Dissertation for the Degree of Doctor of Philosophy

Trophic dynamics of fisheries resources in coastal ecosystems of Korea: Application of stable isotope and stomach content analyses

by

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February, 2023

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(한국 연근해 수산자원의 영양동태 연구: 안정동위원소와 위내용물 분석 기법 적용)

Advisor: Prof. Chang Geun Choi

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CONTENTS

LIST OF FIGURES

LIST OF TABLES

한국 연근해 수산자원의 영양동태 연구: 안정동위원소와 위내용물 분석 기법 적용

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요약

본 연구는 2020년부터 2021년까지 한반도 주변해역(동해, 남해)에서 저층트롤에 의해 어획된 어류와 잠재먹이원을 대상으로 어류 군집 및 먹이망 구조의 계절 변동과 분포 특성 그리고 주요 상업종인 갈치와 살오징어의 먹이원과 영양단계의 시·공간 변동 연구를 탄소 및 질소 안정동위원소와 위내용물 분석 기법을 활용하여 수행하였다.

동해 해역 내 두 개 정점과 남해 해역 한 개 정점을 대상으로 2020년 5월과 10월에 어류 군집의 먹이망 구조를 파악하고 해역별 생태학적 지위를 비교하기 위해 각각의 정점에서 어류와 잠재먹이원을 채집하여 탄소 및 질소 안정동위원소 분석을 실시하였다. 남해 해역 어류의 δ^{13}C 범위는 −22.4 ~ −15.3‰, δ^{15}N 범위는 7.4 ~ 13.8‰이었으며, 동해 해역 어류의 δ^{13}C 범위는 −22.1 ~ −18.0‰, δ^{15}N 범위는 9.8 ~ 13.6‰로 분석되어, 두 해역 간에 공간적인 차이를 보였다. 잠재먹이원인 입자유기물질, 동물플랑크톤의 δ^{13}C 및 δ^{15}N 범위도 두 계절 간에 유의한 차이를 보였다 (PERMANOVA, $p < 0.05$, in all cases). 또한, 어류의 δ^{13}C 과 δ^{15}N 값을 기반으로 계산한 trophic niche 값은 동해에 비해 남해 해역에서 상대적으로 높게 나타났다. 결국, 이러한 먹이망 특성의 차이는 어류 종조성과 해양환경 요인들의 차이에 기인하는 것으로 판단된다.

남해 해역 갈치를 대상으로 성장에 따른 계절별 먹이원 변동 특성을 파악하기 위하여 2021년 2월, 5월, 8월, 11월 안정동위원소와 위내용물 분석을 실시하였다. 갈치의 경우, 위내용물 분석을 통해 2월과 11월에는 어류, 5월에는

난바다곤쟁이류가 주요 먹이원으로 분석되었다. 갈치의 탄소 안정동위원소 비값은 계절적으로 차이를 보였으며, 특히 5월에는 성장에 따라 부유성 기원의 먹이기여가 높아지는 상관관계가 나타났다(r^2 = 0.594, $p < 0.001$). 5월에 난바다곤쟁이류의 기여가 매우 높게 나타난 위내용물 분석과도 일치하는 결과로 파악되었다.

남해 해역 살오징어의 크기와 계절에 따른 먹이 조성, 영양단계, 그리고 성장에 따른 먹이원 변화 등을 파악하기 위하여 2021년 2월, 5월, 8월 안정동위원소와 위내용물 분석을 실시하였다. 전반적으로 살오징어의 식성은 어류(37.9 ~ 94.0%)와 두족류(6.0 ~ 61.0%)의 기여가 매우 높게 나타났다. 그러나 8월의 경우, 10cm 그룹에서 대부분 갑각류(95.5%)의 기여가 높게 나타났는데, 이는 계절별, 크기군별로 주요 먹이원의 변화가 있음을 의미한다.

본 연구는 기후변화 및 환경변화에 따른 해양 생태계 군집 변화와 영양단계 변화를 이해하기 위한 중요한 기초자료로 활용이 가능하며, 우리나라 해역에 서식하는 주요 종의 생태계 기반 수산자원관리를 위한 과학적인 자료를 제시하였다. 그리고 안정동위원소 분석기술이 해양생태계 내에서 여러 생물들의 섭식활동 및 에너지 공급원 등을 파악하는데 효과적인 분석방법임을 확인하였다. 동시에 위내용물 분석 기법과 병행하였을 때 더 효과적으로 수산자원의 섭식생태 연구를 진행할 수 있음을 보여주었다. 따라서 본 연구 결과는 기후변화 등의 해양환경 변화에 따른 해양생태계 반응을 이해하고 다양한 환경변화가 시공간적으로 어떻게 변화할 수 있는지에 대한 이해를 높이는 데 도움이 될 것이다. 향후 DNA barcoding 기술과 안정동위원소 분석 기술을 적용하면 다양한 환경의 먹이망 시스템에서 생물들간의 에너지 이동과 공급원을 파악하는데 더욱 정확하고 자세한 단서를 찾아낼 수 있을 것이다. 나아가서 생태공학 분야를 접목시킨 수산자원 관리 방안, 생태계 복원, 청정생산 기술 등 생태계를 이해하는데 중요한 접근법을 제시할 수 있으며, 장기적인 관점에서 생태계 변화를 예측하기 위한 생태계 모델링 결과 도출을 개선하는데 크게 기여할 수 있을 것으로 판단된다.

ABSTRACT

Despite its importance, fish food web structure and feeding ecology have been relatively less researched. The research aimed to provide new insights into trophic relationships and feeding strategies within fish assemblages sampled in Korean coastal areas located in the western North Pacific since the study of food webs allows a better understanding of ecosystems.

This dissertation assessed seasonal variation in the food-web structure and ecological interaction of fish assemblages in the East and South Seas of Korea, a large coastal ecosystem that has recently undergone considerable shifts in fish abundance and composition. Specifically, this dissertation examined the diet composition, trophic position, and ontogenetic dietary shifts of two economically important species (*Trichiurus japonicus* and *Todarodes pacificus*) using the stable isotope technique and stomach content analysis during four seasons (winter, spring, summer, and autumn) in South Sea of Korea. Fish and potential food sources were collected from the study areas in 2020 and 2021.

