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Seascape connectivity: ontogenetic migration for *Haemulon flavolineatum*

Diana Carolina Rodriguez-Torres^{1*}  and Alberto Acosta¹

Abstract

In the seascape, species migrate between ecosystems to complete their life cycles, and such ontogenetic migrations create functional connections between ecosystems. Nevertheless, the scarcity of information on patch distribution, species life history and ecology limits its application in Marine Protected Areas (MPA) management. We use a potential connectivity network approach to analyze how *Haemulon flavolineatum* might move through a complex and diverse seascape by simulating part of its life cycle migrations among three ecosystems (reef, mangrove, and seagrass) in the MPA of Bahía Portete-Kaurre (BPK), Colombia. We used available ecosystem cover maps to conduct habitat fragmentation analyses and evaluate structural connectivity in BPK using eight indices that describe ecosystem patches and how they are related. With published information on the *H. flavolineatum* home range and its ontogenetic migration distances, we estimated the potential functional connectivity (CONNECT and migration distances) between ecosystems by building bipartite graphs. The benthic habitat configuration of the BPK could allow *Haemulon flavolineatum* to complete at least two stages of its life cycle (stage 5 mangroves to reefs being more likely than stage 4 seagrass to mangroves). Ontogenetic migrations is possible since, patches of different ecosystems were highly intermixed (76%) rather than grouped (58%); reefs showed higher values of structural indices (patch area, largest patch, shape complexity, functional links) than mangrove (shortest distance to the nearest neighbor) and seagrass (representativeness); and juveniles migrate from mangroves to reef patches along the bay, but they could be isolated by distance when moving from particular seagrass to mangrove patches. Our methodological approach, which integrates ecological information (evidence-based ranges of species migration distances between habitat patches) and the seascape (spatial configuration of habitat patches and fragmentation) is novel for a marine fish species with ontogenetic migration to search for the likelihood of completing its life cycle stages. We discuss the need for ecological information on French grunts and the need to validate future models and scenarios.

Keywords French grunt, Marine protected area, Structural configuration, Reef, Seagrass, Mangrove

Background

Because the seascape is heterogeneous, some habitats and patches may provide the right conditions and resources for certain species to be considered suitable

habitats [10, 76]. Suitable habitats can be understood in terms of the performance of a species (assessed via presence, abundance, fitness, and growth rate) [73]. These variables reflect habitat quality (good or bad) and depend on the species' niche breadth [112]. A seascape composed of suitable habitats sustains species throughout their entire life cycle, a situation that will be reflected in terms of productivity. Within the seascape, core areas (patches rich in resources) can maintain high productivity, which is partly explained by habitat connectivity, and are often targeted by fishing [50]. In seascape studies, an

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integration of landscape ecology and conservation biology is just emerging [9, 103], and the developing connectivity theory is gaining recognition as a relevant integrator of these areas [141]. Connectivity has also become a central conceptual tool for marine protected areas (MPAs), although most approaches do not provide information on the relative ecological importance of species ecosystems and habitats [16]. One example of connectivity between habitats of different ecosystems occurs in the form of ontogenetic migration [98]. Thus, conservation strategies must consider interconnected habitat mosaics, as these interact in the seascape [11, 103, 143] and affect species behavior and survival. For instance, in the strategies to manage the Australian Roviana and Vonavona reserves, the inclusion of knowledge drawn from connectivity among ecosystems (mangrove, reef, and seagrass) has increased the abundance of 17 fish species [102].

Ontogenetic migrations of marine species are the movements of individuals of a given species through habitats (ecosystems) where they fulfill different stages of their life cycle [101]. These migrations help us understand connectivity between and within habitats, their functioning, and how matter and energy flow among them, as well as their contribution to the food web [74, 104]. Furthermore, ontogenetic migration is affected by species-intrinsic and species-extrinsic variables. Intrinsic variables entail species attributes such as genotype, phenotype, mortality rate, development, reproductive output, behavior, and dispersal-migratory strategies [33, 80, 135]. Extrinsic variables are seascape attributes and include discontinuity due to habitat fragmentation (increases in the number of patches, decreases in size), bottom topography, habitat structure, habitat quality (conditions and resources), habitat permeability (structural connectivity), predator-prey interactions, competition, and disturbances [46, 80, 135]. Three coastal habitats known to be connected by ontogenetic migrations are reefs, mangroves and seagrasses, the latter two serving as nurseries for reef fishes [15, 59, 99]. These ecosystems, due to their proximity to the coast, are particularly vulnerable to disturbance due to urban development, aquaculture, overfishing, ports, maritime transportation [52, 79, 82, 113] and direct discharge of pollutants and tourism, which in most cases tends to be unsustainable and irresponsible [29, 123, 138, 144]. The cumulative and chronic degradation of ecosystems causes this large expanse of habitat to transform into a series of smaller and more dispersed patches, limiting fish species dispersion [105].

According to Halpern and Warner [56], the movement patterns and dispersion distances of larvae, juveniles, and adults of a given fish species among ecosystems in the MPA seascape (*i.e.*, ontogenetic migrations) must

be well understood in order to appropriately identify the areas to be protected under the MPA. However, obtaining this exact information can be challenging because species' ontogenetic migration distances in the marine environment are intensely modified by habitat fragmentation and loss of resources (food and shelter), directly and indirectly affecting ecosystem functioning, stability, and diversity [2, 134]. To date, evidence-based ranges of species migration distances between habitat patches have not been used to analyze connectivity in the seascape. However, efforts have been made to determine these ranges between nurseries (mangroves and seagrasses) and breeding areas (reefs) that allow species with ontogenetic migrations between these habitats to thrive (*e.g.*, [12, 132]). The potential use of connectivity given by ontogenetic migrations has also been described for the design of MPAs [95]. There are two complementary views of seascape connectivity: structural connectivity and functional connectivity [53]. The first is a measure of habitat permeability and involves the physical characteristics and spatial configuration of habitat patches within ecosystems [26, 60]. Functional connectivity, on the other hand, describes the response of genes, gametes, propagules, or individuals to the landscape structure, as reflected in survival, reproduction, dispersal, migration, and settlement/recruitment [26, 143]. Whereas real functional connectivity directly quantifies the movements of organisms, potential functional connectivity uses indirect knowledge about the dispersal or migration ability of the organisms and the species' life history data to simulate and predict its connectivity in a seascape, which is particularly useful in remote areas with limited access to species ecological information [7, 38].

The French grunt *Haemulon flavolineatum* (Desmarest 1823) makes ontogenetic migrations among different ecosystems (Fig. 1), where different stages develop [54]. Its geographic distribution according to Lindeman and Toxey [81] includes South Carolina, the Bahamas, Bermuda, and the Gulf of Mexico throughout much of the West Indies and the coasts of Central and South America to Brazil. The *H. flavolineatum* live cycle begins with reproduction and larval dispersal (stage 1), which occurs between the reef (reproduction) and the water column (larval dispersal). This process is favored by surface currents during the pelagic phase and it is assumed the larvae disperse up to 37 km [114]. The next stage is larval settlement (stage 2) between the water column and hard and soft bottoms with rubble or sand (noncoral) [58]. Here, the larvae prefer to settle at depths of approximately 8 m to reduce the risk of predation [70], feeding on plankton brought by local currents [54]. When the larvae reach approximately 2 cm in length, they migrate from the soft bottom with rubble to the seagrass meadow

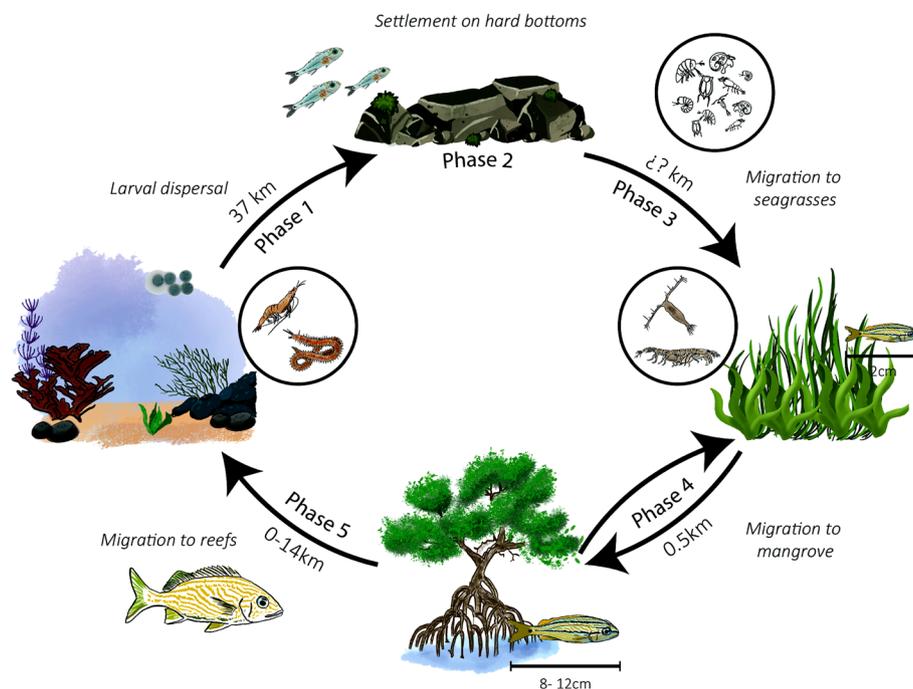


Fig. 1 Representation of *Haemulon flavolineatum* ontogenetic migrations during its life cycle in the Caribbean, when three habitats are present (seagrass, coral reef, and mangrove). Distances above arrows indicate average movement between habitats reported in the literature, and circles indicate fish diet in each phase

