


Research Article

Role of Trophic Niche Plasticity in Shaping Individual Performance: Insights From Juvenile *Mugil cephalus* in Mangrove Habitats

Fengming Liu,¹ Jiao Qin,² Xiaodong Yang,¹ Zhuoxin Sun,¹ Lingwei Kong,¹ Junhao Li,¹ Yanping Zheng,¹ and Yunrong Yan ^{1,2}

¹College of Fisheries, Guangdong Ocean University, Zhanjiang, China

²Mangrove Conservation and Research Center, Southern Marine Science and Engineering Guangdong Laboratory (Zhanjiang), Zhanjiang, China

Correspondence should be addressed to Yunrong Yan; yryan_gdou@163.com

Received 3 January 2024; Revised 16 January 2024; Accepted 28 July 2025

Academic Editor: Jorge Paramo

Copyright © 2025 Fengming Liu et al. Journal of Applied Ichthyology published by John Wiley & Sons Ltd. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Trophic niche plasticity is a critical mechanism that enables fish species to adapt to diverse food resources in heterogeneous habitats; however, its specific implications for the performance of migratory juveniles through mangroves remain unclear. Thus, we comprehensively analyzed the population density, trophic niche characteristics, and body condition assessments of two juvenile populations of *Mugil cephalus* (Flathead grey mullet) inhabiting mangroves on the east and west coasts of Leizhou Peninsula, China. Our findings demonstrate a notable difference in niche metrics between populations with different population densities: the population with high population density had a narrower trophic niche space, higher niche redundancy, and higher trophic plasticity than the population with low density. Juveniles with high population density exhibited low Fulton condition index, indicating poorer body conditions. These empirical results support observations commonly documented in unstable environments with limited food resources, where intraspecific competition for resources tends to be prevalent. Our work contributes to the understanding of trophic niche variations among juvenile fish populations, provides valuable insights for conservation initiatives, and highlights the importance of considering the interplay among population size, trophic niche characteristics, and individual performance when designing protected areas with the aim of maximizing the nursing value for targeted species.

Keywords: individual performance; kernel utilization density; mullet; trophic niche; trophic plasticity

1. Introduction

Mangroves, one of the most productive ecosystems in tropical and subtropical regions, function as spawning, foraging, and nursery grounds as well as migratory corridors for a diverse range of fish species [1, 2]. In these habitats, 3161 fish species were identified, which accounted for 9.6% of the total species recorded in FishBase [3]. On a global scale, acknowledging that mangroves play a pivotal role in supporting the livelihoods of approximately 4.1 million individuals residing in local fishing communities is

imperative [4]. However, the ecological integrity of mangrove ecosystems has been severely compromised in recent decades due to various human activities, including urban development, aquaculture, mining, and the excessive exploitation of timber resources. Furthermore, ever-escalating climate change has played a considerable role in these ecosystems [5–7]. Mangroves encompass a range of microhabitats, each providing diverse food resources, such as mangrove detritus, plankton, crustaceans, and other macrofauna, which serve as essential nutrients for juvenile fish. These dietary factors profoundly influence the life history

characteristics of juvenile fish, including survival rates, growth patterns, and reproductive allocation [8]. Consequently, a comprehensive understanding of the trophic ecology of juvenile fish is critical for the assessment of habitat quality in mangrove-associated fish populations and the formulation of strategies to ensure their sustainable exploitation [9, 10].

The concept of a trophic niche, constituting one quantifiable dimension within the n-dimensional hypervolume framework, is paramount in elucidating trophic roles in ecosystem functioning [11]. It has provided insights into the breadth of their dietary niches and trophic positions [1]. Inquiries into resource utilization patterns and trophic dynamics in mangrove fish populations span a spectrum from individual to community scales and encompass a range of significant topics, including ontogenetic shifts [12, 13], niche partitioning among coexisting species [14, 15], and the broader trophic structure of the community. Furthermore, species within these ecosystems exhibit remarkable trophic plasticity, which enables them to adapt their foraging strategies to variations in trophic resource availability [16, 17]. Spatial and temporal fluctuations in food availability can profoundly influence the composition of ingested food and dietary preferences. Such plasticity may arise from shifts in direct predation dynamics driven by factors such as alterations in prey abundance or interspecific competition [18] or via indirect predation mechanisms involving changes in the diet or trophic levels of prey species [17]. Growing evidence suggests that some mangrove fish species exhibit an expanded dietary spectrum and trophic plasticity in response to changing environmental conditions [19]. However, comprehensive quantitative investigations of trophic plasticity remain limited. Research has provided insights into the dynamics of trophic plasticity in the context of changing environments with respect to mangrove sedentary carnivorous fish species, exemplified by *Acentrogobius viridipunctatus* [20]. This study underscores the substantial role of trophic plasticity in optimizing energetic returns [21, 22], with potential repercussions on individual performance. Nevertheless, a significant gap exists in understanding the interplay among population size, trophic niche characteristics, and individual performance in juvenile mangrove fish populations.

The flathead mullet, *Mugil cephalus*, exhibits a cosmopolitan distribution, inhabiting coastal waters across tropical, subtropical, and temperate regions of major oceans globally [23]. This species primarily spawns in near-shore marine environments [24]. Individuals at early life stages, including eggs and larvae, drift in ocean currents and migrate onshore during the post-flexion larval stage. Subsequently, early juveniles temporarily occupy the surf zone [25]. During the juvenile and sub-adult life stages, *M. cephalus* predominantly inhabits estuarine waters, with an affinity for mangrove ecosystems, where juveniles are commonly reported to be dominant in catches [26]. *M. cephalus* occupies a foundational position in the food pyramid because it consumes organic matter, detritus, and benthic microalgae and possesses high-quality fish protein available to apex predators, which plays an important role in

facilitating energy and nutrient transfer between adjacent aquatic ecosystems. Furthermore, this species holds economic importance in the fisheries and aquaculture sectors of many countries. Adult *M. cephalus* are primarily targeted by small-scale fisheries, and larvae are captured for aquaculture purposes [27, 28]. However, due to overfishing and habitat alterations, *M. cephalus* stocks experienced substantial global declines [29]. A substantial gap remains in understanding the trophic dynamics of *M. cephalus* juveniles in heterogeneous environments, particularly in mangrove ecosystems. This knowledge deficit hinders the ability to quantitatively assess the nursery value provided by mangroves and devise sustainable exploitation strategies for *M. cephalus* juveniles.

