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Trophic ecology of largehead hairtail *Trichiurus japonicus* in the South Sea of Korea revealed by stable isotope and stomach content analyses

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Largehead hairtail (*Trichiurus japonicus*) is one of the most commercially important fishes in the western North Pacific. To identify the dietary changes across ontogeny and seasons, we investigated its stomach contents and stable isotope signatures (δ^{13}C and δ^{15}N) in the South Sea of Korea. The index of relative importance revealed that the dietary composition of largehead hairtail consisted mainly of Pisces (1.6%–84.8%) and Euphausiacea (3.0%–93.0%). However, the proportions of dietary items differed by season and anal length (ALs), suggesting a trophic adaptability response to seasonal food availability and size-related trophic variation, respectively. Our isotopic results showed that the largehead hairtail is placed intermediately between pelagic and benthic fishes and was more ^{13}C and ^{15}N-depleted than other carnivorous fishes, suggesting a high consumption of pelagic species. Similarly, seasonal variations were observed in the δ^{13}C and δ^{15}N values of the largehead hairtails (PERMANOVA, *p*= 0.001). Interestingly, their δ^{13}C values in spring decreased significantly with ALs (r^2 = 0.594, *p*< 0.001), suggesting an ontogenetic change due to the increased proportion of Euphausiacea to the nutrition of largehead individuals during this specific season. Based on a combination of stomach contents and stable isotope signatures, overall results provide new insights into the feeding characteristics of the largehead hairtail, which improves our understanding of its trophic ecology depending on season and body size.

1. Introduction

The family Trichiuridae, known as hairtail, is an economically important teleost fish group with a worldwide distribution generally inhabiting tropical and temperate continental shelves and shallow coastal waters (Nakamura and Parin, 1993). In 2016, the estimated annual catch of hairtail worldwide was approximately 1,280,000 t, making it one of the most caught marine fish species (FAO, 2019). In particular, the largehead hairtail (*Trichiurus japonicus*) is one of the most commercially important fishery resources in the western North Pacific (Lin et al., 2007). This species is widely distributed in the Bohai Sea, Yellow Sea, East China Sea, and South Sea of Korea. In Korea, its annual catch was approximately 120,000 t in the 1980s; since then, the annual catch has declined gradually from an average of approximately 60,000–80,000 t in the 2000s to an average of approximately 44,000 t in the last five years (KOSIS, 2019). Due to its increasing commercial value and decreasing catch volumes, the basic ecology, life history, population dynamics, habitat, and environmental conditions of the largehead hairtail are being widely studied (Kim et al., 2005; He et al., 2014; Kim et al., 2020; Sun et al., 2020; Mammel et al., 2022). In addition to basic biological knowledge, trophic ecology is essential for the effective management and conservation of this specific fish population.

In general, scientific data on the quality and quantity of diets available for fish populations are needed to evaluate the effects of environmental changes on biological processes, including growth and reproduction (Beverton and Holt, 1957; Darnaude, 2005; Persson and De Roos, 2006). Hairtails are high trophic level predators that play a key role in the marine food web, as they control lower trophic level species (e.g., fish, shrimp, and squid) through top-down processes (Martins et al., 2005; Yan et al., 2011). Since the survival and abundance of the hairtail can potentially affect the population dynamics of other fish, understanding their feeding ecology, based on energy flow within marine ecosystems, is critical for the assessment of commercial fisheries resources (Mammel et al., 2022). Accordingly, many studies have addressed the feeding characteristics, dietary composition, ontogenetic changes, and spatiotemporal variations in the diet of hairtails (Lee, 1978; Bakhoum, 2007; Liu et al., 2009; Yan et al., 2011; Hamaoka et al., 2014; Mammel et al., 2022). However, most of the research was limited to Chinese hairtail populations inhabiting China and the Yellow Sea. For the successful management of a given fish population, it is important to understand the spatial variability in its feeding characteristics resulting from the differences in prey composition in the feeding ground and habitats (Liu et al., 2009). Despite the importance of this information, very little is known about the feeding strategy of hairtail populations in Korean coastal waters (Huh, 1999).

Stomach content analysis has been commonly used to investigate the feeding habits of fish species and provide detailed information on their dietary composition (Hyslop, 1980; Buckland et al., 2017). This is the most widely accepted tool for generalizing the feeding ecology of consumer species (Baker et al., 2014). However, this technique can only reflect transient diet, and the digested and unidentifiable stomach contents may cause uncertainty in the taxonomic identification of the dietary items (Deb, 1997; Davenport and Bax, 2002). Stable isotope analysis has been adopted as an alternative method to overcome the limitations of stomach content analysis, providing a long-term view of feeding characteristics by evaluating actual assimilated dietary items among a variety of food sources during the feeding season (Michener and Schell, 1994; Layman et al., 2012). Stable carbon isotope (δ^{13}C) can be used to infer the dietary source for consumer nutrition, which generally increases from prey to consumer by a slight enrichment of less than 1.0‰ (DeNiro and Epstein, 1978; Fry and Sherr, 1984). In contrast, stable nitrogen isotope (δ^{15}N) can offer information on the trophic position (TP) of animals, which exhibits a high isotopic discrimination of 2–4‰ between prey and consumers (Minagawa and Wada, 1984; Post, 2002). Stable isotope analysis has been increasingly used to assess the trophic role of fish species and their ontogenetic dietary shifts (Jennings et al., 2002; Darnaude, 2005; Chiang et al., 2020; Estupiñán-Montaño et al., 2021). Stable isotope analysis supported by stomach content analysis is among the most powerful tools for improving the interpretation of feeding studies for fish species (Davis et al., 2012; Santos et al., 2013; Park et al., 2018).

The objective of this study was to examine the trophic ecology of the largehead hairtail in the South Sea of Korea. We investigated stable isotope signatures (δ^{13}C and δ^{15}N) and stomach contents of largehead hairtail. Specifically, considering its seasonal growth dynamics (Huh, 1999), we focused on the changes in its dietary composition and TP across ontogeny and seasons. A combination of stable isotope and stomach content analyses has rarely been applied to this species (Hamaoka et al., 2014). In addition, most studies have investigated the feeding characteristics of *T. lepturus*, whereas information on the trophic ecology of *T. japonicus* is very limited (Mammel et al., 2022). We anticipated that if the dietary composition of *T. japonicus* changes in association with its ontogeny and season, its tissue isotopic signatures would reflect this change. To the best of our knowledge, this is the first study to identify the trophic ecology of the largehead hairtail that may play an important role in the marine food web of Korean coastal waters.

