Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

The relationship between age-growth and feeding habits of the robust tonguefish, Cynoglossus robustus in the coastal waters of Yeosu, South Korea

Seung-Jo Han
National Institute of Fisheries Science
Hae-Won Lee
roundsea@korea.kr

National Institute of Fisheries Science

Research Article

Keywords:

Posted Date: November 25th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11744452/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: No competing interests reported.

The relationship between age-growth and feeding habits of the robust tonguefish, *Cynoglossus robustus* in the coastal waters of Yeosu, South Korea

Seung-Jo Han[1] · Hae-won Lee[*]

S. J. Han
South Sea Fisheries Research Institute, National Institute of Fisheries Science, Yeosu 59780, Republic of Korea

H.W. Lee(✉)
Fisheries Resources Research Center, National Institute of Fisheries Science, Tongyeong 53064, Korea
Corresponding author: Tel: +82. 55. 650. 2220 Fax: +82. 55. 650. 2206
e-mail: roundsea72@gmail.com (Hae Won Lee)

Running title: Relationship between age-growth and feeding habits of robust tonguefish

Abstract

This study comprehensively investigated the relationship between the age, growth, and feeding characteristics of the robust tonguefish (*Cynoglossus robustus*), a commercially important species in the coastal waters of Yeosu, to improve understanding of its ecological adaptation strategies. Gonadosomatic index (GSI) and marginal index (MI) analyses identified the main spawning season as June–August, requiring approximately 1.08 years were required for the formation of first annulus. Back-calculated von Bertalanffy growth parameters exhibited distinct sexual dimorphism, with females (L_∞ = 46.23 cm, k = 0.220 year) reaching a larger asymptotic length than males (L_∞ = 36.91 cm, k = 0.287/year). These sex- and age-specific growth patterns were closely associated with ontogenetic dietary shifts. During early growth (G1–G2),both sexes predominantly consumed amphipods, before gradually shifting to larger prey items, primarily polychaetes and Brachyura. Permutational Multivariate Analysis of Variance (PERMANOVA) and Canonical Analysis of Principal Coordinates (CAP) analyses revealed significant dietary variations driven by ontogenetic somatic growth and seasonal factors. During the peak metabolic spawning season (May–July), mature individuals (G3 and older) consumed small amphipods to minimize foraging costs and alleviate physical gut compression from enlarged gonads. After spawning (August–September), they exhibited compensatory feeding on larger brachyurans to replenish their energy reserves. Collectively these findings indicate that the species exhibits high trophic adaptability and optimizes energy allocation by flexibly adjusting its feeding strategies in response to morphological development, reproductive constraints, and environmental changes.

Keywords: *Cynoglossus robustus*, age and growth, von Bertalanffy growth model, feeding habits, ontogenetic dietary shift, Yeosu.

1. Introdution

To comprehend fluctuations in fishery resources and manage them effectively, analyzing the age structure of a specific fish population is critical for understanding its ecological characteristics and formulating appropriate management strategies (King 2013; Lee et al. 2024). Research on the age and growth of fish provides the foundational data necessary to identify parameters, such as age at recruitment and maturity (Kim et al. 2024), lifespan (La Mesa and Eastman 2024), growth rate (Froese 2006; Flinn and Midway 2021), and mortality rate (Ragheb et al. 2024). Consequently, these data are essential for evaluating population productivity and resilience to fishing pressure (Zhang 2012).

In general, marine organisms are subjected to various environmental changes within their habitats throughout their growth and development (Chasco et al. 2022; Li et al. 2022). Fish growth is heavily influenced not only by prey availability, which supplies the energy required for both somatic growth and reproductive allocation (Kuzuhara et al. 2019; Slesinger et al. 2022), but also by environmental factors such as water temperature and photoperiod. Growth pattern may also exhibit spatiotemporal variation driven by these environmental factors, as well as by harvest-induced evolution resulting from persistent fishing pressure (Daufresne et al. 2009; Audzijonyte et al. 2013; Eikeset et al. 2016; Hočevar and Kuparinen 2021).

The growth trajectory of fish cannot be adequately explained by a simple increase in body length with age (Morrongiello and Thresher 2015; Lorenzen 2016). Rather, growth is strongly influenced by changes in prey availability and differences in feeding intensity among life stages, particularly through ontogenetic dietary shifts and seasonal patterns of prey use (Graeb et al. 2004; Denechaud et al. 2020; Nunn et al. 2012; Loutrage et al. 2024).

The target species in the present study, the robust tonguefish (*Cynoglossus robustus*), belongs to the family Cynoglossidae within the order Pleuronectiformes. According to fishery statistics for the past decade, this species is primarily harvested using coastal and offshore gill nets, improved coastal stow nets, and large trawl nets. In particular, the species has an average annual production of approximately 1,536 tons in the southern coastal waters of Korea, accounting for 83.0% of the total domestic catch and highlighting its commercially importance (KOSIS 2026).

Previous studies have generally examined age and growth or feeding ecology separately.

Studies on age and growth were predominantly conducted in the early 2000s in the coastal

water of Yeosu (Baeck 2003; Seo et al. 2007) and adjacent Japanese waters (Katayama and Yamamoto 2012; Park et al. 2013). Research on feeding ecology has been conducted in select regions, including the South Sea of Korea (Choi et al. 2024), Yeosu coastal waters (Baeck and Huh 2004; Han and Moon 2026), and Japan's Seto Inland Sea (Baeck et al. 2011). However, simultaneously investigate age, growth, and feeding ecology are still scarce.

Notably, most existing studies on age and growth are based on data collected 10-20 years ago, limiting their ability to reflect recent changes in the marine environment and the associated ecological characteristics of current populations. Therefore, a comprehensive understanding of the contemporary life-history traits of this species requires an integrated analysis of age, growth, and feeding ecology.

Because long-term changes in marine environment and ecosystems can alter prey communities and fish feeding behavior, there by influencing growth patterns (Hunt et al. 2025; Taniguchi et al. 2026). Therefore, a comprehensive understanding of the life-history strategies and resource status of a specific species, requires an integrated approach that goes beyond examining age and growth alone and concurrently evaluates ontogenetic shifts in feeding ecology and growth patterns.

Taking these into consideration, the present study aimed to investigate the age and growth characteristics of *C. robustus* using otolith analysis, together with its feeding ecology in the coastal waters of Yeosu, a major habitat for this species. In addition, dietary shifts associated with different growth stages were examined to elucidate the relationship between growth and feeding ecology. Through this integrated approach, the study provides baseline information on regional and seasonal variation and feeding characteristics, contributing to a better understanding of the life-history traits of the population and supporting effective resource management.

2. Materials and methods

2.1 Sample collection

The specimens used in this study were collected monthly from September 2023 to December 2024 in the coastal waters of Yeosu (Naro, Baek, and Geomun Islands) using coastal gill nets and shrimp beam trawls (Fig. 1). Of the total specimens collected, 1,019 individuals sampled from September 2023 to August 2024 were used for age and growth analysis, whereas 1,210

individuals sampled from January to December 2024 were used for feeding ecology analyses.

The collected specimens were transported to the laboratory, where total length (TL) was measured to the nearest 0.1 cm, while body weight (BW) and gonad weight (GW) were measured to the nearest 0.01 g. The gonadosomatic index (GSI) was calculated using the following equation (Eq. 1).

$$GSI = (GW/BW) \times 100 \quad (1)$$

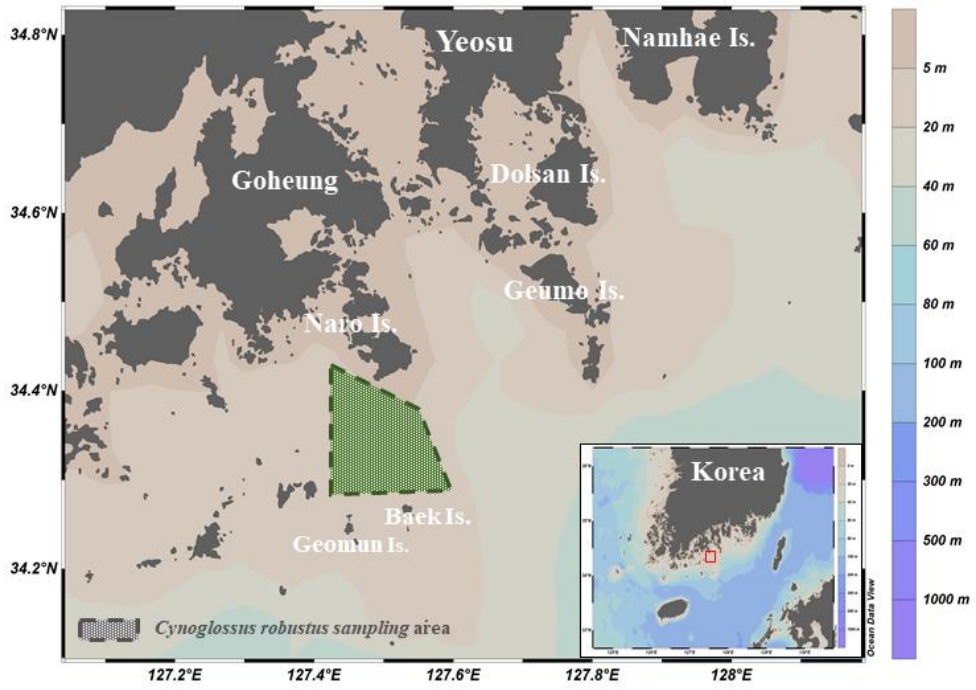


Fig. 1. Map showing the sampling locations of in the coastal waters of Yeosu, South Korea.