This dissertation comprises the following three parts. The first study assessed seasonal variation in the food-web structure of fish assemblages in the East (two sites) and South (one site) Seas of Korea, and compared the isotopic niche areas between the regions. To accomplish this, we analyzed the community structures and carbon and nitrogen stable isotope values of fish assemblages and their potential food sources collected during May and October 2020. There were spatial differences in the diversity and dominant species of fish assemblages between the two seas. The fish assemblages in the South Sea had relatively wide ranges of δ^{13}C and δ^{15}N (−22.4 to −15.3‰ and 7.4 to 13.8‰, respectively) compared with those in the East Sea (−22.1 to −18.0‰ and 9.8 to 13.6‰, respectively). The δ^{13}C and δ^{15}N values of suspended particulate organic matter, zooplankton, and fish assemblages differed significantly among sites and seasons (PERMANOVA, $p < 0.05$, in all cases). Moreover, the isotopic niche indices were relatively higher in the South Sea than in the East Sea. Such differences in food-web characteristics among sites are likely due to the specific environmental effects (especially, major currents) on the differences in species compositions.

The second study investigated stomach contents and stable isotope signatures (δ^{13}C and δ^{15}N) of largehead hairtail (*Trichiurus japonicus*), which is one of the most commercially important fishes in the western North Pacific, to determine dietary changes across ontogeny and seasons. Our isotopic results revealed that the largehead hairtail is placed intermediately between pelagic and benthic fishes and was more δ^{13}C and δ^{15}N-depleted than other carnivorous fishes, suggesting high consumption of pelagic species. Similarly, seasonal variations were observed in the δ^{13}C and δ^{15}N values of the largehead hairtail (PERMANOVA, $p = 0.001$). Notably, their δ^{13}C values in spring decreased significantly with ALs ($r^2 = 0.594$, $p < 0.001$), suggesting an ontogenetic change due to the increased proportion of Euphausiacea in the nutrition of largehead individuals during this specific season.

The third study evaluated the diet composition, trophic position, and ontogenetic dietary shifts of common squid (*Todarodes pacificus*) across different body sizes (mantle length, ML) and seasons (winter, spring, and summer 2021) in the South Sea of Korea using stable isotope and stomach content analyses. Regardless of the season,

the common squid diet predominantly comprised Pisces (37.9–94.0%) and Cephalopoda (6.0–61.0%). However, in the smallest group (ML < 10 cm), the stomach contents in August were primarily Crustacea (95.5%), suggesting a seasonal difference in dietary composition and ontogenetic dietary shifts only during the summer. Similarly, our isotope results revealed seasonal isotopic variation among sampling periods and significant positive correlations between ML and both $\delta^{13}C$ and $\delta^{15}N$ values in common squid during summer. These results suggest seasonal variability of major diet components among size groups of common squid and that their feeding strategy is likely adjusted in response to diet availability on a temporal scale.

This dissertation work allows for a deeper understanding of the changing trophic diversity and community structure of faunal assemblages caused by environmental changes. Moreover, this study improves our understanding of the feeding ecology of *Trichiurus japonicus* and *Todarodes pacificus,* which provides valuable information for ecosystem-based fishery management of these commercially important species.

This study confirmed that the stable isotopes technique is a powerful tool for identifying feeding activities and energy sources of various organisms in marine ecosystems. The integrated use of stable isotope techniques and stomach content analysis is crucial for improving the interpretation of feeding studies for fisheries resources.

Therefore, this dissertation will enhance our understanding of the impacts of outside influences on marine ecosystems, such as climate change, and how those interactions may change in time, space, and under different environmental conditions. In the future, more accurate and detailed clues can be found regarding the energy transfer among organisms in marine food webs in various environments using DNA barcoding and stable isotope techniques. Furthermore, these methods can be used for ecological engineering to enhance the design of ecosystems for the mutual benefit of humans and nature. Finally, we can improve marine ecosystem modeling to analogize long-term change perspectives.

I. General introduction

1.1 Coastal ecosystem

Coastal ecosystems that extend to the margins of continental shelves are complex ecosystems in which biotic and abiotic factors are generally characterized by strong spatial and seasonal heterogeneity and variability. This results in the organization of the community structure of aquatic assemblages (McLusky and Elliott, 2004; Akin et al., 2003). In addition, coastal ecosystems provide nursery habitats and refuge for commercially important fish species, which is one of the most important ecosystems for supporting commercial fish and enhancing the productivity of fisheries resources (Beck et al. 2001; Seitz et al. 2014; Park et al. 2020).

However, various natural and anthropogenic disturbances, such as climate change, eutrophication, overfishing, and industrial and urban discharge, may lead to changes in the number and biomass of marine organisms. Such occurrences can also change the distribution of marine organisms through trophic interactions as mediators between biodiversity and ecosystem functioning (Dunson and Travis, 1991; Thompson et al., 2012).

1.2 Fisheries resources

The global trend in capture fisheries has gradually fluctuated from 86,000,000 to 93,000,000 t per year since the late-1980s. However, the total global capture fisheries production reached its highest level at 96,400,000 t in 2018 (FAO 2020). The increase in 2018 was primarily caused by marine capture fisheries (FAO 2020). The catch data for fishery resources in South Korea gradually decreased from 1,725,820 t in 1986 to 941,069 t (KOSIS, 2021) (Figure 1.1).

In particular, the largehead hairtail (*Trichiurus japonicus*) and common squid (*Todarodes pacificus*) are commercially important species that are widely distributed in the South Sea of Korea. Nevertheless, the total catch of the largehead hairtail (*T. japonicus*), a warm-water fish, has decreased continuously since 1983. The common squid *Todarodes pacificus* (*T. pacificus*), a cold-water species, rapidly increased after the late 1980s, owing to the response of marine ecosystems to climate regime shifts; however, this species has decreased since 1996 (Jung et al., 2017, KOSIS, 2019) (Figure 1.2).

It is necessary to assess and manage a variety of commercially important species and the different elements of the marine ecosystem, such as climate change, habitat, energy flow, and food web, to maintain the health of the ecosystem and support the sustainable use of fisheries resources (Park et al., 2020). Therefore, many scientists have focused on conservation efforts and the development of fisheries management practices. Two species (largehead hairtail and common squid) were considered the target for examination in this study.

