



# Stable isotopes track the ontogenetic movement of three commercially important fishes along a coastal Tanzanian seascape

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**ABSTRACT:** Coastal habitats serve a variety of functions for fisheries species including the provision of foraging areas. Numerous studies have demonstrated that fish species shift their habitat preferences as they age, and this paradigm is also common in commercially important species. In this study, the timing and magnitude of ontogenetic movements in 3 coastal fishes (thumbprint emperor *Lethrinus harak*, crescent perch *Terapon jarbua*, and dory snapper *Lutjanus fulviflamma*) was examined in Tanzania. A combination of carbon and nitrogen stable isotope analysis, Bayesian mixing models, and niche metric analysis was used to quantify the ontogenetic timing and magnitude of shifts in each species' habitat niche. Results from this work identified an ontogenetic shift in the relative importance of mangrove and seagrass habitat use between smaller, younger individuals and larger, older individuals across all 3 species. However, the ontogenetic timing of this shift varied between species, with thumbprint emperor exhibiting the most abrupt shift in habitat use with increasing body size, followed by dory snapper and crescent perch. Management approaches that emphasize the conservation of seascapes are suggested to support sustainable fisheries in coastal Tanzania.

**KEY WORDS:** Fisheries ecology · Mixing models · Stable isotopes · Ontogenetic shift · Habitat use

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## 1. INTRODUCTION

Tropical coastal habitats such as mangroves, seagrass beds, and coral reefs are commonly regarded as highly productive ecosystems that support a wide variety of services for fish species (Moberg & Folke 1999, Rönnbäck 1999). These services include the provision of foraging grounds for various fishes (Verweij et al. 2006, Vaslet et al. 2012), nursery areas for juvenile fishes (Beck et al. 2001, Grol et al. 2014), and recruitment areas for larvae (Robertson & Duke 1990), among other services. However, some habitats are functionally better than others at providing certain services to fishes, and thus movement of fishes among habitats during ontogeny is common. For

example, in the Caribbean, French grunt *Haemulon flavolineatum* settle on rubble habitats as larvae before moving out to seagrass habitats for food, then to mangroves to avoid predation, and sometimes back to rubble habitats as a final stop before reaching coral reefs to reproduce (Grol et al. 2014). Different habitats offer advantages that are maximized at different stages of a given species' development (Dahlgren & Eggleston 2000, Haywood & Kenyon 2009, Grol et al. 2014), although each habitat has trade-offs. For example, juvenile fish may seek mangrove habitats for protection from predators at the cost of scarcer and less nutritious prey items (Grol et al. 2011). As fish grow, the costs of predator avoidance may begin to outweigh the nutritional needs re-

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quired for growth, which can motivate movement to adjacent habitats (Dahlgren & Eggleston 2000). This movement of species from one habitat to another as their ecological and physiological requirements change with maturity is known as an ontogenetic habitat niche shift (Werner & Gilliam 1984, Dahlgren & Eggleston 2000, Hammerschlag-Peyer et al. 2011).

Four general ontogenetic habitat niche shift scenarios are possible between size and/or age classes in coastal fishes: (1) no change in habitat niche (i.e. habitat use is independent of ontogeny), (2) habitat niche shift (i.e. primary habitat changes with ontogeny), (3) habitat niche expansion or contraction (i.e. variability in habitat use changes with ontogeny), or (4) an asymmetrical expansion or contraction (i.e. both primary habitat and variability in habitat use changes with ontogeny) (Fig. 1) (Werner & Gilliam 1984, Hammerschlag-Peyer et al. 2011, Marques et al. 2013, Polito et al. 2013, Balza et al. 2020, Pensinger 2020). However, tracking ontogenetic shifts between habitats in coastal fishes can be challenging. Traditional approaches consist of gut content analyses (Wine-miller 1989), visual census techniques (Macpherson 1998), cage and tethering experiments (Dahlgren & Eggleston 2000), and acoustic tracking (Dance & Rooker 2015). While these approaches can elucidate specific aspects of ontogenetic movements, they often only reflect habitat use instantaneously or within a short duration of time.

Stable isotope analyses are a complementary tool for studying ontogenetic movements, as the resulting data are representative of diets and habitat use of consumers over longer time periods than traditional methods (Hammerschlag-Peyer et al. 2011, Vander Zanden et al. 2015). In particular, carbon stable isotope values ( $\delta^{13}\text{C}$ ) are useful measures of habitat use as the  $\delta^{13}\text{C}$  values of primary producers travel through food webs relatively unmodified (Peterson & Fry 1987, Layman et al. 2012). In contrast, nitrogen stable isotope values ( $\delta^{15}\text{N}$ ) are useful proxies of trophic level as they increase with each trophic step (Post 2002). These stable isotope values have been used to identify ontogenetic changes in animal dietary and habitat niches through the analysis of generated convex hulls

or standard area ellipses in  $\delta$ -space ( $\delta^{13}\text{C}$  vs.  $\delta^{15}\text{N}$ ), which are interpreted as proxies of habitat use (Hammerschlag-Peyer et al. 2011, Jackson et al. 2011). The  $\delta$ -space convex hulls and standard ellipses can be used to detect changes in niche width, shifts, and overlap between groups (Bearhop et al. 2004, Turner et al. 2010, Hammerschlag-Peyer et al. 2011, Jackson et al. 2011).

Even so, habitat niche analyses using  $\delta$ -space are particularly challenging for a few reasons. Isotope niche measurements depend on sources being sufficiently contrasting in  $\delta$ -space in order to detect a difference in use (i.e. it is difficult to distinguish between sources with similar isotope values). However, if sources are sufficiently contrasting, consumers of both may appear to have a wide niche width when the primary driver of the width is simply a result of sources being far apart in  $\delta$ -space (Newsome et al. 2007). Lastly, while it is easy to see how groups of organisms separate in  $\delta$ -space, quantifying how spe-

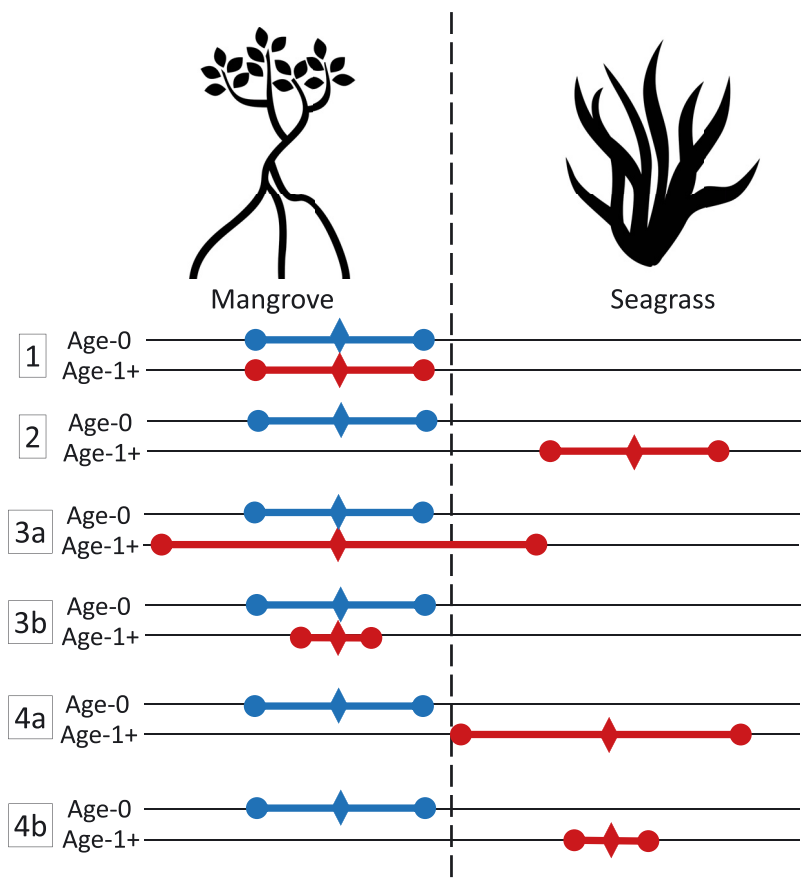


Fig. 1. Theoretical framework for each of the ontogenetic habitat niche scenarios: (1) no change, (2) habitat niche shift, (3a) habitat niche expansion, (3b) habitat niche contraction, (4a) shift with expansion, (4b) shift with contraction. Significant distances ( $>0$ ) between centroids (diamonds) indicate a shift, while changes in bar width between age classes indicate an expansion or contraction