(stage 3) and switch to a benthic diet, composed mainly of copepods and tanaidaceans, abundant in these ecosystems [54]. Subsequently, juveniles with an approximate size of 8 to 12 cm migrate from the seagrass to the mangrove (stage 4), which provides shelter, making these juveniles less vulnerable to predation by species such as *Epinephelus striatus*, *Epinephelus guttatus*, *Aulostomus maculatus*, *Mycteroperca bonaci*, *Mycteroperca tigris* or *Mycteroperca venenosa* [13, 28, 54, 78, 117]. However, during stage 4, juveniles perform nocturnal migrations from mangroves to seagrass and feed on copepods (e.g., *Pseudocyclops* sp.), ostracods (e.g., *Actionoseta* sp.), gastropods and decapod larvae [36]. The reported average ranges of these migrations are 0 - 500 m [17, 30, 54, 139, 140]. Finally, ontogenetic migrations occur between mangrove and reef patches (stage 5), where juveniles reach sexual maturity, become adults and reproduce on the reef by broadcast spawning [22, 23, 69, 116, 140], Fig. 1). Distances of 2 to 4 km between nursery areas (mangroves or seagrasses) and reefs could maintain high biomass of *H. flavolineatum*, although, this biomass could approach zero in reefs located more than 14 km away from the nursery areas [99]. Adults continue nocturnal migrations to seagrass arguably to avoid reef ectoparasites such as blood-feeding gnathiid isopods (with higher night activity at reefs, [130] and feed preferentially on crustaceans

such as tanaids, harpacticoid copepods, crabs, shrimps and other groups such as sipunculans and ophiuroids, so *H. flavolineatum* is considered a generalist [57].

Knowledge and tools from terrestrial landscape ecology aid the analysis of connectivity in the seascape [111]. Two of these approaches are the patch mosaic model and graph theory. The patch mosaic analysis considers the size of the habitat (i.e., area and perimeter), the degree of the ecosystem fragmentation, the geometry of the patches, and their degree of isolation, given the distances within and between patches of different ecosystems [27]. The patch mosaic is used in marine spatial planning, prioritizing habitats and ecosystems [12], it underlines the importance of morphological and habitat heterogeneity in connectivity (resistance to movement), so that fish species could develop their life cycles and viability [126]. Graph theory displays a network of connected nodes, nodes representing habitat patches, and the connections between nodes are called links [133, 137]. A bipartite graph approach is used, as a complement to the patch mosaic, to study linkages in fragmented habitats, particularly between patches of two ecosystems, but not within the same ecosystem. In practice, when ecological connectivity between different habitats is strong (graphic network between ecosystems), the entire system is more resilient [34, 75], which helps to make informed management decisions [61].

In Colombia, as in other parts of the world, the lack of information on connectivity hinders its use in the planning and management of MPAs for tropical species of ecological and economic interest, preventing the incorporation of this knowledge into environmental policies and decision-making for the conservation and sustainable use of marine ecosystems [102, 122, 143]. Given the above, it is pertinent to ask whether analyzing potential structural-functional connectivity in the seascape using *H. flavolineatum*, an ecologically and economically important fish species in the Caribbean [42, 55], will help to understand how juveniles might move through a complex and diverse seascape. It can also highlight important knowledge gaps about this species' life cycle requirements, particularly if we are thinking about its sustainable use in an MPA with management conflicts between actors. To do so, we built a connectivity network based on literature migration thresholds for *H. flavolineatum* and habitat maps (reef, mangrove, and seagrass) of the marine protected area Bahía Portete-Kaurrele (BPK), Colombian Caribbean. BPK - it is a remote area with restricted access, including the presence of crocodiles (*Crocodylus acutus*), which makes diving activities risky. Therefore, there is not much detailed information available for the management of any species of economic-ecological importance. That is the reason for using the potential connectivity approach (structural and functional) as a tool to generate a baseline that helps us define the habitat that *H. flavolineatum* needs to fulfill part of its lifecycle.

Materials and methods

Selection of the MPA in Colombia

We examined the National Registry of Protected Colombian Areas (RUNAP) to select one MPA for analysis. The criteria to choose the MPA were public, coastal, located in the Colombian Caribbean, and containing the three ecosystems of mangrove, seagrass, and reef. We discarded MPAs without the three ecosystems because we sought to examine their connectivity as revealed by a species that uses all the three of them [96]. Of 19 MPAs in the Colombian Caribbean, 8 met the established inclusion criteria. The final criterion for choosing the Bahía Portete-Kaurrele MPA (BPK) was the presence of *H. flavolineatum* [109], the representativeness of the three ecosystems and computing limitations for running the networks.

Located in the North of the Department of La Guajira, Colombian Continental Caribbean (12°13'8.24 "N, 71°55'42.60 "O), BPK spans 14 km at its widest point (Fig. 2). It has two contrasting climatic seasons, characterized by the influence of trade winds from the North

and South. The dry season occurs at the beginning of the year (January to March), with north solid trade winds and upwelling, leading to low water temperatures and acidic pH, accompanied by higher dissolved oxygen concentrations [44]. The area's rainy season (from September to November) influences southern trade winds, resulting in higher water temperature, salinity and pH but low dissolved oxygen concentrations [44, 63]. The water presents high turbidity caused by sediment resuspension with a maximum visibility of 4 m [109]. BPK is a shallow bay with a maximum depth of 20 m (Centro de Investigaciones Oceanográficas e Hidrográficas-CIOH nautical charts - charts 229 and 603) and harbors the largest share of seagrasses in Colombia and a considerable extension of mangroves and coral reefs in the department of La Guajira [31, 131]. BPK connects to the open sea through a 2 km wide mouth [66, 131], Fig 2). The surface current flows north to south, then enters the bay moving through the west and center toward the south, and then leaves the bay through the northeast, generating a cyclonic gyre, with the highest speeds occurring in July (see [44] for details on the currents map). The soft bottom consists of clay-type sediments [109].

A mangrove forest borders the bay, dominated by the *Rhizophora mangle* at the waterfront, while *Avicennia germinans* (black mangrove) is found landward, along with patches of *Laguncularia racemosa* (white mangrove; [109]). Shallow seagrasses, dominated by *Thalassia testudinum* and *Syringodium filiforme*, face the forest [32, 47]. *Thalassia* had an average height of 30 cm, and in *Thalassia* and *Syringodium* mixed patches, the latter grew 60 cm on average (Table 1). A high seagrass cover includes scattered colonies of *Millepora alcicornis* and gorgonians (*Antillologorgia*, *Plexaura*, and *Briareum*) and occasionally *Siderastrea* limiting toward the reef crest. In the meadow, it is also possible to find encrusting and erect sponges (INVEMAR, in press). In the southern and western parts of the bay, seagrass meets the reef crest, with significant extensions dominated by *M. alcicornis* and sporadic colonies of *Porites astreoides*, *P. porites*, and *Favia fragum*. Massive coral colonies of *Orbicella faveolata*, *Pseudodiploria strigosa*, *Colpophyllia natans* (2 m diameter), and *Pseudodiploria clivosa* dominate a fringing reef toward the slope. These colonies showed disease symptoms (white plague and dark spots) and mechanical damage by anchors (INVEMAR, in press, Table 1). Other observed sources of degradation in the bay include ship passage to Puerto Nuevo, harpoon fishing, and aromatic hydrocarbons in the sediment (Table 1, [109]). The reef's maximum depths are approximately 4 m (INVEMAR, in press, [131]).

