

# Functional digestive morphology and feeding intensity of the halfbeak *Zenarchopterus clarus* (Hemiramphidae) in a tropical estuarine habitats, southern Vietnam

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**ABSTRACT.** This study examines the functional digestive morphology and feeding intensity of the halfbeak *Zenarchopterus clarus* (Hemiramphidae) in a tropical estuarine habitats of southern Vietnam. A total of 892 specimens were collected monthly from August 2024 to July 2025 at two estuarine sites. The species exhibited a superior mouth with an elongated lower jaw, dense conical dentition, well-developed pharyngeal tooth plates, and numerous gill rakers. The digestive tract consisted of a muscular esophagus and a short intestine, lacking a clearly differentiated stomach, indicating rapid processing of soft prey. Feeding intensity was evaluated using the gut-somatic index (GI) and analyzed with generalized linear mixed models. The model indicated significant variation in GI ( $p < 0.001$ ). The GI differed significantly between sexes and sampling locations, with higher values in females and at Dam Doi. Although the season had no significant main effect, a significant sex  $\times$  season interaction indicated contrasting seasonal feeding patterns between males and females. Morphological traits and GI collectively suggest that *Z. clarus* is adapted for surface-oriented feeding on small, mobile prey in dynamic estuarine environments. However, the feeding strategy was inferred from morphological traits and GI, as diet composition was not directly examined. These findings provide baseline insights into the digestive morphology and feeding ecology of an estuarine hemiramphid fish.

**Keywords:** digestive morphology, feeding intensity, gut-somatic index, Hemiramphidae, *Zenarchopterus clarus*

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## 1. Introduction

Digestive tract morphology is a key determinant of feeding strategy and trophic adaptation in fishes, particularly in environmentally dynamic systems such as estuaries. Estuarine ecosystems are characterized by high environmental variability, supporting diverse fish assemblages and complex trophic interactions (Dien, 2024; Nguyen et al., 2024). Within these systems, feeding strategy and digestive morphology play crucial roles in determining trophic performance and energy allocation. Structural features of the digestive tract, including mouth orientation, dentition, gill rakers, and intestinal configuration, are closely associated with dietary habits and feeding mechanisms in teleost fishes (Nikolsky, 1963; Berkovitz and Shellis, 2023). Moreover, variation in digestive morphology often reflects ecological adaptation to specific feeding niches (Amundsen et al., 2004; Day et al., 2011).

The family Hemiramphidae comprises surface-oriented fishes widely distributed in tropical and subtropical coastal and estuarine waters (Talwar and Jhingran, 1991; More et al., 2022). Many species within this family exhibit characteristic morphological adaptations, including an elongated lower jaw and specialized dentition associated with surface feeding. Previous studies have described digestive morphology and feeding traits in several hemiramphid species, including *Hyporhamphus limbatus* (Nguyen et al., 2025) and related taxa (Tibbetts and Carseldine, 2003; Buddery et al., 2009), demonstrating considerable interspecific variation linked to trophic specialization. However, detailed functional information integrating digestive morphology and feeding intensity remains limited for many regional species.

*Zenarchopterus clarus* (Mohr, 1926) is a common halfbeak species inhabiting brackish and estuarine waters of the Mekong Delta, Vietnam (Nguyen, 2005;

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Tran et al., 2013). Despite its frequent occurrence in coastal ecosystems, detailed descriptions of its digestive tract morphology and quantitative assessments of feeding intensity remain lacking. Feeding intensity in fishes can be estimated using somatic indices, such as the gut-somatic index (GI), which reflects the relative development of digestive organs in relation to body weight and provides insight into energy allocation and feeding activity (Desai, 1970; Egerton et al., 2018). Differences in feeding intensity between sexes and seasons have been documented in several fish species and are often associated with reproductive investment and environmental variation (Gebremedhin and Mingist, 2014; Hua et al., 2023).

To date, no study has examined simultaneously digestive tract morphology and seasonal variation in the GI in *Z. clarus* from the Mekong Delta. Therefore, this study aims to: (i) describe the functional digestive tract morphology of *Z. clarus* in relation to feeding strategy, and (ii) evaluate the effects of sex, season, and sampling location on GI using generalized linear mixed models. By integrating morphological descriptions with quantitative analysis, this study provides functional insights into trophic adaptation and feeding ecology of *Z. clarus* in estuarine environments.

