



Mangroves as nursery habitats for Galapagos reef fishes

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ABSTRACT: Mangroves offer key ecosystem services such as the provision of feeding, breeding, and nursery grounds to marine fish populations. The role of mangroves as fish nursery habitats is not ubiquitous and depends on factors such as species, geographic location, and environmental conditions. Studies of this nursery role for fish species are limited in the Tropical Eastern Pacific and particularly scarce for the Galapagos Islands. We used underwater visual censuses to survey fish species composition within mangrove forests and adjacent shallow rocky reefs across 6 of the Galapagos Islands. Adult densities of 3 commercially important reef fishes (*Lutjanus argentiventris*, *L. novemfasciatus*, and *Mycteroperca olfax*) were also surveyed in adjacent deep rocky reefs to investigate the relative importance and potential of mangroves in supporting their populations. Our study provides evidence that mangroves play a role as nursery habitats for reef fish species. Specifically, we identified *Eucinostomus dowii*, *L. argentiventris*, *Mugil* spp., *Mycteroperca olfax*, *Sphoeroides annulatus*, *Stegastes arcifrons*, and *Scarus ghobban* as mangrove nursery species, as their juvenile densities were significantly higher in mangroves than in shallow rocky reefs. Additionally, 19 other fish species, primarily juveniles, were exclusively observed within mangrove habitats. We found that the extent of mangrove perimeter within 10 km of deep reefs positively influenced the densities of adult *L. argentiventris* and *M. olfax*. Our results argue for the need to consider nursery ecosystem function in the design and management of the Galapagos Marine Reserve, since mangroves will directly contribute to the fisheries management of economically important species.

KEY WORDS: Essential habitats · Underwater visual census · UVC · Fisheries · MPA

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1. INTRODUCTION

Many marine species undertake ontogenetic migrations from one habitat to another. During their juvenile stages, some of these species use shallow-water habitats such as mangroves, seagrass beds, coral reefs, or salt marshes before migrating to deeper reefs as adults (Cocheret de la Morinière et al. 2002, Saenger et al.

2013, Bradley et al. 2020). Mangroves in particular are one of the most important coastal ecosystems in tropical and subtropical latitudes because they offer key resources to marine fish populations by providing feeding, breeding, and nursery grounds (Moberg & Rönnbäck 2003, Barbier et al. 2011, Lefcheck et al. 2019) that can even offset losses of adult habitat quality (Rogers & Mumby 2019).

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The role of mangroves as nursery habitats has been studied worldwide, with most research focused on the Caribbean and Indo-Pacific region (Nagelkerken 2009, Whitfield 2017, Bradley et al. 2024). While some evidence suggests ecosystem equivalence in mangroves supporting fish assemblages across different regions (Sheaves 2012), there is also evidence that the contribution of mangroves to reef fish assemblages is higher in the Caribbean than in the Indo-Pacific region (Igulu et al. 2014, Dubuc et al. 2019a). This can be partly explained by the fact that mangroves in the Indo-Pacific region often experience significant tidal fluctuations that can leave habitat emergent at low tide (Igulu et al. 2014, Bradley et al. 2024). Additionally, these situations often result in challenging environmental conditions such as low dissolved oxygen (DO) levels, potentially causing environmental hypoxia (Dubuc et al. 2019b, 2021). As a result, several studies have shown that seagrass beds play a more significant role in supporting fish nurseries in the Indo-Pacific region (Dorenbosch et al. 2005, Nanjo et al. 2011, Igulu et al. 2014).

The differential role that mangroves play as nursery habitats is not ubiquitous and depends on several environmental factors such as temperature, tidal regime, or wave energy (Nagelkerken 2009, Igulu et al. 2014, Bradley et al. 2020). Furthermore, this role is influenced by geographic location, species interactions, habitat size, isolation, and proximity to adjacent habitats (Chittaro et al. 2005, Lee et al. 2014, Bradley et al. 2024). In mangroves, these conditions are dynamic and change over time and space, complexifying the characterization of mangroves roles (Bradley et al. 2020, Dubuc et al. 2021). Despite potentially challenging conditions, juvenile fish of some species can thrive in mangroves because of the high abundance of food, complex root systems, high turbidity, and high primary productivity, which satisfies the juveniles' need for low-predation pressure, shelter, and food supply (Blaber & Blaber 1980, Nagelkerken & Faunce 2008, Lee et al. 2014). As a result, many commercially important reef fish species use mangrove areas as juveniles, increasing their biomass, survival, and growth as adults in deeper waters (Mumby et al. 2004, Aburto-Oropeza et al. 2008, Brown et al. 2019). It is important to note that adjacent ecosystems such as shallow reefs, seagrass meadows, salt marshes, macroalgae beds, and mud and sand flats have also been identified as potential nursery habitats (Kimirei et al. 2015, Bradley et al. 2017, Sambrook et al. 2020). These studies highlight the complexity of habitat-use patterns of juvenile reef fish. Nevertheless, a higher number of studies around the world have reported distinct spe-

cies and higher densities of juvenile fish within mangroves compared to adjacent ecosystems (Thayer et al. 1987, Dubuc et al. 2019a, Whitfield et al. 2023).

The functioning of potential nursery habitats has not been evaluated in the Tropical Eastern Pacific (TEP) as extensively as in other regions (Faunce & Serafy 2006, Castellanos-Galindo et al. 2013, Zu Ermgassen et al. 2020). This is particularly problematic considering the alarming mangrove deforestation rates in the region, with a loss of ~40% of mangrove cover in the last 40 yr in Ecuador alone (Shervette et al. 2007). Over the last decades, approximately 35% of worldwide mangrove cover has been lost due to a combination of anthropogenic and natural causes (Valiela et al. 2001, Alongi 2008). Global mangrove cover was 163 925 km² in 2014 (Hamilton & Casey 2016); by 2020, it had decreased to 147 359 km² (Bunting et al. 2022). However, recent conservation efforts have reduced the annual average loss rate from 0.21 to 0.04% (Bunting et al. 2022). Globally, mangrove forests have been replaced by aquaculture, agriculture, tourism, and urban development (Alongi 2002, Giri et al. 2011, Goldberg et al. 2020), while climate change processes such as sea-level rise, severe storms, and increased temperatures are also impacting mangrove ecosystems at regional scales (Lovelock et al. 2015, Ward et al. 2016). Overexploitation and pollution further contribute to the degradation of mangrove forests, culminating in an unsustainable condition for the provision of ecosystem services (Goldberg et al. 2020).

Underestimating the importance of mangroves in supporting fish populations might lead to further declines in fish species along with a significant economic loss for fishers. Although the economic valuation of the nursery function provided by mangroves is complex and often biased due to generalizations, outdated assumptions, and the neglect of other coastal habitats that also contribute to fish assemblages (Sheaves et al. 2020), mangrove cover and fisheries catch data have been used to predict fisheries value per hectare. In Malaysia, the estimated annual return of mangrove habitat was US \$846 ha⁻¹ (Carrasquilla-Henao & Juanes 2017). Similarly, in the Gulf of California, Aburto-Oropeza et al. (2008) found a positive correlation between the abundance of commercial fish species in mangroves and fish landings, estimating the annual economic value of mangrove fringe at \$37 500 ha⁻¹. This approach may not provide the most accurate estimate, but it offers a baseline for the economic value of an ecosystem service that is often undervalued.