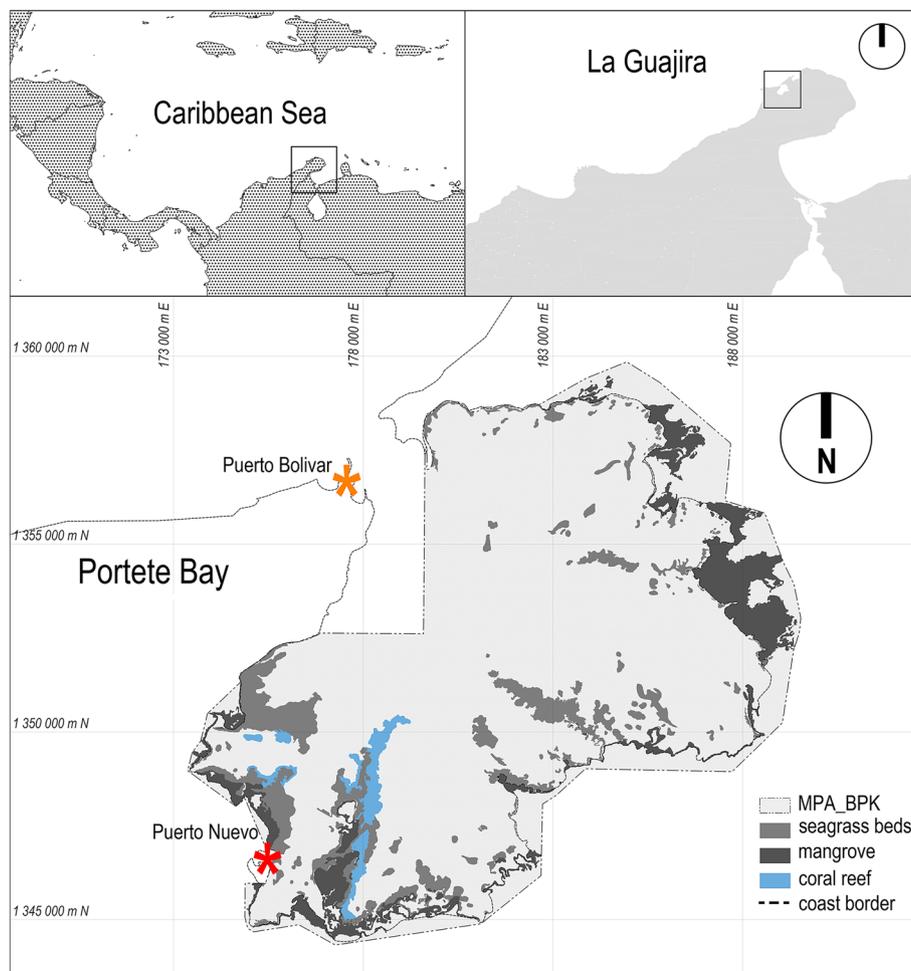


Fig. 2 Map of the spatial location of three habitats (reef-blue, seagrass-gray, mangroves-dark gray) of interest in the Bahía Portete-Kaurrele MPA. The two main ports of the bay are shown, Puerto Nuevo (red asterisk) and Puerto Bolívar (orange asterisk)

Species

The French grunt *Haemulon flavolineatum* (Desmarest 1823) was chosen to analyze connectivity among BPK ecosystems because of its well-documented presence in the Caribbean and sufficient data about its life history, life cycle, and ontogenetic migrations [4, 5, 17, 23, 51, 54, 99, 118]. Furthermore, *H. flavolineatum* is ecologically important in marine food webs [43] and is an important food source of the Wayuu indigenous people in the MPA-BPK [55, 109].

INVEMAR conducted surveys in 2022 to count the presence/absence and relative abundance of *H. flavolineatum* in the bay (see detail of the method used at INVEMAR [68] and Sanchez-Valencia et al. [124]). *H. flavolineatum* individuals were observed in the three ecosystems with relative abundances of 10 individuals in 2500 m² [119, 120]. The bay's ichthyofauna features primarily Haemulidae species, followed by Pomacentridae and Labrisomidae species. According to the literature,

the possible predators of *H. flavolineatum* in BPK are fishes of the genus *Epinephelus* (groupers); while *H. flavolineatum* preys are fishes of the family Clupeidae (sardines) or decapods (anomura) [45, 57, 117].

Structural connectivity analysis

In this study, data from each of the three ecosystems in BPK correspond to a spatial layer, namely, the coral reef layer [65], the seagrass layer [49], and the mangrove layer [67]. The base layer for the analysis was constructed from the cartography generated in projects carried out by INVEMAR and other institutions between 2005 and the present, with scales ranging from 1:10,000 to 1:500,000. Since these layers were not equally scaled, because they come from different sources, unwanted information and ecosystem overlaps were trimmed off using ArcGIS 10.7.1. The resulting maps used for the metrics had a scale of 1:80000 (seagrass to mangrove graph, Fig. 5) and 1:250000 (mangrove to reef graph, Fig. 6).

Table 1 Characteristics of the benthic, reef, seagrass, and mangrove habitats of the Bahía Portete-Kaurrele MPA

	Ecosystems - benthic habitats				
	Seagrass	Fringing Reef	Mangrove Roots	Soft bottom	Literature
Ecosystems benthic area (Bay Total = 14080 ha)	1152 Extensive and continuous meadows	201	1227	9904 Lithoclastic & lithobioclastic	[2]
Relative percent cover of potentially used habitats by <i>H. flavolineatum</i>	45	8	47		
Major structural species	3 (seagrasses)	11 (scleractinian corals)	1 (mangrove)		
Confirmed presence of <i>H. flavolineatum</i>	Yes (juvenile- see photo & adults)	Yes (juvenile & adults around <i>Orbicella-Colpophyllia</i> & <i>Siderastrea</i>)	Yes (juvenile)		
Habitat used by <i>H. flavolineatum</i>	Yes	Yes	Yes	No (Not suitable habitat)	
Species composition (coast toward middle of the bay)	<i>Thalassia</i> <i>Thalassia & Syringodium</i> <i>Thalassia & Millepora</i> <i>Thalassia & Sponges</i> <i>Thalassia & Octocorals</i> <i>Thalassia & coral patch</i> <i>Thalassia & Siderastrea</i>	Reef crest with <i>Millepora</i> (50% cover) & <i>Porites</i> (5%) Big massive coral colonies: <i>Orbicella-Pseudodiploria-Colpophyllia</i> Slope - coral-rubble-sand	<i>Rhizophora mangle</i>		
Habitat Depth (m)	0-2.5	0-4	1	5-20	
Bottom substrate type	Clay>Silt>sand	Gravel-sand	Silt-clay	Silt-clay-rubble	
<i>Thalassia</i> Leaf average height (range & average; cm)	22-36; 26				
<i>Syringodium</i> leaf height (range & average; cm)	59-64.5; 62				[1]
<i>Thalassia</i> Shoot density (range & average - 25x25 cm)	30-105; 50				[1]
Shoot density (range & average - m²)	120-420; 200				
Dominant species in the habitat	<i>Thalassia testudinum</i> <i>Syringodium filiforme</i> <i>Millepora alcornis</i> <i>Altilogorgia</i> <i>Plexaura</i> <i>Briareum</i> Erect and encrusting sponges <i>Siderastrea siderea</i>	<i>Porites astreoides</i> <i>Porites porites</i> <i>Favia fragum</i> <i>Orbicella faveolata</i> <i>Pseudodiploria strigosa</i> <i>Colpophyllia natans</i> (2m diameter) <i>Diploria clivosa</i> <i>Siderastrea siderea</i>	<i>Rhizophora mangle</i>	NA	
Fish community	Gobiidae, Haemulidae y Scaridae	NA			[1]
Fish richness	217 (67 families)	NA	NA NA	NA NA	[2]
Other <i>Haemulon</i> observed	<i>Haemulon bonariense</i> <i>Haemulon sciurus</i> <i>Haemulon plumierii</i> <i>Haemulon aurolineatum</i> (large groups)	NA NA NA NA	NA NA NA NA	NA NA NA NA	[1]

Table 1 (continued)

	Ecosystems - benthic habitats				Literature
	Seagrass	Fringing Reef	Mangrove Roots	Soft bottom	
Fish juveniles observed	Surgeons and snappers	NA	NA	NA	[1]
Dominant fish trophic guilds	Omnivores (<60%) and carnivores (18%)	NA	NA	NA	[1]
<i>H. flavolineatum</i> habitat quality based on relative density (ind/2500m²)	10	NA	NA	NA	[1]
Percent of relative abundance of <i>H. flavolineatum</i> (respect to the total species sampled)	1.8	NA	NA	NA	
Habitat conservation status (scale from 0-10; 10=highest value)	10	10 (<i>Millepora crest</i>) - 6 (massive corals)	10	NA	
(qualitative assessment from an expert; Navas-Camacho, R.)					
Habitat health	No presence of fungus (<i>Labyrinthula sp.</i>)	40 - 50% Live coral cover (Reef crest) <i>C. natans</i> (white plague)	NA		
Rehabilitation	Neccesary (North)	Only to massive corals along the crest	Neccesary (Central)		
Stressor	Sedimentation Artesanal indigenous fishing Fishing - nets, line, fork type harpoon Boat and ships transit Marine waste - plastic	Anchor damage Fishing Hurricanes	Pollution - oil		

The structural characteristics and status of the habitats are presented. The relative coverage of each habitat was calculated from the patch size data extracted from the ecosystem maps. Most information comes from field sampling (August 2022, INVEMAR in press), and few data come from the literature ([1] Sanchez-Valencia et al. [124], [2] Parque Nacionales Naturales de Colombia [109]), as indicated in the rows. NA means no available information

Two structural connectivity analyses were performed: at the bay level and zones (explained in the following section). The structural indices selected describe characteristics between and within each ecosystem (mangrove, coral reef, and seagrass), e.g., relative percent cover of each ecosystem, respects the sum of the coverage of the three ecosystems in the entire bay (PLAND, units 0 - 100%); relative percent cover occupied by the largest patch, respects the total cover of each ecosystem (LPI, 0 - 100%); average size of the patches (AREA, ha) at each ecosystem; average distance to the nearest neighbor between patches of the same ecosystem (ENN, m); number of patches of each ecosystem (NP), average shape complexity of the patches for each ecosystem, when adjusted to a squared standard (SHAPE, = 1 Square Shape, >1 Irregular Shape). The structural CONTAG and IJI indices analyze the aggregation of cells (raster pixels), corresponding to patches, and the interspersión degree of patches from different ecosystems, respectively (0 - 100%). The CONTAG and IJI indices were applied to assess features at the bay level (the sum of the three ecosystem coverages). All structural indices were analyzed

with Fragstats 4.2.1.603 [89]. Fragstats are widely used in fragmentation studies in terrestrial ecosystems [1, 25, 40] and can be used in aquatic environments [107].

