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Feeding habits of Pacific anchovy, *Engraulis japonicus* (Actinopterygii: Clupeiformes: Engraulidae), captured off the southern coasts of Korea

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Abstract

Understanding the feeding ecology of anchovies in the southern waters of Korea is crucial for improving ecosystem management. However, to date, few studies have examined seasonal changes in the diet of Pacific anchovy, *Engraulis japonicus* Temminck et Schlegel, 1846, in Korean waters, with the majority of these focusing on the larval and adult stages. The presently reported study provides updates on the feeding habits of *E. japonicus* off the southern coast of Korea. We analyzed 347 individuals. One-way analysis of similarity was performed to evaluate the differences in diet composition among size classes and seasons of *E. japonicus*, and correspondence analysis was conducted using the matrix of the percentage by number (%*N*) data for prey with occurrence of less than 10% to determine the distribution of prey across all size classes and each season. The diet of *E. japonicus* was investigated according to season and four size classes. The fork length of these specimens ranged from 5.4 to 14.1 cm. A total of 55 prey taxa of varying sizes between 0.33 mm (diatom *Coscinodiscus* spp.) and 5.8 mm (fish larvae) were recorded. Anchovies were exclusively planktivorous, and copepods were the most common prey, comprising 82.1% of the identified food items and 84.3% of anchovy stomach contents analyzed. However, their occurrence and abundance varied according to season and Pacific anchovy size class. According to the percentage of the index of relative importance (%IRI), the most important prey items were the copepods *Calanus sinicus* (48.0%), *Paracalanus orientalis* (31.7%), bivalve larvae (5.8%), *Ditrichocorycaeus affinis* (4.2%), and calanoid copepods (2.4%). Analysis of similarities and similarity percentage analysis indicated that a distinct diet of Pacific anchovy in the southern waters of Korea is potentially driven by differences in hydrological conditions. Correspondence analysis revealed that anchovies had the most significant impact on the differences between size classes. The results deepen our understanding of prey species diversity and intraspecific food competition off the southern coast of Korea.

Keywords

copepods, diet, Pacific anchovy, southern waters of Korea

Introduction

The Pacific anchovy, *Engraulis japonicus* Temminck et Schlegel, 1846, is a widely distributed pelagic fish abundant in the coastal and offshore waters of the western North Pacific (Zenitani and Kimura 1997; Kim and Lo 2001; Wan and Bian 2012; Yamamoto et al. 2018). This anchovy is one of the commercially most important fish species present in Korean waters, where it is exploited using anchovy drag and offshore stow nets (Kim and Lo 2001). The total annual catch of *E. japonicus* was 209 102 to 250 106 tonnes from 2003 to 2013, and almost 187

849 tonnes from 2014 to 2021 from Korean waters (KOSIS 2023). The majority of the catch is taken from the southern coast of Korea, which occupies approximately 87% of Korean waters (KOSIS 2023). Pacific anchovies are an important intermediate link between zooplankton and higher-level fish species in marine food webs, and they are one of the main keystone species within the marine ecosystem (Tang et al. 2005; Wan and Bian 2012; Shin et al. 2021).

Studies on the feeding habits of fish may play a key role in understanding resource partitioning between and within species (Harmelin-Vivien et al. 1989; Wu et al. 2018), prey selection (Takasuka et al. 2003), predator–prey size relations (Scharf et al. 2000; Jin et al. 2010), distribution of feeding patterns with latitude (Pauly and Christensen 2000), ontogenetic diet shift (Jin et al. 2010), and habitat selection (Labropoulou et al. 1999; Zhang et al. 2007). They are also particularly important when establishing fishery management plans for exploited species that are important for their economic value (Lassalle et al. 2011; Bachiller and Irigoien 2015).

The fundamental publication on fish feeding was that by Hyslop (1980) who reviewed, summarized, and critically analyzed the methods used in studies on fish stomach contents. Hyslop (1980) divided the "objective" methods into four categories: 1) occurrence methods, 2) numerical methods, 3) volumetric methods, and 4) gravimetric methods. Among "subjective" methods he listed the index of relative importance (IRI).

The trophic ecology of *E. japonicus* has been studied to understand the functional ecology of the pelagic ecosystem (Ma et al. 2019). This is particularly subject to highly variable recruitment success, and therefore, environmental variability causes substantial stock fluctuations (Takasuka and Aoki 2006; Wang et al. 2021a). *Engraulis japonicus* is one of the most important small pelagic species in Korean waters, with respect to biomass and commercial interest (Kim and Lo 2001; Kim et al. 2005). The diet and recruitment of *E. japonicus* are affected by variations in the environmental processes governing plankton abundance (Uotani et al. 1978; Tanaka et al. 2006; Kim et al. 2013). However, most of these studies have been conducted in Japanese waters (Uotani et al. 1978; Aoki and Miyashita 2000; Islam and Tanaka 2009; Yasue et al. 2010) and the Yellow Sea (Wang et al. 2021b). To date, few studies have examined seasonal changes in the diet of *E. japonicus* in Korean waters, with most of these focusing on the larval (Park and Cha 1995; Kim et al. 2005; Yoo and Jeong 2016) and adult stages (Chang et al. 1980; Kim et al. 2013). *Engraulis japonicus* predominantly feeds on plankters, such as the diatoms such as *Coscinodiscus* spp. (Bacillariophyta) and copepods, such as *Calanus sinicus*, *Ditrichocorycaeus affinis*, and *Paracalanus orientalis* (= *Paracalanus parvus* sensu lato) along the southern coast of Korea (Kim et al. 2013). Understanding the feeding ecology of anchovies in the southern waters of Korea is crucial for improving ecosystem management.