2.2 Otolith preparation and reading

Right otoliths (ocular side) were extracted, cleaned of organic matter, washed with distilled water and alcohol, and stored in 24-well plates. The otoliths were embedded in a silicone molds coated with a release agent (Buehler) using a mixture of epoxy resin (EpoThin™ 2 Epoxy Resin, Buehler) and hardener (EpoThin™ 2 Epoxy Hardener, Buehler), and were cured for 72 hours. Subsequently, the embedded otoliths were ground to the core using a grinder (ISOMET 1000, Buehler) and sandpaper (CarbiMet™, P400–P4000). The surfaces were polished with alumina (MicroPolish 0.05 μm, Buehler, Germany) and mounted on glass slides.

120 The annulus was identified as the boundary between translucent and opaque zones. The
121 otolith radius (OR) and the radius of each ring (r_n) from the core to the posterior edge were
122 measured using a stereomicroscope (SZX16, Olympus) equipped with image analysis software
123 (RisingView, Rising Technology). To validate the timing of annulus formation, the monthly
124 marginal index (MI) was calculated using the following equation (Eq. 2).

125 $$MI = \frac{OR - r_n}{r_n - r_{n-1}} \quad (2)$$

126 (OR: otolith radius; r_n: distance from the core to nth annulus)

127

128 2.3 Growth equation and growth performance index

129 The von Bertalanffy (1938) growth equation (Eq. 3) was fitted using the back-calculated
130 mean total length for each age group. The parameters of the growth equation were optimized
131 via least-squares nonlinear regression using the Solver tool in Excel (Microsoft, Redmond, WA,
132 USA) based on initial estimates derived from a Walford plot (Walford 1946). The Solver
133 options were configured as follows: the GRG Nonlinear solving method, convergence criterion
134 of 0.0001, central derivatives, population size of 100, and random seed of 0.

135 $$L_t = L_\infty(1 - e^{-k(t-t_0)}) \quad (3)$$

136 (L_t : total length at age t, L_∞: theoretical maximum total length, *k*: growth coefficient, t_0:
137 theoretical age at zero length)

138

139 To compare the estimated growth parameters with those of previous studies, the growth
140 performance index (Φ') proposed by Munro and Pauly (1983) was calculated using Eq. 4.

141 $$\Phi' = \log k + 2\log L_\infty \quad (4)$$

142

143 2.4 Stomach content analysis

144 For the monthly stomach content analysis, individual stomachs were extracted, fixed in 10%
145 neutral buffered formalin, and dissected under a stereomicroscope (SZX16, Olympus
146 Corporation, Tokyo, Japan). The prey organisms were identified using standard taxonomic
147 guidelines (Kim et al. 2005; Hong et al. 2006). The number of individuals of each prey item
148 was counted, and the wet weight of each taxonomic group was measured to the nearest 1.0 μg
149 using a microbalance (XP26, Mettler-Toledo International Inc., Greifensee, Switzerland) after
150 removing excess moisture with filter paper (Whatman GF/F glass microfiber filters, Cat. No.

1825-047, 47 mm). The results of the stomach content analysis were expressed as frequency of occurrence (*%F*), percentage by number (*%N*), and percentage by wet weight (*%W*), which were calculated using the following equations (Eqs. 5–7).

$$\%F = A_i / N \times 100 \quad (5)$$

$$\%N = N_i / N_{total} \times 100 \quad (6)$$

$$\%W = W_i / W_{total} \times 100 \quad (7)$$

(A_i: number of stomachs containing prey *i*, *N*: total number of stomachs containing food, N_i: number of individuals of prey *i*, N_{total}: total number of all prey individuals, W_i: wet weight of prey *i*, W_{total}: total wet weight of all prey)

The index of relative importance (*IRI*) for each prey item was calculated following Pinkas et al. (1971) (Eq. 8). The calculated *IRI* values were expressed as percentages (*%IRI*) (Eq.9).

$$IRI = (\%N + \%W) \times \%F \quad (8)$$

$$\%IRI = (IRI_i + \sum_{i=1}^{n} IRI) \times 100 \quad (9)$$

2.5 Statistical analysis of dietary variations

Two-way permutational multivariate analysis of variance (ANOVA) was conducted to test for differences in diet across age groups and seasons. To reduce the frequency of zero values in the stomach content data and to enhance the robustness of the multivariate analysis, the mean percentage of wet weight (*%W*) was calculated for small, randomly pooled groups of five individuals categorized by age, month, and sex (White et al. 2004; Marshall et al. 2008).

To reduce data bias, the dietary data were $log_{(x+1)}$-transformed, and a Bray–Curtis similarity matrix was generated. PERMANOVA was used to analyze the variance explained (R^2) by the main factors (age, month, and sex) and their interactions. When a statistically significant difference was detected ($p < 0.05$), a CAP was performed to visualize group separation.

The major prey taxa driving the dietary differences were identified using overlay vectors with a Spearman's correlation coefficient of 0.4 or greater. All statistical analyses were performed using the 'vegan' package (version 2.6–8) in the R programming environment (version 4.4.1) (R Core Team 2024; Oksanen et al. 2024).

3. Results

3.1 Total length composition and spawning season

A total of 1,419 individuals were used in this study, with the total length (TL) ranging from 13.8 to 43.8 cm and a mean TL of 30.7 ± 4.2 cm (Fig.2). Among them, the 30.0–35.0 cm length class accounted for the highest proportion, with 605 individuals (42.6%), followed by the 25.0–30.0 cm class, with 441 individuals (31.1%) (Table 1).

The monthly mean TL was lowest in November 2023 at 28.1 ± 3.2 cm and highest in February 2024 at 35.8 ± 2.6 cm. Regarding sex-specific differences, the mean TL of females (32.4 ± 2.5 cm) was significantly greater than that of males (29.5 ± 2.1 cm) (t-test, $p < 0.05$).

Monthly changes in the GSI were analyzed to determine the spawning season of females and males. In both sexes, the GSI began to increase in June 2024, peaked in July at 5.7 ± 2.3 for females and 0.27 ± 0.0 for males, and then decreased to its lowest levels in September. Consequently, the spawning season was estimated to occur between June and August (Fig. 3).

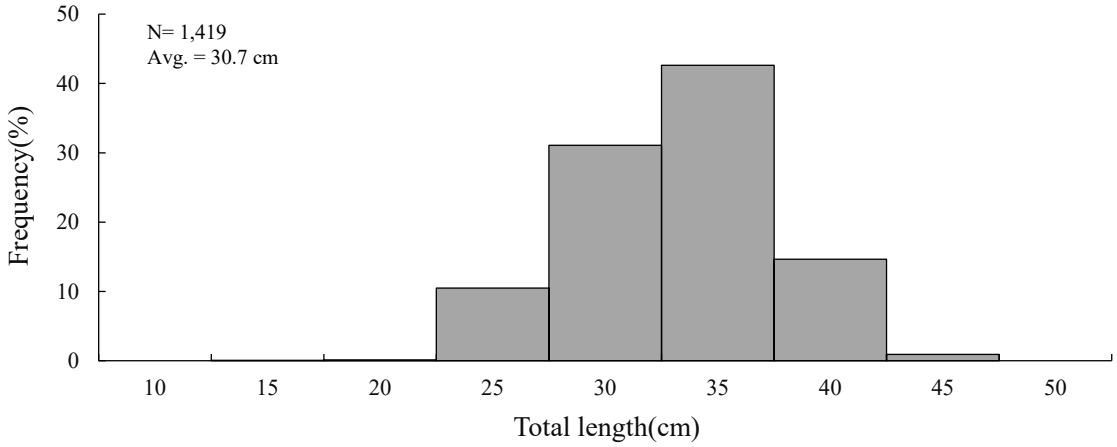


Fig. 2. Length frequency distribution of *C. robustus* from the coastal waters of Yeosu, South Korea.

