Seascape connectivity: ontogenetic migration model for Haemulon flavolineatum

Carolina Rodríguez-Torres (ro_diana@javeriana.edu.co)  
UNESIS (Unidad de Ecología y Sistemática)

Alberto Acosta  
UNESIS (Unidad de Ecología y Sistemática)

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Abstract

In the seascape, species migrate between ecosystems to complete their life cycles, such ontogenetic migrations create functional connections between ecosystems. Nevertheless, the scarcity of information on patch distribution, species life history and ecology limit its application in MPA management. We use a potential connectivity model approach to predict how Haemulon flavolineatum might move through a complex and diverse seascape, by simulating part of its life cycle among three ecosystems (reef, mangrove, and seagrass) in the MPA of Bahía Portete-Kaurrele (BPK). We used available ecosystem cover maps to conduct habitat fragmentation analyses and evaluate structural connectivity in BPK (PLAN D, LPI, AREA, ENN, NP, SHAPE, CONTAG and UJ indices). With published information on 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. Patches of different ecosystems were highly intermixed (76%) rather than grouped (58%) reflecting appropriate structural connectivity; particularly for reefs followed by mangrove and seagrass; this seascape promote the potential migration of stage 5, juveniles from mangroves to the reefs (328 links, mainly in the BPK’s southern zone). Meanwhile, the structural configuration could reduce functional connectivity of stage 4 juveniles from seagrass to mangrove (mainly in the northern and central zone; 94 and 49 links respectively). Our model is a novel methodological approach for marine species with ontogenetic migration, which integrates ecological information and the seascape to predict their life cycle. We discuss the need for ecological information of French grunts to validate future models.

1 Introduction

In seascape studies, an integration of landscape ecology and conservation biology is just emerging (Olds et al. 2016; Balbar and Metaxas 2019), and the developing connectivity theory is gaining recognition as a relevant integrator of these themes (Virtanen et al. 2020). Furthermore, connectivity has become a central conceptual tool for ecosystem-level management. 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 (Olds et al. 2014).

There are two complementary views of seascape connectivity: structural connectivity and functional connectivity. The first is a measure of habitat permeability and involves the physical characteristics and spatial configuration of habitat patches within ecosystems. Structural connectivity also considers the disturbances (natural and anthropogenic) that a habitat experiences and the conditions and resources specific to a landscape that are necessary for organisms to move, survive, reproduce, and fulfill their life cycles (Hilty et al. 2019). 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 (Crooks and Sanjayan 2006; Weeks 2017). 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 (Fagan and Calabrese 2006; Assis et al. 2021) and the species’ life history data to simulate, model, and predict its connectivity in a seascape, particularly useful in remote areas with limited access to species ecological information.

Because the seascape is heterogeneous, some habitats and patches can offer certain species the right conditions and resources. Habitats with the necessary quality, quantity, and availability of resources for any species are considered suitable habitats. Here, suitable habitats can be understood in terms of the performance of a species (assessed via presence, abundance, fitness, and growth rate). The values of these species-performance variables reflect habitat quality (good or bad) and depend on the species’ niche breadth (Klinka et al. 1989). A seascape composed of suitable habitats sustain species throughout their entire life cycle, situation that will be reflected in productivity. Within the seascape, core areas are rich in resources, can maintain elevated productivity, and are often targeted by fisheries, which is partly explained by habitat connectivity. Thus, conservation strategies must consider interconnected habitat mosaics, as these are interacting in the seascape (Berkström et al. 2013; Olds et al. 2016; Weeks 2017) and affect species’ behavior and survival. Connectivity between habitats can occur in the form of ontogenetic migrations (Nagelkerken et al. 2015).

Ontogenetic migrations of marine species are the movements of individuals of given species through habitats where they fulfill different stages of their life cycle. These guarantee the exchange of genetic material between populations-metapopulations and ensure their adaptation to threats (Pérez-Ruzafa et al. 2006; Sale et al. 2010). Furthermore, ontogenetic migrations help us understand connectivity between habitats, their functioning, and how matter and energy flow among them, as well as their contribution to the food web (Kneib 1997; Olds et al. 2018). For instance, two habitats known to be connected by ontogenetic migrations are mangroves and seagrasses, serving as nurseries for reef fishes (Nagelkerken et al. 2017; Bradley et al. 2019; Hemingson and Bellwood 2020).

According to Halpern and Warner (2003), in a Marine Protected Area (MPA), the movement patterns and dispersion distances of larvae, juveniles, and adults of a given fish species among ecosystems in the seascape (i.e., ontogenetic migrations) must be well understood. 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 (Thompson et al. 2017). To date, optimal species migration distances between habitat patches have not been employed to analyze connectivity in the seascape. However, efforts have been made to determine the ideal distances between nursery (mangroves and seagrasses) and breeding areas (reefs) that allow species conducting ontogenetic migrations between these habitats to thrive (Berkström et al. 2020).

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 (Di Franco et al. 2012; Liggins et al. 2015; Treml et al. 2015). Extrinsic variables are seascape attributes and include discontinuity due to habitat fragmentation, bottom topography, habitat structure, habitat quality (conditions and resources), matrix resistance to movement (structural connectivity), predator-prey interactions, competition, and, as already illustrated above, disturbances (García et al. 2013; Liggins et al. 2015; Treml et al. 2015). Coastal and insular ecosystems around the globe are affected by
urban development, aquaculture, overfishing, ports, and transportation, which degrade and cause the loss of these ecosystems (Polidoro et al. 2010; Loh et al. 2015; Griffiths et al. 2020). Mangrove, coral reefs, and seagrass are particularly vulnerable to these disturbances. Since they are close to coasts, they receive a direct discharge of pollutants and tourism that, on most occasions, tends to be unconscious and irresponsible (Zaneveld et al. 2016; De et al. 2020; Uribe et al. 2020; Santos-Andrade 2021).

Knowledge and tools from terrestrial landscape ecology aid the analysis of connectivity in the seascape (Pittman 2018). Two of which are the patch mosaic model and graph theory. The patch mosaic model allows understanding the population dynamics of species of economic and ecological interest that require several marine ecosystems to complete their life cycles and maintain viable populations. This model supports habitat and ecosystem prioritization in marine spatial planning and fisheries management (Berkström et al. 2020). The patch mosaic model is suitable to study connectivity because the latter can be a function of the ease or difficulty of the movement of organisms (resistance) in space through different habitats and matrix elements. The model also considers habitat size (i.e., area and perimeter), the degree of ecosystem fragmentation, the geometry of the patches, and their degree of isolation, given the distances within and between patches of different ecosystems (Cushman et al. 2009).