2. Materials and methods

2.1. Study area and sample collection

Field surveys were performed on the continent shelf of the South Sea of Korea (Northern East China Sea, 33° 49´N, 127° 13´E)

(Figure 1). The water temperature, salinity, and chlorophyll *a* levels in the sampling area were obtained using a CTD (SBE 911 Plus, Seabird Electronics Inc., Bellevue, WA, USA). The sampling area had low tidal amplitude (less than 30 cm) and water depth approximately 94–102 m. All specimens of largehead hairtail *T. japonicus* (a total of 422 individuals) and other fish were collected during February, May, August, and November 2021. Sampling was conducted using a trawl net (12 cm mesh in the main body, 8 cm mesh in the intermediate part, and 6 cm mesh in the cod end with a 2 cm cod end liner of the net) from a research vessel (R/V *Tamgu 22*) for over 30 min at 3 knots. The fishing depth for sampling ranged from 91.1 m to 98.2 m. The total length and weight of each individual was measured on board to the nearest 0.1 cm and 0.1 g, respectively. The collected fish samples were stored in a deep freezer (−60°C) and transported to the laboratory. For the collection of dominant zooplankton groups, sampling was conducted through oblique towing on each occasion using a Bongo net (2.0 m² mouth opening, 500 μm mesh) equipped with a flowmeter. The collected zooplankton samples were frozen in 1 L polyethylene bottles in a deep freezer (−60°C) for processing.

2.2. Laboratory processing

The collected fish samples for stable isotope analysis were dissected, and only muscle tissues were obtained from the anterior dorsal region. The stomachs were separated from the largehead hairtail individuals, and their contents were preserved in 10% formalin for stomach content analysis. For the zooplankton samples, two dominant groups of copepods and euphausiids for stable isotope analysis were identified under a dissecting microscope. The fish and zooplankton samples for isotope analysis were dried in an oven for 72 h at 50–60°C, ground into a homogeneous powder using a mortar and pestle, and kept frozen in a deep freezer (−70°C) to avoid contamination damage until the next stage.

2.3. Stomach content analysis

In the laboratory, the preserved stomach contents were identified to the lowest possible taxonomic level under a stereomicroscope (LEICA 12; Wetzlar, Germany). The wet weight of each food item was measured to the nearest 0.1 mg using an analytical balance (ME204TE/00; Mettler Toledo, Greifensee, Switzerland). Fresh and partially digested prey were used to reduce bias in the stomach content analysis. Food components were estimated by the percent frequency of occurrence (% *F*, number of stomachs in which a particular food item occurred as a percentage of the total number of stomachs examined), percent numerical frequency (% *N*) of each prey item to the total number of identifiable food items, and percent wet
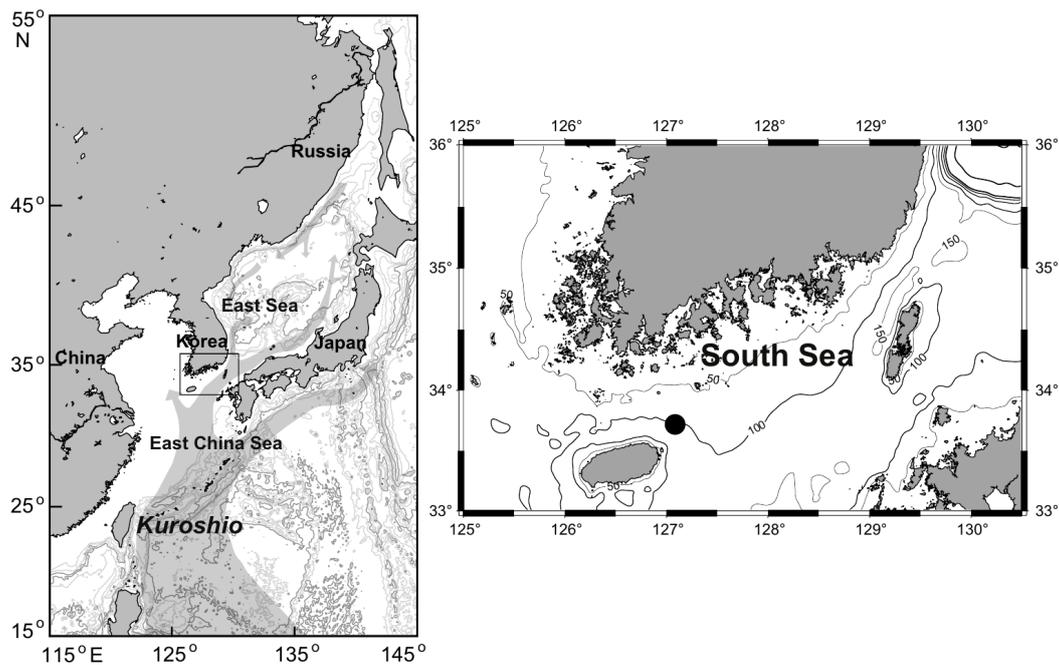

FIGURE 1

Map of the sampling area in the South Sea of Korea. Field circle indicates the sampling site collected for zooplankton, large-head hairtail (*Trichiurus japonicus*), and other fishes.

weight (% *W*) of each prey item to the total wet weight of the identifiable food items. An index of relative importance (IRI) for all food components was calculated for each prey type [*IRI = (% N+% W)× % F*] and expressed as a percentage (% *IRI*) as follows: % *IRI = IRIi*/$\sum_{i=1}^{n}$*IRIi*   100 (Pinkas et al., 1971), where n is the total number of food components categorized as class levels. Size-related dietary changes were examined by dividing the largehead specimens into three size classes:<10 cm, 10–15 cm, and ≥15 cm, based on their anal lengths (ALs).

2.4. Stable isotope analysis

Powdered zooplankton and fish samples (0.5–1.0 mg) were wrapped in tin combustion capsules (5 Ã–9 mm, D– H). All sealed samples were combusted at 1020°C using a CNSOH elemental analyzer (EA Isolink, Bremen, Germany), and the resultant gases were analyzed using a linked continuous-flow isotope ratio mass spectrometer (CF-IRMS; DELTA V PLUS, Bremen, Germany). The stable isotope ratios are expressed in δ notation relative to conventional standard reference materials (Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen) as follows: X (‰) = $[(\frac{R_{sample}}{R_{standard}}) - 1] \times 10^3$, where X is ^{13}C or ^{15}N, and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The international standards of sucrose (NIST-8542, $C_{12}H_{22}O_{11}$) and glucose (BCR-657, $C_6H_{12}O_6$) for $\delta^{13}C$ measurements and ammonium sulfate (NIST-8547, $[NH_4]_2SO_4$) and L-glutamic acid (USGS-40, $C_5H_9NO_4$) for $\delta^{15}N$ measurements were used as reference standards to calibrate the analyzed isotope values. The analytical precision based on 20 urea (a laboratory reference) replicates was within 0.15‰ and 0.18‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Due to bias in the $\delta^{13}C$ values for fish species resulting from interspecific differences in the concentration of ^{13}C-depleted lipids, we performed lipid correction by Post et al. (2007) if their C:N ratios were more than 3.5. The lipid correction was performed as follows: $^{13}C_{normalized}= ^{13}C_{untreated} -3.32+0.99 \times C$:N (*ratios*) , where $^{13}C_{untreated}$ and $^{13}C_{normalized}$ are the measured and lipid-normalized values of the sample, respectively.