Usually, the AREA, SHAPE, and (EEN) indices are calculated using the average; however, this measure may be biased by the maximum and minimum values. In our case, we observed wide variability in the patch size. Therefore, we also decided to use the median, which is less sensitive to extreme data and shows a better distribution of our ecological data for interpretation. We then performed Kruskal–Wallis and Mann–Whitney U tests (R studio) to examine significant differences between ecosystems for each of the three indices. The use of the median was not applied to other indices since they are expressed in relative percentages (PLAND, LPI, CONNECT) or total counts (NP) or have a unique value (CONTAG, IJI) [89]. Furthermore, based on patch sizes, we calculated the relative coverage of each habitat potentially used by *H. flavolineatum* in the entire bay and for zone. The patch area within each habitat was calculated to have an idea of the minimal patch size potentially used by the species in the bay [119].

Potential functional connectivity analysis

The functional variables were the CONNECT index and *H. flavolineatum* migration distance. The functional CONNECT index provides information within the same ecosystem, namely, connectivity between patches. For the CONNECT index, we used four arbitrary distances (100, 250, 500, and 1000 m) to simulate different possible home range scenarios, in addition to the one reported for *H. flavolineatum* (0–500 m). We simulated home ranges based on reported migration distances for fish families living in the ecosystems of interest, such as Haemulidae (1000 m), Lutjanidae (500 m), and Serranidae (100 m) [44, 51].

Based on graph theory, which involves a set of nodes (patches) and links (potential connections and distances between patches), we built a bipartite graph to represent the potential functional connectivity using published information on the *H. flavolineatum* juveniles home range (0–500 m) from seagrass to mangrove (stage 4) and its ontogenetic migration distances (up to 14 km) from mangrove to reefs (stage 5). We only simulated these two stages due to information available in the literature. For the first potential functional connectivity analysis, we took seagrass cover as one set and mangrove cover as the other set in the graph, and for the second analysis, we took mangrove cover as the first set and reef cover as the second set. Therefore, there are no within-set (ecosystem) nodes with links between them, which is ideal for examining potential functional connectivity between ecosystems. To know the distance of the links between neighboring patches or any pair of ecosystems (nodes), we used the edge of the patches as a reference (perimeter/border) to calculate the closest distance to another patch. Consequently, multiple edges were used for the same patch, trying to measure the shortest distance between patches (different ecosystems). Dataset analysis could be found at Rodríguez-Torres and Acosta [121].

Potential functional connectivity analysis of *Haemulon flavolineatum* juvenile migration from seagrass to mangroves (stage 4)

Using a theoretical migration threshold of 0 to 500 m reported for juveniles, the connectivity analysis in the bay showed three groups of patches isolated by distance (exceeding 500 m); which we called the South, Central, and North zone for a more detailed connectivity analysis within them. Seagrass and mangrove patches within each zone were more likely to be connected, but patches between zones were not. In each zone, linear distances from seagrass patches to mangrove patches were drawn as links, assuming a linear juvenile movement behavior. A single seagrass patch could have several links to different mangrove patches. Five nonoverlapping arbitrary

distance ranges were proposed for *H. flavolineatum* juveniles (0 to 100, 101 to 200, 201 to 300, 301 to 400, and 401 to 500 m) to establish the distance range with the most drawn links. Linear distances were calculated in ArcGIS using its Measure tool with geodetic measurement calibration. Finally, we identified the highest valency patch in each ecosystem. Valency is the sum, across distance ranges, of the number of links drawn to a single patch. We excluded isolated patches (*i.e.*, located at distances greater than 500 m) from this analysis.

Potential functional connectivity analysis of *Haemulon flavolineatum* juvenile migration from mangroves to reefs (stage 5)

To represent ontogenetic stage 5 *H. flavolineatum* migration, a bipartite graph, with a single zone (component; the whole bay) was built since all nodes (patches) of both ecosystems (mangrove and reef) are connected within 14 km, the maximum reported *H. flavolineatum* juvenile migration distance [99]. Three thresholds (linear distance) were proposed to examine the distance range with the most links, 0 to 4 km plus two arbitrary ranges (4.1 to 8 km and 8.1 to 14 km), to cover the reported maximum migratory distance for *H. flavolineatum*. Linear distances were calculated in ArcGIS 10.7.1 using its Measure tool with geodetic measurement calibration. In this analysis, obtaining the highest valency patch in each set (ecosystem) was unnecessary because all mangrove patches are connected to the reef patches and would have the same valency value (number of links). Only two isolated mangrove patches located at distances greater than the threshold of 14 km were excluded from the analysis.

Our connectivity network representation among BPK ecosystems does not allow us to consider all the intrinsic or extrinsic variables that are known to influence functional connectivity and the species' habitat use. The essential extrinsic variables included directly or indirectly in our connectivity network were habitat structure (number of patches, distribution, size, type of ecosystem), habitat fragmentation (indirect relationship between the number of patches and size), quality of the habitat (larger patches will have better conditions and resources for migration), habitat permeability (structural connectivity) (see [46, 80, 135]). Other extrinsic (predator-prey interactions, competition and disturbances) and intrinsic variables (species genotype, phenotype, mortality rate, development, reproductive performance, behavior and migratory dispersal strategies) [33, 80, 135] were not considered due to: (i) this information is currently not available in the literature and its collection in the field is outside the scope of our work. (ii) connectivity networks must first consider robust data to explain basic ecological processes [90] and predict [127].

Assumptions

To build the network, based on the literature [68] and field data (juveniles and adults in different ecosystems; Table 1), we assume: 1. Larvae could disperse throughout the bay given the current pattern [44], which is supported by the juveniles and adults presence in the three ecosystems [120], in consequence patches of different ecosystems could be ecologically connected by juveniles along the bay. 2. *H. flavolineatum* could find suitable habitats at BPK, as defined in the introduction, meaning the conditions and resources necessary for this species (to complete its life cycle and to allow population growth) are present. 3. We assume that even small patches could be nodes in the network. In consequence, we did not exclude patches due to size or set a minimum patch size threshold because, to our knowledge, this has not been reported in the literature. In our study, we identified the smallest patch size in each ecosystem: 3.2 m² for seagrass (south), 340 m² for mangroves (center), and 61006 m² for reefs (south) and were included in the network. 4. In the network, we assume as a valid approximation of patch size the total mangrove area, since the dominant species is *Rhizophora mangle*, and the underwater roots are very shallow (1-2 m deep), so *H. flavolineatum* juveniles could make use of all this habitat, as observed in the field. The total mangrove patch area (appropriate patch size metric) was used to estimate structural connectivity indices (PLAND, LPI, AREA and SHAPE), to avoid bias due to underestimation, by using the outer edge of the mangrove patch as used in other studies [6, 8]. 5. We assumed that smaller juveniles (stage 4) movement was hindered by distance for seagrass to mangrove migrations [12], since exceed 500 m, and the matrix is a soft/muddy bottom [48]. According to Burke [17] and Kimirei et al. [72] soft/muddy bottom is mostly inhabited by adults and late juveniles (stage 5), not small juveniles. 6. We assume that links at short moving distances are more likely to occur than links at longer distances. This is because the risk increases with distance, when moving between patches and the matrix. Shorter distance traveled by immature juveniles will mean a higher survival probability of reaching the reef, maturing, and reproducing [19, 54]. Then, nearby and connected patches, from different ecosystems, are those that should be prioritized for stages 4 and 5.

Results

Structural connectivity

Seagrass

In the total BPK area of 14080 ha, seagrass had 197 patches and was the most representative ecosystem, with the highest coverage share in the seascapes (8.93%), but it had the highest level of fragmentation. Seagrass had the

lowest average patch size (6.59 ± 23.04 ha), with a median of 1.17 ha, a maximum value of 244.67 ha and a minimum value of 0.001 ha, showing high data dispersion (Tables 2 and 3). It had an ENN of 79.63 ± 109.87 m, and it had the lowest average shape index of 1.89 ± 0.81 (1.64 for median). Concerning the total seagrass cover, the most sizable seagrass patch accounted for 21.20% of the ecosystem. Of the three bay zones, South seagrass patches had the highest ENN index value (107.76 ± 177.03 m), although they had a median of 48.02 m, the most extensive seagrass patches on average (12.23 ± 36.25 ha), the greatest coverage by extension (602 ha), the largest seagrass patch in the bay (244.21 ha), and the most natural and complex nonintervened patch forms (*i.e.*, curvilinear or amoeboid), with an average shape index value of 2.02 ± 0.93 (1.77 for median). These results revealed less fragmentation in the South. In contrast, the North contained patches with the smallest average size (2.17 ± 4.99 ha) with the lowest median (0.58 ha; max value of 39.42 ha and min value of 0.003 ha), the highest number of patches (98), the lowest coverage by share and extension (26%; 215 ha), and the most geometric patch forms, with a shape index value of 1.74 ± 0.74 . However, it had the shortest average distance to the nearest neighbor (61.30 ± 64.63 m), with a median of 38.01 m, a maximum value of 420.52 m and a minimum value of 2.23 m. Overall, these values revealed significant fragmentation in the northern zone of the bay. The central zone of the bay had the largest coverage of seagrass of the three zones by share (80%) and the highest median distance to the nearest neighbor (62.76 m; max value of 342.81 m and min value of 2.23 m) (Tables 2 and 3, Fig. 3).

