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Mangrove fish assemblages reflect the environmental diversity of the Galapagos Islands

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ABSTRACT: Mangroves are important habitats for a variety of ecologically, commercially and culturally important fishes. However, little is known about their role within the Tropical Eastern Pacific (TEP), and particularly in the Galapagos Archipelago, the westernmost limit for mangroves in the Americas, and the only oceanic islands in the TEP where mangroves are present. We describe patterns of fish composition in the 2 Galapagos bioregions where mangroves are present and assess potential environmental factors influencing fish community composition. Underwater Visual Census and Stereo Baited Remote Underwater Video stations (stereo-BRUVS) were used to sample fish communities. We identified 35 029 fish representing 93 species, 67 genera and 36 families. Pomacentridae, Mugilidae, Haemulidae and Lutjanidae were the most common families. Juveniles made up 43 % of the fish, 30 species were of importance to local artisanal fisheries and 80 % of species were associated with reef habitats, suggesting mangroves in Galapagos may provide nursery habitats for economically valued species. Fish assemblage composition varied across bioregions, with 6 taxa responsible for driving these differences, including species of economic importance: *Lutjanus novemfasciatus* and *Mycteroperca olfax*. Species richness was 17 % higher in the Central-Southeastern than in the Western region; while higher species richness, Shannon-Wiener diversity and Pielou's evenness were detected with BRUVS than through visual censuses. Our results highlight the role of mangroves as a habitat for a unique fish community composed of young, endemic and commercially important species, whose composition is likely driven by the isolation of the islands and its location in a convergence zone.

KEY WORDS: Fisheries · Nursery habitat · Marine protected area · MPA · Underwater Visual Census · UVC · Stereo-Baited Remote Underwater Video stations · Stereo-BRUVS · Tropical Eastern Pacific

1. INTRODUCTION

Mangrove forests are considered to be amongst the most productive and diverse ecosystems on Earth (Alongi 2002). Mangroves can be found globally along intertidal areas in tropical and subtropical regions, where they provide a variety of key ecosystem services (Alongi 2002). One such service is the provision of nursery habitats to various ecologically and economically important species of fish and crustaceans, thus making mangroves an important contributor to the recruitment of fish and invertebrate populations (Aburto-Oropeza et al. 2009, Saenger et al. 2013, Nagelkerken et al. 2015, zu Ermgassen et al. 2020). Despite their ecological importance, an estimated 50 % of mangrove forests worldwide have

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*Corresponding author: denisse.fierro@fcdarwin.org.ec been lost in the past 50 yr (López-Portillo et al. 2017), largely as a result of human activities (Saenger et al. 2013, Chowdhury et al. 2017). The resilience of mangrove ecosystems are also negatively affected by anthropogenic pressures, making them vulnerable to the effects of climate change (Jennerjahn et al. 2017). It is predicted that by the end of this century the combination of human pressures and climate change impacts will have a significant negative effect not only on mangrove distribution, but also on the ecosystem services they provide (Jennerjahn et al. 2017).

The Tropical Eastern Pacific (TEP), a marine ecoregion extending from southern Baja California (Mexico) to northern Peru (Robertson & Cramer 2009), contains ~7% of global mangrove coverage (Giri et al. 2011). In the TEP, mangroves are found along the continental coastline of the Americas, and on one set of oceanic islands, the Galapagos Islands (Giri et al. 2011). As widely reported in locations across the Caribbean and the Indo-Pacific, mangroves are also known to play an important ecological role in marine ecosystems of the Eastern Pacific (Dorenbosch et al. 2004, 2005, Mumby et al. 2004, Aburto-Oropeza et al. 2008, Nagelkerken et al. 2008). However, very little is known about their influence on the composition of fish community assemblages across most of the TEP, and in particular on mangrove fish communities of the Galapagos Archipelago.

The Galapagos Marine Reserve (GMR) is a multiple use reserve established in 1998 to protect the Galapagos Archipelago and its surrounding waters (Heylings et al. 2002). The GMR covers a total area of 138 000 km^2 where no industrial fishing is allowed (Heylings et al. 2002). The Galapagos Archipelago is located about 1000 km west of the South American Pacific coast (see Fig. 1), and it is made up of 13 large islands and over 100 islets of volcanic origin (Snell et al. 1996). The Galapagos is the only tropical archipelago located in a convergence zone where various cool and warm water oceanic currents meet (Andersen & Hamann 1986, Edgar et al. 2004a). The distinct oceanographic conditions together with the local geological features result in markedly different environmental conditions across the archipelago (Banks 2002, Schaeffer et al. 2008). This spatial variability in environmental conditions has a strong influence on the distribution of marine fauna, such as shallow reef fishes and sharks (Banks 2002, Edgar et al. 2004a, Palacios et al. 2006, Acuña-Marrero et al. 2018). These patterns in faunal distribution are consistent enough to allow for the separation of the marine areas of the archipelago into 3 main bioregions (see Fig. 1): (1) far-northern (not shown in Fig. 1), (2) Central-Southeastern (CSE), which includes the northern subregion, and (3) Western, including the Elizabeth subregion (Edgar et al. 2004a).

Mangroves cover about 35% of the Galapagos coastlines, and in contrast with global trends, their coverage on the islands is estimated to have increased by 24% between 2004 and 2014 (Moity et al. 2019). This overall increase was likely the result of the protected status of the Galapagos Islands, and the lack of human interference in mangrove areas (Moity et al. 2019). Despite this upward trend in coverage, mangroves in the Galapagos are particularly vulnerable to climate change because of their location in a convergence zone, where they are regularly subjected to environmental conditions at the edge of their physiological tolerance (Andersen & Hamann 1986, Doney et al. 2012, Moity et al. 2019). Since mangroves are severely understudied in the Galapagos, we cannot be certain of the ecological role they currently play in the marine systems of the archipelago, or how its ecological function will be affected by global climate change. Mangrove fish assemblages have not been fully described yet, and the potential spatial variation of these assemblages across the archipelago has not been examined either. The few studies conducted to date in the archipelago are mostly available as part of the grey literature, and either focus on a small subset of islands (Suárez-Moncada 2012, Aguaiza 2015, Llerena-Martillo et al. 2018), or on a selected group of fish species (Llerena-Martillo et al. 2015). This knowledge gap represents a challenge, as without accurate data about the diversity of mangrove fish populations and the relationship between fish assemblages and mangrove habitat conditions, it is not possible to identify key areas deserving additional protections; or to design, support and improve conservation strategies that are effective in protecting these marine communities (Ley 2005, Banks et al. 2009). An improved understanding about the ecological role of mangroves in the Galapagos could also be used to assess future alterations to this ecosystem brought by a changing climate (Visbeck 2018).

To avoid any negative impacts inside protected areas, such as the GMR, derived from permanently removing individual fish as a result of sampling, the use of non-destructive sampling methods are deemed more suitable (Mallet & Pelletier 2014). Underwater Visual Census (UVC) and Stereo-Baited Remote Underwater Video stations (stereo-BRUVS) are 2 non-destructive techniques widely used to obtain information about the composition of fish assemblages in a variety of marine systems (Mallet & Pelletier 2014). UVC is a relatively inexpensive and easy method to sample fish communities in clear, shallow water areas; however, observations are influenced by the presence of divers, and it is prone to inconsistencies between observers (Murphy & Jenkins 2010, Mallet & Pelletier 2014).

Advantages of using stereo-BRUVS include a wider range of species sampled due to the presence of bait, higher accuracy and consistency in both identifications and length measurements, as videos can be revised by multiple observers, thus ensuring mistakes are minimised or avoided (Mallet & Pelletier 2014). Nonetheless, stereo-BRUVS also have some disadvantages, including the unknown influence of the bait plume, the time required to analyse videos and the high costs of purchasing required equipment and software (Langlois et al. 2010, Watson et al. 2010).

Here, we combined UVCs and stereo-BRUVS to sample fish communities during the warm season (December to April) of 2015 across mangroves in the GMR. Our study had 5 objectives: (1) describe the Galapagos fish communities across all islands where mangroves are present, (2) compare results about fish community structure obtained with UVC and stereo-BRUVS, (3) compare the composition of fish assemblages across the 2 bioregions where mangroves are present, (4) investigate the environmental factors that may influence fish community composition and (5) explore the potential nursery function of Galapagos mangroves for 3 taxonomic groups important to local artisanal fisheries. We hypothesised that the composition of fish communities in Galapagos mangroves would vary between bioregions due to their consistently different environmental and oceanographic conditions (Edgar et al. 2004a). We also expected community composition to vary between sampling methods, as they have been reported to sample different subsets of the fish community (Colton & Swearer 2010, Langlois et al. 2010). Given that the Galapagos does not have many structured estuarine and coastal areas that may offer nursery habitats for fishes and invertebrates (Beck et al. 2001, Danulat & Edgar 2002, Lefcheck et al. 2019), we anticipate finding evidence supporting the role of Galapagos mangroves as nursery habitats to species of local commercial interest, as has been reported for other areas of the planet (Aburto-Oropeza et al. 2009, Nagelkerken et al. 2015, zu Ermgassen et al. 2020). Furthermore, we expect our results to be used as a reference point to assess the effectiveness of the GMR in protecting fish diversity in mangrove areas from local human pressures (e.g. tourism and artisanal fishing), and to evaluate the effects of climate change in this ecosystem.

2. MATERIALS AND METHODS

2.1. Study area

The Galapagos represents the westernmost limit for mangroves in the Americas (Lacerda et al. 1993). Here, mangroves are often exposed to environmental conditions at the limit of their physiological tolerance, including little protection from direct wave energy, seasonal exposure to temperatures as low as 18°C, lack of major freshwater sources and low soft sediment availability (Andersen & Hamann 1986, Schaeffer et al. 2008, Moity et al. 2019). The Galapagos has a semidiurnal mesotidal regime (Banks 2002) with an average tidal range spanning from 1.8 to 2.4 m (Wellington 1975), which coincides with the prevailing mesotidal regime in most of the TEP (Castellanos-Galindo & Krumme 2015). Only 4 species of mangrove trees have been reported on the islands, *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove), *Laguncularia racemosa* (white mangrove) and *Conocarpus erectus* (button mangrove) (Andersen & Hamann 1986). Due to these suboptimal environmental conditions, mangroves on the islands are mostly underdeveloped across the archipelago, and they often form small, narrow vegetated areas growing directly on lava fields. In fact, it was found that over three-quarters of mangrove patches in the archipelago were smaller than 0.25 ha, and 50% of total mangrove coverage was found within 100 m of the coastline (Moity et al. 2019). However, a few enclosed bays exist on Isabela Island, where mangroves are largely sheltered from direct wave energy, and they are able to reach heights of up to 25 m and form well developed forests (Moity et al. 2019).