cific sources drive a separation between groups is not feasible with this approach. An alternative method is to convert consumer isotope values ( $\delta$ -values) to proportional contributions of isotopically unique resources ( $p$ ) via stable isotope mixing models. Analyses in  $p$ -space vs.  $\delta$ -space offer the benefit of analyzing multiple habitat axes at once, avoid issues of physiology, and are generally easier to interpret (Newsome et al. 2007). In addition, while the common niche metric analyses used in  $\delta$ -space detailed by Hammerschlag-Peyer et al. (2011) are transferable to  $p$ -space, this approach is generally underutilized (Newsome et al. 2007). Therefore, there is great potential to use the  $p$ -space approach with fish that differ in size and/or age classes to identify niche shifts based on the 4 general ontogenetic habitat niche shift scenarios outlined above.

Quantifying habitat use in commercially valuable fishes throughout their respective lifetimes is often a critical first step needed to link sustainable fisheries production and habitat conservation (Adams et al. 2006, Berkström et al. 2012). However, despite supporting the livelihoods of many people living along the Tanzanian coast, fisheries and fish ecology are generally under-researched relative to other regions (Jacquet et al. 2010, Berkström et al. 2012). A greater understanding of the habitat use patterns of commercially important fishes in coastal Tanzania is of increased importance due to the deforestation of coastal mangroves, destruction of seagrass beds, and other exploitative practices that have the potential to imperil fisheries production (Jiddawi & Öhman 2002,

Cinner 2009, Mangora 2011). This study quantified shifts in habitat use within 3 commercially valuable fish species: thumbprint emperor *Lethrinus harak* ('changu doa' in Kiswahili), crescent perch *Terapon jarbua* ('kui'), and dory snapper *Lutjanus fulviflamma* ('janja') in coastal Tanzania. For the purposes of this study, we define habitat use as the energetic contributions towards any individual or species of fish originating from an ecologically and isotopically unique environment. A combination of stable isotope mixing models and habitat niche  $p$ -space geometry analyses was used to address 2 research questions: (1) Does coastal habitat use change in thumbprint emperor, crescent perch, and dory snapper with increasing body size? (2) When the habitat use of a fish changes with ontogeny, which niche shift scenario best describes the observed differences between size and age classes?

## 2. MATERIALS AND METHODS

### 2.1. Study site

This study focused on Kipumbwi-Sange Estuary, located in the Pangani District of Tanzania near the village of Kipumbwi (Fig. 2). Kipumbwi operates as a hub for many fishing activities in the area, including the collection, sale, and export of daily catches (Nurse & Kabamba 2001). The Kipumbwi-Sange Estuary has a semidiurnal tide with a tidal amplitude of up to 4 m (Ochieng & Erfteemeijer 2003). Six spe-

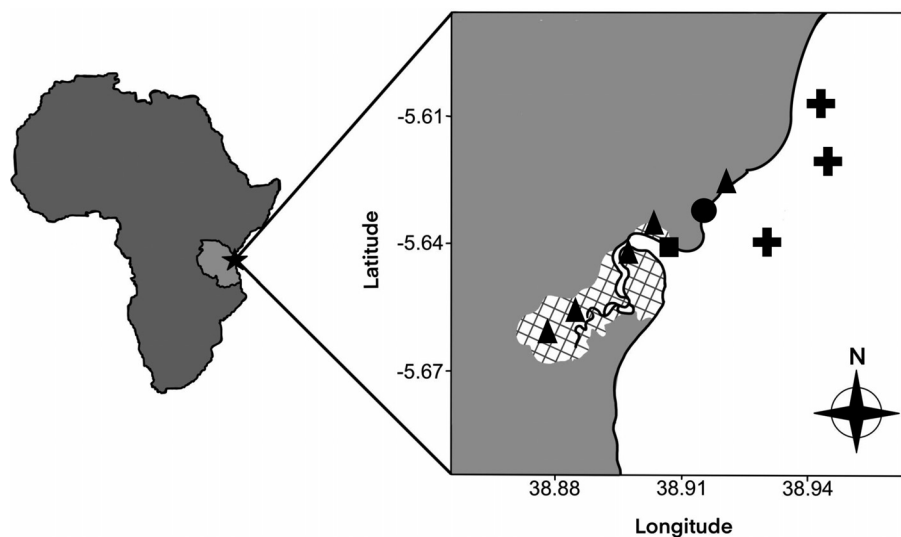


Fig. 2. Coastline with sampling sites near the village of Kipumbwi (circle) within the Pangani District of Tanzania. The square, triangles, and crosses represent mud/sand flat, mangrove, and seagrass sites, respectively. Grey shading represents land, and the gridded areas represent mangrove coverage

cies of mangroves are located throughout the estuary, with distributions conditional on geomorphology. At the mouth of Kipumbwi-Sange Estuary, *Sonneratia alba*, *Rhizophora mucronata*, and *Avicennia marina* dominate. The middle reaches consist of *Ceriops tagal*, while the head of the estuary is occupied by *Xylocarpus granatum* and *Bruguiera gymnorhiza*. Estuary channels are dominated by mud and sandflats. Patchworks of seagrass beds make up the area along the coast of the estuary, consisting of *Sphyrngodium isoetifolium*, *Halophila ovalis*, and *Thalassodendron ciliatum*.

## 2.2. Sample collection and processing

Thumbprint emperors (N = 60), crescent perch (N = 176), and dory snappers (N = 68), were collected in August of 2016 and 2017, which coincides with the dry season in Tanzania (Rohli et al. 2019). Fish were collected from mangrove habitats using a 6.4 mm mesh seine net measuring 3.3 m wide and 1.2 m tall with a 1.2 m by 1.2 m central pocket, sampled along 100 m sections of estuary creek at low tide (Fig. 2). Collapsible fish traps (45.7 cm by 25.4 cm with 6.4 cm openings and 5 mm mesh) were also used to supplement seine net sampling within the estuary's creeks and channels. Fish were collected from seagrass habitats adjacent to the estuary with the assistance of local fishermen using a 100 m seine net with approximately 6.4 mm mesh, sampled over a distance of 500 m at each location (Fig. 2). Total length of each individual was measured to the nearest millimeter. Fish samples were packed into polyurethane bags, kept in a cooler filled with ice for <6 h, and then dissected to obtain white muscle tissue samples. Fish muscle tissue samples were dried using an Excalibur 2400 food dehydrator at 70°C for 6 h and then homogenized using a mortar and pestle prior to stable isotope analysis.