## 2. Materials and Methods

### *Study area and sample collection*

Specimens of *Z. clarus* were collected monthly from August 2024 to July 2025 at two estuarine locations in Ca Mau Province, southern Vietnam: Vinh Phuoc (VP; 9°26'47.8"N, 105°27'03.4"E) and Dam Doi (DD; 9°05'00.0"N, 105°09'00.0"E) (Fig. 1). These sites

represent brackish-water habitats within the Mekong Delta estuarine system and differ in local hydrological conditions. Tidal processes and freshwater input influence both Dam Doi and Vinh Phuoc; however, spatial variation in water exchange, sediment characteristics, and local hydrodynamics may result in differences in turbidity, nutrient availability, and prey distribution between sites. These environmental variations are expected to influence feeding conditions and digestive traits in *Z. clarus*.

Fish were captured using hand nets (mesh size 1.0 cm) during late afternoon, when individuals were less active. Immediately after capture, specimens were euthanized following approved ethical procedures of Can Tho University (CTU–AEC25025) using tricaine methanesulfonate (10 g/L). All samples were fixed in 4% formaldehyde and transported to the laboratory for analysis. Species identification and sex determination were performed as described by Tran et al. (2013). A total of 892 individuals were examined. Specimens were collected consistently across months and sites to ensure representative sampling coverage.

### *Morphological examination*

Total body weight ( $W$ ,  $\pm 0.01$  g) was recorded prior to dissection using an electronic balance (AND EK-610). Morphometric measurements included lower jaw length (LJ,  $\pm 0.01$  cm), upper jaw length (UJ,  $\pm 0.01$  cm), and mouth width between corners (AB,  $\pm 0.01$  mm). Measurements were taken using digital calipers (MOORMAN-110-15DP) and a measuring ruler (TPS-R021). Mouth diameter (MD) was calculated following Shirota (1970):  $MD = AB \times \sqrt{2}$ , where AB represents the linear mouth width measured as the distance between the left and right mouth corners (mm).

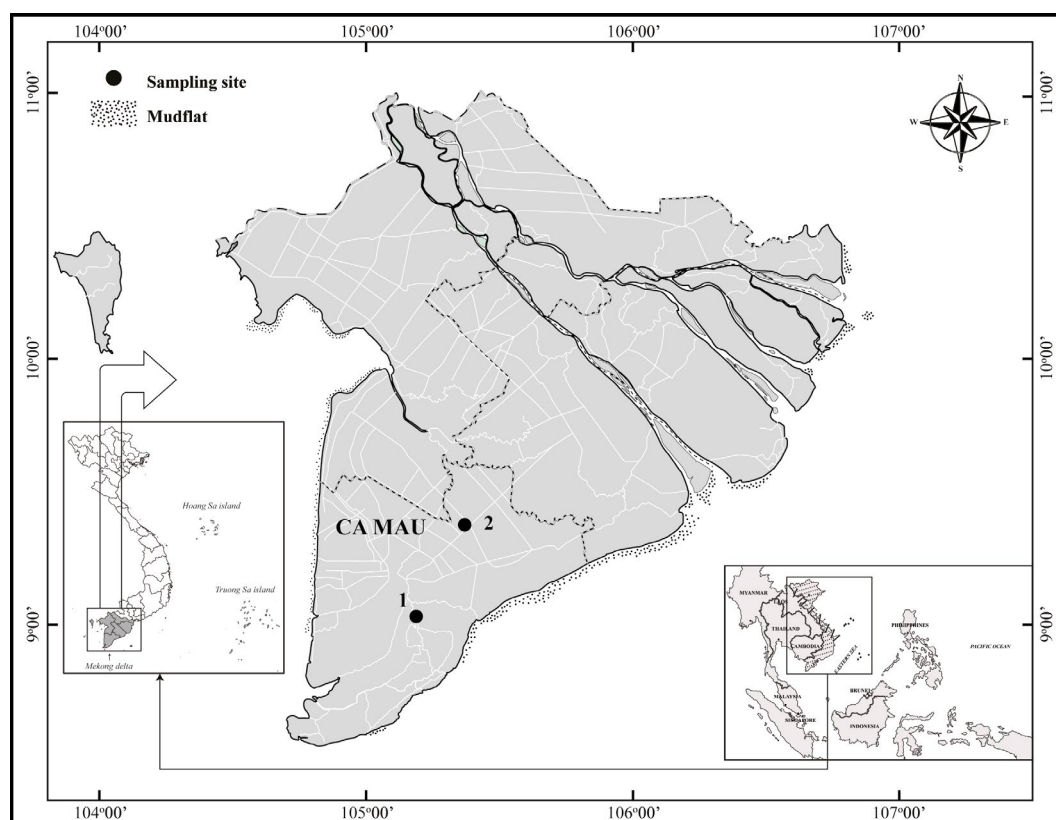


Fig.1. Map of sampling sites in Ca Mau Province, Vietnam (1: Dam Doi; 2: Vinh Phuoc; modified from Dinh (2018)).