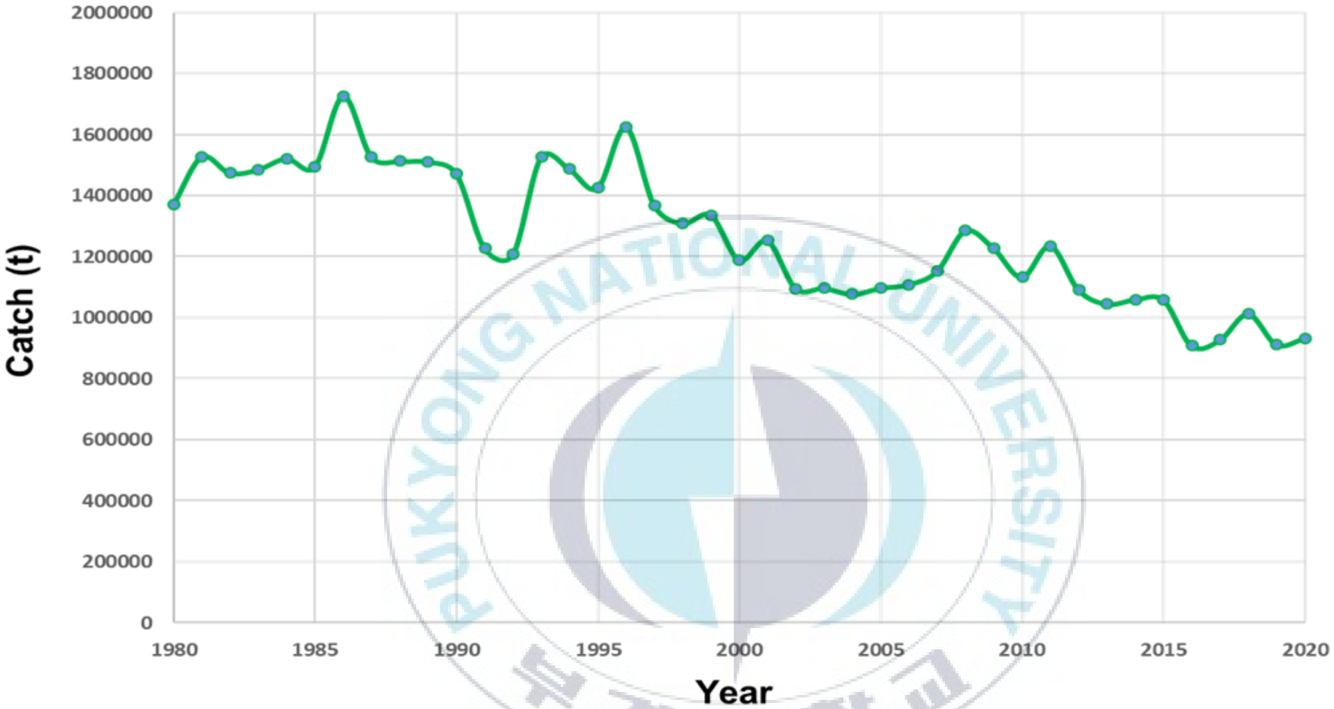


Figure 1.1. Change in catches of the fisheries resources in Korean coastal waters from 1980 to 2020.

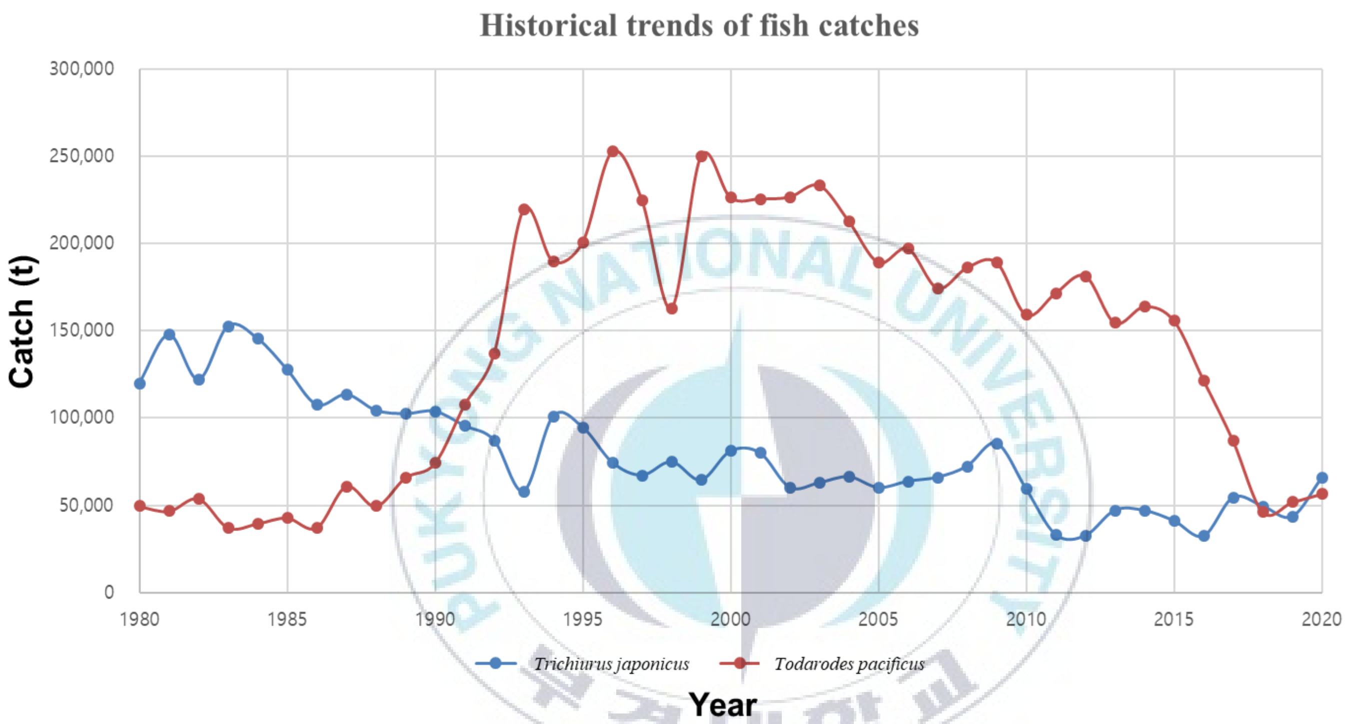


Figure 1.2. Change in catches of the largehead hairtail (*Trichiurus japonicus*) and common squid (*Todarodes pacificus*) in Korean coastal waters from 1980 to 2020.