The Leizhou Peninsula, between latitudes 21° 15' to 21° 20' N and longitudes 109° 22' to 110° 27' E, marks the southernmost extent of mainland China and experiences a unique climate that combines northern tropical and subtropical conditions. Covering an expansive land area of 12,470 km², this region boasts vast intertidal flats spanning 867 km² and an extensive coastline stretching for 1556 km. The numerous sheltered bays and muddy inlets along this broad coastline fostered the development of extensive mangrove ecosystems. Recent estimates indicate that the mangrove coverage on the Leizhou Peninsula encompasses approximately 7800 ha, constituting 33% of the total national mangrove area of China [30]. Mangrove ecosystems display high levels of productivity and biodiversity, particularly in fishery populations, and play a crucial role in sustaining inshore fisheries and mariculture [31]. However, this region experienced decades of human-induced impacts, including wetland reclamation, aquaculture expansion, urbanization, and a series of mangrove restoration initiatives, which significantly altered the habitats of mangrove-associated fish. Furthermore, environmental conditions such as tidal regimes, salinity fluctuations, and mangrove tree community composition vary considerably between the eastern and western mangroves of the Leizhou Peninsula [20]. Thus, three primary objectives were considered in the present study with regard to assessing juvenile *M. cephalus* inhabiting mangrove habitats along the eastern and western coasts of the Leizhou Peninsula: (1) investigate variations in the population size, density, body length, and body condition of juvenile *M. cephalus* populations within these mangrove habitats; (2) comparatively assess the trophic niches of these juvenile *M. cephalus* populations throughout the four seasons; and (3) quantitatively evaluate and compare the trophic plasticity exhibited by these heterogeneous juvenile populations. This multifaceted investigation was designed to elucidate the intricate relationships among the population size, trophic niche characteristics, and individual performance of juvenile *M. cephalus* populations. The insights derived from this study not only enhance the understanding of trophic niche variations within these juvenile populations but also provide valuable guidance for formulating conservation strategies, particularly in designing protected areas aimed at optimizing the nursing value for targeted species.

2. Materials and Methods

The sampling areas included two distinct mangrove forests on the eastern and western coasts of the Leizhou Peninsula, Fucheng (FC), and Gaoqiao (GQ) (Figure 1). These two sites differ significantly in environmental factors, including tidal rhythm, fluctuations, tidal range, mangrove tree composition, and ocean currents. The FC mangrove forest, on the eastern coast of the Leizhou Peninsula (approximately 109°42'–110°23'E and 20°26'–21°11'N), is in proximity to Leizhou Bay. The area has a rainy season from April to October, with a mean annual rainfall of 1711.6 mm and irregular semidiurnal tides with a mean tidal range of 3.12 m. Dominant mangrove plants include *Avicennia marina*, *Kandelia obovata*, *Aegiceras corniculatum*, and *Sonneratia apetala* [32]. The GQ mangrove forest is within the core area of the Guangdong Zhanjiang National Mangrove Forest Nature Reserve (from 109°45' to 109°48'E and 21°31' to 21°35'N). The annual average precipitation in this region ranges from 1700 to 1800 mm, and is concentrated primarily from May to September. Tidal patterns follow a regular diurnal tide regime, characterized by an average tidal range of 2.53 m, with the maximum tidal range reaching 6.25 m [33]. The dominant mangrove tree species in this region are *A. corniculatum*, *Bruguiera gymnorrhiza*, and *Kandelia obsoleta*.

Juvenile fish were collected during four seasons: autumn 2021, winter 2022, spring 2022, and summer 2022. Three locations in each region were sampled over 3 consecutive days. To efficiently capture these juveniles, we used five 8-m nets with a 5-mm mesh size in small intertidal mangrove creeks during the ebb tide, intercepting them as they exited during low tide. Upon capture, we identified, measured (length in cm), weighed (g) the fish, and promptly froze the fish for analysis. We adhered to the ethical standards of the Animal Ethics and Welfare Committee of Guangdong Ocean University (Approval No. 2023A1515010580). Following the AVMA Guidelines for Euthanasia of Animals published in American Veterinary Medical Association 2020, specific manipulation first anesthesia with MS-222, and then animals humane euthanasia by intraperitoneal injection of sodium pentobarbital, we strictly followed the 3R principles (replacement, reduction, refinement) and ensured humane treatment according to international experimental animal welfare standards. Fulton's condition factor was calculated by Mozsar et al. [34] as follows: $K\text{-factor} = (\text{weight (g)}/\text{standard length (mm)}^3) \times 100,000$.

Dorsal muscle tissue samples were randomly selected and preserved at -20°C . Subsequently, these samples underwent freeze-drying in a freeze dryer (Alpha1-4/2-4LD Plus, Christ, Germany) at -45°C under vacuum conditions for 48 h, removing all moisture until the sample weight stabilized. The dried muscle tissue was transformed into a fine powder using a bead homogenizer (BIO SPEC MiniBeadbeater-16, USA). Approximately 0.42 ± 0.02 mg of this powdered sample was accurately weighed using a Mettler Toledo microscale (Mettler Toledo, XPE26DR, Germany) and enclosed within a tin capsule for isotopic analysis. Stable isotope analysis was performed using an

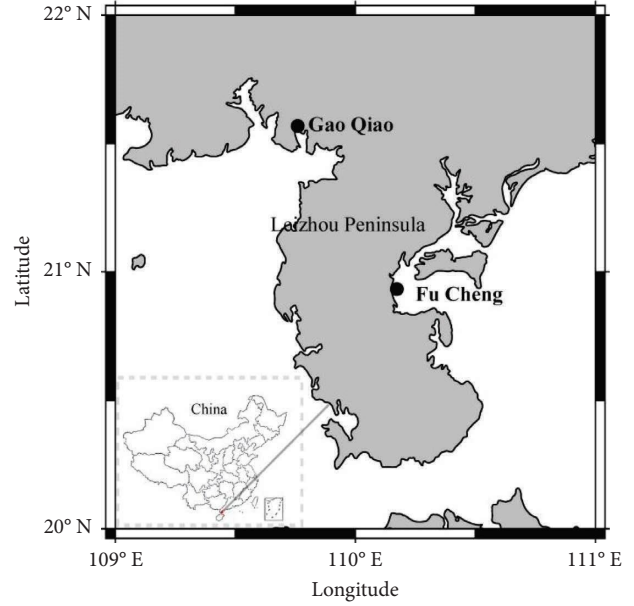


FIGURE 1: Solid circles indicating two sampling sites, Fu Cheng (FC) and Gaoqiao (GQ), in two mangroves on Leizhou Peninsula, China.

elemental analyzer (EA Isolink CNHO) connected to an isotope ratio mass spectrometer (DELTA V Advantage) at our dedicated isotope laboratory. All stable isotope values are reported in the δ notation format:

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

where R_{sample} and R_{standard} are the ratios of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively, and the standards are atmospheric nitrogen and Pee Dee Belemnite.

Trophic level (TL) was calculated using the formula

$$\text{TL} = \frac{(\delta^{15}\text{N}_{\text{sample}} - \delta^{15}\text{N}_{\text{baseline}})}{\Delta^{15}\text{N}} + \lambda, \quad (2)$$

where $\delta^{15}\text{N}_{\text{sample}}$ is the adjusted nitrogen stable isotope ratio for each individual, $\delta^{15}\text{N}_{\text{baseline}}$ is the estimated mean $\delta^{15}\text{N}$ value for the baseline organism *Cyclina sinensis* (differences between the two habitats were not significant [t -test, $p = 0.287$], with means of 8.61‰ and 8.81‰ for FC and GQ, respectively), $\Delta^{15}\text{N}$ denotes the nitrogen isotope enrichment (3.4‰) (usually taken as 3.4‰) [35], and λ is the trophic level of the baseline organism, typically 2.