Mangrove

The mangroves had 55 patches, covering 7.96% of the BPK seascape. The shortest average distance to the nearest neighbor of 52.27 ± 60.08 m (30, 338.89, 2 m for median, max and min value, respectively) was significantly different when compared to reef and seagrass patches ($H = 11.83$, $N = 258$, $p = 0.00269$). The average patch size was 18.41 ± 62.67 ha (0.80, 443.63, and 0.0334 ha for the median, max and min values, respectively), showing high data dispersion, where 50% of the patches had sizes considerably smaller than average. The average shape index was 2.34 ± 1.52 (1.62, 6.81, and 1 for the median, max and min values, respectively). Concerning the total mangrove cover, the most sizable patch accounted for 35.49% of the ecosystem. Of the three zones, the North had the most extensive mangrove patch on average (36.35 ± 105.54 ha), with the greatest median value (0.82 ha), the greatest coverage by extension (617 Ha), the largest patch that occupies 70% of the ecosystem's extension, and the shortest

Table 2 Fragmentation analysis (Fragstats) at ecosystems and seascape level in the Bahía Portete-Kaurrele MPA

Coverage	PLAND (%)	NP (#)	LPI (%)	AREA (Ha)			SHAPE (=1/>1)					ENN (m)						
				Mean	SD	Min	Max	Median	SD	Min	Max	Median	Mean	SD	Min	Max	Median	
CR	1.43	6	49.5	33.52	32.35	18.87	99.68	6.11	3.30	1.18	3.78	4.70	1.49	256.54	190.69	215.54	601.99	85.04
SG	8.93	197	21.20	6.59	23.04	1.17	244.67	0.001	1.89	0.81	1.64	5.07	1	79.63	109.87	47.51	1050.83	2.23
M	7.96	55	35.49	18.41	62.67	0.80	443.63	0.033	2.34	1.52	1.62	6.81	1	52.27	60.08	30	338.89	2
Seascape	CONTAG (%)		58.18	IJI (%)	76.55													

CR Coral reefs, M Mangrove, SG Seagrass, descriptions of each index (PLAND, NP, LPI, AREA, SHAPE, ENN, CONTAG and IJI) as in text. Seascape (bay) refers to the sum of the coverage of the three ecosystems. In bold are the significantly higher values of area and shape for the reef compared to the other two ecosystems, which would imply better conditions for the species, while the shorter distance to the nearest neighbor is significantly better for the connectivity of the species in the mangrove (statistical details supplement Tables 3, [121]).

Table 3 Fragstats analysis at ecosystems level giving by zones in Bahía Portete-Kaurrele MPA seascape

	SOUTH	NP (#)	LPI (%)	AREA (Ha)			SHAPE (=1/>1)			ENN (m)			PLAND								
				Mean	SD	Median	Max	Min	Mean	SD	Median	Max	Min	Ha	%						
	CR	6	49.5	33.5	32.35	18.87	99.49	6.1	3.30	1.18	3.78	4.70	1.49	256.84	190.72	215.54	601.99	84.95	15%	201	
	SG	59	40.53	12.23	36.25	1.46	244.21	0.001	2.07	0.93	1.77	4.86	1	107.76	177.03	48.02	1050.83	2.23	45%	602	
	M	28	34.9	14.54	35.32	0.81	172.70	0.15	2.39	1.66	1.51	6.63	1	58.07	68.38	34.65	338.89	3.16	40%	494	
	CENTRAL																				
	SG	40	39.64	8.37	21.8	2.06	132.48	0.002	1.87	0.75	1.70	4.25	1	72.62	64.62	62.76	342.81	2.23	80%	334	
	M	11	47.49	6.43	11.22	0.64	39.79	0.034	2.47	1.59	1.75	6.8	1.18	66.66	56.90	39.62	156.40	3.16	20%	83	
	NORTH																				
	SG	98	18.33	2.17	4.99	0.58	39.42	0.003	1.74	0.74	1.52	5.08	1	61.30	64.63	38.01	420.52	2.23	26%	215	
	M	16	70	36.35	105.54	0.89	435.60	0.089	2.30	1.20	1.66	5.13	1.26	37.64	41.46	29.42	171.81	2	74%	617	

CR Coral reefs, SG Seagrass, M Mangrove). Description of each index (NP, LPI, AREA, SHAPE, ENN, PLAND) as in the text

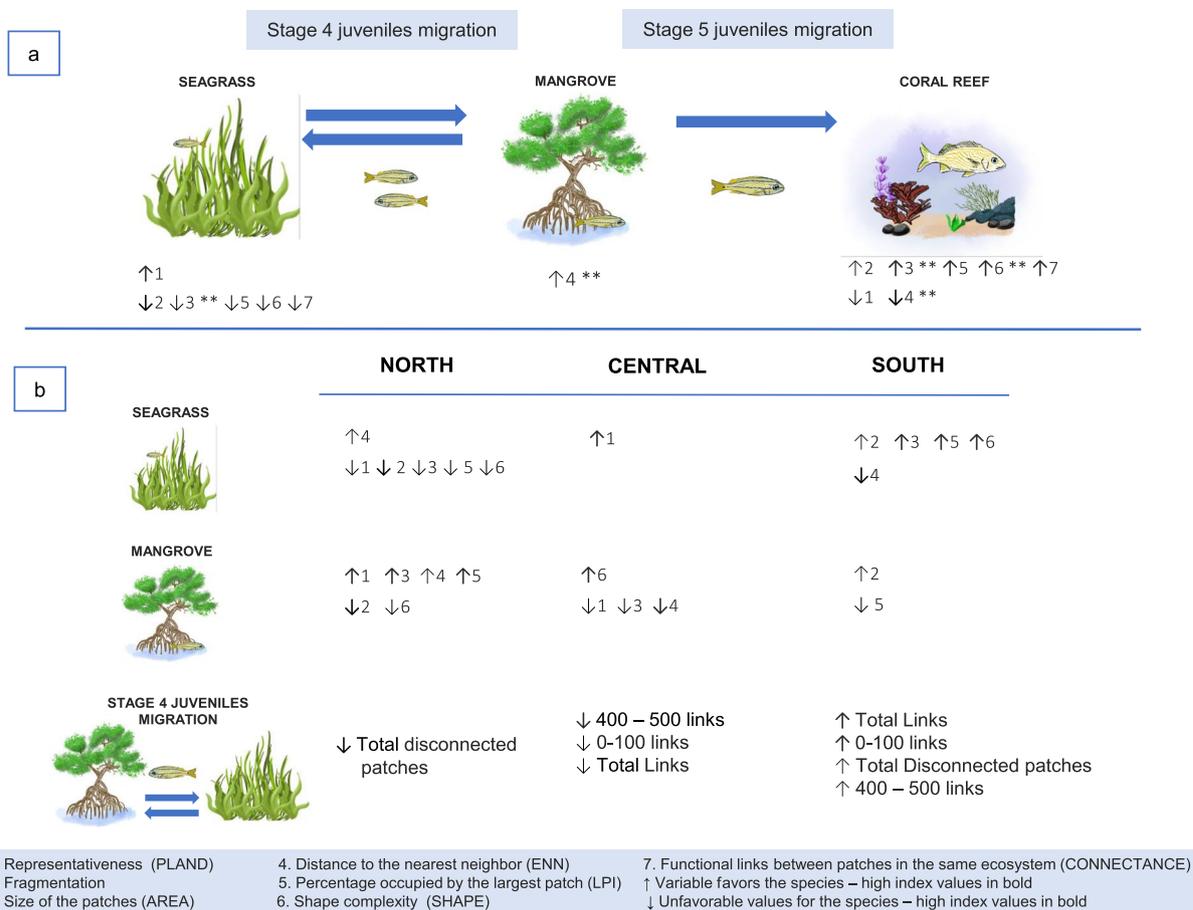


Fig. 3 Summary graph of the variables analyzed for the connectivity representation of *Haemulon flavolineatum* migratory potential in the Bahía Portete-Kaurrele MPA. The sum of the arrows indicates whether the variables are beneficial (up arrows) or detrimental (down arrows) to the species. Part A summarizes and compares the structural and functional connectivity indices for each ecosystem. This could be interpreted as the quality of the habitat where the juvenile lives (according to the measured indices), as well as the habitat conditions that the juveniles will experience when migrating. The species use all three ecosystems as observed in the field; therefore, in theory, they could fulfill life stages four and five. However, the indices suggested that the reef is a relatively better habitat for the species in the MPA. Part B summarizes and compares the structural and functional connectivity indices of seagrass and mangroves between the bay areas. Note that mangroves are better in the northern zone and worse in the central zone, while seagrasses are better in the south and worse in the north. The migration of *H. flavolineatum* juveniles is favored mainly in the south. In the scheme, representativeness refers to the coverage (ha) of each ecosystem in each zone of the bay, and fragmentation is the relation between coverage and the number of patches. Asterisks refer to significant differences

average distance to the nearest neighbor ($37.64 \pm 41,46$ m) with the lowest median (29.42 m). These results show less fragmentation in the North. The central zone, in contrast, contained patches of the smallest average size (6.43 ± 11.22 ha) with the lowest median (0.64 Ha) and the lowest coverage by share and extension (20%; 83 ha), and it had the highest ENN index value (66.66 ± 56.90 m). However, the Central had the greatest shape index value (2.47 ± 1.59). Overall, these values show significant fragmentation in the central zone of the bay. The South mangrove had the smallest percentage occupied by its largest patch (34,9%) and the lowest median shape index (1.51) (Tables 2 and 3, Fig. 3).