The Galapagos Islands have been protected as a National Park since 1959 by the Ecuadorian govern-

ment. The entire archipelago is protected from industrial activities, but an artisanal fishery that targets reef fish species is allowed in 99% of the 142 759 km² Galapagos Marine Reserve (GMR) that surrounds the islands (Edgar et al. 2004, Moity et al. 2019, Palacios & Cantor 2023). Rocky shores are the main coastal habitats in the Galapagos Islands, followed by relatively pristine mangroves that only display evidence of deforestation around the few coastal settlements (Moity et al. 2019). Seagrass beds and salt marshes do not occur in the Galapagos. Moreover, the separation of the Galapagos Islands into distinct proposed bioregions (Edgar et al. 2004) separated by deep water helps attribute the abundance of fish on the reef to the local habitats available. Fierro-Arcos et al. (2021) investigated fish composition patterns within mangroves in 2 Galapagos bioregions, comparing the proportion of juveniles between mangroves and adjacent rocky reefs. The study identified 6 economically significant fish species in mangrove habitats, including *Mycteroperca olfax* and *Lutjanus* spp. Another study utilized experimental fishing methods to evaluate fish assemblages on Santa Cruz Island, recording 26 species in mangroves, of which 9 held high commercial value (Llerena-Martillo et al. 2018). However, that study did not differentiate between juvenile and adult individuals, nor did it compare habitat utilization across different environments. According to nursery habitat definitions, the mere presence of juveniles in a habitat is insufficient to classify it as a nursery habitat (Beck et al. 2001). Instead, a contribution to the adult population of a specific juvenile area compared to other habitats (Sheaves et al. 2006) and the connectivity among habitat types is essential for a comprehensive assessment of fish nursery function (Sheaves 2005, Nagelkerken et al. 2015).

This study aims to contribute robust evidence regarding the role of mangroves in the Galapagos Islands as nursery areas. We surveyed reef fish species composition in mangroves and adjacent shallow rocky reefs using underwater visual censuses (UVCs) and assessed adult reef fish species using diver-operated videos (DOVs) in outer reefs at 20 m depth across the Galapagos Islands. We compared juvenile fish densities among habitat types and bioregions in the Galapagos Islands to identify mangrove nursery species, updated the list of these species, and predicted their densities in each habitat and bioregion. Furthermore, we assessed the effect of mangrove perimeter and the distance to mangrove habitats from outer reefs on the density of 3 economically significant adult fish species: *Lutjanus argentiventris*, *L. novemfasciatus*, and *M. olfax*.

2. MATERIALS AND METHODS

2.1. Study site

The study was conducted in the Galapagos Islands, located 1000 km off the coast of Ecuador in the TEP Ecoregion (1° 40' N–1° 36' S, 89° 16' W–92° 01' W). The Galapagos Islands were declared a National Park in 1959 and a UNESCO World Heritage Area in 1978. The Ecuadorian government created the 138 000 km² GMR in 1998, where industrial fishing is prohibited within 40 nautical miles (~74 km) around the islands. Tourism and artisanal fishing are allowed within the GMR only in designated areas under the current zoning scheme. The GMR is made up of 13 large islands and more than 100 islets and rocks (Fig. 1). These islands were formed by plume-volcanic activity and are located south of the Nazca Plate in an isolated unique geographic position where ocean currents meet (Snell et al. 1996, Harpp et al. 2014). The major currents that contribute to the variability of weather, climate, biodiversity, and productivity in the islands are the warm, nutrient-poor Panama Current coming from the northeast, the cool, nutrient-rich Humboldt Current coming from the Southern Ocean, and the Cromwell Current coming from the west, which is rich in nutrients because of sub-equatorial upwelling (Edgar et al. 2004, Heumann 2011).

Exposed lava coastline and rocky reefs are the main coastal formations in the Galapagos Islands, followed by mangroves and sandy beaches (Moity et al. 2019). Most Galapagos mangrove forests grow on lava fields, while more developed mangroves grow in enclosed sand or clay bays protected from wave action (Moity et al. 2019). Regional biogeography of shallow-reef fish communities has also been proposed with 3 main groupings: the northern, central-southeastern, and western areas (Edgar et al. 2004). The western region, including the island of Fernandina and west of Isabela, is characterized by abundant mangrove habitats and high numbers of endemic fish species; while the central-southern bioregion including Santa Cruz, Santiago, Cristobal, Floreana, and the east coast of Isabela is characterized by 'Panamic' fish species, with distributions extending north to Central America. (Edgar et al. 2004). The total mangrove cover in the Galapagos Islands is 3657 ha, amounting to 35% of the coastline. In total, 80% of mangrove cover is found in Isabela, followed by Santa Cruz, Santiago, Fernandina, San Cristobal, and the Floreana Islands (Moity et al. 2019). These mangrove forests constitute 4 main species of mangroves: *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove), *Laguncularia*

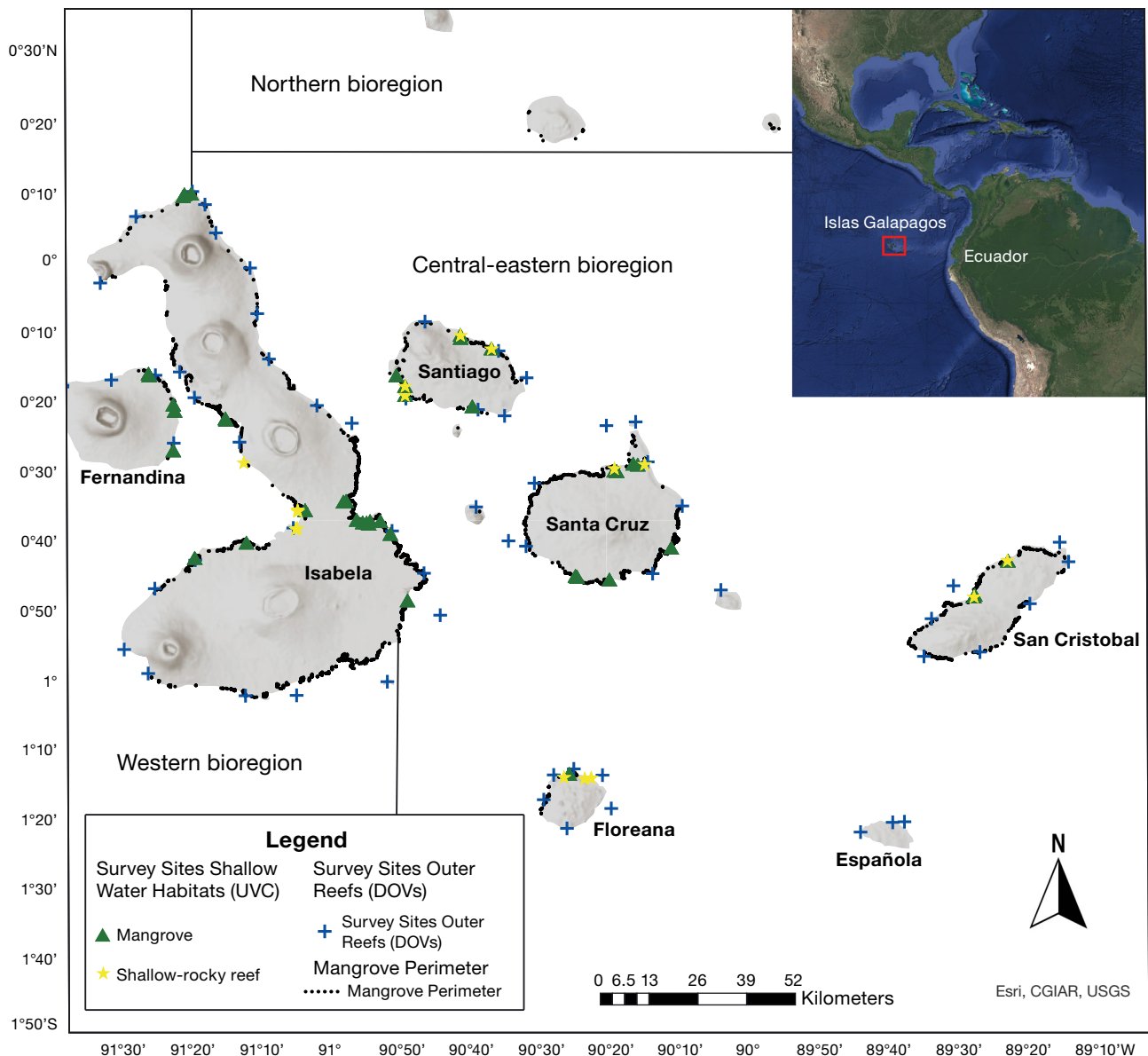


Fig. 1. Study area showing underwater visual census (UVC) survey sites in mangrove habitats and shallow rocky reefs (green and yellow), diver-operated videos (DOVs) in outer reefs (blue), and mangrove perimeter (dark outline) in each island. Inset map illustrates the geographic position of the Galapagos Islands in the Tropical Eastern Pacific region

racemosa (white mangrove), and *Conocarpus erectus* (buttonwood mangrove) (van der Maarel 1993).