We employed t -tests to assess the differences in population density and body length between the two habitats across the four seasons. Additionally, we used analysis of covariance (ANCOVA, standard length as a covariate) to evaluate variations in condition factors among the habitats and seasons. We conducted a permutational multivariate analysis of variance (PERMANOVA) to assess the significance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variations across the four seasons and two locations. This analysis was conducted using the “Adonis2” function in the R package “vegan” [36], using the methodology outlined by Haubrock et al. [37]. To define

population niches, we employed Layman's metrics and the corrected standard ellipse area (SEAc) by using the R package "SIBER" [38]. These metrics included the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ranges (NR and CR, respectively), mean distance to the centroid (CD), total area encompassing individual measurements (TA), mean nearest neighbor distance (MNND), and standard deviation of the nearest neighbor distance (SDNND). These metrics collectively provide insights into the degree of trophic redundancy (i.e., interindividual competition) and niche breadth, with SEAc considering the core 40% of the data points while minimizing the influence of extreme values. We conducted a spatial analysis of the kernel isotope niche by using a bivariate normal kernel utilization density estimator to determine the "estimated isotopic homing ranges" at the 50%, 75%, and 95% levels for each population. This analysis, conducted with the R package "rKIN" [39], involved assessing kernel utilization density (KUD) overlap between populations in different seasons. The KUD was used to define the trophic niche of each population, indicating their specific resource utilization within their respective sites. Additionally, we introduced a novel metric, the isotopic plasticity index (IPI), calculated as the ratio between total homing (based on 95% of the data) and the core range (based on 50% of the data), using the approach outlined by Haubrock et al. [37]. A higher IPI indicates a greater ability to utilize diverse resources. The IPI was used to compare trophic plasticity among the four seasons of two populations, enhancing the understanding of trophic adaptations in these heterogeneous mangrove ecosystems.

All statistical analyses were performed using the software R (Version 4.1.2, R Core Team, 2021).

3. Results

In total, 505 *M. cephalus* individuals were captured: 366 from FC and 139 from GQ. Of these, 105 individuals were randomly selected for isotope analysis: 57 and 48 from the FC and GQ groups, respectively (Table 1). Observations revealed that the standard length was consistently larger in FC than in GQ across all four seasons (*t*-test, $p < 0.05$; Figure 2(a)). This pattern was also observed when individual densities were assessed (Table 1). Conversely, juveniles in the FC exhibited poorer body conditions (ANCOVA, $p < 0.05$, Table 2), suggesting reduced individual performance.

The population arrangement within the isotopic space differed significantly between FC and GQ juveniles. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values exhibited significant spatial-temporal variations (PERMANOVA, $p < 0.05$, Table 2), indicating niche differentiation at the foundational level of the food web and in trophic length. The trophic level of *M. cephalus* in the two mangrove forests showed a significant difference outside the spring, with maximum and minimum values of 3.70 and 2.88 occurring in the spring and autumn, respectively, at GQ (Figure 3, Table 1); further, the changes in trophic level relative to standard length showed the same pattern as that for the individual developmental changes except in summer in FC (Figure 3). Examination of the size of the isotopic space, quantified using TA and SEAc (Table 3), revealed that

the FC population occupied a substantially smaller area. This observation indicated a lower degree of trophic diversity within the FC population than that within the GQ population. Furthermore, the smaller values of the mean nearest neighbor distance and the standard deviation of the nearest neighbor distance in the FC population than that in the GQ population (Table 3) indicate a higher level of individual redundancy, implying that individuals frequently form pairs with similar trophic preferences.

The isotopic homing range, which serves as a proxy for the occupied trophic niche, exhibited pronounced variation between the two locations across the four seasons. No overlap was observed in the 50% KUD area in any season (Figure 4). However, the estimated values for the 95% KUD area ranged from 3% in summer to 65% in autumn (Figure 4). These findings provide compelling evidence that the trophic niche of the population differs significantly between the two locations. Furthermore, consistently higher IPI values were recorded in FC than in GQ across all seasons (except for winter) (Table 1). This suggests that between the FC and GC populations, the former has a greater capacity to utilize a more diverse range of resources than that by the latter.

4. Discussion

In this study, we investigated the differences in juvenile *M. cephalus* population sizes between two heterogeneous mangrove locations, FC and GQ. Our findings indicated that of FC and GC, the former had a higher density of large individuals but exhibited a lower body condition than that in the latter. Based on the $\delta^{15}\text{N}$ value, the *M. cephalus* individuals in the two habitats showed a lower trophic level in FC, and different patterns of individual development were exhibited during summer. Additionally, we comprehensively analyzed the trophic niches and plasticity of these juvenile populations across the four seasons. Our results revealed that FC displayed a narrower niche space, greater nutrient redundancy, and higher IPI than those for GQ. The higher abundance of larger juveniles in FC than in GQ could be probably attributed to the fluctuating availability of food resources associated with irregular semi-diurnal tides. In such environments, juvenile *M. cephalus* may increase their body size to enhance their food capture efficiency. This increased body size probably contributes to their adaptability to dynamic conditions, leading to improved survival rates and an increased population density, which aligns with the findings of our study. The findings of Stuthmann et al. [15] also support our findings; they reported that the overall body size of the fish community in mangroves under a semi-diurnal tidal regime was larger than that in mangroves under regular diurnal tides. As aforementioned, these findings suggest that body size strongly influences utilization of mangrove ecosystems by the fish at the population and community levels.

Trophic diversity, derived from individual stable isotope values, directly indicates a trophic structure of the population [40]. Our study revealed significant spatial-temporal differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among juvenile

TABLE 1: Number of individuals, isotopic plasticity indices, and means (\pm s.d.) of standard length (SL, mm), $\delta^{13}\text{C}$ (‰), $\delta^{15}\text{N}$ (‰), trophic level (TL), and Fulton's condition factor (K-factor) of *Mugil cephalus* collected in four seasons in Fucheng and Gaoqiao.

Habitat	Abundance	N (for isotope analysis)/season	Standard length (mm)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	K-factor	TL	IPI
			Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD	
Fucheng	69	Spring ($n=20$)	71–124 (94.55 \pm 12.86)	-18.60 \pm 1.71	11.95 \pm 0.95	1.750 \pm 0.21	3.56 \pm 0.27	4.08
	16	Summer ($n=10$)	59–95 (85.10 \pm 9.25)	-19.46 \pm 4.90	9.69 \pm 0.85	2.02 \pm 0.26	2.89 \pm 0.24	4.16
	124	Autumn ($n=10$)	86–138 (107.6 \pm 15.74)	-18.24 \pm 1.62	11.83 \pm 1.33	1.76 \pm 0.15	3.52 \pm 0.37	4.41
	157	Winter ($n=17$)	79–124 (101.64 \pm 16.098)	-18.88 \pm 1.69	11.82 \pm 1.01	1.71 \pm 0.18	3.52 \pm 0.29	3.73
Gaoqiao	45	Spring ($n=10$)	55–106 (93.40 \pm 15.30)	-21.16 \pm 2.45	14.60 \pm 1.42	1.62 \pm 0.19	3.70 \pm 0.40	3.67
	8	Summer ($n=8$)	28–123 (58.75 \pm 29.59)	-22.91 \pm 2.34	13.00 \pm 0.58	2.50 \pm 0.22	3.23 \pm 0.16	3.78
	68	Autumn ($n=15$)	33–110 (57.53 \pm 26.74)	-23.25 \pm 2.78	11.81 \pm 1.29	2.05 \pm 0.38	2.88 \pm 0.37	4.17
	18	Winter ($n=15$)	41–98 (61.53 \pm 18.79)	-21.81 \pm 2.33	12.94 \pm 0.87	1.79 \pm 0.37	3.21 \pm 0.25	4.49