Graph theory is the basis of other connectivity analysis methods, such as circuit theory and least-cost routing (Urban and Keitt 2001). Graphs display a network of connected nodes, representing habitat patches, and the connections between nodes are called links (Urban and Keitt 2001; Theobald 2006). A bipartite graph can be used to study links between patches of two opposed fragmented habitats (two ecosystems), with patches linked across habitats but not within (same ecosystem). Additionally, these graphs may reveal sub-graphs, consisting of patch bunches strongly linked across habitats that are loosely linked or not linked to other patch bunches. These sub-graphs are relevant because, according to graph theory, when connectivity between habitats is strong and connected habitat patches neighbor each other, the whole ecosystem is more resilient (Koch et al. 2009; Earp et al. 2017). In practice, the loss of ecological connectivity (graph network) and biodiversity is often a consequence of management decisions and policies (Hilty et al. 2020).

In Colombia, as in other parts of the world, the scarcity of information regarding 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 policy and decision-making for the conservation and sustainable use of marine ecosystems (Romero-Torres and Acosta 2012; Olds et al. 2014; Weeks 2017). Given the above, it is pertinent to ask whether modeling potential structural-functional connectivity in the seascape, using Haematonon flavolineatum, an ecologically and economically important fish species in the Caribbean (Guerra et al. 1990; Friedlander et al. 2010) will help to predict and understand how juveniles might move through a complex and diverse seascape, and highlight important gaps in the knowledge of the species to meet its life cycle, particularly if we are thinking about its sustainable use in an MPA with management conflicts between actors. To do so, we build a model based on literature migration thresholds for H. flavolineatum and habitat maps (reef, mangrove, and seagrass) of the marine protected area Portete-Kaurrele Bay (BPK), Colombian Caribbean.

2 Materials And Methods

2.1 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 using them (Nagelkerken et al. 2004). Of 19 MPAs in the Colombian Caribbean, 8 met the established inclusion criteria. The final criterion for choosing the Portete Kaurrele Bay MPA (BPK) was the presence of H. flavolineatum (Parques Nacionales Naturales de Colombia 2022) the representativeness of the three ecosystems and the available RAM and level of performance of our computing devices in dealing with file weights and data processing as they run our model.

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. 1). 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 (Gallego and Giraldo 2018). 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 (IDEAM n.d.; Gallego and Giraldo 2018). The water presents high turbidity caused by sediment resuspension with maximum visibility of 4 meters (Parques Nacionales Naturales de Colombia 2022).

BPK is a shallow bay with a maximum depth of 20 m (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 (Solano 1994; Díaz-Pulido 1997). BPK connects to the open sea through a 2-km wide mouth (Fig. 1; Solano 1994; INEMAR 2004). The surface current flows north to south, moves along the coast and center, then moves to the northeast to exit the bay, generating a cyclonic gyre, with the highest speeds occurring in July (Gallego and Giraldo 2018). The soft bottom consists of clay-type sediments (Parques Nacionales Naturales de Colombia 2022).

A mangrove forest borders the bay, dominated by Rhizophora mangle at the waterfront, while Avicennia germinans (black mangrove) is found landward, along with patches of Laguncularia racemosa (white mangrove; Parques Nacionales Naturales de Colombia 2022). Shallow seagrasses, dominated by Thalassia testudinum and Syringodium filiforme face the forest (Garzón-Ferreira 1989; Díaz 1990). Thalassia had an average height of 30 cm, and in Thalassia and Syringodium mixed patches, the latter grew 60 cm on average (Table 1). INEMAR 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 Sanchez-Valencia et al. 2019 and INEMAR 2022). H. flavolineatum individuals were observed in the three ecosystems with relative abundances of 10 individuals in 2500 m² (Supplementary Table 1; https://doi.org/10.6084/m9.figshare.21046438.v1 and Supplementary Fig. S1; https://doi.org/10.6084/m9.figshare.21047332.v1). A high seagrass cover includes scattered colonies of Millepora alcicornis and gorgonians (Antillogorgia, Plexaura, and Briareum) and occasionally Siderastrea limiting towards the
reef crest. In the meadow, it is also possible to find encrusting and erect sponges (INVEMAR in press). In the southern and western part 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 meters diameter), and *Pseudodiploria clivosa* dominate a fringing reef towards the slope. These colonies show diseases symptoms (white plague and dark spots) and mechanical damage by anchors (INVEMAR in press; Table 1). Other observed sources of degradation in the bay included ship passage to Puerto Nuevo, harpoon fishing, and aromatic hydrocarbons in the sediment (Table 1; Parques Nacionales Naturales de Colombia 2022). The reef’s maximum depths are approximately 4 m (Solano 1994; INVEMAR in press). The bay’s ichthyofauna features primarily Haemulidae species, followed by Pomacentridae and Labrisomidae species. The most abundant species are *Anisotremus virginicus* and *Stegastes sp.*, and the most relevant species of commercial interest in the bay are *Bairdiella ronchus, Balistes capricious, Trachurus lathami, Trichiurus lepturus, Opisthonema oglinum, Sardinia brasiliensis*, and *Sardinia aurita* (Gallego et al. 2018).

### 2.2 Model species

The French grunt, *Haemulon flavolineatum* (Desmarest 1823), was chosen as the model species 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 (Burke 1995; Appeldoorn et al. 2009; Grol et al. 2014; Green et al. 2015; Nagelkerken et al. 2017, Robertson et al. 2019; Appeldoorn and Bouwmeester 2022). Furthermore, *H. flavolineatum* is ecologically important in marine food webs (Friedlander et al. 2010) and is the principal food source of the Wayuu indigenous people in the MPA-BPK (Guerra, 1990; Parques Nacionales Naturales de Colombia 2022).

*H. flavolineatum* uses a variety of habitats throughout its life cycle. Juveniles and adults feed on seagrasses, and in reefs adults fulfill their reproductive phase (Burke 1995). Furthermore, during their ontogenetic migrations, *H. flavolineatum* individuals can shift among available habitats for shelter in the seascape, for instance, from seagrass to the coral reef, seagrass to sand/rubble flats, or seagrass to rubble piles (Appeldoorn et al. 2009). Also, they can move from mangroves to the coral reef (Jaxon-Harm et al. 2012). Therefore, we modeled *H. flavolineatum* juvenile ontogenetic migrations among three ecosystems only (seagrass, reef, and mangrove) since no rubble piles and sand/rubble flats were present in the bay, and most of the benthic bottom is silty and muddy (Garzón-Ferreira and Díaz 2003).