The TP for fish species was calculated using the equation: $TP_i=(\delta^{15}N_i- \delta^{15}N_{baseline})/\Delta^{15}N+2$, where $\delta^{15}N_i$ represents the mean $\delta^{15}N$ of the target species, $\delta^{15}N_{baseline}$ is the mean $\delta^{15}N$ of trophic baseline consumers (i.e., copepod group), $\Delta^{15}N$ is the enrichment factor (3.4‰) in $\delta^{15}N$ per TP, and 2 represents the baseline TP (Post, 2002).

2.5. Data analysis

Data were analyzed using SPSS software (version 23.0, IBM, Armonk, NJ, United States) and PRIMER version 6 + PRIMER add-on (PRIMER-e, Auckland, New Zealand). Prior to statistical analyses, all data were tested for normality and homogeneity of variance using the Shapiro-Wilk and Levene's tests, respectively. One-way analysis of variance (ANOVA) was used to test for significant differences in the TP values and ALs of largehead hairtails, followed by Tukey's honest significant difference (HSD) multiple-comparison *post hoc* test to evaluate differences among variables. To examine the size-based trophic dynamics of the largehead hairtails, linear regressions were used to examine the relationships between their ALs and isotope values ($\delta^{13}C$ and $\delta^{15}N$). All values are presented as the mean ± standard deviation. Significant differences in the $\delta^{13}C$ and $\delta^{15}N$ values of zooplankton, largehead hairtails, and other fish consumers among seasons were tested using permutational multivariate analysis of variance (PERMANOVA).

3. Results

3.1. Environmental conditions

The water temperature was lowest at the surface (16.2°C) in February and highest (27.6°C) in August (**Table 1**). In contrast, during the four seasons, the bottom layer water temperature ranged from 15.2°C in August to 15.9°C in February. The salinities in the surface layer varied between 30.6 in August and 34.8 in February. In the bottom layer, the salinity was fairly constant (34.4 in August and 34.8 in February). Chlorophyll *a* concentration of the surface water ranged from 0.8 μg/L in August to 1.2 μg/L in November.

3.2. Dietary compositions

Of the 747 largehead hairtail stomachs sampled, 322 (43.1%) were empty. A total of 14 prey taxa groups were identified based on class (**Figure 2**). The diet of the largehead hairtail (based on IRI, %) consisted mainly of Pisces (1.6% in May to 84.8% in February) and Euphausiacea (3.0% in February to 93.0% in May) over the four seasons. The minor components of the stomach contents were Macrura (1.6% in May to 26.8% in November) and Amphipoda (0.1% in February to 7.4% in August). Size-related stomach compositions also showed that Pisces and Euphausiacea were preferred by the three AL groups (10 cm, 10–15 cm, and > 15 cm). While the small and mid-groups of largehead hairtails represented 5.5–93.4% and 22.1–94.6% for Pisces and 0–24.7% and 1.0–69.5% for Euphausiacea, respectively; the preferred prey composition of their largest group was 4.3 to 92.5% for Euphausiacea and 2.4 to 81.3% for Pisces.

3.3. Stable isotope ratios

3.3.1. Zooplankton

The $\delta^{13}C$ and $\delta^{15}N$ values of both zooplankton groups (calanoid copepods and euphausiids) differed significantly among

TABLE 1 The environmental conditions (water temperature, salinity, and chlorophyll *a*) at the surface and bottom layers in the South Sea of Korea during February, May, August, and November 2021.

Month	Water temperature (°C)		Salinity		Chlorophyll *a* (µg/L)
	Surface	Bottom	Surface	Bottom	Surface
February	16.2	15.9	34.8	34.8	0.7
May	16.9	15.6	34.5	34.6	0.6
August	27.6	15.2	30.6	34.4	0.8
November	21.1	15.6	34.1	34.5	1.2

FIGURE 2
Size-related (anal length, AL; 10 cm, 10−15 cm, and > 15 cm) and total **(E)** compositions of the stomach contents of large-head hairtail (*Trichiurus japonicus*) by the index of relative importance (%IRI) expressed as a percentage of the sum of the IRI values in the South Sea of Korea during winter (**A**, February), spring (**B**, May), summer (**C**, August), and autumn (**D**, November) 2021.
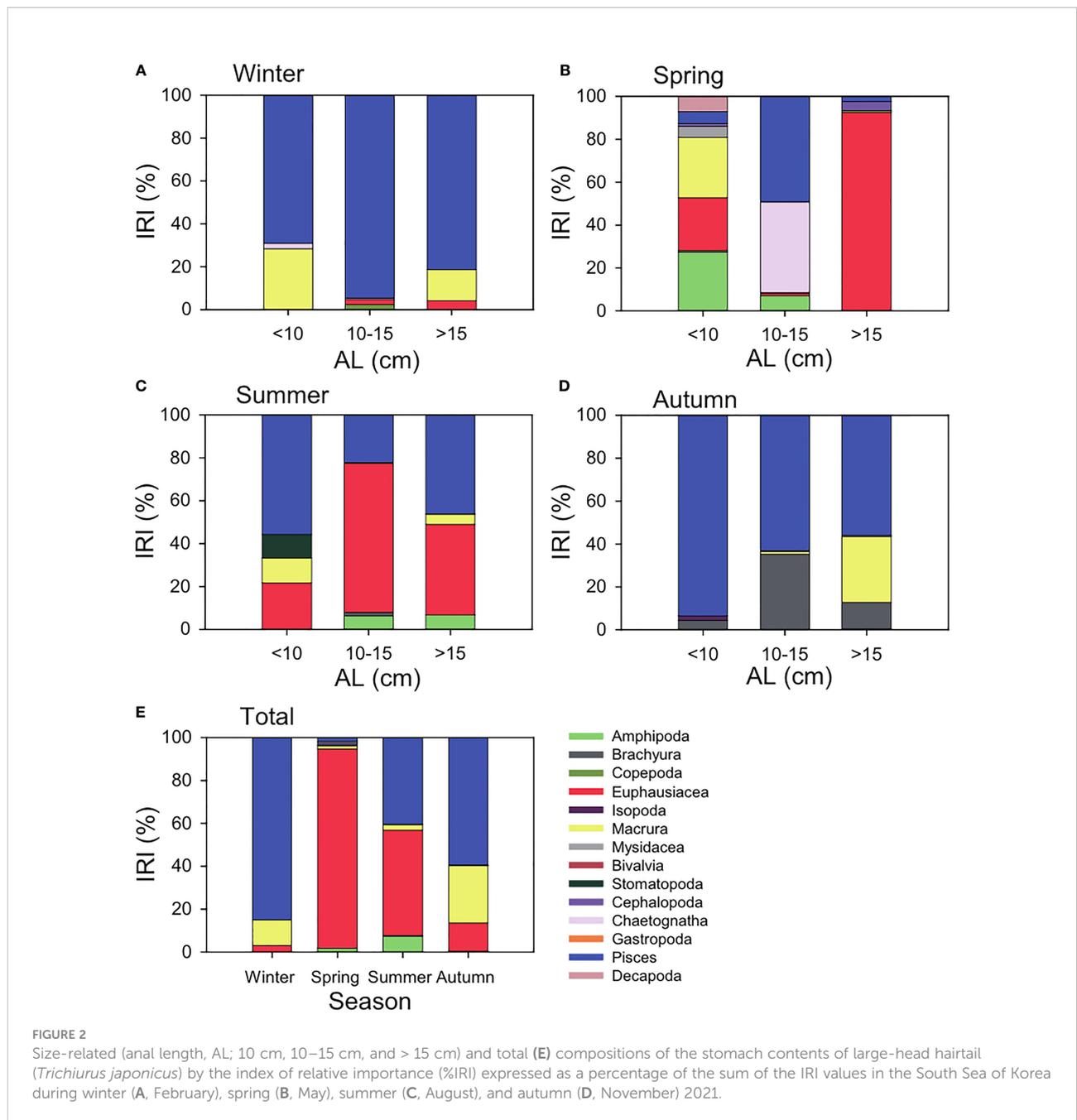
the four seasons (PERMANOVA, pseudo-$F_{3,\,48}$ = 12.29, p = 0.001 and pseudo-$F_{3,\,35}$ = 9.36, p = 0.001, respectively) (Table 2). The mean δ^{13}C and δ^{15}N values of copepods ranged from −22.5 ± 0.5‰ (November) to −20.2 ± 1.2‰ (February) and from 6.4 ± 0.5‰ (February) to 8.0 ± 0.9‰ (August), respectively. The euphausiids showed mean δ^{13}C and δ^{15}N values of −21.3 ± 0.9‰ (May) to −20.4 ± 1.0‰ (February) and 6.1 ± 0.6‰ (November) to 8.5 ± 0.9‰ (August), respectively.