Hence, in the presently reported study, the feeding habits of Pacific anchovy, *E. japonicus*, were studied in terms of size and seasonally in Korean waters. This is the first study to analyze annual dietary changes of Pacific anchovy off the southern coast of Korea. We aimed to provide feeding data of *E. japonicus* regarding the important ecological and economic role of pelagic fish. These data can contribute to the already emphasized need for the development of ecosystem-based fishery management.

Material and methods

Sample collection. The specimens of Pacific anchovy, *Engraulis japonicus*, were collected monthly from November 2020 to October 2021 using a set net, anchovy boat seine, and bottom trawl in the southern waters of Korea during daylight hours (Fig. 1; Table 1). The stomachs of 347 *E. japonicus* individuals were analyzed. The anchovies were measured to the nearest 0.1 cm (FL, fork length), and their stomachs were immediately preserved in 10% formalin. All stomach contents were washed out onto a Petri dish, and aliquots comprising 20~100% of the total volume of each pool were taken to be examined under the Olympus SZX10 (Tokyo, Japan) stereomicroscope at 100× magnification. The stomach contents were identified to the lowest feasible taxonomic level, and prey items were counted and measured under the stereomicroscope. All the prey items in the aliquots were counted and identified up

Table 1. Sampling information of Pacific anchovy, *Engraulis japonicus*, from the southern waters of Korea.

Date	Depth [m]	Fishing gear	Sample number	Sample size (FL) [cm]
27 Nov 2020	18	Anchovy boat seine	20	7.1–13.8
23 Dec 2020	23	Anchovy boat seine	30	5.4–9.2
12 Jan 2021	28	Anchovy boat seine	25	6.9–12.7
19 Feb 2021	20	Bottom trawl	30	5.5–13.0
23 Mar 2021	27	Anchovy boat seine	30	8.0–14.1
13 Apr 2021	17	Set net	30	7.7–11.4
21 May 2021	19	Set net	30	8.9–13.0
17 Jun 2021	16	Set net	30	7.4–11.5
29 Jul 2021	24	Anchovy boat seine	30	7.3–11.4
20 Aug 2021	16	Bottom trawl	30	6.2–10.8
9 Sep 2021	28	Anchovy boat seine	30	8.0–11.5
14 Oct 2021	15	Set net	32	9.6–11.2

FL = fork length.

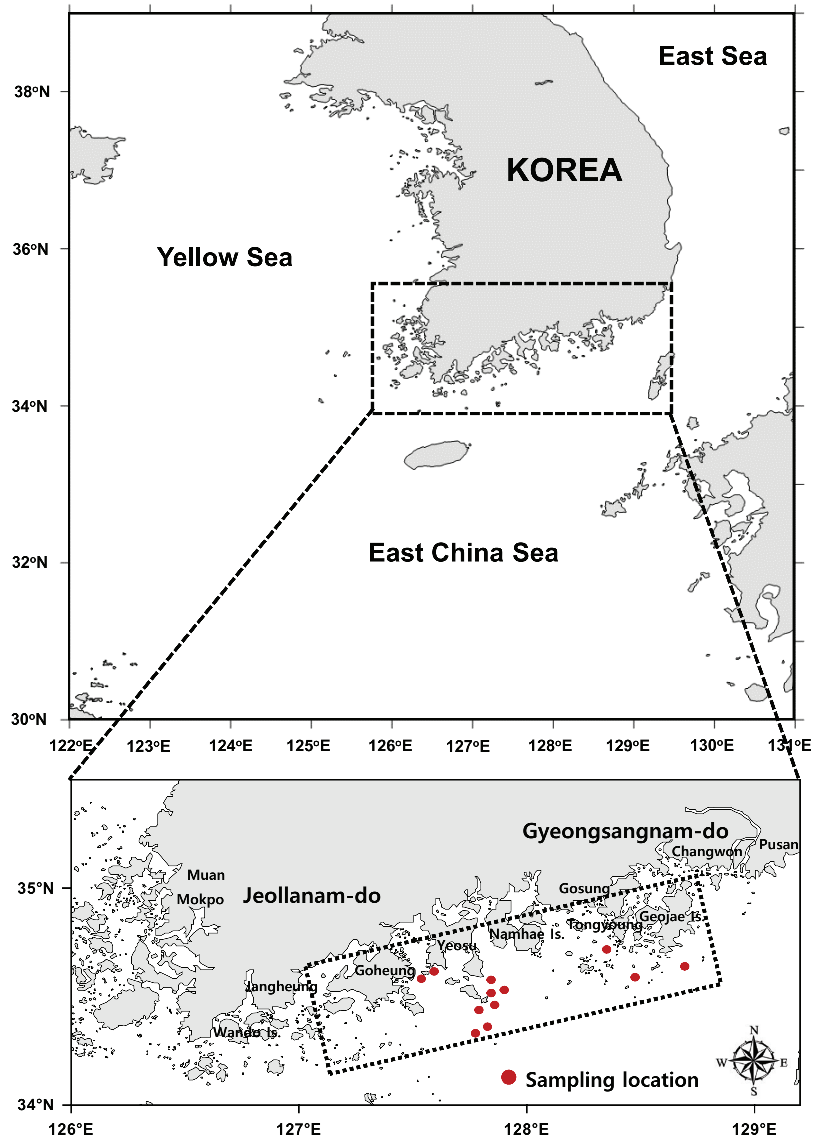

Figure 1. Map of the sampling area (dotted line) of the Pacific anchovy, *Engraulis japonicus*, in the southern waters of Korea. Note: East Sea is otherwise known as the Sea of Japan.

to the lowest possible taxa, and their widths and lengths were measured [µm], if distinguishable, using the software ImageJ (Abràmoff and Magalhães 2004). Prey dry weight (DW) [µg] was obtained from estimations by James (1987), Uye (1982), Pinchuk and Hopcroft (2007), and Borme et al. (2009). The diet was described using the relative contribution of a food item to total stomach content.