The digestive tract was dissected and examined under a stereomicroscope (Motic DM143). Detailed images of dentition were obtained using an Olympus CX41 microscope equipped with a digital camera (Olympus U-CMAD3). The following structures were observed and described: mouth, dentition, tongue, gill arches, esophagus, and intestine. Digestive morphology was described following standard ichthyological criteria outlined by Nikolsky (1963).

Gill rakers and gill filaments were counted on each gill arch. Pharyngeal teeth were examined and quantified. Intestinal configuration was recorded to determine the presence or absence of stomach differentiation. Gill raker and pharyngeal tooth counts were recorded from a randomly selected subsample of 67 specimens. These measurements were conducted as an additional post hoc analysis; therefore, metadata on sex and sampling site were not retained for this subsample.

#### Gut-somatic index

Feeding intensity was assessed using the gut-somatic index (GI), calculated according to Desai (1970):  $GI = (Wg / W) \times 100$ , where *Wg* is intestinal weight (g), and *W* is total body weight (g). GI was used as a proxy for relative digestive development and feeding intensity.

#### Statistical analysis

All statistical analyses were performed using Jamovi version 2.6.44 with the GAMLj module (The jamovi project, 2024). To evaluate variation in MD, a generalized linear mixed model (GLMM) with a Gamma error distribution and log link function was applied, with sex as a fixed effect and month as a random intercept. The GI, a continuous positive variable, was analyzed using a similar GLMM framework. Fixed effects included sex (male, female), season (dry, wet), and location (VP, DD), along with their two-way and three-way interactions. The month was included as a random intercept to account for temporal variation and repeated monthly sampling. Estimated marginal means (EMMs) were calculated on the response scale, and pairwise comparisons were conducted using Tukey-adjusted tests. Statistical significance was set at  $p < 0.05$ . Model assumptions and goodness-of-fit were evaluated using residual diagnostics and model fit indices.

### 3. Results

#### Digestive tract morphology

The mouth of *Z. clarus* was superior, with the

upper jaw approximately one-quarter the length of the elongated lower jaw (Fig. 2A–B). The upper jaw was flattened and triangular, whereas the lower jaw was pointed and projected upward. Mean lower jaw length was  $3.39 \pm 0.01$  cm (SE). GLMM analysis revealed a significant difference in MD between sexes ( $\chi^2 = 14.07$ ;  $df = 1$ ;  $p < 0.001$ ). Estimated marginal means indicated that males exhibited larger MD values than females ( $8.54 \pm 0.57$  mm (SE) vs.  $8.12 \pm 0.55$  mm (SE)). MD did not vary significantly among months, seasons, or sampling locations ( $p > 0.05$ ).

Teeth were small, conical, and densely distributed on both upper and lower jaws (Fig. 3A–D). Teeth were elongated, with pointed tips and broad bases firmly attached to the jaw margins. In the upper jaw, tooth size increased from the inner to the outer margin (Fig. 3A–B). In the lower jaw, teeth were sparser near the mouth edge and denser toward the inner region (Fig. 3C). High-magnification images revealed pointed tooth tips and dense packing along the jaw margins (Fig. 3D). Tooth density on the outer jaw surface averaged  $25 \pm 0.6$  (17–39) N/mm<sup>2</sup> in the upper jaw and  $22 \pm 0.4$  (14–32) N/mm<sup>2</sup> in the lower jaw. Inner tooth density averaged  $24 \pm 0.5$  (15–33) N/mm<sup>2</sup> in the upper jaw and  $24 \pm 0.6$  (16–39) N/mm<sup>2</sup> in the lower jaw. The lower pharyngeal tooth plate (LPT) was triangular with rounded lateral margins and a blunt anterior apex, whereas the upper pharyngeal tooth plate (UPT) exhibited a three-lobed triangular structure (Fig. 4A–B). Both plates were covered with densely packed conical teeth. Mean counts of pharyngeal teeth were  $88 \pm 1.7$  (54–120) in the upper plate and  $131 \pm 2.4$  (84–162) in the lower plate.