3.3.2. Largehead hairtail

Largehead hairtails of 18 (August) to 37 (November) individuals were prepared for stable isotope analysis during the four seasons (Figure 3). Seasonal variations were observed in δ^{13}C and δ^{15}N values of the largehead hairtail (pseudo-$F_{3,\,94}$ = 9.03, p = 0.001). The δ^{13}C values of largehead hairtail ranged from −19.8 ± 0.8‰ (May) to −18.2 ± 0.3‰ (August), whereas the δ^{15}N values varied between 10.8 ± 0.7‰ (May) and 11.3 ± 1.2‰ (February). The TPs of largehead hairtails, calculated based on the lowest δ^{15}N values of zooplankton, showed significant differences among seasons (Tukey's HSD test, $p<$ 0.01), ranging from 2.8 ± 0.2 in August to 3.5 ± 0.2 in November.

There were significant differences in the mean ALs of analyzed largehead hairtails among seasons (one-way ANOVA, p = 0.001), ranging from 11.6 ± 4.0 cm (5.8 to 19.3 cm in February) to 17.9 ± 7.3 cm (6.8 to 28.4 cm in May). The δ^{13}C values in May decreased significantly with AL (r^2 = 0.594, $p<$ 0.001), whereas there were no significant correlations between ALs and δ^{13}C in February, August, and November (r^2 = 0.033, p = 0.461; r^2 = 0.002, p = 0.929; r^2 = 0.006, p = 0.147, respectively; Figure 4). In contrast, significant positive relationships were found between ALs and δ^{15}N in May, August, and November (r^2 = 0.441, p = 0.002; r^2 = 0.244, p = 0.033; r^2 = 0.420, $p<$ 0.001, respectively). However, in February, there was no significant relationship between the AL and δ^{15}N (r^2 = 0.115, p = 0.148).

3.3.3. Dual isotope plot for largehead hairtail and other fish consumers

Dual isotope plots for all fish consumers showed variable ranges of δ^{13}C and δ^{15}N values (Figure 5), which were significantly different among the seasons (PERMANOVA, pseudo-$F_{3,\,179}$ = 7.52, p = 0.001). The range of δ^{13}C values of fish consumers during February (−21.8‰ to −16.6 ± 0.4‰) and May (−20.8‰ to −17.3 ± 0.3‰) were broader than those during August (−19.4‰ to −17.4 ± 0.2‰) and November (−18.6 ± 0.4‰ to −16.6 ± 0.2‰). Similarly, relatively wide ranges were observed for δ^{15}N values during February (8.8‰ to 13.8 ± 0.7‰) and May (9.5‰ to 13.3 ± 0.4‰) compared with those during August (9.6‰ to 12.3 ± 0.2‰) and November (10.1‰ to 12.6 ± 0.3‰). The mean TP values of fish consumers (except for largehead hairtail) differed significantly among seasons (Tukey's HSD test, $p<$ 0.01), ranging from 2.90 ± 0.2 in August (2.46 − 3.27) to 3.59 ± 0.2 in November (3.20 − 3.93).

TABLE 2 δ^{13}C and δ^{15}N values of zooplankton (calanoid copepods and euphausiids) collected during February, May, August, and November 2021 in the South Sea of Korea. PERMANOVA test of δ^{13}C and δ^{15}N values for each zooplankton among seasons.

Zooplankton	February δ13C Mean	SD	δ15N Mean	SD	n	May δ13C Mean	SD	δ15N Mean	SD	n	August δ13C Mean	SD	δ15N Mean	SD	n	September δ13C Mean	SD	δ15N Mean	SD	n	PERMANOVA pseudo-F	p
Copepods	−20.2	1.2	6.4	0.5	12	−22.1	1.1	7.4	0.5	18	−21.3	1.0	8.0	0.9	10	−22.5	0.5	7.5	0.6	9	12.29	**0.001**
Euphausiids	−20.4	1.0	7.1	0.8	7	−21.3	1.1	6.7	0.6	13	−20.5	0.8	8.5	1.0	8	−21.2	0.4	6.1	0.6	8	9.36	**0.001**