Feeding habits. To examine the ontogenetic variations in the feeding ecology of Pacific anchovy, individuals were divided into the following four FL classes

- <6 cm (group 1),
- 6.0–8.9 cm (group 2),
- 9.0–11.9 cm (group 3), and
- ≥12.0 cm (group 4).

The size groups were analyzed in accordance with the standard by establishing the maturing size of anchovies (Moon et al. 2022b) in 2-cm increments. The diet of *E. japonicus* was investigated according to season and the four size classes. The qualitative importance of each prey item in the *E. pacificus* diet was described using the relative frequency of occurrence (%F), the percentage by number (%N), and the percentage by (dry) weight %W_D (Hyslop 1980). We define the relative frequency of occurrence (%F) as the percentage of stomachs containing one or more individuals of a given food category; the percentage by number (%N)—as the percentage of the total individuals in all food categories; and the percentage by (dry) weight %W_D—as the percentage of the (dry) weight of total individuals in all food categories.

These indies were then integrated into the index of relative importance (IRI) modified by Borme et al. (2009) (based on Pinkas et al. 1971)

$$\mathrm{IRI} = (\%N + \%W_D) \times \%F$$

where %IRI_i is the percentage of the index of relative importance, i is the number of a specific food category, and n is the total number of food categories.

For comparison, the IRI values calculated for each prey item were transformed to its percentage (%IRI) values using the following equation by Cortés (1999)

$$\% \text{ IRI} = \text{IRI}_i / \sum_{i=1}^{n} \text{IRI}_i \times 100$$

To assess the feeding strategy of *E. japonicus*, we used the graphical analysis described by Amundsen et al. (1996). In mathematical terms, the prey-specific abundance is calculated as

$$P_i = 100\Sigma S_i \times \Sigma S_{ti}^{-1}$$

where P_i is equal to the prey-specific abundance of prey *i*, S_i is the weight of prey *i* in stomachs, and S_{ti} is the total weight of prey in the stomachs of predators that contain prey *i*.

Statistical analysis. One-way analysis of similarity (ANOSIM) was performed to evaluate the differences in diet composition among size classes and seasons of *E. japonicus*. Typifying and distinguishing the prey for each size class were performed using the similarity-percentages procedure (SIMPER). This procedure was established by the average contribution of each prey item to the similarity and dissimilarity among size classes and seasons. Correspondence analysis (CA) was conducted using the matrix of the percentage by number (%*N*) data for prey with an occurrence of less than 10% to determine the distribution of prey across all size classes and each season. Sea water temperatures in the southern sea of the Korean Peninsula show distinct seasonal patterns (Kim et al. 2011; Han and Lee 2020), so we analyzed data from winter (December to February), spring (March to May), summer (June to August), and autumn (September to November). PRIMER software package (Version 6.1.9) (Clarke and Warwick 2001) was used to perform cluster, SIMPER, and ANOSIM analyses. CA was performed using CANOCO software (Version 4.5).

Results

A total of 347 specimens of Pacific anchovy, *Engraulis japonicus*, measuring between 5.4 and 14.1 cm FL were examined for diet composition. Overall, 15.7% of stomachs were empty, and prey items included one phytoplankter, 50 crustaceans, one chaetognath, two mollusks, and two vertebrates (Table 2). The dominant zooplankton prey groups included calanoid copepods (%*F* = 59.1, %*N* = 60.0, %IRI = 82.8) and cyclopoid copepods (%*F* = 29.7, %*N* = 10.6, %IRI = 5.1). The abundant prey items were *Calanus sinicus* (%*F* = 19.9, %*N* = 30.8, %IRI = 48.0), *Paracalanus orientalis* (%*F* = 28.0, %*N* = 22.8, %IRI = 31.7), bivalve larvae (%*F* = 17.9, %*N* = 7.7, %IRI = 5.8), *Ditrichocorycaeus affinis* (%*F* = 14.1, %*N* = 7.5, %IRI = 4.2), other calanoid copepods (%*F* = 11.8, %*N* = 2.2, %IRI = 2.4), and copepods eggs (%*F* = 7.5, %*N* = 6.2, %IRI = 1.5).

Diet composition in relation to fish size and season. The diet composition for size classes concerning the cumulative percentage IRI is depicted in Fig. 2A. A total of 5 stomachs from the group with a fish length below 6 cm (FL) were examined, revealing 4 prey items. According to the %IRI, the most significant prey items in this group were diatoms *Coscinodiscus* spp. (44.3%), copepods *Ditrichocorycaeus affinis* (35.4%), and Harpacticoida (8.9%). For group 2 (6.0–8.9 cm FL), comprising 156 stomachs, 28 prey items were identified. The primary prey consisted of copepods *Paracalanus orientalis* (46.1%), *Ditrichocorycaeus* spp. (20.4%), *D. affinis* (11.7%), and other calanoid copepods (11.1%). Group 3 (9.0–11.9 cm FL) included 172 stomachs with 47 prey items. The dominant prey items were the copepods *Calanus sinicus* (44.9%), *P. orientalis* (42.9%), *D. affinis* (4.4%), and diatoms *Coscinodiscus* spp. (1.9%). Finally, in group 4 (≥12.0 cm FL), 14 stomachs were analyzed, and 17 prey items were found. The most important prey items were the copepods *P. orientalis* (43.3%) and *C. sinicus* (43.1%).