Mangroves cover 35% of the Galapagos coastlines, with a total area of 3657.10 ha, where 52% are found in the Western bioregion and 48% in the CSE. Mangroves become less common north of the equatorial line, so the northern subregion of the CSE contains <1% of mangrove coverage, and no mangroves are present in the far-northern region (Moity et al. 2019). Due to their remoteness, mangroves in the Galapagos are relatively unaffected by human activities (Lacerda et al. 1993). Mangrove patch size varies greatly across the archipelago as a function of the geological age of the island, with younger islands having more mangrove cover than older ones (Moity et al. 2019). It is hypothesised that this is due to mangroves acting as pioneer vegetation because of their ability to withstand the difficult and highly dynamic environmental conditions characteristic of intertidal environments (Moity et al. 2019). However, mangroves are not strong competitors, and they are usually outcompeted for light by other species, particularly in the higher parts of the intertidal area, where they are also at risk of desiccation (Duke 2017). Therefore, to ensure an accurate representation of the natural variability of fish communities occupying mangrove habitats in the Galapagos, we sampled a variety of mangrove patch sizes, but concentrated our efforts in the Western and CSE regions, excluding the northern subregion, where the vast majority of mangrove areas are located.

2.2. Sampling of fish communities

Sampling took place during the warm season in daylight hours between 10 and 27 April 2015 in mangrove habitats on 7 islands and across 2 bioregions (Fig. 1) using UVC and stereo-BRUVS. We chose these 2 methods as research on clear water reef systems suggests that they complement each other by sampling different sections of the fish community under study, thus offering a more complete indication of the overall fish assemblage composition (Colton & Swearer 2010, Langlois et al. 2010, Watson et al. 2010, Walsh et al. 2017). Most surveys took place within 2 h of slack high tide, to ensure mangrove roots were inundated. Whenever possible, individual fish were identified to the finest taxonomical level (i.e. species). Length measurements were also estimated for each individual sampled as detailed below.

2.2.1. UVCs

We surveyed a total of 22 mangrove bays across 6 islands (Fig. 1) using UVCs. At each site, fish surveys were conducted by 2 researchers snorkelling side by side, at the same speed and parallel to the mangrove fringe, following protocols of previous mangrove surveys within the TEP (Aburto-Oropeza et al. 2007, 2009). Four replicate 50 × 2 m transects were surveyed at each site. Replicates were separated by at least 10 m from one another to avoid detecting the same individual fish across replicates. Total transect

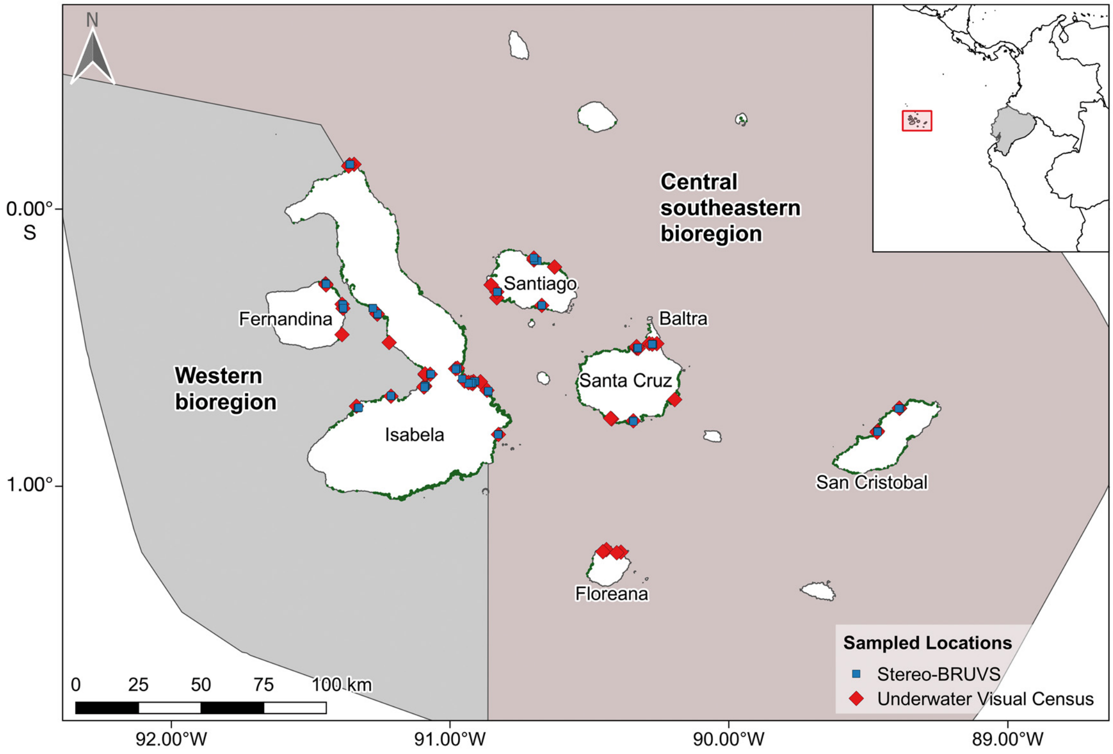

Fig. 1. Mangrove sites where fish communities were surveyed across 2 bioregions of the Galapagos Archipelago (Edgar et al. 2004a). Coastal green areas: mangrove patches across the archipelago

length was measured using a measuring tape, which researchers attached to one end of the mangrove area being sampled. Researchers identified, counted and estimated total length (TL) for all individual fish located within 1 m of either side of the transect, surveying a total area of 100 m^2 per transect. Surveys were carried out at a maximum depth of 2 m to minimise low visibility conditions, which could affect the accuracy of the data obtained.

Sampling occurred parallel to the mangrove fringe due to the small size and high root density of most mangrove patches in our study area. Researchers were often physically unable to enter mangrove areas and sample among their roots. However, because transects were laid immediately next to the mangrove fringe, fish up to 1 m inside the mangrove roots were included in our surveys.

To reduce observer bias, all UVCs were conducted by only 2 researchers, who were experienced at visually surveying fish assemblages in the TEP and at accurately estimating fish length. Additionally, to ensure TL estimation was consistent between the 2 observers, a plastic transparent ruler and a PVC tube representing 22 size classes, ranging from 2 to 125 cm, were used as reference by researchers when estimating fish sizes (Aburto-Oropeza et al. 2009).

2.2.2. Stereo-BRUVS

Stereo-BRUVS systems were deployed in 20 mangrove bays across 5 islands (Fig. 1). We completed 3 replicate deployments per site. Individual stereo-BRUVS deployments were separated by a minimum distance of 500 m to avoid the overlap of bait plumes and to reduce the likelihood of detecting the same individual fish across multiple replicates (Langlois et al. 2018).

The stereo-BRUVS systems consisted of 2 GoPro Hero 4 black edition cameras mounted inside PVC waterproof housings located 0.70 m apart on a steel base and inwardly converging at a 6° angle (SeaGIS). Each system was deployed from a dinghy at depths ranging from 1 to 4.5 m, and at an average distance of 2 m from the mangrove roots, as due to the small size of mangrove patches, it was often impossible to place stereo-BRUVS among the roots. Stereo systems were left to film for a minimum soaking time of 100 min while floating about 1 m above the sea floor as described by Acuña-Marrero et al. (2018). To keep consistency with previous monitoring programs in the Galapagos, 800 g of yellowfin tuna *Thunnus albacares* was used as bait, which was placed inside a PVC canister with holes to allow dispersion into the water column.

2.2.3. Video analysis

Stereo-BRUVS systems were calibrated following Harvey & Shortis (1998) using the specialised CAL software (SeaGIS). Videos were analysed using EventMeasure software (SeaGIS). The lead author conducted all video analyses to ensure results were consistent and fish identifications were validated by several fish experts. A total of 90 min of video was analysed per deployment, the first 5 min of footage after the system settled on the seafloor and the last 5 min prior to collection were discarded to minimise any potential disturbance to behaviour of animals in the area. All fish that could be clearly seen by the analyst were counted and identified using Grove & Lavenberg (1997), Robertson & Allen (2015) and Froese & Pauly (2019) as identification guides. MaxN, which is described as the maximum number of individuals of the same taxon present within a single video frame, was used as a measure of relative abundance. MaxN is a conservative measure of abundance, but it allows us to avoid counting the same individual fish multiple times if they re-enter the field of view (Cappo et al. 2003).

Fork length measurements were obtained only from individuals recorded at the time of MaxN for each species whenever allowed by visibility and position of the animal in relation to the cameras (i.e. individual appears as straight as possible in both cameras and their body is parallel to the cameras). Because visibility (i.e. the furthest distance from the cameras to which we could clearly see an object) did vary across individual stereo-BRUVS drops, we only used measurements if the calculated root mean square (RMS), a measure of the performance of our estimates (Skiena 2017), was ≤100, and the precision value was a maximum 10% of the length measured. If either condition was not met, measurements were rejected.

2.3. Collection of environmental data

Based on previous publications, we identified the following variables to be potentially influential on fish community composition: total mangrove area and length of mangrove fringe (Ley 2005, Aburto-Oropeza et al. 2008), tidal stage (Castellanos-Galindo & Krumme 2015, Ramirez-Martínez et al.

2016) and visibility (Gladstone et al. 2012). Furthermore, sea surface temperature (SST) and chlorophyll *a* were identified as another set of potentially influential environmental factors, because they are known to differ greatly across the archipelago (Banks 2002), and can influence the distribution of fishes across space and time (Currie et al. 2004, Tittensor et al. 2010).

Depth, time and location (latitude and longitude) were recorded immediately prior to each deployment and transect, but we were unable to collect environmental data *in situ*. However, open source, remotely sensed environmental data were used to investigate if they had any potential correlations with fish assemblage composition across bioregions. Although, remotely sensed data may not capture the distinctive environmental conditions of sites in waters close to the coastline (Thakur et al. 2018), we decided to use it as an exploratory tool that would allow us to identify the variables that show a potential correlation with the composition of fish communities in mangroves, and are thus worth monitoring over the long-term (LaDeau et al. 2017).