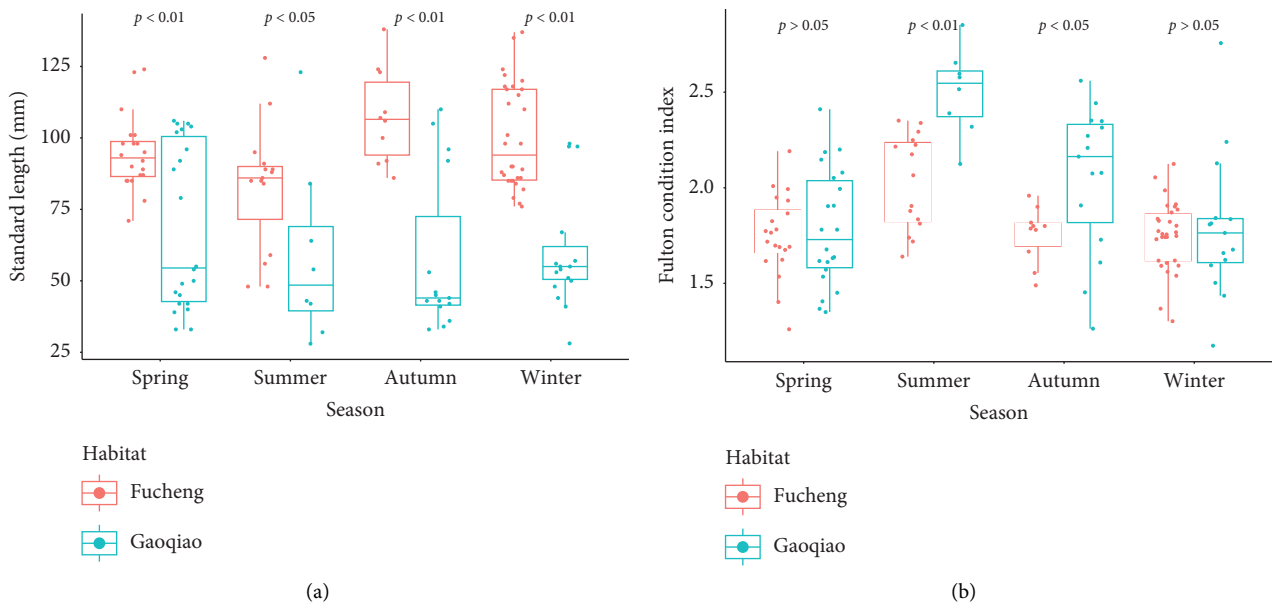


FIGURE 2: Results of variability in standard length (a) and Fulton's condition index (b) between seasons in two habitats, Fucheng and Gaoqiao. The boxplot shows the median (solid thick line), 25th and 75th quantiles (box); the solid dots represent eigenvalues for the corresponding season. Statistically significant effects are indicated in bold " p " ($\alpha=0.05$).

TABLE 2: Permutational multivariate analysis of variance (PERMANOVA) results from the differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Source of variation	df	Mean square error	F	Probability ($> F$)
$\delta^{13}\text{C}$				
Sites	1	41.677	30.389	0.001***
Seasons	3	11.318	2.220	0.038*
Sites: seasons	3	5.016	1.265	0.229
Residual	97	128.237		
Total	104	182.934		
$\delta^{15}\text{N}$				
Sites	1	10.148	13.190	0.001***
Seasons	3	7.360	3.021	0.001***
Sites: seasons	3	11.930	6.654	0.001***
Residual	97	57.970		
Total	104	89.400		
K-factor				
Sites	1	21,046	69.83	1.01e⁻¹³***
Seasons	3	1429	4.74	0.00363**
Sites: seasons	3	1697	5.63	0.00118**
Residual	126	301		

Note: Statistically significant effects are in bold ($\alpha=0.05$). An analysis of covariance (ANCOVA) results from the differences in Fulton's condition factor (K-factor) of juvenile *Mugil cephalus* by habitats and seasons. Asterisks (*, **, ***) are widely used markers to denote the level of statistical significance in hypothesis testing. They conventionally represent the following p value thresholds: * for $p < 0.05$ (statistically significant), ** for $p < 0.01$ (highly statistically significant), and *** for $p < 0.001$ (very highly statistically significant).

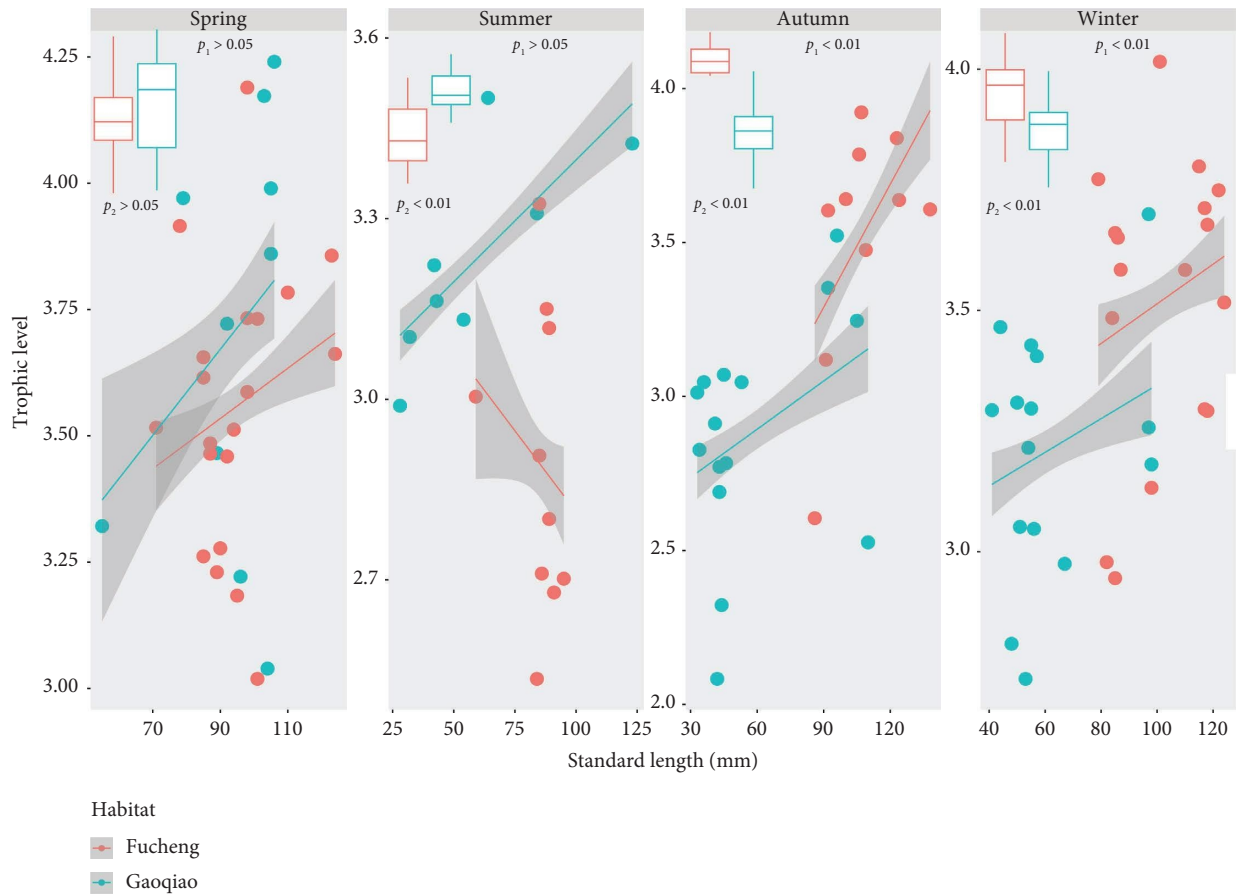


FIGURE 3: Results of trophic level variation with standard length (t -test analyzed the result as “ p_1 ”) in different seasons in two habitats, Fucheng and Gaoqiao, and boxplots (t -test analyzed the result as “ p_2 ”) between habitats. The boxplot shows the median (solid thick line), 25th and 75th quantiles (box), and minimum and maximum values excluding outliers (whiskers); the solid dots represent the trophic levels for the corresponding season. Statistically significant effects are indicated in bold “ p ” ($\alpha = 0.05$).