The variations in diet composition according to size class were determined using ANOSIM, which showed that the diets differed significantly in prey number between the size classes (Table 3). The SIMPER analysis showed that *P. orientalis*, bivalve larvae, *Ditrichocorycaeus* spp., *C. sinicus*, and *D. affinis* were the prey items that contributed the most to discriminating the size classes (Table 3).

A total of 90, 90, 82, and 85 stomachs from the spring, summer, autumn, and winter seasons, respectively, were analyzed (Fig. 2B). According to %IRI, the most important prey items in each season were the copepods *C. sinicus* (67.9%), *D. affinis* (16.0%), *P. orientalis* (10.3%), and the euphausiid *Euphausia pacifica* (3.8%) in spring; *C. sinicus* (37.8%), *Ditrichocorycaeus* spp. (11.7%), calanoid copepods (7.1%), and *D. affinis* (5.5%) in summer; *C. sinicus* (41.2%), *P. orientalis* (36.6%), *D. affinis* (4.7%), and copepod eggs (4.1%) in autumn; and *Coscinodiscus* spp. (48.7%), *C. sinicus* (18.7%), *P. orientalis* (9.8%), *Ditrichocorycaeus* spp. (6.6%), and bivalve larvae (3.9%) in winter. ANOSIM showed that there were no significant differences between the seasons for stomach content (Table 4). According to SIMPER analysis, the stomach contents that contributed the most to the diet were *C. sinicus*, copepods eggs, *D. affinis*, *P. orientalis*, and *Coscinodiscus* spp.

The relative prey importance of *E. japonicus* is graphically represented in Fig. 3, where prey-specific abundance (P_i) is plotted against the frequency of occurrence. *Calanus sinicus* is situated in the upper right corner of the diagram for the spring, summer, and autumn seasons. It constitutes the dominant prey item, making up more than

Table 2. Stomach contents (and associated parameters) of Pacific anchovy, *Engraulis japonicus*, from the southern waters of Korea.

Taxon	Prey items	%*F*	%*N*	IRI	%IRI
Bacillariophyta	*Coscinodiscus* spp.	7.5	7.5	56.4	1.8
Cladocera	*Pseudevadne* spp.	0.9	0.0	0.0	1.8
	Pseudevadne tergestina	0.3	0.0	0.0	0.0
	Podon polyphemoides	0.6	0.0	0.0	0.0
Copepoda	Total	71.5	82.1	11 005.7	98.1
Calanoida	Total	59.1	60.0	7654.4	82.8
	Acartia omorii	0.9	0.1	0.1	0.0
	Acartia pacifica	0.9	0.2	0.2	0.0
	Acartia erythraea	0.9	0.8	1.2	0.0
	Acartia sp.	2.9	0.5	1.7	0.1
	Calanus sinicus	19.9	30.8	1648.8	48.0
	Candacia bipinata	1.2	0.5	3.8	0.1
	Candacia sp.	0.3	0.0	0.0	0.0
	Centropagus dorsispinatus	4.3	0.8	11.0	0.4
	Centropagus furcatus	1.7	0.2	0.5	0.0
	Centropages abdominalis	0.3	0.0	0.0	0.0
	Centropages sp.	0.3	0.0	0.0	0.0
	Clausocalanus furcatus	0.0	0.0	0.0	0.0
	Euchaeta rimana	0.3	0.7	1.5	0.0
	Labidocera sp.	0.3	0.0	0.1	0.0
	Paracalanus orientalis	28.0	22.8	969.4	31.7
	Paracalanus sp.	1.2	0.1	0.2	0.0
	Pseudodiaptomus marinus	0.3	0.0	0.0	0.0
	Temora discaudata	0.9	0.1	0.3	0.0
	Temora turbinata	1.2	0.2	0.5	0.0
	Tortanus forcipatus	0.3	0.0	0.0	0.0
	Other calanoid copepods	11.8	2.2	74.1	2.4
Cyclopoida	Total	29.7	10.6	372.0	5.1
	Oithona similis	0.9	0.1	0.1	0.0
	Oithona sp.	2.3	0.2	0.6	0.0
	Oncaea sp.	2.3	0.2	0.5	0.0
	Oncaea venella	0.6	0.1	0.0	0.0
	Oncaea venusta	0.9	0.3	0.3	0.0
	Triconia sp.	1.4	0.1	0.2	0.0
	Ditrichocorycaeus affinis	14.1	7.5	128.0	4.2
	Ditrichocorycaeus spp.	11.2	2.1	26.0	0.9
Harpacticoida	Total	9.2	5.2	51.4	1.0
	Microsetella sp.	4.9	1.6	8.5	0.3
	Unidentified harpacticoids	5.8	3.6	22.2	0.7
Copepoda larvae	Total	8.1	6.3	51.0	1.5
	Unidentified copepodids	0.9	0.1	0.1	0.0
	Calanus nauplii	0.6	0.0	0.0	0.0
	Copepod eggs	7.5	6.2	46.7	1.5
Cirripedia	Total	6.9	0.6	4.1	0.1
	Cirripedia nauplii	2.6	0.2	0.6	0.0
	Cirripedia cyprii	4.0	0.3	1.4	0.0
Decapoda	Total	6.6	0.8	15.8	0.0
	Decapod zoea and mysis	3.7	0.4	4.7	0.0
	Crab megalopa	2.3	0.1	0.4	0.2
	Decapod eggs	0.3	0.0	0.0	0.0
	Unidentified Decapoda	0.3	0.3	0.3	0.0
Ostracoda	Ostracoda	0.9	0.1	0.1	0.0
Cumacea	Cumacea	2.0	0.2	1.1	0.0
Euphausiacea	Total	1.2	0.3	23.4	0.8
	Euphausia pacifica	1.2	0.3	19.9	0.7
	Euphausia sp.	0.6	0.1	1.8	0.1
Amphipoda	Total	1.4	0.1	0.5	0.0
	Unidentified gammarids	1.4	0.1	0.4	0.0
	Unidentified hyperiids	0.3	0.0	0.0	0.0
Chaetognatha	*Adianosagitta* sp.	0.3	0.0	0.0	0.0
Mollusca	Total	18.4	7.7	184.1	6.0
	Gastropod larvae	0.6	0.0	0.0	0.0
	Bivalve veliger	17.9	7.7	177.7	5.8
Fishes	Total	2.0	0.3	4.7	0.2
	Unidentified fish eggs	1.2	0.2	0.8	0.0
	Unidentified fish larvae	0.9	0.2	1.4	0.0
Other items	Total	13.5	0.2	24.8	0.8