Samples of dominant basal carbon sources were also collected in each habitat. Specifically, seagrass blades, live and dead mangrove leaves, and water-column suspended particulate organic matter (POM) were sampled (see Table S1 in the Supplement at [www.int-res.com/articles/suppl/m670\\_p139\\_supp.pdf](http://www.int-res.com/articles/suppl/m670_p139_supp.pdf)). Seagrass and mangrove samples were rinsed with deionized water, dried at 70°C for 48 h, and then homogenized using a Retsch MM200 ball grinder. POM was collected by passing 500–1500 ml of water per sample through a pre-combusted Whatman GF/F filter and then dried at 70°C for 48 h.

## 2.3. Stable isotope analysis

Homogenized muscle, plant, and POM samples were flash-combusted using a COSTECH Elemental Analyzer and analyzed via an interfaced Thermo Scientific Delta V Advantage Isotope Ratio Mass Spectrometer. Stable isotope values are expressed in  $\delta$ -notation, which is calculated as:

$$\delta X = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000 \quad (1)$$

where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  refer to the ratio of heavy to light isotopes in a sample or standard, respectively. Stable isotope values are relative to the standards Vienna Pee Dee belemnite for  $\delta^{13}\text{C}$  and atmospheric air for  $\delta^{15}\text{N}$ , respectively. Raw isotope values were normalized on a 2-point scale using depleted and enriched glutamic acid standards USGS 40 and USGS 41, respectively. Repeated analysis of sample and reference materials resulted in precisions of 0.1 and 0.2‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. The C:N ratios for all samples analyzed ranged from a minimum of 2.91 to a maximum of 3.91. Of the 304 total fish muscle samples, 146 were corrected for lipid content following Post et al. (2007) as they had C:N ratios that were larger than 3.2 (Table 1).

Mangrove leaves served as a mangrove habitat proxy, seagrass blades were used as seagrass habitat proxies, and POM obtained from filtered water was used as a proxy for the pelagic resources which can be found across both mangrove and seagrass habitats. All statistical analyses were conducted using R software version 3.6.3 (R Core Team 2020). Habitat-specific proxies (i.e. mangrove leaves, seagrass blades, and POM) all differed statistically in their  $\delta^{13}\text{C}$  ( $p < 0.01$ ) and  $\delta^{15}\text{N}$  values ( $p < 0.1$ ), with an exception for  $\delta^{15}\text{N}$  values between mangrove and seagrass ( $p = 0.40$ ), using Kruskal-Wallis and post hoc Mann-Whitney  $U$ -tests.

## 2.4. Mixing model analysis

Three mixing models were fitted to the carbon and nitrogen stable isotope data using the 'MixSIAR' package (Stock & Semmens 2016a) in R to address the 2 research questions. We used a 'body-size' model, which fits total length (mm) as a continuous covariate and individuals as random effects, an 'age-class' model, which uses a binary age classification as a covariate and individuals as random effects, and a 'null' model, which is simply used to assess the

Table 1. Mean stable isotope values and C:N ratios with standard deviations by species and size class for coastal Tanzania; total length (TL) values are in millimeters; N refers to the total number of samples collected;  $p$ Mangrove,  $p$ Seagrass, and  $p$ POM refer to median percent habitat usage from the age-class model with 95% credible intervals in brackets from 3000 posterior draws for each species and age class combination; POM: particulate organic matter

Species	N	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N ratio	$p$ Mangrove (%)	$p$ Seagrass (%)	$p$ POM (%)
Thumbprint emperor							
All	60	$-10.6 \pm 2.0$	$8.3 \pm 0.5$	$3.11 \pm 0.07$	1.4 [ $<1.0, 15.8$ ]	98.2 [84.1, 99.9]	$<1.0$ [ $<1.0, <1.0$ ]
Age 0 (TL < 120)	20	$-12.3 \pm 2.4$	$8.0 \pm 0.4$	$3.16 \pm 0.03$	10.4 [3.2, 17.2]	89.5 [82.7, 96.7]	$<1.0$ [ $<1.0, <1.0$ ]
Age 1+ (TL $\geq$ 120)	40	$-9.8 \pm 1.0$	$8.4 \pm 0.5$	$3.09 \pm 0.07$	$<1.0$ [ $<1.0, <1.0$ ]	99.9 [99.2, 99.9]	$<1.0$ [ $<1.0, 1.0$ ]
Crescent perch							
All	176	$-18.9 \pm 2.6$	$10.2 \pm 1.5$	$3.24 \pm 0.09$	20.3 [2.1, 39.6]	28.7 [21.9, 35.7]	50.2 [29.7, 70.7]
Age 0 (TL < 71)	94	$-20.0 \pm 2.0$	$9.8 \pm 1.3$	$3.26 \pm 0.06$	33.8 [26.5, 41.4]	27.5 [20.9, 34.1]	38.7 [27.2, 49.8]
Age 1+ (TL $\geq$ 71)	82	$-17.6 \pm 2.7$	$10.8 \pm 1.4$	$3.23 \pm 0.11$	8.5 [1.0, 15.8]	30.1 [23.2, 36.3]	61.4 [50.4, 73.0]
Dory snapper							
All	68	$-14.8 \pm 3.0$	$9.7 \pm 1.0$	$3.19 \pm 0.10$	10.6 [ $<1.0, 24.1$ ]	63.2 [38.2, 87.0]	25.2 [8.0, 45.9]
Age 0 (TL < 124)	33	$-17.1 \pm 2.1$	$9.9 \pm 1.2$	$3.18 \pm 0.05$	18.8 [12.4, 25.6]	45.6 [36.5, 54.1]	35.9 [23.4, 48.4]
Age 1+ (TL $\geq$ 124)	35	$-12.6 \pm 1.7$	$9.5 \pm 0.7$	$3.20 \pm 0.13$	3.6 [ $<1.0, 9.4$ ]	79.7 [70.1, 89.1]	16.2 [5.4, 26.5]

effectiveness of the selected covariates. All 3 models have the following form:

$$Y_{ij} \sim N\left(\sum_k p_{ik} (\mu_{jk} + \lambda_{jk}), \sum_k p_{ik} (\omega_{jk}^2 + \tau_{jk}^2) \times \xi_j\right) \quad (2)$$

where  $Y_{ij}$  is the value of each of  $j$  isotopes for  $i$  consumers,  $p_{ik}$  is the diet proportion of source  $k$  to the consumer  $i$ ,  $\mu_{jk}$  is the mean value of isotope  $j$  for source  $k$ ,  $\lambda_{jk}$  is the mean trophic enrichment factor for isotope  $j$  in source  $k$ ,  $\omega_{jk}^2$  is the variance around isotope  $j$  for source  $k$ ,  $\tau_{jk}^2$  is the variance around the trophic enrichment factor, and  $\xi_j$  is a multiplicative error term (Stock & Semmens 2016b). The goal of these mixing models is to estimate proportional contributions ( $p$ ) of each habitat ( $k$ ) to the diet of each fish ( $i$ ). Estimations of  $p$  vary depending on the model used but are generally derived from a flat Dirichlet distribution, transformed to isometric log-ratio parameters, modified based on covariates, and then back-transformed into  $p$ -space values (Stock et al. 2018). For example, estimations of  $p$  for the body-size model would take the form of:

$$p_i = \text{inverse ILR}(\beta_0 + \beta_1 \text{'Total Length'}_i) \quad (3)$$

where ILR is the isometric log-ratio,  $\beta_0$  is the base contribution of a given source, and  $\beta_1$  is the modification to the base contribution based on a certain total length. The age-class model takes a similar form for estimating  $p$ :

$$p_i = \text{inverse ILR}(\beta_0 + \beta_1 \text{'Age'}_i) \quad (4)$$

where  $\beta_0$  is the same base contribution but  $\beta_1$  is now a modification based on a binary age classification. The null model only generates the base  $\beta_0$  values so

it can be used as a baseline to test for model performance using a leave-one out information criterion (Vehtari et al. 2017). For more information on the general parameterization of mixing models in MixSIAR, see Parnell et al. (2013), Stock & Semmens (2016a,b), and Stock et al. (2018).

