

Spatial trophic variability of a coastal apex predator, the giant trevally *Caranx ignobilis*, in the western Indian Ocean

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ABSTRACT: Top predators have substantial downstream effects on the structure, function, and resilience of ecosystems. The influence of top predators on an ecosystem can vary if they occur within multiple habitat types and have a wide niche breadth due to spatiotemporal changes in diet. We examined spatial patterns in trophic position and niche width for an economically important reef-associated fishery species, the giant trevally *Caranx ignobilis*. We sampled 4 localities in the western Indian Ocean representing different habitats: coral atolls, coastal reefs, and granitic islands. We analyzed isotopic ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$), and performed compound-specific amino acid stable isotope analysis (AA-CSIA) to control for baseline nitrogen variation. Our analysis of 12 juveniles and 43 adults revealed wide variation in trophic niche breadth between sampling sites and an offshore to coastal gradient in carbon that drove niche distinctiveness between localities. We observed niche width patterns suggestive of ontogenetic changes in diet and habitat utilization and larger niche sizes at the oceanic island sites than the coastal site. Trophic position estimates ranged from 3.5–5, expanding the trophic range of *C. ignobilis* relative to previous studies using AA-CSIA and placing it at the equivalent trophic level as many predatory sharks. Our study corroborates prior evidence that *C. ignobilis* is an important apex predator in reef and island ecosystems. Additionally, we show how evaluating spatiotemporal components of trophic ecology of marine predators is critical for characterizing their functional role and ecosystem influence, allowing for targeted conservation efforts.

KEY WORDS: Compound-specific stable isotope analysis · Amino acids · Reef fishes · Apex predators · Trophic position · Trevally

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1. INTRODUCTION

The removal of top predators can lead to substantial changes in the structure, function and resilience of ecosystems (Parsons 1992, Frank et al. 2005, Estes et al. 2011, Maureaud et al. 2017). This is particularly relevant throughout the world's oceans where the abundances of many predatory fish species are in global decline due to industrialized fishing (Pauly et al. 1998, Myers & Worm 2003, Sibert et al. 2006, Queiroz et al. 2019). Understanding the trophic position and niche breadth of top predator species is criti-

cal for determining the functional role they play in their environment and for predicting future changes to ecosystem structure and resilience (Heithaus et al. 2008, Estes et al. 2011, Ripple et al. 2014). Yet, the downstream impacts of top predators can vary spatiotemporally due to factors such as resource availability, species composition, variation in diet, and predator biomass (Shurin et al. 2002, Duffy et al. 2007, Baum & Worm 2009, Ferreira et al. 2017).

Some marine species such as tunas, billfishes, and sharks consume primarily pelagic food sources and are consistently considered top predators throughout

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their entire ranges (Kitchell et al. 2006, Torres Rojas et al. 2013, Lorrain et al. 2015, Bird et al. 2018). Yet, the trophic position of many species considered top predators can be geographic and habitat dependent (Bolnick et al. 2003, Farmer & Wilson 2011, Papastamatiou et al. 2015, Trystram et al. 2015, Ferreira et al. 2017). Intraspecific spatial variability in trophic position and niche breadth is unknown for many fish species due to the localized geographic focus of most studies. However, characterizing spatiotemporal patterns in trophic position and niche breadth is critical for understanding community structure, food web dynamics, and energy flow (Peterson & Fry 1987, Vander Zanden & Rasmussen 1996, Post 2002).

One ecologically and economically important predatory fish is the giant trevally *Caranx ignobilis*. This species is considered semipelagic, inhabiting tropical and sub-tropical marine waters throughout the Indian and Pacific Oceans and often associated with coral and rocky reefs but also frequently using estuaries and coral atolls as both juveniles and adults (Blaber & Cyrus 1983, Smith & Parrish 2002, Meyer et al. 2007, Lédée et al. 2015). Reaching up to 80 kg, *C. ignobilis* is often considered an apex predator on reefs and translocates nutrients across varying spatial scales (Sudekum et al. 1991, Papastamatiou et al. 2015, Sackett et al. 2017).

C. ignobilis exhibits high site fidelity with varying degrees of migratory behavior, which convolutes where and when feeding primarily occurs (Sudekum et al. 1991, Holland et al. 1996, Meyer et al. 2007, Lédée et al. 2015, Daly et al. 2018a). Stomach content analyses of *C. ignobilis* in Hawaii, USA (Sudekum et al. 1991, Meyer et al. 2001), and throughout the Indian Ocean (Whitfield & Blaber 1978, Blaber & Cyrus 1983, Blaber 1986, Blaber et al. 1990, Farmer & Wilson 2011) show a wide range of dietary preferences and trophic positions. In general, *C. ignobilis* is viewed as a piscivorous predator that also feeds to a varying degree on benthic invertebrates. Adult and juvenile *C. ignobilis* in the northwestern Hawaiian islands primarily prey upon fishes (69.1%; Sudekum et al. 1991), whereas in Oahu, Hawaii, adults primarily prey upon crustaceans (88.9%; Meyer et al. 2007). In an estuary in South Africa, juvenile and subadult *C. ignobilis* consume mostly fishes but also high numbers of crustaceans and mollusks, while in North West Australia, approximately 75 % of the prey of adult and juvenile *C. ignobilis* are teleost fishes (Whitfield & Blaber 1978, Farmer & Wilson 2011). Differences in stomach contents could reflect a number of factors including prey availability, shifts in *C. ignobilis* diet over time, lifespan, season, and the influ-

ence of feeding location on diet. Biological, seasonal, spatial, and temporal (e.g. diurnal) factors contributing to diet variability are relevant for understanding the trophic ecology of *C. ignobilis*, which, because of its status as a top predator, can have substantial downstream effects on fish community structure (Sudekum et al. 1991). *C. ignobilis* can be difficult to catch in numbers large enough for stomach content analysis, which makes stable isotope analysis a more feasible method for estimating trophic variability of this species. Stable isotope studies have revealed a split between coastal and offshore foraging individuals of *C. ignobilis*, as well as spatial differences in depth utilization (Papastamatiou et al. 2015, Trystram et al. 2015, Sackett et al. 2017).