%*F* = the relative frequency of occurrence of each food item, %*N* = the percentage by number of each food item, IRI = index of relative importance, %IRI = the percentage of the index of relative importance.

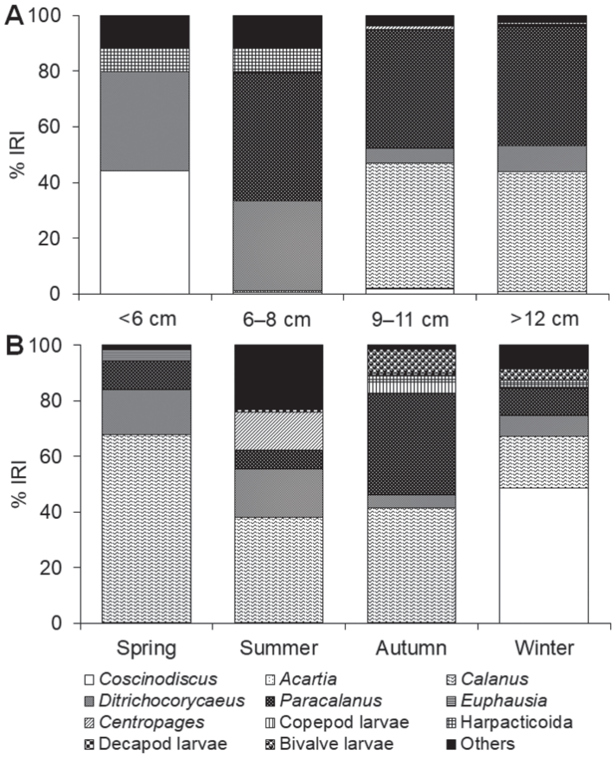

Figure 2. Changes in composition of stomach contents by %IRI of Pacific anchovy, *Engraulis japonicus*, in the southern waters of Korea: (**A**) size classes, (**B**) seasons.

40% by P_i and 20% by FO (frequency of occurrence) of the stomach contents. In contrast, *Acartia* sp., decapod larvae, cirriped larvae, and Harpacticoida were infrequent prey items for all seasons. *Euphausia pacifica* (spring and summer) and *P. orientalis* (autumn) are positioned in the upper left and right parts of the graph, respectively.

Canonical analysis (CA) of *N*% (number percentage) of prey items identified groups of prey species that were discriminated between each season with ontogenetic variation (Fig. 4A). Ontogenetic changes in the diet were investigated in the Pacific anchovy (*E. japonicus*) collected. Copepods were the most frequently observed prey item across all fish sizes. CA analysis of *N*% of prey items showed the groups of prey that distinguished each ontogenetic variation. Factors 1 and 2, illustrated by the eigenvalues on the first and second axes, explained 0.185 and 0.092 of the variance, respectively. The size of all groups was clearly apparent on the CA graph. Group 1 was distinctly separated into the positive part of Axis 1, distinguished by diatoms *Coscinodiscus* spp. Groups 2 and 4 were separated into the negative part of Axis 3, distinguished by copepod larvae, *Centropages*, *Paracalanus*, and *Ditrichocorycaeus*. Group 3 was separated into the positive part of Axis 2, distinguished by *Acartia* and decapod larvae. The data according to season are shown in the CA graphs (Fig. 4B). Spring was separated into the positive part of Axis 1, showing the consumption of Euphausiids, *Euphausia*, *Ditrichocorycaeus*, copepods, and *Calanus*. Summer was separated into the positive part of Axis 2, showing the consumption of *Centropages* and decapod larvae. Autumn was separated into the negative part of Axis 3, owing to the consumption of *Acartia* and bivalve larvae. Winter was separated into

Table 3. Comparison of diet composition of Pacific anchovy, *Engraulis japonicus*, from the southern waters of Korea among size classes by one-way ANOSIM (*R* and *P* value) and SIMPER. Global $R = 0.277$, $P < 0.001$.