1.3 Study area and survey design

The Korean Peninsula is surrounded by the East, South, and Yellow Seas, which have different environmental characteristics. This study was conducted in the South Sea and East Sea in Korean waters. The South Sea shows regional characteristics of diverse marine environments and ecosystems that are mostly influenced by the North Korean Cold Current (EKWC), a branch of the Kuroshio Current. Seasonal fluctuations in the Kuroshio current influence the South Sea. Warm and salty subtropical seawater flows from the south along the Kuroshio Current. The South Sea is influenced by the Changjiang River, which is the longest river in Asia, and coastal waters from mainland China and Korea. In contrast, the East Sea has two major currents of the EKWC: one of the branches of the Kuroshio Current from south to north and the North Korea Cold Current (NKCC), which is strengthened during the winter from the north to south (Figure 1.3).

In this study, Stable Isotope Surveys (SIS) were conducted in two coastal regions (South and East Seas) of the Korean Peninsula (Figure 1.4). Pre-trial SIS was performed at three sites in the South and East Seas in May and October 2020. The next SIS was conducted at six sites on the continental shelf of the South Sea in February, May, August, and November 2021. In this study, SIS was performed at 13 sites in the South, East, and Yellow Seas in February, May, August, and November of 2022. Samples of all fish and zooplankton species were collected from Tamgu 20 (885 t) and Tamgu 22 (1,458 t) research vessels of the Fisheries Resources Research Center of the National Institute of Fisheries Science (NIFS). Fish and zooplankton samples were collected using the trawl net and Bongo net (trawl net: 12 cm mesh in the main body, 8 cm mesh in the intermediate part, and 6 cm mesh in the cod end with a 2 cm cod end liner, Bongo net: 2.0 m^2 mouth opening, 500 μm mesh). All collected fish and zooplankton samples were stored in a freezer (−20 °C). They were then transported to the laboratory for processing.

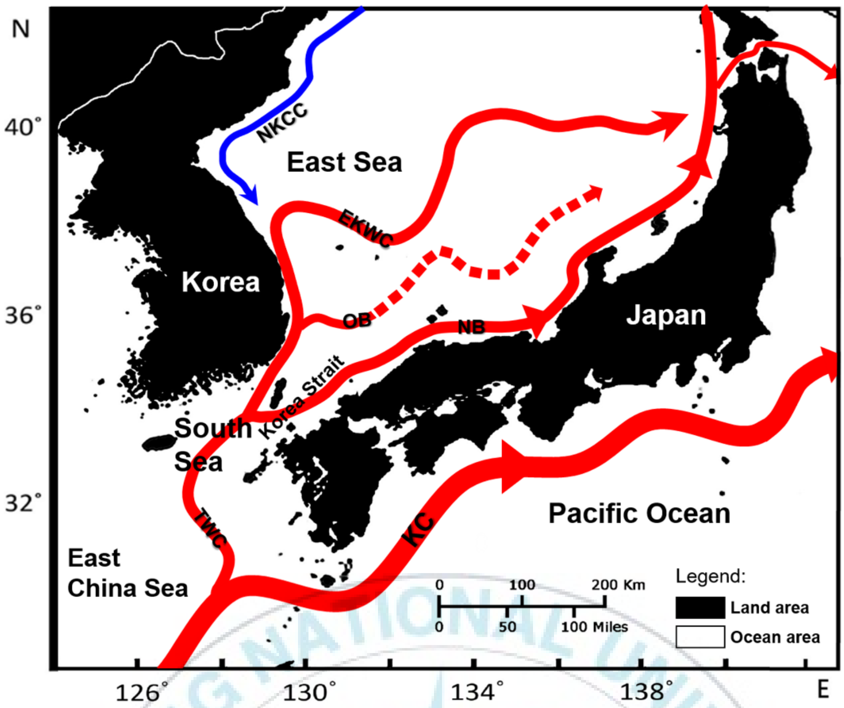


Figure 1.3. A schematic current map with cold (blue) and warm (red) currents (TWC: Tsushima Warm Current, EKWC: East Korea Warm Current, NKCC: North Korea Cold Current, and KC: Kuroshio Current) (modified from Lee et al., 2019), where the line width represents the overall strength of the current.

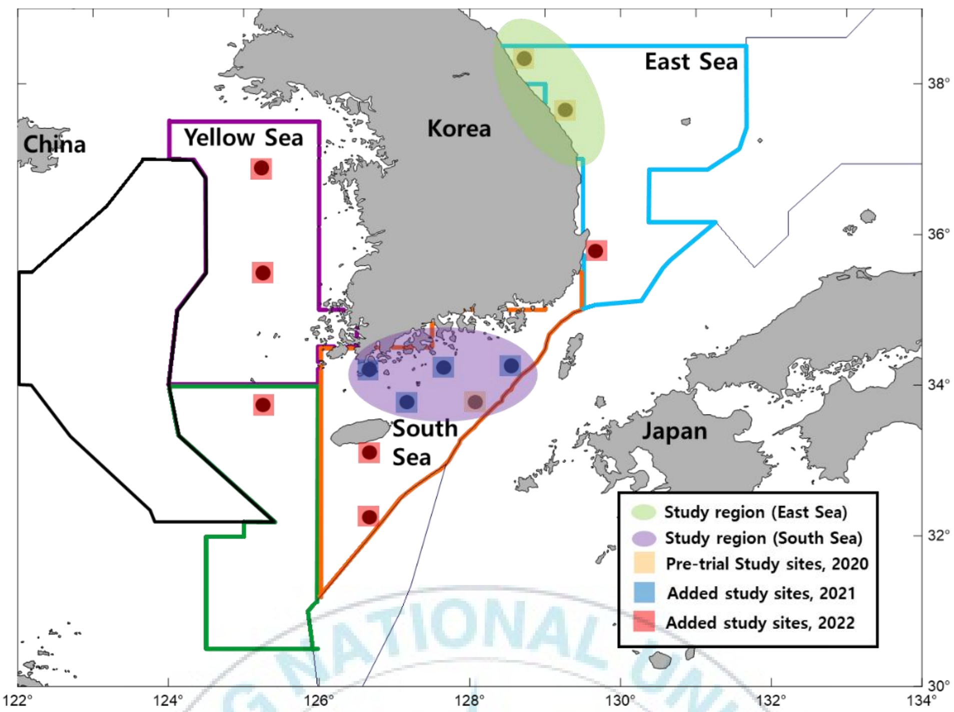


Figure 1.4. Survey area and sampling sites for this study from 2020 to 2022.

