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Thesis for the Degree of Doctor of Engineering

Population Ecology of John dory, *Zeus faber*, in the coastal waters of Korea

by

Han Ju Kim

Interdisciplinary program of Marine-Bio,
Electrical & Mechanical Engineering

The Graduate School

Pukyong National University

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[한국 연안에 서식하는 달고기의 자원생태학적 연구]

Advisor: Prof. Chul-Woong Oh

by

Han Ju Kim

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Han Ju Kim

Approved by:

(Chairman) Jin-Koo Kim

(Member) Hyun-Woo Kim

(Member) Gun Wook Baeck

(Member) Young Il Seo

(Member) Chul-Woong Oh

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김한주

부경대학교 대학원 의생명기계전기융합공학과정

초록

달고기과 어류는 전 세계적으로 2속 6종이 보고되고 있고, 대서양, 인도양 태평양에서 서식하는 것으로 알려져 있으나 우리나라에는 단 두 종만 (*Zeus faber, Zenopsis nebulosa*) 보고되었다. 두 종은 주로 50-100 m 사이에서 가장 흔하게 발견되지만, 어린 개체들의 경우에는 연안의 얕은 수심대에서 서식하기도 한다. 달고기와 민달고기의 체형은 타원형으로 매우 측편으로 되어있고, 체고는 높으며, 주둥이의 모양, 체색, 큰 둥근 흑색 반점의 유무 등으로 쉽게 동정할 수 있다.

두 어종 중 식용으로 많이 이용되는 어종은 달고기이며, 상업적으로 중요한 가치가 있는 어류이다. 달고기는 일본에서 고급어종으로 소비되고 있으며 동중국해 지역에서 200-300 t의 많은 양이 어획된다. 한국에서는 2018년에 열린 남북정상회담에서 달고기가 만찬의 요리로 이용되면서 수요가 증가하고 지속적으로 수산자원으로서의 가치가 증가하고 있지만, 현재 어획량의 통계자료는 전무한 실정이다. 지속적인 자원관리와 회복을 위해서라도 이들에 대한 명확한 어획량 기록과 생태학적 특성에 대한 연구가 필수적이다. 달고기의 생태학적 연구는 많은 표본 개체와 장기간의 연구가 필요해 주요 상업어종에 비해 상대적으로 부족한 실정이다. 따라서, 국내 달고기 어류를 대상으로 생물학적 특징, 연령과 성장, 성숙과 산란, 그리고 섭이 특성에 대하여 연구를 수행하였다.

본 연구는 2017년 2월부터 2018년 1월까지 상업적 트롤 네트를 이용하여, 총 838마리를 채집하였다. 암컷은 593마리, 수컷은 245마리로 암컷이 수컷보다 많았다. 암컷의 평균체장은 34.85 ± 4.44 cm, 평균체중은 723.51 ± 299.31 g, 수컷의 평균체장은 31.17 ± 299.31 cm, 평균체중은 512.34 ± 195.29 g로 나타나며, 암컷이 수컷보다 더 큰 최대체장을 보였고, 40 cm 이상의 개체들은 모두 암컷이었다. 상대 성장식은 암컷: $\mathrm{BW} = 0.0212TL^{2.9248}$, 수컷: $\mathrm{BW} = 0.019TL^{2.9548}$로 추정되었고, 암·수 간의 차이가 있었다.

달고기의 연령과 성장에 대한 연구는 일본, 터키, 영국에서 진행되었지만, 국내에는 전무한 실정이다. 달고기의 이석은 모양이 불규칙하고 윤문의 대응성이 맞지 않아 연령을 판별하기에는 적합하지 않다고 알려져 있기 때문에 대부분의 이전연구에서는 7번 척추골을 이용하여 달고기의 연령을 분석하였다. 본 연구에서도 7번 척추골을 이용하여 연령 판독과 성장식을 추정하였다. 7번 척추골은 투명한 륜과 불투명한 륜이 명확하게 구분되었으며, 체장과 연령이 증가함에 따라 척추골의 지름도 증가하는 것을 확인하여, 연령을 판독하는데 적합한 형질이라 판단되어졌다. Marginal increment index (MI)를 통해 성장륜이 1년에 한 번 겨울에 형성되는 것을 확인하였으며, 달고기의 최대 연령은 암컷 14세, 수컷 8세로 추정되었다. 달고기의 본 버틀란피 성장식은 암컷: $L_t = 50.13(1 - e^{-0.17(t+0.36)})$, 수컷: $L_t = 40.97(1 - e^{-2.56(t+0.57)})$으로 추정되었다. 암·수간의 성장 매개변수에는 유의한 차이가 있었다.

본 연구에서는 달고기의 생식소를 조직학적으로 관찰하여 성숙정도를 5단계로 구분하는 기준을 만들고, 달고기의 생식에 대한 연구를 진행하였다. 생식소는 나비 모양이

었으며, 성숙할수록 생식소는 비대해졌다. 또한, 알이 명확하게 보였으며, 핏줄이 뚜렷해졌다. 성숙한 생식소에서는 비동시적 난모세포의 발달이 보였으며, 난모세포의 단계 및 난경이 모두 달랐다. 이러한 결과를 통해 달고기가 다회산란 어종임을 알 수 있었다. 산란기는 11월부터 5월까지이고, 주 산란기는 1월부터 3월로 나타났으며, 군성숙 체장은 30.8 cm (age 5)로 추정되었다. 체장이 증가함에 따라 알의 수도 많아지며, 완숙한 생식소의 알 수는 42,215-336,986개로 추정되었다.

달고기의 위내용물을 종수준까지 동정하였으며, 어류, 갑각류, 두족류 순으로 많이 섭이 하였다. 달고기의 먹이생물 중 어류는 82.8%로 높은 %IRI를 차지하였다. 따라서, 달고기는 어류를 주로 섭이하는 어식성 어종임을 알 수 있었다. 주로 갈치와 전갱이는 모든 체장과 계절에서 섭이되는 주요 먹이로 보이며, 갑각류 중 북쪽분홍새우는 17.5% (%IRI)나 섭이하는 특징이 나타났다. 이전 연구에서 14 cm 이상의 개체들은 어류만 섭이한다는 연구 결과가 있지만, 다른 연구에서는 먹이 전환이 되는 시기를 명확하게 알 수 없으며, 어린 개체일 때 섭이했던 갑각류를 성어가 되어서도 지속적으로 섭이하는 것으로 보고했으며, 본 연구는 후자의 결과와 일치하였다. 38 cm 이상의 개체들에서 기름가자미가 자주 출현하였고, 체장이 커질수록 더 깊은 수심에서 서식하는 것으로 판단된다. 생활사에 따라 달고기의 섭이 강도가 달라 질 것으로 예상하여, 성비, 크기, 계절에 따른 섭이 강도 변화를 분석하였다. 암컷이 수컷보다 더 높은 섭이강도를 보였고, 산란기간인 봄과 겨울에 더 높은 강도를 보였다. 따라서, 달고기의 섭이는 생활사의 영향을 받을 것으로 생각된다.

I. Introduction

Zeid fishes have a wide distribution range, occurring in the Atlantic, Indian, and Pacific. It consists of 6 species in 2 genera worldwide (Nelson 1994). Fish belonging to Zeidae live and feed mainly on the bottom of the seafloor. They inhabit at depths of up to 800 m. In Korea, only two species, *Zeus faber* and *Zenopsis nebulosa* are found.

Z. faber and *Z. nebulosa* have distinct morphological differences. *Z. faber* has an oblique head from eye to occipital region, scales with small round shape, gray body and black spots (Gang 2005). *Z. nebulosa* has concave head form eye to occipital region, no scales, body color is silver, and no block spots (Gang 2005). The ecological difference cannot be explained clearly, because ecological studies on the two species are lacking.

The *Z. faber* has a wide range of distribution that includes the Eastern Atlantic and Western Pacific Oceans and the Mediterranean Sea (Ismen et al. 2012; Silva 1999; Stergiou and Fourtouni 1991). It is a demersal species, inhabiting depths between 5 and 400 m, and is most commonly found between 50 and 100 m (Akyol 2001; Vrgoč et al. 2006). In Korea, they are distributed in the Southern Sea and East Sea of Korea (Choi et al. 2002).

The John dory, *Z. faber* is of commercial importance in England, Turkey, and Japan

(Akyol 2001; Dunn 2001; Yoneda et al. 2002). Especially, in the Japan, *Z. faber* is used as a high-quality fish resource and caught in the trawl fishing. Japanese fisheries harvest *Z. faber* intensively in the East China Sea. Annual catch from this region was about 1,000 tons in the mid-1980s but has since gradually decreased to about 200–300 tons per year (Tokimura 1999) due to increased fishing pressure. Japanese trawlers range from the East China Sea to the Yellow Sea (Tokimura 1999), an area that overlaps with Korean fishing waters. This overlap must be taken into account in the management of *Z. faber* fisheries in Korea. In Korea, the commercial value of *Z. faber* has recently increased, making this species a potentially valuable resource. However, it is treated as bycatch in Korea, and the catch is not recorded. No biological information on this species in Korea is currently available.

Ecological characteristics vary depending on the environment, and other regions have different consequences. Ecological study of *Z. faber* was performed on age and growth, maturity, feeding habits, distribution, but the results of the previous study were inconsistent. Therefore, the results of previous studies are difficult to apply to resource management of Korea.

Yoneda et al. (2006) studied age and growth of *Z. faber* according to latitude in East China Sea, which reported that the higher the latitude, the slower the growth.

It is indicated that even in linked waters, the growth rate can vary depending on population.

In the case of maturation, *Z. faber* spawned twice a year in Turkey (Akyol 2001, Ismen et al. 2012) and once a year in Japan (Yoneda et al. 2006). The size at sexual maturity in England (Female: 34.5 cm TL) was larger than that in Turkey (Female: 26.0 cm TL) (Dunn 2001, Ismen et al. 2012). These studies have different results because of different regions and ecological adaptation. There is a lack of research on maturation, and previous findings are not clear.

Z. faber is piscivorous fish, which often fill the role of higher predators within trophic food webs. Previous studies focused on ontogenic diet composition. *Z. faber* from the Mediterranean were found to switch gradually from feeding on zooplankton to small demersal fish, and when >140 mm, to feeding exclusively on benthic and demersal fish (Stergiou and Fourtouni 1991). On the other hand, the diets of *Z. faber* in the Portuguese area do not show distinct changes, as large specimens feed mainly on pelagic fish (Silva 1999).

For the above mentioned reasons, we need to research biological study of *Z. faber* which inhabit in Korea. The purpose of this study is to investigate age and growth, maturation, and feeding habits of *Z. faber* in the coastal waters of Korea.

II. Materials and methods

2.1 Sample collection

A total of 838 samples were monthly collected between February 2017 and January 2018 in Busan fish markets, Korea. These samples were caught using a commercial bottom trawl net in coastal waters of Korea (Fig. 1). All samples were collected randomly and brought in thermos cool boxes to the laboratory.

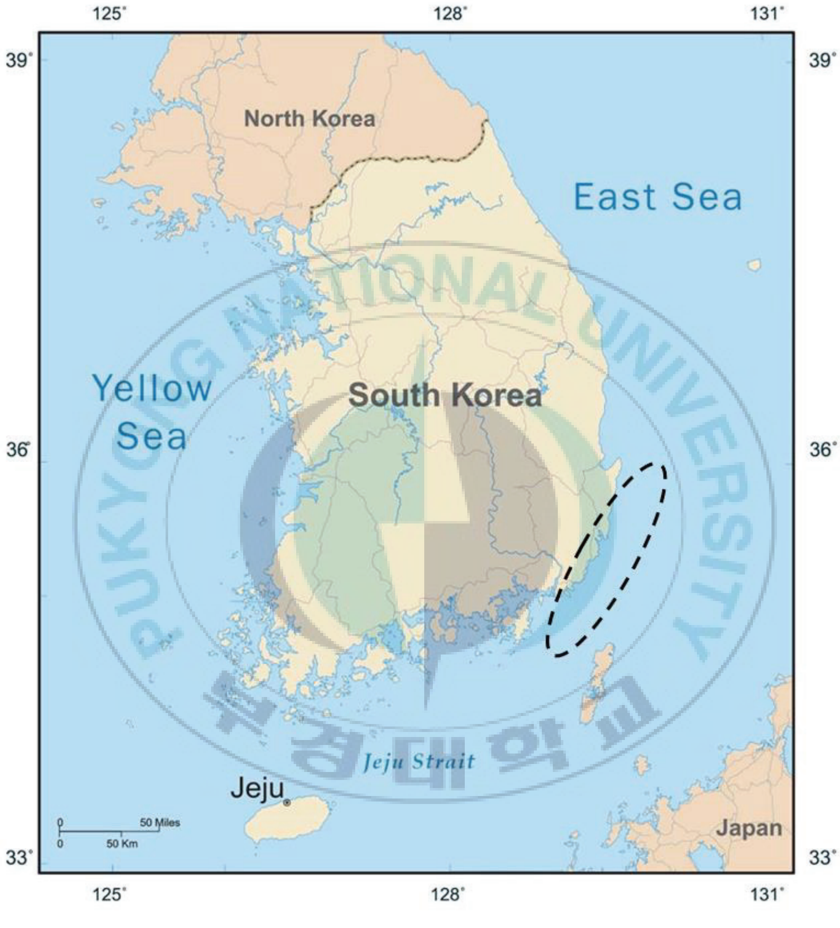

Fig.1. Sampling area of *Zeus faber* in the coastal waters of Korea.

2.2 Biological data

In the laboratory, total length (TL) was measured to the nearest 0.1 mm for all fish samples (838 individuals). The body weight (BW) and gonad weight (GW) were measured to the nearest 0.01 g with electronic balance, respectively. The sex was determined using the gonad morphological shape of each specimen. The difference in sex ratio was examined using a Chi-square test. The Kolmogorov- Smirnov two sample test was applied to test differences in the size frequency distributions between sexes.

The length-weight relationship was described by the equation:

$$BW = aTL^b$$

where BW is body weight, TL is the total length, b is the growth exponent or length-weight factor and a is a constant. Analysis of covariance (ANCOVA) was applied to test the difference in a length-weight relationship and in growth curve between sexes.

2.3 Age and growth

The vertebra of 380 females and 123 males were taken for age and growth studies. Vertebrae of *Z. faber* were excised from the only 7th of each fish. Prior to examination, each collected vertebra was cleaned with a 4% solution of potassium hydroxide and a 70% solution of ethanol, and then dried at 40℃ for 10 hours.