Bold-face font indicates significance at p < 0.05. Data represent mean ± 1SD.
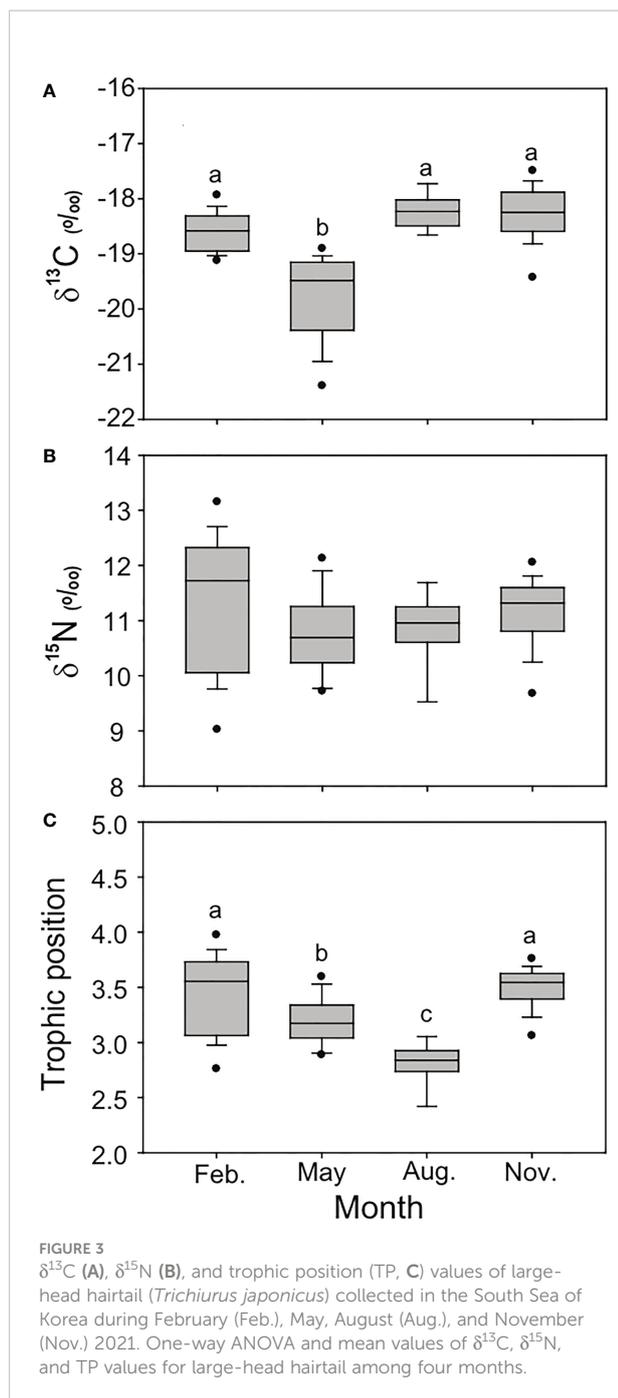
Overall, the largehead hairtails showed intermediate δ^{13}C and δ^{15}N positions in the dual isotope plots during all seasons.

4. Discussion

This study revealed the feeding ecology of largehead hairtail (*T. japonicus*) in the southern coast of Korea through the combined use of stable isotope and stomach content analyses.

The feeding characteristics observed in the species may be explained by seasonally varying patterns of feeding dynamics, ontogenetic dietary shifts, and dietary composition. A wide range of prey compositions for largehead hairtail as a carnivorous species has been reported from several other seas, identifying principal prey items, including zooplankton, shrimps, cephalopods, and fish, based on stomach content analysis (Martins et al., 2005; Mammel et al., 2022). Our study provides valuable information for understanding population variations in the dietary composition and trophic position (TP) of largehead hairtails in different foraging areas resulting from opportunistic and variable feeding behavior.

4.1. Seasonal effects on the dietary compositions of largehead hairtail

Overall, in the present study, the major diet of largehead hairtail was Pisces (1.6–84.8%) and Euphausiacea (3.0–93.0%) over the four seasons, regardless of the size effect. However, the proportions of dietary items differed by season and AL, as identified under microscopic observation. A clear seasonal distinction in the prey composition of the hairtail may be closely associated with its trophic adaptability response to food availability (Yan et al., 2012). Although we did not perform a seasonal analysis of the relationship between environmental variables and distributions of dietary items for the species, they have been identified as generalists due to their fluctuating feeding intensity as per prey availability (Hamaoka et al., 2014; Mammel et al., 2022). In addition, dietary preference shifts for largehead hairtails were likely related to their spawning season or maturation size. The major spawning periods for the species in the South Sea of Korea has been reported to be from May to September and the minimum ALs at sexual maturity is more than 25.0 cm (Cha and Lee, 2004; Kim et al., 2020). The seasonal and size-related prey compositions observed on stomach content analysis in our study may coincide with the known major spawning season. Most fish species, including hairtails, require additional nutritional energy for gonad development and maturation (Mohammed Koya et al., 2018). Accordingly, despite Pisces and Euphausiacea being the preferred diet of longhead hairtails, the diet composition showing contrasting results across seasons and size classes may be regulated by two important factors: seasonal food availability and size-related trophic variation.

In this study, stable isotope analysis revealed seasonal changes in the feeding ecology of largehead hairtail. Significant seasonal differences in the δ^{13}C and δ^{15}N values of the largehead hairtail suggest that its diet is flexible. Hairtails and largehead hairtails inhabiting the East Asian Marginal Seas are generally known to exhibit different spatiotemporal feeding habits due to differences in reliance on pelagic and benthic production, mainly through consuming pelagic and benthic fishes and *Eupausia pacifica* (Yan et al., 2011; Hamaoka et al., 2014). Several studies
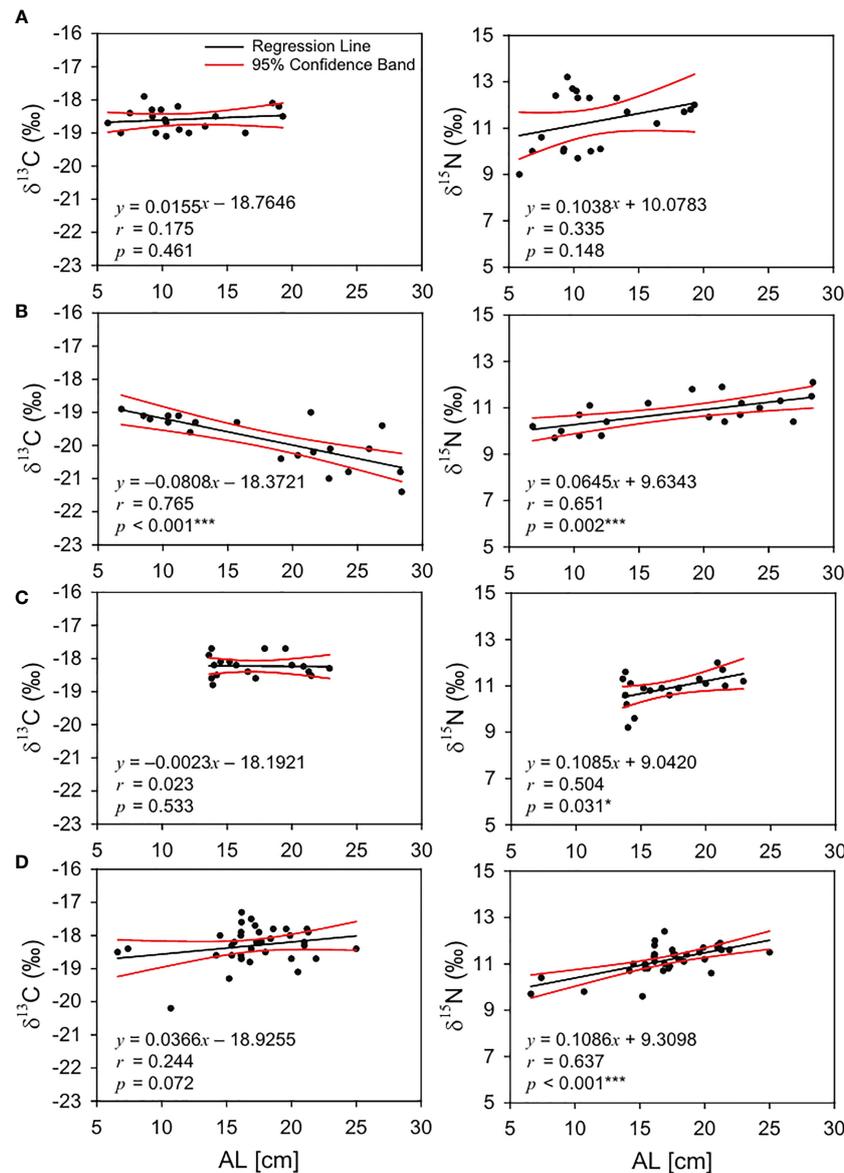
FIGURE 4