The binary age classes 'age-0' and 'age-1+' were estimated for each species using published von Bertalanffy age and growth models. Total length cut-off values were 124, 120, and 71 mm for dory snapper, thumbprint emperor, and crescent perch, respectively (Kamukuru et al. 2005, Midway et al. 2018, Fortaleza et al. 2019). Fish longer than the cut-offs were classified as 'age-1+' and below as 'age-0' in the age-class model. Proportional contribution of sources (i.e.  $p$ Mangrove,  $p$ Seagrass, and  $p$ POM) were the dependent variables in each model. The body-size model was used to address the first research question by identifying the ontogenetic timing and magnitude of fish movements between habitat types. The age-class model was used to address the second research question by identifying which of the 4 possible ontogenetic habitat niche shift scenarios occurred between age-0 and age-1+ fish.

Each model was run using the 'very long' setting in the 'MixSIAR' package (Stock & Semmens 2016a) which generates 3 Markov chains over 1 000 000 iterations with the first 500 000 values used as burn-in and the remaining 500 000 thinned by 500 resulting in 3000 posterior data points for each parameter in each model. In addition to variation by age class and variation by body size, individual variation was assessed by treating individuals as random effects for each model. Trophic discrimination factors (mean  $\pm$  SD) of



$0.8 \pm 1.3\%$  and  $6.8 \pm 1.0\%$  were applied to consumer  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, respectively. This represents an increase of +0.4 for  $\delta^{13}\text{C}$  and +3.4 for  $\delta^{15}\text{N}$  for each of the 2 trophic steps assumed between basal habitat sources (Post 2002) and the 3 fish species' trophic position ( $\sim 3.0$ ) examined as reported on FishBase (Froese & Pauly 2012). Prior to analysis,  $\delta$ -space plots were examined for each species to ensure consumers were contained within the source polygons as an indication that the selected trophic discrimination factors were appropriate (Phillips & Gregg 2003, Semmens et al. 2013, Phillips et al. 2014) (Fig. S1 in the Supplement). Convergence was assessed using the Gelman-Rubin diagnostic and Geweke diagnostics (Geweke 1991, Gelman et al. 2013). The MixSIAR 'Residual Only' error structure was used for each model as a conservative approach to estimating source contributions (Stock & Semmens 2016b).

## 2.5. Niche analyses

Posterior data (i.e. 3000 possible compositions for each species' age class) from the age-class model were used to generate geometries for age-0 and age-1+ classes. Due to the posterior data being compositional and thus only having 2 variables that can vary freely, an isometric log-ratio (ILR) transformation was applied, which allows for the use of Euclidean metrics as well as reducing the number of axes from 3 to 2 (Egozcue et al. 2003). The resulting point clouds from this approach represent 6 unique, 2-dimensional geometries which can be interpreted as proxies for habitat niches for each species/age class combination (see Fig. 4). The resulting age-0 and age-1+ habitat niche proxies were then compared using 3 Euclidean metrics: distance between centroids, mean distance to centroid, and overlap as measured by standard ellipses encompassing  $\sim 40\%$  of the transformed data (Batschelet 1981, Turner et al. 2010, Hammerschlag-Peyer et al. 2011, Jackson et al. 2011).

## 2.6. Hypothesis testing

To test for shift in habitat use between age classes, we followed the approach of Turner et al. (2010) and Hammerschlag-Peyer et al. (2011) using the ILR-transformed  $p$ -space values instead of stable isotope data directly. Specifically, the ILR-transformed points that compose each species' age-0 and age-1 habitat niche proxy were compared using established residual permutation procedures to test for a significant

distance between centroids and difference in mean distance to centroid (Turner et al. 2010). Significance was determined using a threshold ( $\alpha$ ) of 0.05 for each of the following metrics. Ontogenetic difference in habitat niche position was quantified using the Euclidean distance (ED) between  $p$ -space centroids of each age class (Turner et al. 2010). Habitat niche positions were considered different if the ED between age classes was  $>0$  after comparison with 999 null distributions generated by a residual permutation procedure (Turner et al. 2010). Ontogenetic difference in habitat niche width was quantified by comparing the mean distance to centroid (MDC) of  $p$ -space point clouds for each age class (Turner et al. 2010). The absolute value of MDC differences between age classes was calculated using residual permutation procedures, with absolute values  $>0$  indicating a significant difference in habitat niche width (Turner et al. 2010). In addition, habitat niche overlap between age classes was calculated using standard ellipses which encompass approximately 40% of the centermost proportional data (Batschelet 1981). Jaccard similarity indices were generated for each of the 3 species, which refer to the total area of shared space between age-class ellipses divided by the total area formed by the 2 age-class ellipses combined. Unique fractions were also calculated for each age class by species, which refers to the area that is 'shared' between age-class ellipses divided by the area of an age-class ellipse of interest (e.g.  $\text{area}_{\text{Age-0}} \cap \text{area}_{\text{Age-1+}} / \text{area}_{\text{Age-0}}$ ).

Following the hypothesis-testing framework outlined by Hammerschlag-Peyer et al. (2011), when non-significant ED values and no differences in MDC values were observed between age classes, this was assumed to indicate no ontogenetic change in habitat niche (Scenario 1). Significant ED values but no differences in MDC values observed between age classes was assumed to indicate a habitat niche shift with ontogeny (Scenario 2). Non-significant ED values, but significant differences in MDC values observed between age classes was assumed to indicate a habitat niche expansion or contraction with ontogeny (Scenario 3). Significant ED values and significant differences in MDC values observed between age classes was assumed to indicate an asymmetrical habitat niche expansion or contraction with ontogeny (Scenario 4). Overlap statistics were used to further confirm the scenarios listed above and quantify the degree to which habitat niche shifts, expansions, and/or contractions between age classes resulted in differences in habitat use between age classes.

### 3. RESULTS

#### 3.1. Ontogenetic timing and magnitude of fish movement

Body-size and age-class models converged for all 3 species based on Gelman-Rubin and Geweke diagnostics (Table S2). The body-size model provided a better fit for the thumbprint emperor and crescent perch data than the null model based on the leave-one out information criterion values (Table S3). The results of the body-size model indicate that all 3 species are characterized by an increase in seagrass use and a decrease in mangrove use with increasing total length (Fig. 3). The body-size model estimated that the smallest thumbprint emperor sampled (~54 mm) consumed resources reflecting a median habitat use of 36% mangrove, 64% seagrass, and <1% water-column POM (Fig. 3). Mangrove habitat use decreased (to 1%), seagrass use increased (to 98%), and water-column POM was similar (to <1%) at the body size (124 mm) reflecting the transition between

age-0 and age-1+ for thumbprint emperor (Fig. 3). The largest thumbprint emperor sampled in this study (310 mm; Fig. 3) consumed resources reflecting a similarly high use of seagrass habitats (99%) over mangrove (<1%) or water-column POM (<1%).