1.4 Stable isotope and stomach content analyzes

Food webs describe the biological networks between predator and prey and transfer the substances and energy from primary food sources to the upper trophic position predator (Govenar et al. 2012). This predator and prey relationship provides crucial information on ecosystem structure and function (Dunne et al. 2002).

Traditionally, stomach content analysis has been used as a method for evaluating the dietary contribution and trophic position of fish species in marine ecosystems (Pasquaud et al., 2008; Baker et al., 2014). Food components were estimated by the percentage frequency of occurrence (%*F*, number of stomachs in which a particular food item occurred as a percentage of the total number of stomachs examined), percentage numerical frequency (%*N*) of each prey item to the total number of identifiable food items, and percentage wet weight (%*W*) of each prey item to the total wet weight of the identifiable food items. In Chapter 3, all food components of the largehead hairtail (*Trichiurus japonicus*) were calculated as an index of relative importance (IRI) and wet weight (W), which were expressed as a percentage (%*IRI* and *%W*). In Chapter 4, all food components of the common squid (*T. pacificus*) are calculated for a ranking index (RI) and wet weight (W), which are expressed as a percentage (%*RI* and *%W*). Size-related ontogenetic dietary changes in these species were examined using three size classes. Despite being a common tool for describing diet composition and feeding ecology, this method requires a large number of species to characterize the dietary composition and may be biased toward their more recently consumed prey (Hertz et al., 2014).

Recently, stable isotope analysis has become useful in ecology and has been combined with the traditional method of stomach content analysis to more effectively clarify the trophic relationships of animals and the food web structure in marine ecosystems (Michener and Schell, 1994; Boecklen et al., 2011; Layman et al., 2012). This technique relies on the assumption that the stable carbon and nitrogen isotope compositions of a consumer species reflect those of its diet with well-known isotopic fractionations (within approximately 1‰ for δ^{13}C and 2–4‰ for δ^{15}N) between them (DeNiro and Epstein, 1978; Fry and Sherr, 1984; Vander and Rasmussen, 2001; Boecklen et al., 2011; Post, 2002) (Figure 1.5). δ^{13}C and δ^{15}N values provide information on the origin of assimilated dietary sources for consumers and their trophic positions, respectively (Peterson and Fry, 1987). Furthermore, this analysis provides an insightful tool for identifying the spatial and temporal variability in the trophic ecology of fish species and the trophic structure of fish assemblages through isotopic monitoring in coastal ecosystems (Willis et al., 2017; Timmerman et al., 2021; Park et al., 2020). Stable isotope techniques have been increasingly used to assess the trophic role of fish species and their ontogenetic dietary shifts (Branch et al., 2002; Darnaude, 2005; Chiang et al., 2020). This method, supported by stomach content analysis, is among the most powerful tools for improving the interpretation of feeding studies for fisheries resources (Davis et al., 2012; Santos et al., 2013; Park et al., 2018).

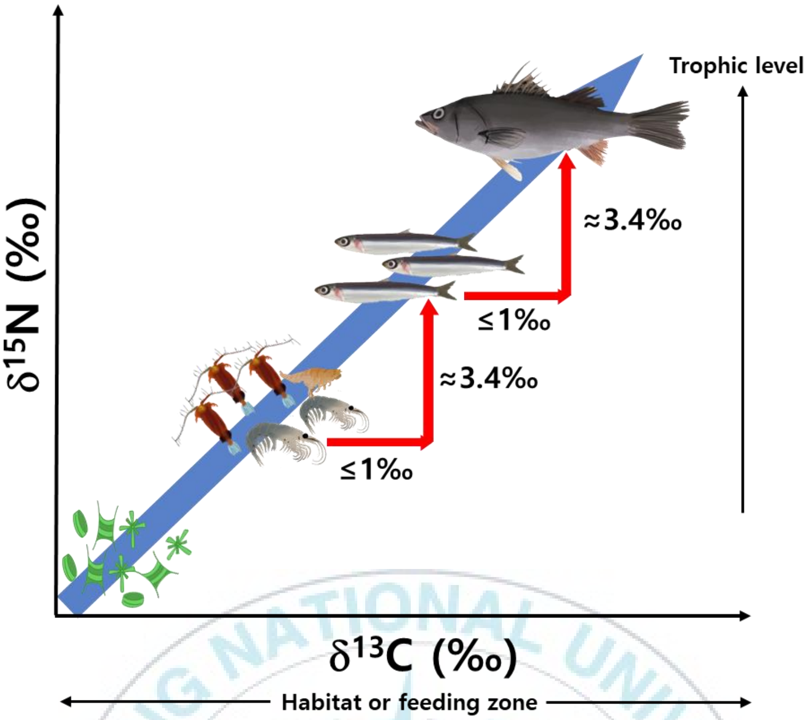


Figure 1.5. Fractionation of carbon and nitrogen stable isotopes by trophic position.

1.5 Objectives and chapter structure

This thesis aimed to understand the ecological role of major species in the fish food web by identifying the spatial and temporal variability of trophic structures and diet sources in coastal ecosystems. This research was performed in the East and South Seas of Korea from May 2020 to November 2021 using multiple techniques, stable isotopes, and stomach content analyses (Figures 1.6 and 1.7).

The three chapters of this study have already been published in peer-reviewed journals. Chapter 2 was published in December 2022 in Water, Chapter 3 in July 2022 in Frontiers in Marine Science, and Chapter 4 in October 2022 in Water. The specific objectives of this dissertation are as follows;

(1) Chapter 2 — The aim of this chapter is to assess seasonal variation in the food-web structure of fish assemblages in the East (two sites) and the South (one site) Seas of Korea, and to compare the isotopic niche areas between the regions. To do this, chapter 2 described the community structures and the $\delta^{13}C$ and $\delta^{15}N$ values for fish assemblages, and their potential food sources collected during May and October 2020.
Corresponding journal article: Shin, D., Park, T. H., Lee, C. I., Hwang, K., Kim, D. N., Lee, S. J., Kang, S. & Park, H. J. (2022). Characterization of Trophic Structure of Fish Assemblages in the East and South Seas of Korea Based on C and N Stable Isotope Ratios. Water, 14(1), 58.;

(2) Chapter 3 — The aim of this chapter is to examine the trophic ecology of the largehead hairtail (*Trichiurus japonicus*) in the South Sea of Korea. Considering its seasonal growth dynamics, chapter 3 focused on the changes in the dietary composition and trophic position of largehead hairtail across ontogeny and seasons based on stable isotope analysis and supplementary stomach content data. All specimens of zooplankton, largehead hairtail and other fish were collected during four seasons (February, May, August, and November) 2021.