Regression relationships between δ¹³C − anal length (cm, left) and δ¹⁵N − anal length (cm, right) of large-head hairtail (*Trichiurus japonicus*) collected in the South Sea of Korea during February **(A)**, May **(B)**, August **(C)**, and November **(D)** 2021, *, $p < 0.05$ and ***, $p < 0.001$.

have reported that consumer species commonly discriminate isotopically between benthic and pelagic food webs, as shown by a higher number of ^{13}C- and ^{15}N-enriched benthic species than pelagic feeders (Davenport and Bax, 2002; Boyle et al., 2012; Park et al., 2020). Benthic consumers may display a tendency to demonstrate increasing δ^{13}C and δ^{15}N values with increasing depth due to the biogeochemical process of sinking phytoplankton-derived organic matter as the basal nutritional source supporting benthic food webs (Polunin et al., 2001; Park et al., 2018). The relatively lower δ^{13}C values of the largehead hairtail in spring compared with those in other seasons were

closely related to the higher reliance on pelagic production. These results were supported by the increased contribution of Euphausiacea to the diet of hairtails, as estimated by stomach content analysis. Furthermore, although hairtails are generally known as top predators, their relatively lower δ^{15}N values than those of other carnivorous fishes were likely related to the higher contribution of pelagic sources to their diets. Dual isotope plots of fish consumers showed that hairtails had intermediate positions between pelagic and benthic fishes and was more ^{13}C and ^{15}N-depleted than other large carnivorous fishes. Thus, these results suggest that largehead hairtails may feed on both
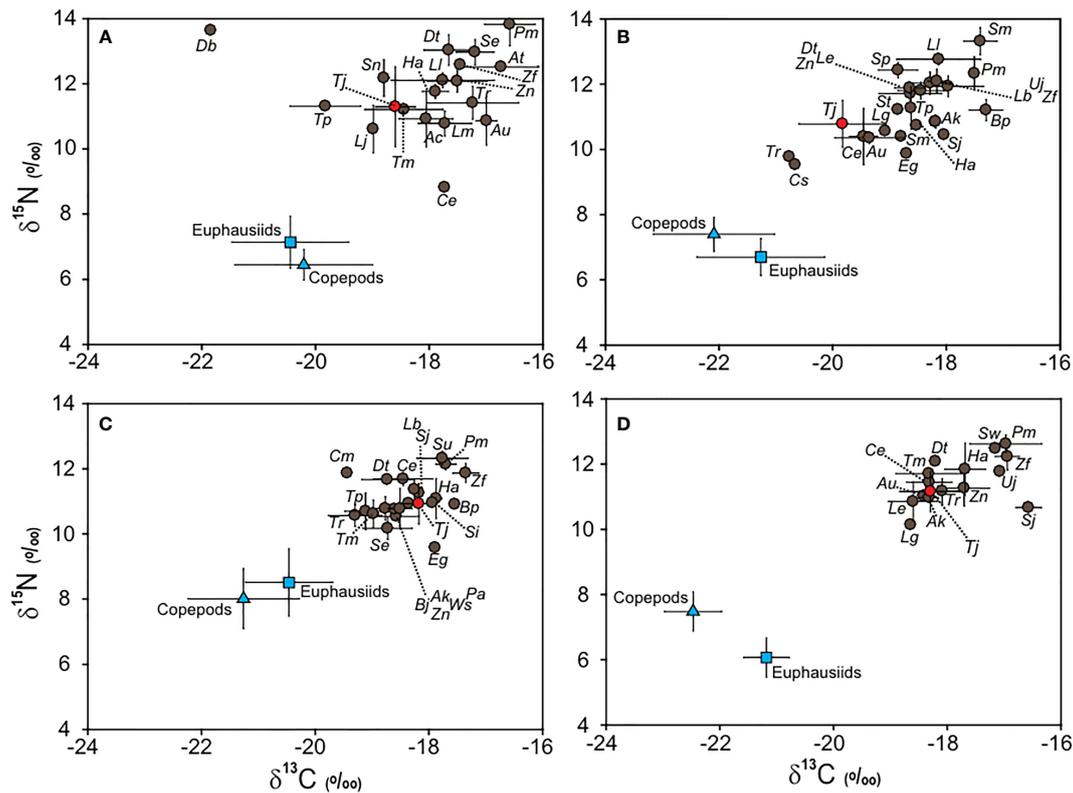
FIGURE 5
Bi-plots of δ¹³C and δ¹⁵N values of zooplankton (blue squares, euphausiids; blue triangles, copepods), large-head hairtail (red circles, *Trichiurus japonicus*), and other fishes (gray circles) in the South Sea of Korea during February **(A)**, May **(B)**, August **(C)**, and November **(D)** 2021. Values are presented as mean δ¹³C and δ¹⁵N (‰ ± 1 SD). Species codes are presented in Table 3.

pelagic and benthic dietary sources and dietary items with a pelagic source affinity (Le Loc'h et al., 2008).