The growth rings of each vertebra were counted twice by the same reader using a stereoscopic microscope (magnification of 10×) (Carl Zeiss Discovery v.8) with an interval of two months. If both readings were in agreement, counts were accepted only. If the first and second readings were different, vertebrae were recounted. If it agrees with one of the previous counts, the final counts were accepted. A paired *t*-test was performed to compare first and second reading. Correlation analysis was used to check whether there is a correlation between total length and vertebra radius. To assess aging precision, the growth increment was counted independently by two readings without knowledge of fish length or sex. The variability of the within-reader age estimates was calculated with the average percentage error (APE) with the equation (Beamish and Fournier 1981):

$$\mathrm{APE}_j(\%) = 100 \times \frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij} - X_j|}{X_j}$$

where R is the number of times each fish is aged, X_{ij} is i (th) age determination of the j (th) fish, and X_j is the mean age calculated for the j (th) fish.

Marginal increment (MI) analysis was used to validate the periodicity of growth:

$$\mathrm{MI} = \frac{R - r_i}{r_i - r_{i-1}}$$

where R represents structure radius, r_i and r_{i-1} are annular radii of the last and penultimate annuli.

To describe the growth of females and males, the von Bertalanffy growth function (VBGF) was fitted to observe TLs at age t using non-linear least square regressions. The growth equation was

$$L_t = L_\infty[1 - e^{-k(t-t_0)}]$$

Where L_t is the length (cm) at age t, L_∞ is the asymptotic length (cm), k is the rate at which the growth curve approaches the asymptotic length (year^{-1}), t_0 is hypothetical age of the fish at zero length. The differences in growth curves between sexes were compared by the method of Kimura's likelihood ratio test.

For comparison with previous studies, the growth performance index (φ) was estimated in each case following the formula (Munro and Pauly 1983):

$$\text{Growth performance Index } (\varphi) = 2\log L_\infty + \log k$$

Where L_∞ is the asymptotic length of von Bertalanffy growth parameter, k is the growth constant of von Bertalanffy growth parameters.

2.4 Maturation

Although macroscopic characteristics of gonad stage in some fishes were described (Zhang 2010, Nancy et al. 2011, Vaz-dos-Santos et al. 2014), standard in detail to determine the gonad stage for *Z. faber* is lacking. Thus, the gonad development was investigated in detail through microscopic and histological observation. The maturation conditions of gonad were classified into 5 stages (I immature, II developing, III mature, IV spawning, V resting).

Gonads of all females were examined by histological analysis. The gonads were preserved in 10% formalin for measurement of the gonad. All gonads were embedded in paraffin, sectioned at 5 μm and stained using Mayer's hematoxylin-eosin. The oocyte diameters of 15 individuals in each stage were measured with a light microscope connected to an image program (magnification: X40). All of the oocytes shown on the screen were measured.

The monthly occurrence percentages of development stages in female were recorded. The gonad somatic index (GSI) was calculated for each sex as follows:

$$GSI = \frac{gonad\ weight}{total\ weight\ of\ fish} \times 100$$

The one-way ANOVA was performed to test for significant monthly differences in

GSI values.

Of 384 specimens collected in the spawning season between November to May, 284 females matured (III, IV, IV) were used to estimate length at sexual maturity.

A logistic curve may be fitted to the proportion (P) of sexually mature individuals by length (King 1995):

$$P = \frac{1}{1 + e^{-r(L-L_m)}}$$

Where r is the slope of the curve in logistic model, and L_m is the mean length at sexual maturity or the length which corresponds to a proportion of 50% in reproductive condition.

Similarly, to estimate age at sexual maturity, the age of individual fish collected in the spawning season was determined by counting the annual ring marks of the 7th vertebra.

For the determination of fecundity, fish in stage IV were considered. Fecundity was estimated by weighing all the eggs in the gonad and also counting samples of eggs from a part of the gonad. Fecundity was estimated using the formula:

$$Fecundity = \frac{Weight\ of\ total\ \ gonad \times Number\ of\ part\ gonad}{Weight\ of\ part\ gonad}$$

2.5 Feeding habits

Stomachs were opened and determined as either present or absent. Prey items in the stomachs were determined to the lowest taxonomic level possible. Biomass and length of all prey items were measured with an electronic balance to the nearest 0.01 g and the nearest mm.

Feeding habits were determined by using the index (Hyslop 1980; Amundsen et al. 1996): (1) the frequency of occurrence (%F) (2) the numerical percentage (%N) (3) the weight percentage (%W) and (4) the index of relative importance (IRI). Indices were calculated for each stomach as follows:

$$(1)\ \%F = \frac{A_i}{N} \times 100$$

$$(2)\ \%N = \frac{N_i}{N_{total}} \times 100$$

$$(3)\ \%W = \frac{W_i}{W_{total}} \times 100$$

$$(4)\ IRI = (\%N + \%W) \times \%F$$

A_i is the number of fish with prey i (th) in their stomach, N, the total number of fish with stomach contents, N_i, the number of prey i (th), N_{total}, the total number of prey items, W_i, the mass of prey i (th) and W_{total}, the total mass of prey items. IRI was converted into a percentage and expressed as %IRI.

To find the differences in the empty rate among the size classes, season and sex were examined using a chi-square test. Two-way contingency table analyses were employed to test for independence between prey types and season or size groups. This statistical technique is simple and can readily identify the source of variation when diets are expressed numerically or according to presence/absence (Crow 1982; Cortés 1997). To avoid too many cells having expected frequencies <5 (Rohlf and Sokal 1995), some prey categories were pooled into a larger category.

To assess feeding activity, the emptiness index was calculated as the number of empty stomachs out of the total number of stomachs. Niche breadth analysis was conducted using the Shannon-Wiener diversity index (*H'*) (Colwell and Futuyma 1971),

$$H' = -\sum_{i=1}^{s} P_i ln P_i$$

Where P_i is the proportion of individuals belonging to *i* th species. *s* is the total number of different prey categories consumed by predatora. The value of *H'* increases with species diversity.

The degree of food niche overlap between seasons was calculated using the Schoener's index (R_o) (Schoener 1970),

$$R_o = 1 - 0.5\sum\left|P_{xi} - P_{yi}\right|,$$

where P_{xi} and $P_{yi}$are the proportions of prey *i* (based on the biomass) found in the diet of groups x and y. Value of R_o range from 0 (no overlap) to 1 (complete overlap). Schoener's index values >0.6 are usually considered to indicate significant overlap (Wallace 1981).

To evaluate the effects of sex, size class and season on feeding intensity, feeding intensity index (FI) was calculated by the following formulae:

$$\mathrm{FI} = \frac{Weight\ of\ stomach}{Body\ weight\ of\ fish} \times 100$$

To investigate variation of diet according to size group, *Z. faber* was divided into four size classes: 24-30 cm, 31-35 cm, 36-40 cm, and 41-47 cm. Seasonal variation of diet also was investigated for four seasons: spring (March-May), summer (June-August), autumn (September-November) and winter (December-February).

III. Results

3.1 Biological characteristics

3.1.1 Sex ratio and length structure

In total, 838 *Z. faber* specimens were captured during the sampling period. The over sex ratio of females (593) to male (245) was 2.42:1, significantly different from 1:1 ($x^2 = 143.69$, *df*=1, $P < 0.001$) (Fig.2). Mean total length was 34.85 ± 4.44 cm (mean ± SD) in females and 31.17 ± 3.20 cm (mean ± SD) in males. There was a significant difference in mean lengths between sexes (F=150.06, $P < 0.001$). Mean body weight was 723.51 ± 299.31 g (mean±SD) in females and 512.34 ± 195.29 g (mean±SD) in males. There was a significant difference in mean body weight between sexes (F=120.12, $P < 0.001$). The Kolmogorov-Smirnov two sample test showed that there were significant differences in size frequency distribution between sexes ($P < 0.001$) (Fig. 3). Seasonal size distributions of specimens were demonstrated a significant difference in size structure among seasons by Kolmogorov–Smirnov tests; however, there was no significant difference between spring and winter (Table 1).

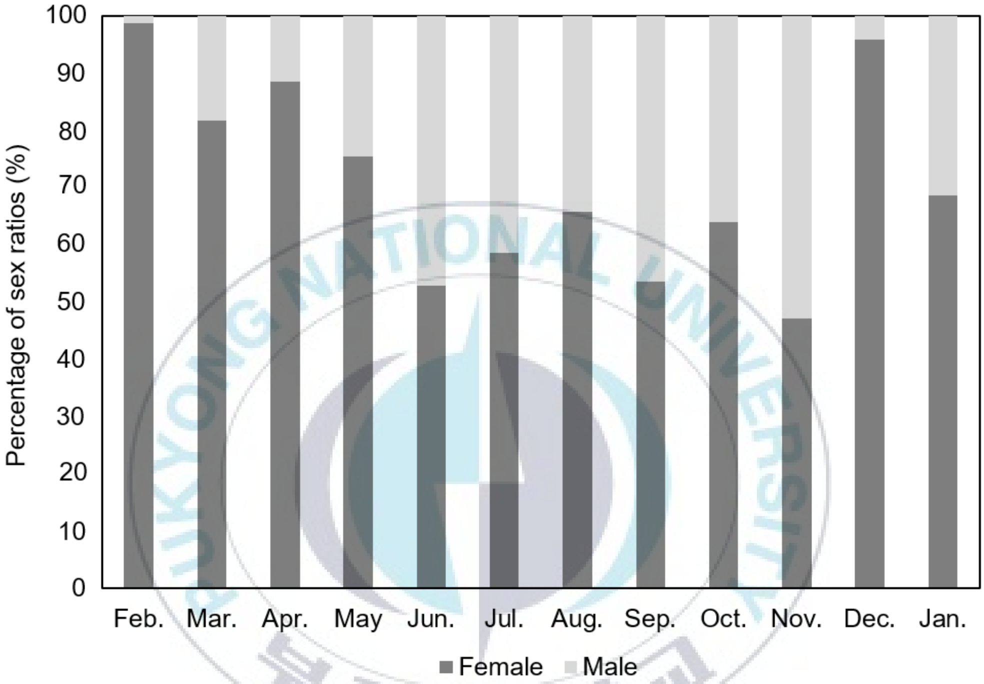

Fig. 2. Monthly sex ratios of *Zeus faber* in the coastal waters of Korea.

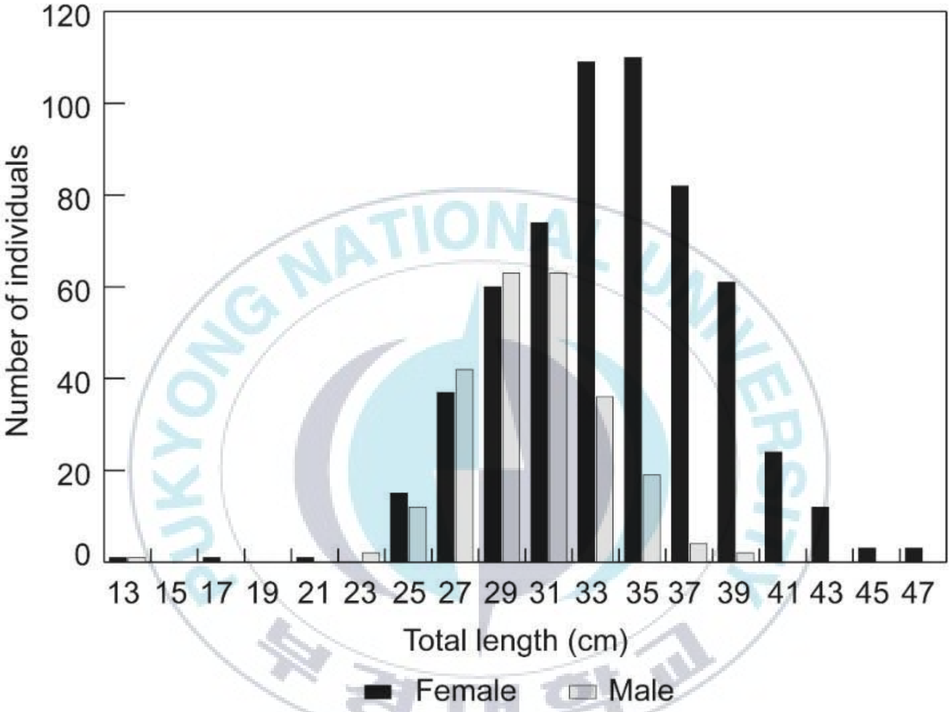

Fig. 3. Size frequency distribution of *Zeus faber* between sexes in the coastal of Korea.

Table1. Kolmogorov-Smirnov two sample tests for the frequency distribution of size between seasons.

Seasons	Spring	Summer	Autumn
Summer	n=150, P<0.001		
Autumn	n=360, P<0.001	n=371, P<0.01	
Winter	n=340, P>0.05	n=351, P<0.001	n=400, P<0.001

3.1.2 Length–weight relationship

The relationship between total length (TL) and body weight (BW) was $\mathrm{BW} = 0.0212TL^{2.9248}$ $(r^2 = 0.89, n = 580, P < 0.001)$ for female, and $\mathrm{BW} = 0.019TL^{2.9548}$ $(r^2 = 0.91, n = 242, P < 0.001)$ for male (Fig. 4). The slope in the relationship between TL and BW was significantly different between the sexes (ANCOVA *F* = 82.14, *P* <0.001).