The smallest crescent perch in this study (~40 mm) was estimated by the body-size model to have consumed resources reflecting a median habitat use of 39% mangrove, 20% seagrass, and 41% water-column POM (Fig. 3). Mangrove habitat use decreased (to 28%), seagrass use increased (to 25%), and water-column POM use increased (to 47%) slightly at the body size (71 mm) reflecting the transition between age-0 and age-1+ for this species (Fig. 3). The largest crescent perch sampled in this study (230 mm; Fig. 3) consumed resources reflecting a low use of mangrove habitats (3%) relative to seagrass (45%) or water-column POM (52%).

The smallest dory snapper in this study (~30 mm) were estimated to have consumed resources reflecting a median habitat use of 33% mangrove, 19% seagrass, and 48% water-column POM. Man-

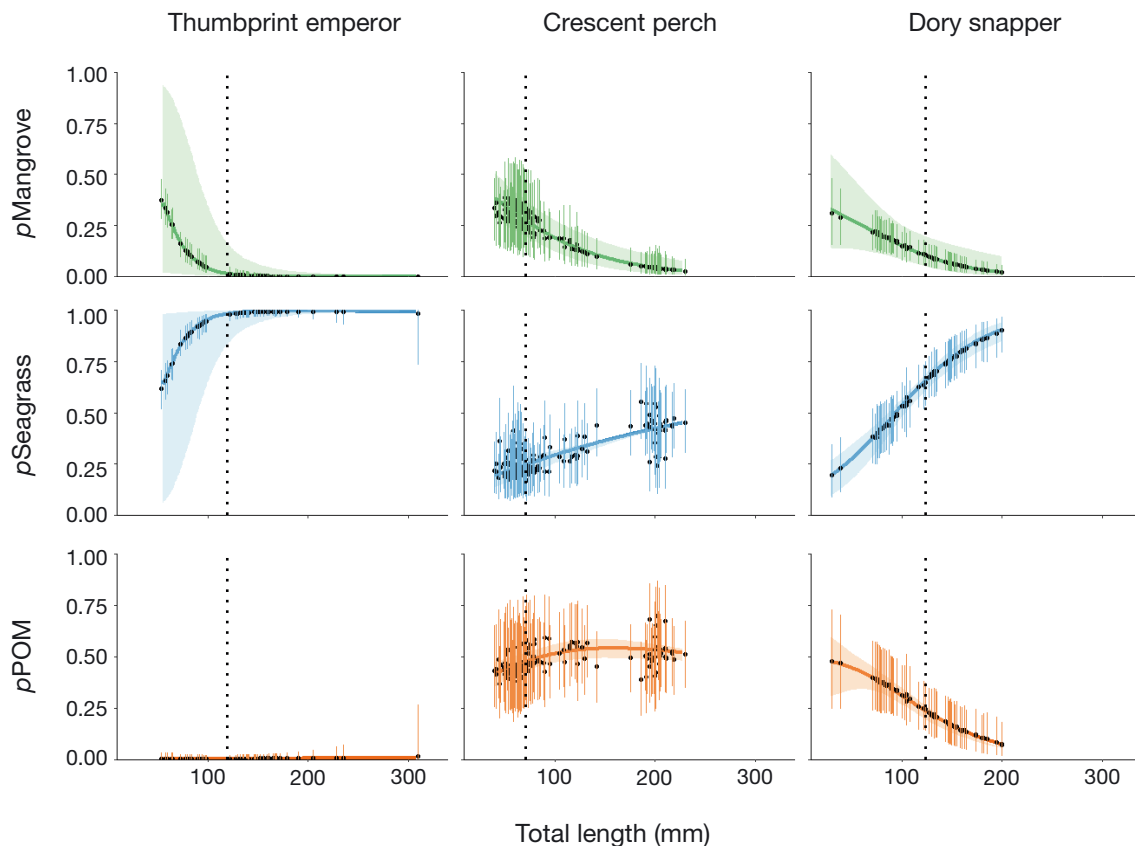


Fig. 3. Changes in proportional contributions of seagrasses, mangroves, and particulate organic matter (POM) with increasing total length for thumbprint emperor, crescent perch, and dory snapper in Tanzania. Solid lines and shaded areas around the lines represent medians and 95% credible intervals. Dots and vertical lines represent individual medians and their respective 95% credible intervals. Vertical dotted lines represent median total length at age-1+

grove habitat use decreased (to 10%), seagrass use increased (to 66%), and water-column POM use decreased (to 24%) at the body-size (124 mm) reflecting the transition between age-0 and age-1+ for this species (Fig. 3). The largest dory snapper in this study (~200 mm; Fig. 3) consumed resources reflecting a median habitat use of 2% mangrove, 90% seagrass, and 8% water-column POM.

### 3.2. Identifying ontogenetic habitat niche shift scenarios

Both the ED between the group centroids as well as the differences in MDC calculated from the ILR-transformed  $p$ -space geometry were significant between age-0 and age-1+ for thumbprint emperor (Fig. 4, Table 2). The Jaccard similarity index (0) and age-class unique fractions (1 and 1 for age-0 and age-1+, respectively) indicated little to no habitat niche overlap between age-0 and age-1+ classes for this species (Table 2). These results, when combined with the larger MDC values for age-1+ fish, suggest a habitat niche shift and expansion with ontogeny in thumbprint emperors (Scenario 4). When comparing individual habitat niche axes derived from mixing model results, median estimates of mangrove habitat use in thumbprint emperors decreased by 10.4% from age-0 to age-1 (Table 1). Seagrass habitat use increased by 10.4% and water-column POM use was negligible in both age classes (Table 1). The 95% credible intervals around median estimates of mangrove and seagrass habitat use did not overlap between age-0 and age-1+ for thumbprint emperor (Table 1).

There was a significant MDC and ED between the group centroids calculated from the ILR-transformed  $p$ -space habitat niches of age-0 and age-1+ crescent perch (Fig. 4, Table 2). The significant MDC differences (age-1+ is larger) and ED indicate a habitat

niche shift and expansion with ontogeny in crescent perch (Scenario 4). The Jaccard similarity index (0.11) and age-class unique fractions (0.67 and 0.86 for age-0 and age-1+, respectively) indicated little habitat niche overlap between age-0 and age-1+ for this species (Table 2). When comparing individual hypervolume axes derived from mixing model results, median estimates of mangrove habitat use by crescent perch decreased by 25.3% between age classes (Table 1). Median estimates of seagrass habitat use were similar in age-0 (27.5%) and age-1+ (30.1%) crescent perch (Table 1), while water-column POM use increased by 22.7% from age-0 to age-1. The 95% credible intervals around median estimates of mangrove habitat and water-column POM use did not overlap between age-0 and age-1+ (Table 1).