Mean SST and mean chlorophyll *a* concentrations per season (warm season from December 2014 to April 2015, and dry season from June to October 2014) were calculated from Aqua MODIS satellite data, which have a resolution of 4 km (NOAA NMFS SWFSC ERD 2017a,b). Mangrove area and mangrove fringe length were measured in QGIS 3 (QGIS Development Team 2019) using a Galapagos mangrove distribution layer by Moity et al. (2019). Information about tides (incoming or outgoing) were obtained from INOCAR (2017) for the day and time when sampling occurred. Mean maximum visibility was calculated for stereo-BRUVS deployments only, as it varied widely not only across sites, but also with time at the same site.

Visibility measurements were not obtained for UVC transects because the relative short duration of sampling using this method allowed us to put measures in place to ensure visibility was consistent across time and space. As stated in the previous section describing UVCs, sampling occurred at a maximum depth of 2 m to minimise low visibility conditions. To calculate maximum visibility values for stereo-videos, we recorded the distance from the cameras to the furthest object/fish that could be clearly seen in our screen using a 3D point in the EventMeasure software. Distance to the furthest object/fish on the screen was recorded every 10 min for the entire duration of the video being analysed. Finally, a mean maximum visibility was calculated using all the maximum visibility values per video.

Draftsman plots were used to visually inspect the distribution of the data for each environmental variable described above and to investigate multicollinearity among predictive variables. If any 2 predictive variables were found to be highly correlated ($r > 0.90$), and this correlation was found to be significant, then only 1 variable was kept for further analysis. Plots were created using the GGally package (Schloerke et al. 2018) and significance of correlations were calculated with the corrplot package (Wei & Simko 2017) in R v3.6 (R Core Team 2020). After inspection of the data, a $\log_e(x + 1)$ transformation was applied to mangrove area measurements to reduce skewness (Clarke & Warwick 2001). Environmental data was normalised and a Euclidian similarity matrix was calculated for use in multivariate analyses.

2.4. Statistical analyses

Raw data obtained by UVCs and stereo-BRUVS are not comparable because fish abundance is not measured in the same way by both methods. Since our focus was on comparing results between sampling techniques and bioregions, we standardised results by calculating relative abundances for each fish species. Relative abundance was obtained by dividing the total abundance per species by the total number of all individual fish of all species found in that transect or deployment. Mean relative abundance was calculated per site sampled, and a fourth root transformation was applied to decrease the influence of more dominant species, highlight the relative importance of rare species and to improve normality and reduce heteroscedasticity in our data (Clarke & Warwick 2001). A Bray Curtis dissimilarity matrix was calculated on the transformed relative abundances for use in multivariate analysis.

Fish species were classified into 4 trophic groups: apex, carnivores, herbivores and omnivores, based on trophic level information available at FishBase (Froese & Pauly 2019). Herbivore species had a trophic level between 2.00 and 2.19, omnivores had a trophic level between 2.20 and 2.79, and carnivores had a trophic level ≥ 2.80 (Palomares 2000). The apex predators group included sharks only, as we were interested in finding out if one method was better than the other at detecting them. Due to the lack of assumptions about data and error distribution, univariate permutational multivariate analyses of variance (PERMANOVA; Anderson 2005) were used to test for differences in the relative proportions of trophic groups between sampling methods and across bioregions. PERMANOVA was performed in the R vegan package (Oksanen et al. 2019) using Euclidian distances. Univariate PERMANOVAs based on Euclidean distances were also used to test for differences in total number of individuals detected, species richness, Shannon-Wiener diversity index (H') and Pielou's evenness (J') between methods and across sites.

A 2-way PERMANOVA based on Bray Curtis dissimilarities was used to test for differences in the fish assemblages between stereo-BRUVS and UVCs (method, fixed), and between the CSE and Western (bioregions, fixed), as well as the effect of the interactions between these terms. PERMANOVA tests used 9999 permutations for each term included in the analysis to calculate p-values. If factors were significant ($p < 0.05$), a test of homogeneity of dispersions, PERMDISP (Anderson 2004), was run to ensure differences were due to differences between levels of a factor, instead of due to differences within levels. If significant interactions involving >2 levels were found, these were further explored using pairwise tests in PERMANOVA. A principal coordinates analysis, PCO (Gower 1966), was used to complement PERMANOVA results and to visually detect patterns in fish assemblage composition across methods and bioregions. A 2-way Similarity Percentages (SIMPER) analysis was performed on the transformed data to identify species responsible for differences in the structure of fish assemblages between sampling methods and bioregions. A species was considered to be a discriminant species for a bioregion or method when the ratio between the average dissimilarity ($\overline{\delta}$) and the standard deviation of dissimilarities (SD δ) was >1, and its percentage contribution was at least 3% (Terlizzi et al. 2005). Relationships between environmental factors and fish communities were investigated using a Distance-based Linear Model (DistLM) which calculates multivariate multiple regressions based on resemblance matrices using permutation methods (Anderson 2016). The most parsimonious model was selected with the corrected Akaike's Information Criterion (AIC_c) using 9999 permutations. To minimise multicollinearity among moderately correlated variables (Spearman correlations < 0.70) and improve results of DistLM, a full model was run that included these moderately correlated variables. From this run only the factor with the highest correlation to the relative abundance data was included in the final model. Factors identified in the final model were then presented on PCO plots to aid in the interpretation of results. This process was performed using data from both sampling methods, and then separately for UVCs and stereo-BRUVS. All multivariate comparisons were conducted using PRIMER 6 with PERMANOVA+ (PRIMER-E).

Kernel density estimates (KDE) were used to compare length frequency distributions between sampling methods and bioregions for Galapagos sailfin grouper *Mycteroperca olfax*, snappers *Lutjanus* spp. and mullets *Mugil* spp. because of their commercial importance. Length estimates obtained through UVCs were converted to fork length (FL) using length-length conversions from FishBase (Binohlan et al. 2011). KDEs were calculated using the sm (Bowman & Azzalini 2018) and KernSmooth (Wand 2015) R packages based on a modified script developed by Langlois et al. (2012). The statistical tests applied determined if length distributions were different between methods and/or bioregions. KDE tests were applied to each taxonomic group or species separately. The plots produced by the sm. density.compare function from the sm R package include a grey polygon representing the null model of no difference between the KDEs constructed for each group under comparison. This polygon has the KDE mean as the centre and it extends to 1 SE either side of the mean, thus it allows us to visually identify the areas of the length frequency distribution that are likely behind a significant result (Langlois et al. 2012). We included a vertical line in these plots representing the approximate size at which individuals change from juveniles to adults. This line was calculated as one-third of the maximum length reported for that species, or the maximum length reported for a taxonomic group following Nagelkerken & van der Velde (2002). The maximum reported lengths were obtained from FishBase (Froese & Pauly 2019). This was done to help us identify if significant differences were driven by the presence of juvenile fish.

To assess if Galapagos mangroves are potentially being used as nursery habitats by these fishes of local economic importance, we compared the proportion of juveniles present in mangroves and adjacent rocky reefs, which were sampled as part of a monitoring campaign around the archipelago in 2014 (P. Salinas-de-León unpubl. data). This monitoring campaign was completed using Diver Operated stereo-Video Systems (stereo-DOVS). This method is similar to UVCs because divers survey a transect of a previously specified length. The difference with stereo-DOVS is that instead of recording fish abundance and estimating individual fish sizes *in situ* as in

UVCs, divers film the transect using stereo-video cameras (Harvey et al. 2002, Salinas-de-León et al. 2016, Goetze et al. 2019). The resulting footage is processed offsite using EventMeasure software to collect information on the identity, abundance and length of fishes (Goetze et al. 2019). Both methods, stereo-DOVS and UVCs, have been shown to produce similar results in species richness, relative abundance and biomass of the species being studied (Grane-Feliu et al. 2019). Thus, data obtained by these 2 methods are deemed comparable.

3. RESULTS

3.1. Abundance and diversity

A total of 35 029 individuals belonging to 92 species, 67 genera and 36 families were recorded in our survey using both sampling methods (Table 1). Fishes of local commercial importance, such as groupers, snappers and mullets, were identified as inhabitants of mangrove habitats, including a high proportion of juveniles. It is worth noting that only about 44 % of fish recorded by stereo-BRUVS were identified to species level, in large part due to poor visibility and/or the location of individual fish within the frame. Additionally, approximately 12 % of fish sampled by stereo-BRUVS were categorised as schooling silvery fish because we were unable to identify them up to family level. They were not excluded from the analysis because they represented a large proportion of the stereo-BRUVS assemblage.

There were significant differences in mean abundance between the CSE and Western bioregions, with a higher number of individuals sampled in the CSE (189 ± 29.4 SE) than in the Western bioregion (87 ± 11.4 SE) regardless of the sampling method used (Table 2A, see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m664p183_supp.pdf). There was no significant difference in mean abundance between methods (Table 2A, Fig. S1A) despite the fact that almost twice as many individual fish were recorded using UVCs than stereo-BRUVS (Table 1).

Statistically significant interactions between the effects of sampling methods and bioregions were detected for species richness (Table 2B, Fig. S2C in the Supplement). Mean species richness was 50 % higher in the CSE regardless of the sampling method used, and stereo-BRUVS detected a higher number of species than UVCs.

Neither the Shannon-Wiener diversity index nor evenness were found to significantly differ between bioregions (Table 2, Figs. S3B & S4B in the Supplement). However, the Shannon-Wiener index was significantly higher for stereo-BRUVS (univariate PERMANOVA, Table 2C, Fig. S3A). Additionally, a statistically significant interaction between the effects of sampling methods and bioregions was detected on evenness (Table 2D, Fig. S4C). However, further inspection of the data indicates that the interaction results may have been influenced by the presence of outliers (Fig. S4). In fact, once outliers were removed this particular interaction became non-significant.