Model	Parameter	Length class [cm]		
		<6 vs. 6.0~8.9	6.0~8.9 vs. 9.0~11.9	9.0~11.9 vs. ≥12
One-way ANOSIM	*R* value	0.417	0.269	0.330
	p value	0.002	0.001	0.002
SIMPER	Discriminating food item 1	Calanoid copepods	*Calanus sinicus*	*Euphausia pacifica*
	Contribution [%]	24.75	16.19	17.17
	Discriminating food item 2	Cirripedia larvae	*Euphausia pacifica*	*Calanus sinicus*
	Contribution [%]	16.22	13.83	15.80
	Discriminating food item 3	*Paracalanus orientalis*	Calanoid copepods	Calanoid copepods
	Contribution [%]	13.09	11.36	12.21

Table 4. Comparison of diet composition of Pacific anchovy, *Engraulis japonicus*, from the southern waters of Korea among seasons by one-way ANOSIM (R and *p* values) and SIMPER. Global $R = –0.059$, $P > 0.001$.

Model	Parameter	Season			
		Spring vs. summer	Summer vs. autumn	Autumn vs. winter	Winter vs. spring
One-way ANOSIM	*R* value	–0.259	–0.259	–0.148	0.222
	p value	ns	ns	ns	ns
SIMPER	Discriminating food item 1	*Calanus sinicus*	*Calanus sinicus*	*Calanus sinicus*	*Calanus sinicus*
	Contribution [%]	42.49	36.40	35.08	46.59
	Discriminating food item 2	*Eurytemora pacifica*	Fish larvae	Fish larvae	*Eurytemora pacifica*
	Contribution [%]	24.59	10.14	12.63	19.42
	Discriminating food item 3	*Centropages abdominalis*	*Paracalanus orientalis*	Bivalvia larvae	*Euchaeta rimana*
	Contribution [%]	6.94	8.61	8.92	19.42

ns = not significant.

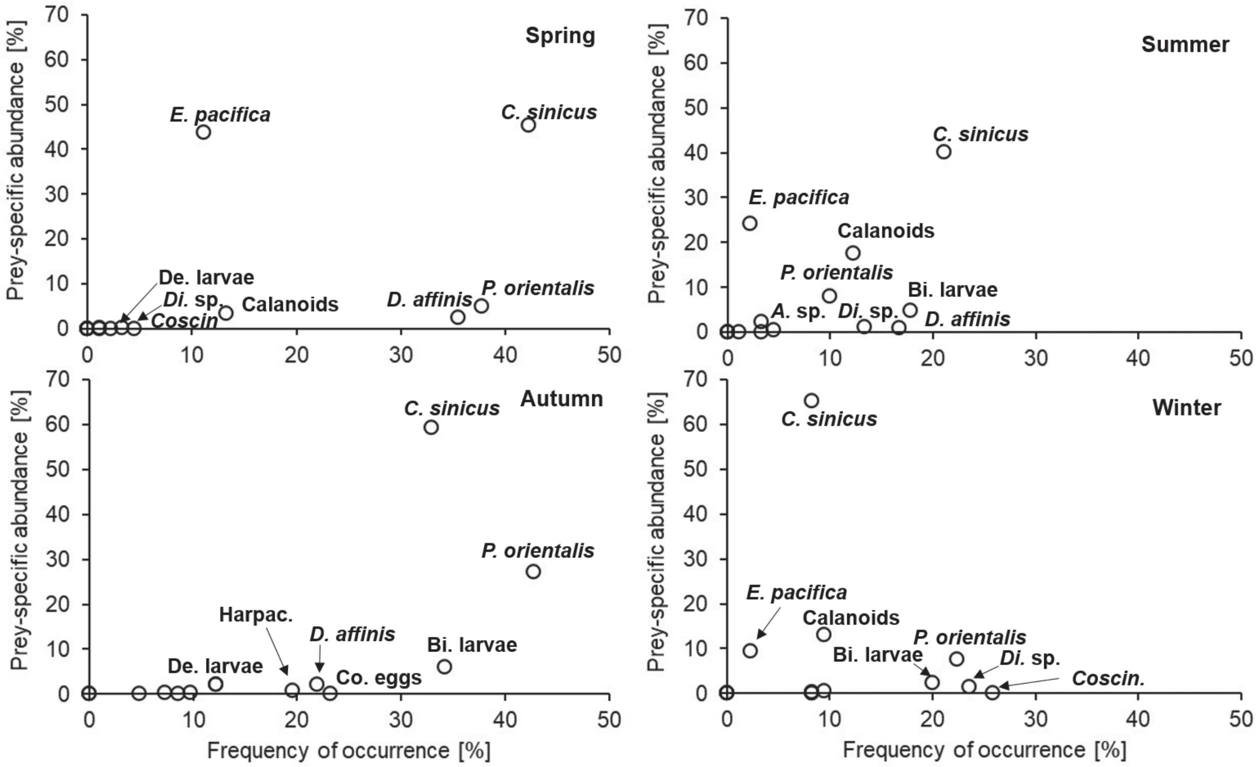

Figure 3. Seasonal changes of percent prey-specific abundance (%P_i) versus the relative frequency of occurrence (%*F*) for Pacific anchovy, *Engraulis japonicus*, from the southern waters of Korea. Abbreviations: *Coscin*. = *Coscinodiscus*, *C. sinicus* = *Calanus sinicus*, *P. orientalis* = *Paracalanus orientalis*, *D. affinis* = *Ditrichocorycaeus affinis*, Harpac. = harpacticoid copepods, *Di*. sp. = *Ditrichocorycaeus* sp., Calanoids = calanoid copepods, Bi. larvae = bivalve larvae, Co. eggs = copepod eggs, *E. pacifica* = *Euphausia pacifica*, De. larvae = decapod larvae.