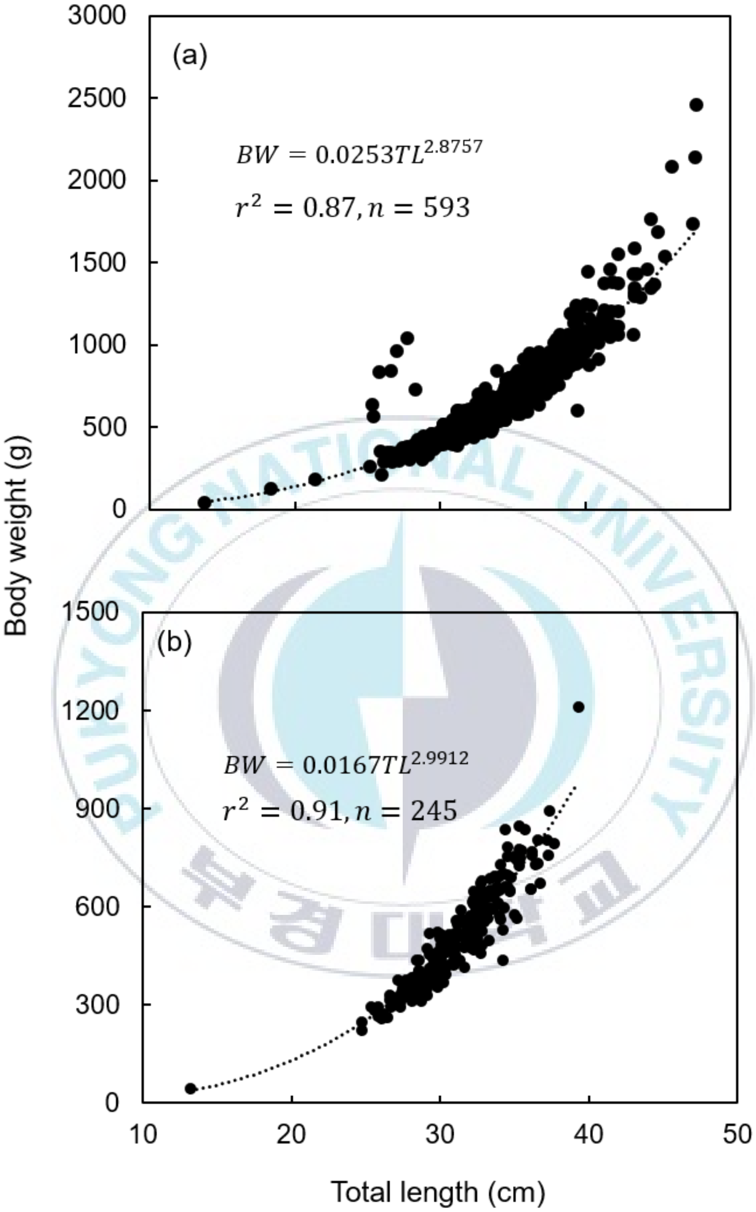

Fig. 4. Relationship between total length (TL) and body weight (BW) for (a) female and (b) male of *Zeus faber* in the coastal waters of Korea.

3.2 Age and growth

3.2.1 Age

Of the 838 *Z. faber* sampled, the number of ring marks recorded for 503 (380 female and 123 male) was consistent through 2 readings. Ring marks in vertebra growth showed the typical pattern of translucent and opaque zones (Fig. 5). As the total length increased, the vertebra radius increased (Fig. 6). There was a significant correlation between total length and vertebra radius ($r = 0.821,\ n = 469, P < 0.001$). The relationship between ring mark radius and vertebra radius was compared to ensure that vertebra can use as an aged character. Each of the ring marks was clearly separated (Fig.7), and even ring marks of the same age have different ring radius. As the vertebra radius increased, the ring mark radius increased. Therefore, the vertebra of *Z. faber* can be used as an aged character to determine the age.

Of the 469 vertebrae examined, similar replicate measurements were 76.81%, there was no significant difference between measurements (t = 0.62, P > 0.05). The average percentage error between the first and second measurements was very low (2.33%), which demonstrated the reliability and the high precision of vertebrae for aging the species.

The marginal increment (MI) was calculated for each month (Fig. 8). MI peaked in

October, and decreased thereafter to the lowest value in January, suggesting that ring mark formed once per year between November and January. Maximum numbers of band pairs counted were 14 for female and 8 for male base on 469 vertebrae.

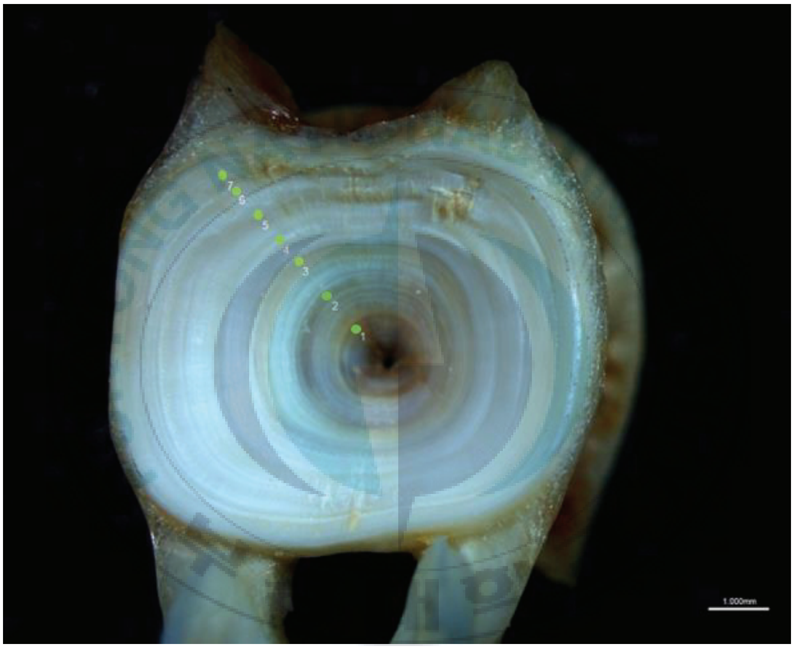

Fig. 5. 7th vertebra of *Zeus faber* with 7 growth rings (Female: 35.7 cm TL).

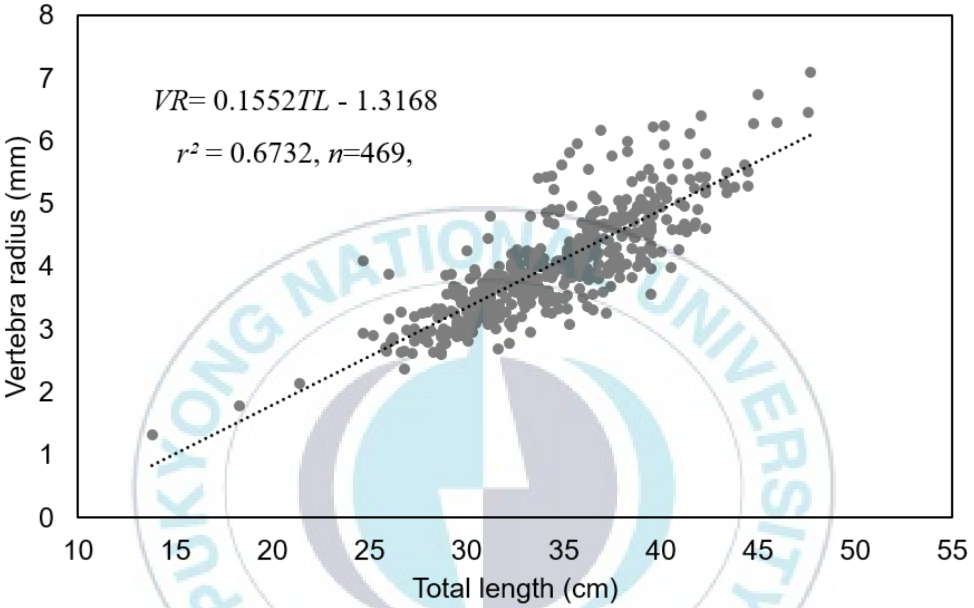

Fig. 6. Relationship between total length (TL) and vertebra radius (VR) of *Zeus faber* in the coastal waters of Korea.

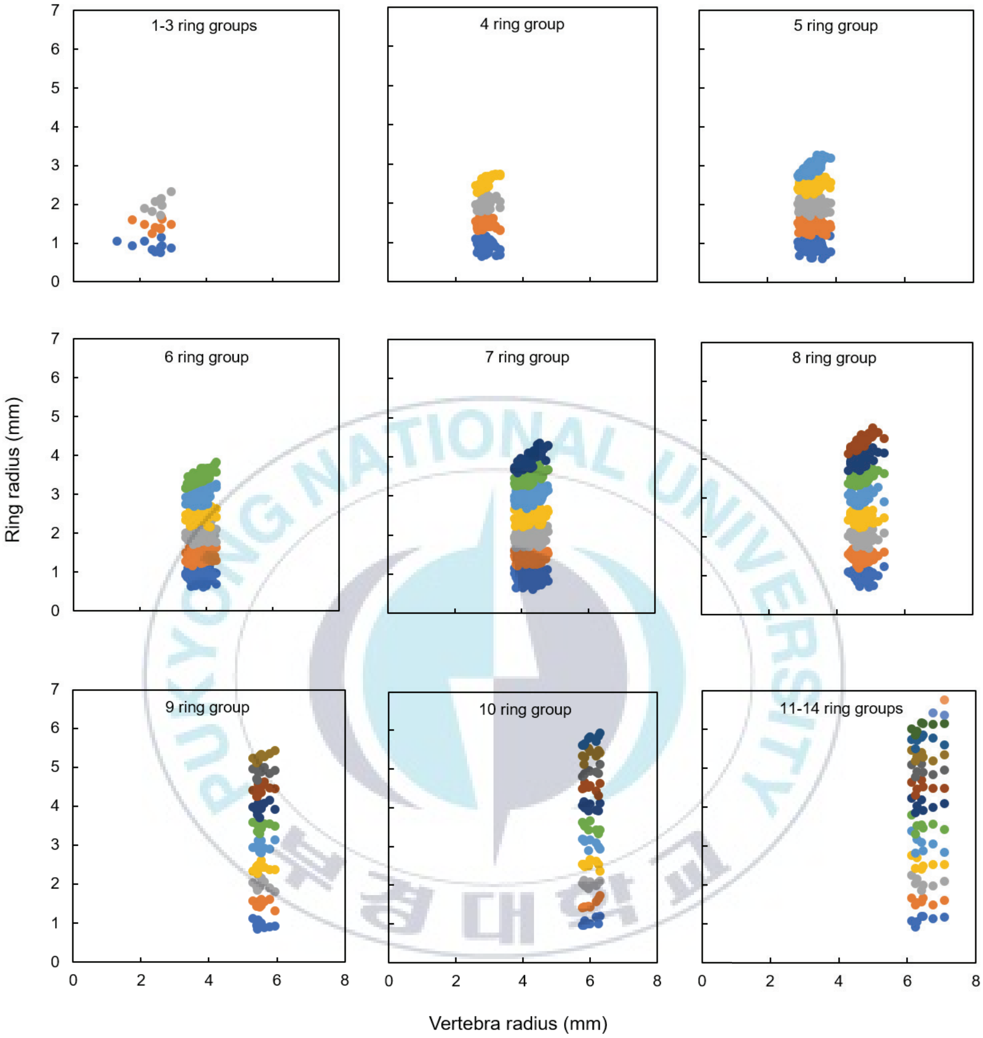

Fig. 7. Relationship between ring radius and vertebra radius of *Zeus faber* in the coastal waters of Korea.

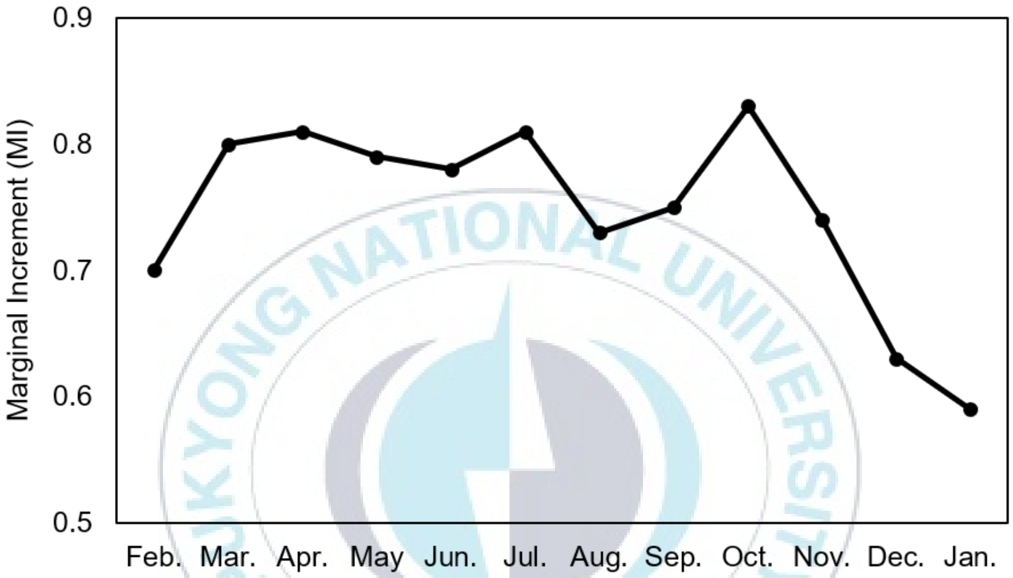

Fig. 8. Monthly change of marginal increment (MI) for *Zeus faber* in the coastal waters of Korea.

3.2.2 Growth parameters

The von Bertalanffy growth model for *Z. faber* was estimated from observed length data at age (Fig. 9). The von Bertalanffy growth functions for female and male were expressed with nonlinear regression according to the equations:

$$\text{Female: } L_t = 50.13(1 - e^{-0.17(t+0.36)})$$

$$\text{Male: } L_t = 40.97(1 - e^{-2.56(t+0.57)})$$

A likelihood test was used to detect the differences in the growth curves for the two sexes. The likelihood test for the nonlinear regression showed that there were significant differences between the sexes in the growth parameters asymptotic length (L_∞; $P < 0.001$), growth rate (K; $P < 0.001$), and hypothetical age (t_0; $P < 0.001$) (Table 2). The asymptotic length value for females was larger than that for males, and the growth rate for females was lower than that for males.

The growth performance indices (φ) for females and males were 2.62 and 2.64, respectively (Table 3).