Although most fish species were recorded by both methods, there were 23 species uniquely identified by UVCs and 20 species were only recorded by stereo-BRUVS (Table S1 in the Supplement). Family diversity was found to be similar across methods and bioregions (Table 1), but there were 3 families uniquely sampled by UVCs (Cirrhitidae, Apogonidae and Sciaenidae) and 6 only recorded by stereo-BRUVS, including Scombridae, Hemiramphidae, Chanidae, Gobiidae, Centropomidae and Mullidae (Table S1). Mugilidae was the only family to contribute at least 5 % of individuals to the overall fish assemblage across methods and bioregions (Fig. 2). UVCs sampled more individuals belonging to the families of

Table 1. Summary of fish data collected by stereo-Baited Remote Underwater Video Stations (stereo-BRUVS) and Underwater Visual Census (UVC) in Galapagos mangroves during the warm season of 2015

	Stereo-BRUVS			UVC		
	CSE	Western	Total	CSE	Western	Total
Individuals	9307	2420	11727	19786	3516	23302
Species	61	42	69	66	41	72
Unique species sampled per method	19	19	20	24	18	23
Families	29	22	33	29	19	30
Unique families sampled per method	5	5	6	5	2	3

Table 2. Univariate PERMANOVA results based on Euclidean distances testing for differences in (A) abundance, (B) species richness, (C) Shannon-Wiener diversity and (D) Pielou's evenness between methods (UVC and stereo-BRUVS) and across bioregions (CSE and Western) of fish collected in Galapagos mangroves during the warm season of 2015. **Bold** values: significant

	df	SS	MS	*F*	R^2	p
(A) Abundance						
Bioregion	**1**	**12.262**	**12.262**	**9.726**	**0.042**	**0.002**
Method	1	3.316	3.316	2.630	0.011	0.108
Bioregion:Method	1	2.685	2.685	2.130	0.009	0.144
Residuals	218	274.830	1.261		0.938	
Total	221	293.092			1.000	
(B) Species richness						
Bioregion	**1**	**73.700**	**73.730**	**5.716**	**0.018**	**0.017**
Method	**1**	**1243.000**	**1243.040**	**96.380**	**0.297**	**<0.001**
Bioregion:Method	**1**	**53.300**	**53.280**	**4.131**	**0.013**	**0.043**
Residuals	218	2811.600	12.900		0.672	
Total	221	4181.700			1.000	
(C) Shannon-Wiener diversity						
Bioregion	1	0.523	0.523	2.126	0.009	0.144
Method	**1**	**4.131**	**4.131**	**16.794**	**0.071**	**<0.001**
Bioregion:Method	1	0.100	0.100	0.408	0.002	0.518
Residuals	218	53.626	0.246		0.919	
Total	221	58.380			1.000	
(D) Pielou's evenness						
Bioregion	1	0.010	0.010	0.460	0.002	0.506
Method	**1**	**0.264**	**0.264**	**11.945**	**0.051**	**0.001**
Bioregion:Method	**1**	**0.094**	**0.094**	**4.263**	**0.018**	**0.039**
Residuals	217	4.788	0.022		0.929	
Total	220	5.155			1.000	

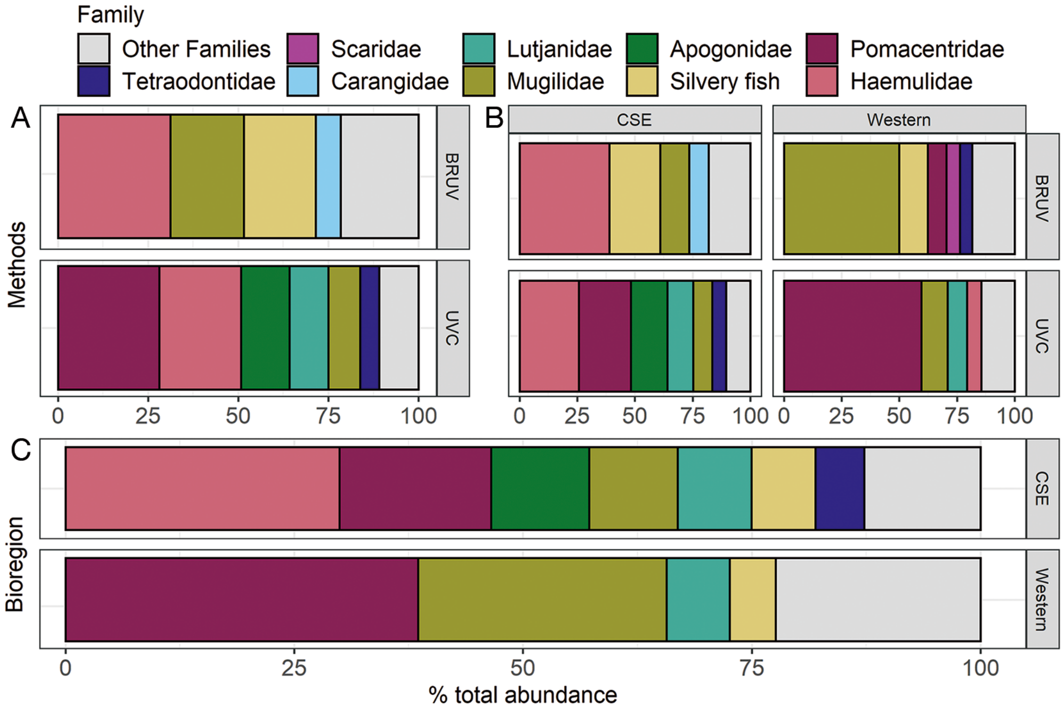

Fig. 2. Relative percentage contributions of fish families to the overall Galapagos mangrove fish assemblage: (A) per sampling method, (B) per method and bioregion, (C) and across bioregions. Families representing <5% of the total assemblage were pooled together under 'Other Families' category. BRUV: stereo-Baited Remote Underwater Video Stations; UVC: Underwater Visual Census; CSE: Central-Southeastern bioregion

Pomacentridae and Apogonidae, which together made up 41.51% of the fish assemblage sampled by this method. Haemulidae, Lutjanidae, Mugilidae and Tetraodontidae were also commonly sampled by this method and were responsible for an additional 47.62% of the fish assemblage (Fig. 2A). The most common families identified by stereo-BRUVS included Haemulidae (31.20%), Mugilidae (20.30%) and Carangidae (6.92%), with silvery fish contributing an additional 19.98% (Fig. 2A). However, dominant families varied within methods and across bioregions and in both cases, it can be seen that the overall pattern seen per method more closely resembles that of the CSE bioregion (Fig. 2B), likely because this bioregion contributes more individuals. The Western bioregion was dominated by 2 families, Mugilidae (27.14%) and Pomacentridae (38.53%) when looking at both methods together, while Lutjanidae contributed just under 7% (Fig. 2C). The most common families for the CSE included Haemulidae, Pomacentridae, Apogonidae, Mugilidae, Lutjanidae and Tetraodontidae, which together represent 80.30% of the fish community of the bioregion as sampled by both methods (Fig. 2C).

3.2. Community composition

Fish assemblage composition was significantly different between sampling methods (PERMANOVA, Table 3). These results were similar to those observed on the PCO biplot for the mean relative fish assemblage composition, which showed clear differences between sampling methods (Fig. 3A). However, it is worth noting that the first 2 PCO axes only explained approximately 31% of the variation, and thus may not reflect all patterns in our data cloud. The PCO also appeared to show that the variance was not homogenous between the 2 sampling methods, which was validated by PERMDISP results ($F_{1,40}$ = 12.15, $p < 0.01$), thus confirming the existence of a dispersion effect (Anderson et al. 2008). When relative abundances from both bioregions were pooled together, the multivariate dispersion across stereo-BRUVS (43.63 ± 1.54) was larger than that from UVCs (36.39 ± 1.40).

Significant differences in fish assemblage composition were also found between bioregions (PERMANOVA, Table 3), and no differences in dispersion were detected by PERMDISP ($F_{1,40}$ = 1.84, $p = 0.23$). These results were not readily apparent on the PCO plot with the pooled data, so separate plots were created for each method (Fig. 3B,C). The resulting figures support both PERMANOVA results, as they show a clear separation of fish assemblages between bioregions. Finally, the method:bioregion interaction was not significant, indicating that the effect of the method used to sample fish assemblages was consistent across bioregions.

Five taxa were identified by SIMPER as being important in differentiating fish assemblages sampled by the 2 sampling methods (Table 4A). Two species, *Lutjanus argentiventris* and *Abudefduf troschelii* were almost twice as likely to be sampled by UVCs as by stereo-BRUVS. In addition, the mean abundance recorded by UVCs for *L. novemfasciatus* was 50% more than that recorded by stereo-BRUVS. The remaining 2 taxa were *Eucinostomus* sp. and *Mugil* sp., both of which were more likely to appear on stereo-BRUVS. It is probable that these last 2 taxa were not in fact detected differently by each sampling method, but rather the resulting numbers were due to poor water clarity. This prevented us from identifying individuals to species level, thus we identified them to a coarser taxonomic level, in this case up to genus. Across bioregions, 6 taxa were found to be important in differentiating assemblages (Table 4B), which included species of local economic interest, such as *Mycteroperca olfax*, *L. novemfasciatus* and *Mugil cephalus*. *M. olfax* and *M. cephalus* showed greatest affinity for the Western bioregion, with reported mean abundances of 3.8 and 2.9 times higher than in the CSE, respectively. Mean abundances were also found to be higher in the Western bioregion for all other differentiating species, *Mugil* sp., *Scarus ghobban*, *Archosargus pourtalesii* and *L. novemfasciatus*, than in the CSE (64.20, 31.03, 28.79 and 1.30% higher, respectively).