Coral reef

The reef ecosystem was underrepresented in the bay, revealing the lowest coverage in the seascape (1.43% of the total BPK area), with only six patches in the southern part of the bay. Compared to seagrass and mangroves, the reef had the highest average patch size of 33.53 ± 32.35 ha (18.87, 99.68, and 6.11 ha for median, max and min values, respectively) and the highest shape index value of 3.30 ± 1.18 (3.78, 4.70, and 1.49 for median, max and min values, respectively). Both indices were significantly different between reefs and seagrass and reefs and mangroves ($H= 11.83, N= 258, p= 0.00269$; $H=7.41, N= 258, p= 0.02457$, respectively; Supplementary Tables 3).

Additionally, the patches of this ecosystem showed that the average distance to the nearest neighbor of 256.54 ± 190.69 m (215.54, 601.99, 85.04 m for median, max and min value, respectively) was significantly different when compared to seagrass and mangrove patches ($H=15.19$, $N=258$, $p=0.0005$), and the values obtained were higher when compared to seagrasses ($Z=2.94$, $U=168$, $p=0.0032$) and mangroves ($Z=3.21$, $U=36$, $p=0.0012$) (Supplementary Tables 3). The reefs had the highest percentage occupied by the largest patch (49.56%). Therefore, the reef reveals less fragmentation. Finally, of the 3 ecosystems, reefs occupy 15% (201 ha) of the cover (refers only to the southern part of the bay; Tables 2 and 3, Fig. 3).

Seascape connectivity

At the seascape level, CONTAG (contagion) was 58.1%, and IJI (intercalation) was 76.5%, implying that patches of different ecosystems were more dispersed and intercalated, thus reflecting high spatial heterogeneity, whereby small patches limited the connectivity between patches of the same ecosystem but increased the connectivity between patches of different ecosystems (Table 2). Although we did not find differences in AREA, SHAPE and ENN indices when comparing bay zones for mangroves and seagrasses (Supplementary Table 3 [121]), the South has the presence of the three ecosystems, less fragmentation and the overall structural characteristics of the seagrass and mangroves that are suitable for *H. flavolineatum* to reach stages 4 and 5 of its life cycle (Fig. 3).

Functional connectivity

Figure 4 illustrates the connectivity in the seascape as revealed by the CONNECT index values. The

connectivity results are directly proportional to distances, meaning that the connectivity between patches of the same ecosystem tends to increase as the distance range increases. These values were higher in the coral reef ecosystem due to its smaller number of patches and its clustering in the southern part of the bay. In contrast, seagrasses and mangroves, with a higher number of patches, were more dispersed throughout the bay and had higher connectance values. However, no ecosystem exceeded 50% connectance within their patches. Then, the structural configuration of coral reef, seagrass, and mangrove patches in BPK tends to be more functional for species with larger home ranges (>1000 m).

Juvenile migration from seagrass to mangroves

84% of seagrass and mangrove patches were found to be functionally connected by *H. flavolineatum* migrations using the 0 to 500 m range, the remaining 16% of patches were outside this range and were considered disconnected in our analysis. The obtained juvenile migration analysis drew 247 links connecting patches between both ecosystems throughout the bay, with almost half the links (117) with migration distances between 0 and 100 m (Table 4), indicating that the configuration of the ecosystem patches would make short migrations more likely. The South patches contained the most functional links (104), concentrated mainly within the 0 to 100 m distance range (48), with 20 links in the longest distance (from 401 to 500 m), and with the fewest disconnected patches (6). The seagrass patch with the highest number of links (9) occurred in the South. The North had the most disconnected patches (23), the mangrove patches with the highest number of functional links (27) and

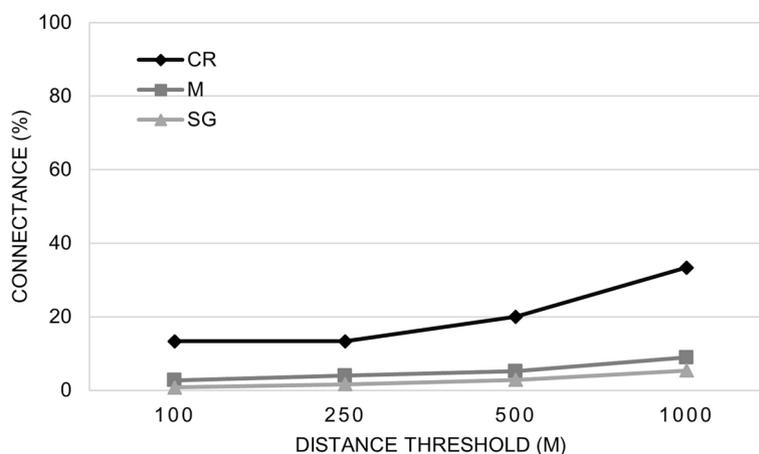


Fig. 4 Connectance (percentage) represents functional links between patches of the same ecosystem at different migration distance thresholds in the Bahía Portete-Kaurrele MPA. The results of the CONNECT index were obtained with Fragstats. CR (coral reefs), M (mangrove), SG (seagrass)

Table 4 Functional links (FL) of the ontogenetic migration from seagrass to mangroves of *Haemulon flavolineatum*

Distance (m)	Number of links			Total FL Bay
	South	North	Central	
0 - 100	48	47	22	117
101 - 200	12	12	7	31
201 - 300	12	15	9	36
301 - 400	12	8	9	29
401 - 500	20	12	2	34
Total FL Zones	104	94	49	247
Disconnected patches	6	23	12	41
Valency SG	9	4	7	
Valency M	11	27	18	

Distance thresholds are based on the limits reported in the literature regarding the migration of *H. flavolineatum* from seagrass to mangrove

concentrated seagrass patches with the lowest number of links (4) (Fig. 5, Table 4).

Highly linked patches also had large perimeters; for instance, the mangrove patches in the North and Central zones were conveniently located close to each other, such as the seagrass patch with the highest number of links in the North (Fig. 5). Because of its salient total number of links, majority of short-distance links, and fewer disconnected patches, the South revealed a great connectivity potential for *H. flavolineatum* juveniles to successfully achieve their ontogenetic migration stage from seagrass to mangrove (Table 4).

Juvenile migrating from mangroves to coral reefs

97% of mangrove and reef patches were found to be functionally connected by *H. flavolineatum* migrations using the 0 to 14 km range, the remaining three percent of patches were outside this range and were

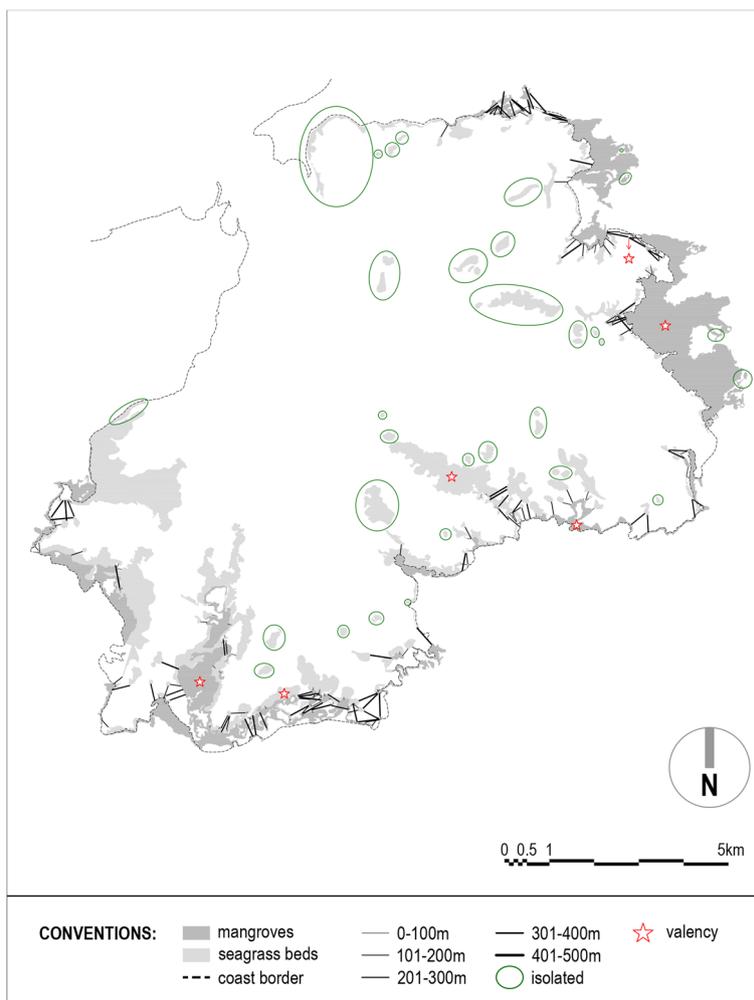


Fig. 5 Functional connectivity of the *Haemulon flavolineatum* ontogenetic migration from seagrass to mangrove in the Bahía Portete-Kaurrele MPA (stage 4 of its life cycle). Line thickness increases with distance thresholds. Green circles represent isolated patches. Scale 1/80000

considered disconnected. But only about half of the mangrove patches had connections to reefs at the shortest distance (0-4 km). The obtained juvenile migration analysis generated 328 links in the bay, with a high prevalence of connections within the 8.1 to 14 km range (125; Fig. 6). At the coral reef patch level, within the shortest migration distance range of 0 to 4 km, patch 6E (Fig. 6) had the highest number of connections (28) and would experience the most visits by

stage 5 *H. flavolineatum* juveniles from the mangrove, while patch 6A (Fig. 6) had the fewest connections (8). For the intermediate migration distance range of 4.1 to 8 km, patch 6C obtained the highest number of links (24; Fig. 6), closely followed by patches 6B (23; Fig. 6) and 6A (20). Within the furthest migration distance range (8.1 to 14 km), patch 6A obtained the most links (25). Only patch 6A, outside the established maximum migration distance, was disconnected from two mangrove patches (Fig. 6, Table 5).