The tongue was poorly developed and firmly attached to the floor of the buccal cavity (Fig. 5). The anterior region exhibited a rough texture, gradually becoming smoother toward the posterior region. This reduced development suggests a limited role in food manipulation, consistent with a feeding strategy that relies primarily on jaw and dentition for prey capture.

Four pairs of gill arches were observed (Fig. 6A–B). Each arch bore two rows of gill filaments and one row of gill rakers. Gill rakers on the first arch were longer and larger than those on subsequent arches (Fig. 6C–D). The arrangement of filaments and rakers is further illustrated in the transverse section of the gill arch (Fig. 6E). Mean gill raker counts were  $118 \pm 1.0$  (97–148) for the first arch,  $109 \pm 2.0$  (88–142) for the second arch,  $96 \pm 2.0$  (70–136) for the third arch, and

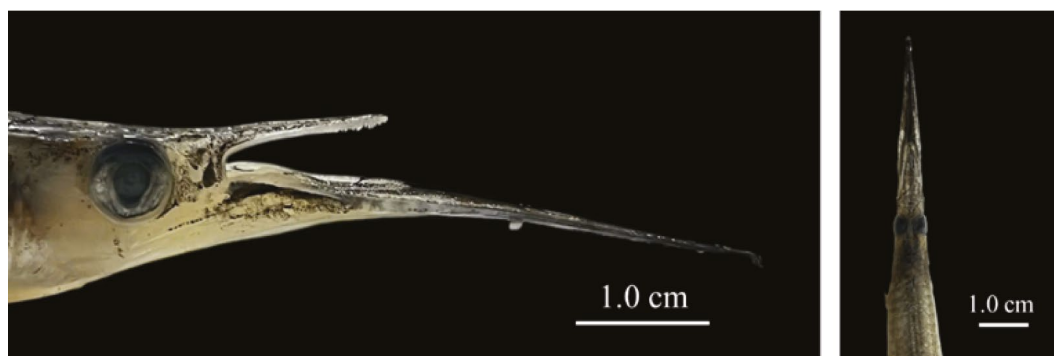
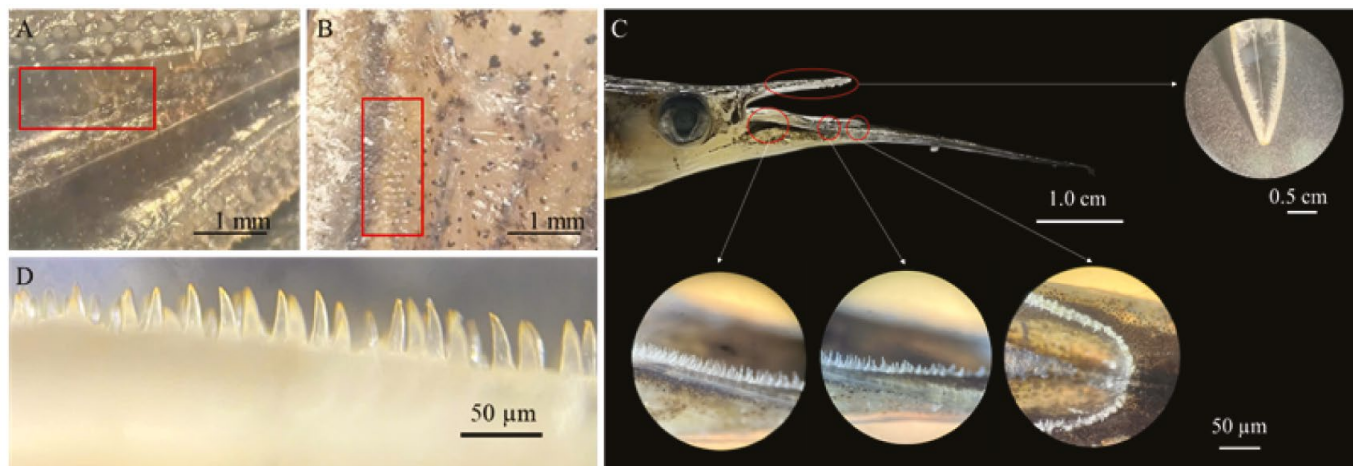


Fig.2. Mouth morphology of *Zenarchopterus clarus* (A: lateral view; B: dorsal view).



**Fig.3.** Dentition of *Zenarchopterus clarus* (Inner teeth: A: upper jaw, B: lower jaw; C: distribution pattern of teeth on the jaws; D: morphology of the upper jaw teeth).