Table 3. PERMANOVA results based on Bray Curtis distances dissimilarities of fourth root-transformed mean relative abundance data testing for differences between methods (UVC and stereo-BRUVS) and across bioregions (CSE and Western) of fish collected in Galapagos mangroves during the warm season of 2015. Significant results are highlighted in **bold**

Source	df	SS	MS	F	p (perm)	Unique
Method	**1**	**11129**	**11129**	**6.936**	**<0.001**	**9908**
Bioregion	**1**	**5651**	**5651**	**3.522**	**<0.001**	**9912**
Method:Bioregion	1	2375	2375	1.480	0.105	9915
Residuals	38	60972	1605			
Total	41	81648				

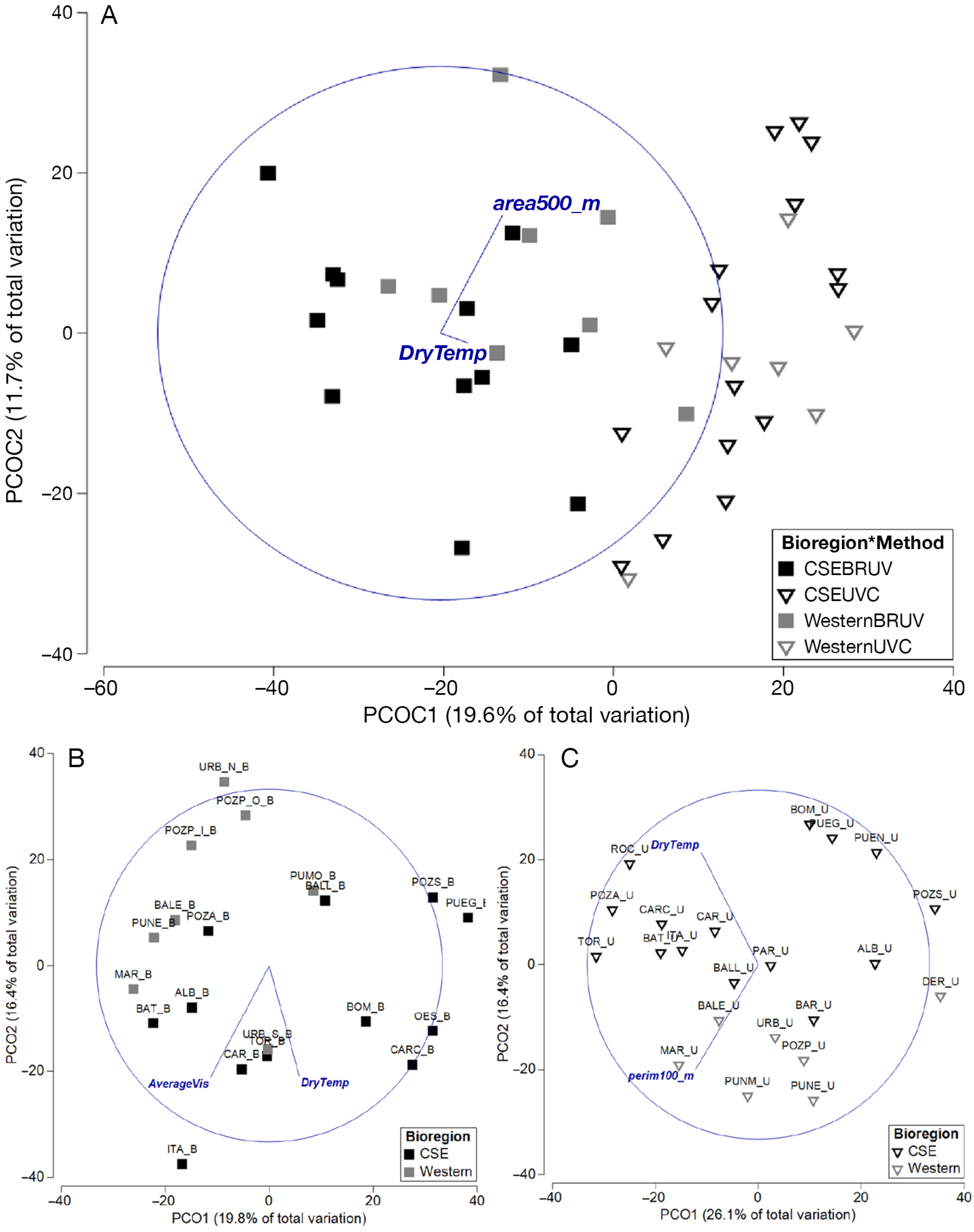

Fig. 3. Principal coordinates (PCO) biplots based on Bray Curtis dissimilarities calculated on fourth root transformed mean relative abundances of fish in mangrove areas of the Galapagos: as recorded by (A) both sampling methods, (B) stereo-Baited Remote Underwater Video Stations (BRUV) and (C) Underwater Visual Census (UVC). Environmental factors identified by distance-based linear models as having a high correlation with biotic data have been overlaid. Blue circles have a radius of one unit and their centers are the origin of the vectors representing correlations. CSE: Central-Southeastern bioregion

The best model from the DistLM analysis using the pooled relative abundance data ($AIC_c = 319.85$, $R^2 = 0.11$) was significant, but represented a poor fit. This model identified the total mangrove area within 500 m of the site sampled ($F = 2.01$, $p = 0.01$) and mean temperature during the dry season ($F = 2.67$, $p < 0.01$) as having a significant correlation with the fish community structure (Fig. 3A). When the data was divided

Table 4. Results of 2-way SIMPER analysis of average Bray-Curtis dissimilarity calculated on fourth root transformed mean relative abundance data (A) between sampling methods (stereo-BRUVS and UVC) and (B) across bioregions (CSE and Western). Species contributing to ≥3 % of the assemblage and with a ratio >1 are considered discriminating species, and are highlighted in **bold**. $\bar{\delta}$: mean dissimilarities between groups; δ: dissimilarities between groups. Refer to section 2.4 for more information

Taxon	Mean abundance Stereo-BRUVS	 UVC	$\bar{\delta}$	$\bar{\delta}$/SD δ	Contribution (%)
(A)					
***Eucinostomus* sp.**	1.03	0.00	2.24	**2.28**	**3.38**
Lutjanus argentiventris	0.86	1.77	2.47	**1.36**	**3.72**
Lutjanus novemfasciatus	0.52	1.00	2.21	**1.33**	**3.34**
Eucinostomus dowii	0.38	1.03	1.86	1.30	2.81
Abudefduf troschelii	0.97	1.87	2.26	**1.28**	**3.42**
***Mugil* sp.**	1.26	0.76	2.38	**1.17**	**3.59**
(B)					
Mycteroperca olfax	0.30	1.14	2.29	**1.59**	**3.84**
Lutjanus novemfasciatus	0.77	0.78	2.06	**1.39**	**3.46**
Chaetodon humeralis	0.56	0.13	1.20	1.30	2.02
Lutjanus argentiventris	1.33	1.34	1.51	1.27	2.53
Abudefduf troschelii	1.45	1.43	1.49	1.23	2.50
Archosargus pourtalesii	0.66	0.85	1.80	**1.21**	**3.02**
Thalassoma lucasanum	0.54	0.61	1.24	1.21	2.08
Scarus ghobban	0.58	0.76	1.87	**1.18**	**3.14**
Bodianus diplotaenia	0.51	0.39	1.08	1.18	1.81
***Mugil* sp.**	0.81	1.33	2.42	**1.16**	**4.06**
Sphoeroides annulatus	1.44	1.19	1.54	1.13	2.59
Eucinostomus dowii	0.89	0.42	1.64	1.12	2.76
Stegastes arcifrons	1.46	1.79	1.62	1.06	2.72
Carcharhinus limbatus	0.44	0.18	0.99	1.06	1.66
Mugil cephalus	0.31	0.91	2.08	**1.01**	**3.50**

based on sampling method, DistLM found that fish assemblages sampled by stereo-BRUVS were best explained by average visibility (F = 2.09, p < 0.01) and mean temperature during the dry season (F = 2.16, p < 0.01); however, this model (AIC_c = 154.45) explained just over 20 % of total variation in the fish communities (Fig. 3B). Total length of the mangrove fringe within 100 m of the site sampled (F = 2.35, p = 0.01) and mean temperature during the dry season (F = 2.53, p < 0.01) were identified as factors significantly influencing fish assemblages sampled by UVCs (Fig. 3C). This model explained 22.23 % of the variation in the data (AIC_c = 160.62).

3.3. Trophic structure

Overall, carnivores made up the largest proportion of mangrove fish assemblages in the archipelago (80.4 %), followed by omnivores (12.7 %) and herbivores (2.7 %). UVCs detected a significantly higher mean relative abundance of carnivores than stereo-BRUVS (Fig. 4, Table S3 in the Supplement). On the other hand, stereo-BRUVS detected significantly higher mean relative abundances of all other groups than UVCs (Table S3). Across bioregions, only herbivores were found in significantly higher proportions in the Western bioregion (Fig. 4, Table S3). The method:bioregion interaction was not found to significantly influence mean proportions in any trophic group.

3.4. Fish length frequency comparisons

Overall, juveniles in mangroves represented over 43 % of all individuals sampled by both methods; however, this percentage varied among species. Mean length frequency distribution and mean FL of *Mycteroperca olfax* were similar between sampling methods and across bioregions (Fig. 5), but a larger size range was recorded by UVCs (50 cm) than by stereo-BRUVS (38 cm) (Table 5). Juveniles of this species represented 98 and 96 % of the CSE and Western bioregions, respectively; both sampling methods were just as likely to detect juveniles (stereo-BRUVS 98 % and UVC 97 %).

Significant differences in the mean FL and length frequency distribution for *Mugil* spp. were detected (Fig. 5). Stereo-BRUVS sampled a large range of sizes for mullets, and, on average, mullets sampled by this method were almost twice as large as those detected by UVCs (Table 5). When comparing bioregions, we found a larger range of sizes and larger mean FL for mullets in the West. Juvenile mullets were found in slightly lower proportion in the Western bioregion (93 %) than in the CSE (97 %).

Length frequency distributions were also significantly different in their mean and distribution for *Lutjanus* spp. between methods and across bioregions (Fig. 5). UVCs detected a smaller range of sizes as well as a smaller mean FL for snappers than stereo-BRUVS (Table 5). On average snappers were 38 % larger in the Western bioregion than those recorded in the CSE, and a slightly higher proportion of juveniles were found in the CSE (91 %) than in the Western bioregion (88 %). UVCs detected a higher proportion of juveniles (91 %) than stereo-BRUVS (71 %).