The life cycle of *H. flavolineatum* occurs among different ecosystems (Fig. 2) where different stages develop (Grol et al. 2014). It 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 is assumed to disperse up to 37 km (Green et al. 2015), although *in situ* larval dispersal is challenging to track. The next life cycle stage is a larval settlement (stage 2) between the water column and hard and soft bottoms with rubble (non-coral). Here, the larvae prefer to settle at depths of 8 m to reduce the risk of predation (Jordan et al. 2012), feeding on plankton brought by local currents (Grol et al. 2014). When the larvae reach approximately 2 cm in length, they migrate from the soft bottom with rubble to the seagrass meadow (stage 3) and switch to a benthic diet, composed mainly of copepods and tanaidaceans, abundant in this ecosystem (Grol et al. 2014). These three *H. flavolineatum* larval stages were not considered in this study due to absence of information. 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* or *Epinephelus guttatus*, among others (Danilowicz and Sale 1999; Laegdsgaard and Johnson 2001; Grol et al. 2014; Bester 2017). However, during stage 4, juveniles perform nocturnal migrations from mangroves to seagrass for feeding. The reported average ranges of these migrations are of 0 - 500 m (Verweij and Nagelkerken 2007; Grol et al. 2014; Green et al. 2015; Vaslet et al. 2015). Finally, ontogenetic migrations occur between mangrove and reef patches (stage 5), where juveniles reach sexual maturity, become adults, and reproduce. Distances of 2-4 km between nursery areas (mangrove or seagrass) and reefs maintain optimal adult biomass in *H. flavolineatum*, in fact, its adult biomass approaches zero in reefs located more than 14 km from the nursery areas (Green et al. 2015; Nagelkerken et al. 2017). Mature adults reproduce on the reef by releasing and dispersing their gametes to recommence the life cycle (Fig. 2). Adults in the reef feed preferentially on benthic worms (Sierra-Rozo et al. 2012; Grol et al. 2014) and continue nocturnal migrations to seagrass, arguably to avoid reef ectoparasites such as blood-feeding gnathiid isopods (with higher night activity; Sikkel et al. 2017).

### 2.3 Structural connectivity analysis

In this study, data from each of the three ecosystems in BPK correspond each to a spatial layer, namely the coral reef layer (MEC Project 1:100. 000; Instituto de Hidrología et al. 2015), the seagrass layer (Proyecto Atlas Pastos Marinos 2014; Gómez-Lopez et al. 2014), and the mangrove layer (SIGMA project layer version 6 - SIGMA Project; INVMAR 2014). The base layer for the analysis was constructed from the cartography generated in projects carried out by INVMAR 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. 4) and 1:250000 (mangrove to reef graph, Fig. 5).

Two structural connectivity analyses were performed, depending on the migration distance of the assessed *H. flavolineatum* life stages. As for the first structural analysis (stage 4), since patch distances exceeded reported juvenile migration distances from seagrass to mangrove (0 – 500 m; Green et al. 2015), we divided the bay into three zones, South, Central, and North. Seagrass and mangrove patches within each zone are likely to connect, whereas seagrass and mangrove patches between zones are not. The inter-zone matrix is soft bottom (*i.e.*, no habitat), rendering the chances of connections across zones close to 0. Thus, we assumed that the movement of the species was impeded by the distance between zones (Berkström et al. 2020). Next, we run the second structural analysis (stage 5) at a whole-bay level. According to Nagelkerken et. al (2017), the maximum migration distance of the species is 14 km, meaning that in the bay, mangroves and reefs are potentially connected (Fig. 4 and 5) since the bay's maximum diameter is 14 km.
To analyze connectivity, we considered ten variables. Eight were structural and two were functional (which will be described in the following section). The structural indices selected describe characteristics of each habitat, e.g., percentage of each habitat in the seascape (PLAND) or average of the size of the patches in a habitat (AREA). The description of each index PLAND, LPI, AREA, ENN, NP; and SHAPE is shown in Table 2. The structural CONTAG and IJI indices analyze the aggregation of cells (raster pixels), corresponding to patches, and the interdispersion degree of patches from different ecosystems, respectively. The CONTAG and IJI indices were applied to assess features at a seascape level. We conducted analyses with the program Fragstats 4.2.1.603. Fragstats is widely used in fragmentation studies in terrestrial ecosystems (Correa et al. 2014; Alonso-F et al. 2017; Fernandez et al. 2022) and can be used in the aquatic environment (Ortiz et al. 2020).

Usually, the AREA, SHAPE, and ENN indices are calculated using the average; however, this measure may be biased by the maximum and minimum values. In our case we observed a 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 to examine significant differences between ecosystems for each of three indices. The use of the median was not applied to other indices since they are expressed in percentages (PLAND, LPI, CONNECT), total counts (NP) or have their own formula (CONTAG, IJI) (McGarigal 2015). Furthermore, based on patch sizes, we calculated the relative coverage of each habitat potentially used by *H. flavolineatum* in the entire bay and for each 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 (Supplementary Table 1).

### 2.4 Potential functional connectivity analysis

The functional variables were CONNECT index and *H. flavolineatum* migration distance. The functional CONNECT index provides information within the same ecosystem, namely connectivity between patches. For CONNECT index we used four arbitrary distances (100, 250, 500, and 1,000 m) to simulate different possible home ranges scenarios, besides the one reported for *H. flavolineatum* (0-500 m). We based modeled home ranges on reported migration distances for fish families living in the ecosystems of interest, such as Haemulidae (1,000 m), Lutjanidae (500 m), and Serranidae (100 m) (Green et al., 2015; Gallego and Giraldo, 2018). We conducted analyses with the program Fragstats 4.2.1.603.

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

As mentioned earlier, we divided the bay into three disconnected zones for the bipartite graph: South, Central, and North. 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 non-overlapping arbitrary distance ranges were proposed for *H. flavolineatum* juveniles home range (0-500 m) from seagrass to mangrove (stage 4) and its ontogenetic migration distances (up to 14 km) from mangroves to reefs (stage 5). We only modeled 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. So, 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 use the edge of the patches as a reference (perimeter) to calculate the closest distance to another patch.

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

To model ontogenetic stage 5 *H. flavolineatum* migration, a bipartite graph with a single zone (component) 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 (Nagelkerken et al. 2017). Three thresholds (linear distance) were proposed to examine the distance range with the most links, 0 to 4 km, according to the literature (Green et al. 2015; Nagelkerken et al. 2017), 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* (Green et al. 2015; Nagelkerken et al. 2017). A shorter distance traveled will mean a higher survival probability of reaching the reef, maturing, and reproducing (Grol et al. 2014). 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 thresholds of 14 km, were excluded from the analysis.