79 ± 2.0 (68–114) for the fourth arch. Mean numbers of gill filaments were 14 ± 1.0 (7–22), 14 ± 1.0 (11–23), 13 ± 1.0 (9–20), and 12 ± 1.0 (8–16) for arches I–IV, respectively.

The digestive tract consisted of a tubular esophagus followed by a short intestine divided into anterior and posterior sections (Fig. 7). The esophagus had a relatively thick wall, whereas the intestinal wall was thinner. No clearly differentiated stomach structure was observed.

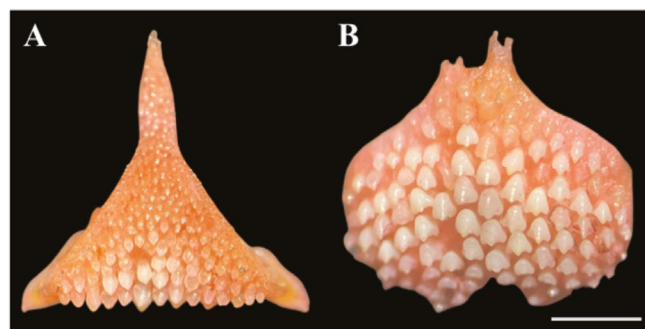
*Gut-somatic index*

The generalized linear mixed model (GLMM) explained a moderate proportion of the variation in GI and was overall significant ( $\chi^2 = 154.97$ ,  $df = 8$ ,  $p < 0.001$ ). Sex had a significant effect on GI (estimate =  $-0.100 \pm 0.036$  (SE), 95% CI:  $-0.171$  to  $-0.029$ ,  $p = 0.006$ ), with males exhibiting lower GI values than females. Estimated marginal means indicated that females had higher GI values ( $2.52 \pm 0.20$  (SE)) compared to males ( $2.28 \pm 0.18$  (SE)). Sampling location also had a significant effect (estimate =  $0.170 \pm 0.038$  (SE), 95% CI:  $0.097$  to  $0.244$ ,  $p < 0.001$ ), with higher GI values observed at Dam Doi ( $2.60 \pm 0.21$  (SE)) compared to Vinh Phuoc ( $2.20 \pm 0.17$  (SE)). Season alone did not significantly influence GI (estimate =  $0.024 \pm 0.152$  (SE),  $p = 0.876$ ). However, a significant interaction between sex and season was detected (estimate =  $0.158 \pm 0.072$  (SE), 95% CI:  $0.015$  to  $0.300$ ,  $p = 0.030$ ), indicating contrasting seasonal trends between sexes. Specifically, female GI decreased during the wet season, whereas male GI increased (Fig. 8). A significant interaction between season and location was also observed (estimate =  $-0.265 \pm 0.075$  (SE), 95% CI:  $-0.413$  to  $-0.118$ ,  $p < 0.001$ ), suggesting that seasonal variation differed between sampling sites. No significant interaction was found between sex and location ( $p = 0.776$ ) or among sex × season × location ( $p = 0.912$ ) (Table 1).

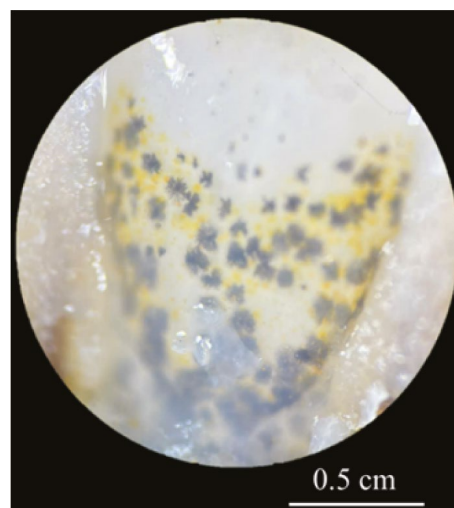
**4. Discussion**

This study integrates digestive morphology and GI variation to characterize the trophic adaptation of *Z. clarus* in the estuarine waters of the Mekong Delta. The combined evidence from jaw configuration, den-