Lastly, there was a significant MDC and ED between the group centroids calculated from the ILR-transformed  $p$ -space habitat niches of age-0 and age-1+ dory snapper (Fig. 4, Table 2). Additionally, the 'age-class' model provided a better fit for dory snapper data than the other models assessed (Table S3). The significant MDC (age-1+ was larger) and ED indicate a habitat niche shift and expansion with ontogeny in dory snapper (Scenario 4). The Jaccard similarity index (0.09) and age-class unique fractions (0.60 and 0.89 for age-0 and age-1+, respectively) indicate low overlap in habitat niches between age-0 and age-1+ for this species (Table 2). When comparing individual hypervolume axes derived from mixing model results, mangrove habitat use decreased by 15.2%. Estimates of seagrass habitat use by dory snapper had the greatest overall change, with a median increase of 34.1% between age classes (Table 1). However, water-column POM use fell by 19.7% between age classes (Table 1). Each of the 95% credible intervals around median estimates of habitat use did not overlap between age-0 and age-1+ for dory snapper (Table 1).

Table 2. Euclidean metrics using the isometric log-ratio (ILR)-transformed proportional space ( $p$ -space) output from the age-class model for Tanzanian fishes; Euclidean distance (ED) between age-class centroids with significance ( $p < 0.05$ ), differences in mean distance to centroid (MDC) between age 0 and age 1+ with significance ( $p < 0.05$ ), and overlap metrics for age-0 and age-1+ habitat niche standard ellipses (~40% of the centermost data) for each species

Species	ED	$p$ -ED	MDC difference	$p$ -MDC	Jaccard overlap	Age-0 unique	Age-1+ unique	Shift type
Thumbprint emperor	11.75	<0.01	4.12	<0.01	<0.01	1	1	Shift + expansion
Crescent perch	1.72	<0.01	0.28	<0.01	0.11	0.67	0.86	Shift + expansion
Dory snapper	2.13	<0.01	0.72	<0.01	0.09	0.60	0.89	Shift + expansion



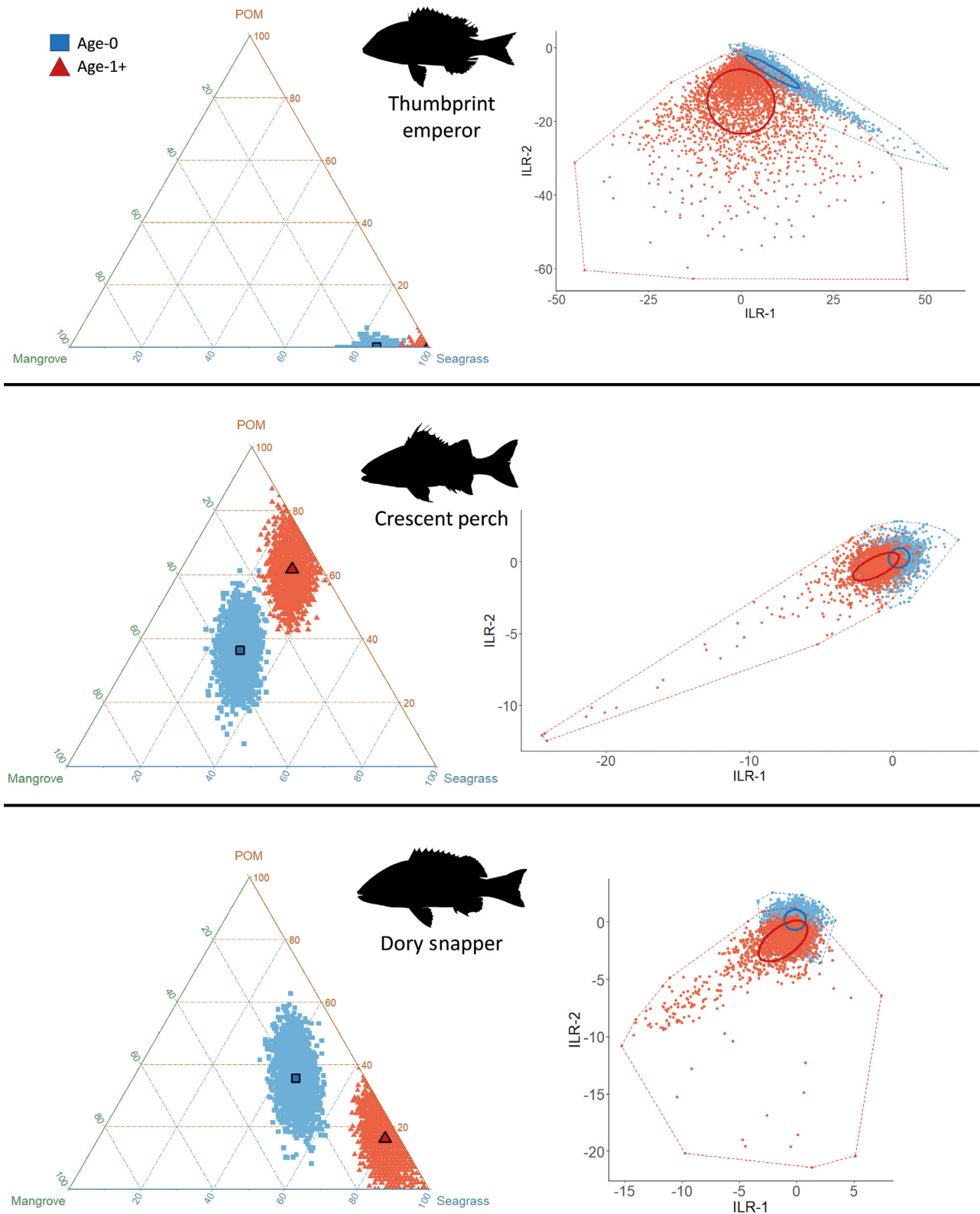


Fig. 4. Habitat niche ternary plots and the respective isometric log-ratio (ILR)-transformed biplots for 3 Tanzanian fish species. Euclidean measures were calculated in ILR-transformed space. Squares and triangles refer to the centroids of Age-0 and Age 1+ point clouds, respectively. Standard ellipses are indicated by solid lines for ILR point clouds which encompass ~40% of the center-most data. Dotted lines in ILR space refer to convex hulls. POM: particulate organic matter

## 4. DISCUSSION

This study identified significant ontogenetic shifts and expansions in coastal habitat use by thumbprint emperor, crescent perch, and dory snapper in coastal Tanzania. Specifically, our results demonstrate a general shift in habitat niche along a mangrove to seagrass habitat gradient with increased body size in all 3 species (i.e. Scenario 4). Even so, the ontogenetic timing and magnitude of niche shifts varied by species, as did the relative importance of mangrove, seagrass, and water column resources between age classes.

### 4.1. Thumbprint emperor

Stable isotope mixing models were used to inform the first research question and identify the timing, relative to body size, and overall magnitude of ontogenetic movements between habitat types along a coastal Tanzanian seascape. Based on the resulting estimates of resource use, the use of seagrass habitats by thumbprint emperors was relatively higher than that of the other species throughout their ontogeny. In contrast, mangrove habitat use was lowest compared to the 2 other fish species examined in this study (Fig. 3). In addition, thumbprint emperors in this study exhibited an early and rapid ontogenetic shift in habitat use with body size, with the smallest fish sampled consuming 36% of their resources from mangrove habitats and age-0/age-1+ transitioning fish consuming exclusively seagrass-derived resources (Fig. 3). These results support previous studies which suggested limited use of mangrove habitats by thumbprint emperors relative to seagrass beds (Unsworth et al. 2009, Kimirei et al. 2011).

