. Oceans* **2015**, *120*, 3987–4002. [CrossRef]
69. Ambriz-Arreola, I.; Gómez-Gutiérrez, J.; del Carmen Franco-Gordo, M.; Plascencia-Palomera, V.; Gasca, R.; Kozak, E.R.; Lavaniegos, B.E. Seasonal succession of tropical community structure, abundance, and biomass of five zooplankton taxa in the central Mexican Pacific. *Cont. Shelf Res.* **2018**, *168*, 54–67. [CrossRef]
70. Aceves-Medina, G.; Jiménez-Rosenberg, S.P.A.; Durazo, R. Fish larvae as indicator species of interannual environmental variability in a subtropical transition area off the Baja California peninsula. *Deep.-Sea Res. II Top. Stud. Oceanogr.* **2019**, *169*, 1046. [CrossRef]
71. Franco-Gordo, C.; Godínez-Domínguez, E. Seasonal hydrographic forcing structures ecological trajectories of fish larvae assemblages in the central Mexican Pacific. *Fish. Res.* **2026**, *301*, 107830. [CrossRef]
72. Fontoura, L.; D'agata, S.; Gamoyo, M.; Barneche, D.R.; Luiz, O.J.; Madin, E.M.; Eggertsen, L.; Maina, J.M. Protecting connectivity promotes successful biodiversity and fisheries conservation. *Science* **2022**, *375*, 336–340. [CrossRef] [PubMed]
73. Chan, W.W.R.; Chang, J.J.M.; Tan, C.Z.; Ng, J.X.; Ng, M.H.C.; Jaafar, Z.; Huang, D. Eyeing DNA bar-coding for species identification of fish larvae. *J. Fish Biol.* **2024**, *105*, 1784–1799. [CrossRef] [PubMed]

74. Mouchet, M.A.; Villéger, S.; Mason, N.W.; Mouillot, D. Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Funct. Ecol.* **2010**, *24*, 867–876. [CrossRef]
75. da Silva, V.E.L.; de Assis, I.O.; Campos-Silva, J.V.; Paulino, G.V.B.; Fabre, N.N. Relative importance of habitat mosaics for fish guilds in the northeastern coast of Brazil. *Reg. Stud. Mar. Sci.* **2022**, *50*, 102145. [CrossRef]
76. Reis-Filho, J.A.; Schmid, K.; Harvey, E.S.; Giarrizzo, T. Coastal fish assemblages reflect marine habitat connectivity and ontogenetic shifts in an estuary-bay-continental shelf gradient. *Mar. Environ. Res.* **2019**, *148*, 57–66. [CrossRef] [PubMed]
77. Nodo, P.; Childs, A.R.; Pattrick, P.; James, N.C. The nursery function of shallow nearshore and estuarine benthic habitats for demersal fishes. *Estuar. Coast. Shelf Sci.* **2023**, *280*, 108168. [CrossRef]
78. Gao, S.; Yu, W.; Li, Z.; Zhang, S.; Fu, K.; Wang, N.; Gu, J. Research progress on habitat connectivity in coastal waters: A review. *Ecohydrology* **2023**, *16*, e2479. [CrossRef]
79. Pitts, P.A. Effects of summer upwelling on the abundance and vertical distribution of fish and crustacean larvae off central Florida's Atlantic coast. *J. Exp. Mar. Biol. Ecol.* **1999**, *235*, 135–146. [CrossRef]
80. Chen, L.-C.; Hu, C.-W.; Weng, J.-S.; Lan, K.-W.; Tseng, C.-T.; Hsieh, H.J. Variations in the Abundance, Biodiversity, and Assemblage Structure of Larval Fish in the Restricted Waters of the Wang-an Light Fishery off Penghu, Taiwan. *J. Mar. Sci. Eng.* **2024**, *12*, 1434. [CrossRef]