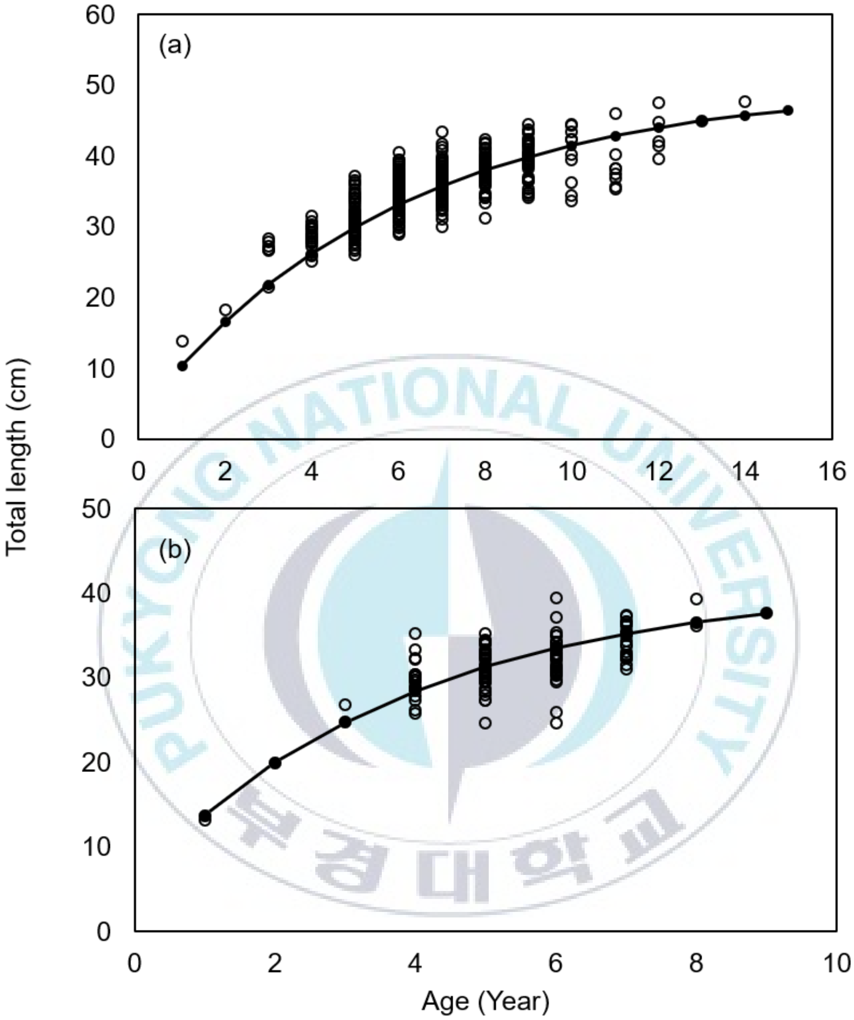

Fig. 9. The von Bertalanffy growth function for (a) female and (b) male of *Zeus faber* in the coastal waters of Korea.

Table 2. Likelihood tests comparing von Bertalanffy growth parameters by non-linear regression estimates for *Zeus faber* females (1) and males (2).

Hypothesis	Linear constraints	$L_{\infty1}$	$L_{\infty2}$	K_1	K_2	$t_{0\,1}$	$t_{0\,2}$	Residual sum of squares (1)	Residual sum of squares (2)	X^2	P
H_0	none	50.13	40.97	0.17	2.56	-0.36	-0.57				
H_1	$L_{\infty1} = L_{\infty2}$	48.85	48.85	0.16	0.16	-1.10	-1.22	32.71	18.96	10.68	<0.001
H_2	$K_1 = K_2$	48.85	47.82	1.17	1.17	-1.10	-1.23	32.72	18.30	9.77	<0.001
H_3	$t_{0\,1} = t_{0\,2}$	48.85	44.48	0.16	0.19	-1.10	-1.10	32.72	16.42	8.95	<0.001
H_4	$L_{\infty1} = L_{\infty2}$ $K_1 = K_2$ $t_{0\,1} = t_{0\,2}$	48.85	48.85	0.17	0.17	-1.10	-1.10	32.72	19.36	10.23	<0.05

Table 3. Growth parameter comparisons of *Zeus faber* reported around the world.

Author	Regions	Parameters			
		L_∞	K	t_0	φ'
Dunn (2001)	Western English Channel	50.8	0.47	-1.47	3.08
Akyol (2001)	Izmir Bay, Turkey	60.7	0.3	0.33	3.04
Yoneda et al. (2002)	East China Sea	58.0 (female)	0.11	-0.77	2.57
		44.7 (male)	0.13	-1.47	2.41
Yoneda et al. (2006)	Northern East China Sea	54.6	0.13	-0.66	2.59
	Southern East China Sea	52.0	0.14	-0.79	2.58
Ismen at al. (2012)	North Aegean Sea, Turkey	58.0 (female)	0.11	-0.99	2.57
		45.0 (male)	0.13	-1.17	2.42
This study	Coastal waters of Korea	50.13 (female)	0.17	-0.36	2.63
		40.96 (male)	0.26	-0.57	2.64

3.3 Maturation

3.3.1 Development stages of gonad

In the females, a total 593 of gonad were analyzed microscopically and histologically. In this paper, the gonads were classified into five stages of development. Results for gonad observations are shown in Table 4, Figure 10, and Figure 11.

Stage I (immature): ovaries showed immature features with small gonad size. In the microscopical analysis, a butterfly-shaped gonad was observed and the color is translucent orange. In the histological, the ovary was filled with primary oocyte (PO), and intervals among oocytes were narrow. Ovarian walls were thin.

Stage II (Developing): ovaries exhibited the developing characteristics during secondary growth. The gonad gradually increased in volume with oocyte growth. At a later stage, eggs appeared opaque and cloudy orange eggs. In the histological analysis, oocytes have reached the cortical alveolar oocyte (CA) and primary (Vtg1) or secondary (Vtg2) vitellogenesis.

Stage III (Mature): gonad showed that the blood vessels in the ovary surface were thick. The eggs were clearly visible to the naked eye. The mature oocytes were filled in the ovary. The mature oocytes contained tertiary vitellogenesis (Vtg3). Intervals among oocytes were narrow because it was pre-spawning. Various types of oocyte presented in an ovary.

Stage IV (Spawning): gonad had hard blood vessels in the ovary surface. Gonad was bigger and opaque orange color. The eggs were distinctly visible to the naked eye. The mature oocytes reached germinal vesicle migration (GVM). Post-ovulatory follicle (POF) and atresia oocyte (AO) were observed in the ovarian tissue. More than 50% of the ovigerous lamellae had vitellogenic oocytes and GVM, which means that the *Z. faber* has spawning capable (spawning or recently spawned individuals).

Stage V(Resting): ovaries reduced in size and were running out. Less than 50% of the ovigerous lamellae had vitellogenic oocytes. PO was observed in the ovarian tissue.

Table 4. A macroscopic and histological description of each stage in the development of female gonad (AO: atresia oocyte; CA: cortical alveolar; GVBM: germinal vesicle breakdown; GVM: germinal vesicle migration; PO: primary oocyte; POF: postovulatory follicle complex; Vtg1: primary vitellogenesis; Vtg2: secondary vitellogenesis; Vtg3: tertiary vitellogenesis;).

Stage	Macroscopic description	Histological description
Ⅰ Immature	Small ovaries, blood vessels indistinct. Color was translucent orange.	Only oogonia and PO present. No AO and POF. Thin ovarian wall.
Ⅱ Developing	Burking up ovaries for maturation starts. Blood vessel becoming more distinct. Color was translucent orange. Egg absence, but presence at after stage and individual egg visible cloudy.	Various types of oocytes were present in the ovaries: PO, CA, Vtg1, Vtg2. Small oil droplet occurrence. No evidence of POFs or Vtg3 oocytes.
Ⅲ Mature	Larger ovaries. Blood vessels were thick. Color was opaque orange. Egg visible.	Various types of oocytes were present in the ovaries and Vtg3 present additionally. Growth of oil droplet and gathering around the nucleus. And Intervals of oocytes was narrow.
Ⅳ Spawning	Mature ovaries with very thick blood vessels. Individual egg was visible clearly. Large and transparent eggs exist. Color was opaque orange.	Intervals of oocytes were wild. Oil droplet united into a big one. Various types of oocytes were present in the ovaries and additionally GVM, GVBD, POF and AO present. More than 50% of the ovigerous lamellae had vitellogenic oocytes and GVM.
Ⅴ Resting	Small ovaries, blood vessels reduced but present. Some eggs were visible. Color was red yellow	Less than 50% of the ovigerous lamellae had vitellogenic oocytes. PO present but AO and POF was existed.

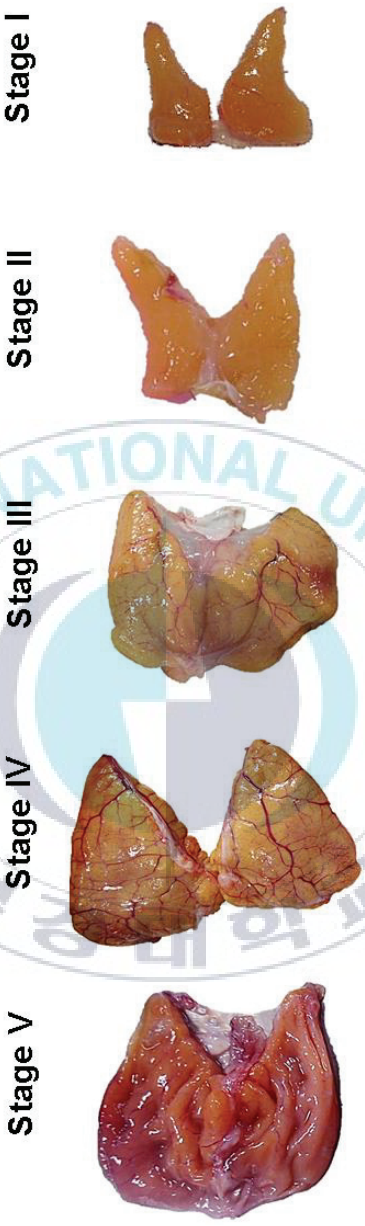

Fig. 10. Microscopical stages of gonad development on female *Zeus faber* in the coastal waters of Korea.

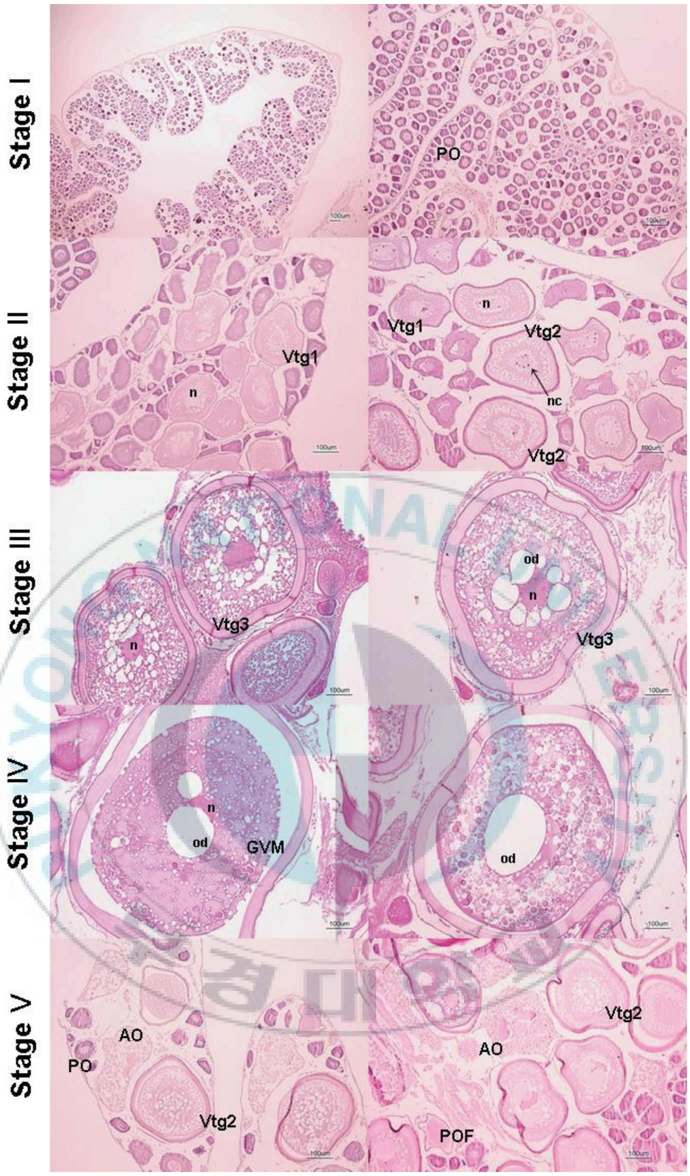

Fig. 11. Histological stages of gonad development on female *Zeus faber* in the coastal waters of Korea. (AO: atresia oocyte; GVM: germinal vesicle migration; n: nucleus; nc: nucleolus; od: oil droplet; PO: primary oocyte; POF: postovulatory follicle; Vtg1: primary vitellogenesis; Vtg2: secondary vitellogenesis; Vtg3: tertiary vitellogenesis).

3.3.2 Annual reproductive cycle

The gonads maturity stages of 593 females were distinguished. The rate of matured gonads (III, IV, V) began to rise in November (Fig. 12). And the highest mature percentage was occurred in January (97%). Females with stage III (mature) of ovaries appeared all through the year and those with stageV occurred between April and August.

The mean GSI for females began to increase gradually from November, peaking in February, after which it dropped rapidly until May (Fig. 13a), which is described highest spawning activity between November and March. The GSI declined sharply after February, which indicated that most eggs had been released, which indicated that the main spawning season is from January to March. The GIS values in females were significantly differences among the months (F= 14.14*,* df=11*,* P<0.05).

The mean GSI for males increased between November and December had a little higher GSI value (Fig. 13b). The GIS values in males were no significant differences among the months (F= 1.01*,* df=11*,* P>0.05), which indicated that the spawning season of males is all the year over.

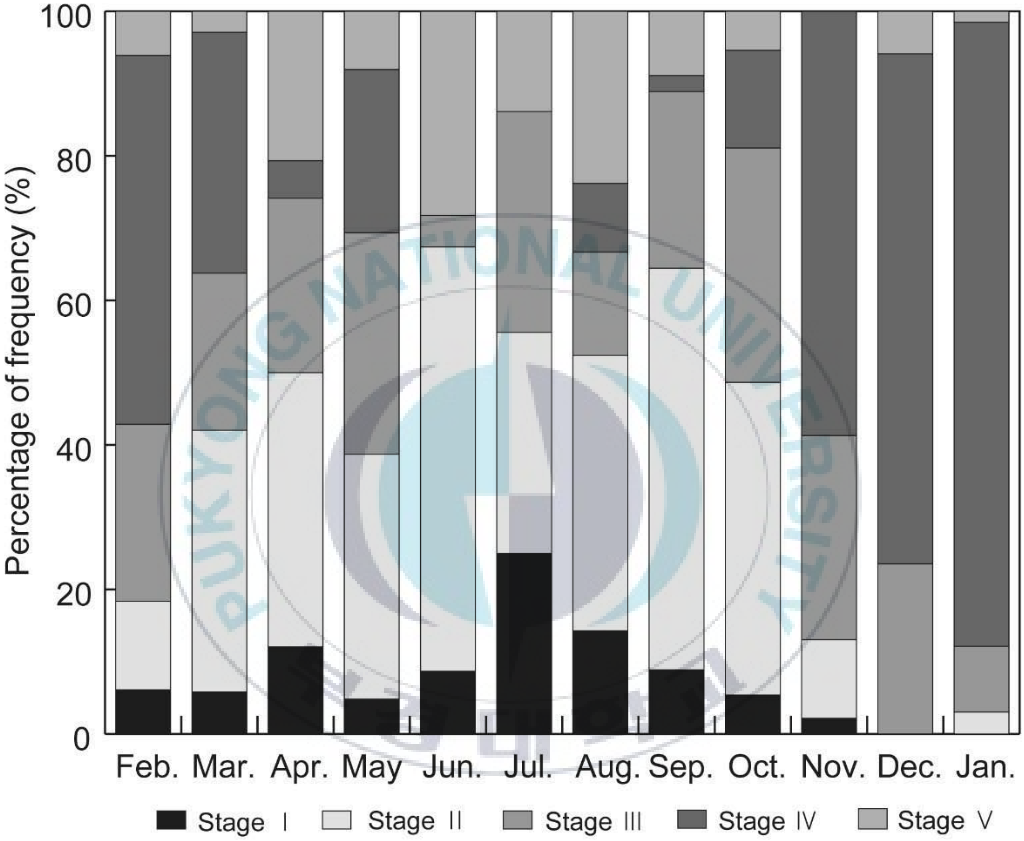

Fig. 12. Monthly frequency variation of development stages for *Zeus faber* in the coastal waters of Korea.