The closest habitat to mangroves in terms of distance is shallow rocky reefs. Decades ago, this habitat was dominated by coral reefs, but El Niño–Southern Oscillation events have caused the decline of more than 90% of the coral reef coverage (Glynn 1994). Coral reefs are still present in the Galapagos Islands, exhibiting cycles of loss, recovery, and potential resilience to extreme thermal events (Rodríguez-Romero et al. 2011).

2.2. Juvenile fish densities in mangroves and shallow rocky reefs

We used UVCs to estimate fish density within mangroves and adjacent shallow rocky reefs. This method is non-destructive, repeatable, and cost-effective (Faunce & Serafy 2006, Langlois et al. 2010). In addition, this method allows observers to enter mangroves that are characterized by high turbidity and root complexity. Two experienced observers conducted 4 replicates of 1×50 m transects, counting

fish within 1 m on each side of the transect. Thus, the sampling area of each UVC transect was 100 m² within mangroves and shallow rocky reefs. Observers recorded species, number, and total length (TL) of all fish observed in each transect. Surveys were performed during daylight hours between 09:00 and 17:00 h, in 2–5 m of water at a total of 58 sites across the islands of Isabela, Fernandina, San Cristobal, Santa Cruz, Santiago, and Floreana (Table 1).

Of all the species observed, statistical analysis could be conducted on 11 fish species. Species that had counts in only one habitat or bioregion were not considered in this statistical analysis since models cannot estimate the effect of covariates in the absence of data. We also reviewed published literature to confirm whether these species (or related species) were possible nursery species in other tropical regions (Nagelkerken & van der Velde 2002, Shibuno et al. 2008, Jones et al. 2010). A total of 11 species were selected as potential mangrove nursery species. Among these species, the sailfin grouper *Mycteroperca olfax*, the yellow snapper *Lutjanus argentiventris*, and the dog snapper *L. novemfasciatus* are commercially important for the local fisheries (Molina et al. 2004). In the Galapagos Islands, *M. olfax*, better known as 'bacalao', has been listed as Endangered by the IUCN, while both snappers *L. argentiventris* and *L. novemfasciatus* are considered less of a concern (Besudo et al. 2010, Rojas et al. 2010, Ramirez et al. 2023). We used the length at first maturity of each species from FishBase to differentiate juvenile from adult abundances (Froese & Pauly 2018; see also Table S1 in the Supplement at www.int-res.com/articles/suppl/m747p099_supp.pdf).

Table 1. Number of sites surveyed per island, bioregion, and habitat using underwater visual census (UVC) and diver-operated video surveys (DOVs) across the Galapagos Marine Reserve

Island/ bioregion	UVC		DOVs Outer reefs (20 m)
	Mangrove	Shallow rocky reef	
Fernandina	5	0	3
Floreana	3	1	6
Isabela	5	18	19
San Cristobal	3	2	3
Santa Cruz	8	2	8
Santiago	7	4	5
Total	31	27	44
Central eastern	11	32	32
Western	5	10	12
Total	16	42	44

2.3. Adult fish biomass in outer deep reefs

Stereo video systems are also known to provide accurate estimates of marine fauna because they provide a more defined sample unit area, higher accuracy, and the opportunity to validate data (Harvey & Shortis 1995, Watson et al. 2005). We used diver-operating stereo-video surveys (stereo-DOV) to capture fish assemblages in outer deep reefs at approximately 18–20 m depth in 54 sites across the GMR. Divers swam 2 min timed transects at a speed of 0.5 m s⁻¹, 1 m above the bottom with cameras slightly tilted downward. Divers towed a surface buoy equipped with a GPS synchronized with the diver's watch allowing them to back-calculate the exact distance covered for each transect (Salinas-De-León et al. 2016).

From the stereo-video footage, we identified individuals of *M. olfax*, *L. argentiventris*, and *L. novemfasciatus*, and calculated relative abundance (number of fish per 100 m²) and TL in ten 50 m long by 5 m wide video transects (sampled area of 250 m² at each sampling site). We used the digital imagery software EventMeasure (Sea GIS) to make 3D measurements of individual fish. Cameras were previously calibrated following the methods in Goetze et al. (2019).

2.4. Mangrove perimeters and distances to outer coral reefs

Using Google Earth and QGIS 3.4 Madeira, we mapped and calculated mangrove perimeters in the Galapagos Islands at a virtual altitude of approximately 2.5 km. Mangrove perimeters in Isabela, Santiago, Fernandina, Santa Cruz, and San Cristobal were 175, 18, 9, 51, and 63 km², respectively. We used QGIS 3.4 Madeira to measure distances between stereo-DOV survey sites in outer reefs less than 10 km away from mangrove habitats to test the hypothesis that fish densities in the adult habitat decrease with increasing distance from mangrove habitats. Mangroves in the Galapagos islands are characterized as fringing, so juvenile fish are found mainly in the submerged prop roots of these mangroves. In that case, area can be misleading, as much of the mangrove is unavailable to fishes. Previous studies have found a link between mangrove perimeter and fish assemblages under these circumstances (Mumby et al. 2004). To avoid bias in calculating habitat area used by juvenile fish species, we used perimeter over area. Mangrove perimeter and area have been used to investigate relationships between mangrove extent and fisheries production, providing similar results (Man-

son et al. 2005). To determine whether mangrove perimeter affects adult fish densities, we quantified the total perimeters of mangroves within 10 km of each site, as carried out in other studies (Mumby et al. 2004, Huijbers et al. 2013). However, we acknowledge that the empirical data on the distance fish travel from mangroves to outer reefs is limited and there remains uncertainty regarding this 10 km criterion.

2.5. Statistical analysis

The nature of our data set was zero-inflated (Table 2). Failure to account for zero inflation can cause bias in parameter estimates and lead to incorrect relationships and inferences (Martin et al. 2005). However, it is a misconception that zero-inflated models are always necessary when a response variable contains many zeros (Zuur & Ieno 2016). The origin of a high number of zeroes in ecological data can stem from (1) real ecological effects causing the occurrence of ‘true zeroes’ and (2) sampling error or observation during data collection causing the presence of ‘false zeroes’ (Lambert 1992, MacKenzie et al. 2002). Additionally, covariates may be able to explain excessive numbers of zeros, and in such cases, generalized mixed models may effectively model the zeros in a specific data set. In our juvenile reef fish data set, we were unable to identify the source of zero observations. Therefore, we developed 2-way nested generalized linear mixed models (GLMMs) and 2 zero-inflated models with either Poisson or negative binomial distributions. We used the Poisson GLMM with a log link function (Eq. 1), as this model considers the mean as the variance, allowing for

some heterogeneity while ensuring positive fitted values typically used for positive count data (Zuur et al. 2009). When the variance was larger than the mean, we observed problems of overdispersion and therefore used the negative binomial distribution (Eq. 2) as a recommended alternative to the Poisson GLMM (Welsh et al. 2000, Zuur et al. 2009). Zero-inflated models combine a Bernoulli distribution with any other distribution (Poisson, negative binomial, binomial, gamma, beta-binomial, lognormal, or Gaussian), and are particularly robust to fit non-linear relationships (Zuur & Ieno 2016).