TABLE 3: Ecological niche metrics and corrected standard ellipse area of *Mugil cephalus*.

Habitat	Season	SEA	SEAc	TA	NR	CR	CD	MNND	SDNND
Fucheng	Spring	4.886	5.157	14.309	3.980	6.422	1.660	0.673	0.543
	Summer	10.564	11.885	18.937	2.684	12.414	4.158	0.948	1.389
	Autumn	4.447	5.002	8.756	4.481	4.999	1.694	0.834	0.564
	Winter	3.122	3.330	7.147	3.640	5.675	1.634	0.442	0.319
Gaoqiao	Spring	10.680	12.015	20.367	4.085	6.385	2.476	1.191	0.885
	Summer	3.957	4.616	6.155	1.739	7.345	1.795	1.098	1.165
	Autumn	10.855	11.689	29.574	4.894	9.701	2.576	1.196	0.851
	Winter	5.605	6.036	15.230	3.275	9.938	1.804	0.797	1.173

Note: SEAc, corrected standard ellipse area; TA, total area encompassing all individual measurements, NR, $\delta^{15}\text{N}$ range; CR, $\delta^{13}\text{C}$ range; CD, mean distance to centroid.

Abbreviations: MNND, mean nearest neighbor distance; SDNND, standard deviation of the nearest neighbor distance; SEA, standard ellipse area.

M. cephalus, implying variations in resource utilization between the two studied locations. Specifically, the FC population exhibited lower isotopic diversity than that by the GQ population, as evidenced by the smaller niche space occupied by FC, indicating a narrowed range of food sources. This observation aligns with the concept of niche redundancy, signifying a higher similarity among individuals in trophic behavior within FC than within GQ. Because of the higher population density in FC than in GQ

and the known school-feeding tendencies of juvenile mullets [41], we can reasonably anticipate increased intraspecific competition within this location. In the literature, resource competition was thought to drive niche diversification among individuals within a population, often resulting in specialization due to intraspecific competition [42, 43]. However, despite higher intraspecific competition levels, our findings deviate from this expectation, revealing reduced niche variation among individuals. This discrepancy may

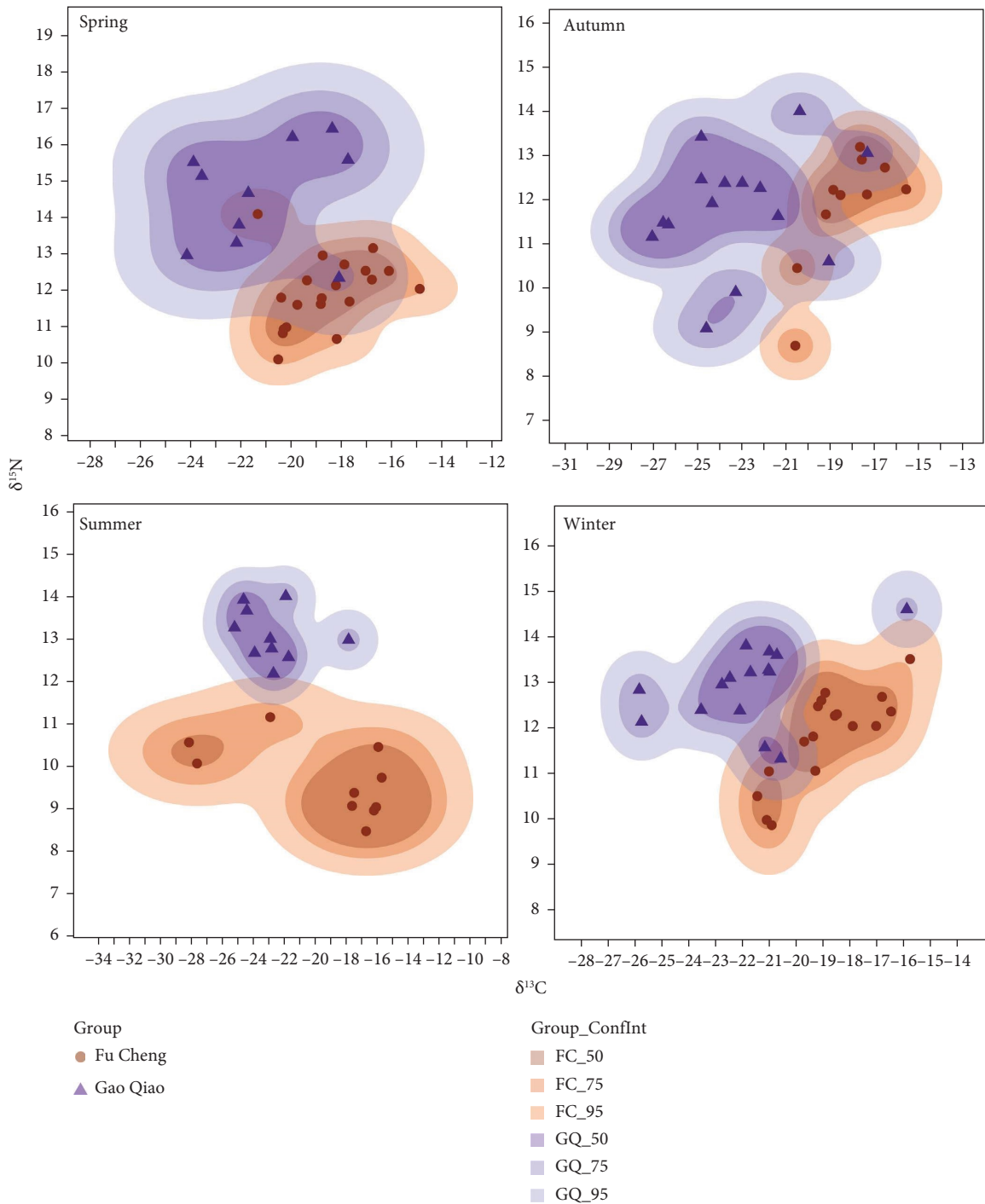


FIGURE 4: Isotopic homing areas based on isotopic coordinates of *Mugil cephalus* among four seasons between two habitats and according to kernel utilization density (KUD). The four seasons are spring, summer, autumn, and winter; the two habitats are Fucheng and Gaoqiao. Dark, intermediate, and light colors represent the percentage of data used for the estimations (50%, 75%, and 95%, respectively).

stem from the feeding habits of juvenile *M. cephalus*, which predominantly engage in benthic foraging, primarily subsisting on detritus, including particulate organic matter, and benthic microalgae such as diatoms [26]. We postulate that this feeding habitat may restrict the broadening of individual niches in juvenile *M. cephalus*. Additionally, tidal rhythms can influence ecological opportunities such as the accessibility of exploitable resources [44], and irregular semi-

diurnal tides can limit certain types of available habitats due to frequent tidal surges [45], potentially favoring larger-bodied individuals of juvenile *M. cephalus* with demersal foraging habits in the FC.