Stable isotope analyses examining carbon and nitrogen can characterize food web dynamics, energy transfer, animal migration, ontogenetic shifts in diet, individual specialization, and biogeochemical variation across space and time (Peterson & Fry 1987, Fry & Sherr 1989, Kelly 2000, Graham et al. 2010, Boecklen et al. 2011, Sackett et al. 2017). Variation in carbon and nitrogen cycling can cause isotopic ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at the base of the food web to vary significantly across small spatial gradients and over short temporal periods (e.g. days to weeks; O'Reilly et al. 2002, Post 2002, Bowen 2010, Magozzi et al. 2017). In marine systems, localized studies have limited power to estimate $\delta^{13}\text{C}$ baselines because carbon gradients vary geographically and are often habitat- and season-dependent, changing with processes such as primary production and upwelling (Goering et al. 1990, Schell et al. 1998, Hill et al. 2006, Bowen 2010, Lorrain et al. 2015, Magozzi et al. 2017). It is therefore important to measure baseline variation at each sampling locality to implement a robust comparative study of trophic positions, particularly for spatiotemporal trophic studies on mobile marine fishes. Baseline measurement is especially pertinent when using $\delta^{15}\text{N}$ to estimate trophic position, due to higher fractionation of $\delta^{15}\text{N}$ than $\delta^{13}\text{C}$, as well as spatiotemporal changes in marine $\delta^{15}\text{N}$ baselines (Post 2002, Bowen 2010). For example, a primary consumer collected from shore as a representative $\delta^{15}\text{N}$ baseline may not reflect the isotopic nitrogen baseline of offshore habitats (Post 2002). Using compound-specific amino acid stable isotope analysis (AA-CSIA; Gaebler et al. 1963, Hare et al. 1991, Fantle et al. 1999, McClelland & Montoya 2002, Popp et al. 2007), one can compare $\delta^{15}\text{N}$ between different amino acids (AAs) to estimate the isotopic baseline using tissue collected from the consumer alone, reducing the need to sample baseline organisms. Com-

pound-specific amino acid stable isotope analysis is therefore a useful, non-lethal technique for estimating trophic positions of organisms such as mobile marine fishes.

Studies using stable isotope analysis to estimate trophic position for *C. ignobilis* have occurred only in Hawaii, USA (Papastamatiou et al. 2015, Sackett et al. 2017) and Réunion (Trystram et al. 2015). Exploring variability in trophic position in other parts of the range of *C. ignobilis* is critical for understanding spatial and behavioral feeding dynamics and niche differences, especially given the variation in movement behavior across this species' range. Moreover, *C. ignobilis* is heavily targeted by recreational, artisanal, and small-scale commercial fisheries throughout the Indo-Pacific and has been overfished in the most-studied part of its range (Hawaii, USA; Friedlander & DeMartini 2002, Nadon 2017), which raises concerns of its conservation status in less-studied areas. One such area is the western Indian Ocean (WIO), where fishing effort is largely unmonitored, and significant knowledge gaps concerning basic aspects of *C. ignobilis* biology remain (FAO 2014). In this region, semipelagic fishes such as *C. ignobilis* are often targeted by artisanal fisheries, and remain vulnerable to overexploitation (Maggs 2013, FAO 2014, Trystram et al. 2015).

Here we evaluated spatial variation in trophic position and niche width across a variety of habitat types (coral atolls, coastal reefs, and granitic islands) for *C. ignobilis* in the WIO. We used AA-CSIA to estimate trophic position and bulk $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to estimate isotopic niche breadth. Using a combination of stable isotope methods, we demonstrate spatial variability in trophic position and niche width across individuals due to heterogeneity in diet and habitat use within and between study sites.

2. MATERIALS AND METHODS

2.1. Study sites

We collected *Caranx ignobilis* muscle tissue samples from 4 localities in the WIO between 2015 and 2018 (Table 1). These sampling localities represent various habitat types including granitic islands (Mahé, Seychelles), coral atolls (St. Joseph Atoll and

Table 1. Collection information for giant trevally *Caranx ignobilis* indicating locality, year, number of adult samples (N_A), number of juvenile samples (N_J), mean fork length (FL) of all samples, as well as minimum (Min) and maximum (Max) FLs by year. MAHE: Mahé, Seychelles; PDO: Ponta do Ouro, Mozambique; PROV: Providence Atoll, Seychelles; STJO: St. Joseph Atoll, Seychelles

Locality	Year	N_A	N_J	FL (mean \pm SD)	Min FL (cm)	Max FL (cm)	Months collected
MAHE		4	11	54.473 \pm 29.051	25.5	110.5	Feb.
	2016	0	8		31	50.4	
	2017	2	0		83	110.5	
	2018	2	3		25.5	105	
PDO		21	0	78.115 \pm 11.336	64.5	98.4	Dec., Jan.
	2015	8	0		67	98	
	2016	9	0		64.5	94	
	2017	4	0		74.5	88	
PROV	2017	9	0	86.333 \pm 6.062	79	95	Mar., Apr.
STJO	2016	9	1	89.250 \pm 19.600	46	120	Feb., Mar., Apr.

D'Arros Island, Seychelles; Providence Atoll, Seychelles), and coastal coralline and rocky reefs (Ponta do Ouro, Mozambique; Fig. 1). All samples were collected during the austral summer months (December–April). Although we were unable to account for short-term environmental and biogeochemical processes

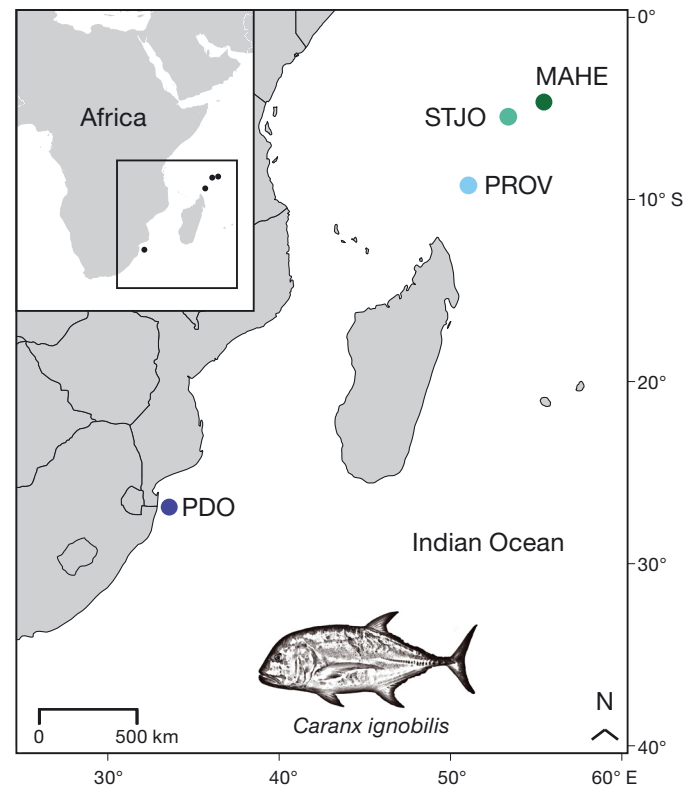


Fig. 1. Sampling localities for *Caranx ignobilis* in Mahé, Seychelles (MAHE), Ponta do Ouro, Mozambique (PDO), Providence Atoll (PROV), and St. Joseph Atoll (STJO)

occurring between sites during these months (e.g. differences in primary productivity), we collected samples during the summer season to minimize seasonality effects. Moreover, samples that were collected over the course of multiple years from a specific site were taken at the same time of year.