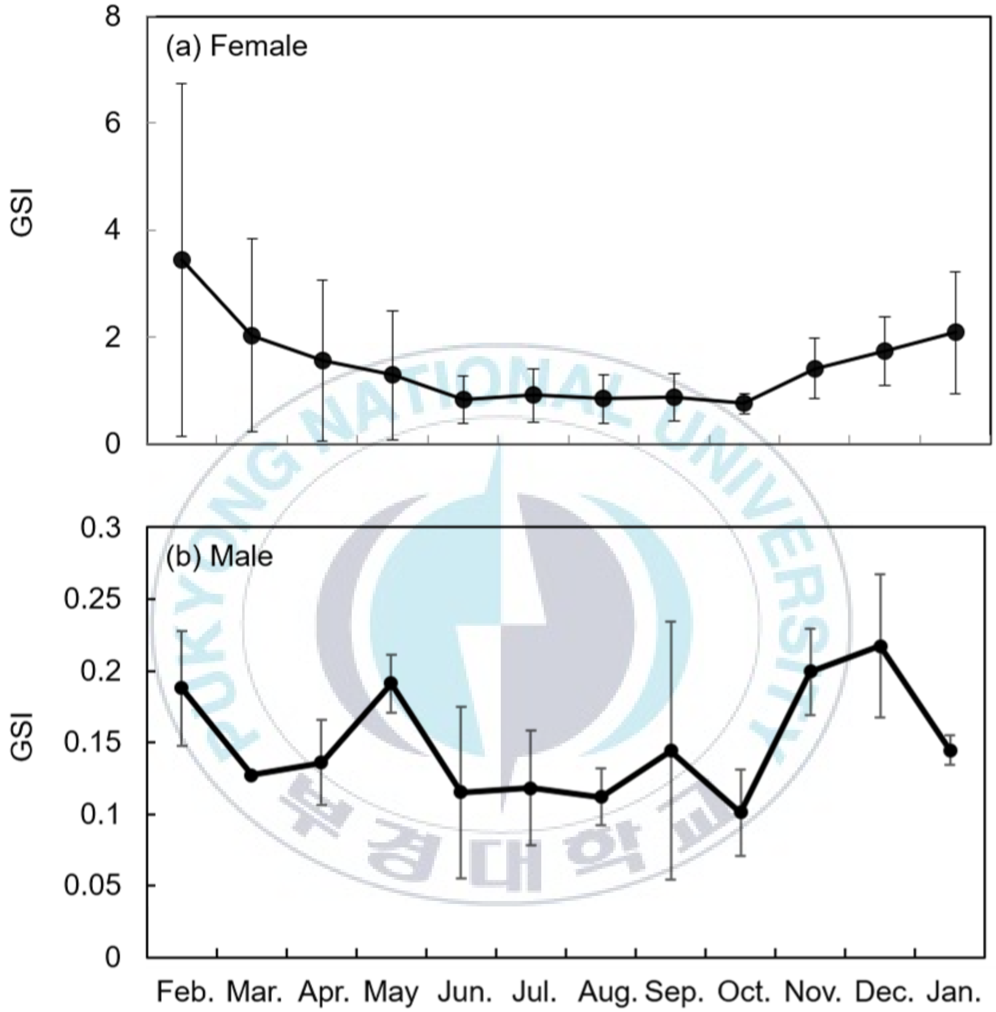

Fig. 13. Monthly changes in the mean gonadosomatic index (GSI) for female (n=583) and male (n=245) of *Zeus faber* in the coastal waters of Korea.

3.3.3 Size-frequency distribution of oocytes

The diameter of oocyte gradually increased with ovarian development (Fig. 14). In stage I, PO were only observed. This results showed that the diameter of oocyte was less than 105 ㎛. Stage II had two modes, which corresponds to the PO and Vtg1 or Vtg2. Because oocytes of various size were existed in the same gonad, several modes could be occurred from stage III to stage IV. Stage V had two modes, which was similar to stage II, the oocyte has shrunk in diameter. Figure 14 shows that *Z. faber* is able to spawn several times in the spawning period, which indicated that they have a multiple-spawning strategy.

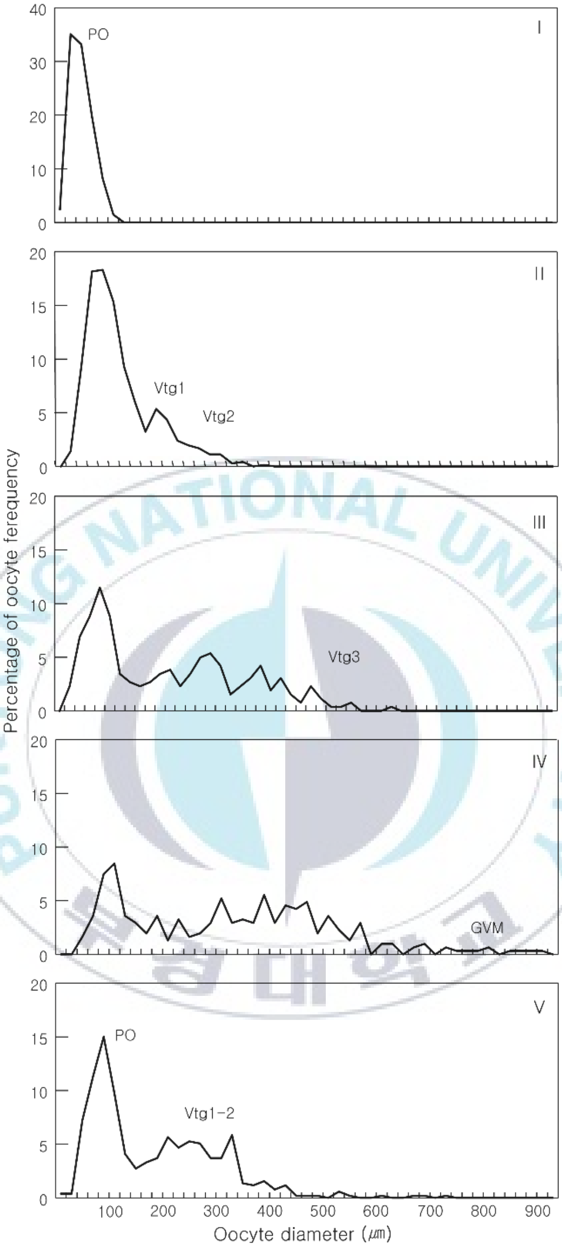

Fig. 14. Diameter distribution of oocyte at each development stage (I immature; II developing; III mature; IV spawning; V resting) for *Zeus faber.* (GVM: germinal vesicle migration; PO: primary oocyte; Vtg1: primary vitellogenesis; Vtg2: secondary vitellogenesis; Vtg3: tertiary vitellogenesis).

3.3.4 Length at sexual maturity

The minimum length and age at sexual maturity for females were 25.8 cm TL and age 4. The length (L_{50}) and age (A_{50}) at sexual maturity for females were 30.8 cm TL (Fig. 15) and age 5 (Fig. 16). All females ≥ 41 cm and age 12 were mature.

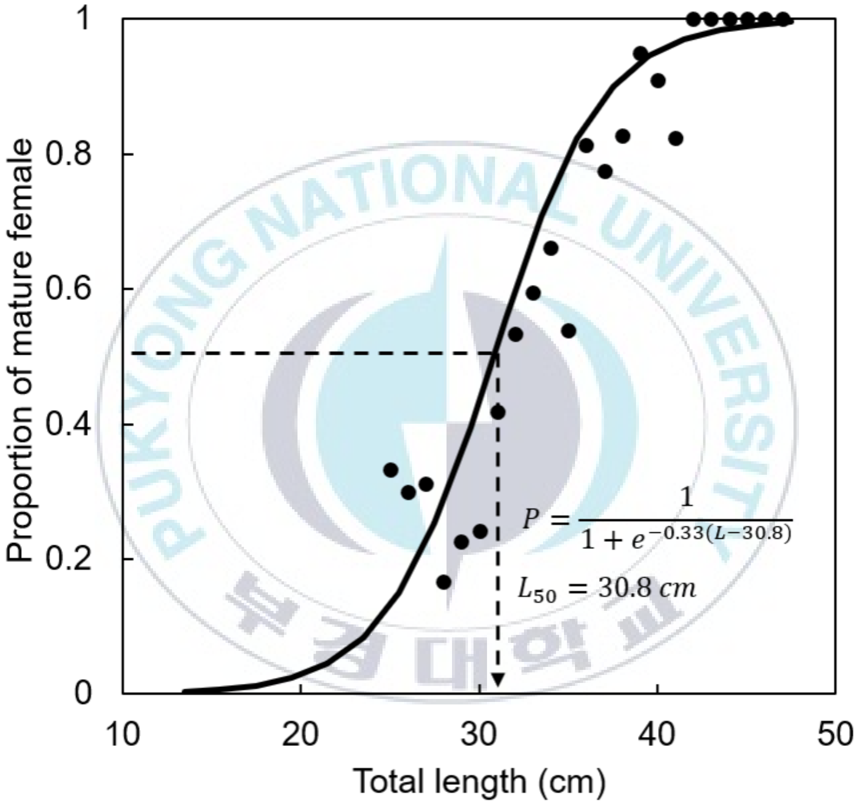

Fig. 15. Length at sexual maturity for female *Zeus faber* in the coastal waters of Korea.

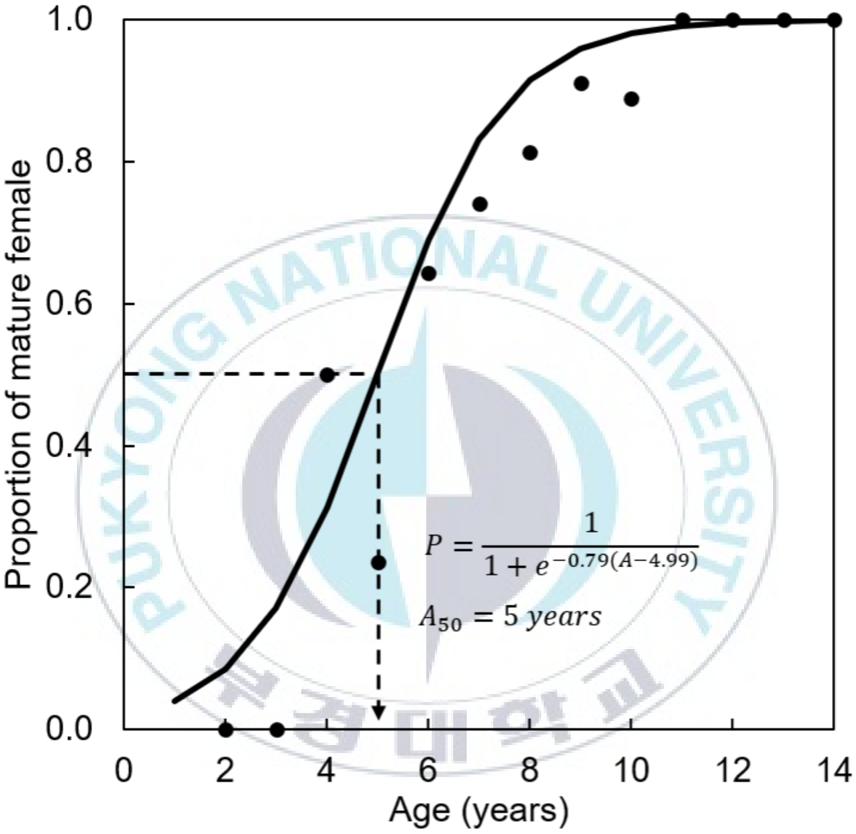

Fig. 16. Age at sexual maturity for female *Zeus faber* in the coastal waters of Korea.

3.3.5 Fecundity

Using 57 specimens with stage IV ovaries collected between November and March, fecundity was estimated. Fecundity ranged from 42,215 to 336,986. The relationship between fecundity and TL was described by the equation (Fig. 17):

$$F = 0.0158TL^{4.3542}$$

$(r^2 = 0.5192, n=57, P<0.001)$

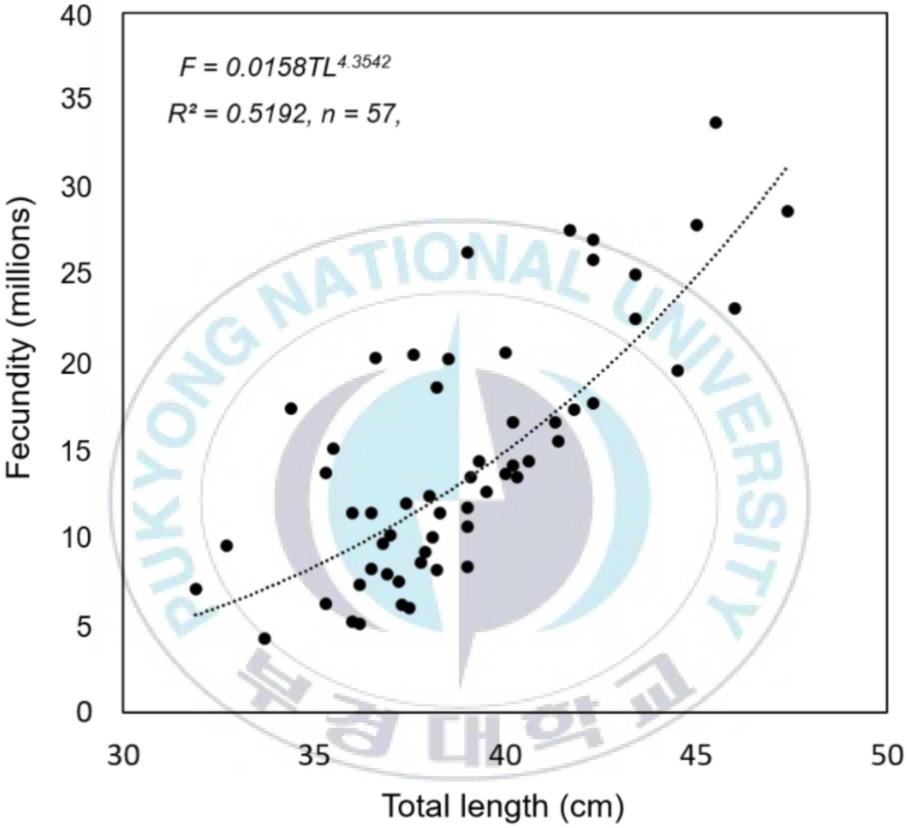

Fig. 17. Relationship between total length and fecundity on *Zeus faber* (n=57) in the coastal waters of Korea.