Our response variable was juvenile counts of each fish species, while fixed covariates were habitat (categorical with 2 levels: mangrove and shallow-rocky reefs) and bioregion (categorical with 2 levels: central-eastern and western). To incorporate the dependency among juvenile counts for each species from sites of the same island, we applied a random effect of site nested within the random effect of island. We used the package ‘glmmTMB’ (Brooks et al. 2017) in the software R (R Core Team 2017) to fit all models.

$$\begin{aligned}
 & \text{JuvD}_i \sim \text{Poisson}(\mu_i) \\
 E(\text{JuvD}_i) &= \mu_i \quad \text{and} \quad \text{var}(\text{JuvD}_i) = \mu_i \\
 \mu_i &= (\eta_i) \\
 (\eta_i) &= \beta_1 + \beta_2 \times f\text{Habitat}_i + \beta_3 \times f\text{Bioregion}_i
 \end{aligned} \tag{1}$$

$$\begin{aligned}
 & \text{JuvD}_i \sim \text{NegBinomial}(\mu_i, k) \\
 E(\text{JuvD}_i) &= \mu_i \quad \text{and} \quad \text{var}(\text{JuvD}_i) = \mu_i + \mu_i^2/k \\
 \mu_i &= \exp(\eta_i) \\
 (\eta_i) &= \beta_1 + \beta_2 \times f\text{Habitat}_i + \beta_3 \times f\text{Bioregion}_i
 \end{aligned} \tag{2}$$

Table 2. Juvenile counts of the 11 fish species selected to determine the importance of mangroves as nursery habitats detailed by habitat and bioregion. Means correspond to associated densities of fish species as the sampling area of each underwater visual census transect was 100 m² within mangroves and shallow rocky reefs

Species name	Habitat				Bioregion				Zero counts (% total)
	Mangrove		Shallow rocky reefs		Central eastern		Western		
	Mean ± SD	Count	Mean ± SD	Count	Mean ± SD	Count	Mean ± SD	Counts	
<i>Abudefduf troschelii</i>	15.10 ± 28.47	2537	12.08 ± 25.10	773	15.63 ± 30.76	2688	10.37 ± 14.55	622	43
<i>Chaetodon humeralis</i>	0.24 ± 1.59	41	0.38 ± 1.86	24	0.30 ± 1.62	51	0.23 ± 1.81	14	90
<i>Eucinostomus dowii</i>	2.88 ± 7.95	483	0.41 ± 2.60	26	2.88 ± 7.99	496	0.22 ± 0.76	13	79
<i>Halichoeres dispilus</i>	0.19 ± 1.39	32	1.45 ± 4.03	93	0.71 ± 2.86	122	0.05 ± 0.29	3	92
<i>Holacanthus passer</i>	0.04 ± 0.24	6	0.44 ± 1.68	28	0.19 ± 1.05	32	0.03 ± 0.26	2	95
<i>Lutjanus argentiventris</i>	7.44 ± 14.42	1250	0.19 ± 1.50	12	6.41 ± 14.16	1102	2.67 ± 6.41	160	58
<i>Mugil</i> spp.	10.09 ± 47.34	1695	1.61 ± 6.92	103	8.69 ± 46.19	1495	5.05 ± 16.06	303	83
<i>Mycteroperca olfax</i>	0.89 ± 1.81	149	1.31 ± 4.52	84	0.25 ± 0.98	43	3.17 ± 4.69	190	73
<i>Scarus ghobban</i>	1.10 ± 3.81	184	0.45 ± 1.36	29	0.72 ± 3.34	123	1.50 ± 3.26	90	85
<i>Sphoeroides annulatus</i>	9.14 ± 21.03	1535	2.70 ± 12.75	173	9.52 ± 21.99	1638	1.17 ± 1.98	70	62
<i>Stegastes arcifrons</i>	4.77 ± 11.27	802	3.41 ± 14.54	218	3.99 ± 10.57	686	5.57 ± 16.16	334	47

As part of the model validation process, we used Akaike's information criteria (AIC) to measure the goodness of fit and model complexity. We plotted Pearson residuals versus fitted values and versus each covariate in the model to assess nonlinear patterns or excessive heterogeneity. Models with clear issues of dispersion were excluded from further analysis. We validated the assumption of each distribution family by calculating the dispersion statistic and checking for over- and under-dispersion based on the dispersion statistic of 1.0 described by Hilbe (2011).

We also simulated the frequency of zeroes in 10 000 simulated data sets generated from each model and compared them with the percentage of zeroes observed in our data set. This comparison helped determine whether our models produce enough true or false zeroes, thus assessing the need for zero-inflated models. To determine the acceptable range of dispersion, we calculated the dispersion statistic in the 10 000 simulated data sets from model selection and assessed how much it fluctuated for the simulation and our models. Histograms of the simulations compared with our observed data were produced to validate whether our models complied with the assumptions of a Poisson and negative binomial distribution. To analyze spatial dependency, we plotted Pearson residuals against the coordinates of each site and looked for any residual spatial correlation. Our analysis indicated no issues with spatial dependency.

For most reef fish species, the covariates habitat and bioregion effectively explained the presence of zeros in the data set, making GLMMs a better fit without violating model assumptions. Zero-inflated models were only necessary for 2 species: *Eucinostomus dowii* and *L. argentiventris*. Both GLMMs and zero-inflated Poisson models produced similar fitted values and were competitive. However, we only present results from models that could handle enough zeros in our data set, as determined by the 10 000 simulations. We calculated estimated parameters, standard errors, and confidence intervals. The count of juvenile fish species already represents a density measure, as it is a count per unit area (100 m²).

A principal coordinates analysis (PCoA) based on Bray-Curtis distances was also performed on the juvenile fish species counts to visualize the differences in community composition between mangroves and shallow rocky reefs as well as between central-eastern and western bioregions. To quantitatively assess the significance of the observed differences in community composition, we conducted a PERMANOVA test to determine whether the differences between habitats and bioregions were statistically significant. These

analyses were performed using the 'vegan' package (Oksanen et al. 2024) in R (R Core Team 2017).

In the analysis of our adult reef fish data set, Poisson or negative binomial GLMs presented serious overdispersion problems while simulated data also failed to model the frequency of zeroes observed in the raw count data. Therefore, we applied a zero-altered Poisson model (ZAP), better known as the hurdle model, consisting mainly of fitting 2 models: one on the absence–presence data using a binary model (Bernoulli GLM), and the other one on the count data only (truncated Poisson GLM) for discrete data. The binary model estimated the statistically significant likelihood of the presence and absence of adult coral reef fish species *L. argentiventris*, *L. novemfasciatus*, and *M. olfax* in outer 20 m deep reefs (Eq. 3), while the second model predicted counts of each species as a function of distance to mangroves and extent of mangrove perimeter (Eq. 4). We used software RStudio v.0.99.486 (RStudio Team 2020) and the 'glmmaADMB' package built on the open-source AD Model Builder nonlinear fitting engine for fitting GLMMs (Fournier et al. 2012, Skaug et al. 2018). Model selection and model interpretation follow similar steps as those used for analyzing juvenile reef fish densities. These include simulating data sets, calculating AIC, visualizing spatial dependency, and plotting Pearson residuals versus fitted values.

$$\begin{aligned} & \text{Adult}_{ijkl} \sim \text{Bernoulli}(\pi_{ijkl}) \\ & E(\text{Adult}_{ijkl}) = \pi_{ijkl} \\ \text{logit}(\pi_{ijkl}) &= \text{distance}(\text{km})_{ijkl} + \text{perimeter}(10 \text{ km})_{ijkl} + \text{Island}_i \\ & \text{Island}_i \sim N(0, \sigma_{\text{Isl}}^2) \end{aligned} \quad (3)$$

$$\begin{aligned} & \text{Adult}_{ijkl} \sim \text{ZeroTruncated Poisson}(\mu_{ijkl}) \\ & E(\text{Adult}_{ijkl}) = \frac{\mu_{ijkl}}{1 - e^{-\mu_{ijkl}}} \\ \text{logit}(\mu_{ijkl}) &= \text{distance}(\text{km})_{ijkl} + \text{perimeter}(10 \text{ km})_{ijkl} + \text{Island}_i \\ & \text{Island}_i \sim N(0, \sigma_{\text{Isl}}^2) \end{aligned} \quad (4)$$

3. RESULTS

3.1. Fish assemblages and juvenile densities in shallow-water habitats

Most of the species surveyed using UVCs were found in both mangroves and shallow rocky reefs. We recorded 75 fish species (29 221 individual counts) across a total of 58 sites, comprising 16 mangrove and 42 shallow rocky reef sites within 6 islands. The aver-

age sizes (cm, TL) of fish observed were within their juvenile length ranges. A detailed description of the number of juvenile species found in each habitat and bioregion can be found in Table S2. We observed several species with high juvenile and adult abundances in mangroves, including *Caranx caballus*, *C. caninus*, *Lutjanus aratus*, and *L. jordani*.