The 3 sampling localities in Seychelles differ in their geographic features and associated oceanographic processes (Kalugina-Gutnik et al. 1992). The granitic island of Mahé (4.6827° S, 55.4804° E; 157.3 km²) is the largest island of the Seychelles Archipelago. Mahé is located on the Seychelles Bank of the Mascarene Plateau and is heavily influenced by the Indian Ocean seasonal monsoon and El Niño Southern Oscillation events. Specifically, the Seychelles Archipelago is characterized by southeast trade winds during the austral winter (May–November) and northwestern winds during the austral summer (December–April). *C. ignobilis* samples were collected around Mahé from locations accessed by foot or by boat from narrow fringing reefs composed of coral and granite rock. We also collected samples by boat from the rocks of a small granitic island, Mamelles (0.06 km²), 14 km north-east of Mahé.

St. Joseph Atoll (5.4365° S, 53.3596° E) and neighboring D'Arros Island (5.4180° S, 53.2962° E) are located on the Amirantes Bank, ~255 km southwest of Mahé. The Amirantes Bank is approximately 180 km long and between 8 and 40 km wide, providing a platform for a chain of 20 islands (Stoddart et al. 1979). St. Joseph Atoll is encompassed by 14 islands and contains shallow sand banks and flat reefs encompassing a sand lagoon. St. Joseph Atoll and D'Arros are approximately 1 km apart, separated by a channel ~70 m deep, and both contain seagrass communities dominated by *Thalassodendron* and *Thalassia* (Kalugina-Gutnik et al. 1992, Daly et al. 2018b). Although St. Joseph and D'Arros make up only ~3 km of land, a recent marine biodiversity assessment recorded >500 fish species from these 2 islands alone, representing approximately 45% of all marine fish species recorded in Seychelles (Daly et al. 2018b). These 2 island groups support a variety of habitat types, from seagrass to lagoon to coral reef, and hereafter are referred to collectively as St. Joseph.

Providence Atoll (9.2231° S, 51.0319° E) is a small, uninhabited coralline island (2.82 km²), located ~705 km southwest of Mahé Island and approximately 345 km northeast of the northern tip of Madagascar. Providence is sandy, lacking elevated reef rock, and is distinguished from St. Joseph by being calcareous with fringing barrier reefs (Stoddart 1967,

Kalugina-Gutnik et al. 1992). The vegetation on Providence is dominated by *Casuarina* and coconut trees, while sea grasses and red and green algae dominate the intertidal community (Stoddart 1967, Kalugina-Gutnik et al. 1992).

Ponta do Ouro, Mozambique (26.8427° S, 32.8860° E), is located in southern Mozambique, neighboring the border of South Africa. This site represents an area of transition between western Indian-Pacific and temperate southern African marine ecoregions, and is subject to upwelling (Spalding et al. 2007). *C. ignobilis* were collected from the Ponta do Ouro Partial Marine Reserve, which contains a reef complex referred to as 'the pinnacles' (Daly et al. 2013). The pinnacles are located ~3.7 km offshore and consist of a 30 m shallow ridge encompassed by deeper water that is 50+ m. These reefs are the location of a large aggregation of *C. ignobilis* that takes place annually during the austral summer, correlated with the full moon and most likely used for spawning (Daly et al. 2018a). Samples were collected from the aggregation concurrently as fish were being fitted with acoustic tags. Preliminary movement data suggest that some *C. ignobilis* individuals are resident here year-round, while others travel >500 km to this site while residing along the coastline and estuaries of South Africa during the rest of the year (Daly et al. 2019).

2.2. Sample collection and preparation

Using primarily hook-and-line fishing with artificial lures, we collected muscle tissue from 43 adult (>60 cm fork length, FL) and 12 juvenile (<60 cm FL) individuals of *C. ignobilis* (Table 1). Eleven of the 12 juveniles were from Mahé, Seychelles, 2 of which were sampled from fish markets. *C. ignobilis* sizes ranged from 25.5–120 cm FL (Table 1). This species becomes sexually mature at approximately 60 cm standard length (Sudekum et al. 1991), and we used this estimate to conservatively assign individuals as adults or juveniles, given that standard length measurements (from tip of the nose to the end of the caudal peduncle) are smaller than FL measurements (from tip of the nose to the fork of the caudal fin). We did not perform bulk analyses on 1 individual from Mahé because of limited tissue. We collected white muscle tissue from the dorsal region of the fish at all localities except Ponta do Ouro and St. Joseph, where white muscle tissue was collected from inside the central ventral cavity as these individuals were being equipped with acoustic tags.

We collected baseline samples in the form of long-lived coastal filter feeders from each site (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m641p195_supp.pdf). We analyzed bulk $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for baseline mussel (*Perna* sp. and *Pinna* sp.) samples collected from 2015–2017 from Mahé (N = 7), Ponta do Ouro (N = 8), and St. Joseph Atoll (N = 3; Table S1). We also analyzed oysters (*Pinctada margaritifera*) from Providence Atoll (N = 3), barnacles (*Tetraclita* sp.) from Mahé (N = 3), as well as gastropods from Mahé (N = 2) and St. Joseph (N = 2; Table S1). Out of these samples, we selected 7 to analyze for AA-CSIA to evaluate the suitability of baselines from each site. We froze all samples of fish and invertebrate muscle tissue upon collection, oven-dried them at 50°C for 48 h, and then homogenized samples using a mortar and pestle before weighing and measuring them for stable isotope analysis. We split and packed homogenized samples in tin capsules for bulk analysis and glass vials for AA-CSIA.

2.3. Bulk tissue analysis

We performed bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements at the Yale Analytical Stable Isotope Center (YASIC) using a Costech ECS 4010 Elemental Analyzer coupled to a Thermo Delta Plus Advantage isotope ratio mass spectrometer. We report isotopic values in conventional δ -notation in units of per mil (‰) relative to the international standards of atmospheric N_2 (Air) for N and Vienna PeeDee Belemnite (V-PDB) for C. The δ -values were computed as:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000 \quad (1)$$

where R is equal to $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Data were corrected using internal glutamic acid reference materials YGA and CN2, which were calibrated to Air and V-PDB using United States Geological Survey (USGS) glutamic acid 40 and USGS glutamic acid 41. Internal reference (trout) served as a quality control check. The precision for each run was within $\pm 0.1\%$ for $\delta^{15}\text{N}$ and $\pm 0.2\%$ for $\delta^{13}\text{C}$ based on the performance of the internal reference materials.

Previous research on *C. ignobilis* and other marine predators has indicated a high lipid content in the muscle tissue, which can interfere with $\delta^{13}\text{C}$ readings (Post et al. 2007, Papastamatiou et al. 2015). We accounted for lipids using the following correction factor designed for aquatic organisms (Post et al. 2007):

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times \text{C:N} \quad (2)$$

where $\delta^{13}\text{C}$ is the raw C value and C:N is the carbon to nitrogen ratio. We applied this equation to samples (39% of data) with a C:N > 3.5 (Post et al. 2007).