Juvenile *M. cephalus* displays trophic plasticity, demonstrating the ability to adapt their trophic niche to varying resources in heterogeneous environments. We found no overlap in 50% of the core regions of the occupied niche space

between the two mangrove species, indicating substantial differences in resource utilization. These distinctions are probably attributable to variations in prey richness and abundance [46], influenced by environmental factors such as tidal regimes, salinity fluctuations, and the composition of mangrove tree communities [47]. This feeding flexibility capacity was further supported by the partial separation observed in 95% of the total area of the trophic space. Trophic plasticity, which reflects the ability of fish species to adapt their diets according to the availability of local resources, is a well-documented phenomenon (e.g., [48]). However, this concept was not extensively explored in the context of the juvenile life stages of mangrove fish. The FC population exhibited a higher IPI than that by the GQ population, indicating that the former possesses greater trophic plasticity than by the latter, allowing the former to effectively utilize fluctuating food resources, particularly in mangroves characterized by irregular semi-diurnal tidal rhythms. Furthermore, our prior research identified an ontogenetic decline in the IPI from juveniles to subadults, which is probably associated with a dietary shift toward increased specialization during ontogeny [20]. In addition to the findings of this study and other related research [37], the IPI has emerged as a robust, practical metric for quantifying trophic plasticity with potential applications at the community scale.

The fish condition index serves as a reliable indicator of the energy status and physical condition of fish, encompassing crucial aspects of their performance, including growth, reproduction, and swimming ability [49–51]. This index is intricately linked to individual food availability, which is contingent upon competition among individuals, considering both the number of individuals and their capacity for food assimilation [51]. In our investigation, we observed a larger population of juvenile fish, denoted by an increased density, coexisting with limited food availability and potentially constrained by irregular semi-diurnal tide characteristics. This scenario probably results in reduced food availability per individual, leading to diminished energy reserves and a density-dependent decline in the condition index [52, 53]. This pattern aligns with observations in food-limited environments, where intraspecific competition for resources prevails, underscoring our findings of a lower condition index in the FC population than in the GQ population. Haberle et al. [51] effectively employed composite modeling to establish a connection between the condition of an individual, represented by the condition index, and the status of the entire population. Their work indicated that the condition index offers insights into stock size relative to environmental carrying capacity. Specifically, a low condition index signifies a population size near or exceeding the carrying capacity of the environment, and a high condition index indicates an overfishing stock. Therefore, we propose that the population of juvenile *M. cephalus* in the FC may have reached the carrying capacity of its habitat, implying a relatively high nursery value.

This work advances our understanding of the role of trophic niche plasticity in shaping the performance of juvenile fish in mangrove habitats. It provides valuable insights into the ecological mechanisms operating within

these complex ecosystems. Furthermore, the implications for conservation initiatives underscore the practical relevance of this research, highlighting the importance of considering trophic dynamics in the design and management of protected areas. Other researchers can leverage the information presented in this paper to further explore trophic interactions and niche dynamics in mangrove ecosystems. They could replicate the study design in different geographical locations in China (or elsewhere) or investigate similar questions in other fish species to assess the broader implications of the findings. Additionally, the methodological approaches employed in this study, such as population density estimation and body condition assessment, could serve as valuable tools for researchers studying fish ecology and conservation in diverse aquatic habitats [54].

Data Availability Statement

All data included in this study are available upon request by contacting the corresponding author.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

Fengming Liu and Xiaodong Yang conceived the idea, analyzed the data, and wrote the draft of the manuscript; Zhuoxin Sun, Lingwei Kong, Junhao Li, and Yanping Zheng helped in stable isotope testing and specimen collection; Yunrong Yan and Jiao Qin provided substantial intellectual input by refining the research framework and methodology.

Funding

This work was supported by Southern Marine Science and Engineering Guangdong Laboratory (Zhanjiang) (013S22003), Guang Dong Basic and Applied Basic Research Foundation (2023A1515010580), Zhan Jiang Science and Technology Program (2022E05015), and Project of Young Innovative Talents in General Universities of Guangdong Province (2022KQNCX025).

Acknowledgments

This work was supported by two grants from Southern Marine Science and Engineering Guangdong Laboratory (Zhanjiang) (013S22003), Guang Dong Basic and Applied Basic Research Foundation (2023A1515010580), Zhan Jiang Science and Technology Program (2022E05015), and Project of Young Innovative Talents in General Universities of Guangdong Province (2022KQNCX025). We sincerely appreciate Editage for their language editing and formatting services for the manuscript.

References

- [1] S. Bearhop, C. E. Adams, S. Waldron, R. A. Fuller, and H. Macleod, "Determining Trophic Niche Width: A Novel