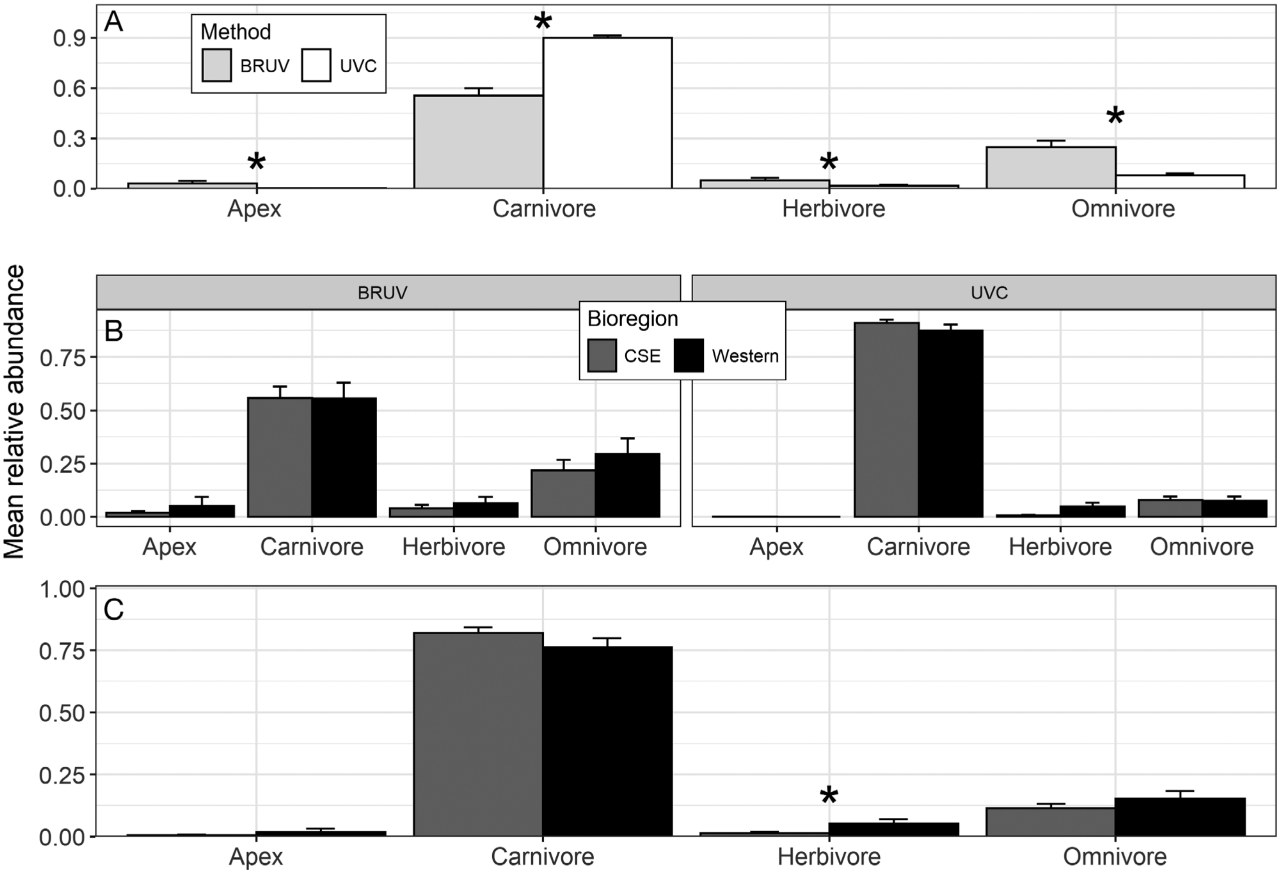

Fig. 4. Proportions of different fish trophic levels comprising mangrove fish assemblages in the Galapagos: (A) per sampling method, (B) per method and bioregion, and (C) across bioregions. Error bars show standard errors; (*) pairs where differences were detected; BRUV: stereo-Baited Remote Underwater Video Stations; UVC: Underwater Visual Census; CSE: Central-Southeastern bioregion

3.5. Juvenile proportion comparisons between mangroves and adjacent reefs

On average in mangrove areas, juveniles of *Mycteroperca olfax*, *L. aratus*, *L. argentiventris*, *L. jordani*, *L. novemfasciatus* and *Lutjanus* sp. represented approximately 85% of all individuals of the aforementioned species, while this proportion dropped to under 40% in adjacent rocky reefs (Table 6). Additionally, some of the snapper species detected in mangrove areas were not present in rocky reefs.

4. DISCUSSION

This is the first study to characterise mangrove fish assemblages at the only oceanic archipelago within the TEP where mangroves naturally occur at the edge of their biogeographical range (Giri et al. 2011). Based on our results, we can conclude that fish assemblages vary between bioregions during the warm season. We also found that the sampling method chosen affects the end results regardless of the bioregion sampled, because they detect a different cross section of the mangrove fish community, as has been reported elsewhere (Colton & Swearer 2010, Langlois et al. 2010, Watson et al. 2010, Walsh et al. 2017). Furthermore, our results suggest mangroves in the Galapagos are used by a higher proportion of juveniles of commercially important fish families when compared to rocky reefs. This indicates that mangroves are potentially functioning as nursery habitats.

4.1. Mangrove fish assemblages

Using both sampling methods, we identified 92 species of fish, most of which were detected in low numbers. The low evenness values calculated from our observations suggest that there is a high prevalence of rare species with only a handful of common

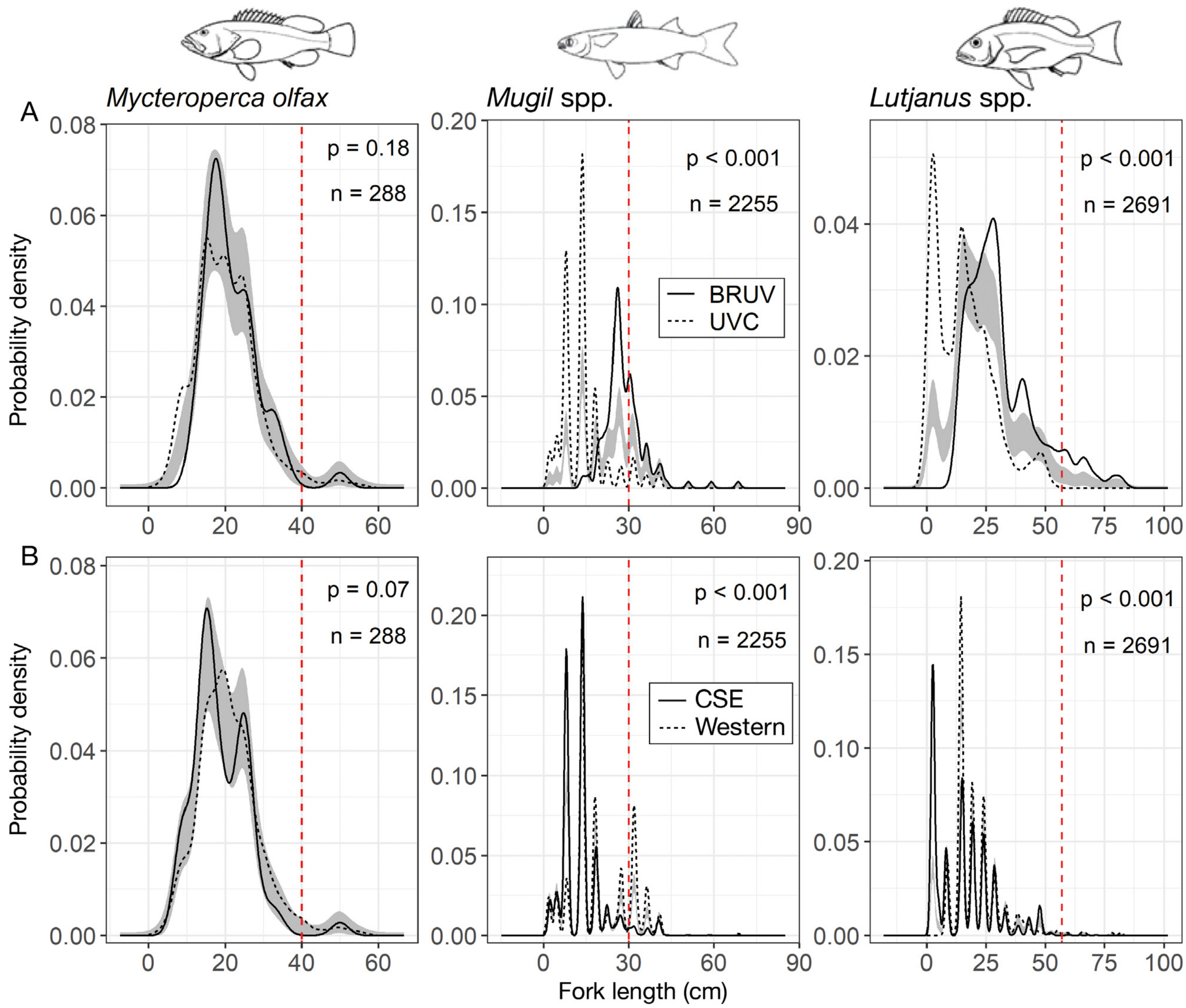

Fig. 5. Comparison of kernel density estimates (KDEs) (A) between methods and (B) across bioregions for *Mycteroperca olfax* (left), *Mugil* spp. (centre) and *Lutjanus* spp. (right) sampled in mangrove areas of the Galapagos. Red dashed line: reproductive size (i.e. juveniles are to the left and adults to the right); Grey shading: 1 SE to either side of the null model. BRUV: stereo-Baited Remote Underwater Video Stations; UVC: Underwater Visual Census; CSE: Central-Southeastern bioregion; n: number of individual fish measurements included in the KDE calculation. Differences in the location and shape of the length-frequency distributions are considered significant at $p < 0.05$ based on permutation tests

species dominating mangrove fish assemblages in the Galapagos. When comparing richness and evenness of Galapagos mangrove fish communities to values reported for other mangrove areas elsewhere in the TEP, we expected that our results would be similar to those from continental Ecuador due to the closer proximity, or northern Mexico as environmental conditions are similar to those found in the archipelago (e.g. low freshwater input, high salinity, smaller mangrove coverage). However, our species richness results were almost 3 times higher than those from northern Mexico and continental Ecuador (Castellanos-Galindo et al. 2013). Instead, we found a similar number of species to central Mexico and Costa Rica, which included sampling sites with a much larger mangrove coverage and a much higher fishing pressure than in the Galapagos (Feutry et al. 2010, Castellanos-Galindo et al. 2013, de la Lanza Espino & Hernandez Pulido 2017, Alms & Wolff 2019). When comparing to areas outside the TEP, species richness in the Galapagos was found to be similar to that reported in subtropical mangrove systems of Southeast Asia, as well as tropical systems in both the West and East Atlantic regions, where at least 100 species of fish have been identified (Ley 2005, Nagelkerken et al. 2008, Castellanos-Galindo