2.4. Compound-specific analysis

We analyzed samples for AA-CSIA at the University of California Davis Stable Isotope Facility. Acid hydrolysis was performed by adding 6M HCl, flushing with N_2 , and incubating for 70 min at 150°C. Samples were then derivatized using esterification-acetylation (N-acetyl amino acid methyl esters; Corr et al. 2007) via the process described by Walsh et al. (2014). We performed analyses of $\delta^{15}\text{N}$ values of individual amino acids by means of GC-combustion isotope ratio mass spectrometry (GC-C-IRMS) using a Trace Ultra GC gas chromatograph (Thermo Electron) coupled to a Thermo Delta V plus isotope ratio mass spectrometer through a GC IsoLink interface (Thermo Electron). Combustion occurred at 1000°C with Ni/NiO/CuO catalyst.

We co-measured 2 mixtures of internal reference materials of pure amino acids of calibrated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all samples. One was used for isotopic calibration of each amino acid and the other was used as the scale normalization standard. L-norleucine was used as an internal standard to calculate provisional values for each sample. A third mixture served as the primary quality assurance standard not used in corrections. In addition, we co-measured 2 well-described materials (whale baleen and fish muscle) as secondary quality assurance materials. Mean SD for sample materials was $\pm 0.55\%$ and mean SD for reference materials was $\pm 0.82\%$. Additional methods are described by Corr et al. (2007) and Yarnes and Herszage (2017).

The methodology described above generated $\delta^{15}\text{N}$ values for 14 amino acids: alanine (Ala), aspartate/asparagine (Asx), glycine (Gly), threonine (Thr), serine (Ser), valine (Val), leucine (Leu), isoleucine (Ile), proline (Pro), methionine (Met), glutamine/glutamic acid (Glx), phenylalanine (Phe), tyrosine (Tyr), and lysine (Lys). We included 6 of these AAs for further analyses, including 3 'source' AAs (Gly, Lys, Phe), which retain the isotopic signature of the primary producer and display minimal fractionation with trophic transfers, and 3 'trophic' AAs (Glx, Leu, Ala).

2.5. Calculation of AA-CSIA trophic position

We calculated trophic position using a variation of the following equation:

$$TP = \left(\frac{\delta^{15}N_{tr} - \delta^{15}N_{sr} - \beta}{TEF} \right) + 1 \quad (3)$$

where TP is trophic position and $\delta^{15}N_{tr}$ and $\delta^{15}N_{sr}$ are the nitrogen isotopic compositions of chosen trophic and source AAs, respectively. The value of β represents the difference in $\delta^{15}N$ values between the trophic and source AAs in primary producers, and the trophic enrichment factor (TEF) represents the average $\delta^{15}N$ enrichment per trophic level between trophic and source AAs.

The choice of TEF and β values can heavily influence the trophic position value, and can vary substantially by organism (Hussey et al. 2014, Bradley et al. 2015, Nielsen et al. 2015, McMahon & McCarthy 2016). To assess the influence of TEF and β values, we generated multiple estimates of trophic position using 4 approaches (Text S1; Fig. S1). After comparing these approaches using ANOVA (Table S2), we conducted all subsequent analyses using the weighted means method (Hayes et al. 1990, Vander Zanden et al. 2013). Specifically, we replaced $\delta^{15}N_{sr}$ and $\delta^{15}N_{tr}$ with weighted means for 3 source (Gly, Phe, Lys) and 3 trophic (Ala, Leu, Glu) AAs, respectively, using the following equation from Hayes et al. (1990):

$$\delta^{15}N_{xw} = \frac{\sum \frac{\delta^{15}N_x}{\sqrt{\sigma_x^2}}}{\sum \frac{1}{\sqrt{\sigma_x^2}}} \quad (4)$$

where $\delta^{15}N_x$ is the nitrogen isotopic composition of a specified AA within the grouping, and σ_x is the standard deviation of the specific AA. We used a β value of 3.6 and TEF value of 5.7 sensu Bradley et al. (2015). These values were calculated specifically for marine teleost fishes, and are similar to those generated in another meta-analysis (McMahon & McCarthy 2016). These β and TEF values are also within the range of those generated by Nielsen et al. (2015) for animals that excrete ammonium (NH_4^+), e.g. marine teleosts. Thus, the equation we used for trophic position in comparative analyses among sampling sites was:

$$TP = \left(\frac{\delta^{15}N_{tr_{xw}} - \delta^{15}N_{sr_{xw}} - 3.6}{5.7} \right) + 1 \quad (5)$$

where $\delta^{15}N_{tr_{xw}}$ and $\delta^{15}N_{sr_{xw}}$ are the weighted means of trophic and source AAs, respectively. We calculated uncertainty in trophic position using the propagation of errors method as detailed in following equation from Blum et al. (2013):

$$\sigma_{TP}^2 = \left(\frac{\partial TP}{\partial \delta^{15}N_{tr}} \right)^2 \sigma_{\delta^{15}N_{tr}}^2 + \left(\frac{\partial TP}{\partial \delta^{15}N_{sr}} \right)^2 \sigma_{\delta^{15}N_{sr}}^2 + \left(\frac{\partial TP}{\partial \beta} \right)^2 \sigma_{\beta}^2 + \left(\frac{\partial TP}{\partial TEF} \right)^2 \sigma_{TEF}^2 \quad (6)$$

In order to calculate $\sigma_{\delta^{15}N_{tr}}^2$ and $\sigma_{\delta^{15}N_{sr}}^2$ we calculated the propagation of errors for $\delta^{15}N_{tr}$ and $\delta^{15}N_{sr}$ by accounting for analytical uncertainty in each of the 3 trophic and 3 source amino acid nitrogen measurements using a minimum of 3 replicates. We used published values of uncertainty for β and TEF from Bradley et al. (2015).

2.6. Statistical analyses

We conducted all analyses in R v 3.5.2 on 2 datasets: one consisting only of adult individuals (FL > 60 cm), and the other composed of both adults and juveniles. Univariate linear models were used to test for correlations between trophic position, $\delta^{13}C$, and fish size (measured by FL). We used ANOVA to assess whether trophic position estimates between sites were significant. We examined trophic niche width and niche overlap with bulk $\delta^{15}N$ and $\delta^{13}C$ data by generating Bayesian ellipse widths using the package SIBER (Jackson et al. 2011). The area of Bayesian ellipses is used as an estimate of niche width, and we used the small sample size corrected ellipses in order to mitigate bias in sample sizes between localities. We then generated Bayesian ellipses using AA-CSIA trophic position estimates and $\delta^{13}C$ in order to control for baseline $\delta^{15}N$ variability. For both bulk $\delta^{15}N$ and $\delta^{13}C$ and AA-CSIA trophic position datasets, we generated ellipses that represent 40 % of the data. Using SIBER, we fit Bayesian multivariate normal distributions to each sampling site to compare isotope niche width between sites. We also used principal component analysis (PCA) to visualize differences between sites and the effects of each variable: carbon, trophic position, sampling year, and weighted means for trophic and source AAs. For PCA, all variables were normalized by dividing by their standard deviation.