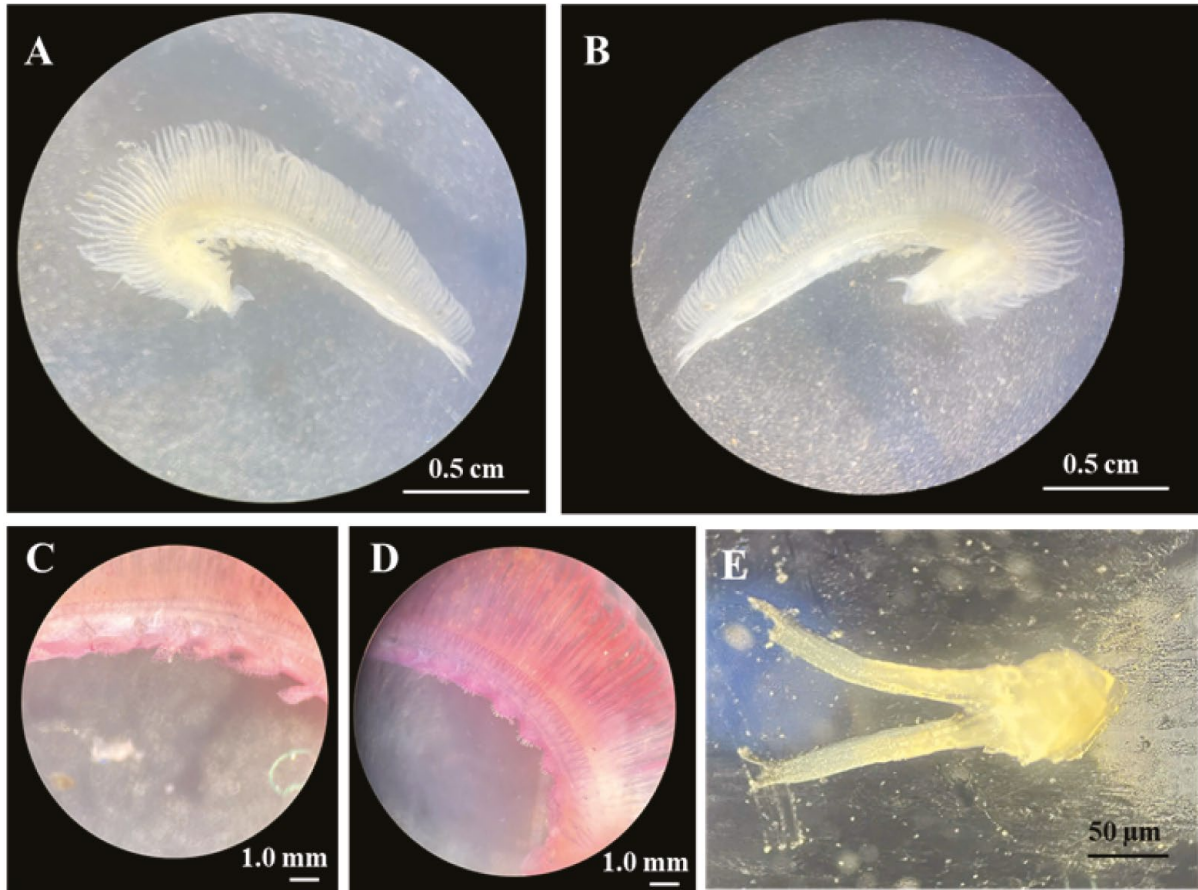
titition, gill structures, intestinal organization, and spatiotemporal GI dynamics indicates that this species is functionally adapted to exploit surface-associated prey under environmentally fluctuating conditions. By linking structural traits with feeding intensity patterns, the present study provides a more comprehensive perspective on trophic strategy in estuarine halfbeaks.



**Fig.4.** Pharyngeal tooth plates of *Zenarchopterus clarus* (scale bar = 1 mm). (A: lower pharyngeal tooth plate; B: upper pharyngeal tooth plate).



**Fig.5.** Tongue morphology of *Zenarchopterus clarus* showing a poorly developed structure with a rough anterior surface and smoother posterior region.



**Fig.6.** Gill structure of *Zenarchopterus clarus* (A: anterior view; B: posterior view; C: Gill rakers in first gill arch; D: Gill rakers in second gill arch; E: Transverse section of the gill arch).