- Approach Using Stable Isotope Analysis,” *Journal of Animal Ecology* 73, no. 5 (2004): 1007–1012, <https://doi.org/10.1111/j.0021-8790.2004.00861.x>.
- [2] R. N. Gibson, R. J. A. Atkinson, and J. D. M. Gordon, eds., “An Evaluation of the Evidence for Linkages Between Mangroves and Fisheries: A Synthesis of the Literature and Identification of Research Directions,” in *Oceanography and Marine Biology* (CRC Press, 2005), 493–524, <https://doi.org/10.1201/9781420037449-12>.
 - [3] M. Sheaves, “How Many Fish Use Mangroves? The 75% Rule an Ill-Defined and Poorly Validated Concept,” *Fish and Fisheries* 18, no. 4 (2017): 778–789, <https://doi.org/10.1111/faf.12213>.
 - [4] Wetlands International, *The State of the World’s Mangroves 2022* (Wetlands International, 2023), <https://www.wetlands.org/publications/the-state-of-the-worlds-mangroves-2022/>.
 - [5] C. E. Lovelock, D. R. Cahoon, D. A. Friess, et al., “The vulnerability of Indo-Pacific mangrove Forests to Sea-Level Rise,” *Nature* 526, no. 7574 (2015): 559–563, <https://doi.org/10.1038/nature15538>.
 - [6] C. Kuenzer, A. Bluemel, S. Gebhardt, T. V. Quoc, and S. Dech, “Remote Sensing of Mangrove Ecosystems: A Review,” *Remote Sensing* 3, no. 5 (2011): 878–928, <https://doi.org/10.3390/rs3050878>.
 - [7] E. L. Gilman, J. Ellison, N. C. Duke, and C. Field, “Threats to Mangroves From Climate Change and Adaptation Options: A Review,” *Aquatic Botany* 89, no. 2 (2008): 237–250, <https://doi.org/10.1016/j.aquabot.2007.12.009>.
 - [8] K. van de Wolfshaar, U. Daewel, S. Hjøllø, et al., “Sensitivity of the Fish Community to Different Prey Fields and Importance of Spatial-Seasonal Patterns,” *Marine Ecology Progress Series* 680 (2021): 79–95, <https://doi.org/10.3354/meps13885>.
 - [9] S. Kanno, A. Schlaff, M. Heupel, and C. Simpfendorfer, “Stationary Video Monitoring Reveals Habitat Use of Stingrays in Mangroves,” *Marine Ecology Progress Series* 621 (2019): 155–168, <https://doi.org/10.3354/meps12977>.
 - [10] S. D. Goecke and S. M. Carstenn, “Fish Communities and Juvenile Habitat Associated With Non-Native *Rhizophora mangle* L. in Hawai’i,” *Hydrobiologia* 803, no. 1 (2017): 209–224, <https://doi.org/10.1007/s10750-017-3182-7>.
 - [11] B. Blonder, “Hypervolume Concepts in Niche- and Trait-Based Ecology,” *Ecography* 41, no. 9 (2018): 1441–1455, <https://doi.org/10.1111/ecog.03187>.
 - [12] M. Hernandez, S. Midway, L. West, H. Tillya, and M. Polito, “Stable Isotopes Track the Ontogenetic Movement of three Commercially Important Fishes Along a Coastal Tanzanian Seascape,” *Marine Ecology Progress Series* 670 (2021): 139–154, <https://doi.org/10.3354/meps13754>.
 - [13] L. A. Sandoval, J. Leal-Flórez, J. F. Blanco-Libreros, J. E. Mancera-Pineda, A. Delgado-Huertas, and C. J. Polo-Silva, “Stable-Isotope Analysis Reveals Sources of Organic Matter and Ontogenic Feeding Shifts of a Mangrove-Dependent Predator Species, New Granada Sea Catfish, *Ariopsis canteri*,” *Journal of Fish Biology* 97, no. 2 (2020): 499–507, <https://doi.org/10.1111/jfb.14404>.
 - [14] C. Berkström, T. Jörgensen, and M. Hellström, “Ecological Connectivity and Niche Differentiation Between Two Closely Related Fish Species in the Mangrove-Seagrass-Coral Reef Continuum,” *Marine Ecology Progress Series* 477 (2013): 201–215, <https://doi.org/10.3354/meps10171>.
 - [15] L. E. Stuthmann, G. A. Castellanos-Galindo, and D. R. Robertson, “The Functional Ecology of Mangrove Fishes Across the Isthmus of Panama,” *Diversity and Distributions* 28, no. 8 (2022): 1663–1679, <https://doi.org/10.1111/ddi.13519>.
 - [16] N. D. Rayl, G. Bastille-Rousseau, J. F. Organ, et al., “Spatiotemporal Heterogeneity in Prey Abundance and Vulnerability Shapes the Foraging Tactics of an Omnivore,” *Journal of Animal Ecology* 87, no. 3 (2018): 874–887, <https://doi.org/10.1111/1365-2656.12810>.
 - [17] C.-A. Timmerman, C. Giraldo, P. Cresson, et al., “Plasticity of Trophic Interactions in Fish Assemblages Results in Temporal Stability of Benthic-Pelagic Couplings,” *Marine Environmental Research* 170 (2021): 105412, <https://doi.org/10.1016/j.marenvres.2021.105412>.
 - [18] D. J. McLeod, A. J. Hobday, J. M. Lyle, and D. C. Welsford, “A Prey-Related Shift in the Abundance of Small Pelagic Fish in Eastern Tasmania?” *ICES Journal of Marine Science* 69, no. 6 (2012): 953–960, <https://doi.org/10.1093/icesjms/fss069>.
 - [19] A. K. Whitfield, K. W. Able, S. J. Blaber, et al., “Feeding Ecology and Trophic Dynamics,” *Fish and Fisheries in Estuaries* 1 (2022): 255–331, <https://doi.org/10.1002/9781119705345.ch5>.
 - [20] Q. Jiao, L. Fengming, B. V. Schmidt, S. Zhuoxin, K. Lingwei, and Y. Yunrong, “Interpopulation Trophic Niches and Ontogenetic Shifts of a Mangrove Fish Predator,” *Journal of Fish Biology* (2022): 1–9, <https://doi.org/10.1111/jfb.15219>.
 - [21] F. S. Scharf and K. K. Schlicht, “Feeding Habits of Red Drum (*Sciaenops ocellatus*) in Galveston Bay, Texas: Seasonal Diet Variation and Predator-Prey Size Relationships,” *Estuaries* 23, no. 1 (2000): 128, <https://doi.org/10.2307/1353230>.
 - [22] P. W. Kelly, D. W. Pfennig, and K. S. Pfennig, “Adaptive Plasticity as a Fitness Benefit of Mate Choice,” *Trends in Ecology & Evolution* 36, no. 4 (2021): 294–307, <https://doi.org/10.1016/j.tree.2021.01.001>.
 - [23] J. C. Briggs, “Fishes of Worldwide (Circumtropical) Distribution,” *Copeia* 1960, no. 3 (1960): 171, <https://doi.org/10.2307/1439652>.
 - [24] A. K. Whitfield, J. Panfili, and J.-D. Durand, “A Global Review of the Cosmopolitan Flathead Mullet *Mugil cephalus* Linnaeus 1758 (Teleostei: Mugilidae), With Emphasis on the Biology, Genetics, Ecology and Fisheries aspects of this Apparent Species Complex,” *Reviews in Fish Biology and Fisheries* 22, no. 3 (2012): 641–681, <https://doi.org/10.1007/s11160-012-9263-9>.
 - [25] N. A. Strydom and B. D. d’Hotman, “Estuary-Dependence of Larval Fishes in a Non-Estuary Associated South African Surf Zone: Evidence for Continuity of Surf Assemblages,” *Estuarine, Coastal and Shelf Science* 63, no. 1–2 (2005): 101–108, <https://doi.org/10.1016/j.ecss.2004.10.013>.
 - [26] E. Lawson and A. Jimoh, “Aspects of the Biology of Grey Mullet, *Mugil cephalus*, in Lagos Lagoon, Nigeria,” *Aacl Bioflux* (2010).
 - [27] G. Katselis, C. Koutsikopoulos, E. Dimitriou, and Y. Rogdakis, “Spatial Patterns and Temporal Trends in the Fisheries Landings of the Messolonghi-Etoliko Lagoons (Western Greek Coast),” *Scientia Marina* 67, no. 4 (2003): 501–511, <https://doi.org/10.3989/scimar.2003.67n4501>.
 - [28] L. Chaoui, H. Kara, É. Faure, and Q. Jean-pierre, “The Fish Fauna of Mellah Lagoon (North-East Algeria): Diversity, Production and Commercial Catches Analysis,” *Cybiium* 30 (2006): 123–132.
 - [29] M. Lang Dos Santos, V. M. Lemos, and J. P. Vieira, “No Mullet, No Gain: Cooperation Between Dolphins and Cast Net Fishermen in Southern Brazil,” *Zoologia* 35 (2018): 1–13, <https://doi.org/10.3897/zoologia.35.e24446>.