Table 1. Monthly variations in mean total length and size range of *C. robustus* sampled from the coastal waters of Yeosu, South Korea, from september 2023 to december 2024. Inds., individuals; TL, total length

Year	Month	Female			Male		
		Mean TL ± SD(cm)	Range of Total length(cm)	No. of Inds.	Mean TL ± SD(cm)	Range of Total length(cm)	No. of Inds.
2023	Sep.	29.4±4.0	19.3-38.2	59	28.8±3.0	21.6-38.3	40
	Oct.	30.3±5.0	18.0-39.4	35	29.1±5.1	13.8-38.2	31
	Nov.	32.7±4.2	26.2-41.0	21	27.7±2.1	25.3-32.0	9
	Dec.	33.2±4.3	25.8-40.2	12	32.6±0.4	32.2-33.0	2
2024	Jan.	32.0±3.5	22.0-38.8	73	28.1±3.7	21.5-36.3	47
	Feb.	36.2±2.6	31.5-42.8	81	34.3±2.0	30.8-38.2	19
	Mar.	29.1±4.4	20.3-39.3	44	27.9±3.8	21.0-42.1	76
	Apr.	35.4±2.7	25.1-43.8	74	30.1±2.7	23.4-35.8	46
	May	30.2±3.2	24.5-38.5	58	28.9±2.5	23.4-34.5	62
	Jun.	31.9±3.4	22.5-38.4	41	27.7±2.6	23.4-33.1	49
	Jul.	34.5±4.5	24.4-42.6	47	28.4±3.1	23.8-33.5	43
	Aug.	34.2±2.6	30.6-40.1	15	30.4±3.1	24.2-36.2	75
	Sep.	33.2±2.0	29.3-39.2	51	31.0±1.5	27.4-35.8	39
	Oct.	31.1±2.3	27.0-35.4	25	28.3±3.4	22.0-34.6	65
	Nov.	28.6±3.5	23.5-35.5	26	28.6±3.4	22.0-34.9	64
	Dec.	29.2±4.2	23.0-35.3	36	29.2±3.6	21.7-34.4	54
Total		32.3±4.3	18.0-43.8	698	29.1±3.5	13.8-42.1	721

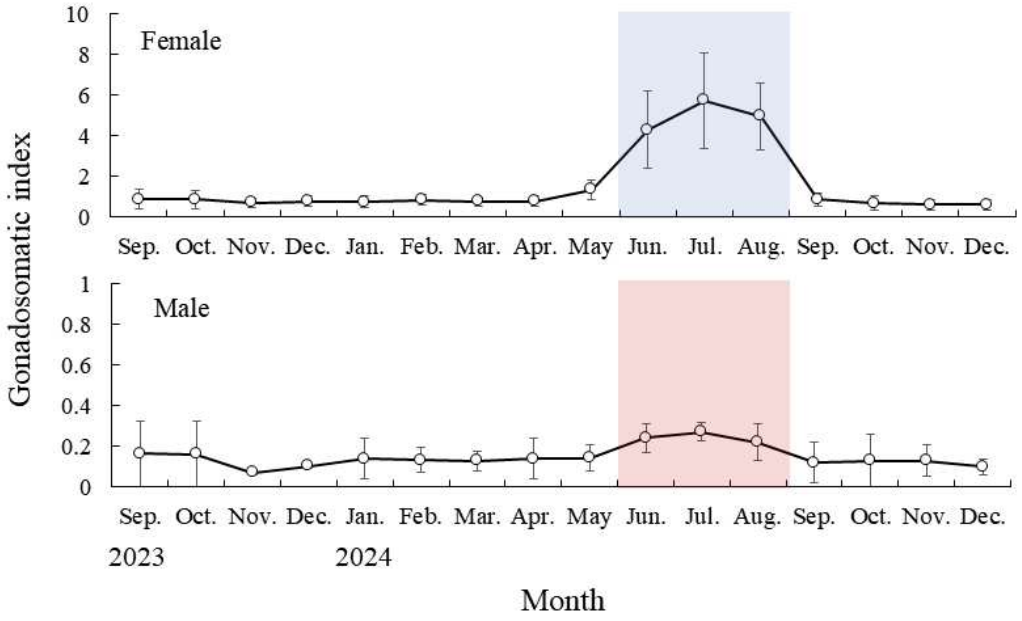


Fig 3. Monthly variations in gonadosomatic index (GSI) of the collected from the coastal waters of Yeosu, South Korea, from september 2023 to december 2024.

3.2 Age and growth

3.2.1 Relative growth

Among the 1,019 specimens collected between September 2023 and August 2024, individuals with damaged or unreadable otoliths were excluded. Consequently, 883 specimens (459 females and 424 males) were analyzed.

To examine the the relationship between body weight and total length, the length-weight relationships of females and males were compared. The results indicated that females grew faster than males in terms of both total length and body weight (Fig.4).

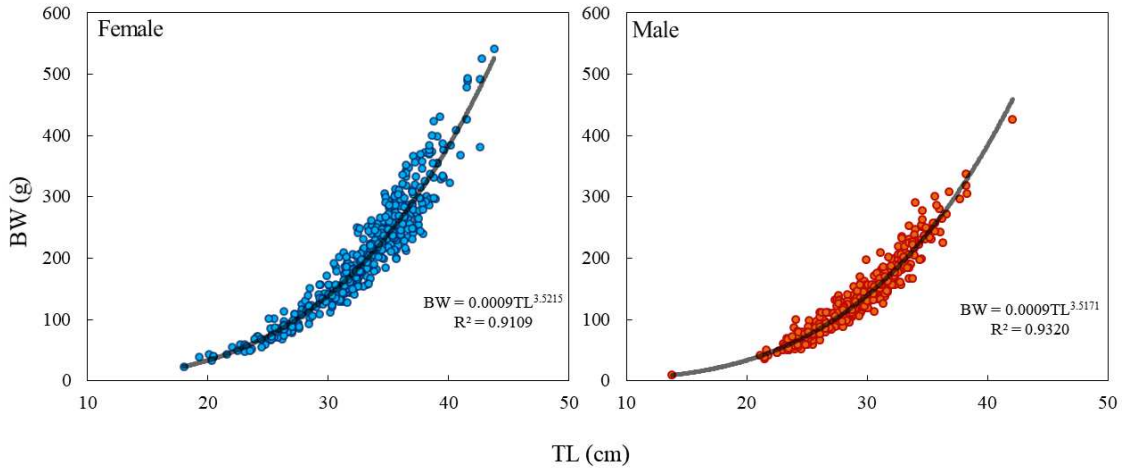


Fig. 4. Relationship between total length and body weight of *C. robustus* in the coastal waters of Yeosu, South Korea.

3.2.2. Period of annulus formation

The monthly marginal index (MI) was calculated to validate the timing of annulus formation. The MI was lowest in September 2023 for both females (0.51) and males (0.49). This finding indicated that one annulus was formed annually in September**.** Considering the peak spawning season (July), it was estimated that approximately 1.08 years (13 months) were estimated to elapse from hatching to the formation of the first annulus (Fig. 5).

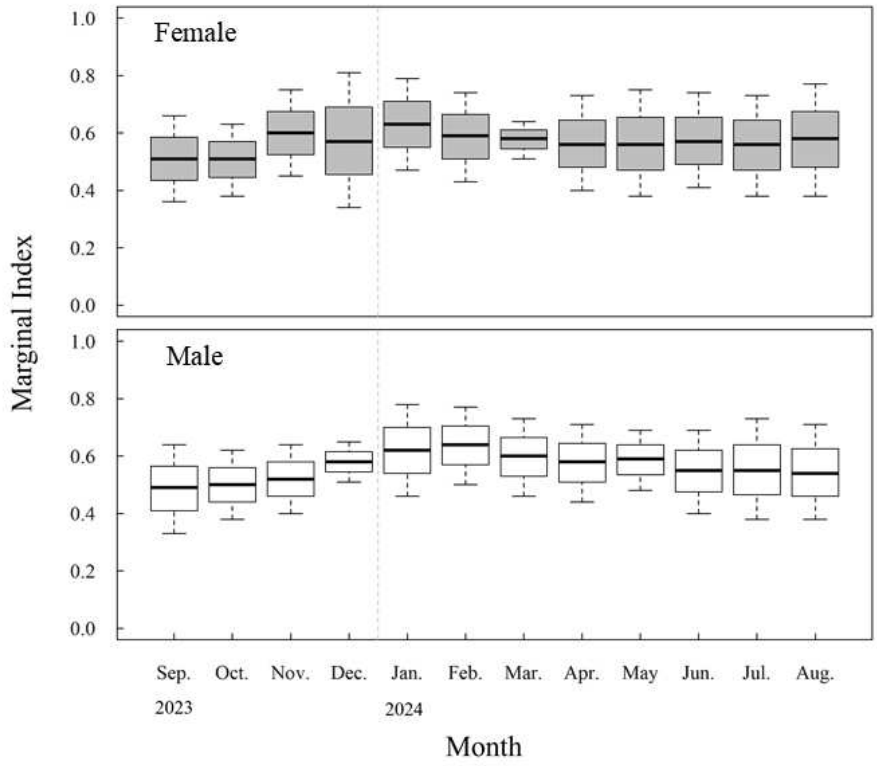


Fig. 5. Monthly changes in marginal index (MI) of *C .robustus* in the coastal waters of Yeosu, South Korea.