3.4 Feeding habits

3.4.1 Diet composition

Of the 711 stomachs examined, 524 (74%) were empty. A total of 24 prey species were found in the remaining 187 stomachs. Prey items were divided into three categories: Pisce, Crustacean, and Cephalopoda. The index of relative importance (IRI) analysis recovered pisce as the most important prey category (82.3%), followed by crustaceans (17.5%) and Cephalopoda (0.3%) (Table 5). Seasonal diet compositions of %IRI are summarized in Table 6.

Table 5. Diet composition in the stomach contents (%F, frequency of occurrence; %N, numerical percentage; %W, percentage weight; %IRI, percentage index of relative importance).

Prey items	%F	%N	%W	%IRI
Pisces				82.3
Acropoma japonicum	4.0	1.7	3.6	1.0
Argentina kagoshimae	1.0	0.3	0.3	0.0
Coelorinchus multispinulosus	0.5	0.2	0.3	0.0
Chelidoperca hirundinacea	0.5	0.2	0.5	0.0
Cleisthenes pinetorum	1.0	0.3	2.9	0.2
Cololabis saira	1.0	2.8	1.7	0.2
Decapterus muroadsi	0.5	0.3	0.9	0.0
Doederleinia berycoides	2.0	0.6	1.6	0.2
Engraulis japonicus	10.9	7.6	6.0	7.2
Glyptocephalus stelleri	5.0	3.0	14.5	4.2
Larimichthys polyactis	2.5	0.9	4.7	0.7
Lepidotrigla guentheri	0.5	0.2	0.2	0.0
Malakichthys wakiyae	1.0	0.3	0.2	0.0
Pagrus major	1.0	0.5	1.0	0.1
Pennahia argentata	1.5	0.5	2.5	0.2
Psenopsis anomala	1.5	0.5	3.5	0.3
Scomber japonicus	0.5	0.2	1.6	0.0
Trachurus japonicus	8.5	2.8	10.4	5.4
Trichiurus japonicus	18.9	7.3	23.9	28.6
Unidentified fish	28.4	9.5	15.0	33.8
Crustacean				17.5
Plesionika izumiae	0.5	2.0	0.1	0.1
Pandalus eous	6.0	57.5	2.4	17.4
Unidentified shrimp	0.5	0.2	0.0	0.0
Cephalopoda				0.3
Todarodes pacificus	2.0	0.6	2.2	0.3
Sepiola birostrata	0.5	0.2	0.0	0.0

Table 6. Percentage index of relative importance (%IRI) of 4 seasonal groups.

Prey items	Spring	Summer	Autumn	Winter
Pisces	100.0	61.7	71.0	100.0
Acropoma japonicum	0.0	0.1	0.0	21.5
Argentina kagoshimae	0.1	0.0	0.1	0.0
Coelorinchus multispinulosus	0.1	0.0	0.0	0.0
Chelidoperca hirundinacea	0.0	0.0	0.0	0.4
Cleisthenes pinetorum	1.2	0.0	0.0	0.0
Cololabis saira	0.0	3.0	0.0	0.0
Decapterus muroadsi	0.0	0.0	0.2	0.0
Doederleinia berycoides	0.6	0.2	0.0	0.3
Engraulis japonicus	0.3	0.9	36.8	0.0
Glyptocephalus stelleri	5.1	1.4	0.2	11.9
Larimichthys polyactis	0.0	0.6	3.0	0.0
Lepidotrigla guentheri	0.0	0.0	0.1	0.0
Malakichthys wakiyae	0.0	0.3	0.0	0.0
Pagrus major	0.0	0.4	0.0	0.3
Pennahia argentata	0.0	0.0	1.8	0.0
Psenopsis anomala	0.0	0.0	1.2	0.5
Scomber japonicus	0.0	0.0	0.4	0.0
Trachurus japonicus	1.7	6.9	0.7	16.8
Trichiurus lepturus	34.9	31.3	16.2	9.2
Unidentified fish	56.0	16.5	10.3	39.1
Crustacean	0.0	32.8	29.0	0.0
Plesionika izumiae	0.0	0.4	0.0	0.0
Pandalus eous	0.0	32.4	29.0	0.0
Unidentified shrimp	0.0	0.0	0.0	0.0
Cephalopoda	0.0	5.4	0.0	0.0
Todarodes pacificus	0.0	5.4	0.0	0.0
Sepiola birostrata	0.0	0.0	0.0	0.0

3.4.2 Difference in diet by size class

For each of the four size classes, *Trichiurus japonicus* and *Trachurus japonicus* were the most common prey by biomass (Fig. 18). *E. japonicus* was an important prey in the 24–30 cm and 31–35 cm size classes, but the occurrence of *E. japonicus* from the 36-40 cm group was greatly reduced. In the large fish (>38 cm), the proportion of *Glyptocephalus stelleri* increased markedly. There is no significant difference in the size of the prey items (*Trichiurus japonicus, E. japonicus, Trachurus japonicus* and *G. stelleri*) according to the TL $(P > 0.05)$. There was a significant difference $(x^2 = 318.24, df = 24, P < 0.001)$ in the proportions of prey categories consumed by the four size classes (Table 7). Among prey items, *G. stelleri* varied the most highly between size classes $(x^2 = 132.88)$, followed by crustaceans $(x^2 = 53.90)$ and *Trichiurus japonicus* $(x^2 = 46.44)$. The *post hoc* contingency table analysis for prey types revealed that other fish, including *E. japonicas*, contributed to the variation between size classes as well as among prey categories (Table 8).

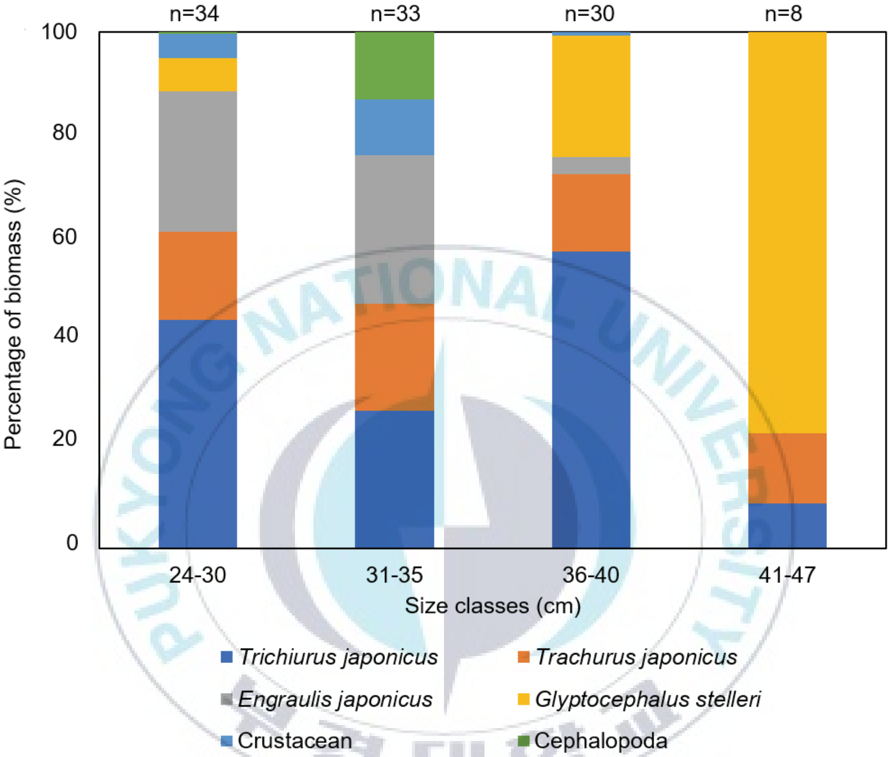

Fig. 18. Variation of the diet composition by the percentage biomass by size classes.

Table 7. Two-way contingency table analysis of the size class variation of nine different prey groups. Values are frequencies of prey groups observed in each size class.

	Size class (cm)					
Prey type	24 -30	31 - 35	36 - 40	41 - 47	N_i	x^2
Trichiurus japonicus	17	9	17	4	47	46.44
Engraulis japonicus	20	19	10	0	49	17.37
Trachurus japonicus	5	6	5	2	18	9.09
Cololabis saira	7	11	0	0	18	4.83
Glyptocephalus stelleri	1	0	8	10	19	132.88
Acropoma japonicum	0	5	4	2	11	14.26
Other fishes	3	12	9	7	31	38.46
Crustacean	78	293	11	0	382	53.90
Cehalopoda	1	4	0	0	5	1.01
N_i	132	359	65	25	580	
x^2	21.48	48.92	93.16	154.68		318.24 ***

***, P<0.001

Table 8. Results of *post hoc* contingency table analysis of the size class variation of nine different prey groups after the elimination of selected rows and/or columns

Row(s) or column(s) eliminated	Significance of x^2	Sample size
Glyptocephalus stelleri	*P*<0.001	561
Glyptocephalus stellerim, Crustacean	*P*<0.001	179
Glyptocephalus stelleri, Crustacean, Trichiurus japonicus	*P*<0.001	132
Glyptocephalus stelleri, Crustacean, Trichiurus japonicus, other fish	*P* <0.05	101
Glyptocephalus stelleri, Crustacean, Trichiurus japonicus, other fish*, Engraulis japonicus*	*P* >0.05	51
Glyptocephalus stelleri, Crustacean, Trichiurus japonicus, other fish*, Engraulis japonicus, Acropoma japonicum*	*P* >0.05	41

3.4.3 Difference in diet by season

In all seasons, *Trichiurus japonicus* and *Trachurus japonicus* were consumed (Fig. 19). *Trichiurus japonicus* was the most common prey item by mass in spring (30.5%) and summer (34.9%). Overall crustacean prey mass was minimal but increased during summer and autumn. In autumn, *Trichiurus japonicus and E. japonicus* dominated the prey mass, making up 18.3% and 15.8% of the total diet, respectively. *G. stelleri* and *Trachurus japonicus* mass increased in winter to 27.8% and 18.9%, respectively. We found a significant difference ($df = 24, P < 0.001$) in the seasonal proportions of prey categories consumed (Table 9). Among the prey categories, the most variables were *Acropoma japonicum* ($x^2 = 148.68$) and *G. stelleri* ($x^2 = 85.93$), as demonstrated by the seasonal changes in these prey items. Among seasons, the most variable was winter ($x^2 = 238.95$). The *post hoc* contingency table analysis revealed that statistical significance was maintained after eliminating this source of variability from the analyses (Table 10).

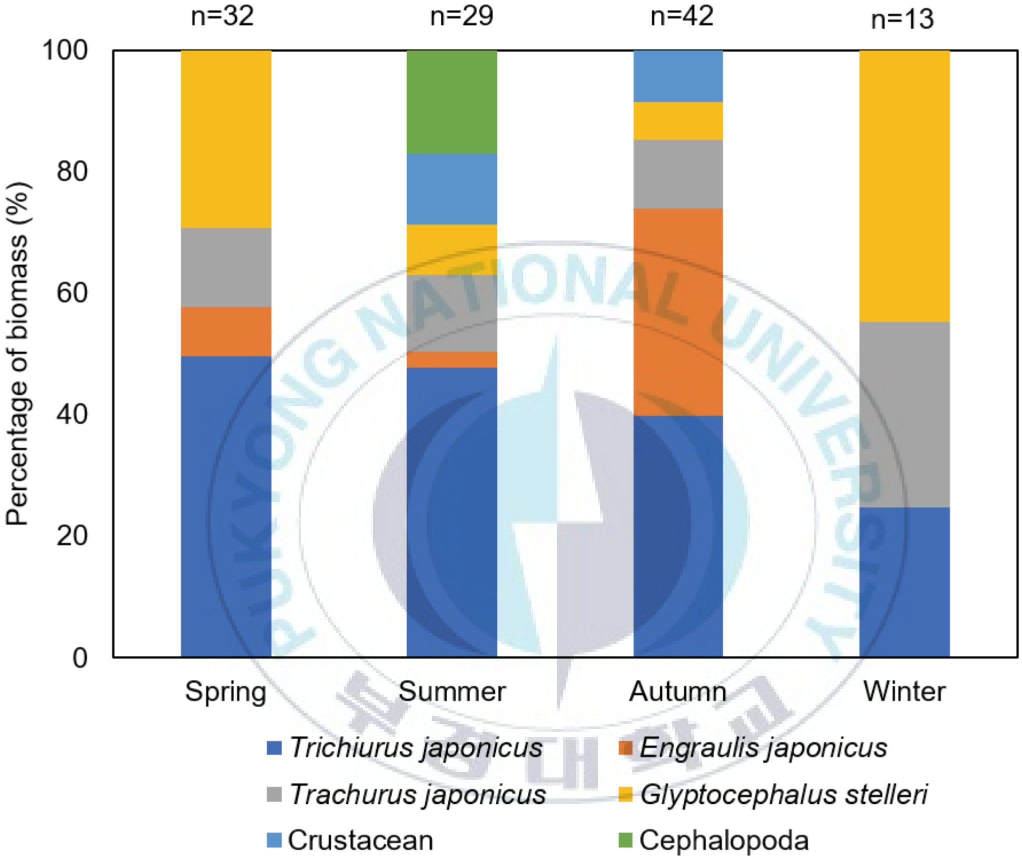

Fig. 19. Seasonal variation in the diet composition by the percentage of biomass.