Table 5. Fork lengths (cm) summary for 3 commercially important taxonomic groups of the Galapagos. Length summaries broken down by method (stereo-BRUVS and UVC) and across bioregions (CSE and Western)

	N	Mean ± SE (min.–max.)
Stereo-BRUVS		
Mycteroperca olfax	55	21.70 ± 0.96 (12.00–49.90)
Mugil spp.	139	28.40 ± 0.62 (13.50–68.50)
Lutjanus spp.	132	31.40 ± 1.28 (13.00–81.80)
UVC		
Mycteroperca olfax	233	20.40 ± 0.53 (5.00–55.00)
Mugil spp.	2116	15.10 ± 0.19 (2.00–45.00)
Lutjanus spp.	2559	16.10 ± 0.25 (2.00–55.00)
CSE		
Mycteroperca olfax	65	19.0 ± 0.91 (9.00–49.90)
Mugil spp.	1777	14.50 ± 0.19 (2.00–59.10)
Lutjanus spp.	2314	16.00 ± 0.27 (2.00–72.10)
Western		
Mycteroperca olfax	223	21.10 ± 0.53 (5:00–55.00)
Mugil spp.	478	21.3 ± 0.51 (2.00–68.50)
Lutjanus spp.	377	22.00 ± 0.56 (9.00–81.80)

Table 6. Comparison of juvenile proportions found in mangrove areas and nearby rocky reefs. Fish data obtained from fish monitoring campaigns using Diver Operated stereo-Video Systems (stereo-DOVS) in rocky reefs across the Galapagos Marine Reserve (P. Salinas-de-León unpubl data). No individuals of the *Mugil* genus were found in rocky reefs

Species	% Juveniles	
	Mangroves	Rocky reefs
Lutjanus aratus	72.70	Not found
Lutjanus argentiventris	80.20	35.58
Lutjanus jordani	78.00	Not found
Lutjanus novemfasciatus	98.50	Not found
Lutjanus sp.	100.00	50.00
Mycteroperca olfax	84.20	32.89

& Krumme 2015). Evenness in the Galapagos had a similar pattern to that reported for northern Mexico and continental Ecuador, where few species dominate the fish assemblage (Castellanos-Galindo et al. 2013).

The reason that our results differed greatly from those previously reported for areas that are geographically close or have similar environmental conditions in the wider TEP is again likely to be the sampling method chosen. Studies using just 1 sampling method or gear type reported 50 species or less; while those using a combination of methods and/or gear type identified at least 75 species (Shervette et al. 2007, Castellanos-Galindo et al. 2013, Castellanos-Galindo & Krumme 2015, Lee et al. 2017). There are other possible explanations, including the location of the Galapagos in a convergence zone (Banks 2002), the unique oceanographic and environmental conditions its mangroves are usually subjected to (Moity et al. 2019) and the spatio-temporal coverage of the study, or a combination of all of these factors.

Although the composition of mangrove fish communities can vary across the TEP with total mangrove coverage and as a result of local environmental conditions (Castellanos-Galindo et al. 2013), there are some families that are commonly found throughout the region, including: Lutjanidae, Tetraodontidae, Mugilidae, Gerreidae, Centropomidae, Ariidae and Clupeidae (Lacerda et al. 1993, Shervette et al. 2007, Castellanos-Galindo et al. 2013, Castellanos-Galindo & Krumme 2015). In the Galapagos mangroves, we found 4 of these families: Lutjanidae, Mugilidae, Gerreidae and Tetraodontidae, and they were among the 10 most abundant and speciose families (7 species for Lutjanidae and 5 species for each of the other 3 families). The Centropomidae family was also found in the mangroves of the archipelago, however it was uncommon, with only 3 individuals of the same species, *Centropomus viridis*, identified at Fernandina Island.

Two families commonly found in mangroves across the TEP, Ariidae and Clupeidae, were notably absent from our surveys. The Clupeidae family does occur in the Galapagos, in fact 5 genera and 6 species, 1 of which is endemic to the islands, have been reported in the archipelago (Robertson & Allen 2015). Given that most of species of the Clupeidae family are reported to occur in coastal shallow waters, often forming large schools, the schools of silvery fish detected in the stereo-BRUVS could possibly have comprised fishes of this family. Due to their distance from the camera and low visibility, we were unable to confirm this, but it is possible that this family does occupy mangroves in the Galapagos. The Ariidae family, on the other hand, has not been reported in the Galapagos, despite the fact that this family is commonly found along the entire continental coastline of the TEP, predominantly in marine and brackish waters (Castellanos-Galindo & Krumme 2015, Robertson & Allen 2015). A likely explanation for their absence in the Galapagos is the lack of brackish waters, as there are no rivers on the islands, and also because the Ariidae family prefers sheltered bays with sandy or muddy substrate (Robertson & Allen 2015), which are not a common feature of mangrove areas of the Galapagos (Moity et al. 2019). Another notable difference is the relative dominance of the

Apogonidae and Pomacentridae families in mangrove fish assemblages of the Galapagos. Although both these families have been reported in mangroves of the TEP, they are mostly associated with rocky and coral reefs (Robertson & Allen 2015). It is likely that these families are common in the Galapagos because mangroves across the archipelago mostly grow directly on lava fields (Moity et al. 2019), thus offering a hard substrate with plenty of crevices that both of these families prefer (Robertson & Allen 2015).

Carnivores were the most common trophic group found in Galapagos mangroves, which is likely the result of local conditions: low soft sediment availability and the absence or shortage of other food sources, such as detritus and benthic producers. These findings are similar to those reported for Colombian mangroves (Castellanos-Galindo & Krumme 2015).

Finally, 80% of the species observed in our study (n = 74) are associated with reef habitats, which suggests a strong connectivity between mangrove and reef habitats in the Galapagos, as has been reported for other parts of the world such as the Caribbean and Indo-Pacific regions (Mumby et al. 2004, Unsworth et al. 2008, Saenger et al. 2013, Nagelkerken et al. 2015). However, further research needs to be conducted to establish the strength of this potential link between these habitats.

4.2. Spatial variability of mangrove fish assemblages

Our results suggest that mangrove fish community composition was significantly different across bioregions, which are known to endure different environmental conditions (Banks 2002, Schaeffer et al. 2008). Fish communities in the CSE were found to have an average of 50% more species and a higher proportion of endemic species (17.63%) than the Western bioregion (7.06%). However, fish assemblages in the West had a significantly higher proportion of herbivores than the CSE.

We identified 6 taxa that were responsible for driving dissimilarities in community composition between bioregions. The discriminating species included 2 taxa of interest to fisheries, the Sailfin grouper *Mycteroperca olfax* and mullets *Mugil* spp., both of which had significantly higher abundances in the Western bioregion than in the CSE. This finding highlights the importance of mangroves in the western side of the archipelago in supporting local fisheries. Another group which just missed the threshold to be considered a discriminating species, but that is worth noting, is juvenile blacktip sharks *Carcharhinus limbatus*. This species appeared to have a higher affinity for the CSE bioregion, where abundance was on average 2.4 times that recorded in the West. This result keeps in line with previous reports of juvenile *C. limbatus* as regular users of mangrove areas in the central area of the Galapagos Archipelago (Llerena-Martillo et al. 2015). *C. limbatus* is a charismatic species with a high economic value as a tourist attraction, thus this result emphasises the importance of mangroves in the CSE in supporting the local tourism industry (Llerena-Martillo et al. 2015, Lynham et al. 2015).

Among the environmental drivers of differences in community composition, mean water temperature during the dry season appeared to be one of the most influential factors, as it was identified as a significant variable by all our exploratory models (Fig. 3). This result indicates that there may be a lag effect of temperature on mangrove fish communities. Similar lags between environmental and ecological variables have been described in other marine systems across the planet (Olden & Neff 2001, Atkinson et al. 2004, Moraes et al. 2012), which further underpins the importance of assessing this lag effect of temperature on fish communities in future studies. Total mangrove area and total length of the mangrove fringe were 2 other factors identified as significant by our exploratory models, both of which have been found to be highly influential on fish communities of the TEP (Aburto-Oropeza et al. 2008, 2009). Visibility was also determined to have a significant, though minor, effect on the community structure detected by stereo-BRUVS. There are 2 potential explanations for this result: (1) visibility does in fact affect the composition of fish assemblages through a decline in visual predators present in the area (Rodríguez & Lewis 1997, Nowicki et al. 2019), or (2) it hinders the ability of researchers to detect fish in the video footage (Mallet & Pelletier 2014). In either case, we recommend further investigation of the effect of visibility of mangrove fish communities.

Although not included in our models, we suggest the influence of soft sediment availability on the fish assemblages is further investigated. Researchers involved in UVC sampling reported that the amount of soft sediment appeared to vary between bioregions. Sites on the western side of the archipelago, including Isabela and Fernandina Islands, were mostly dominated by lava fields, while sites on the eastern side of the archipelago had more soft sediment available. High variability in soft sediment has been previously reported across the archipelago, but no clear spatial pattern has been identified (Costa et al. 2019, Moity et al. 2019). Researchers have hypothesised that variability in soft sediment availability may be the result of local bathymetry and geomorphology, which shelter coastal areas from physical disturbances caused by wave action (Costa et al. 2019). Moity et al. (2019), on the other hand, proposed that soft sediment may be related to island age, as they found that the younger islands on the western side of the archipelago had a higher proportion of lava cover above the water line than older islands to the east. Given the reported relationship between soft sediment and bioregions, we recommend that future studies include soft sediment as an abiotic factor potentially influencing fish community composition in Galapagos mangroves.