3.2.3 Growth equations

To back-calculate the total length at the time of annulus formation, the relationship between otolith radius (*R*) and total length (TL) was determined. The relationship equations for females and males are presented in Eqs. 10 and 11, respectively (Fig. 6).

$$\text{Female} \quad : \quad \text{TL} = 10.727\text{R} + 1.0666\,(\text{R}^2 = 0.8157) \qquad (10)$$

$$\text{Male} \quad : \quad \text{TL} = 10.579\text{R} + 1.4701\,(\text{R}^2 = 0.6917) \qquad (11)$$

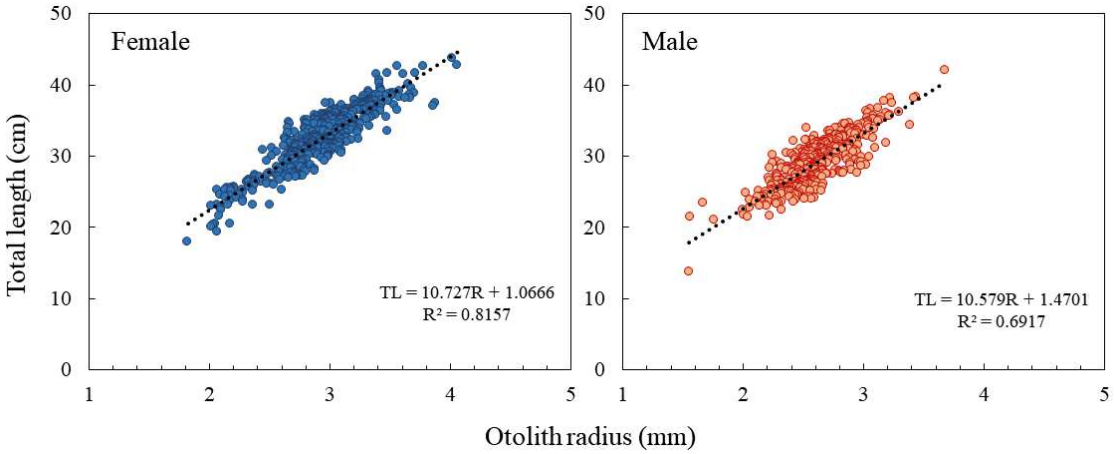


Fig. 6. Relationship between otolith radius and total length of *C. robustus* in the coastal waters of Yeosu, South Korea.

Based on the growth parameters estimated from the Walford plot using these back-calculated lengths, the von Bertalanffy growth equations for females and males were established using Eqs. 12 and 13.

$$\text{Female} \quad : \quad L_t = 46.23(1 - e^{-0.220(t+1.886)}) \qquad (12)$$

$$\text{Male} \quad : \quad L_t = 36.91(1 - e^{-0.287(t+1.682)}) \qquad (13)$$

For female, the estimated growth parameters were a theoretical maximum total length (L_∞) of 46.23 cm, a growth coefficient (k) of 0.220/year, and a theoretical age at zero length (t_0) of –1.886 years. For males, the theoretical maximum total length (L_∞) was estimated at 36.91 cm, the growth coefficient (k) at 0.287/year, and the theoretical age at zero length (t_0) at –1.682 years (Fig.7).

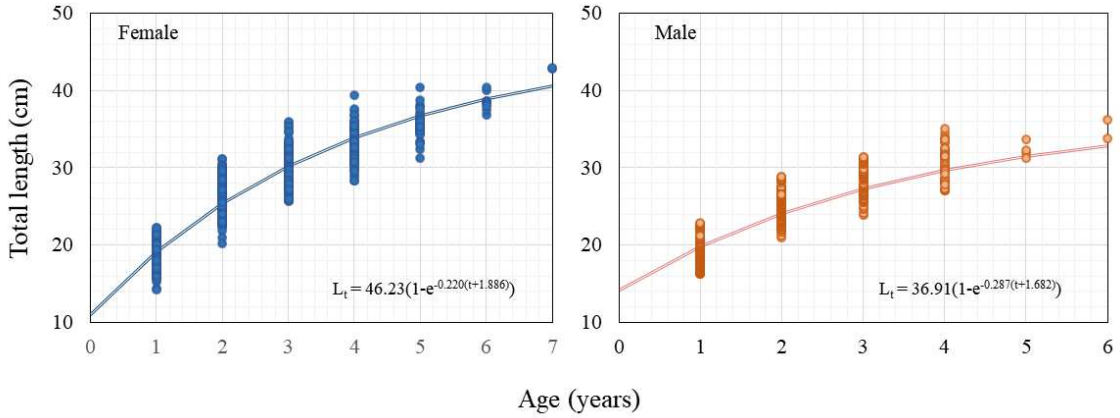


Fig. 7. von Bertalanffy growth curves in total length of *C. robustus* in the coastal waters of Yeosu, South Korea, estimated by non-linear regression method

Subsequently, to statistically test for differences in the von Bertalanffy growth curves between females and males, an analysis of the residual sum of squares (ARSS) and likelihood ratio test (LRT) were conducted concurrently. Through the ARSS, the statistical significance of the residuals between the models was evaluated using an *F*-test, whereas the LRT was used to analyze the joint differences in the parameters based on a chi-square test. Both analyses indicated significant sex-related differences in growth ($p < 0.05$) (Table 2).

Table 2. Estimated von Bertalanffy growth parameters and statistical comparison between sexes for *C. robustus* in the coastal waters of Yeosu, South Korea

Species	Sex	No. of Inds.	Growth Parameters			Method					
						ARSS			LRT		
			L_∞	k	t_0	*F*-value	*df*	*p*-value	χ^2-value	*df*	*p*-value
C. robustus	Female	459	46.23	0.220	-1.866	22,489.9	31,013	<0.05	4,293.5	3	<0.05
	Male	424	36.91	0.287	-1.682						

3.3 Dietary shifts across age groups

Based on the back-calculated total lengths, the stomach contents of 1,210 specimens collected from January to December 2024 were categorized into seven age groups: G1 (≤ 22 cm and below, ≤ year), G2 (22–27 cm, 2 years), G3 (27–31 cm, 3 years), G4 (31–34 cm, 4 years), G5 (34–37 cm, 5 years), G6 (37–40 cm, 6 years), and G7 (≥ 40 cm, ≥ 7 years). The

analysis revealed distinct ontogenetic dietary shifts and sex-specific differences in feeding habits.

Regarding the overall dietary pattern, Amphipoda dominated the diets of the G1 and G2 groups (≤ 27 cm), accounting for 68.4% and 58.6% of the index of relative importance (*%IRI*), respectively. From G3 onwards, the proportion of amphipods progressively decreased. In contrast, the consumption of Polychaeta and Brachyura increased; the proportion of polychaetes increased significantly in G6 (36.8%) and G7 (53.3%), whereas that of brachyuras increased from G3 (9.4%) to G5 (28.3%). Additionally, prey such as bivalves were consumed as supplementary items, depending on age group and sex (Fig.8).

Regarding sex-specific dietary shifts with increasing age, females showed a decreasing reliance on amphipods, which declined from 45.9% in G2 to 25.2% and 22.0% in G6 and G7, respectively. Conversely, the consumption of polychaetes (24.9% in G6 and 41.1% in G7), Brachyura (33.5% in G6), and stomatopods (2.5% in G6) increased with age.

For males, after amphipods dominated the diets in G1 (44.6%) and G2 (52.6%), they remained a major dietary component in G5 (34.7%) and G6 (17.8%). Furthermore, prey items such as Caridea (10.6% in G5) and Cumacea (4.0% in G4) were also consumed.

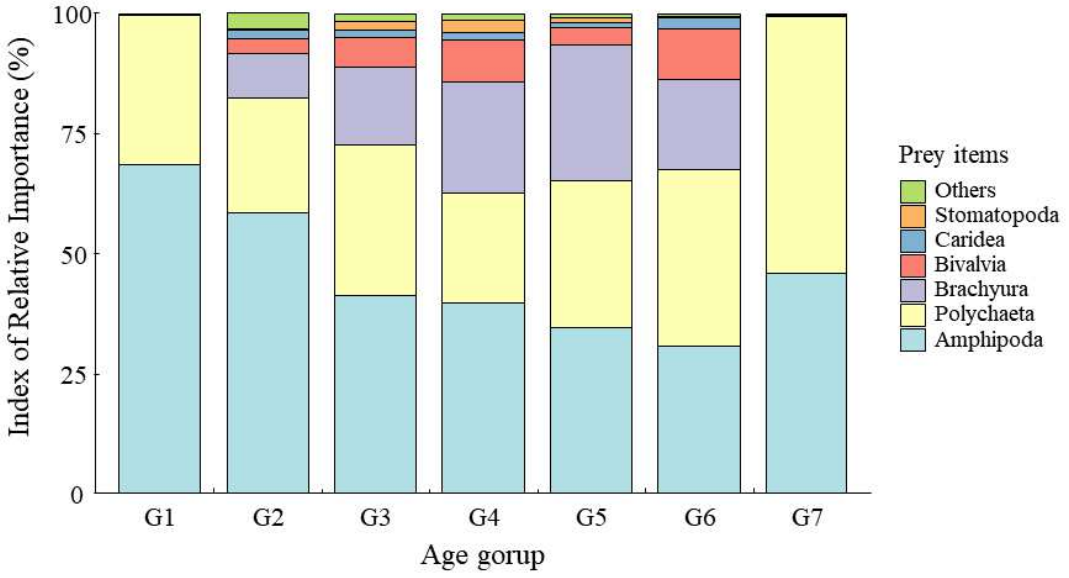


Fig. 8. Ontogenetic dietary shifts in *C. robustus*, in the coastal waters of Yeosu, South Korea, based on the percentage of index of relative importance (*%IRI*) across age groups (G1–G7).