### 2.5 Model assumptions
BPK - it's a remote area with a restrict access, including the presence of crocodiles (Crocodylus acutus) which makes diving activities risky. So, there is not much detail information available for management of any species of economical-ecological importance. This is the reason to use potential connectivity as a tool to help us to predict and use the results in management and conservation. Our approach (structural and potential functional connectivity) can help us to define what ecological information is relevant for the species and the necessary habitat required by H. flavolineatum to fulfill its life cycle, particularly if we are thinking in a sustainable use of the species worldwide. To build the model, based on the literature (INVEMAR 2022) and field data (juveniles and adults in different ecosystems; Table 1) we assume that H. flavolineatum could find suitable habitats at BPK, as defined in the introduction, meaning necessary conditions and resources to be there and achieve its life cycle and population growth.

In this study we assumed that juveniles could disperse throughout the bay, given the current pattern (Gallego and Giraldo 2018), which is supported by the presence of juveniles and adults in the three ecosystems (Supplementary Fig. S1). In other world locations, mangroves may not be present, so the species could replace mangroves with any other habitat with the necessary condition-resources; in consequence in this case the migration distances between the new habitats should be known, included, and modeled.

We did not exclude patches due to size nor 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 at each ecosystem: 3.2 m² for seagrass (South), 340 m² for mangrove (Center), and 61006 m² for reefs (South) and assume that small patches can function as stepping stones, allowing H. flavolineatum juveniles to reach reefs farther South. However, the minimum BPK patch size should be validated in the field and in different habitats to identify which areas provide sufficient resources (quantity, quality, and availability) to individuals, schools, and populations.

In the model we assume as valid the total mangrove area as an approximation of ecosystem size, 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 this whole habitat, as was observed in the field. If fishes like grunts only use the outer edge, say a maximum of 2 m deep into the mangrove area, the water-edge perimeter could be an appropriate metric for patch size, as in our case study the whole ecosystem (if this not the case, mangrove patch water-edge perimeter is a more appropriate metric for size). Since we use patch edge perimeter to evaluate functional connectivity – juvenile movement distance among patches, the functional connectivity indices calculated were not affected. However, the structural connectivity indices (PLAND, LPI, AREA and SHAPE) would be bias in cases where the patch size are underestimated, resulting in greater ecosystem fragmentation and degradation.

### 2.6 Model limitations

Ecosystem connectivity for the first three stages of H. flavolineatum’s life cycle: larval dispersal, larval settlement, and ontogenetic migration from soft bottoms with gravel to grasses, was not modeled due to a lack of information on these processes in the literature, and the absence of field data for H. flavolineatum.

Also, the simplicity of our potential connectivity model among BPK ecosystems with the limited ontogenetic migration data from H. flavolineatum does not allow us to consider several of the intrinsic and extrinsic variables known to influence functional connectivity and the species’ habitat use (see the introduction for a list of them; Liggins et al. 2015; Treml et al. 2015). This is why, we decided to keep these variables out of our model because: (i) These data are currently unavailable, and their gathering from the field is beyond our work’s scope. (ii) General models must first consider essential variables to be able to make predictions (Sekund and Pittman 2017) and keep the basic factors to explain ecological processes (Meentemeyer and Box 1987). We are aware the need to validate our model (detail field data) to have accurate predictions and to build a more robust connectivity model.

### 3 Results

#### 3.1 Structural connectivity

##### 3.1.1 Seagrass

In the total BPK area of 14080 ha, seagrass had 197 patches and it was the most representative ecosystem, with the highest coverage share in the seascape (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, max value of 244.67 ha and min value of 0.001 ha, showing high data dispersion (Tables 3 and 4). It had an average distance to the nearest neighbor (ENN) of 79.63 ± 109.87 m and it had the lowest average SHAPE index 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) though, it had a median of 48.02 m, the most extensive seagrass patches in 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 non-intervened 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 an acceptable seagrass configuration and structural connectivity in the South. In contrast, the North patch in the bay (244.67 ha), and the most natural and complex non-intervened patch forms (Table 1) we assume that H. flavolineatum could find suitable habitats at BPK, as defined in the introduction, meaning necessary conditions and resources to be there and achieve its life cycle and population growth.

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3.1.2 Mangrove

Mangrove had 55 patches, covered 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; Supplement Tables 2 and 3; https://doi.org/10.6084/m9.figshare.22533610.v1). The average patch size was 18.41 ± 62.67 ha (0.80, 443.63, 0.0334 ha for median, max and min value, respectively), showing high data dispersion, where 50% of the patches have sizes considerably smaller than average. The average SHAPE index was 2.34 ± 1.52 (1.62, 6.81, 1 for median, max and min value, respectively). Concerning the total mangrove cover, the most sizable mangrove patch accounted for 35.49% of the ecosystem. Of the three zones, the North revealed the most extensive mangrove patch in average (36.35 ± 105.54 ha), with the greatest median value (0.82 ha), the greatest coverage by extension (617 Ha), the largest patch which occupies 70% of the ecosystem's extension, the shortest average distance to the nearest neighbor (37.64 ± 41.46 m) with the lowest median (29.42 m). These results revealed an appropriate mangrove configuration and structural connectivity 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), 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 revealed significant fragmentation in the central zone of the bay. The South mangrove had the smallest percentage occupying by its largest patch (34,9%) and the lowest median shape index (1.51) (Tables 3 and 4, Fig. 3).

3.1.3 Coral Reef

The reef ecosystem was underrepresented in the bay, revealing the lowest coverage in the seascape (1.43%), 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, 6.11 ha for median, max and min value, respectively) and the highest shape index value of 3.30 ± 1.18 (3.78, 4.70, 1.49 for median, max and min value, respectively) both indices 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 2 and 3). Also, 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 seagrasses and mangroves patches (H= 15.19, N= 258, p= 0.0005); were 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 2 and 3). The reefs had the highest percentage occupying by its largest patch (49.56%). Therefore, the reef reveals less fragmentation. Finally, off the sum of the 3 ecosystems, reefs occupy 15% (201 ha) of the cover (Tables 3 and 4, Fig. 3).