Out of all the species observed, 11 fish species were suitable for statistical analysis. These potential nursery species comprised 15578 individuals from the families Chaetodontidae, Gerridae, Labridae, Lutjanidae, Mugilidae, Serranidae, Scaridae, and Pomacentridae. Densities of *Eucinostomus dowii* (negative binomial [nbn] coefficient -2.9 , $p = 0.002$), *L. argentiventris* (nbn coefficient -5.4 , $p < 0.001$), *Mugil* spp. (nbn coefficient -2.4 , $p = 0.052$), *Mycteroperca olfax* (nbn coefficient -1.4 , $p = 0.041$), *Spheroides annulatus* (nbn coefficient -2.3 , $p = 0.002$), and *Stegastes arcifrons* (nbn coefficient -2.3 , $p = 0.005$) were greater in mangroves than in shallow rocky reefs (Fig. 2, Tables S3 & S4). *Mugil* spp. represented the species with the highest juvenile density in mangrove habitats, with a mean (\pm SE) of 4.9 ± 0.8 in the central bioregion and 3.4 ± 1.5 in the western bioregion. The density of commercial *L. argentiventris* per 100 m² in the central bioregion was 2.5 ± 0.4 in mangrove habitats compared to 0.01 ± 1.0 in shallow rocky reefs, while in the western bioregion, the density was 2.5 ± 0.6 in mangrove habitats and 0.01 ± 1.1 in shallow rocky reefs. The density of the commercial parrotfish *Scarus ghobban* was also higher in mangrove habitats than in shallow rocky reefs for both bioregions, at 0.3 ± 0.3 and 0.1 ± 0.1 individuals, respectively in the central-eastern region, and 5.1 ± 5.1 and 1.5 ± 1.5 individuals in the western region. However, this effect was only significant for the factor bioregion (coefficient 2.9, $p = 0.002$).

The only species that showed significantly higher density in shallow reefs than in mangrove forests was *Halichoeres dispilus* (nbn coefficient 3.6, $p = 0.014$). In the central-eastern region, juvenile *H. dispilus* density was 0.6 ± 1.5 compared to juveniles found in mangroves (0.02 ± 1.6 ind.). Likewise, in the western region, *H. dispilus* density was higher in shallow rocky reefs (0.1 ± 2.0 ind.) than in mangrove habitats (0.0 ± 2.6 ind.). *Abudefduf troschelli*, *Chaetodon humeralis*, and *Holacanthus passer* densities were not significantly different between habitat or bioregion.

Juveniles of *A. troschelli*, *E. dowii*, and *S. ghobban* made up about 90% of all recorded fish. All individuals of *C. humeralis*, *M. olfax*, and *S. annulatus* recorded were juveniles, while the percentage of individuals at a juvenile stage for *Mugil* spp., *H. dispilus*,

and *L. argentiventris* were 85, 79, and 68%, respectively. *H. passer* and *S. arcifrons* showed lower juvenile percentages of 40 and 20%, respectively.

When considering the distribution of juvenile fish densities per bioregion, *E. dowii* and *S. annulatus* had significantly higher juvenile densities in the central-eastern bioregion than the western bioregion (nbn coefficient -2.5 , $p = 0.004$ and nbn coefficient -1.6 , $p = 0.025$, respectively). In contrast, densities of *M. olfax* and *S. ghobban* were significantly higher in the western bioregion (nbn coefficient 3.5, $p < 0.001$ and nbn coefficient 2.9, $p = 0.002$, respectively). All juvenile densities in these bioregions were higher in mangrove habitats compared to shallow rocky reefs (Table S2). There was no detectable bioregion effect on the densities of the remaining 6 species (*A. troschelli*, *C. humeralis*, *H. dispilus*, *L. argentiventris*, *H. passer*, or *Mugil* spp.).

The negative binomial GLMM model had the best fit and the lowest AIC value for most species. Both model structures were comparable for only 3 species (*C. humeralis*, *H. passer*, and *M. olfax*; Fig. S1). Model validations showed no violations of assumptions for any of the models (Fig. S1). To analyze spatial dependency, we plotted Pearson residuals against the coordinates of each survey site but did not find any residual spatial correlation.

PCoA based on Bray-Curtis dissimilarity was used to analyze the fish community compositions across different habitats and bioregions. The first 2 principal coordinates explained 25.75 and 14.03% of the variation in the data, respectively (Fig. 3). The analysis revealed distinct clusters for samples from mangroves and shallow rocky reefs, indicating different species compositions between these habitats. Additionally, the central-eastern bioregion and western bioregion also suggested biogeographical differences, although this difference was moderate. Galapagos reef fish species *E. dowii*, *M. olfax*, and *L. argentiventris* were strongly associated with mangrove habitats, while *A. troschelli* and *S. ghobban* were more associated with shallow rocky reefs. Additionally, *C. humeralis* and *S. arcifrons* were primarily associated with the central-eastern bioregion, whereas *H. passer* and *H. dispilus* were associated with the western bioregion.

Statistical analysis using PERMANOVA confirmed the significant differences in fish community compositions between habitats ($F_{1,200} = 11.96$, $p = 0.001$) and bioregions ($F_{1,200} = 7.10$, $p = 0.001$). Additionally, the interaction between habitat and bioregion was significant ($F_{1,200} = 2.18$, $p = 0.023$), suggesting that the influence of habitat on species composition varies between bioregions.