3.4 Seasonal dietary shifts across age groups

Two-way PERMANOVA results (Table 3) revealed that dietary composition differed significantly across both age groups and seasons (months) ($p < 0.05$). The interaction between age group and season was also significant for both sexes (females, $p < 0.05$; males, $p < 0.05$). A comparison of the variance explained (R^2) by each factor showed that the seasonal factor (females: R^2= 0.4617; males: R^2= 0.4149) was substantially higher than the age group factor (females: R^2= 0.0493; males: R^2= 0.0602). This indicates that seasonal effects exerted a strong influence on dietary shifts in *C. robustus* than age-related factor (Table 3).

Table 3. Results of a two-way PERMANOVA based on a Bray-Curtis similarity matrix of prey composition in male and female collected from the coastal waters of Yeosu, South Korea. Shown are the degrees of freedom (*df*), sums of squares (SS), R^2, *F*-values, and *p*-values

Source	Female					Male				
	Df	**SS**	**R^2**	***F*-value**	***p*-value**	**Df**	**SS**	**R^2**	***F*-value**	***p*-value**
Age group	5	0.9296	0.0493	1.8773	0.0251	5	1.2163	0.0602	2.0857	0.0053
Month	11	8.7047	0.4617	7.9900	0.0001	11	8.3824	0.4149	6.5336	0.0001
Age group x Month	35	5.0606	0.2684	1.4599	0.0123	28	4.3050	0.2131	1.3182	0.0438
Residual	42	4.1597	0.2206			54	6.2982	0.3118		
Total	93	18.8546	1.0000			98	20.2020	1.0000		

Based on the PERMANOVA results, a canonical analysis of principal coordinates (CAP) based on the Bray–Curtis similarity matrix was performed. The first axis (CAP1) explained 49.46% of the total variance and the second axis (CAP2) explained 26.08%, together accounting for 75.54% of the total variance. Differences in dietary composition among age groups were primarily separated along CAP1, with polychaetes and Brachyuran crabs serving as the main contributors to group discrimination.

When monthly variations were pooled into seasonal groups, the second axis (CAP2) clearly distinguished the dietary characteristics of the spring–winter group from those of the summer–autumn group. Specifically, greater contributions of polychaetes and amphipods during spring and winter resulted in a clear separation between the seasonal groups. In contrast, Brachyura and Stomatopoda contributed relatively more to the diet during summer and autumn (Fig.9).

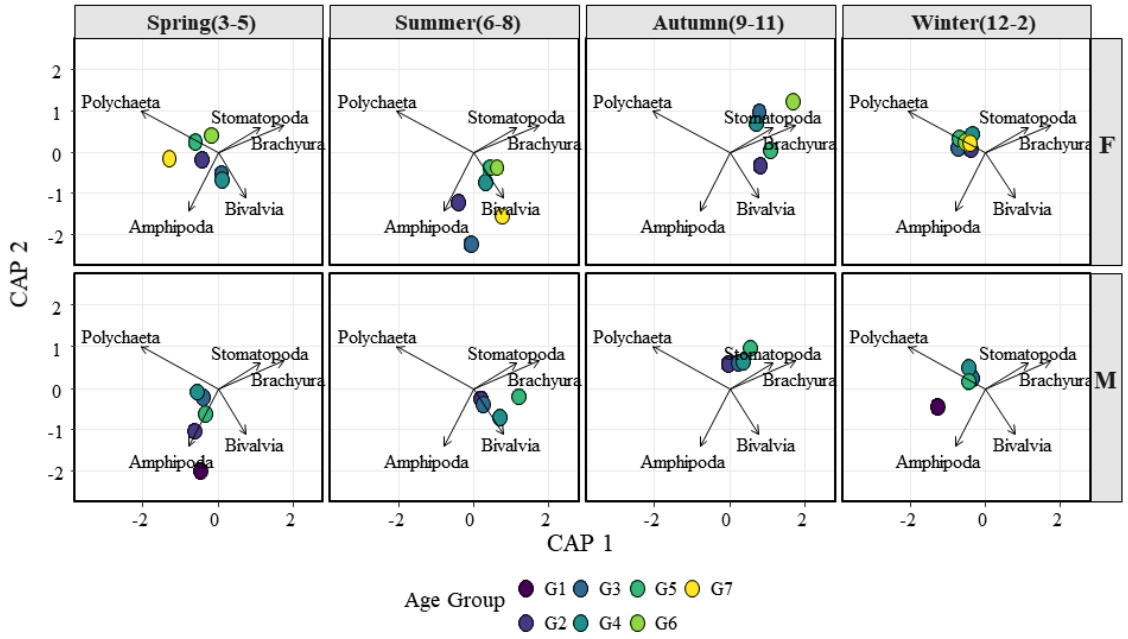


Fig. 9. Canonical analysis of principal coordinates (CAP) based on a Bray-Curtis similarity matrix of prey composition in female (F) and male (M) *C. robustus* collected from the coastal waters of Yeosu, South Korea. Samples are grouped by age class and season.

3.5 Correlation between age groups and major prey composition

Correlation analysis was conducted to examine the relationship between age groups (G1–G7) of *C. robustus* and the percentage wet weight (*%W*) of the five major prey taxa that were previously identified as key distinguishing factors in the CAP. The results revealed a distinct correlation between age and changes in dietary composition, indicating ontogenetic shifts in prey use (Fig.10).

The consumption proportions of Polychaeta, Brachyura, and Bivalvia showed significant positive correlations with age, increasing significantly across age groups ($p < 0.05$). In particular, Bivalvia (R_{mean}= 0.779) and Polychaeta (R_{mean}= 0.763) exhibited strong positive correlations, indicating that their contributions as major prey items increased substantially in older age groups. Conversely, Amphipoda exhibited a strong negative correlation with age, with its consumption proportion decreasing markedly (R_{mean}= –0.764, $p < 0.05$). Stomatopoda also exhibited a negative correlation, although this was not statistically significant (R_{mean}= –0.067, $p > 0.05$).

Consequently, the correlation analysis of the major prey taxa, aligned with the CAP results,

confirmed a distinct ontogenetic shift in the diet of *C. robustus*. The diet transitioned from being dominated by amphipoda in G1 to an increasing reliance on polychaetes and brachyuran in G2–G5, and ultimately to a diet dominated by polychaetes, brachyuran, and bivalves in G6 and G7.

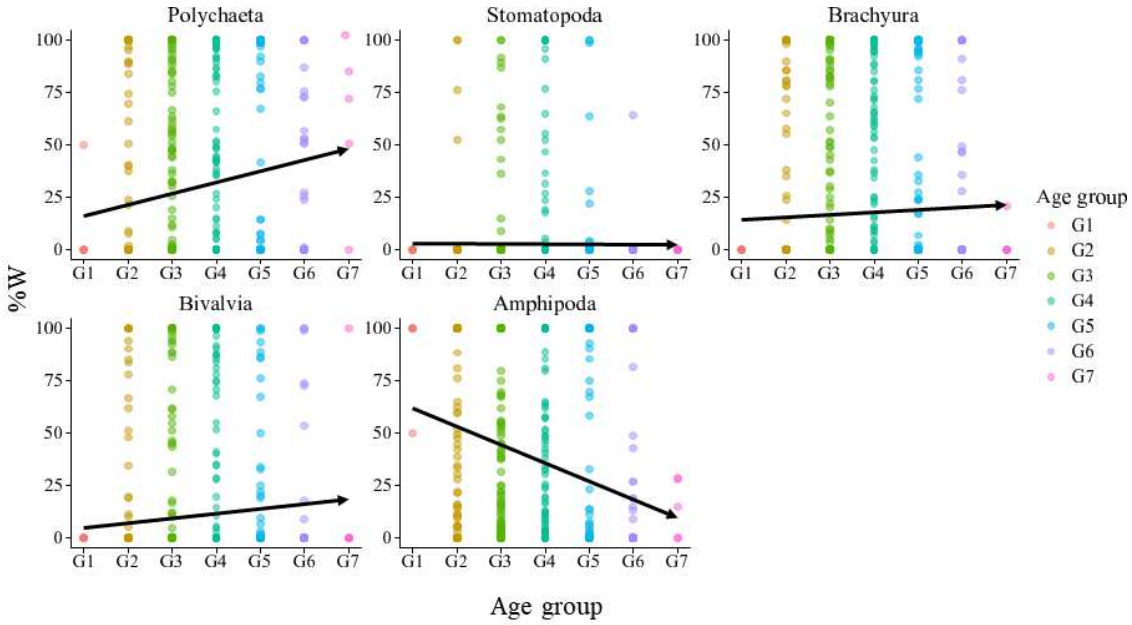


Fig. 10. Relationship between age group and dietary composition (*%W*) of the five major prey groups in *C. robustus* collected from the coastal waters of Yeosu, South Korea.