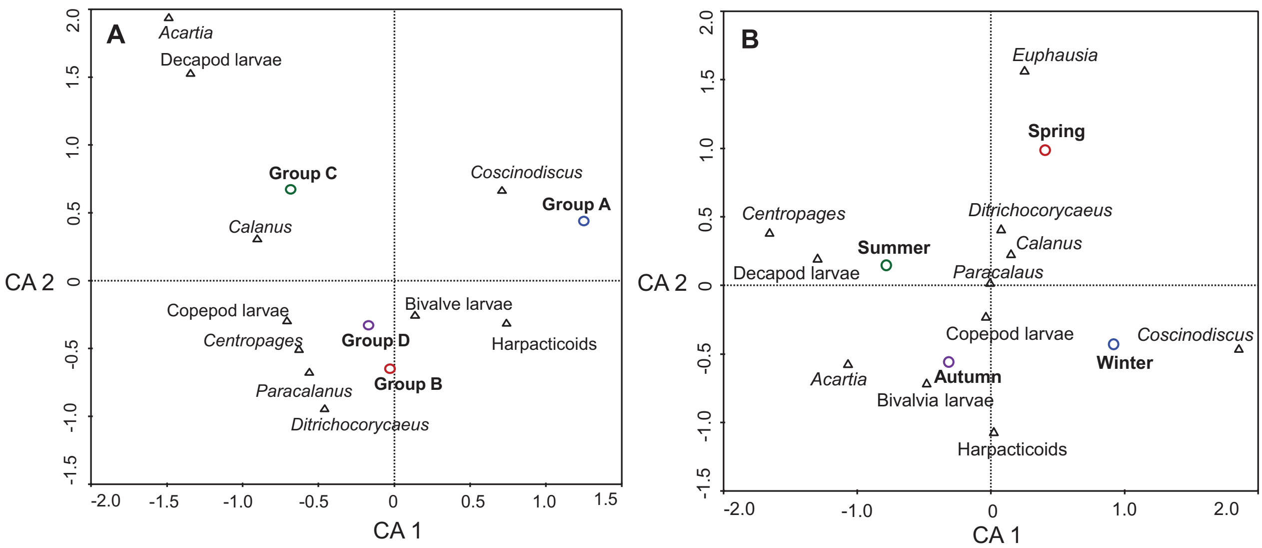

Figure 4. Correspondence analysis biplot for prey items of Pacific anchovy, *Engraulis japonicus*, from the southern waters of Korea, based on the percentage numerical frequency (%*N*). (**A**) size classes, (**B**) season. Abbreviations: Group A = fork length < 6 cm, Group B = fork length 6–8.9 cm, Group C = fork length 9–11.9 cm, Group D = fork length ≥ 12 cm.

the negative part of Axis 4 owing to the consumption of the phytoplanktonic *Coscinodiscus* spp. (Bacillariophyta). The other prey items are halfway between the four groups, which comprise general prey that were consumed in similar proportions in all seasons.

Discussion

Several studies have reported the feeding habits of Pacific anchovy, *Engraulis japonicus*, at various locations (Uotani et al. 1978; Aoki and Miyashita 2000; Yasue et al.

2010; Kim et al. 2013; Wang et al. 2021b). In this study, we found that anchovies were exclusively planktivorous, and the primary prey items were copepods, diatoms (such as *Coscinodiscus* spp.), and to a lesser extent mollusk larvae. The main prey items for anchovy were *Calanus sinicus*, *Paracalanus orientalis*, bivalve larvae, *Ditrichocorycaeus affinis*, and copepod eggs. The food items of Pacific anchovy were not only small and medium prey (<2 mm, such as *Coscinodiscus* spp., *P. orientalis*, and *D. affinis*), but also large prey (>2 mm, such as *C. sinicus* and bivalve larvae). Some individuals contained relatively large prey (>4 mm, such as decapod larvae, amphipods, and *Euphausia pacifica*) along with much smaller prey. Graphical analysis of the diet composition showed that *E. japonicus* is an opportunistic and specialized predator characterized by strong individual feeding specialization. *Engraulis japonicus* from the southern coast of Korea employs two feeding modes: selective feeding on large prey or filter feeding on small prey, as suggested for Pacific anchovy of Sagami Bay (Mitani 1988), *Engraulis encrasicolus* (Linnaeus, 1758) in the Gulf of Lions (Mediterranean Sea) (Plounevez and Champalbert 2000), and Cape anchovy, *Engraulis capensis* Gilchrist, 1913 (see James 1987). According to Kim et al. (2013), Cirripedia larvae and *C. sinicus* were present during summer, with large phytoplankters (such as *Coscinodiscus* spp.) and *Pseudodiaptomus marinus* present during autumn. In particular, *C. sinicus* is situated in the upper right corner of the diagram for the spring, summer, and autumn seasons, indicating specialization within the *E. japonicus* population. *C. sinicus* has been previously described as particularly important for the Pacific anchovy diet (Islam and Tanaka 2009; Kim et al. 2013; Yoneda et al. 2022). In the southern waters of Korea, the abundance of bivalves is very important, as is evident from the abundance of bivalve larvae presented in the results on the zooplankton community by Moon et al. (2010, 2022a). In this study, prey items of anchovies showed no significant difference between the seasons of the stomach contents by performing an ANOSIM test. These results showed that the dominant prey items according to the season in this study were *C. sinicus*, *E. pacifica*, *P. orientalis*, bivalve larvae, and *D. affinis.*