Corresponding journal article: Shin, D., Park, T. H., Lee, C. I., Jung, J., Lee, S. J., Kang, S. & Park, H. J. (2022). Trophic ecology of largehead hairtail *Trichiurus japonicus* in the South Sea of Korea revealed by stable isotope and stomach content analyses. Frontiers in Marine Science, 10, 3159.;

(3) Chapter 4 — The aim of this chapter is to examine the dietary composition, trophic position and ontogenetic dietary changes of common squid *Todarodes pacificus* in the South Sea of Korea. To do this, chapter4 analyzed stomach contents and stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) across different body sizes (mantle length, ML) and seasons (winter, spring and summer) in 2021.

Corresponding journal article: Shin, D., Park, T. H., Lee, C. I., Jo, J., Choi, C., Kang, S. & Park, H. J. (2022). Feeding Ecology of Common Squid *Todarodes pacificus* in the South Sea of Korea Determined through Stable Isotope and Stomach Content Analyses. Water, 14(19), 3159.

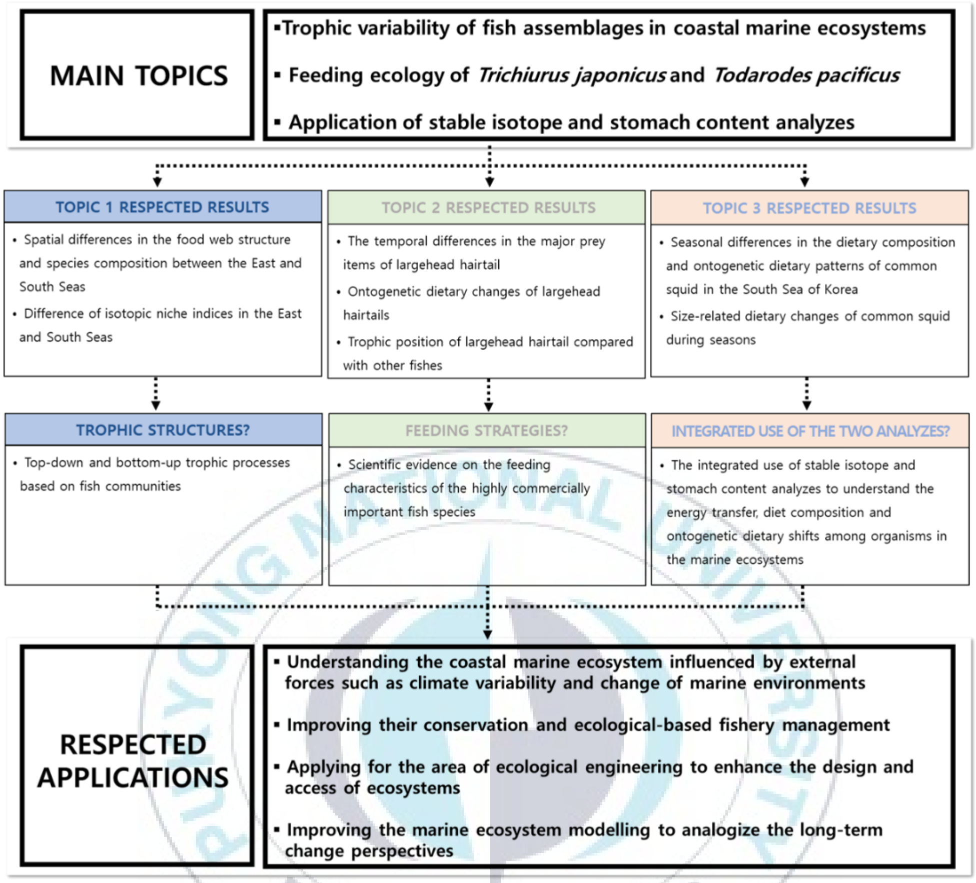


Figure 1.6. Schematic diagram of the main topics, respected results, and applications of this study.