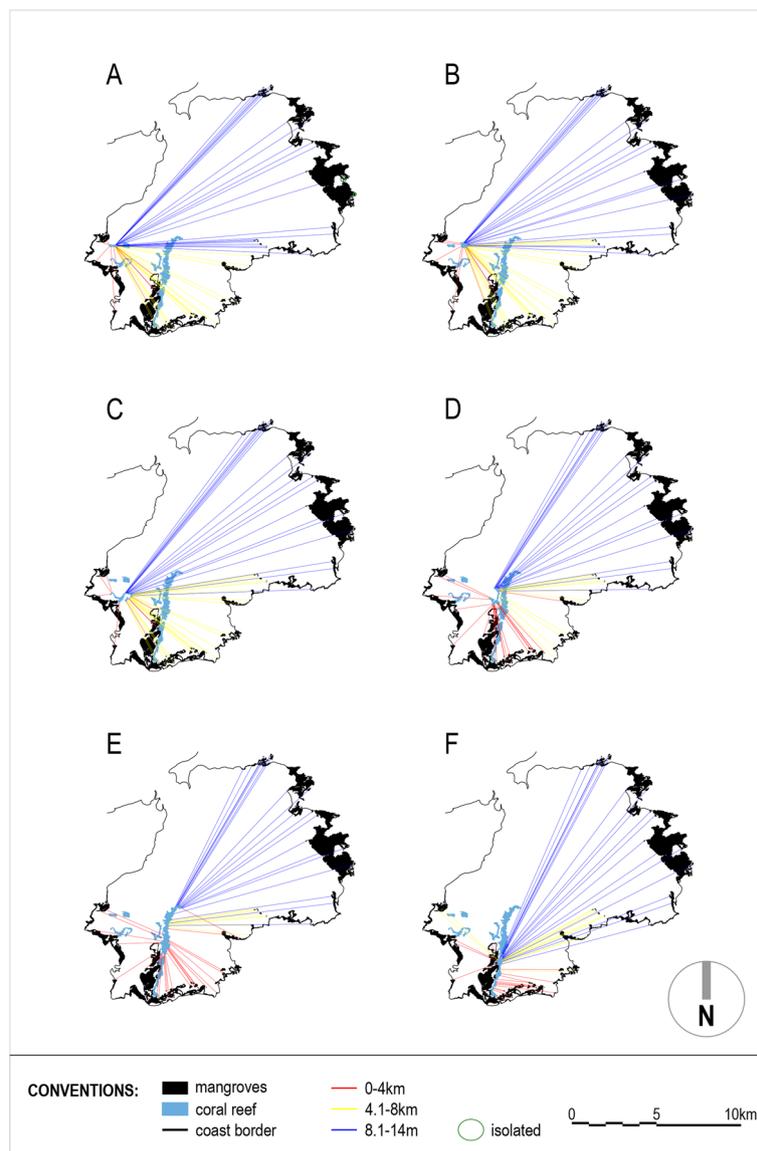


Fig. 6 Functional connectivity of the *Haemulon flavolineatum* ontogenetic migration from mangrove to reefs in the Bahía Portete-Kaurrele MPA (stage 5 of its life cycle). Coral reef (Blue), Mangrove (Black). Distance thresholds from 0 to 4 km (red lines), 4.1 to 8 km (yellow lines), and 8.1 to 14 km (blue lines). Patch representation listed from left to right and top to bottom: (A) Patch 6A, (B) patch 6B, (C) patch 6C, (D) patch 6D, (E) patch 6E, (F) patch 6F. Scale 1/250000

Table 5 Functional links (FL) of the ontogenetic migration from mangroves to coral reefs of *Haemulon flavolineatum*

Distance (km)	Number of links per patch						Total LD
	5A	5B	5C	5D	5E	5F	
0 - 4	8	11	11	24	28	23	105
4,1 - 8	20	23	24	11	8	12	98
8,1 - 14	25	21	20	20	19	20	125
Total LP	53	55	55	55	55	55	328
Disconnected patches	2	0	0	0	0	0	

Distance thresholds are based on the limits reported in the literature regarding the migration of *H. flavolineatum*. Total LD (number of links for each distance range), Total LP (number of links for each patch)

Discussion

We assessed potential functional connectivity at MPA BPK and ontogenetic migrations for *H. flavolineatum*, revealing that the bay has a spatial configuration that theoretically allows *H. flavolineatum* juveniles to complete stages 4 and 5 of their life cycle. Three lines of evidence support this statement. (i) The obtained CONTAG and IJI index values (58.18% and 76.55, respectively) indicate great connectivity between patches of different habitats, in accordance with a high spatial heterogeneity seascape configuration, with smaller, more interspersed and dispersed patches [89]. (ii) The short distances between seagrass and mangroves and between mangroves and the reef could facilitate the ontogenetic migrations of *H. flavolineatum* life stages 4 and 5. (iii) Although the CONNECT index showed low values (Fig. 4), indicating reduced connectivity between patches of the same habitat, the presence of *H. flavolineatum* in the three habitats studied [120] suggests that connectivity would occur between patches of different ecosystems. The bay hypersalinity conditions [44] could also favor the presence of juveniles in nursery areas (mangrove), as has been reported in other Caribbean sites [64]. However, movement restrictions within or between habitats (e.g., soft bottom matrix, predators, distance) or low reef total area can affect the *H. flavolineatum* population size and partially explain the low relative densities observed (Table 1) compared to other observations in nursery habitats in the Caribbean [18, 69].

Migrations during stages 4 and 5 of *H. flavolineatum* juveniles are more likely to occur in the southern BPK, where there is low fragmentation, the presence of large patches, and the spatial arrangement of mangroves and seagrass (with scattered hard corals and debris) could make this area more suitable for juvenile migration, the latter corroborated by the greatest number of connections found in the smallest distance threshold (0-100 m; Table 4 and Fig. 5). The importance of seagrass and mangroves as nursery habitats for different fish species, including *H. flavolineatum*, has been demonstrated in

the archipelago of San Andres and Providencia [129], and other studies support this view (e.g., [42, 87, 116]). In addition, Kendall et al. [71] showed that *H. flavolineatum* juveniles are more abundant near mangroves or seagrass (nursery areas), and similar results have been obtained for this species in La Parguera (Puerto Rico), Providencia and Santa Catalina (Colombia), and Honduras [3, 69, 110] and for other migratory species (e.g. *Plectorhinchus* spp and *Apogon* spp) in the Bazaruto Archipelago (Mozambique) and in Kaledupa (Indonesia) [12, 136]. Coral reef patches occur only in the south of the BPK, where the 6E reef patch is relevant for functional connectivity due to its higher number of short-distance connections (0-4 km, Table 5 and Fig. 6). Nagelkerken et al. [99] found that this species is more likely to avoid migrating from its nursery areas to very isolated reefs if there are patches nearby that provide conditions and resources for growth and survival. In addition, Zollner and Lima [146] highlight the trade-off between safety and risk (relative costs of moving between different habitats) and the benefit of moving to adjacent and nearby patches to reduce the chance of mortality during migration. The south has similar values than the north in most mangrove indices (Fig. 3), but the south has the higher values in most of the seagrass indices compared to the northern and central zone, also, we found less disconnected patches for seagrass to mangrove migration and it has the coral reef patches closer. As stated by Nagelkerken et al. [97], the spatial arrangement of habitat patches determines fish-mediated connectivity between different marine ecosystems. Thus, the southern BPK ecosystems could allow the fulfillment of stages 4 and 5 of *H. flavolineatum* juveniles.

Isolation by distance has been a critical factor for connectivity in other fish species [12, 84]. Caldwell and Gergel [19] hypothesized that if the total cost of displacement due to distance is too high, organisms will not move across the seascape. This may be occurring for juveniles (stage 5) in the northern mangrove patches of the BPK, where the number of long-distance links (8.1 to 14 km, less likely to occur) exceeds the number of short-distance

links (0 to 4 km, Fig. 6), and may also be the case during seagrass to mangrove migration (stage 4, Fig. 5). However, movement flexibility may occur depending on the quality, quantity, and availability of resources within the patches, the possibility of conducting stepping-stone movements [77] and the plasticity of *H. flavolineatum* in the use of habitats to fulfill its life cycle [72]. Tagging juveniles and following them along the seascape may be a way to check several hypotheses, the use of resources within and between ecosystems, stepping-stone movements, patch isolation, predation risk, matrix negative effects, and the use of different ecosystems besides those analyzed. Opposite to what was proposed, Shulman [128] suggests that predation on *H. flavolineatum* decreases with distance from the reef, and argues for the avoidance of nursery areas (mangrove or seagrass) close to the reef, as they have a higher predation rate due to the presence of a greater number of predators on the reefs [86]. This hypothesis should also be evaluated since fishes can shift over multiple resident and feeding areas over intermediate time frames, thus revealing considerable navigation skills [4].