3. Discussion

In this study, otoliths were used as aging structures for *C. robustus*. Based on the spawning season (as inferred from the GSI) and the marginal index (MI), the time required for the formation of the first annulus was estimated to be approximately 1.08 years (13 months). This is highly consistent with previous studies conducted in the Yeosu coastal waters, which reported 1.27 years (14 months) (Baeck 2003) and 1.25 years (15 months) (Seo et al.2007). The formation of the annulus in September is thought to result from physiological changes and shifts in energy allocation following the peak spawning season in July, which subsequently influences otolith growth (Hüssy et al.2020).

The theoretical maximum total length (L_∞) and growth performance index (Φ') estimated from the growth equations in this study differed from those reported by Seo et al.(2007) (L_∞: 44.29 cm for females, 37.29 cm for males; Φ': 2.57 for females, 2.58 for males). In the present study, the female L_∞ and Φ' values were higher than the previously reported values (46.23 cm

and 2.67, respectively) than those in the previous study, whereas the male parameters were similar (36.91 cm and 2.59, respectively). This discrepancy in growth estimates is likely attributable to the choice of aging structure and annulus reading criteria. Although the present study utilized otoliths, which effectively captured early growth information, including the first annulus, Seo et al.(2007) employed scales and excluded the first annulus from their analysis. Because scales can be lost and regenerated during growth, which affects the accuracy of age determination (Kerr and Campana 2014), and excluding the first annulus fails to adequately reflect early growth data (Thomas and Swearer 2019), these methodological differences likely caused the observed disparities in growth estimates.

The growth coefficient (k) was higher for males (0.287/year) than females (0.220/year), indicating that males experienced an earlier deceleration in growth, whereas females continued to grow toward their maximum length. This sexual dimorphism, characterized by superior female growth, is a common biological trait across the family Cynoglossidae, as observed in *Cynoglossus arel* and *Cynoglossus lida* off the eastern coast of China (Rajaguru 1992), *Cynoglossus semilaevis* in Indian waters (Meng and Ren 1988),and *Cynoglossus abbreviatus* in Jiaozhou Bay (Zhu and Ma 1992). Such sex-specific growth differences are closely related to variations in maturation timing and reproductive energy allocation (Kahl and Radke 2006). In the present study, stomach content analysis revealed that during the early growth stages (G1–G2), both sexes exhibited a similar diet dominated by small prey, specifically amphipods. However, an ontogenetic dietary shift occurred with increasing age; in the older age groups (G6 and G7), females transitioned to larger prey items, such as polychaetes and brachyura, whereas males maintained a diet centered on relatively smaller prey. This pattern suggests that the larger theoretical maximum total length (L_∞) observed in females may be supported by a feeding strategy that secures the energy required for continued growth and reproduction through the increased utilization of larger prey after maturation

Furthermore, b parameter of the length-weight relationship equations indicated positive allometry ($3 < b$) for both sexes (3.2212 for females and 3.1171 for males), implying that body weight increased relatively faster than total length. Such allometric patterns can vary depending on the fishing pressure on the population (Cacciamani et al. 2025), sampling location (James et al. 2025), and fishing gear used (Munubi and Nyakibinda 2020), and are tightly regulated by both environmental conditions and trophoecological characteristics (Denechaud et al. 2020).

The sandy and muddy sedimentary environments of the southern coast, including the Yeosu coastal waters, provide favorable conditions for major prey organisms, such as amphipods, polychaetes, and brachyura (Lee et al. 2025). The continuous availability of benthic food resources in this habitat is is likely to promote somatic growth in *C. robustus*.

Correlation analysis across age groups based on back-calculated lengths demonstrated a distinct relationship between the growth and feeding characteristics of *C. robustus*. Given that amphipods occur at high densities and biomass and are widely distributed throughout benthic ecosystems (Ritter and Bourne 2024), their use as a primary food source by *C. robustus,* a benthic fish with a relatively narrow home range and limited mobility (Ruffino et al. 2025) is considered an efficient exploitation of food resources. This aligns with optimal foraging theory (Pyke 2019), which posits that foraging efficiency is maximized within a restricted activity range.

Concurrently, although amphipods were primarily consumed during the early growth stages, their proportions exhibited a strong negative correlation with age. Conversely, the proportions of polychaetes, brachyuran crabs and bivalves were significantly positively correlated with age. This ontogenetic dietary shift toward larger benthic prey is likely the result of the development of feeding structures (Alsafy et al. 2024) and swimming capabilities (Voesenek et al. 2018) as the fish grow, enabling them to meet increasing metabolic demands (Karachle and Stergiou 2011). Thus, *C. robustus* exhibits a high dependence on small benthic prey, such as amphipods, in its early stages, but transitions to a greater reliance on larger prey, such as polychaetes and brachyuran crabs, as it grows.

However, the two-way PERMANOVA results indicated that the variance explained (R^2) for dietary composition shifts was higher for the seasonal factor (0.4617 for females, 0.4149 for males) than for the age group factor (0.0493 for females, 0.0602 for males). This demonstrates that the dietary composition of *C. robustus* fluctuates significantly, not only because of ontogenetic dietary shifts but also because of seasonal factors. Canonical analysis of principal coordinates (CAP) also clearly separated the spring–winter diets, dominated by polychaetes and amphipods, from the summer–autumn diets, dominated by brachyuran crabs and stomatopods**,** along the second axis (CAP2). Such seasonal dietary fluctuations are closely linked to energy trade-offs and the physiological demands of the spawning cycle (Kindsvater et al. 2024).

Furthermore, the feeding patterns before and after the spawning season were distinct between the G1 and G2 groups and the G3 and older groups, marking the onset of full-scale ontogenetic dietary shifts. In the G1–G2 groups, the exceptionally high proportion of amphipods consumed between May and July (including the peak spawning season) reflects the inherent feeding strategy of these age groups which prioritize early somatic growth, rather than physiological changes associated with the spawning cycle.

Conversely, even in the G3 and older groups, the dietary proportion of amphipods increased between May and July. During the spawning season, when metabolic demands surge, energy is preferentially allocated to gonadal development (Birnie-Gauvin et al. 2023; Slesinger et al. 2022). Swollen gonads compress the digestive tract within the abdominal cavity, limiting the ingestion of large, bulky prey (Wootton and Smith 2015; Shimose 2024). In addition, enlarged gonads may compromise swimming performance. Therefore, to minimize foraging costs, these older individuals consume amphipods, a dense, abundant, and easily accessible benthic prey resource, to secure the minimum energetic requirements prior to spawning.

However, from August to September (immediately following the spawning season), G3 and older age groups, which were physically constrained from consuming large prey during spawning, rapidly transitioned to a diet on large brachyuran crabs. This pattern is attributed to a compensatory feeding strategy unique to older age groups aimed at rapidly replenishing energy reserves depleted during spawning and securing substantial energy required for physiological recovery (Choi et al. 2024). This rapid dietary shift in older individuals may provide the ecological advantage of alleviating food competition with younger growing individuals (G1–G2), thereby facilitating efficient niche partitioning of resources within a shared habitat.

In conclusion, *C. robustus* inhabiting the Yeosu coastal waters efficiently utilizes its habitat by shifting its diet from amphipods to larger benthic organisms, such as polychaetes and brachyuran crabs, as it grows. However, the overall dietary composition of a population is governed by both age-related changes and seasonal factors linked to the spawning cycle.

Furthermore, beyond merely altering its diet in accordance with somatic growth, *C. robustus* flexibly adjusts its feeding strategies to meet the heightened physiological demands of the spawning season and respond to varying prey availability within its habitat. This trophoecological adaptation is thought to be a core strategy that enables the optimal allocation

449 of energy between somatic growth and reproduction under constrained environmental
450 conditions, thereby supporting a stable life history strategy for the population.

4. Conclusions

The results demonstrate that as *C. robustus* grows, it undergoes an ontogenetic dietary shift from small prey, predominantly amphipods, to larger benthic organisms, such as polychaetes and brachyuran crabs, to meet increasing metabolic demands. This active utilization of large prey resources may provide a core nutritional foundation that supports the superior growth of females, thereby contributing to observed sexual dimorphism.