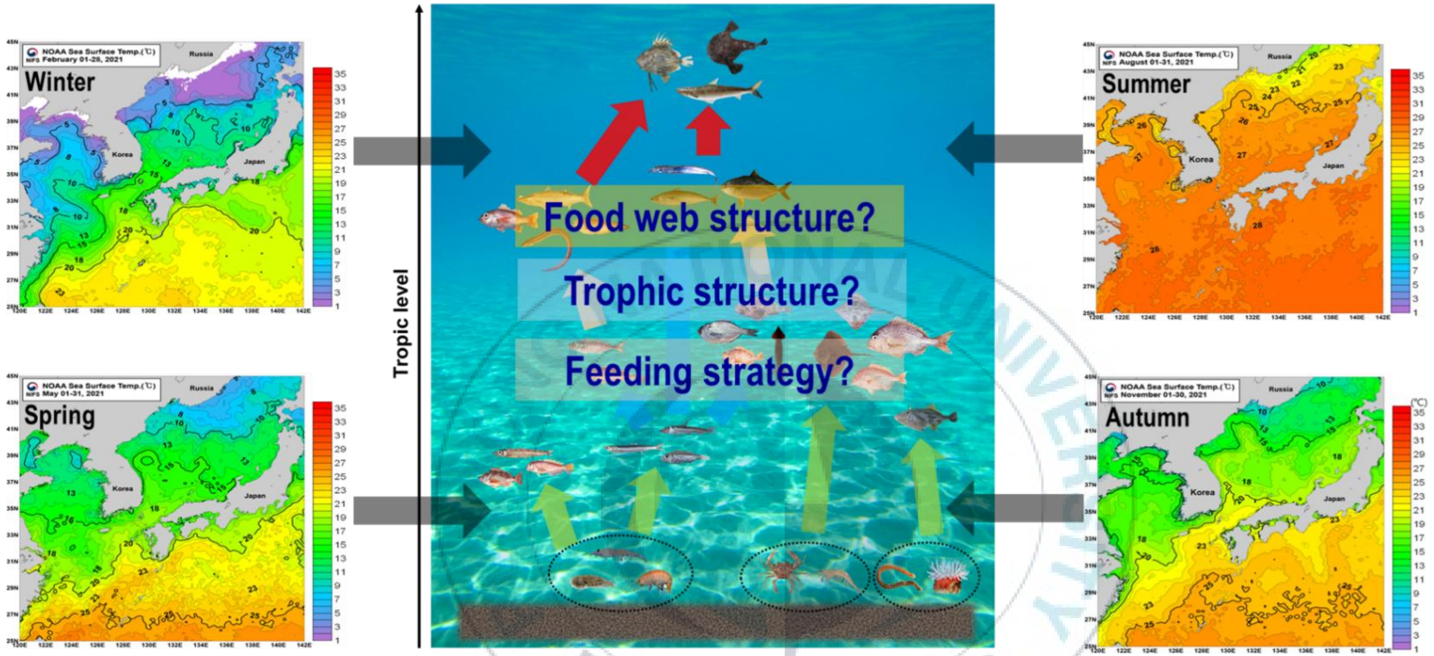


Figure 1.7. Schematic diagram of the generalized fish food web in Korean coastal waters. Sea Surface Temperature (SST) near Korea in four seasons in 2021 is sourced from NOAA Optimum Interpolation.

II. Characterization of trophic structure of fish assemblages in the East and South Seas of Korea based on C and N stable isotope ratios

2.1 Introduction

Coastal zones that extend to the margins of continental shelves are complex ecosystems in which biotic and abiotic factors are generally characterized by strong spatial and seasonal heterogeneity, and variability. These result in the organization of the community structure of aquatic assemblages (McLusky and Elliott, 2004; Akin et al., 2003). These areas are among the most productive systems, and play an important role in sustaining high secondary production and biodiversity (Costanza et al., 1997). However, a variety of natural and anthropogenic disturbances, such as climate change, eutrophication, overfishing, and industrial and urban discharges may lead to changes in the number and biomass of marine organisms. Such occurrences can also change the distribution of marine organisms with trophic interactions between organisms as mediators between biodiversity and ecosystem functioning (Dunson and Travis, 1991; Thompson et al., 2012). Characterizing the spatial and temporal variability of trophic networks related to several ecological processes of bottom-up or top-down effects, and predator–prey relationships, is essential to improving our understanding of ecosystem functioning (McMeans et al., 2015; Willis et al., 2017). Furthermore, the alteration of trophic interactions due to changes in community patterns has a significant effect on the structure and functioning of food webs (Johnson and Seinen, 2002; Timmerman et al., 2021). Thus, knowledge of comprehensive trophic information by the assessment of trophic interactions between coexisting organisms, their nutrition, and their spatial and temporal changes is needed for the sustainable management of marine ecosystems.

Because there are many commercially important fishes in coastal ecosystems, fisheries management actions on fish stock and harvest regulation should be considered for sustaining resources for fisheries. Additionally, fish are ecologically important consumers in marine ecosystems, and information about their dietary sources and trophic interactions is crucial for predicting the top-down consequences of many potential anthropogenic drivers (Johnson and Seinen, 2002; Garrison and Link, 2000). Several studies have consistently emphasized the need for information on changed food web structures through trophic cascades related to changes in community structure and the replacement, depletion, and addition of specific fish species (Willis et al., 2017; Pace et al., 1999; Park et al., 2020). Local fish population abundance and species compositions are being increasingly influenced by changes in ambient environmental conditions, as well as food densities, competitors, and predators (Pasquaud et al., 2008; Last et al., 2011). In particular, climate change phenomena due to ocean warming can directly or indirectly influence fish abundance and composition through spatial and temporal shifts in the habitats and feeding strategies of component species, and their trophic interactions (Cury et al., 2008). Accordingly, spatial and temporal variability in the community-level interactions of fishes, with the inflow of energy through fish food webs in response to environmental gradients and anthropogenic pressures, is still a central point in terms of major drivers of coastal ecosystem functioning and their ecological roles.

Traditionally, stomach content observation has been used as a common tool for evaluating the dietary composition of fish species and trophic-based structures in marine ecosystems (Pasquaud et al., 2008; Baker et al., 2014). Despite the standard practice for describing fish trophic ecology, this method requires a large number of organisms to characterize the dietary composition and may be biased toward their more recently consumed prey (Hertz et al., 2014). Recent applications to overcome this bias have used stable isotope analysis, based on actual assimilated diets over longer periods, to elucidate the trophic relationships and functioning of animals, and the food web structure in marine ecosystems (Michener and Schell, 1994; Boecklen et al., 2011; Layman et al., 2012). This technique relies on the assumption that the stable carbon and nitrogen isotope compositions of a consumer species reflect those of its diet with the well-known isotopic fractionations (within approximately 1‰ for $\delta^{13}C$ and 2–4‰ for $\delta^{15}N$) between them (DeNiro and Epstein, 1978; Fry and Sherr, 1984; Vander and Rasmussen, 2001; Boecklen et al., 2011; Post, 2002). The $\delta^{13}C$ and $\delta^{15}N$ values provide information on the origin of assimilated dietary sources for consumers and their trophic positions, respectively (Peterson and Fry, 1987). Furthermore, this analysis provides an insightful tool for identifying the spatial and temporal variability in the trophic ecology of fish species, and the trophic structure of fish assemblages, through isotopic monitoring in coastal ecosystems (Willis et al., 2017; Timmerman et al., 2021; Park et al., 2020).

The South and East Seas of Korea are a part of the East Asian Marginal Seas, included in the western North Pacific, which are among the most productive fisheries in the world (Jung et al., 2017). The South Sea shows regional characteristics of diverse marine environments and ecosystems that are mostly influenced by the Tsushima Warm Current (TWC), a branch of the Kuroshio Current. Conversely, the East Sea has two major currents of the TWC from south to north and the Liman Cold Current (LCC) from north to south, which are generally separated by a subpolar front. Thus, there are considerable environmental differences in the oceanographic and geographical features between the two regions (Jung et al., 2017; Jian et al., 2006). Moreover, because the spatial and temporal responses of marine ecosystems to environmental gradients can vary regionally due to differences in major currents, it is very important to understand the properties of these systems through comparisons with the dynamics of the fish food web structures.