3.1.4 Seascape connectivity

At the seascape level, both CONTAG (contagion) and IJI (intercalation) index values exceeded 50%, CONTAG was 58.1%, and IJI 76.5%, implying that patches of different ecosystems were more dispersed and intercalated, thus reflecting a 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 3). Figure 4 illustrates the connectivity in the seascape as revealed by CONNECT index values. These values were higher in the coral reef ecosystem due to its smaller number of patches and its clustering in the South part of the bay. In contrast, with a higher number of patches, seagrasses and mangroves were more dispersed throughout the seascape. However, no ecosystem exceeded 50% connectance within its patches.

Although we do not found differences in AREA, SHAPE and ENN indices when comparing bay zones for mangroves as well as for seagrasses (Supplementary Table 4; https://doi.org/10.6084/m9.figshare.22533610.v1), the South has the presence of the three ecosystems, representativeness, 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). We hypothesized that juveniles experienced a reduced predation risk as they moved between these habitats in this part of the bay.

3.2 Functional Connectivity as revealed by *Haemulon flavolineatum*

3.2.1 Juvenile migration model from seagrass to mangroves

The obtained juvenile migration model between seagrass and mangroves drew 247 links connecting patches in both ecosystems throughout the bay, with almost half the links (117) marking migration distances from 0 to 100 m. (the number of links in each migration distance range is shown in Table 5). The South contained the most (104) functional links, concentrated mainly within the 0 to 100 m distance range (48), entailed the most links (20) in the longest distance (from 401 to 500 m), and revealed the least number of disconnected patches (6). The North had the most disconnected patches (23), the mangrove patches with the highest number of functional links (27) and concentrated the seagrass patches with the lowest number of links (4). However, the seagrass patch with the highest number of links (9) occurred in the South (Fig. 5, Table 5).

Highly linked patches were had also 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). It was impossible to calculate the total connectivity between the seagrass-mangrove network because of the seascape division into three zones and the distances between patches of these two ecosystems exceeding the reported *H. flavolineatum* home range. However, 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 5).
3.2. Juvenile migrating model from mangroves to coral reefs

The obtained juvenile migration model between mangroves and the reef 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 5E had the highest number of links (28), whereas patch 5A had the least connections (8). For the intermediate migration distance range of 4.1 to 8 km, patch 5C obtained the highest number of links (24), closely followed by patches 5B (23) and 5A (20). Within the furthest migration distance range (8.1 to 14 km), patch 5A obtained the most links (25). Only patch 5A, outside the established maximum migration distance, was disconnected from two mangrove patches (Fig. 6, Table 6).

The bay is potentially fully connected by the ontogenetic migration of *H. flavolineatum* from mangrove to reef. However, it is intuitive to think the species may prefer to move through nearby patches to avoid predators. The migration model results supported the view that coral patch 5E experiences the most visits of stage 5 *H. flavolineatum* juveniles from the mangrove and patch 5A the least (Fig. 5). Being closer to the reefs, the mangrove patches in the south part of the bay generate the links at the shortest distances (0 – 4 km), so it would be more likely that the migration of stage 5 juveniles would occur in this zone.

4 Discussion

We assessed potential functional connectivity at MPA BPK based on the modelling of *H. flavolineatum* ontogenetic migrations, revealing that the bay has a spatial configuration that theoretically allows *H. flavolineatum* juveniles to complete stages 4 and 5 of their life cycle thanks to functional connectivity. Two lines of evidence support this statement. (i) The obtained CONTAG and IJI index values (58.18% and 76.55, respectively) indicate ample connectivity between patches of different habitats, agreeing with seasearch configurations with high spatial heterogeneity and smaller, more intercalated, and dispersed patches (McGarigal 2015). (ii) The short distances between seasearch and mangroves and between mangroves and the reef could facilitate the ontogenetic migrations of *H. flavolineatum* life stages 4 and 5. The presence of both juvenile-to-adult stages in the ecosystems may help to corroborate these model predictions (Supplementary Fig. S1). (iii) Although, the CONNECT index show low values (Fig. 4) indicating reduced connectivity between patches of the same habitat, the presence of *H. flavolineatum* in the three habitats studied (Supplementary Fig. S1) suggest that the existing connectivity could be sufficient for the species. However, movement restrictions within habitats (e.g., soft bottom matrix) or low reef total area can affect the *H. flavolineatum* population and likely explain in part the low relative densities observed (Table 1), which in turn modulate its ecological role as prey of Lutjanid species (Fridlander et al. 2010), therefore altering food webs (Stallings 2009; Lamb and Johnson 2010).

Migration from seagrass to mangrove potentially occurs during stage 4 of *H. flavolineatum*’s life cycle in BPK. Low fragmentation, large patches, and the spatial configuration of mangroves and seasearch meadows could make the South more suitable for juveniles than the rest of the bay. In the South, patches of the two habitats are located at shorter distances from one another (0-100 m), facilitating juvenile presence (Fig. 3). Our results support the idea that the spatial arrangement of habitat patches determines fish-mediated connections between different coastal ecosystems (Nagelkerken et al. 2008) and drives regional differences between seasearches (Igulu et al. 2014; Shideler et al. 2017). For instance, in the archipelago of San Andres and Providencia, Sierra-Rozo et al. (2012) demonstrated the importance of seagrass and mangroves as nursery habitats for different fish species, including *H. flavolineatum*, finding significant juvenile abundances; additional studies support this view (e.g., Fridlander et al. 2003). Furthermore, Kendall et al. (2003) indicated that there is a prominent presence of *H. flavolineatum* juveniles in hard-bottoms (refuge zones) nearby ample soft-bottoms (feeding zones). Similar results were obtained in the Bazaruto Archipelago (Mozambique), Kaledupa (Indonesia), Florida (United States), and Providencia and Santa Catalina (Colombia) (Appeldoorn et al. 2003; Pittman et al. 2007; Unsworth et al. 2008; Jaxon-Harm et al. 2012; Berkström et al. 2020). Also, our results agree with Martin et al. (2015), who found that fish assemblages improve when mangroves are close to reefs (< 500 m).

As suggested by our model, a mangrove to reef juvenile migration may occur during stage 5 of the life cycle of *H. flavolineatum* in BPK. Coral reef patches occur in the South, there the 5E reef patch could be relevant for the functional connectivity of *H. flavolineatum* because of its higher number of short-distance links. The benefit of moving to adjacent and nearby mangroves is to diminish the chance of mortality during migration. This result agrees with Zollner and Lima (2005), who found that the relative cost of moving through different habitats in the seasearch comes from predation risk offsetting food/shelter benefits. Nagelkerken et al. (2017) found that fish are more likely to avoid migrating from their nursery areas to very isolated reefs if there are nearby patches that present the necessary conditions and resources to grow and survive. In BPK, most of the mangrove patches are 2 to 4 km away from the reefs, and *H. flavolineatum* juveniles’ optimal migration distance may surpass the 4 km mark, as reported in Aruba, Curaçao, Grand Cayman, and Bermuda (Nagelkerken et al. 2017).