Table 9. Two- way contingency table analysis of the season variation of nine different prey groups. Values are frequencies of prey groups observed in each size class.

Prey type	Spring	Summer	Autumn	Winter	N_i	x^2
Trichiurus japonicus	16	14	12	5	47	74.64
Engraulis japonicus	1	4	44	0	49	65.23
Trachurus japonicus	3	7	2	6	18	31.69
Cololabis saira	0	18	0	0	18	15.59
Glyptocephalus stelleri	7	3	1	8	19	85.93
Acropoma japonicum	0	1	0	10	11	148.68
Other fish	6	7	13	4	30	19.15
Crustacean	0	252	131	0	383	54.35
Cehalopoda	0	5	0	0	5	4.15
N_i	33	311	203	33	580	
x^2	137.51	58.89	64.07	238.95		499.41***

***, *P*<0.001

Table 10. Results of *post hoc* contingency table analysis of the season variation of nine different prey groups after the elimination of selected rows and/or columns.

Row(s) or column(s) eliminated	Significance of x^2	Sample size
Acropoma japonicum	*P* <0.001	569
Acropoma japonicum, Glyptocephalus stelleri	*P* <0.001	550
Acropoma japonicum, Glyptocephalus stelleri, Trichiurus japonicus	*P* <0.001	503
Winter	*P* <0.001	547
Winter, *Acropoma japonicum*	*P* <0.001	546
Winter, *Acropoma japonicum, Glyptocephalus stelleri,*	*P* <0.001	535

3.4.4 Trophic diversity and dietary niche overlap

Trophic diversity was generally low. Among the size classes, trophic diversity was highest in the 31–35 cm group and lowest in the 24–30 cm group (Fig. 20a). This confirmed that as body size increased, dietary variability also increased. Niche overlap among the size groups showed differences between the 41–47 cm group and other groups. The lowest values of trophic diversity were observed for the 41–47 cm group (Table 11), indicating that this group consumed different prey items to the other groups.

In terms of season, autumn and summer yielded the highest trophic diversity (Fig. 20b), indicating that more prey items were consumed during this time period than in other seasons. Niche overlap comparisons between seasons demonstrated that prey items consumed during spring were similar to those during summer and winter (Table 12).

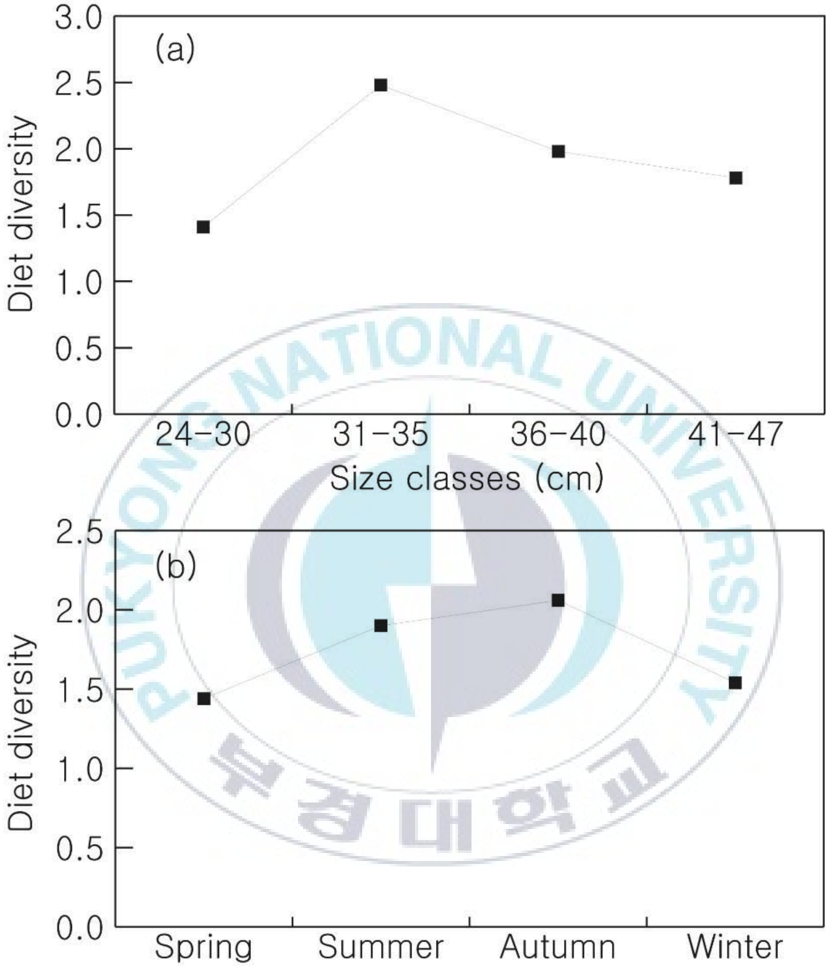

Fig. 20. Trophic diversity of prey items; (a) size classes and (b) seasons.

Table11. Niche overlap between size classes of *Zeus faber*, using Schoener's overlap index (R_0).

Size class (cm)	24-30	31-35	36-40	41-47
24-30		0.67	0.69	0.29
31-35			0.47	0.25
36-40				0.47

Table 12. Niche overlap between seasons of *Zeus faber*, using Schoener's overlap index (R_0).

season	Spring	Summer	Autumn	Winter
Spring		0.64	0.48	0.63
Summer			0.41	0.46
Autumn				0.10

3.4.5 Effects of sex, size class, and season on feeding intensity

The occurrence of empty stomachs among females (69.8%) was lower than that among males (81.59%) (Fig. 21a). There was a significant difference in the empty rate between males and females ($x^2 = 42.81, df = 1, P < 0.001$). The values of the feeding intensity index (FI) differed between females (8.16) and male (7.82), indicating that females were more active predators than males.

There were significant differences in the occurrence of empty stomachs between size classes of specimens ($x^2 = 183.37, df = 3, P < 0.001$). This empty rate was highest in the 31–35 cm group and lowest in the 41–47 cm group (Fig. 21b). The 31-35 cm group (8.58) of FI was higher than other size groups of that (24-30 group: 7.59; 36-40 cm group: 7.36; 41-47 cm group: 7.27).

There was no statistically significant difference in the occurrence of empty stomachs between seasons ($x^2 = 1.15, df = 3, P > 0.05$). The empty rate was highest in winter (Fig. 21c). Seasonal differences in FI were observed, with the highest value for spring (8.35), followed by winter (8.28), summer (7.68), and autumn (7.59).

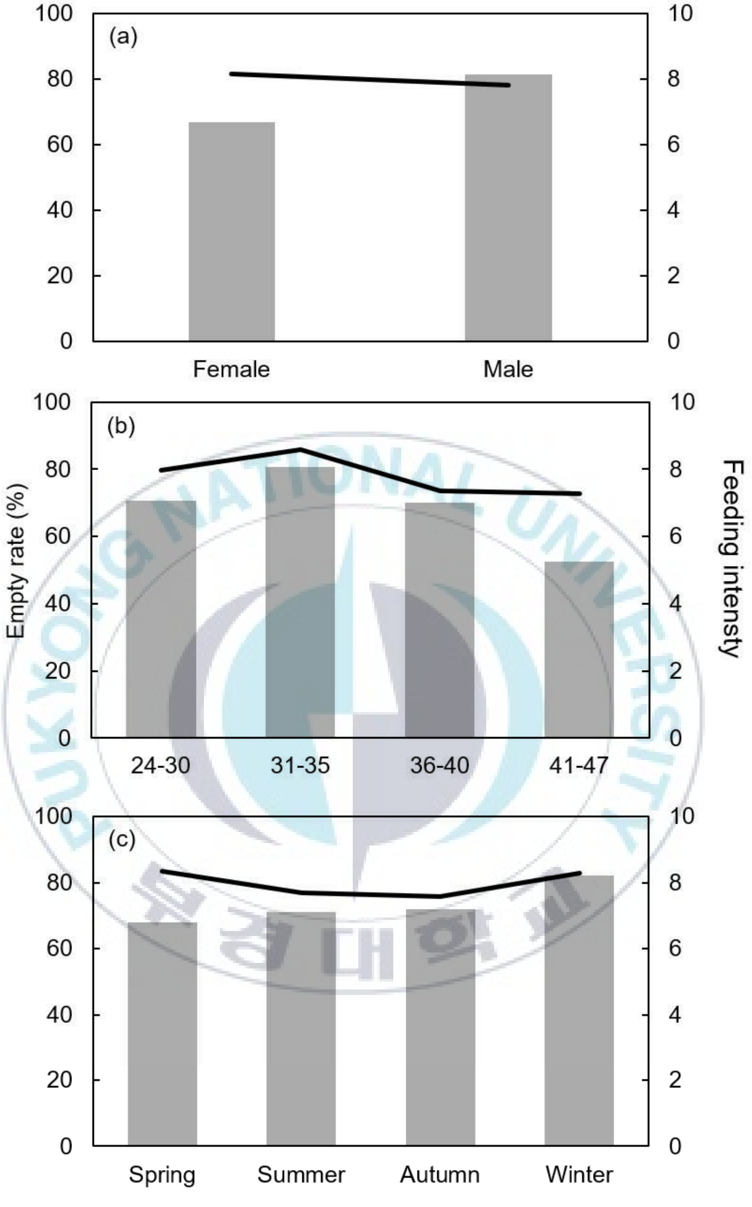

Fig. 21. Empty rate of stomach and feeding intensity for (a) sex, (b) size classes, and (c) season.

IV. Discussion

4.1 Biological characteristics

The result of the sex ratio revealed the intrinsic pattern of *Z. faber* in the coastal waters of Korea, which is important information for understanding the population structure. The number and length of female were more than that of male, and up to 40 cm individuals were all female. These differences could occur in various factors, such as differential growth rate, lifespan, fishing pressure, and habitat preference. In the present study, samplings were done with a commensal trawl. The previous studies reported that as the depth increases, the length of the zeid fish is longer (Kim et al. 2013, Martins & Schwingel 2012, Vaz-dos-Santos et al. 2014). Therefore, there are a high rate that females were most likely more fishing. The previous studies of *Z. faber* have been similar results (Ismen et al. 2012, Vrgoč et al. 2006, Yoneda et al. 2002). This pattern is a bigger-deeper paradigm, which is affected by the competition, food availability and preferred water depth (Vaz-dos-Santos et al. 2014).

4.2 Age and growth

Common techniques used to determine the age of fish are to analyze growth zones of structures such as vertebra, fin rays, scales, otoliths, and other skeletal (Zhang 2010). To use any of these features to estimate age, ring marks must be clearly recognizable, and the feature must be of a certain size in proportion to total body length, among other requirements (Zhang 2010). According to Yoneda et al. (2002), the otoliths of *Z. faber* are small in size and irregular in shape, and they do not have clear ringmarks, leading to underestimations of fish age. In this study, we used vertebra for the age determination of *Z. faber*. Vertebral ring marks are easy to read in this species, with clearly discernible opaque and translucent bands. Vertebra size increases with body length. Therefore, vertebrae are the most suitable feature to use to estimate the age of *Z. faber* specimens (Ismen et al. 2012).

Marginal increment analysis confirmed the deposition periodicity of growth marks, revealing an annual pattern. It also showed that the opaque band is formed between November and December, suggesting that one ring is formed each year. This is consistent with the results of Yoneda et al. (2002), who found that opaque bands were formed during winter. Annuli formation is associated with environmental factors and endogenous rhythms (Kim et al. 2016), and it is affected by winter water temperatures (Kim et al. 2016). Incremental growth during summer is affected by the spawning season and is consistent with the period of peak gonadosomatic index (GSI). The growth rate slows during the spawning period because energy is diverted from growth to maturation.

We estimated that there were 14 age classes of *Z. faber* (ages 1–14 years). The maximum age was 14 years in females and 8 years in males. Previous studies, using vertebra to measure age, have reported a maximum age of 15 years in females and 13 years in males in the East China Sea and 18 years in females and 17 in males in the North Aegean Sea (Yoneda et al. 2002, Ismen et al. 2012). Akyol (2001) and Hanchet et al. (2001), using otoliths to measure age, estimated the maximum age at 6 years and 9 years, respectively. These results concluded that age estimated using otolith was smaller than 10 years. In previous studies using otolith, individuals with a total body length of 42 cm were about 5 years old. Most other studies, using vertebra to measure age, have estimated fish of this size to be about 11 years old. It seems probable that the use of otolith measurement leads to significant underestimation of age in this species (Yoneda et al. 2002). This study judged that *Z. faber* is long-lived fish that lives over 14 years old.

Growth patterns and equations in this study indicate that *Z. faber* of both sexes grow rapidly during the two years of life and slowly thereafter (Hanchet et al. 2001; Yoneda et al. 2002). We found significant differences between males and females in all three growth parameters analyzed in this study (Table 2). Our results indicate that males grow faster and reach their maximum length at a younger age than do females. The same results have been observed from Turkey, the North Aegean Sea, and the East China Sea (Akyol 2001; Ismen et al. 2012; Yoneda et al. 2002). For age 7 years females have larger in body size than the male. The maximum length of females in this study was larger than that of males. The size-frequency distribution showed that individuals over 40 cm long were likely to be female. Because the maximum age of females was greater than that of males, females have longer lifespans than males and thus are able to have a longer growth period. This phenomenon is commonly seen in demersal fish species, such as *Lophiomus setigerus* (Yoneda et al. 1998), *Dipturus chinensis* (Hara et al. 2018), *Doederleinia berycoides* (Choi et al. 2012).

In this study, growth performance index was 2.63 in female and 2.64 in male. The range of growth performance index is from 2.42 to 3.08, and our result is similar value to East china Sea and North Aegean Sea (Yoneda et al. 2002; Ismen at al. 2012). However, the value of Western English Channel (Dunn 2001) was the highest, and the study of Dunn (2001) used the length frequency distribution was suggested that *Z. faber* grew to 34 cm in the first year. These results are similar to those of Silva (1992). Silva (1992) observed a modal length of 10–14 cm in summer growing to 18–22 cm by the autumn, and reach in 23–26 cm by the following summer. Because *Z. faber* has a long spawning period and is long-lived fish, year class cannot be clearly confirmed by length frequency method.