3. RESULTS

3.1. Trophic position

Across the 4 sampling sites of Mahé, Ponta do Ouro, St. Joseph and Providence, we detected significant differences in trophic position of *Caranx ignobilis*, supported by ANOVA for both the adult-only ($F_{3,38} = 7.86$, $p < 0.001$) and adult and juvenile ($F_{3,50} = 9.022$, $p < 0.0001$) datasets. Post hoc Tukey tests indicated significant differences ($p < 0.05$) in the adult dataset between Ponta do Ouro and St. Joseph, as well as be-

Table 2. Bulk $\delta^{13}\text{C}$, bulk $\delta^{15}\text{N}$, and compound-specific amino acid stable isotope analysis trophic position (TP) minimum, maximum, range, mean (\pm SD), and size-corrected standard ellipse area (SEAc) for each locality for the adult dataset and the adult and juvenile dataset

	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		TP		Mean TP	SEAc (Bulk $\delta^{15}\text{N}$)	SEAc (TP)
	Min-max	Range	Min-max	Range	Min-max	Range			
Adult									
Ponta do Ouro	-17.986 to -15.502	2.484	12.134-15.358	3.225	4.036-5.085	1.048	4.531 ± 0.290	2.006	0.623
Mahé	-17.495 to -15.072	2.425	13.955-14.917	0.774	3.927-4.828	0.901	4.359 ± 0.399	1.734	1.475
Providence	-13.847 to -10.110	3.737	12.330-13.381	1.051	3.571-4.343	0.772	4.039 ± 0.274	1.713	1.31
St. Joseph	-15.312 to -12.216	3.096	13.458-14.322	0.865	3.792-4.644	0.851	4.132 ± 0.238	0.839	0.531
Adult and juvenile									
Ponta do Ouro	-17.986 to -15.502	2.484	12.134-15.358	3.225	4.036-5.085	1.048	4.531 ± 0.290	2.006	0.623
Mahé	-17.495 to -12.321	5.174	13.897-15.859	1.962	3.530-4.828	1.297	4.079 ± 0.376	3.707	1.507
Providence	-13.847 to -10.110	3.737	12.330-13.381	1.051	3.571-4.343	0.772	4.039 ± 0.274	1.713	1.31
St. Joseph	-15.312 to -10.551	4.760	12.748-14.322	1.574	3.792-4.644	0.851	4.15 ± 0.231	1.504	1.145

tween Ponta do Ouro and Providence. In the dataset including juveniles, Ponta do Ouro was significantly different ($p < 0.05$) from all other sites (Mahé, St. Joseph, and Providence) while none of the other sites were significantly different from each other.

For adult fish, mean trophic position was highest in Ponta do Ouro (4.531 ± 0.290) followed by Mahé (4.359 ± 0.399), St. Joseph (4.132 ± 0.238), and Providence (4.039 ± 0.274 ; Table 2). Trophic position range among adult individuals was greatest in Ponta do Ouro (1.048), followed by Mahé (0.901), St. Joseph (0.851), and Providence (0.772; Table 2). There was

no significant relationship between trophic position and adult fish size when combining data from all localities ($r^2 = 0.005$, $p = 0.768$; Fig. 2A), or within individual sites except for Mahé, where trophic position and size (FL) were negatively correlated ($r^2 = 0.994$, $p = 0.003$; Fig. 2A). Mahé contained the broadest range of sizes of individuals collected in this study, specifically because juvenile fishes were sampled. When juveniles were included, Mahé exhibited the largest range in trophic position (1.297; Table 2) and a positive correlation between trophic position and fish size ($r^2 = 0.256$, $p = 0.0543$; Fig. 2B).

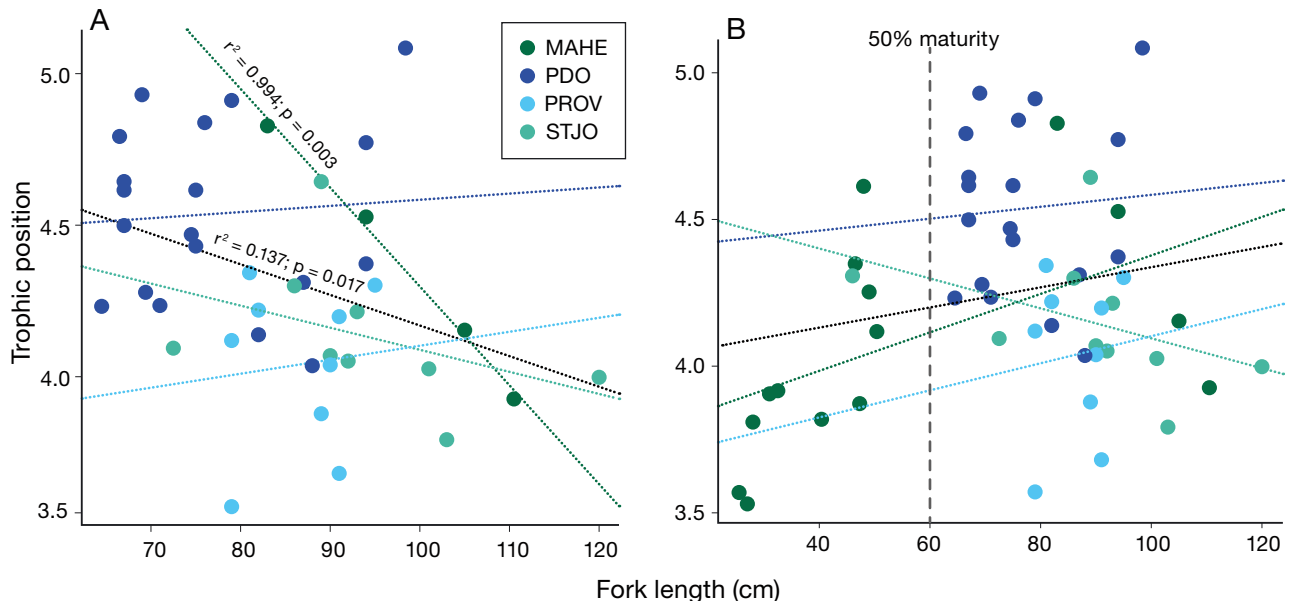


Fig. 2. Relationship between compound-specific amino acid stable isotope analysis trophic position and fork length of *Caranx ignobilis* collected from Mahé, Seychelles (MAHE), Ponta do Ouro, Mozambique (PDO), Providence Atoll (PROV), and St. Joseph Atoll (STJO) for (A) the adult-only dataset and (B) the adult and juvenile dataset. The colored dotted lines represent the best fit lines for the linear models of trophic position versus fork length for each site. The dotted black line is the best fit line for all sites combined. Linear model results are shown for significant relationships