Isolation by distance has been a critical factor for connectivity (Lowe et al. 2003; Berkström et al. 2020), which could be the case for the reef patches 5A and 5B in BPK (Fig. 6), where the number of long-distance links (8.1 to 14 km) exceeds the number of short-distance links (0 to 4 km). These patches are farther from the northern mangrove patches (Fig. 1). The model also shows that compared to the south and the central zone, the north zone had the worst structural configuration of seagrass patches, so it is possible that juvenile isolation could occur there, as well as in the mangrove patches of the central zone (Fig. 3). Nagelkerken et al. (2017) suggest that *H. flavolineatum* densities decreased sharply on reefs that exceeded distances from 2 to 4 km from nursing areas. However, movement flexibility may occur depending on the quality, quantity, and availability of resources within the patches, the possibility of conducting stepping-stone movements and the plasticity of *H. flavolineatum* in the use of habitats to fulfill its life cycle (Kimrei et al. 2011). Caldwell and Gergel (2013) hypothesized that if the total cost of the displacement is too high because of distance, organisms will not move in the seasearch. Tagging juveniles and following them along the seasearch may be a way to check the use of resources and ecosystems (patch isolation, stepping-stone movements, and the use of habitats other than those modelled). There is, however, an alternative hypothesis; Shulman (1985) suggests that predation on *H. flavolineatum* decreases as the distance from the reef increases, arguing for the avoidance of nursery patches (mangrove or seasearch) located nearby the reef because they have a higher predation rate (Manson et al. 2005). 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 (Appeldoorn et al. 2009). So, juveniles could move from reefs (South) to mangroves (North) by using those patches surrounding the bay to avoid deep, non-habitat areas.
Some limitations of the model 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 lose functionality for *H. flavolineatum* and imply more energy for migration, explaining why the northern seagrass has the highest number of links, reducing its potential use. Fragmentation effects have been observed with the massive loss of *Zostera marina* in Morro Bay in California, USA, where species composition changed without loss of fish biomass, which in the long term could affect the levels and trophic chains of the area (O’Leary et al. 2021). Second, if the area/perimeter ratio is small, the reduced amount of suitable space maybe not suffice to support vital ecological processes. For instance, patches with the higher valency marked with a star in Fig. 6 will have more edge effects than the core area, and habitat edges are known to have lower nursery benefits due to high predation risk (Olson et al., 2019). Additionally, all functional links were considered as direct linear distances and not considering erratic fish movements, which depends on the cost-benefit energy ratio.

Detailed studies are needed to determine whether a habitat patch (a place with all the conditions and resources necessary for the survival, development, reproduction, and establishment of local populations; Batzli and Lesieutre 1991) meets *H. flavolineatum*’s minimal requirements (Laegdsgaard and Johnson 2001; Nagelkerken et al. 2004; Vaslet et al. 2012), which may vary depending on the species life stage (Borland et al. 2021). Moreover, it is necessary to measure *H. flavolineatum* population parameter differences between patches, habitats, and ecosystems (Morris 2003) and conduct more in-depth studies of the physicochemical variables that affect habitat conditions (Fabricius et al. 2005; Huijbers et al. 2008). All the above, considering *H. flavolineatum* vulnerability to disturbances because of its high fidelity to specific sites (Krumme 2009). The parameters of our fish migration potential model must also consider a stepping-stone movement when adjusting theoretical maximum migration distances. Stepping-stone movements will allow juveniles to perform longer migrations and short displacements between patches while facing lower risks (Saura et al. 2014). 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 (Fodrie et al. 2009; Nagelkerken et al. 2015).

Accelerated climate change challenges ecosystems to increase their resilience and species to adapt to unstable environmental conditions and dynamic landscape structures (Hilty et al. 2020). Strongly connected areas are more resilient to climate change because important ecological processes for the ecosystem’s stability are more likely to occur there (Walker and Salt 2006). The bay’s south zone has the highest connectivity potential and requires management and protection. In Puerto Nuevo, south of the bay (Fig. 1), intended dredging (so that large vessels can access the existing harbour) will negatively affect most coastal ecosystems (Moreira et al. 2021). 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 (McFarland and Hills 1982). Also, an increase in the sedimentation rate decreases benthic organism fixation, recruitment, and survival (Escobar et al. 2016). Puerto Nuevo is precisely where our model predicts 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 (Friedlander et al., 2010). The South, with a higher number of short links (considered by Melia et al. 2016 as an effective area) would be a valuable zone for the protection of *H. flavolineatum*.

Understanding how seascape configuration influences *H. flavolineatum* ontogenetic migrations is crucial to validating connectivity within the MPA BPK. Target 11 of the Aichi Targets states that “By 2020, at least 17% of terrestrial and inland water and 10% of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative, and well-connected systems of protected areas and other effective area-based conservation measures and integrated into the wider landscapes and seascapes” (CBD 2010). Balbar and Metaxas (2019) 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” (Cardique et al. 2016). Even though connectivity is now integrated into conservation endeavours (Canal de videos Conexión BioCaribe 2020; FAO 2021), more research effort and investment are needed in the marine realm (Zárrate and Ochoa 2020). In other cases, around the world, connectivity mediated by larval dispersal is a criterion for establishing marine conservation areas (Magris et al. 2018; Osipina-Alvarez et al. 2020).

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 (Magris et al. 2018). Our study on potential functional connectivity considering *H. flavolineatum* is one of the first approaches to understanding ecosystem links within an MPA by modelling the ontogenetic migration of a species that uses different marine-coastal habitats. Our results could be a tool to guide the planning or evaluation of MPAs. By studying BPK’s potential functional connectivity, the model predicts that it is possible that this MPA meets the requirements for *H. flavolineatum* to fulfill at least two stages of its life cycle. We also can put forward the need to preserve the south ecosystem’s mosaic, with its ecological processes (nursery areas) and its biodiversity (Ministerio de Ambiente y Desarrollo Sostenible 2014). Furthermore, because *H. flavolineatum* occurs in most Caribbean marine ecosystems (Robertson et al. 2019), we propose this species’ life cycle fulfillment as an indicator to validate ecosystem connectivity in the present and future Caribbean MPAs.