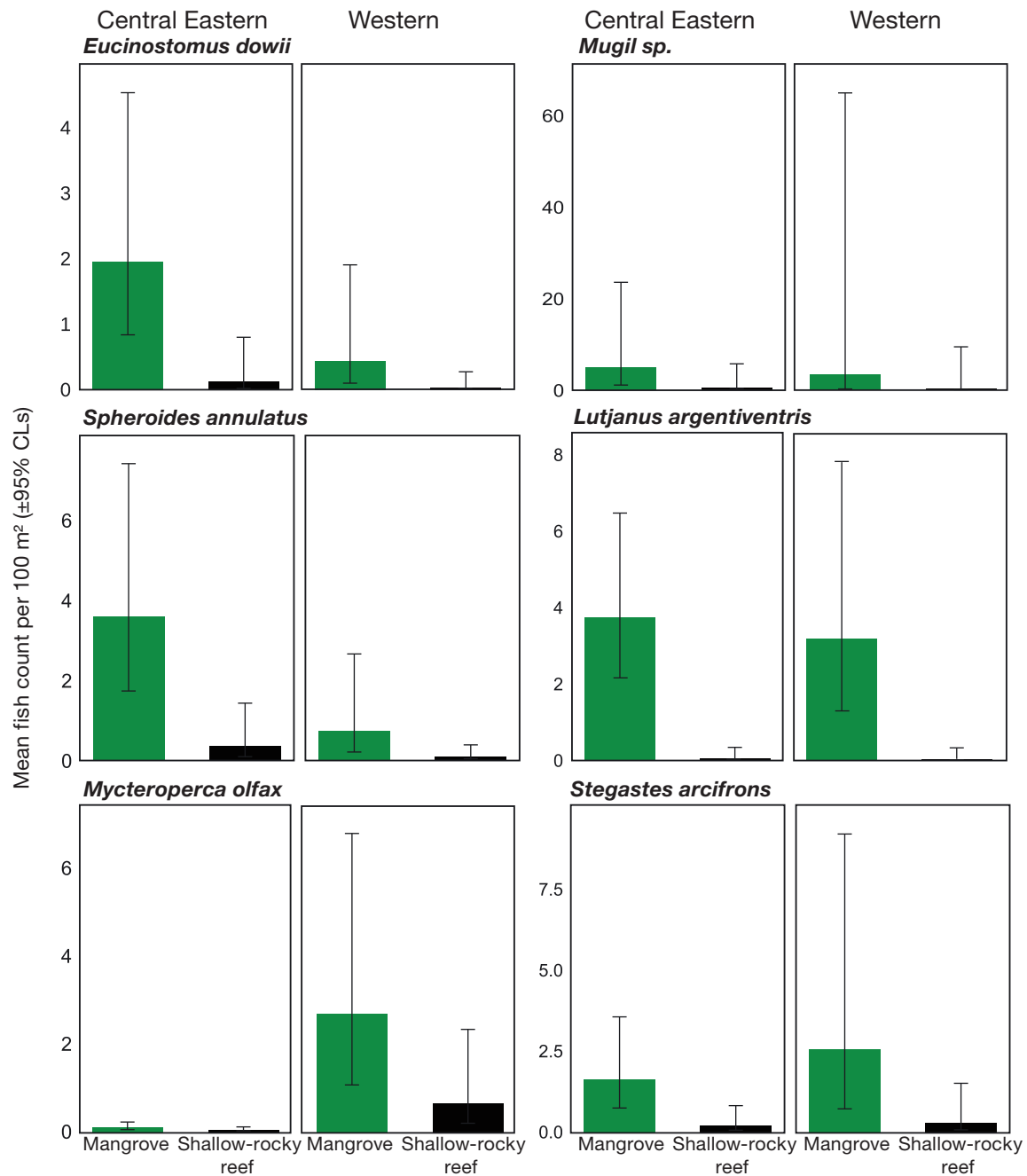


Fig. 2. Mean fish count for the 7 species that exhibited significantly higher juvenile counts in mangrove habitats compared to shallow coral reefs. These counts are estimated densities given the context of the area in which counts were observed (100 m²). Estimates were predicted by generalized linear mixed models using juvenile counts from both mangroves and shallow rocky reefs across both bioregions in the Galapagos Islands

3.2. Adult fish densities in deep rocky reefs

A total of 44 outer-deep reef sites were sampled using DOVs, with 32 sites in the central-eastern bioregion and 12 sites in the western bioregion. Counts of *L. argentiventris*, *L. novemfasciatus*, and *M. olfax* were also zero-inflated with 83, 97, and 69% zeroes,

respectively out of their total counts. The observations of *L. novemfasciatus* were so low that statistical results were unreliable and showed severe issues of overdispersion. Therefore, we chose to exclude these results from the study. From the binary model, we found a significant negative effect of the distance to mangrove habitats on the probability of the presence

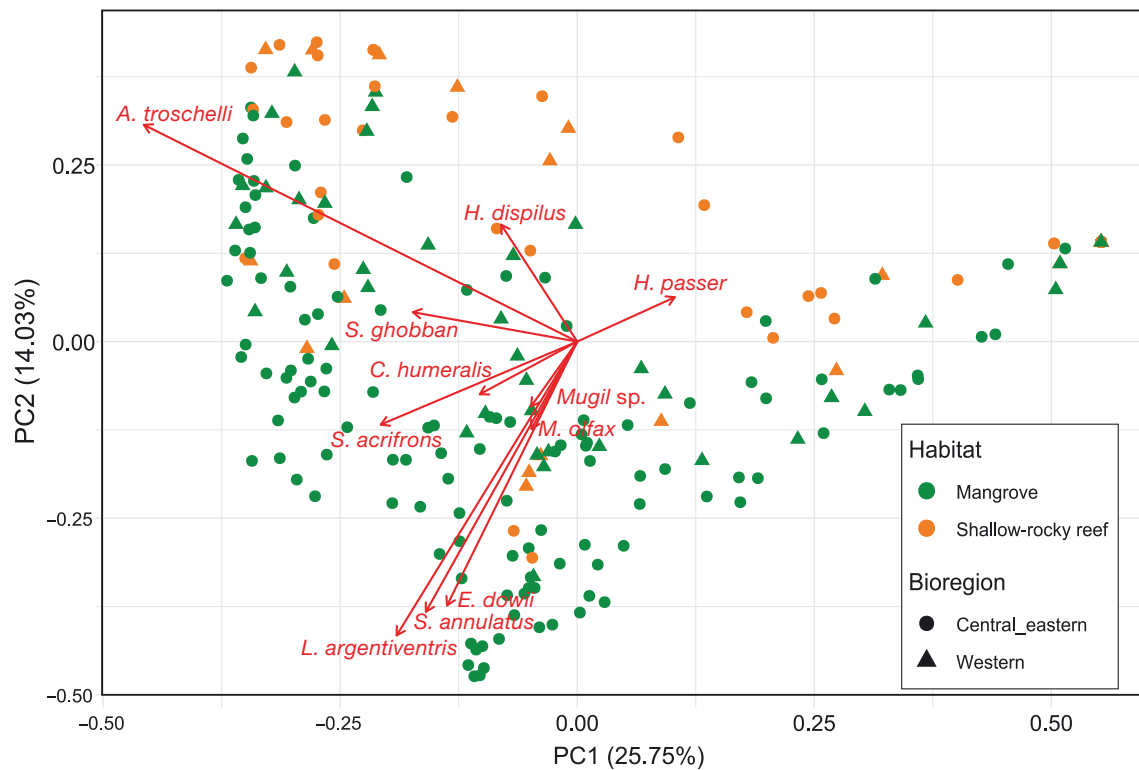


Fig. 3. Principal coordinates analysis (PCoA) based on Bray-Curtis dissimilarity showing fish species counts in mangroves (green), shallow rocky reefs (orange), central-eastern (circles) and western (triangles) bioregions. Species vectors indicate the contribution of individual species to community structure (see Table 2 for full species names)

for both *L. argentiventris* (coefficient -0.183 , $p = 0.013$) and *M. olfax* (coefficient -0.085 , $p = 0.043$). The likelihood of encountering these species decreased as the distance from mangroves increased, indicating that these species prefer deep outer reef sites closer to mangroves (Fig. 4). The effect of distance to mangroves from outer reefs was not significant on the count component of the hurdle model for both *L. argentiventris* and *M. olfax*.

The extent of the mangrove perimeter within a 10 km radius from deep outer reef sites where *L. argentiventris* and *M. olfax* were identified was not significant for the binary model but was significant for the count model of these species. Although the mangrove perimeter was not significant in predicting the presence–absence of *M. olfax* and *L. argentiventris*, it was a significant predictor in the count model for both species: *L. argentiventris* (coefficient 0.029, $p < 0.001$) and *M. olfax* (coefficient 0.015, $p = 0.016$) (Fig. 4, Table S5). These results show that although the presence of these species might not be directly influenced by the extent of the mangrove perimeter available for reef fishes, their abundance within those areas is significantly enhanced by larger mangrove perimeters. The highest estimated mean (\pm SD) den-

sity per 250 m² was 0.52 ± 0.13 for *M. olfax*, followed by *L. argentiventris* with an estimated mean density of 0.39 ± 0.51 , and *L. novemfasciatus* with 0.06 ± 0.13 . All model validations indicated no violation of statistical assumptions for these species (Fig. S2). We combined the fitted values of the individual components to obtain the overall fitted values of the ZAP GLMM.