4.2. Size-related dietary compositions of largehead hairtail

Our isotopic results revealed a significant positive relationship between ALs and δ¹⁵N values of largehead hairtails, coinciding with higher δ¹⁵N values in larger individuals, except in February. Since higher δ¹⁵N values of carnivorous consumers are closely related to larger and higher TP dietary items, such ontogenetic dietary shifts are likely to be a general trend in the feeding characteristics of common fish species (Link and Garrison, 2002; Graham et al., 2007). The ecological function of increasing fish body and mouth size can allow individuals to capture a wider range of prey sizes and types for energy optimization (Gerking, 1994). Studies of the hairtail species *T. margarites*, *T. lepturus*, and *T. japonicus* show that with growth-related increasing body length, noticeable ontogenetic dietary changes have been observed by increasing the consumption of larger prey items (Yan et al., 2011; Mammel et al., 2022).

However, except in May, the δ¹³C values of largehead hairtails in our study did not reflect isotopic changes with body size. This result suggests that they may feed on similar dietary sources among size classes and that their dietary overlap may be relatively high. Although many fish species tend to have the potential for resource and trophic niche partitioning because of differences in their size-dependent distribution depths and feeding behaviors, no correlations in the δ¹³C values among size classes of largeheads were inconsistent with the stable isotope and/or stomach content results indicated by several previous studies (Pinnegar and Polunin, 2000; Bode et al., 2004; Collins et al., 2005; Park et al., 2018). This tendency may increase intraspecific competition and cannibalism of feeding behavior for largehead hairtails, with no size-dependent patterns in resource use. Cannibalism has been reported as a general phenomenon in the hairtail species in coastal waters to efficiently control population stock and species abundance (Lin et al., 2005; Yan et al., 2012; Mammel et al., 2022). However, in our study, such cannibalism was not observed in any size class during the stomach contents analysis of largehead hairtails (Chiou et al., 2006).

TABLE 3 δ^{13}C and δ^{15}N values and trophic position (TP) of large-head hairtail *Trichiurus japonicus* and other fish consumers collected during February, May, August, and November 2021 in the South Sea of Korea.

Month	Species name	Code	n	δ^{13}C		δ^{15}N		TP
				Mean	S.D.	Mean	S.D.	
February	*Trichiurus japonicus*	Tj	20	−18.6	0.4	11.3	1.2	3.43
	Acropoma japonicum	Ac	3	−18.1	0.5	10.9	0.9	3.32
	Ateleopus japonicus	At	3	−16.7	0.7	12.5	0.1	3.79
	Aulopus japonicus	Au	3	−17.0	0.2	10.9	0.7	3.30
	Caranx equula	Ce	1	−17.7		8.8		2.70
	Dentex tumifrons	Dt	3	−17.7	0.4	13.0	0.5	3.94
	Doederleinia berycoides	Db	1	−21.8		13.6		4.12
	Hoplobrotula armata	Ha	3	−17.9	0.2	11.8	0.2	3.56
	Lepidotrigla microptera	Lm	3	−17.7	0.5	10.8	0.4	3.28
	Loligo japonica	Lj	3	−19.0	0.0	10.6	0.7	3.23
	Lophius litulon	Ll	3	−17.8	0.9	12.1	0.2	3.67
	Pagrus major	Pm	3	−16.6	0.4	13.8	0.7	4.17
	Saurida elongata	Se	2	−17.2	0.3	13.0	0.4	3.92
	Scomberomorus niphonius	Sn	3	−18.8	0.1	12.2	0.6	3.69
	Thamnaconus modestus	Tm	3	−18.4	0.7	11.2	0.1	3.40
	Todarodes pacificus	Tp	3	−19.8	0.6	11.3	0.1	3.43
	Trachurus japonicus	Tr	3	−17.2	0.8	11.4	0.5	3.46
	Zenopsis nebulosa	Zn	3	−17.5	0.5	12.1	0.3	3.66
	Zeus faber	Zf	1	−17.5		12.6		3.81
May	*Trichiurus japonicus*	Tj	20	−19.8	0.8	10.8	0.7	3.20
	Argentina kagoshimae	Ak	3	−18.2	0.1	10.9	0.2	3.22
	Aulopus japonicus	Au	3	−19.4	0.6	10.4	0.2	3.07
	Beringraja pulchra	Bp	3	−17.3	0.3	11.2	0.3	3.33
	Caranx equula	Ce	3	−19.5	0.2	10.4	0.9	3.09
	Champsodon snyderi	Cs	1	−20.7		9.5		2.83
	Dentex tumifrons	Dt	3	−18.6	0.3	11.9	0.2	3.53
	Eopsetta grigorjewi	Eg	3	−18.4	0.5	10.2	0.4	3.02
	Hoplobrotula armata	Ha	1	−18.5		10.7		3.19
	Lepidotrigla guntheri	Lg	3	−19.1		10.6		3.14
	Loligo bleekeri	Lb	3	−18.3	0.4	12.0	0.3	3.57
	Loligo edulis	Le	3	−18.4	0.4	11.8	0.3	3.50
	Lophius litulon	Ll	3	−18.1	0.7	12.8	0.2	3.78
	Pagrus major	Pm	3	−17.5	0.0	12.3	0.5	3.66
	Saurida microlepis	Sm	3	−17.4	0.3	13.3	0.4	3.95
	Sebastiscus tertius	St	1	−18.9		11.2		3.33
	Sepiella japonica	Sj	1	−18.2		10.8		3.22
	Sphyraena pinguis	Sp	3	−18.9	0.3	12.4	0.2	3.69
	Synodus macrops	Sm	3	−18.8	0.1	10.4	0.1	3.09
	Todarodes pacificus	Tp	3	−18.6	0.1	11.3	0.7	3.34
	Trachurus japonicus	Tr	1	−20.8		9.8		2.90
	Upeneus japonicus	Uj	3	−18.2	0.2	12.1	0.4	3.59
	Zenopsis nebulosa	Zn	3	−18.6	0.5	11.7	0.2	3.47
	Zeus faber	Zf	3	−18.0	0.6	11.9	0.3	3.54
August	*Trichiurus japonicus*	Tj	18	−18.2	0.3	10.9	0.6	2.82
	Argentina kagoshimae	Ak	1	−18.6		10.8		2.81

(Continued)