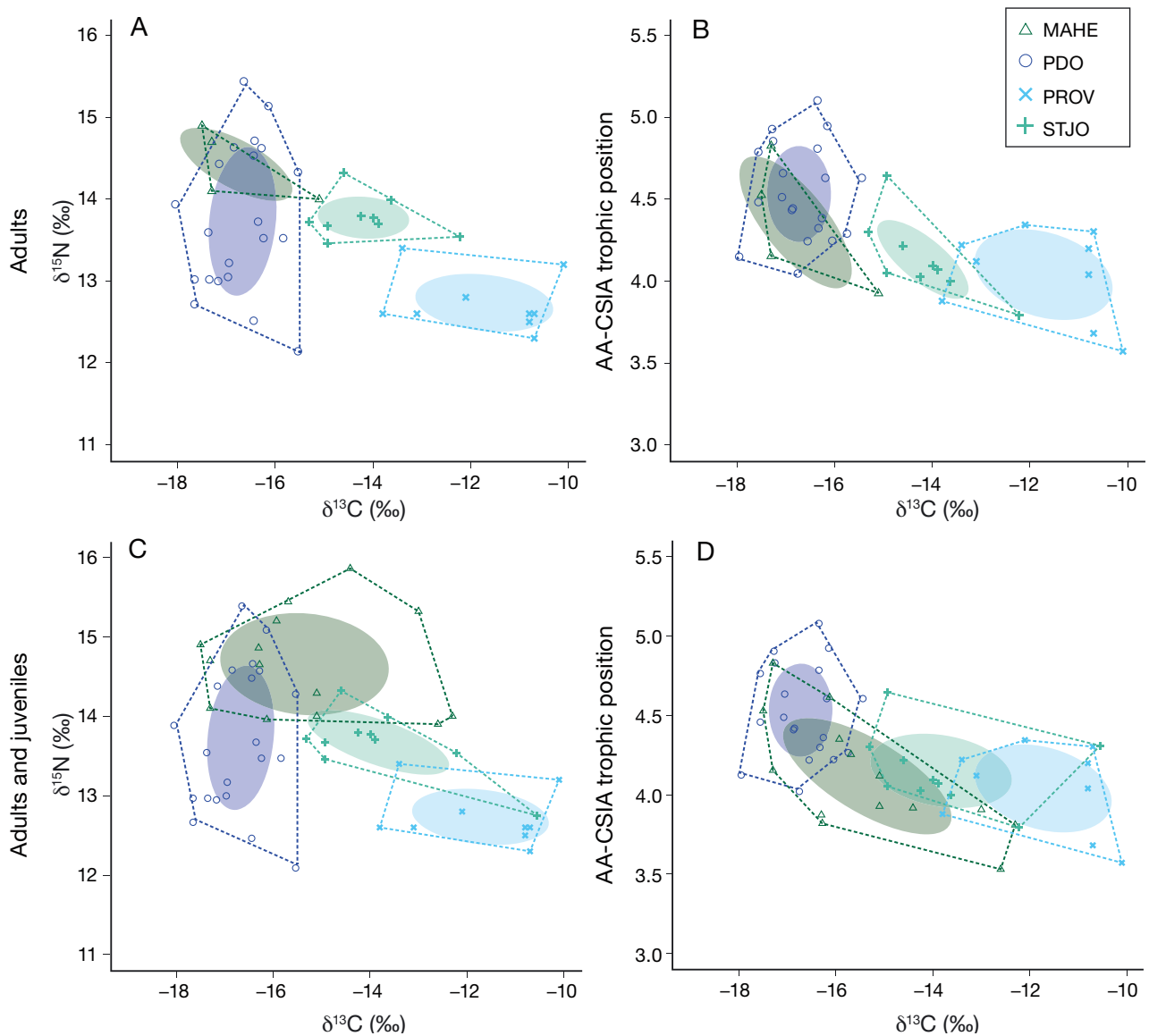


Fig. 3. Size-corrected standard ellipse areas for the (A,B) adult-only dataset and the (C,D) adult and juvenile dataset calculated using (A,C) bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and (B,D) AA-CSIA trophic position and bulk $\delta^{13}\text{C}$. Niche widths (shaded circles) denote Bayesian ellipses representing 40 % of the variance of the data, while dotted lines represent convex hulls. Site abbreviations as in Fig. 1

3.2. Bulk isotopic niche width

We detected differences in the isotopic niche width of *C. ignobilis* across our 4 sampling sites based on bulk $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. Size-corrected niche width of adults using bulk nitrogen was largest at Ponta do Ouro (2.007), followed by Mahé (1.734), Providence (1.713), and St. Joseph (1.504; Table 2). When including juveniles, Mahé had the largest niche width (3.707; Table 2). The spatial differences in niche width were driven primarily by variation in $\delta^{13}\text{C}$, and in Mahé and St. Joseph by inclusion of

juveniles (Fig. 3A,C). For the adult dataset, Providence had the widest range of $\delta^{13}\text{C}$, followed by St. Joseph, Ponta do Ouro, and Mahe (Table 2). When including juveniles, Mahé had the widest range of $\delta^{13}\text{C}$, followed by St. Joseph, Providence, and Ponta do Ouro (Table 2). St. Joseph and Providence had similar values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, but, due to a single juvenile individual, St. Joseph samples exhibited a wider range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Table 2). When only adult fish were examined, the ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were wider in Providence than St. Joseph (Table 2).

The ranges of $\delta^{13}\text{C}$ values from each site are reflective of differences in carbon biogeochemistry due to habitat and feeding characteristics. Ponta do Ouro individuals had a narrow range of $\delta^{13}\text{C}$ values (-17.986 to -15.502), reflecting offshore carbon sources, whereas Providence individuals had values ranging from -13.847 to -10.110 , reflecting more of a coastal carbon signature (Table 2). This variation in $\delta^{13}\text{C}$ signature from offshore to coastal sources was also reflected strongly across samples collected from Mahé, due to juveniles exhibiting coastal carbon signatures (Table 2). Individuals with the highest $\delta^{13}\text{C}$ values were juveniles collected from estuaries, whereas those with the lowest $\delta^{13}\text{C}$ values were adults sampled from Mamelles Island, 14 km from Mahé. From our AA-CSIA analysis of sample baselines, we observed considerable variability in $\delta^{13}\text{C}$ values of baseline species between sampling sites (Fig. S2; Table S3). Moreover, the range of $\delta^{13}\text{C}$ values of *C. ignobilis* was not reflected by the range of baselines at some locations. For example, $\delta^{13}\text{C}$ values from mussels from the coastline of Mahé ranged from -14.803 to -12.856 (Table S3), whereas *C. ignobilis* collected from Mamelles Island exhibited more of an offshore $\delta^{13}\text{C}$ signature (-17.495 to -15.072).