The age-class model corroborates much of what was found in the body-size model. A habitat niche shift driven by a reduction in mangrove use and an increase in seagrass use was present in this species (Table 1) (Fig. 4). This low degree of habitat niche overlap was further evident when examining the ILR-transformed  $p$ -space geometries (Fig. 4). While evidence of a habitat niche expansion can be found in ILR space, this result translated into a very slight shift towards seagrass habitats when converted to  $p$ -space. This may be due to the observation that thumbprint emperors use seagrass habitats to a high degree even when they are small and young (Unsworth et al. 2009). For example, while larger and older individuals may exclusively use seagrass habi-

tats, the potential net difference in niche volume between age classes may be limited by the high degree of habitat specialization already present in age-0 fish.

These results highlight the overall importance of seagrass habitats to thumbprint emperors throughout their ontogeny. Previous habitat studies on thumbprint emperors support this general paradigm (Nanami & Yamada 2009, Unsworth et al. 2009, Kimirei et al. 2013b). Thumbprint emperors regularly consume decapods, echinoderms, and small fishes, which are all abundant in seagrass beds (Nagelkerken et al. 2000a, Froese & Pauly 2012). While sample sizes of large fish were relatively low, mixing model results did suggest a slight shift toward POM resources in the largest individuals sampled (Fig. 3). It is possible that thumbprint emperors may begin to forage in coral reef habitats farther from the coast where phytoplankton often serves as a primary basal carbon source (McMahon et al. 2016). Prior studies also suggested a shift from seagrass to coral reef habitats by larger and older individuals (Unsworth et al. 2009). However, it was not possible to confirm these trends due to the lack of sampling in coral reef habitats and the low number of >300 mm individuals in this study despite the persistent efforts of local fishermen to obtain them.

### 4.2. Crescent perch

Crescent perch exhibited a more gradual transition from mangrove to POM habitat use with body size relative to the other 2 study species, matched with a slight increase in the use of seagrass resources throughout ontogeny. Crescent perch often consume shrimp, and this dietary preference could prolong the use of mangrove habitats where shrimp are abundant (Macia et al. 2003). Additionally, crescent perch have slower growth rates relative to the other 2 species examined, which could also prolong mangrove habitat use (Fortaleza et al. 2019). However, in this study, crescent perch consumed a consistently high proportion of water-column-derived resources regardless of size, unlike thumbprint emperor and dory snapper. A possible explanation for this observation is the propensity of crescent perch to consume the scales of filter-feeding fishes such as mullets (Whitfield & Blaber 1978).

A significant habitat niche shift and expansion was found in crescent perch between age-classes (Scenario 4). Specifically, the age-class model and subse-

quent habitat niches indicated minimal overlap between age classes and decreasing mangrove habitat use from age-0 to age-1+. POM use increased with age class, while seagrass habitat use was consistent between age-0 and age-1+. It is evident from both the body-size and age-class models that mangrove habitat use decreases with body size/age and POM is an important basal resource for crescent perch. A diet that heavily depends on the scales of filter-feeding fishes would explain the results of both models well (Whitfield & Blaber 1978). Under this paradigm, habitat niche width could change with ontogeny if crescent perch continue to target fish scales from various habitats as a preferred diet item. However, as crescent perch grow, they may begin targeting prey more readily found in seagrass habitats. In addition, the slight differences observed between the body-size and age-class models may be a result of the cut-off size used for the age-class model. There were a few small age-1+ individuals with stable isotope values and predicted habitat niches that were similar to those of age-0 crescent perch. This may have led the age-class model to overestimate the ontogenetic change in water-column POM resource use while underestimating the change in seagrass resource use relative to the body-size model.

### 4.3. Dory snapper

Shifts in dory snapper habitat use with body size were intermediate of those observed in thumbprint emperor and crescent perch. Like these 2 species, dory snappers increasingly used seagrass habitats at the expense of mangrove habitats with increased body size. Even though mangrove habitat use was lowest for the smallest individuals (33%), use of this habitat decreased with body size in dory snappers more gradually than observed in thumbprint emperors, but more rapidly than observed in crescent perch. Upon reaching the body size reflecting the age-0 and age-1+ transition, seagrass habitat resource use had increased up to 66% (Fig. 3). Dory snapper water-column POM resource use remained intermediate between the other 2 fish species throughout ontogeny.

Similarly, the age-class model and subsequent habitat niche analyses identified a significant shift and expansion in habitat niche between age-0 and age-1+ (Scenario 4). Like crescent perch, dory snapper experienced an incomplete habitat niche shift with a small amount of overlap between age-0 and

age-1+ habit niches in ILR space (Fig. 4). Dory snappers also experienced a 19.7% decrease in water-column POM resource use from age-0 to age-1+, an ontogenetic trend not found in the other fish species examined.

Even so, dory snappers in Tanzania are suggested to consume a variety of invertebrate prey items at smaller body sizes before moving on to consuming mostly teleost fishes at larger body sizes (Kamukuru & Mgaya 2004). While occupying mangrove habitats, small dory snappers may focus their diets on available invertebrate prey resources such as shrimp and other crustaceans (Laegdsgaard & Johnson 2001). However, mangrove habitats may become suboptimal foraging habitats for larger dory snappers, which could motivate their eventual ontogenetic movement to seagrass beds.

### 4.4. Coastal seascape habitats

The direction of ontogenetic movements from mangrove to seagrass habitats was similar across all 3 species, and as such there may be a shared ecological and/or physiological driver. In addition, a large body of research has identified mangrove habitats worldwide as important nursery habitats for juvenile fish, including other commercially important species (Laegdsgaard & Johnson 2001, Nagelkerken 2009, Iglu et al. 2014). Three non-exclusive hypotheses are commonly proposed to explain these observations (Beck et al. 2001, Laegdsgaard & Johnson 2001): (1) juvenile fish are attracted to the structural heterogeneity of mangrove habitats, (2) predation risk is lower in mangroves due to the shallower water, higher turbidity, and structural complexity relative to unvegetated habitats, and (3) the abundance of food items in mangrove habitats is high relative to adjacent habitats.

While these drivers are often difficult to disentangle, it is possible that fish species examined in this study benefit from lower predation pressure in mangrove habitats at small sizes, but move to adjacent seagrass habitats where the threat of predation becomes lower at larger body sizes (Laegdsgaard & Johnson 2001, Unsworth et al. 2009). Shallow seagrass beds in coastal Tanzania generally have higher fish densities and diversity than adjacent mangrove habitats, suggesting a general preference of this habitat type (Dorenbosch et al. 2005, Lugendo et al. 2005). A higher diversity of prey items in seagrass habitats could also explain the increased variation found in age-1+ fishes when examined in ILR space.

This could indicate that the production of prey items is higher in seagrass beds, or that that seagrass beds are preferred feeding habitats because of their more extensive surface areas relative to mangrove habitats (Nagelkerken 2009). The results of our study suggest that these shared drivers of ontogenetic movements from mangrove habitats to adjacent seagrass beds are mediated by species-specific life histories and dietary preferences that lead to variation in the timing and magnitude of ontogenetic movements.

Tidal regime has also been identified as an important factor when considering fish movements from mangroves to adjacent seagrass habitats (Igulu et al. 2014). Access to the Kipumbwi-Sange Estuary is periodically cut off from the ocean at its lowest tide, which results in the formation of shallow pools of water. As such, the use of creeks and pools in this estuary may be constrained by fish body size. These creeks and pools may act to concentrate smaller fishes and invertebrates at low tides but may be too shallow for larger fish to persist in for an extended period of time. This may explain why the slower-growing crescent perch transitions more gradually to adjacent seagrass habitats relative to thumbprint emperor or dory snapper. This gradual pattern may also apply to other slow-growing fishes, such as trevally and grouper species, in Tanzania (Mwijage et al. 2018).