TABLE 3 Continued

Month	Species name	Code	n	δ¹³C Mean	δ¹³C S.D.	δ¹⁵N Mean	δ¹⁵N S.D.	TP
	Beringraja pulchra	Bp	1	−17.5		10.9		2.85
	Branchiostegus japonicus	Bj	3	−18.8	0.2	10.8	0.4	2.82
	Caranx equula	Ce	3	−18.5	0.5	11.7	0.2	3.08
	Conger myriaster	Cm	1	−19.4		11.9		3.13
	Dentex tumifrons	Dt	3	−18.7	0.4	11.7	0.1	3.08
	Eopsetta grigorjewi	Eg	1	−17.9		9.6		2.46
	Hoplobrotula armata	Ha	3	−17.9	0.1	11.1	0.6	2.90
	Loligo bleekeri	Lb	3	−18.3	0.1	11.4	0.3	2.99
	Pagrus major	Pm	3	−17.7	0.2	12.1	0.2	3.21
	Psenopsis anomala	Pa	1	−18.4		10.9		2.86
	Saurida undosquamis	Su	3	−17.8	0.4	12.3	0.2	3.27
	Scorpaena izensis	Si	1	−17.9		11.0		2.87
	Sepia esculenta	Se	3	−18.7	0.4	10.2	0.3	2.64
	Sepiella japonica	Sj	1	−18.2		11.3		2.95
	Thamnaconus modestus	Tm	3	−19.0	0.1	10.6	0.4	2.77
	Todarodes pacificus	Tp	3	−19.1	0.4	10.7	0.6	2.79
	Trachurus japonicus	Tr	3	−19.3	0.5	10.6	0.3	2.75
	Watasenia scintillans	Ws	3	−18.5	0.2	10.8	0.6	2.81
	Zenopsis nebulosa	Zn	3	−18.6	0.4	10.5	0.0	2.74
	Zeus faber	Zf	3	−17.4	0.2	11.9	0.3	3.13
November	***Trichiurus japonicus***	Tj	37	−18.3	0.5	11.2	0.6	3.50
	Argentina kagoshimae	Ak	3	−18.3	0.2	11.0	0.0	3.44
	Aulopus japonicus	Au	1	−18.4		11.0		3.46
	Caranx equula	Ce	3	−18.3	0.4	11.4	0.2	3.58
	Dentex tumifrons	Dt	3	−18.2	0.0	12.1	0.1	3.77
	Hoplobrotula armata	Ha	3	−17.7	0.4	11.8	0.8	3.70
	Lepidotrigla guentheri	Lg	1	−18.6		10.1		3.20
	Loligo edulis	Le	3	−18.6	0.4	10.9	0.6	3.41
	Pagrus major	Pm	5	−17.0	0.6	12.6	0.3	3.93
	Saurida wanieso	Sw	1	−17.2		12.5		3.89
	Scomber japonicus	Sj	3	−16.6	0.2	10.7	0.1	3.35
	Thamnaconus modestus	Tm	3	−18.3	0.6	11.7	0.0	3.66
	Trachurus japonicus	Tr	3	−18.1	0.3	11.2	0.4	3.50
	Upeneus japonicus	Uj	1	−17.1		11.8		3.68
	Zenopsis nebulosa	Zn	6	−17.7	0.4	11.3	0.6	3.53
	Zeus faber	Zf	10	−16.9	0.2	12.2	0.4	3.81

Data represent mean ± 1SD.

Interestingly, the significant negative correlation between the size and δ¹³C of largehead hairtails in May could disagree with the observations of common fishes that can feed on a variety of food types through opportunistic strategies by enhanced prey-catchability with growth (Le Loc'h et al., 2008; Boyle et al., 2012). Moreover, for some fish species, larger individuals may generally inhabit deeper waters than smaller individuals, to divide habitats and dietary resources (Adin and Mueter, 2007; Park et al., 2018). The enhanced swimming ability of largeheads with growth may allow large individuals to feed on pelagic fishes rather than on dominant zooplankton groups (Yan et al., 2011). However, the high contribution (approximately 93%) of Euphausiacea to the diet of the largest group (AL, > 15 cm) in May, observed by stomach content analysis, may support our isotopic results. Such a large proportion of Euphausiacea as a food source for largehead hairtails may result in a relationship that has lower δ¹³C values compared with the smaller groups and other benthic/benthopelagic feeders. In addition, the relatively high contribution and low diversity of Euphausiacea as a dietary source during a specific season can be explained by food availability due to their dense patch distribution

(Martins et al., 2005), leading to a tight connection between pelagic prey sources and large individuals. Thus, despite the seasonal variability of prey composition and isotope values for largehead hairtails, Euphausiacea may be its most important dietary component in the South Sea of Korea.

4.3. Seasonal and size-related variability in the TPs of largehead hairtail

The TP value of a species is generally influenced by changes in prey items, feeding strategies, and environmental factors (Lorrain et al., 2015; Park et al., 2018; Wang et al., 2022). The $\delta^{15}N$ values of fish consumers based on the enrichment of ^{15}N due to prey-predator interactions have been used for the calculation of TP (Post, 2002). Most fish species commonly have a positive relationship between body length and TP, resulting from increased $\delta^{15}N$ values as they grow (Pinnegar and Polunin, 2000). Our study also showed positive relationships between TPs and ALs in each season, except in winter, suggesting an ontogenetic change in largehead hairtail diets with increasing body length. However, the seasonal TPs of this species may not be affected by general size, because of the discrepancy in the AL distributions and TPs between February (11.6 ± 4.0 cm and 3.4 ± 0.4, respectively) and August (17.0 ± 3.2 cm and 2.8 ± 0.2, respectively). The relatively high TPs for largehead hairtails in February with small ALs likely resulted from the large contribution of Pisces to their diets, as observed by stomach analysis. Moreover, temporal variation in the $\delta^{15}N$ values of trophic baselines (i.e., phytoplankton) has been previously reported in coastal waters of temperate regions (Fry and Sherr, 1984; Kang et al., 2009), likely resulting in seasonal variability in the $\delta^{15}N$ values of dominant zooplankton groups due to trophic interactions, as shown by our isotopic results. The seasonal variability in the TPs of largehead hairtails in our study may be explained by differences in major prey items with seasonally different $\delta^{15}N$ values.

5. Conclusion

Our study revealed the seasonal and size-related patterns in the feeding strategy and dietary composition of largehead hairtails in the South Sea of Korea, exhibiting temporal contrasting differences in the major prey items of Pisces and Euphausiacea, and ontogenetic dietary changes through the combination of stomach and stable isotope analyses. The feeding ecology of largehead hairtails may be opportunistic carnivorous feeding on available dietary species. Stomach content analysis showed no evidence of cannibalism throughout all seasons. Our isotopic results showed greater ^{13}C- and ^{15}N-depleted signatures in largehead hairtails than in other large carnivorous fishes, suggesting a high consumption of dietary items with pelagic source affinity. Similarly, this species had intermediate or lower TP values than pelagic and benthic fishes or

other fishes. Overall, our study provides scientific evidence on the feeding characteristics of the highly commercially important fish species largehead hairtails in the western North Pacific, which improves our understanding of their conservation and ecological-based management.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Ethics statement

The animal study was reviewed and approved by Ministry of Oceans and Fisheries, South Korea.

Author contributions

DS and HJP designed the experiments and drafted the manuscript. DS, S-JL, and SK designed field collection and analyzed faunal assemblages. JMJ analyzed the fish stomach contents. THP and C-IL performed the statistical analyses. DS, THP, and HJP wrote the main manuscript text. HJP supervised all processes. All authors analyzed the data and reviewed the manuscript. All authors have read and agreed to the published version of the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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