4. DISCUSSION

4.1. Juvenile reef species densities

Our study shows that mangroves are nursery habitats for reef fish species in the Galapagos Islands. We identified *Eucinostomus dowii*, *Lutjanus argentiventris*, *Mugil* spp., *Mycteroperca olfax*, *Sphoeroides annulatus*, *Stegastes arcifrons*, and *Scarus ghobban* as mangrove nursery species, as their juvenile densities were significantly higher in mangroves than in shallow rocky reefs. Additionally, 19 other fish species, primarily juveniles, were exclusively observed within mangrove habitats. We suggest that these species are highly associated with mangrove habitats and utilize these areas as nursery grounds. Among these man-

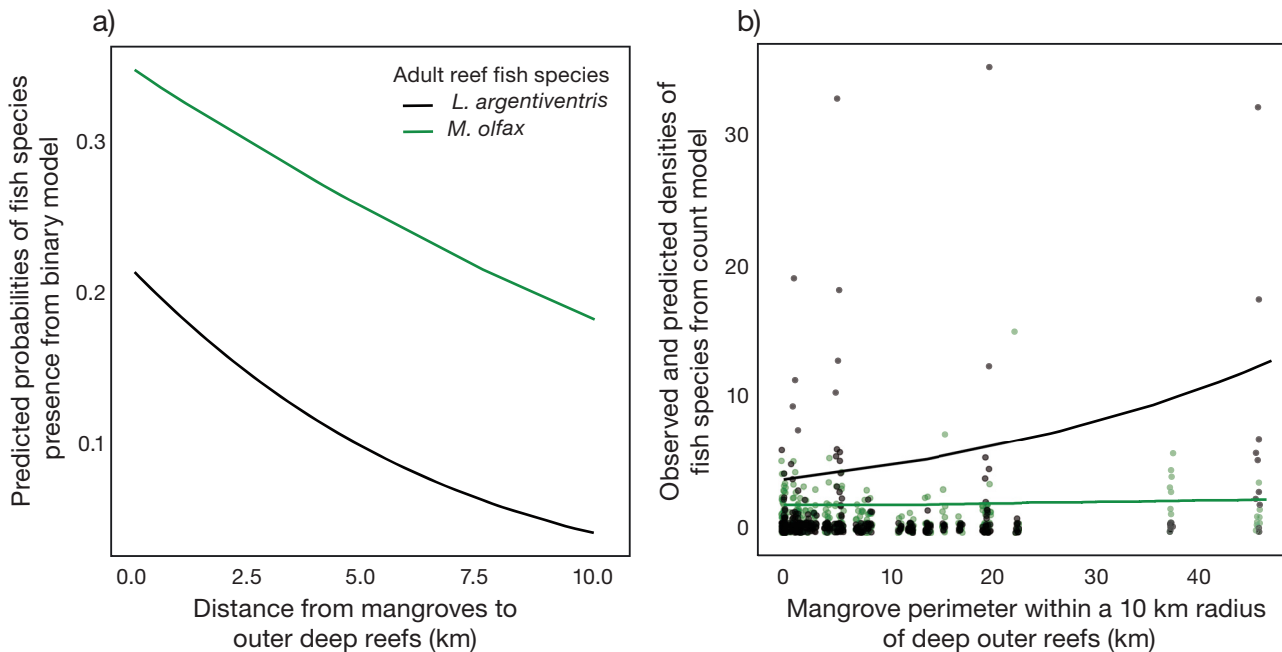


Fig. 4. (a) Effect of distance from mangroves on the presence–absence probability of *Lutjanus argentiventris* and *Mycteroperca olfax*. (b) Effect of the extent of mangrove within a 10 km radius from deep outer reef sites on the densities for *M. olfax* and *L. argentiventris*. Predicted densities (line) and observed counts (dots) are shown for both species

grove nursery species, 6 are of high commercial importance in the Galapagos Islands: the snappers *L. argentiventris*, *L. aratus*, *L. jordani*, and *L. novemfasciatus*, the mullet *Mugil* spp., and the grouper *M. olfax*, which is also listed as Endangered under the IUCN Red List (Ramírez et al. 2023). Species of low commercial importance included the mojarra *Gerres cinereus* and the parrotfish *S. ghobban* (Molina et al. 2004, Llerena-Martillo et al. 2018).

Research on the role of mangroves in the Galapagos Islands is limited. Fierro-Arcos et al. (2021) was the first study that reported patterns of fish compositions in mangroves and assessed the environmental factors influencing fish assemblages in these habitats. Their study observed differences in juvenile proportions between mangroves and adjacent rocky reefs and showed that *L. argentiventris* and *M. olfax* were highly associated with mangroves, with juvenile proportions of 80.2 and 84.3%, respectively. In contrast to the findings of Fierro-Arcos et al. (2021), our study identified more reef fish species that use mangroves as nursery habitats, and we used predictive models to estimate their densities across habitats and bioregions. Llerena-Martillo et al. (2018) also recorded several of our species on the island of Santa Cruz, but their survey was limited to mangrove habitats only and juvenile counts were not differentiated from adult ones. On the southern coast of Ecuador, Shervette et al. (2007)

compared fish densities in remnant wetlands with and without mangroves and reported that 21 out of 34 species were exclusive to mangrove habitats in their juvenile stage.

In the TEP, research on the role of mangroves as nursery habitats is also limited, especially when compared with other tropical regions (Castellanos-Galindo et al. 2013, Zu Ermgassen et al. 2020). The only meta-analysis in the TEP region found 315 fish species associated with mangroves (Castellanos-Galindo et al. 2013). In the Gulf of California, 6 species have been identified as mangrove nursery species, one of them being the yellow snapper *L. argentiventris* (Thomson et al. 2000). One study investigated the recruitment and ontogenetic habitat shifts of *L. argentiventris* and found that this species settles in pebbles after their pelagic larval stage (Aburto-Oropeza et al. 2009). Upon reaching a length of 2 cm, they grow to approximately 10 cm while present in mangroves, shift as subadults to shallow rocky reefs, and subsequently transition to deep coral reefs as adults (Aburto-Oropeza et al. 2009). Our findings also suggest a high level of dependence on mangroves for *L. argentiventris* in the Galapagos—a finding consistent with other studies on snapper species (Nagelkerken & van der Velde 2002).

When comparing our findings with other tropical regions, we found substantial evidence for the role of mangroves as nursery habitats. A meta-analysis by

Igulu et al. (2014) found that juvenile densities of nursery species were significantly higher in mangroves than in seagrass beds in the Caribbean. Another meta-analysis reported that 10 out of 15 studies in the Caribbean had higher juvenile densities of reef fish species in mangroves only (Nagelkerken et al. 2000, Nagelkerken 2009) including species from the Lutjanidae, as reported in our study. Additionally, some studies indicated that few species had the highest densities in seagrass or channel habitats, while others were common in multiple shallow-water habitats, highlighting the diversity in habitat use among juvenile fish (Nagelkerken 2009). By contrast, juvenile fish densities in the Indo-Pacific region were significantly higher in seagrass beds than in mangroves (Igulu et al. 2014). Other studies reported that the availability of seagrass during low tide and mangroves during high tide makes both habitats essential nursery areas for several fish species (Unsworth et al. 2008, Kimirei et al. 2013, Huijbers et al. 2015). Another meta-analysis concluded that seagrass appeared to be more valuable than other nursery habitats in temperate and subtropical regions (McDevitt-Irwin et al. 2016). Igulu et al. (2014) concluded that tidal regime is a major global driver, regardless of biogeographic region, influencing the number of reef species and individuals utilizing mangrove habitats within a mosaic of marine habitats.

In the Galapagos Islands, complex mangrove prop roots and high water turbidity that provide food, shelter, and lower predation risk likely explain the preference of some reef fish species for mangroves over shallow rocky reefs (Parrish 1989, Blaber 2000, Nagelkerken & Faunce 2008). In addition, juvenile fish can distinguish chemicals linked to specific habitats, and these cues play an essential role in the preference of a fish species to a certain nursery habitat (Huijbers et al. 2008). Lastly, environmental conditions such as salinity, temperature, DO, and abiotic factors such as depth and sediment type also explain the distribution of fish in marine habitats (Roff & Evans 2002, Dubuc et al. 2019a). These environmental factors may help explain a bioregional pattern in our data that is superimposed upon the mangrove nursery functioning.