The diet of *E. japonicus* from the southern coast of Korea differed from that of previous studies in Japanese waters (Yasue et al. 2010; Islam and Tanaka 2009), Chinese waters (Wang et al. 2021b), and Korean waters (Chang et al. 1980; Kim et al. 2013). Phytoplankters are generally known to contribute only sporadically to the diet of Pacific anchovy (Bulgakova 1993; Kim et al. 2013). The copepods used as the primary prey in this study are consistently dominant on the southern coast of Korea throughout the year. However, their species composition undergoes seasonal changes, as documented by Moon et al. (2010, 2022a). The prevalent copepod species include *P. orientalis*, *D. affinis*, and *C. sinicus*, as reported by Moon et al. (2010, 2022a) and Shin et al. (2022). In particular, *C. sinicus*, which was abundant in anchovies larger than 9 cm FL, showed high occurrence on the southern coast of Korea from winter to spring (Shin et al. 2022). The calanoids, including the genera *Calanus* and *Paracalanus*, have been previously described as a major for anchovy diets (Uotani et al. 1978; Mitani 1988; Takasuka and Aoki 2006; Kim et al. 2013). In addition, diatoms *Coscinodiscus* spp. also occurred highly in the winter of Korean waters (Park and Lee 1990), and Japanese waters (Nishikawa et al. 2000; Fukao et al. 2012). Diatoms *Coscinodiscus* spp. are predominantly found on the southern coast of Korea during the winter season (Park and Lee 1990), so it is believed that anchovies are utilized along with other prey items. Bivalve and decapod larvae were present in the anchovy diets, as shown by %IRI in all anchovy size classes (see Table 2; Fig. 2). The prey items of *E. japonicus*, which generally comprise zooplanktonic prey, may also be of importance in the species composition and community structure of zooplanktons in the southern coast of Korea (Kim et al. 2013). Off the southern coast of Korea, the spatial and temporal variability of zooplankton populations was associated with changes in phytoplankton composition and density and with the combined effects of regional climatology and local hydrography (Moon et al. 2022a; Shin et al. 2022). These findings deepen our knowledge on the feeding plasticity of *E. japonicus* (see Mitani 1988; Tanaka et al. 2006).

Investigation of the feeding behavior of the Pacific anchovy indicates that raptorial feeding is dominant over filter feeding and that prey appears to be selected primarily based on size. Anchovies selectively fed on phytoplankton (*Coscinodiscus* spp.) and zooplankton, especially calanoid copepods (Uotani et al. 1978; Takasuka and Aoki 2006; Kim et al. 2013). As the anchovies grew, calanoid copepods were steadily substituted by large crustaceans, such as euphausiids and bivalve larvae, which became more frequent in the diets of group 2 (6.0–8.9 cm) and group 3 (9.0–11.9 cm). The increase in the abundance of potentially important prey species is suggested by James (1987) and Plounevez and Champalbert (2000). The southern waters of Korea are temperate and highly productive, and due to seasonal changes in water quality, hydrodynamics, nutrients, and phytoplankton primary productivity change strongly (Park and Lee 1990; Yang and Kim 1990; Baek et al. 2010); zooplankton abundance also varies (Moon et al. 2010; 2022a; Shin et al. 2022). The abundance and distribution of zooplankton were correlated with phytoplankton composition and density (Zenitani et al. 2011). In particular, phytoplankton can be consumed by zooplankton, which is the primary food item for most marine fish larvae and small pelagic fish, such as anchovies. In the southern waters of Korea, the abundance and distribution of zooplankton were strongly associated with environmental factors, such as sea temperature, salinity, and chlorophyll-a concentration (Moon et al. 2022a). Copepods were the dominant prey of anchovies during all seasons, but there was no significant difference between seasons. Notably, anchovies exhibited similar diets in winter and spring, including *C. sinicus* and *E. pacifica*. This selectivity for larger nutrient-rich prey can be explained by the energy requirements of *E. japonicus* for successful reproduction. Our results suggest that *E. japonicus* has a narrow food niche and is a specialized feeder, with copepods being the dominant prey for all seasons.

Pacific anchovies are an essential link between primary production and energy transfer to higher trophic levels (Zenitani and Kimura 1997). The majority of studies of the population dynamics of larvae, juvenile, and adults of *E. japonicus* confirm the important role of copepods as the main link between phytoplankters and anchovy production (Zenitani and Kimura 1997; Takasuka and Aoki 2006).

Conclusions

Through this study, we found that anchovies inhabiting the southern coast of Korea are phyto- and zooplankton-feeders and have the flexibility to utilize various prey depending on prey availability, which may vary depending on the size of the anchovies. However, this study did not include larval stages of *E. japonicus* off the southern coast of Korea, and studies of the diet of anchovy larvae are needed to understand the overall diet of anchovies. The relation between various environmental influences and anchovy population dynamics in this study emphasizes the need to increase our understanding of the feeding ecology of *E. japonicus* off the southern coast of Korea in relation to plankton dynamics and environmental factors.

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