- [30] Q. Chen, G. Xu, Z. Wu, et al., "The Effects of Winter Temperature and Land Use on Mangrove Avian Species Richness and Abundance on Leizhou Peninsula, China," *Wetlands* 40, no. 1 (2020): 153–166, <https://doi.org/10.1007/s13157-019-01159-6>.
- [31] W. Xiong, D. Xie, G. Chen, and D. He, "Freshwater Fish Biodiversity in the Leizhou Peninsula of China," *Aquatic Ecosystem Health and Management* 22, no. 2 (2019): 160–170, <https://doi.org/10.1080/14634988.2019.1632666>.
- [32] T. G. Lun, G. Wei, M. Jing, Z. J. Mao, and B. L. Weng, "Carbon Storage and Influence Factors of Major Mangrove Communities in Fucheng, Leizhou Peninsula, Guangdong Province," *Ecology and Environmental Sciences* 26, no. 6 (2017): 985–990, <https://doi.org/10.16258/j.cnki.1674-5906.2017.06.011>.
- [33] Z. Zhu Yaojun, Z. Zhao Feng, G. Guo Julan, W. Wu Gaojie, and L. Lin Guangxuan, "Below-Ground Organic Carbon Distribution and Burial Characteristics of the Gaoqiao Mangrove Area in Zhanjiang, Guangdong, Southern China," *Acta Ecologica Sinica* 36, no. 23 (2016): 7841–7849, <https://doi.org/10.5846/stxb201511102276>.
- [34] A. Mozsar, G. Boros, P. Saly, L. Antal, and S. A. Nagy, "Relationship Between Fulton's Condition Factor and Proximate Body Composition in Three Freshwater Fish Species," *Journal of Applied Ichthyology* 31, no. 2 (2015): 315–320, <https://doi.org/10.1111/jai.12658>.
- [35] D. M. Post, "Using Stable Isotopes to Estimate Trophic Position: Models, Methods, And Assumptions," *Ecology* 83, no. 3 (2002): 703–718, [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2).
- [36] J. Oksanen, G. L. Simpson, F. G. Blanchet, et al., "Vegan: Community ecology package [Manual]," (2022), <https://CRAN.R-project.org/package=vegan>.
- [37] P. J. Haubrock, P. Balzani, S.-I. S. Matsuzaki, A. S. Tarkan, M. Kourantidou, and P. Haase, "Spatio-Temporal Niche Plasticity of a Freshwater Invader as a Harbinger of Impact Variability," *Science of the Total Environment* 777 (2021): 145947, <https://doi.org/10.1016/j.scitotenv.2021.145947>.
- [38] A. L. Jackson, R. Inger, A. C. Parnell, and S. Bearhop, "Comparing Isotopic Niche Widths Among and Within Communities: SIBER-Stable Isotope Bayesian Ellipses in R: Bayesian Isotopic Niche Metrics," *Journal of Animal Ecology* 80, no. 3 (2011): 595–602, <https://doi.org/10.1111/j.1365-2656.2011.01806.x>.
- [39] C. A. Eckrich, S. Albeke, E. Flaherty, R. T. Bowyer, and M. Ben-David, "rKIN: Kernel-Based Method for Estimating Isotopic Niche Size and Overlap," *Journal of Animal Ecology* 89, no. 3 (2020): 757–771, <https://doi.org/10.1111/1365-2656.13159>.
- [40] J. Cucherousset and S. Villéger, "Quantifying the Multiple Facets of Isotopic Diversity: New Metrics for Stable Isotope Ecology," *Ecological Indicators* 56 (2015): 152–160, <https://doi.org/10.1016/j.ecolind.2015.03.032>.
- [41] Wallace, "The Estuarine Fishes of the East Coast of South Africa. I. Species Composition and Length Distribution in the Estuarine and Marine Environments. II. Seasonal Abundance and Migrations," *Investigational Report series of the Oceanographic Research Institute* 40 (1975): 1–72.
- [42] R. Costa-Pereira, M. S. Araújo, F. L. Souza, and T. Ingram, "Competition and resource Breadth Shape Niche Variation and Overlap in Multiple Trophic Dimensions," *Proceedings of the Royal Society B: Biological Sciences* 286, no. 1902 (2019): 20190369, <https://doi.org/10.1098/rspb.2019.0369>.
- [43] A. Mendes, I. M. Fernandes, J. Penha, and L. Mateus, "Intra and Not Interspecific Competition Drives Intra-Population Variation in Resource Use by a Neotropical Fish Species," *Environmental Biology of Fishes* 102, no. 8 (2019): 1097–1105, <https://doi.org/10.1007/s10641-019-00892-5>.
- [44] G. A. Castellanos-Galindo and U. Krumme, "Tides, Salinity, and Biogeography Affect Fish Assemblage Structure and Function in Macrotidal Mangroves of the Neotropics," *Ecosystems* 18, no. 7 (2015): 1165–1178, <https://doi.org/10.1007/s10021-015-9887-4>.
- [45] C. Elston, P. D. Cowley, R. G. Von Brandis, and J. Lea, "Stingray Habitat Use Is Dynamically Influenced by Temperature and Tides," *Frontiers in Marine Science* 8 (2022): 754404, <https://doi.org/10.3389/fmars.2021.754404>.
- [46] S. R. Vollrath, B. Possamai, F. Schneck, D. J. Hoeinghaus, E. F. Albertoni, and A. M. Garcia, "Trophic Niches and Diet Shifts of Juvenile Mullet Species Coexisting in Marine and Estuarine Habitats," *Journal of the Marine Biological Association of the United Kingdom* 101, no. 2 (2021): 431–441, <https://doi.org/10.1017/S0025315421000242>.
- [47] I. Nagelkerken, S. J. M. Blaber, S. Bouillon, et al., "The Habitat Function of Mangroves for Terrestrial and Marine Fauna: A Review," *Aquatic Botany* 89, no. 2 (2008): 155–185, <https://doi.org/10.1016/j.aquabot.2007.12.007>.
- [48] T. Pool, G. Holtgrieve, V. Elliott, et al., "Seasonal Increases in Fish Trophic Niche Plasticity Within a Flood-Pulse River Ecosystem (Tonle Sap Lake, Cambodia)," *Ecosphere* 8, no. 7 (2017): e01881, <https://doi.org/10.1002/ecs2.1881>.
- [49] R. W. Schloesser and M. C. Fabrizio, "Condition Indices as Surrogates of Energy Density and Lipid Content in Juveniles of Three Fish Species," *Transactions of the American Fisheries Society* 146, no. 5 (2017): 1058–1069, <https://doi.org/10.1080/00028487.2017.1324523>.
- [50] L. Bavčević, S. Petrović, V. Karamarko, U. Luzzana, and T. Klanjšček, "Estimating Fish Energy Content and Gain From Length and Wet Weight," *Ecological Modelling* 436 (2020): 109280, <https://doi.org/10.1016/j.ecolmodel.2020.109280>.
- [51] I. Haberle, L. Bavčević, and T. Klanjšček, "Fish Condition as an Indicator of Stock Status: Insights From Condition Index in a Food-Limiting Environment," *Fish and Fisheries* 24, no. 4 (2023): 567–581, <https://doi.org/10.1111/faf.12744>.
- [52] C. R. E. Hazlerigg, K. Lorenzen, P. Thorbek, J. R. Wheeler, and C. R. Tyler, "Density-Dependent Processes in the Life History of Fishes: Evidence From Laboratory Populations of Zebrafish *Danio rerio*," *PLoS One* 7, no. 5 (2012): e37550, <https://doi.org/10.1371/journal.pone.0037550>.
- [53] S. A. L. M. Kooijman, "The standard Dynamic Energy Budget Model has No Plausible Alternatives," *Ecological Modelling* 428 (2020): 109106, <https://doi.org/10.1016/j.ecolmodel.2020.109106>.
- [54] A. Adite, A. Gbankoto, I. I. Toko, and E. D. Fiogbe, "Diet Breadth Variation and Trophic Plasticity Behavior of the African bonytongue *Heterotis niloticus* (Cuvier, 1829) in the Sô River-Lake Hlan Aquatic System (Benin, West Africa): Implications for Species Conservation and aquaculture Development," *Natural Science* 05, no. 12 (2013): 1219–1229, <https://doi.org/10.4236/ns.2013.512149>.