Coral reefs are also generally regarded as an important habitat for coastal fish in Tanzania (Wagner 2004) and other tropical coastal seascapes (Wilson et al. 2006). For example, fishes inhabiting mangrove and/or seagrass habitats as juveniles often eventually recruit to coral reef habitats (Nagelkerken et al. 2000b, Cocheret de la Morinière et al. 2003, Mumby et al. 2004). However, in our study, it was not possible to explicitly quantify the ontogenetic potential for movements to coral reef habitats by thumbprint emperor, crescent perch, and dory snapper. This was because, despite direct sampling efforts and the efforts of contracted local fishermen, we were unable to obtain any individual fish of these species which could be confirmed to have been captured from patch reefs adjacent to the Kipumbwi-Sange Estuary. In addition, using these same methods, it was not possible to obtain the largest size classes of thumbprint emperor and dory snapper that are most likely to use coral reef habitats (Unsworth et al. 2009, Kimirei et al. 2013a). No individuals were collected between the common and maximum body sizes in coastal Tanzania for thumbprint emperor (400–600 mm total length, TL), crescent perch (250–360 mm TL), and dory snapper (250–350 mm TL) as reported in published field guides (Bianchi 1985,

Eccles 1992, Lieske & Myers 2002). While large thumbprint emperor and dory snapper are likely to recruit to coral reef habitats at large body sizes (Unsworth et al. 2009, Kimirei et al. 2013a), little is known as to the potential for large crescent perch to use coral reef habitats. However, given the catadromous reproductive cycle found in crescent perch, it is likely that this species generally prefers estuarine habitats during much of its lifespan (Whitfield & Blaber 1978, Miu et al. 1990, Fortaleza et al. 2019).

All 3 fish species in this study are of importance to commercial and artisanal fishers in coastal Tanzania, and thus a greater understanding of their ecology is essential to their conservation as a source of food and revenue (Froese & Pauly 2012). We found that all 3 species used more than one coastal habitat during ontogeny. At the smallest sizes and youngest ages, all 3 fish species in this study used mangrove habitats, with the relatively highest use of mangrove habitats found in dory snappers and crescent perch. Tanzania has a history of aggressive mangrove harvesting to build structures and create firewood (Mangora 2011), and the loss of coastal mangroves as essential nursery habitat has the potential to negatively impact fisheries production (Nagelkerken et al. 2002, Sundblad et al. 2014). In addition, all 3 species in this study heavily relied on seagrass habitats at the largest sizes and oldest ages examined. Due to the accessibility and high productivity of seagrass beds, these habitats are often targeted using drag nets, which uproot seagrasses and indiscriminately catch many fisheries species (de la Torre-Castro et al. 2014, Fisheries Development Division–Statistics Section–Tanzania 2016). The general scarcity of the largest size classes of thumbprint emperor, crescent perch, and dory snapper during this study may reflect the consequences of the high fishing pressure present in the Kipumbwi-Sange Estuary and adjacent coastal areas. In support of this hypothesis, Kamukuru et al. (2005) found that dory snapper are highly vulnerable to overfishing, with fewer larger individuals found in heavily fished areas relative to a marine protected area at Mafia Island, Tanzania.

#### 4.5. Caveats

Resource use was employed as a proxy for habitat use in this study. As fish can use habitats for non-consumptive purposes, it is possible that the proportion of basal dietary resources assimilated from a habitat may not fully reflect the proportion of time spent in that same habitat. For example, important habitat

functions such as the provision of spawning grounds or shelter from predators are not reflected in the tissue stable isotope values of fishes, such that estimates of habitat use may be underestimated. In addition, as species-specific trophic discrimination factors were not available, we used generalized discrimination factors representing average values across aquatic consumers (Post 2002). However, these generalized discrimination factors were likely appropriate given that the fish stable isotope values were contained within the convex hull in  $\delta$ -space defined by the 3 habitat sources used in the mixing analyses (Phillips & Gregg 2003, Semmens et al. 2013, Phillips et al. 2014) (Fig. S1). Even so, any variation from these assumed trophic discrimination factors as well as the assimilation of basal resources other than the 3 dominant sources examined (i.e. mangroves, seagrasses, POM) may add additional uncertainty around the stable isotope mixing model predictions (Wyatt et al. 2010, Bond & Diamond 2011, Phillips et al. 2014, Busst & Britton 2016). Regardless, our results should be interpreted as conservative baseline estimates of habitat use for each species and relative measures of change in habitat use with ontogeny.

Contrary to expectations, when transforming  $p$ -space values into ILR values, a habitat niche expansion was found for each species (Table 2) (Fig. 4). This is curious because the variability was generally highest for age-0 fishes in the 'body-size' model, which would indicate a broader habitat niche (Fig. 3). A potential reason for this outcome could lie in the transformation from proportional values ( $p$ ) to ILR values, which changes the range over which data can vary from 0,1 to all real numbers (Egozcue et al. 2003). As a result, values in ILR space, regardless of how variable they may be in real coordinate space, are still tempered by the condition that values are no less than 0 and no greater than 1 when transformed into  $p$ -space. Evidence of this can be seen when comparing the same data in ternary plots vs. ILR biplots (Fig. 4). That said, it is possible that age-1+ fishes demonstrate greater flexibility in habitat use than age-0 fish, which is afforded by higher diet plasticity having larger body sizes and, consequently, reduced predation vulnerability (Juanes 1994). Ultimately, these are habitat use metrics estimated by what each of these species is consuming, which is likely more variable for larger fishes.

Lastly, the 'age' variable in the age-class model is derived from TL measurements using von Bertalanffy age-growth models, so it is likely that these variables are correlated. As a result, both models indicate a shift from mangrove habitats to seagrass

habitats. However, we believe the distinction is necessary to help visualize and quantify the general nature of the ontogenetic shift for each species in a similar fashion to established methods (Turner et al. 2010, Hammerschlag-Peyer et al. 2011).

#### 4.6. Conclusions

The objective of this study was to quantify ontogenetic variation in habitat use within 3 commercially valuable fish species in coastal Tanzania. Our results suggest a general pattern of habitat niche shifts with expansions (i.e. Scenario 4) in all 3 species examined from resources derived from mangrove habitats in smaller, younger individuals to those derived from seagrass habitats in larger, older individuals. This research provides additional support for the general role of mangrove habitats as important nursery habitats for juvenile fish in coastal Tanzania (Lugendo et al. 2006, Kimirei et al. 2013b, Igulu et al. 2014) and the importance of seagrass habitat in supporting coastal fisheries production in East Africa (Gullström et al. 2002, de la Torre-Castro & Rönnbäck 2004, de la Torre-Castro et al. 2014). In addition, our results indicate that the benefits and costs of mangrove and seagrass habitats at specific size and/or age classes are mediated by species-species life histories and dietary preferences. Specifically, thumbprint emperors had the most rapid ontogenetic shift from mangrove to seagrass habitats, followed by dory snappers and crescent perch. Given the ontogenetic variation in habitat use observed in these 3 fish species, management approaches that emphasize the conservation of seascapes, rather than individual habitats, is suggested to support sustainable fisheries in coastal Tanzania (Berkström et al. 2012, de la Torre-Castro et al. 2014, Nagelkerken et al. 2015).

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