Although the importance of validating the model in the proposed study area needs to be considered, we highlight some lessons learned from the development of our potential functional connectivity model, 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; Fernandez et al. 2022; Nucci et al. 2022) in ontogenetic migratory species. (ii) the use of potential functional connectivity approach could help to identify areas of ecological importance (Loher 2022) and key relevant information we need to fully understand the life cycle of ontogenetic species.

### 5 Conclusion

Our model is a novel methodological approach for marine species with ontogenetic migration, which integrates ecological information and the seascape (structural data) to predict their life cycle. The model predicts that, Portete Kaurrele Bay MPAs benthic habitats configuration could allow *Haemulon*...
flavolineatum to complete at least two stages of its life cycle based in the known home ranges for this fish species (stages 4 and 5). The spatial configuration of the patches of the three ecosystems (coral reefs, mangrove, and seagrass) likely facilitates the movement of H. flavolineatum individuals, being 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 the high isolation of seagrass and mangrove patches, and the absence of coral reefs, resulting in unsuitably long migratory distances.

In remote areas, with few ecological available data, the use of models could contribute to make predictions for ontogenetic migratory species, information that has the possibility to be integrated into the MPA planning and management. With the model predictions 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. Even though future research must focus on the distribution and size structure of French grunts in the BPK to validate our model. 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 to validate future models.

Declarations

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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.

Author Contributions

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

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Supplementary Material

The Supplementary Material for this article can be found online at:
Supplementary Table 1
https://doi.org/10.6084/m9.figshare.21046438.v1
Supplementary Tables 2, 3 and 4
https://doi.org/10.6084/m9.figshare.22533610.v1
Supplementary Figure S1
https://doi.org/10.6084/m9.figshare.21047332.v1

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Tables

Table 1. Characteristics of the benthic, reef, seagrass, and mangrove habitats of Portete Kaurrele Bay MPA used by H. flavolineatum during stages 4 and 5 of its life cycle (juveniles). 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, INVEMAR in press) and few data from the literature ([1] Sanchez-Valencia et. al. 2019; [2] Parque Nacionales Naturales de Colombia, 2022) as indicated in the rows.
<table>
<thead>
<tr>
<th>Ecosystems - benthic habitats</th>
<th>Seagrass</th>
<th>Fringing Reef</th>
<th>Mangrove Roots</th>
<th>Soft bottom</th>
<th>Literature</th>
</tr>
</thead>
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<tr>
<td>Ecosystems benthic area (Bay Total = 14080 ha)</td>
<td>1152</td>
<td>201</td>
<td>1227</td>
<td>9904</td>
<td>[2]</td>
</tr>
</tbody>
</table>

Extensive and continous meadows

| Relative percent cover of potentially used habitats by *H. flavolineatum* | 45 | 8 | 47 |

| Major structural species | 3 (seagrasses) | 11 (scleractinian corals) | 1 (mangrove) |

| Confirmed presence of *H. flavolineatum* | Yes (juvenile- see photo & adults) | Yes (juvenile & adults around *Orbicella-Colpophyllia & Siderastrea*) | Yes (juvenile) |

| Habitat used by *H. flavolineatum* | Yes | Yes | Yes | No (Not suitable habitat) |

| Species composition (coast towards middle of the bay) | Thalassia | Reef crest with *Millepora* (50% cover) & *Porites* (5%) | Rhizophora mangle |

| Thalassia & *Syringodium* | Big massive coral colonies: *Orbicella-Pseudodiploria-Colpophyllia* |

| Thalasssia & *Millepora* | Slope - coral-rubble-sand |

| Thalassia & *Sponges* |

| Thalassia & *Octocorals* |

| Thalassia & coral patch |

| Thalassia & *Siderastrea* |

| Habitat Depth (m) | 0-2.5 | 0-4 | 1 | 5-20 |

| Bottom substrate type | Clay>Silt>sand | Gravel-sand | Silt-clay | Silt-clay-rubble |

| *Thalassia* Leaf average height (range & average; cm) | 22-36; 26 |

| *Syringodium* leaf height (range & average; cm) | 59-64.5; 62 | [1] |

| *Thalassia* Shoot density (range & average - 25x25 cm) | 30-105; 50 | [1] |

| Shoot density (range & average - m2) | 120-420; 200 |

| Dominant species in the habitat | *Thalassia testudinum* | *Porites astreoides* | *Rhizophora mangle* |

| *Syringodium filiforme* | *Porites porites* |

| *Millepora alcicornis* | *Favia fragum* |

| *Altilogorgia* | *Orcibella faveolata* |

| *Plexaura* | *Pseudodiploria strigosa* |

| *Briareum* | *Colpophyllia natans* (2m diameter) |

| Erect and incrusting sponges | *Diploria clivosa* |

| *Siderastrea siderea* | *Siderastrea siderea* |

| Fish community | Gobiidae, Haemulidae y Scaridae | [1] |

<p>| Fish richness | 217 (67 families) | [2] |</p>
<table>
<thead>
<tr>
<th>Other Haemulon observed</th>
<th>Haemulon bonariense</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Haemulon sciurus</td>
</tr>
<tr>
<td></td>
<td>Haemulon plumierii</td>
</tr>
<tr>
<td></td>
<td>Haemulon aurolineatum (large groups)</td>
</tr>
</tbody>
</table>

| Fish juveniles observed                     | Surgeons and snappers |

| Dominant fish trophic guilds               | Omnivores (<60%) and carnivores (18%) |

| H. flavolineatum habitat quality based on relative abundance (ind/2500m2) | 10 |
| Percent of relative abundance of H. flavolineatum (respect to the total species sampled) | 1.8 |
| Habitat conservation status (scale from 0-10; 10=highest value) | 10 (Millepora crest) - 6 (massive corals) | 10 |
| Habitat health | No presence of fungus (Labyrinthula sp.) | 40 - 50 % Live coral cover (Reef crest) |
| Neccesary (Central) | C. natans (white plague) |
| Rehabilitation | Neccesary (North) Only to massive corals along the crest |
| Stressor | Sedimentation | Anchor damage | Pollution - oil |
| Stressor | Artesanal indigenous fishing | Fishing |
| Fishing - nets, line, fork type harpoon | Hurricanes |
| Boat and ships transit | |
| Marine waste - plastic | |