Most studies have found that the growth rate decreases as latitude increases; it is common for growth to be faster in warmer waters (Hjernquist et al. 2012; Trip et al. 2014). However, in this study, we found that *Z. faber* grew faster in more northern latitudes. The area from the East China Sea to the coastal waters of Korea is influenced by the high temperatures of the Kuroshio Current, and in this region, higher temperatures are found at higher latitudes (Yoneda et al. 2006). Our study area is linked to the area studied by Yoneda et al. (2006), who found a similar relationship between latitude and growth. These results suggest that the marine environment in the coastal waters of Korea is highly suitable for *Z. faber*. Both prey diversity and the density of potential predators vary with latitude. Due to the meeting of warm and cold currents in the Southern Sea of Korea (Cho 1994; Kim et al. 1991), this region hosts various and abundant resources (Cha 2010). In addition, interpopulation differences in *Z. faber* metabolism, driven by temperature variations, may cause differences in growth, maturation rates, and life span. Information on differences in metabolic rates between populations is beyond the scope of this study, but our results support the existence of a strong link between latitude and growth.

4.3 Maturation

Due to the standard of development stage of gonad was not present, microscopical and histological analyses were conducted in this study. Histological research was performed to account for maturation strategy or phylogeny. Five stages were identified as color, shape, existence of eggs, primary growth, secondary growth, existence of oil droplet, oocyte diameter, interval between oocyte, existence of AO, POF, and so on. Compared to microscopical and histological analysis, it agreed 87.6%.

Spawning season of *Z. faber* was from November to May. GSI of female was peaked in February, which indicated that the main spawning period was from January to March. The previous study in East China Sea has similar results. Yoneda et al (2006) in East China Sea reported that spawning season is from November to May, and the main spawning season is March to April. However, the studies carried out in Turkey found that spawning season is spring and autumn (Akyol 2001, Ismen et al. 2012). Ismen et al (2012) found that spawning season is from February to May and August to September. In Korea and Japan, the spawning season appeared only once per year. This difference of spawning season can be influenced by a multiplicity of different factors such as the latitude, water temperature and light regimes (Otterå et al. 2006, Yoneda et al. 1998). In the case of *Lophius litulon*, the spawning season varies according to latitude in Japan (Yoneda et al. 2001). Spawning rhythms of genus *Amphiprion* are different according to local adaptations, and fecundity and clutch size among the same species are varied according to high latitude and climate

(Richardson et al. 1997). Although differences of spawning season with other areas are common among marine fishes (Thresher 1988), explanations for the reason of this pattern are difficult. The timing of spawning is generally determined by optimal environmental conditions allowing the greatest survival and fitness for larvae, juveniles and adults (McEvoy & McEvoy 1992). Therefore, the difference in spawning season is due to local adaptations.

The *Z. faber* is multiple spawners, as zeid fishes are also multiple spawners (Martins & Schwingel 2012). The use of various techniques combined (mature stage, GSI, histology) consider multiple spawning within a season. The *Z. faber* has long spawning period, and ovaries were staged by histology showed that various size of oocytes was presented. In stage III and IV, distributions of oocyte diameters have various mode, which is evidence of multiple spawning species (Zúñiga-Flores et al. 2011). In stage IV, there were various types of oocytes and spawning evidence such as AO and POF existed. This study showed that *Z. faber* has asynchronous ovary development. The multiple spawning is possible when there is a long period of adequate food supply for the larvae (Nikolsky 1969). Therefore, a long spawning period of *Z. faber* has the advantage of abundant food and the survival of the larvae. Nikolsky (1969) reported that long-lived species have a strategy of multiple spawning due to adaptation under labile conditions for the survival of the eggs and high recruitment variability. Due to the maximum age of *Z. faber* is 15 years (Yoneda et al. 2002) and the habitat depth increases with growth (Kim et al. 2013), *Z. faber* has a multi-spawning strategy.

The present study revealed that length at maturity of females was 30.8 cm. In the previous studies, length at sexual maturity was 32.6 cm and 34.0 cm in the East China Sea (Yoneda et al. 2006) and 25.4 cm (Ismen et al. 2012) and 31 cm (Akyol 2001) in the Aegean Sea. In the waters of England and Wales, length at sexual maturity was 34.5 cm (Dunn 2001). This study showed that length at sexual maturity in Korea was smaller than the most previous ones, with difference of 3-4 cm. The length at sexual maturity in Turkey had lowest. The small values of length at sexual maturity is thought to be a sign of excessive fishing. If the resources are reduced, growth and length at sexual maturity tend to increase due to density-dependent effects (Zhang 2010). Therefore, the continuous monitoring is necessary for the management of resources in *Z. faber.*

4.4 Feeding habits

The diet of *Z. faber* consisted of three prey categories: (1) pisces, (2) crustaceans, and (3) cephalopods. Despite the fact that *Z. faber* fed on a range of prey items, fish dominated the diet in all seasons. In particular, *Trichiurus japonicus, Trachurus japonicus*, and *E. japonicus* were consumed in all seasons, which was similar to all results performed in Korea (Huh et al. 2006a; Choi et al 2011; An et al. 2012). This suggests that *Z. faber* is a piscivorous predator. As *Z. faber* has a large mouth, suction capabilities, and extensive swimming maneuverability (Stergiou and Fourtouni 1991; An et al. 2012), it can swallow fish whole. Prey items in the stomach were therefore well preserved.

In the present study, *Trichiurus japonicus* was the most commonly consumed species, as reported previously (Huh et al. 2006a; Choi et al 2011; An et al. 2012). *T. japonicus* inhabits the Southern Sea at depths of 40 to 120 m (Martins and Haimovici 1997), which overlaps the habitat of *Z. faber* (50 to 140 m) (Vrgoč et al. 2006; Kim et al. 2013). Fishes with a long body swim in a head-up state with limited swimming capabilities (Wilson 1958). In addition, the body of *T. japonicus* is thin, long, and reflective. Therefore, *Z. faber* can efficiently detect *T. japonicus* at any depth (Stergiou and Fourtouni 1991). In the eastern Mediterranean, long body fishes such as *Cepola macrophthalma* are most commonly consumed by *Z. faber* (Stergiou and Fourtouni 1991).

Z. faber consumed *Trichiurus japonicus* and *E. japonicus,* which is schooling fish. *Z. faber* has a stalking ability to consume prey fish selected in a school or group (Russell 1983).

Two species inhabit the wild layer of the ocean, indicating that *Z. faber* moves to the surface layer to feed. Previous studies have found Jack Mackerel (*Trachurus symmetricus*) in the eastern Mediterranean and along the Portuguese coastline (Stergiou and Fourtouni 1991; Silva 1999). *Trichiurus japonicus* and *E. japonicus* the most abundant species in the coastal waters of Korea (Cha 2010), which indicates that *Z. faber* is an opportunistic feeder by energy effectivity.

Crustaceans were commonly consumed by *Z. faber* during summer and autumn. Stergiou & Fourtouni (1991) found that only individuals up to 14 cm consumed tiny crustaceans, but this study yielded different results, as crustaceans were consumed by specimens of *Z. faber* up to 38 cm, and up to 168 crustaceans were consumed at a time. Along the Portuguese coastline, crustaceans are also an important food source for specimens up to 25 cm (Silva 1999). The short period of research in the Mediterranean has yielded different results to this study and a previous study of *Z. faber* along the Portuguese coastline. Crustaceans were the dominant species in summer and autumn in this study, possibly because of the behavior and life history of crustacean prey (Xue et al. 2005; Blasina et al. 2010). *P. eous* used as prey mainly migrate to inshore (<50 m) for the larval hatch during late winter and early spring (Park et al. 2012; Richards 2012). The density of crustaceans increases as the hatched crustaceans recruit in summer. Therefore, larger individuals of *Z. faber* can consume small crustaceans abundantly. Bergstrom (2000) reported that *Pandalus* species are important food items for demersal fish and constitute integral parts of marine food webs found on the continental shelves.

Occurrence of empty stomach was higher (74%) in the present study than that in previous studies, which ranged from 34.6% (Stergiou and Fourtouni 1991) to 71% (Kim et al. 2013). This seems to be a common phenomenon observed in piscivorous fishes (*Lophius litulon*, 64.3%; *Scomberomorus niphonius*, 45.4%; *Sphyraena pinguis*, 34.1%) (Baeck and Huh 2004; Choi et al. 2011; Huh et al. 2006b). As *Z. faber* has high energy content, it allows them to survive without feeding constantly (Baeck and Huh 2004, Choi et al. 2011; Huh et al. 2006b). Thus, *Z. faber* has a relatively higher empty rate. *Z. faber* is a nocturnal predator (Pejdo et al. 2016), but a sampling of our study was carried out at day. So higher empty rate of *Z. faber* could be derived from the sampling time without considering their activity behavior. Feeding ecology should be investigating with understanding their activity behavior.

In the present study, predation by *Z. faber* was not significantly dependent on prey size. As there are no distinct morphological changes related to feeding ability with growth (Stergiou and Fourtouni 1991), large specimens of *Z. faber* expand their prey options by altering feeding behavior. In this study, individuals less than 30cm preferred surface fish as *E. japonicus*, while specimens of *Z. faber* up to 38 cm were found to feed on the benthic species *G. stelleri*. According to previous studies, as body size increased, *Z. faber* preferred fish lived deep water such as *Conger myriaster* (Huh et al 2006), *Micromesistius poutassou* (Silva 1999). This indicates that *Z. faber* can exploit the entire water column when feeding.

This partial dietary change can reduce intraspecific competition by resource partitioning (Gerking 1994). After consuming a diet of small fish and zooplankton during the juvenile stage, adult *Z. faber* (>24 cm) undergo a transformation in prey selection to reduce intraspecific competition.

Feeding activity of *Z. faber* was changed according to life-history pattern. The empty rate was lower for larger specimens, which indicate that as *Z. faber* grow, they have a high hunting ability. *Z. faber* consumed more prey items during summer and autumn than in other seasons. Some fish inhabited Korea tent to spend the winter in near Jeju Island and East China Sea. In the spring, as temperature rise, they come back to the Southern Sea of Korea due to form spawning ground (Noh et al. 2013). Therefore, species abundance in summer becomes higher, compared with winter. The empty rate and FI in winter were higher than that of other seasons. Winter was the main spawning period of *Z. faber*, which indicated that feeding activity was influenced by the spawning period (Oh et al. 2001). Silva (1999) reported that the *Z. faber* fed more actively during the spawning season, which asserted that *Z. faber* during spawning period demand higher energy requirements to support gonad development and multi-spawning. Similarly, the values of FI in this study showed high values during the spawning season. However, the empty rate also increased during the winter. Due to gonad size of *Z. faber* was larger in the abdominal cavity, the empty rate increased during the spawning season to avoid compression of the mature gonads (Yamamura et al. 1998) and to limit the space available for stomach expansion

(Olaso et al. 2000).

V. General discussion

The demand for *Z. faber* has increased in recent years and they became the potential and valuable resource. However, there is no fishing industry targeting *Z. faber*, and which is classified as bycatch in Korea. The records on catch and monitoring for *Z. faber* are difficult. In addition, sampling of *Z. faber* is not easy. The present study had insufficient small individuals due to sampling time and using a trawl net. Therefore, this study is an ecological study that focuses on the adult (>24 cm) of *Z. faber*.

Of the 838 *Z. faber*, sex ratio of female to male was 2.42:1. The range of total length was wider for females than for males, and the size-frequency distribution for females was also wider than that for males. All the individuals more than 40 cm were females. These results can be explained by age, growth rate and feeding habits. The maximum age was 14 years in female and 8 years in male, which seems to have a long growth period and lifespan in females. In addition, feeding intensity of female was higher than that of male.

Previous studies of age and growth have reported a maximum age of 15 in East China Sea and 18 years in Turkey (Yoneda et al. 2002, Ismen et al. 2012). These results were similar to the current one, except for the paper using otolith. Due to otoliths of *Z. faber* have small and irregular shape, age may be underestimated (Yoneda et al. 2002). However, there is a lack of research on otolith, which should be carried out later.

The study of Yoneda (2006) performed in the Northern and Southern Sea of East China

Sea, the growth rate between two populations was different depending on their latitude. As the higher latitude, as the faster growth rate, however, the result of *Z. faber* was the opposite (Yoneda et al. 2006). The sampling area of this study was linked to the area of previous study (Northern Sea of East China Sea) and was higher latitude, and growth rate was higher in the Korea. This phenomenon can be explained as the cause of different environments such as water temperatures, food diversity, current and so on. Due to the coastal waters of Korea is a good environment where meets warm and cold current (Cho 1994; Kim et al. 1991), prey diversity and density in coastal waters is higher than that in East China Sea.

Z. faber has gonochorism and strategy of multiple spawning. The reproductive system begins to develop in November and ends its spawning season in May, which has long spawning season. *Z. faber* has butterfly-shaped gonad, and histologically, matured gonads have oocytes of various types (Vtg1-3, GVM, POF, AO and so on). In addition, the frequency distribution of egg size in each mature stage appeared from several modes, which indicated that *Z. faber* has a strategy of multiple-spawning. The previous studies on gonad maturation carried out in Turkey and East China Sea. Yoneda et al (2006) reported that the spawning period was from January to March in East China Sea. Although there are slight differences between the two results, which have similar spawning season. The smaller size of maturity in Korea was 25.8 cm and it was 4 years. The length at sexual maturity in females was 30.8 cm and age was 5 years. In addition, the length at sexual maturity for all individuals was 41 cm and age was 12 years. The length at sexual maturity for female was 25.4 cm (5 years) in Turkey (Isman et al. 2012) and 34.0 cm (6 years) in Japan (Yoneda et al. 2006). This study recommends the minimum catch size of 30 cm for resource management.

The *Z. faber* was a piscivorous predator. The most important prey category was fish, which accounted for 82.3% (%IRI). The most common fish prey were *Trichiurus japonicus, Trachurus japonicus* and *E. japonicus*. In this study, individuals less than 30cm preferred surface fish as *E. japonicus*, while specimens of *Z. faber* up to 38 cm were found to feed on the benthic species *G. stelleri*. These results indicated that as body size increased, *Z. faber* preferred fish lived deep water. This phenomenon can avoid interspecific competition by choosing to consume benthic and demersal fish (Gerking 1994). Trophic diversity in summer and autumn was increased, in which the prey rate of crustacean was increased. The density of crustacean increases due to the hatched crustacean recruit in the summer. It was found that the feeding of *Z. faber* varies slightly depending on the size and season.

This paper was studied on the population structure, age and growth, maturation, and feeding habits of *Z. faber*. By revealing the biological characteristics and life history of *Z. faber,* we can understand the life-histology strategy of *Z. faber*. It will provide basic data for efficient management of fishery resources of *Z. faber*.

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