3.3. Compound-specific isotopic niche width

We observed a strong effect of the source AA phenylalanine (N_{phe}) on bulk $\delta^{15}\text{N}$, controlling for locality, suggesting that some variability in bulk $\delta^{15}\text{N}$ is due to nitrogen cycling processes (ANCOVA: $F_{1,3} = 33.14$, $p < 0.001$; Fig. S3). Indeed, analyses of source and trophic amino acids versus $\delta^{13}\text{C}$ indicated large shifts in baseline $\delta^{15}\text{N}$ values between offshore versus nearshore sampling localities, particularly in Mahé (Fig. S4). Niche width relationships also changed when removing the variation in $\delta^{15}\text{N}$ using AA-CSIA and examining trophic position versus $\delta^{13}\text{C}$. (Fig. 3B,D). These adjusted niche visualizations highlight the differences in trophic position between sampling sites after accounting for $\delta^{15}\text{N}$ variation, such as the wide trophic range of individuals from Ponta do Ouro (Fig. 3A,C). With AA-CSIA data, Mahé exhibited the largest size-corrected niche width, followed by Providence and, when including juveniles, St. Joseph (Fig. 3D), or, when excluding juveniles, Ponta do Ouro (Fig. 3B, Table 2). Accounting for baseline nitrogen variation and inclusion of juveniles changed the extent of niche overlap between sampling sites (Fig. 3).

The $\delta^{13}\text{C}$ gradient within and between sites had a large impact on niche width. The large niche width

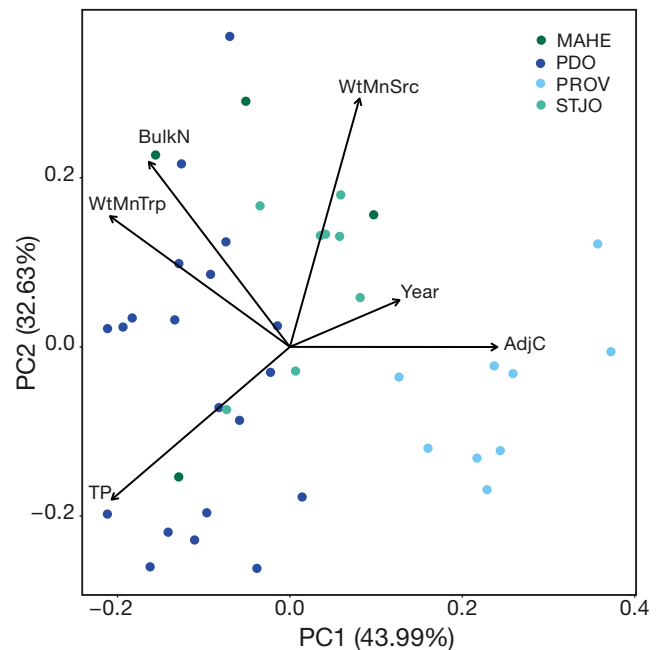


Fig. 4. Principal component analysis of *Caranx ignobilis* adult individuals (>60 cm fork length) showing the first 2 principal components (PC1 and PC2) to visualize differences between samples collected from Mahé (MAHE), Ponta do Ouro (PDO), Providence (PROV), and St. Joseph (STJO). The following variables are overlaid: year (YEAR), bulk $\delta^{13}\text{C}$ (AdjC), bulk $\delta^{15}\text{N}$ (BulkN), AA-CSIA trophic position (TP), and weighted means for trophic (WtMnTrp) and source (WtMnSrc) amino acids

on Mahé was driven by the expansion of $\delta^{13}\text{C}$ by juveniles. When only considering adult fish from Mahé (>60 cm FL), the range of trophic positions was 0.901, close to the range of Ponta do Ouro (1.048). In comparison, Providence had a narrower trophic position range but, due to a wider $\delta^{13}\text{C}$ range, a larger niche width than Ponta do Ouro (Table 2). PCA further corroborated differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ driving variability between adult individuals across the 4 sampling sites (Fig. 4). PC1 accounted for 43.99% of the variance and was driven by $\delta^{13}\text{C}$. PC2 accounted for 32.63% of the variance and was driven by $\delta^{15}\text{N}$. Bulk $\delta^{15}\text{N}$ was correlated with weighted means for trophic and source AAs.

4. DISCUSSION

While previous studies using stable isotope data and stomach content analyses have shown *Caranx ignobilis* to be a generalist feeder, the extent to which this variation in diet is due to habitat, movement behavior, life history characteristics, or other behavioral

and ecological factors has remained unaddressed in the WIO. Our 4 primary sampling localities in the WIO are distinguished from one another by unique habitat features (e.g. coral atolls, coastal reefs, granitic islands) as well as different patterns of habitat utilization by *C. ignobilis* (e.g. resident versus migratory fish). At these sampling localities, 3 of which are within the same archipelago, individual *C. ignobilis* exhibit considerable variation in trophic position and niche width. By using compound-specific methods to account for variation in baseline nitrogen values between sites, our study highlights the wide extent of trophic variability in one predatory species across a range of habitat types, although we are unable to account for variability due to biological factors such as stress, feeding rate, and individual fractionation rate. Our estimates of trophic position span 3.5–5, placing the species in between secondary and tertiary piscivores and expanding the trophic range of *C. ignobilis* compared to previous studies, which estimated trophic positions of adult individuals spanning 3.5–4.6 (Papastamatiou et al. 2015, Sackett et al. 2017). Many large individuals of *C. ignobilis* from Mahé and Mozambique exhibit the same trophic level as several large predatory sharks such as mako, tiger and blacktip sharks, which affirms the status of *C. ignobilis* as an important predator in reef and island ecosystems in the WIO (Hussey et al. 2011, 2015, Daly et al. 2013, Trystram et al. 2015). Similar trophic expansions have been demonstrated using a comparable methodology for sharks (Hussey et al. 2015). Such expansions have relevant downstream effects for understanding trophic cascades and predator–prey dynamics, and for developing classes of functional groups for marine fishes in a given habitat type.

Understanding spatiotemporal variation in ecological niches and the linkages between habitats is essential for marine spatial planning and fisheries management, and our findings have significant potential consequences for fisheries management on coral reefs across the Indo-Pacific range of *C. ignobilis* (Crowder & Norse 2008). For example, in Hawaii, it was estimated that the population of *C. ignobilis* in French Frigate Shoals (~130 000 individuals) consumed a substantial amount (~19 600 t) of prey species per year (Sudekum et al. 1991). Therefore, a large change in population size of *C. ignobilis*, potentially due to overfishing, from a location such as Seychelles would have substantial cascading effects on prey species abundance and reef community composition. Carangid fishes are heavily targeted in Seychelles, with catches comprising between ~1190 and 2100 t yr⁻¹, which is approximately 25% of all arti-

sanal fisheries catches in the country (Le Manach et al. 2015). Our observed differences in diet and habitat use by *C. ignobilis* on Mahé, the most populated island in Seychelles, can help fishery managers implement measures such as catch size limits and no-take zones in order to protect specific size-classes of *C. ignobilis*, such as preserving areas that provide habitat for the largest individuals (e.g. Mamelles Island) and for juvenile individuals (e.g. coastal inlets and fringing reefs). Our confirmation of *C. ignobilis* as an apex predator also sparks the need for research on its abundance in the WIO, coupled with diet studies, to examine direct top-down impacts of this fish on other commercially important species.