**Table 2.** List of structural analysis indices (Fragstats). Coverage refers to each ecosystem (mangrove, coral reef, and seagrass), while landscape (bay) refers to the sum of the three ecosystems coverage.
Index | Description | Level | Units
--- | --- | --- | ---
PLAND | Percentage of each cover in the landscape | Coverage | 0 - 100 %
LPI | Percentage occupied by the largest patch in each coverage | Coverage | 0 - 100%
AREA | Average of the size of the patches in a coverage | Coverage | ha
ENN | Average distance to the nearest neighbor of the same coverage | Coverage | m
NP | Number of patches in a coverage | Coverage | Number
SHAPE | Average of the shape complexity adjusted to a squared standard of the patches in a coverage | Coverage | = 1 Square Shape >1 Irregular Shape
CONNECT | Functional links between patches in the same coverage | Coverage | 0 - 100 %
CONTAG | Degree of aggregation of adjacent cells corresponding to patches of different coverages | Landscape | 0 - 100 %
IJI | Degree of interspersion of adjacent patches of different coverages | Landscape | 0 - 100 %

Table 3. Fragmentation analysis (Fragstats) at ecosystems and seascape level in the Portete Kaurrele Bay MPA. CR (coral reefs), M (mangrove), SG (seagrass), descriptions of each index (PLAND, NP, LPI, AREA, SHAPE, ENN, CONTAG and IJI) as in Table 2. Seascape (bay) refers to the sum of the three ecosystems coverage. In bold 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 2 and 3).

<table>
<thead>
<tr>
<th>Coverage</th>
<th>PLAND (%)</th>
<th>NP (#)</th>
<th>LPI (%)</th>
<th>AREA (Ha)</th>
<th>SHAPE (=1/1)</th>
<th>ENN (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>SD</td>
<td>Median</td>
<td>Max</td>
<td>Min</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>CR</td>
<td>1.43</td>
<td>6</td>
<td>49.5</td>
<td>33.52</td>
<td>32.35</td>
<td>18.87</td>
</tr>
<tr>
<td>SG</td>
<td>8.93</td>
<td>197</td>
<td>21.20</td>
<td>6.59</td>
<td>23.04</td>
<td>1.17</td>
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<tr>
<td>M</td>
<td>7.96</td>
<td>55</td>
<td>35.49</td>
<td>18.41</td>
<td>62.67</td>
<td>0.80</td>
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</tbody>
</table>

Table 4. Index values (Fragstats Analysis) and coverage analysis of Portete Kaurrele Bay MPA Seascape. CR (coral reefs), SG (Seagrass), M (Mangrove). Description of each index (NP; LPI, AREA, SHAPE, ENN, PLAND) as in Table 2.

Table 5. Functional links (FL) of the bipartite graph (South, Central and North) that model’s ontogenetic migration from seagrass to mangrove of *Haemulon flavolineatum* at five distance thresholds (see also Figure 4). The later based on the limits reported in the literature regarding the migration from seagrass to mangrove of *H. flavolineatum* (Grol et al., 2014; Green et al., 2015; Vaslet et al., 2015).
Table 6. Functional links of the bipartite graph that model's ontogenetic migration from mangrove to reefs of *Haemulon flavolineatum* at three distance thresholds (see also Figure 5) within the reported limits for ontogenetic migration of *H. flavolineatum* (Green et al., 2015; Nagelkerken et al., 2017). Total LD (number of links for each distance range), Total LP (number of links for each patch).

<table>
<thead>
<tr>
<th>Distance (m)</th>
<th>Number of links</th>
<th>Total FL Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>South</td>
<td>North</td>
</tr>
<tr>
<td>0 - 100</td>
<td>48</td>
<td>47</td>
</tr>
<tr>
<td>101 - 200</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>201 - 300</td>
<td>12</td>
<td>15</td>
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<tr>
<td>301 - 400</td>
<td>12</td>
<td>8</td>
</tr>
<tr>
<td>401 - 500</td>
<td>20</td>
<td>12</td>
</tr>
<tr>
<td>Total FL Zones</td>
<td>104</td>
<td>94</td>
</tr>
<tr>
<td>Disconnected patches</td>
<td>6</td>
<td>23</td>
</tr>
<tr>
<td>Valency SG</td>
<td>9</td>
<td>4</td>
</tr>
<tr>
<td>Valency M</td>
<td>11</td>
<td>27</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Distance (km)</th>
<th>Number of links per patch</th>
<th>Total LD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5A</td>
<td>5B</td>
</tr>
<tr>
<td>0 - 4</td>
<td>8</td>
<td>11</td>
</tr>
<tr>
<td>4.1 - 8</td>
<td>20</td>
<td>23</td>
</tr>
<tr>
<td>8.1 - 14</td>
<td>25</td>
<td>21</td>
</tr>
<tr>
<td>Total LP</td>
<td>53</td>
<td>55</td>
</tr>
<tr>
<td>Disconnected patches</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>

Figures
Figure 1

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

Representation of *H. flavolineatum* ontogenetic migrations during its life cycle in the Caribbean, when three habitats are present (seagrass, coral reef, and mangrove); although other possibilities for its life cycle may exist (coral reef-seagrass or coral reef-seagrass-sand/rubble flats, as stated by Appeldoorn et al., 2009). Distances above arrows indicate average movement between habitats reported in the literature, and circles indicate diet (Grol et al., 2014; Green et al., 2015; Nagelkerken et al., 2017)
Figure 3

Summary graph of the variables analyzed for the connectivity model of the migratory potential of Haemulon flavolineatum in the Portete Kaurrele Bay MPA. The sum of the arrows indicates whether it is 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 the reef as a relatively better habitat for the species in the MPA. Part B summarizes and compares the structural and functional connectivity indices of seagrass and mangrove 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. In addition, migration of H. flavolineatum juveniles is favored mainly in the south. Therefore, due to the presence of reefs only in the southern zone, the model predicts that this zone is of ecological importance for the species to fulfill phases 4 and 5. 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.
Figure 4

Connectance (percentage) represent functional links between patches of the same ecosystem at different migration distance thresholds in the Portete Kaurrele Bay MPA. Results made in Fragstats for the CONNECT index. CR (coral reefs), M (mangrove), SG (seagrass)
Figure 5

Functional connectivity of the ontogenetic migration of *H. flavolineatum* from seagrass to mangrove in Portete Kaurrele Bay MPA (stage 4 of its life cycle). Distance thresholds are 0 to 100 m (blue lines), 101 to 200 m (red lines), 201 to 300 m (purple lines), 301 to 400 m (yellow lines), and 401 to 500 m (black lines). Yellow circles represent isolated patches. Scale 1/80000
Figure 6

Functional connectivity of the ontogenetic migration of *H. flavolineatum* from mangrove to reefs in Portete Kaurrele Bay 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 5A, (B) patch 5B, (C) patch 5C, (D) patch 5D, (E) patch 5E, (F) patch 5F. Scale 1/250000