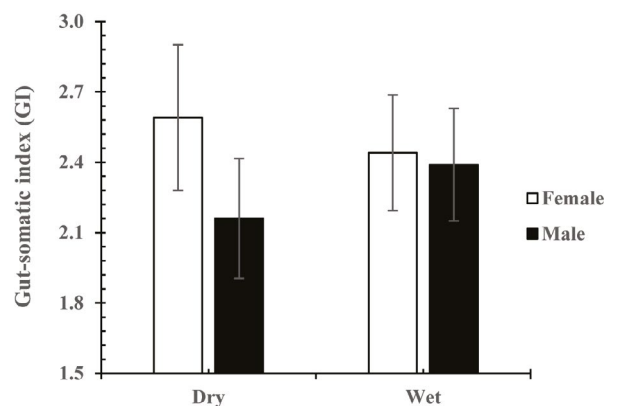
*Morphological integration and surface-oriented feeding strategy*

The superior mouth orientation and elongated lower jaw observed in *Z. clarus* are consistent with the surface-feeding functional guild typical of hemiramphids (Talwar and Jhingran, 1991; More et al., 2022). In estuarine systems characterized by turbidity, tidal mixing, and surface aggregation of invertebrates, prey resources are commonly concentrated near the air-water interface. The elongation of the lower jaw likely enhances prey detection and capture efficiency within this narrow vertical feeding zone. The MD, which differed significantly between sexes, may influence prey size selection or handling efficiency rather than representing a shift in trophic niche.

Dentition further supports a carnivorous or insectivorous feeding mode. The densely distributed conical teeth on both jaws and the high counts of pharyngeal teeth suggest specialization for grasping and retaining mobile prey (Berkovitz and Shellis, 2023). Similar pharyngeal modifications have been described in other hemiramphids with functional pharyngeal mills, in which mechanical reinforcement during intraoral processing enhances prey-handling efficiency (Tibbetts and Carseldine, 2003; Buddery et al., 2009). Compared with *Hyporhamphus limbatus* from Southwest Vietnam (Nguyen et al., 2025), *Z. clarus* exhibits a comparable pattern of dense dentition and well-developed pharyngeal plates, suggesting conserved trophic traits within the family. Such morphological consistency may reflect phylogenetic constraints combined with ecological convergence toward surface-oriented carnivory.



**Fig.7.** Digestive tract of *Zenarchopterus clarus* (A: esophagus; B: anterior intestine; C: posterior intestine).



**Fig.8.** Seasonal variation in gut-somatic index by sex in *Zenarchopterus clarus*.

Gill raker morphology provides additional insight into prey size retention. The relatively high number of gill rakers, particularly on the first arch, is consistent with retention of small prey items (Amundsen et al., 2004). Although diet composition was not directly examined in the present study, the combination of numerous gill rakers and sharp dentition supports the interpretation that *Z. clarus* captures and retains small, mobile prey efficiently in surface microhabitats.

The absence of a clearly differentiated stomach and the presence of a short intestine indicate rapid food throughput, a condition observed in several stomachless or weakly stomach-differentiated teleosts (Day et al., 2011). In estuarine environments where prey patches may be spatially and temporally unpredictable, rapid digestion and turnover may confer an adaptive advantage by allowing individuals to exploit transient feeding opportunities. Thus, the digestive organization of *Z. clarus* appears well suited for high-frequency feeding on soft-bodied prey rather than prolonged gastric processing.

*Energy allocation, reproductive investment, and spatial heterogeneity*

The GI differed significantly between sexes, with females exhibiting higher values than males. In teleost fishes, somatic indices are commonly associated with feeding activity and physiological condition (Gebremedhin and Mingist, 2014). Higher GI values in females may indicate increased feeding or digestive activity, particularly during periods related to reproductive development. Similar patterns have been reported in other fish species, where females exhibit higher feeding indices under certain biological conditions (Gebremedhin and Mingist, 2014; Hua et al., 2023). Differences in GI between sampling locations suggest spatial variation in feeding conditions. Estuarine habitats are characterized by environmental heterogeneity, including variation in hydrodynamics, turbidity, and food availability (Nguyen et al., 2024). Such differences may influence feeding activity and digestive development in fish. The higher GI values observed at Dam Doi may therefore reflect more favorable feeding conditions at this site. Comparable spatial variation in feeding intensity has been reported in other estuarine fish species (Hua et al., 2023).

*Seasonal interaction and adaptive plasticity*

Although no significant seasonal effect on GI was detected, the significant interaction between sex and season indicates differences in feeding patterns between males and females. Female GI decreased during the wet season, whereas male GI increased. Seasonal variation in feeding intensity has been documented in many fish species and is often associated with changes in environmental conditions and biological cycles (Gebremedhin and Mingist, 2014; Hua et al., 2023). The observed differences between sexes suggest that males and females may respond differently to seasonal changes in estuarine environments. In particular, reproductive processes may influence feeding activity, leading to variation in digestive indices between sexes (Gebremedhin and Mingist, 2014). In estuarine systems, seasonal changes in rainfall and nutrient input