In particular, the feeding ecology of *C. robustus* is not restricted to a single variable of age but is flexibly regulated in response to the substantial energy expenditure and the physiological and physical constraints caused by gonadal enlargement during the spawning season. The strategy wherein adult fish (G3 and older) temporarily consume small prey during the spawning season (May–July), when the ingestion of large prey is physically restricted, and rapidly recover energy through compensatory feeding immediately after spawning (August–September), appears to represent an optimal energy allocation mechanism for survival and reproduction. Furthermore, these seasonal dietary fluctuations and rapid feeding shifts offer the ecological advantage of alleviating intraspecific food competition with younger growing individuals (G1–G2). This facilitates effective niche partitioning, thereby maximizing resource-utilization efficiency for the entire population within a limited coastal ecosystem.

Consequently, it is evident that such advanced trophoecological adaptability may underpin the ability of *C. robustus* populations along the southern coast to maintain a stable life history despite exposure to environmental changes and continuous fishing pressure. To accurately predict the future dynamics of these populations and establish effective fisheries management policies, it is imperative to move beyond fragmentary assessments focused solely on total length or age structure. Instead, an integrated approach is recommended, wherein the spatiotemporal variability of prey resources which is inextricably linked to the ontogenetic dietary shifts and spawning cycles identified in this study, is incorporated as an essential ecological indicator.

Funding

This study was supported by a grant from the National Institute of Fisheries Science (NIFS), Korea [grant number R2026011].

Author contributions

Seung Jo Han: Sample collection, identification, formal analysis, methodology, visualization, Writing – original draft, and writing – review and editing. **Hae Won Lee**: Conceptualization, funding acquisition, sample collection, identification, methodology, formal analysis, project administration, resources, supervision, validation, visualization, writing – original draft, and writing – review and editing.

Declaration of Competing Interest

The authors declare that they have no conflicts of interest.

Data availability

Data will be made available on request.

Ethics approval

No live animals were used in this study. The specimens obtained from commercial catches by professional fishers and were handled in accordance with applicable South Korean regulations governing fish disposal.

Acknowledgements

We express our gratitude to the Fisheries Resources Laboratory at the South Sea Fisheries Research Institute (NIFS) for its support and assistance in collecting the *Cynoglossus robustus* used in this study.

References

Alsafy MA, Seif MA, El-Mansi AA, El-Beskawy M, El Dakroury M, Eldesoqui MB, Ez Elarab SM, El-Gendy SAA (2024) Macro- and micro-morphological comparison of the detailed structure of the oral cavity roof in two different feeding habits marine fishes: *Pagrus pagrus* and *Boops boops*. J Exp Zool A Ecol Integr Physiol 341:783–797. https://doi.org/10.1002/jez.2822

Audzijonyte A, Kuparinen A, Fulton EA (2013) How fast is fisheries-induced evolution? Quantitative analysis of modelling and empirical studies. Evol Appl 6:585-595. https://doi.org/10.1111/eva

Baeck GW (2003) Comparative fisheries ecology on three tonguefish species, genus Cynoglossus, from the Yeosu coast, Korea, and the Seto Inland Sea, Japan. Dissertation, Hiroshima University

Baeck GW, Park JM, Hashimoto H (2011) Feeding ecology of three tonguefishes, genus Cynoglossus (Cynoglossidae) in the Seto Inland Sea, Japan. Anim Cells Syst 15:325-336. https://doi.org/10.1080/19768354.2011.611173

Birnie-Gauvin K, Berthelsen C, Larsen T, Aarestrup K (2023) The physiological costs of reproduction in a capital breeding fish. Physiol Biochem Zool 96:40-52. https://doi.org/10.1086/722136

Cacciamani R, Caserta V, Guizzardi S, Santojanni A, Colella S, Domenichetti F, Donato F, Angelini S (2025) How fishing pressures and environmental changes can impact the mean size of fish resources: a case study of small pelagics in the Adriatic Sea. Front Mar Sci 12:1703481. https://doi.org/10.3389/fmars.2025.1703481

Chasco B, Burke B, Crozier L, Zabel R (2021) Differential impacts of freshwater and marine covariates on wild and hatchery Chinook salmon marine survival. PLoS One 16:e0246659. https://doi.org/10.1371/journal.pone.0246659

Choi CH, Kim HJ, Lee JH, Baek GW (2024) Diet composition and trophic level of bluefin searobin (*Chelidonichthys spinosus*) in the South Sea of Korea. J Korean Soc Fish Ocean Technol 60:397–404. https://doi.org/10.3796/KSFOT.2024.60.4.397

532 Daufresne M, Lengfellner K, Sommer U (2009) Global warming benefits the small in aquatic
533 ecosystems. Proc Natl Acad Sci 106:12788-12793. https://doi.org/10.1073/pnas.0902080106

534 Denechaud C, Smoliński S, Geffen AJ, Godiksen JA, Campana SE (2020) A century of fish
535 growth in relation to climate change, population dynamics and exploitation. Glob Chang Biol
536 26:5661-5678. https://doi.org/10.1111/gcb.15298

537 Eikeset AM, Dunlop ES, Heino M, Storvik G, Stenseth NC, Dieckmann U (2016) Roles of
538 density-dependent growth and life history evolution in accounting for fisheries-induced trait
539 changes. Proc Natl Acad Sci 113:15030-15035. https://doi.org/10.1073/pnas.1525749113

540 Flinn SA, Midway SR (2021) Trends in growth modeling in fisheries science. Fishes 6:1.
541 https://doi.org/10.3390/fishes6010001

542 Froese R (2006) Cube law, condition factor and weight–length relationships: history, meta-
543 analysis and recommendations. J Appl Ichthyol 22:241-253. https://doi.org/10.1111/j.1439-
544 0426.2006.00805.x

545 Graeb BD, Dettmers JM, Wahl DH, Cáceres CE (2004) Fish size and prey availability affect
546 growth, survival, prey selection, and foraging behavior of larval yellow perch. Trans Am Fish
547 Soc 133:504-514. https://doi.org/10.1577/T03-050.1

548 Han SJ, Moon SY (2026) Seasonal and Size-Related Variation in Diet Composition and
549 Feeding Strategies of the Robustus Tonguefish, *Cynoglossus robustus* in the Yeosu Coast,
550 Korea. Fishes 11:50. https://doi.org/10.3390/fishes11010050

551 Hočevar S, Kuparinen A (2021) Marine food web perspective to fisheries-induced evolution.
552 Evol Appl 14:2378-2391. https://doi.org/10.1111/eva.13259

553 Hong SY, Park KY, Park CW, Han CH, Suh HL, Yun SG, Song CB, Jo SG, Lim HS, Kang
554 YS, Kim DJ, Ma CW, Son MH, Cha HK, Kim KB, Choi SD, Park KY, Oh CW, Kim DN, Choi
555 IY (2006) Marine Invertebrates in Korean Coasts. Academy Publishing Co., Seoul

556 Hunt GL, Polunin NV, Engelhard GH, Wigham BD, Pinnegar JK (2026) Century-scale
557 changes in the feeding patterns of demersal fish species in the western North Sea. Fish Fish
558 27:99-115. https://doi.org/10.1111/faf.70035

559 Hüssy K, Limburg KE, De Pontual H, Thomas OR, Cook PK, Heimbrand Y et al (2021)

560 Trace element patterns in otoliths: the role of biomineralization. Rev Fish Sci Aquac 29:445-
561 477. https://doi.org/10.1080/23308249.2020.1760204

562 James T, Steele E, Zhang J, Lilkendey J, Lequesne B, Trip EDL, Sabetian A (2025) Age-
563 based growth dynamics analysis of recreationally-vs commercially-caught snapper
564 (*Chrysophrys auratus*) in SNA1 management zone. N Z J Mar Freshwater Res 59:1334-1340.
565 https://doi.org/10.1080/00288330.2025.2503159

566 Kahl U, Radke RJ (2006) Is bigger better?–Sex-specific growth of perch and roach. Int Ver
567 Theor Angew Limnol Verh 29:1367-1371. https://doi.org/10.1080/03680770.2005.11902905

568 Karachle PK, Stergiou KI (2011) Feeding and ecomorphology of seven flatfish species in
569 the North-North-West Aegean Sea, Greece. Afr J Mar Sci 33:67-78.
570 https://doi.org/10.2989/1814232X.2011.572338

571 Katayama S, Yamamoto M (2012) Age, growth and stock status of robust tongue sole
572 *Cynoglossus robustus* Gűnther, 1873 in Japan determined by a new otolith observation
573 technique. Asian Fish Sci. https://doi.org/10.33997/j.afs.2012.25.2.009

574 Kerr LA, Campana SE (2014) Chemical composition of fish hard parts as a natural marker
575 of fish stocks. In: Stock identification methods. Academic Press, pp 205-234.
576 https://doi.org/10.1016/B978-0-12-397003-9.00011-4