Our study generally showed higher juvenile counts in the central-eastern bioregion than in the western bioregion. However, only estimated densities of *E. dowii* and *S. annulatus* were statistically significantly higher in the central-eastern bioregion, while *M. olfax* and *S. ghobban* were statistically significantly higher in the western bioregion. These findings align with Fierro-Arcos et al. (2021), who identified 50% more species in the central-eastern region. The PCoA

based on Bray-Curtis dissimilarity further supports these findings by revealing distinct patterns in the fish species composition across different habitats and bioregions (Fig. 3). Environmental factors such as warmer water temperatures and more stable conditions in the central-eastern bioregion can explain higher species richness in this region as well as potentially more connectivity among mangroves and other important marine habitats.

Other studies suggest that some species developed unique anti-predator tactics, allowing them to use any available shallow habitat (Nanjo et al. 2011). This could explain why species such as *Chaetodon humeralis*, *Halichoeres dispilus*, and *Holacanthus passer* in our study did not display higher juvenile densities in mangroves but rather in shallow rocky reefs. It is important to note that few studies do not support the mangrove nursery hypothesis (Huxham et al. 2004, Nanjo et al. 2011). Thus, assuming mangroves or any shallow-water habitats will offer the same nursery role is equivocal, as this role varies at local scales and depends on habitat availability, as well as the biological, geographical, and/or environmental needs of each species (Chittaro et al. 2005, Sheaves et al. 2006, Dubuc et al. 2021).

4.2. Adult fish densities in deep rocky reefs

M. olfax was the most abundant adult species at 20 m depth, among the 3 species quantified in the DOV surveys. Although we were limited to compare juvenile densities with adult densities due to different sampling methods, all observations of *M. olfax* in mangroves were juveniles and were significantly higher than in shallow rocky reefs. The density of *M. olfax* reported by Salinas-De-León et al. (2015) in the northernmost islands of the GMR was 8 times higher than the mean density reported in our study across 6 Galapagos Islands. Lower densities of *M. olfax* in our study could be explained by the artisanal fishing pressure and the decline that this commercial species has experienced over the last decades (Ramírez et al. 2023) or by the fact that the northern islands are spawning aggregation sites for this species (Salinas-De-León et al. 2015). Densities of *L. argentiventris* and *M. olfax* were significantly higher at sites closer to mangroves. Our results thus provide valuable insights into the spatial distribution and connectivity of reef fish species populations to mangrove forests and are further supported by studies such as Olds et al. (2013) in sub-tropical Australia, who found snappers (Lutjanidae) to be the most abundant species in reserve reefs close to mangroves.

Even in fished areas, a positive effect of the proximity of mangroves on fish biomass suggests that this effect is greater than the effect of no-take marine reserves on fish populations that do have proximity to nursery habitats (Nagelkerken et al. 2012). Although our study did not analyze the effect of marine reserves, we recommend conducting further studies to improve the design and efficiency of the GMR.

The life history and biology of each species can explain the migration of adult species from one habitat to another (Sheaves et al. 2015), given the fact that snappers *Lutjanus* spp., for instance, have a strong swimming capacity and have been reported to disperse 10s of km from their nursery site (Mumby et al. 2004, Huijbers et al. 2013). We observed *M. olfax* up to 20 km away from mangrove sites while Claydon et al. (2015) reported *Scarus guacamaia* as far as 42 km away. In contrast, densities of most fish species were close to zero at approximately ~14 km from mangrove habitats (Nagelkerken et al. 2017). Our results are consistent with studies that indicate that populations of mangrove nursery species are denser within a few kilometers of mangrove habitats (Nagelkerken & van der Velde 2002, Dorenbosch et al. 2004, Aburto-Oropeza et al. 2009, 2015).

Our study also considered the extent of mangrove perimeter within a 10 km radius as a factor influencing adult fish populations in outer reef habitats. Our models predicted higher densities of *L. argentiventris* and *M. olfax* with increasing mangrove perimeter. These findings align with those of Fierro-Arcos et al. (2021), who determined the length of mangrove fringe as a significant factor driving fish assemblages in the Galapagos Islands. A key difference between our study and Fierro-Arcos et al. (2021) is the scale of the area considered. Their study considered mangrove perimeters within 100 m of the sampled mangrove sites, while our study examined the mangrove perimeter within a 10 km radius from adult fish populations in deep outer reefs. Nevertheless, these findings highlight the importance of mangrove abundance in providing habitat and resources to reef fish species.

Sandy beaches, salt flats, and lagoons were not surveyed in our study. We acknowledge that all habitats should be assessed to fully evaluate the potential nursery role for particular species. As suggested by several studies (Sheridan & Hays 2003, Mumby & Hastings 2008, Carrasquilla-Henao & Juanes 2017), we reinforce the call for further research into the importance of other factors driving nursery use by fishes, including predation rates (especially from predators that use nursery habitats on a transient basis), freshwater input, tidal regime, and salinity.

4.3. Implications for management

In the Galapagos, although mangrove trees are protected from human activities, only ~5% of mangrove fringe cover is fully protected from fishing in no-take areas (Moity et al. 2019). Despite a ban on industrial fishing after the creation of the GMR in 1998, artisanal fishing continues to exert pressure on commercially important fish species such as the Galapagos grouper *M. olfax*, snappers (Lutjanidae), and mullets (Mugilidae) (Salinas-De-León et al. 2015, Tanner et al. 2019). While fishers typically do not target juvenile fish, some fishing methods in mangroves can inadvertently capture juvenile individuals, potentially leading to an economic impact on local fisher's revenue. A recent study estimated the annual catch of *M. olfax* to be \$624 367 ha⁻¹ of mangrove, representing 69% of the annual net demersal finfish fishery benefit in the Galapagos Islands (Tanner et al. 2019). Additionally, overfishing, and thereby the decline of predators such as *M. olfax*, in the Galapagos Islands directly impacts fish community structures and, indirectly, other species (e.g. sea urchins) due to a trophic cascading effect whereby these species are targeted by predators (Ruttenberg 2001). Protecting mangroves not only contributes to the sustainability of fisheries but also to the stability of adult reef fish populations that play important ecological roles. Whether as predators (e.g. snappers *Lutjanus* spp.) or grazers (e.g. parrotfishes *Scarus* spp.), these fish contribute to the maintenance of coral reefs (Lamb & Johnson 2010, Harborne et al. 2016). Given the decline of Galapagos coral reefs and ongoing threats such as global warming, sea level rise, and invasive species, the conservation of mangrove habitats is critical. We strongly suggest a better understanding of ecological interactions, continuing monitoring, and implementing proactive management strategies to ensure long-term Galapagos mangrove conservation.

Habitat structure and connectivity of nurseries to adult habitats are also essential for adequate functioning and provisioning of ecosystem services (Beets et al. 2003, Barbier et al. 2011, Ward et al. 2016). Evaluating the linkages between habitats use during reef fish life cycles has important implications for the zoning scheme for the GMR. Although we suggest that mangroves play a major role as nurseries in the absence of seagrass beds, we do not intend to undervalue the role of shallow rocky reefs as nursery habitats, as we found these habitats were more favorable to other non-commercial species such as *C. humeralis*, *H. passer*, and *H. dispilus*. Several studies also agree that juvenile coral reef fish species use diverse non-reef habitats (Nagel-

kerken et al. 2000, Lefcheck et al. 2019, Sambrook et al. 2019). Therefore, it is important to study and protect all these habitats together.

4.4. Conclusions

Our study highlights the importance of mangroves as nursery habitats for 7 reef fish species. We identified at least 7 species exhibiting significantly higher juvenile densities in mangroves compared to shallow rocky reefs. Furthermore, our findings reveal the exclusive association of 19 other juvenile fish species with mangrove habitats. We contribute knowledge about the mangrove nursery function in the Galapagos Islands and the TEP region that aligns with other studies worldwide where the role of mangroves as nursery habitats has been evaluated. We highly recommend incorporating the nursery concept in the design and management of the GMR, including a seascape model considering all habitats and their interactions. As the main nursery habitats for some commercially important, endangered, or endemic species, mangroves play a significant role in the ecology, economy, and tourism of the Galapagos Islands. Our study calls for proactive management, continuous monitoring, regulation, and enforcement that safeguards the long-term conservation of Galapagos mangroves.

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