So far, our results related to differences in fish assemblages across bioregions reflect observations from previous studies of marine ecosystems of the Galapagos. However, the higher proportion of endemic species we detected in the CSE directly opposes findings by Edgar et al. (2004a), whose study was used to first define the bioregions of the Galapagos Archipelago. Edgar et al. (2004a) identified a total of 10 endemic species, 5 of which were not detected during our surveys: *Paralabrax albomaculatus*, *Lythrypnus gilberti*, *Lepidonectes corallicola*, *Acanthemblemaria castroi* and *Odontoscion eurymesops*. Of these undetected species, only *P. albomaculatus* has been reported to be a mangrove dweller, while the rest are more closely associated with rocky and coral reefs (Robertson & Allen 2015). Thus, it is reasonable to assume that the patterns detected by Edgar et al. (2004a) reflect the spatial distribution of endemic species associated with rocky reefs, and these do not necessarily replicate in mangrove habitats. We suggest that studies in other marine areas, such as the oceanic pelagic zone, are carried out to establish if the patterns in fish assemblage composition detected by Edgar et al. (2004a) are common to other marine habitats of the Galapagos.

The discrepancy in the distribution of endemics could also be explained by major differences between studies, including the habitats surveyed (mangroves vs. rocky reefs), methods used for fish sampling (UVCs and stereo-BRUVS vs. UVCs), depths sampled (<5 m vs. up to 20 m) and the temporal scale of the study (1 survey vs. multiple surveys over 18 mo). Furthermore, sampling for these studies occurred at opposing phases of the El Niño Southern Oscillation (ENSO). While Edgar et al. (2004a) sampled fish communities during a relatively cold period associated with La Niña conditions, our study took place exclusively during the warm season and during a warm ENSO period (NOAA 2019). In fact, an El Niño event was officially declared just a few weeks after our sampling campaign was completed (Bureau of Meteorology 2015). It is likely that a combination of the factors described above resulted in significantly different environmental conditions during sampling. ENSO phases, in particular, are linked to strong changes in water temperature across the archipelago (Banks 2002), which would in turn influence the composition of fish assemblages (Attrill & Power 2002, Edgar et al. 2004a, Collie et al. 2008).

Finally, it is worth emphasising that our study investigated mangrove fish assemblage composition during daylight hours, at similar tidal stages and during the warm season. Thus, our findings should be taken as representative of these conditions, but they could be used as a base to further examine the factors that are likely having a global effect on the composition of fish communities of Galapagos mangroves. We suggest future studies examine the effect of tides, time of day (including dusk and dawn) and seasonality on assemblage composition to determine if these factors become more or less influential across time and space.

4.3. Differences between sampling methods

Our results suggest that the sampling method chosen (UVCs vs. stereo-BRUVS) determined the mangrove fish communities we observed. This effect was consistent across bioregions, with stereo-BRUVS detecting a higher number of species, as well as a more even distribution of species across all sites. When looking at average abundance per deployment/transect, stereo-BRUVS detected a slightly higher, though non-significant, abundance than UVCs, regardless of the bioregion sampled. The higher mean abundance detected by stereo-BRUVS could be due to the absence of a diver, which is known to influence results in UVCs (Mallet & Pelletier 2014). The use of bait, longer sampling time and local hydrographic conditions (e.g. tide and current speed) affect the total area of influence of the bait plume, which could also result in higher mean abundance as fish are attracted over a larger area (Taylor et al. 2013).

We also found that although the vast majority of species identified in this study were sampled by UVCs and stereo-BRUVS, there were some species uniquely identified by just 1 method (Table S1). Stereo-BRUVS consistently sampled significantly higher proportions of apex predators (i.e. sharks), herbivores and omnivores, with mullets *Mugil* spp. detected as a discriminating species for this method (Table 4). UVCs, however, were better at detecting carnivores, in particular *Lutjanus argentiventris* and *L. novemfasciatus*, with recorded abundances twice as high in UVCs. We did not expect stereo-BRUVS to detect a lower proportion of carnivores as this contradicts previous studies (Harvey et al. 2007, Langlois et al. 2010, Andradi-Brown et al. 2016). However, previous work in marine protected areas have found that carnivorous fishes, like snappers, are actively attracted to divers (Cole et al. 1990).

We also found that variability of our data was not homogenous, with stereo-BRUVS showing a larger dispersion in comparison to UVCs. When reviewing PCO results (Fig. 3A), we saw a clear separation of data points based on the sampling method. The difference in the dispersion of the data between methods was also readily apparent in this plot. Thus, the differences detected between methods by the PERMANOVA are likely due to a combination of differences between methods and the heterogeneity of data dispersions (Anderson et al. 2008). These results confirm findings from previous studies suggesting each method chosen in this study samples a different subset of the overall population (Langlois et al. 2010, Watson et al. 2010). This finding is particularly relevant when designing monitoring strategies of mangrove fish assemblages in the future, as it shows that although each sampling method has its biases, they will remain constant regardless of differences in environmental conditions as long as the same habitat is sampled (Harvey et al. 2007).

Given that these 2 methods sampled different subsets of the mangrove fish communities, it is recommended that future sampling campaigns use them together as they will provide a more complete view of the fish assemblages under study.

4.4. Potential nursery role of Galapagos mangroves

Studies across the world have determined that structured, coastal and estuarine areas near the coast provide important nursery habitats to a variety of vertebrate and invertebrate species. These areas include seagrass meadows, marshes, kelp beds, coral reefs and mangroves (Nagelkerken et al. 2000, Beck et al. 2001, Dorenbosch et al. 2004, Lefcheck et al. 2019). Considering that most of the previously mentioned nursery habitats are not found in the Galapagos (Danulat & Edgar 2002), and that mangroves are used as nurseries in other parts of the TEP (Shervette et al. 2007, Aburto-Oropeza et al. 2009, Ramirez-Martínez et al. 2016), we hypothesised that mangroves in the archipelago may provide nursery grounds to local fish communities. Our results support this hypothesis, with juveniles found to represent approximately 43% of all individuals sampled in our study. This juvenile proportion is similar to that reported for mangroves of tropical regions, such as the Caribbean and the Indo-Pacific (Dorenbosch et al. 2005).

We further explored the role of Galapagos mangroves as potential nursery habitats for 6 species of economic interest to local fisheries, including *Mycteroperca olfax* and 5 species of the *Lutjanus* genus, by comparing juvenile proportions between mangroves and adjacent rocky reefs. We focused on these species because together they contribute about US$1.3 million per year to the local economy (Tanner et al. 2019), thus potentially providing an economic incentive to protect mangrove areas. In the mangrove areas, we found that approximately 85% of individuals belonging to these taxa were juveniles. This represented over twice the juvenile proportion found in nearby shallow rocky reefs (Table 6). These findings are similar to those of Aguaiza (2015), who found juveniles of *L. argentiventris* and *M. olfax* in significantly higher proportions in mangrove habitats than in nearby shallow rocky reefs.

Mangroves also appeared to work as nursery grounds for blacktip sharks *C. limbatus*. All blacktip sharks we detected in mangrove areas were considered to be juveniles based on their size. Our findings are in line with previous studies in the archipelago, which found evidence of mangroves being used as nurseries by blacktip sharks, as well as 2 more shark species: *Triaenodon obesus* and *Sphyrna lewini* (Llerena-Martillo 2009, Ketchum et al. 2014).

4.5. Management implications

The current coastal zoning plan for the Galapagos only includes waters up to 2 nautical miles from the coastline. This zoning was approved for the GMR in 2001 with the aim of allowing multiple users to coexist with minimal conflict (Heylings et al. 2002, Moity 2018). However, the 2001 plan gives full protection to <1% of the marine area inside the reserve (~1323 km^2) (Moity 2018), with only ~5% of mangrove habitats receiving this full protection against fishing (Moity 2018, Moity et al. 2019). This lack of protection is a problem as mangrove bays are commonly fished by artisanal fishers to obtain baitfish for the handline fishery, and to catch mullets and grunts for local markets (Andrade & Murillo 2002, Heel 2012, Llerena-Martillo et al. 2015). At least 26 fish species are used as bait, including at least 4 endemics, all of which are classified as either Vulnerable or Endangered by the IUCN Red List of Threatened Species (Heel 2012). Additionally, the fishing gear used has very low selectivity, thus a variety of fish species and size ranges are usually caught (Andrade & Murillo 2002, Zimmerhackel et al. 2015). This lack of selectivity is concerning because we have identified a number of species using mangroves during their juvenile stage. Poorly selective fishing may risk these juveniles being removed from populations prior to reproduction. Removal can further complicate the management of fish stocks that are already showing signs of overexploitation, including most notably *M. olfax*, a species also listed as Vulnerable by the IUCN (Burbano et al. 2014, Salinas-de-León et al. 2015, Schiller et al. 2015, Zimmerhackel et al. 2015, Usseglio et al. 2016, Eddy et al. 2019, Ramírez-González et al. 2019).

We recommend that mangrove protection should be expanded across the archipelago. This protection should include areas in the western part of the archipelago, which may be providing important nursery habitats for sailfin grouper, as well as areas in the central part of the archipelago where we have found an important proportion of juveniles for snappers and juvenile blacktip sharks, which are important species to fisheries and the tourism sector in the Galapagos. We also recorded a variety of other non-fish species and charismatic megafauna, such as green turtles *Chelonia mydas*, Galapagos penguins *Spheniscus mendiculus*, Galapagos sea lions *Zalophus wollebaeki* and the flightless cormorant *Phalacrocorax harrisi*, that actively use mangrove forests to rest, feed and breed. This provides evidence that Galapagos mangroves are an important habitat not only to a vast number of fishes, but also to some marine mammals, sea birds and invertebrates (Table S2). Our results show mangroves in the Galapagos support highly diverse fish communities, including species of local commercial and of tourism interest.

Although not a baseline study, results from this first assessment of fish communities in mangrove habitats can be used as a reference point to evaluate the effectiveness of the current zoning plan in protecting mangroves and its inhabitants, and to identify key areas (i.e. due to the provision of habitat to species of interest for fisheries and/or tourism) that are not currently protected from extractive use. This assessment should be considered a pressing issue, as questions have been raised about the influence of some users in the design of the different management zones in the GMR (Edgar et al. 2004b).

Our work has resulted in an improvement in our understanding of a habitat that has been largely understudied in the Galapagos. Our results support the development of management strategies that aim to protect fish biodiversity and ensure the long-term sustainability of local artisanal fisheries under a changing climate (Harvey et al. 2012, Schiller et al. 2015, Salinas-de-León et al. 2020). Furthermore, identifying the environmental factors with the highest influence on the composition of fish communities could help us recognise areas that are more vulnerable to anthropogenic pressures or global climate change (Moore et al. 2016), thus worthy of additional protection measures.

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