A similar approach combining spatial and habitat data made inferences on *C. ignobilis* movement and trophic behavior at a remote atoll in the northwestern Hawaiian Islands (Papastamatiou et al. 2015). At this location, *C. ignobilis* exhibited seasonal patterns of mesophotic and shallow reef habitat utilization correlated with water temperature differences, but showed variability in diel vertical movement behavior (Papastamatiou et al. 2015). Moreover, they occupied a wide range of trophic positions (3.5–4.6), which was attributed to individual dietary specialization (Papastamatiou et al. 2015). In our study, we also observed wide ranges in trophic position at all of our study sites, even the atolls of Providence and St. Joseph, in spite of these atolls lacking the habitat variability more characteristic of the much larger granitic island of Mahé or the Mozambican and South African coastlines. Acoustic tagging data indicate that 2 of the largest fish from St. Joseph Atoll undertook movements to Marie-Louise Island, ~89 km away, also located on the Amirantes Bank (SOSF 2017). These 2 fish had lower trophic positions than other individuals from St. Joseph, whose average dispersal distances were shorter (7–61 km). Thus, *C. ignobilis* individuals from St. Joseph Atoll may have developed local feeding strategies to use resources at neighboring islands, as observed in Hawaii (Papastamatiou et al. 2015). Individual specialization in diet has also been documented for other predatory fishes and attributed to resource abundance, competition, and ontogenetic factors (Bolnick et al. 2003, Woo et al. 2008, Matich et al. 2011).

Our findings generally show larger niche sizes at oceanic island sites compared to coastal Mozambique, which could be indicative of ecological niche expansion commonly associated with islands (MacArthur et al. 1972, Scott et al. 2003, Papastamatiou et al. 2015, Andrades et al. 2019). Diet specialization is one mechanism attributed to population-scale niche

expansion, particularly for island ecosystems (van Valen 1965, Andrades et al. 2019). A recent meta-analysis of island and mainland marine communities off the coast of South America found that niche width and resource exploitation range ($\delta^{13}\text{C}$) were both higher at oceanic island sites than coastal mainland sites (Andrades et al. 2019). Individuals sampled at the coastal mainland site, Ponta do Ouro, Mozambique, exhibit a smaller niche width than expected, since this site hosts a spawning aggregation of *C. ignobilis* and samples are representative of a regional pool that consists of both resident and transient individuals (Daly et al. 2018a). While some individuals appear to be resident and presumably feed close to Ponta do Ouro, several individuals travel hundreds of kilometers to this site from the coastline and estuaries of neighboring South Africa (Daly et al. 2019). Diet variability between Ponta do Ouro and other locations, where many *C. ignobilis* individuals are resident throughout most of the year, likely accounts for the wide range in trophic position, since the height of the niche ellipse was greatly reduced once baseline nitrogen variation was accounted for. However, the niche width at this site remains small due to the narrow range of $\delta^{13}\text{C}$ (Fig. 3).

In concordance with previous studies that have examined the relationship between trophic position and size of *C. ignobilis* (Papastamatiou et al. 2015, Trystram et al. 2015), we found no significant relationships between trophic position and size of adult fish, except 4 individuals from Mahé, which displayed a negative trend. When including juveniles, there was a positive correlation between trophic position and fish size on Mahé. We observed a strong coastal-offshore gradient in Mahé correlated with fish size and sampling location. Larger fish were collected from offshore habitats while smaller fish were collected from nearshore coastal sites. The patterns we observed suggest ontogenetic shifts in habitat utilization and diet from juvenile to adult life history stages, which is widely recorded in fishes and other animals (Werner & Gilliam 1984, Hammerschlag-Peyer et al. 2011). By visualizing trends in source and trophic AAs, we are able to characterize shifts and gradients in baseline nitrogen and carbon within Mahé and the other study sites. Although our estimates of trophic niche width are limited by the fact that it was not possible to sample a breadth of baseline samples to characterize the $\delta^{13}\text{C}$ isoscape at our sample sites, carbon variability is most responsible for niche distinctiveness between sites, which is likely reflective of $\delta^{13}\text{C}$ sources differing due to habitat heterogeneity and a $\delta^{13}\text{C}$ isoscape that varies at a

fine scale (e.g. nearshore to offshore at a scale of kilometers). The correlation between habitat features and fish size on Mahé corresponds with the strongest within-site $\delta^{13}\text{C}$ gradient compared to the other sampling sites. Smaller individuals (<40 cm FL) were caught from shallow channels and reefs along the coastline, and displayed nearshore $\delta^{13}\text{C}$ signatures. Larger fish (40–60 cm FL) were caught on rocky and coral reefs slightly offshore, and displayed intermediate $\delta^{13}\text{C}$ offshore and nearshore signatures, while the majority of adult fish (>60 cm FL) were caught on small granitic rock islands and exhibited offshore $\delta^{13}\text{C}$ signatures.

On the other hand, fish from coastal Mozambique exhibited the narrowest $\delta^{13}\text{C}$ gradient—half the range of that observed in Mahé—and every individual reflected an offshore carbon signal. These $\delta^{13}\text{C}$ values are comparable to representative species used for offshore $\delta^{13}\text{C}$ baselines (Hussey et al. 2011). In a previous study, values of $\delta^{13}\text{C}$ sampled from suspended particulate matter showed a decreasing gradient moving northwards up the eastern coastline of South Africa, although this gradient dissipated ~10 km offshore (Hill et al. 2006). This natural carbon gradient likely explains the offshore signature we observed from Ponta do Ouro individuals, which were collected ~4 km offshore but traveled away from that reef site to various extents. We did not observe any relationship between average distance traveled from Ponta do Ouro and $\delta^{13}\text{C}$ signature. Even Providence and St. Joseph displayed differences in $\delta^{13}\text{C}$, although they are both coralline atolls in the Seychelles. The lower $\delta^{13}\text{C}$ signatures of fish from Providence are likely due to the calcareous features of the atoll, since carbon isoscapes on coral reefs can vary greatly due to reef composition and fine-scale habitat complexities (Briand et al. 2015).

5. CONCLUSIONS

Our study highlights the complexity of trophic dynamics for an important top predator species due to habitat heterogeneity, life history characteristics, and movement behavior. We demonstrate that AA-CSIA provides a powerful way to understand the trophic niche breadth of species such as migratory, semipelagic fishes that are difficult to study in a spatiotemporal context. However, the large amount of variation we observed between trophic position estimation methods, as well as between sampling sites, highlights the challenges of using this metric for meta-analyses that aggregate trophic position by

species at a global scale (e.g. Pauly et al. 1998, Branch et al. 2010, Maureaud et al. 2017). Our confirmation that *Caranx ignobilis* is a top predator across multiple habitat types is a starting point to help prioritize the management and conservation of this understudied species in the WIO.

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