577 Kim ES, McDonald JC, Muñoz-Abril L, Drymon JM, Albins MA, Powers SP (2024) Age,
578 growth, maturity, and mortality of an understudied Gray Snapper fishery from the north-central
579 Gulf of Mexico. Mar Coast Fish 16:e10324. https://doi.org/10.1002/mcf2.10324

580 Kim IS, Choi Y, Lee CL, Lee YJ, Kim BJ, Kim JH (2005) Illustrated Book of Korean Fishes.
581 Kyohak Press Co., Seoul

582 Kindsvater HK, Juan-Jordá MJ, Dulvy NK, Horswill C, Matthiopoulos J, Mangel M (2024)
583 Size-dependence of food intake and mortality interact with temperature and seasonality to drive
584 diversity in fish life histories. Evol Appl 17:e13646. https://doi.org/10.1111/eva.13646

585 King M (2013) Fisheries biology, assessment and management. John Wiley & Sons.
586 https://doi.org/10.1002/9781118688038

587 Korean Statistical Information Service (KOSIS) (2026) Fishery production survey.

588 http://kosis.kr. Accessed 1 October 2026

589 Kuzuhara H, Yoneda M, Tsuzaki T, Takahashi M, Kono N, Tomiyama T (2019) Food
590 availability before aestivation governs growth and winter reproductive potential in the capital
591 breeding fish, Ammodytes japonicus. PLoS One 14:e0213611.
592 https://doi.org/10.1371/journal.pone.0213611

593 La Mesa M, Eastman JT (2024) Assessing current knowledge and future challenges of age
594 determination, life span and growth performance in notothenioid fishes: a review. Rev Fish
595 Biol Fish 34:575-596. https://doi.org/10.1007/s11160-023-09829-9

596 Lee H, Maunder MN, Piner KR (2024) Good practices for estimating and using length-at-
597 age in integrated stock assessments. Fish Res 270:106883.
598 https://doi.org/10.1016/j.fishres.2023.106883

599 Lee JY, Lim HS, Lee JH, Shin HC (2025) Spatio-Temporal Distribution and Dominant
600 Species of the Macrozoobenthic Communties on a Soft Bottom of the Korean Coasts. Sea J
601 Korean Soc Oceanogr 30:174-198. https://doi.org/10.7850/jkso.2025.30.3.174

602 Li N, Wang Y, Fang Z, Chen XJ, Feng ZP (2022) Relationships between daily growth of
603 different groups of swordtip squid (*Uroteuthis edulis*) and environmental variables in the East
604 China Sea. Acta Oceanol Sin 41:52-61. https://doi.org/10.1007/s13131-021-1905-0

605 Lorenzen K (2016) Toward a new paradigm for growth modeling in fisheries stock
606 assessments: embracing plasticity and its consequences. Fish Res 180:4-22.
607 https://doi.org/10.1016/j.fishres.2016.01.006

608 Loutrage L, Brind'Amour A, Chouvelon T, Spitz J (2024) Ontogenetic shift or not? Different
609 foraging trade-offs within the meso-to bathypelagic fish community. Ecol Evol 14:e11129.
610 https://doi.org/10.1002/ece3.11129

611 Marshall AD, Kyne PM, Bennett MB (2008) Comparing the diet of two sympatric urolophid
612 elasmobranchs (*Trygonoptera testacea* Müller & Henle and Urolophus *kapalensis Yearsley &*
613 *Last*): evidence of ontogenetic shifts and possible resource partitioning. J Fish Biol 72:883-898.
614 https://doi.org/10.1111/j.1095-8649.2007.01762.x

615 Morrongiello JR, Thresher RE (2015) A statistical framework to explore ontogenetic growth

variation among individuals and populations: a marine fish example. Ecol Monogr 85:93-115. https://doi.org/10.1890/13-2355.1

Munro JL, Pauly D (1983) A simple method for comparing the growth of fishes and invertebrates. Fishbyte 1:5-6.

Munubi RS, Nyakibinda JN (2020) Assessment of body size and catch per unit effort of Nile perch (*Lates niloticus*) caught using different fishing gears at Magu district in Lake Victoria, Tanzania. Afr J Biol Sci 2:73-83. https://doi.org/10.33472/AFJBS.2.4.2020.73-83

Nunn AD, Tewson LH, Cowx IG (2012) The foraging ecology of larval and juvenile fishes. Rev Fish Biol Fish 22:377-408. https://doi.org/10.1007/s11160-011-9240-8

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D et al (2024) vegan: Community Ecology Package. R package version 2.6-8. https://CRAN.R-project.org/package=vegan

Park JM, Hashimoto H, Jeong JM, Kim HJ, Baeck GW (2013) Age and growth of the robust tonguefish *Cynoglossus robustus* in the Seto Inland Sea, Japan. Anim Cells Syst 17:290-297. https://doi.org/10.1080/19768354.2013.826281

Pinkas L, Oliphant MS, Iverson IL (1971) Food habits of albacore, bluefin tuna, and bonito in California waters. Fish Bull

Pyke G (2019) Optimal foraging theory: an introduction. In: Encyclopedia of animal behavior. Elsevier Academic Press, pp 111-117. https://doi.org/10.1016/B978-0-12-809633-8.01156-0

R Core Team (2024) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.r-project.org

Ragheb E, El-Samman A, El-Betar TA (2024) Age, growth and population aspects of *Fistularia commersonii* (Rüppell, 1838) from the Eastern Mediterranean region, Alexandria, Egypt. Egypt J Aquat Res 50:538-544. https://doi.org/10.1016/j.ejar.2024.10.003

Rajaguru A (1992) Biology of two co-occurring tonguefishes, *Cynoglossus arel* and *C. lida* (Pleuronectiformes: Cynoglossidae), from Indian waters. Fish Bull 90:328-367.

643 Ritter CJ, Bourne DG (2024) Marine amphipods as integral members of global ocean
644 ecosystems. J Exp Mar Biol Ecol 572:151985. https://doi.org/10.1016/j.jembe.2023.151985

645 Ruffino C, Abba M, Candiotto A, Spairani M, Bovero S, Fenoglio S, Comoglio C, Nyqvist
646 D (2025) Movement and habitat use of native and non-native small benthic fish in a high
647 conservation value agricultural environment. J Limnol 84:2216.
648 https://doi.org/10.4081/jlimnol.2025.2216

649 Seo YI, Kim JI, Oh TY, Lee SK, Kim ST, Joo H (2007) Age and growth of the robust
650 tonguefish, *Cynoglossus robustus* in the southern sea of Korea. Korean J Ichthyol 19:324-331.

651 Shimose T (2024) Feeding ecology of two reef-associated snappers (*Lutjanus fulviflamma*
652 and *L. fulvus*): Influence of lunar phase on feeding activity. Fish Oceanogr 33:e12670.
653 https://doi.org/10.1111/fog.12670

654 Slesinger E, Bates K, Wuenschel M, Saba GK (2022) Regional differences in energy
655 allocation of Black Sea Bass (*Centropristis striata*) along the US Northeast Shelf (36 N to 42
656 N) and throughout the spawning season. J Fish Biol 100:918-934.
657 https://doi.org/10.1111/jfb.15023

658 Taniguchi A, Yoneda M, Nishikawa T, Nakamura M, Morioka T, Tomiyama T (2025) Local
659 environmental changes boost predation risk in forage fish: application to the sand lance in the
660 eastern Seto Inland Sea. Mar Environ Res 107827.
661 https://doi.org/10.1016/j.marenvres.2025.107827

662 Thomas OR, Swearer SE (2019) Otolith biochemistry—a review. Rev Fish Sci Aquac
663 27:458-489. https://doi.org/10.1080/23308249.2019.1627285

664 Voesenek CJ, Muijres FT, Van Leeuwen JL (2018) Biomechanics of swimming in developing
665 larval fish. J Exp Biol 221:jeb149583. https://doi.org/10.1242/jeb.149583

666 Von Bertalanffy L (1938) A quantitative theory of organic growth (inquiries on growth laws.
667 II). Hum Biol 10:181-213.

668 Walford LA (1946) A new graphic method of describing the growth of animals. Biol Bull
669 90:141-147. https://doi.org/10.2307/1538217

670 White WT, Platell ME, Potter IC (2004) Comparisons between the diets of four abundant

671 species of elasmobranchs in a subtropical embayment: implications for resource partitioning.
672 Mar Biol 144:439-448. https://doi.org/10.1007/s00227-003-1218-1

673 Wootton RJ, Smith C (2014) Reproductive biology of teleost fishes. John Wiley & Sons.
674 https://doi.org/10.1002/9781118891360

675 Zhang CI (2012) Marine Fisheries Resource Ecology. Pukyong National University Press,
676 Busan

677 Zhu X, Ma D (1992) Studies on age, growth, and age class structures of the tonguefish,
678 *Cynoglossus abbreviatus* (Day) in the Jiaozhou Bay waters. Mar Sci 1:49-53.