Some connectivity network limitations are discussed below. First, the number of patches in each zone may bias the number of functional links. As the number of patches increases, so does the probability of more links, especially if these patches are within the proposed threshold distances. A high level of ecosystem fragmentation is a negative aspect since smaller patches (small area/perimeter ratio e.g. Figure 5, higher valency seagrass patch, marked with a star in the northern zone or smallest mangrove patches in the central zone) lose functionality for *H. flavolineatum*. The latter because smaller fragmented patches will have less complexity and less core suitable area (diminishing nursery benefits), limiting their habitat use for feeding and refuge, and increasing the risk to predators as suggested by Olson et al., [106]. Fragmentation effects, such as those observed in the Bay, have been observed with the massive loss of the *Zostera marina* ecosystem in Morro Bay, California, USA, resulting in changes in species composition (restricting population connectivity and leading to range contraction) with long-term effects on trophic chains [105].

Detailed studies are needed to determine whether a habitat (a place with all the conditions and resources necessary for the survival, development, reproduction, and establishment of local populations; [10] meets *H. flavolineatum*'s minimal requirements [78, 96, 139], which may vary depending on the species life stage [14]. Moreover, it is necessary to measure *H. flavolineatum* population parameter differences between patches, habitats, and ecosystems [94] and conduct more in-depth studies of the physicochemical variables that affect

habitat conditions [37, 62]. Our analysis did not consider a stepping-stone movement when adjusting theoretical maximum migration distances, but future studies should evaluate distances above 500 m - stage 4 and 14 km - stage 5, as stepping-stone movement could allow juveniles to perform longer migrations or displacements within or between different habitats, while facing lower risks and avoid intraspecific competition [125].

Ecosystem connectivity network for the first three stages of *H. flavolineatum*'s life cycle, larval dispersal, larval settlement, and ontogenetic migration from soft bottoms with gravel to seagrasses, was not studied due to a lack of information on these processes in the literature and the absence of field data for *H. flavolineatum* as stated previously. We must identify the habitats *H. flavolineatum* uses in the early stages of the life cycle, the bottleneck pressure on its populations, and the sink areas for larvae, recruits, and juveniles [41, 98]. Elsewhere in the world, there may be no mangroves, so the species could replace them with any other habitat (for food or shelter), consequently, they must be included in the connectivity analyzes of stages 4 and 5. A further step will be to include *H. flavolineatum* distribution and abundance data and physicochemical variables for the habitat patches [24, 115] to better interpret the species ecology.

Accelerated climate change challenges species to adapt to extreme environmental conditions and dynamic landscape structures and ecosystems to increase their resilience [61]. Strongly connected areas and habitats are more resilient to climate change because important ecological processes for ecosystem stability are more likely to occur there [142]. The bay's southern zone has the highest connectivity potential and requires management and protection. In Puerto Nuevo, south of the bay (Fig. 2), intended dredging (so that large vessels can access the existing harbor) will negatively affect most coastal ecosystems [93]. Sediment mobilization will increase water turbidity, further limiting the proper development of ecosystems (reefs and seagrass) and fish navigation, making juveniles more susceptible to predation [88]. Additionally, an increase in the sedimentation rate decreases benthic organism fixation, recruitment, and survival [35]. The South, with a higher number of short links (considered by [91] as an effective area), would be a valuable area for the protection of *H. flavolineatum*, particularly when considering the species' vulnerability to disturbances because of its high fidelity to specific sites [77]. The expansion of the port could result in the degradation and/or disappearance of patches, thus increasing the migration distances of the species, or in the worst-case scenario eliminating the coral reef, which would result in the interruption of the species final migration stage. Puerto Nuevo is precisely where our network representation shows the best

potential for ecosystem connectivity, so it is necessary to integrate ecosystem welfare in future sustainable development actions in the area. A healthy *H. flavolineatum* population will positively impact the local food web and fishery [43].

Understanding how seascape configuration influences *H. flavolineatum* ontogenetic migrations is crucial to validating connectivity within the MPA BPK. Balbar and Metaxas [9] recently assessed 746 MPAs, where only 11% incorporated connectivity within their management plans. Colombia is no exception since structural and functional connectivity has been overlooked when creating (and evaluating) effective MPA management plans. Nevertheless, one of the proposed conservation objectives for MPAs intends to "guarantee ecological processes, to maintain connectivity of marine and coastal biodiversity" [21]. Although connectivity is now integrated into conservation efforts [20, 39], more research effort and investment are needed in the marine realm [145]. In other cases in the Mediterranean Sea and in open-access areas and MPAs, off Mallorca Island (Spain) connectivity mediated by larval dispersal is a criterion for establishing marine conservation areas [85, 108]. The challenge of integrating the growing knowledge on functional connectivity with the ecological evidence necessary to make management decisions has been mentioned and added to the current concern for short-range species [85]. Our study on potential functional connectivity considering *H. flavolineatum* is one of the first approaches to understanding ecosystem links within an MPA by representing the ontogenetic migration of a species that uses different marine-coastal habitats and the first study in this Bay. Our results could be a tool to guide the planning or evaluation of MPAs, since they suggest that it is possible that BPK meets the requirements for *H. flavolineatum* to fulfill at least two stages of its life cycle. We can also put forward the need to preserve the southern ecosystem's mosaic, with its ecological processes (nursery areas) and biodiversity [92]. Furthermore, because *H. flavolineatum* occurs in most Caribbean marine ecosystems [118], we propose this species' life cycle fulfillment as an indicator to validate ecosystem connectivity and fragmentation effects in the present and future Caribbean MPAs.

Although the importance of validating the results in the proposed study area needs to be considered, we highlight some lessons learned from the development of our potential functional connectivity analysis, namely, (i) it is possible to apply connectivity indices derived from landscape ecology and secondary information to predict the effect of a particular seascape (multi-habitat mosaic; [40, 100] in ontogenetic migratory species, (ii) the use of a potential functional connectivity approach could help to

identify areas of ecological importance [83], particularly in remote areas, with few ecologically available data, the use of potential connectivity network could contribute to making predictions for ontogenetic migratory species, information that has the possibility to be integrated into MPA planning and management; and (iii) key relevant information is needed to fully understand the ontogenetic species life cycle.

Conclusion

Our network connectivity representation is a novel methodological approach for marine species with ontogenetic migration that integrates ecological information and the seascape (structural data) to analyze the migration in *Haemulon flavolineatum* late juvenile stages. The network analyzes that the benthic habitat configuration of the BPK could allow *Haemulon flavolineatum* to complete at least two stages of its life cycle (stages 4 and 5), based on the known home ranges and habitat preferences of this fish species.

The spatial configuration of the patches of the three ecosystems (coral reefs, mangroves, and seagrass) likely facilitates the movement of *H. flavolineatum* individuals, which is evident in the bay's southern zone. Unfortunately, these southern habitats overlap substantially with zones of human activity, creating a potential management conflict (*i.e.*, opposing use vs. conservation interests) between different actors. The northern and central bay zones seem less suitable for *H. flavolineatum* due to fragmentation and isolation of seagrass and mangrove patches and the absence of coral reefs, resulting in unsuitably long migratory distances (stage 4). With the analysis results, we can generate two basic local recommendations regarding the management of this MPA. (i) Decrease the stressors within the southern zone to guarantee *H. flavolineatum* survival, as it is a species of economic and cultural importance for the indigenous communities in the area, and (ii) avoid dredging within this MPA when expanding its port. In the short term, this intervention could lead to the local extinction of species that require several ecosystems to complete their life cycles. Future research must focus on the distribution and size population structure of French grunts in the BPK to validate our results. In addition, we need a better understanding of *H. flavolineatum* life history, as well as the conditions and resources it needs in different ecosystems to complete the life cycle, and include this information in future models.

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Authors' contributions

Carolina Rodríguez and Alberto Acosta contributed to the conception and design of the study. Carolina Rodríguez organized the database and performed the analysis. Carolina Rodríguez wrote the first draft of the manuscript. Carolina Rodríguez and Alberto Acosta contributed to manuscript revision and read and approved the submitted version.

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Availability of data and materials

Data was obtained from a third party. The data analyzed in this study were obtained from INVEVAR, and the following licenses/restrictions apply [The layers are suitable for working with other sources of geographic information at a scale of 1:100,000 or less detailed (1:100,000, 1:500,000, etc.). INVEVAR is not responsible for the inappropriate use of this information. The overall accuracy of the data is not guaranteed. The data are provided as stored and have not been adjusted or modified to serve a particular purpose. The applicant is advised of possible errors in the data provided and assumes responsibility for making the necessary checks to detect, correct and interpret them accordingly. The applicant makes use of the data under his/her own responsibility. The applicant accepts the existing limitations on the data, whether arising from their nature or imposed as a result of this agreement. INVEVAR reserves the right to audit and determine whether the data are being used in accordance with this agreement. In no event shall INVEVAR assume liability for direct or indirect incidental damages that may result from the transfer or operation of the data or the supporting instructions given for its administration. The datasets generated during the current study are available in the figshare repository [119–121].

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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