**Table 1.** Fixed effects from the GLMM for gut-somatic index

Factor	Estimate	SE	95% CI	p
Sex (M-F)	-0.100	0.036	-0.171 – -0.029	0.006
Season (Wet-Dry)	0.024	0.152	-0.274 – 0.321	0.876
Site (DD-VP)	0.170	0.038	0.097 – 0.244	<0.001
Sex × Season	0.158	0.072	0.015 – 0.300	0.030
Season × Site	-0.265	0.075	-0.413 – -0.118	<0.001

can affect food availability (Hua et al., 2023), which may contribute to the patterns observed in the present study. However, because reproductive status and diet composition were not directly examined, the mechanisms underlying these differences remain unclear. Further studies incorporating reproductive and dietary data would help clarify the factors influencing seasonal variation in feeding intensity in this species.

*Comparative context within Hemiramphidae*

Within Hemiramphidae, morphological specialization for surface feeding is well documented (Talwar and Jhingran, 1991; Tibbetts and Carseldine, 2003). The morphological patterns observed in *Z. clarus* align with those described in other halfbeaks, suggesting a conserved functional design optimized for exploiting surface-associated prey. However, the integration of morphological evidence with quantitative GI analysis in the present study extends beyond descriptive anatomy by linking structure to the dynamics of feeding intensity. Compared with other estuarine fishes in the Mekong Delta, including gobiid taxa exhibiting variable gut length and somatic indices (Nguyen et al., 2020; Hua et al., 2023), *Z. clarus* demonstrates a trophic profile consistent with rapid surface-oriented carnivory rather than benthic or detritivorous feeding modes. This distinction reinforces its ecological role within the surface trophic network of estuarine systems.

*Ecological implications and limitations*

By integrating morphological and functional indicators, this study provides baseline evidence of trophic adaptation in *Z. clarus* in estuarine ecosystems. The coordinated expression of surface-feeding morphology, dense dentition, numerous gill rakers, and sex-specific GI dynamics suggests that this species exhibits both structural specialization and functional plasticity in response to environmental heterogeneity. Nevertheless, gill raker and pharyngeal tooth counts were derived from a subsample, and metadata were not retained for those specimens, preventing evaluation of spatial or sexual variation in these traits. In addition, diet composition and reproductive stage were not directly quantified. Therefore, the feeding strategy in this study was inferred from morphological traits and GI and should be considered a functional interpretation rather than direct evidence. Future studies incorporating stomach content analysis, reproductive staging, and stable isotope approaches would help clarify trophic niche breadth and seasonal energy allocation in this species.

## 5. Conclusion

The species *Z. clarus* exhibits digestive morphological traits consistent with surface feeding, including an upturned mouth, dense conical dentition, numerous gill rakers, and a short intestine without a clearly differentiated stomach. The GI varied significantly between sexes and sampling locations, and a significant sex × season interaction was detected, indicating sex-specific seasonal feeding strategies. Overall, these findings highlight the functional significance of digestive tract morphology for surface-oriented feeding and provide baseline evidence for sex-specific seasonal variation in feeding intensity in an estuarine hemiramphid fish.

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## Animal Ethics statement

The study was approved by the Animal Ethics Committee of Can Tho University (CTU-AEC25025) and conducted in accordance with relevant animal welfare guidelines.

## Author contributions (CRediT taxonomy)

Vinh Nguyen Quoc: Conceptualization, Methodology, Investigation, Writing - Original Draft, Writing - Review & Editing, Project administration; Anh Ngoc Tran: Conceptualization, Methodology, Investigation, Writing - Original Draft, Writing - Review & Editing; Hung Tran Gia Nguyen: Methodology, Investigation, Writing - Original Draft, Writing - Review & Editing; Think Quoc Nguyen: Methodology, Investigation, Writing - Original Draft, Writing - Review & Editing; Han Thi Kim Nguyen: Methodology, Investigation, Writing - Original Draft, Writing - Review & Editing; Quang Minh Dinh: Conceptualization, Supervision, Writing - Review & Editing.

## Declaration of Generative AI and AI-assisted technologies

During the preparation of this work, the authors used ChatGPT to improve English language clarity and academic writing style. The prompts were related to grammar correction. After using this tool, the authors reviewed and edited the content as needed and took full responsibility for the final manuscript.

## Pre-print server/online repository

This manuscript has not been deposited in any pre-print server or online repository.

## Conflict of interest

The authors declare no conflict of interest.

## Informed consent

Not applicable.

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