In the present study, we assessed and compared the spatial and temporal variability in the trophic structure of fish assemblages in the East Sea and South Sea of Korea. We hypothesized that differences in environmental conditions due to contrasting major currents would affect the trophic characteristics (i.e., trophic relationship and isotopic diversity) of fish assemblages. We accomplished this by analyzing the composition of fish assemblages, and their carbon and nitrogen isotope ratios, in the two seas during two seasons (summer and autumn).

2.2 Materials and methods

2.2.1 Study Sites

Sampling was performed at two eastern (St. A and St. B) coastal regions and one southern (St. C) coastal region of the Korean peninsula (Figure 2.1). Each sampling area had low tidal amplitude (less than 30 cm) and water depth ranging from approximately 100 m to 170 m. In the East Sea sampling sites, the vertical structure of the current generally shows a two-layer system with a branch of the East Korean Warm Current (TWC) in the upper layer and a branch of the LCC (the North Korean Cold Current) in the deeper layer (Lee, 2016). In contrast, the South Sea is a region of diverse marine environments with a branch of the TWC flowing through the sampling area into the East Sea (Jung et al., 2017). The environmental conditions of the sampling sites are listed in Table 2.1. During both seasons, the surface layer water temperatures in the South Sea were relatively high (20.3 °C in May and 24.7 °C in October) compared to those in the East Sea (14.9–15.3 °C in May and 16.2–16.5 °C in October). In case of the bottom layer water temperature, it was highest (24.5 °C at St. C) in October and lowest (1.0 °C at St. B) in May. The salinities of the surface water ranged from 32.4 (St. B) to 34.5 (St. A) in May and from 32.6 (St. B) to 33.8 (St. C) in October, while those of the bottom water were relatively constant (34.0 in St. A and B and 34.4 to 34.5 in St. C). Chlorophyll a (Chl *a*) concentrations of the surface layers varied between 0.7 μg/L (St. B) and 1.4 μg/L (St. A) in May, and between 0.3 μg/L (St. A) and 0.7 μg/L (St. B) in October.

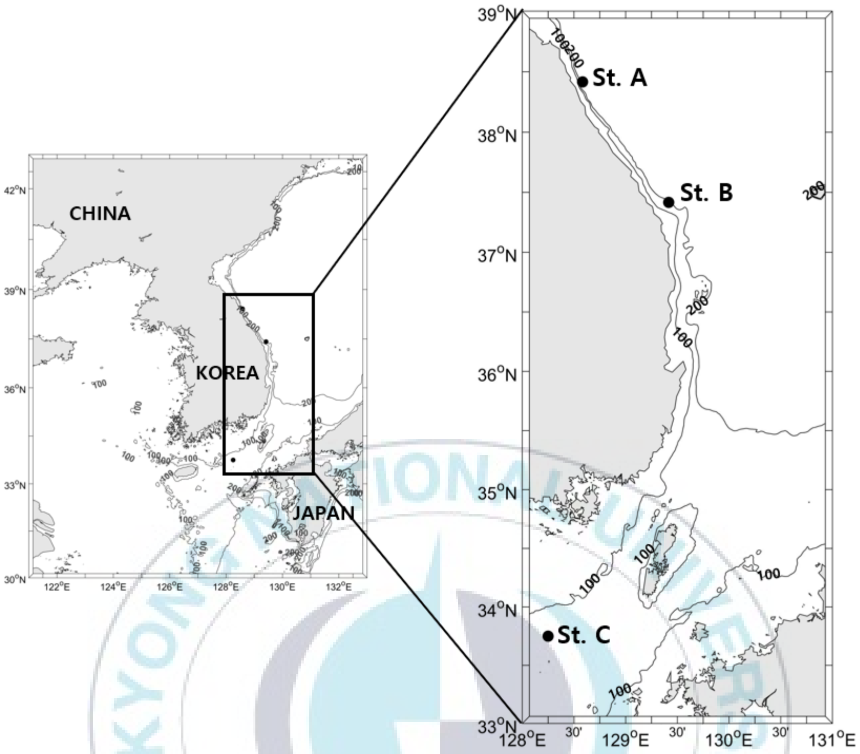


Figure 2.1. Map of the sampling sites in the East Sea (St. A and St. B) and the South Sea (St. C). Filled circles indicate the sampling sites collected for suspended particulate organic matter (SPOM) and consumers (zooplankton and fish).

Table 2.1. The surface and bottom environmental conditions (water temperature, salinity, and chlorophyll *a*) in the East Sea (St. A and St. B) and the South Sea (St. C) of Korea during May and October 2020.

Month	Water temperature (°C)				Salinity				Chl *a* (μg/L)	
	Surface		Bottom		Surface		Bottom		Surface	
	May	October	May	October	May	October	May	October	May	October
St. A	15.3	16.2	3.0	15.7	34.5	32.7	34.0	34.0	1.4	0.3
St. B	14.9	16.5	1.0	16.6	32.4	32.6	34.0	34.0	0.7	0.7
St. C	20.3	24.7	14.8	24.5	33.9	33.8	34.5	34.4	1.0	0.6

2.2.2 Sample collection and processing

Field surveys were performed on board the R/V Tamgu 22 at the three sites during two cruises in May and October 2020. Temperature and salinity data were obtained using a CTD (SBE 911 Plus, Seabird Electronics Inc., Bellevue, WA, USA). To collect chl *a* and suspended particulate organic matter (SPOM), seawater samples (approximately 20 L) were collected from the subsurface layers on each sampling occasion. Subsequently, the water samples were pre-filtered through a 200 μm mesh sieve to remove zooplankton and large particles. The pre-filtered samples were re-filtered on pre-combusted (450 °C for 4 h) Whatman GF/F glass fiber filters, using a vacuum pump, which were then frozen in a deep freezer (–20 °C) for later processing. In the laboratory, the chl a from the filter samples was extracted with 90% acetone overnight in darkness and sonicated for 5 min. After the extraction, the chl *a* concentration was determined using a fluorometer (Model 10 AU 005; Turner Designs, USA). The filtered samples for stable isotope analysis were acidified by fuming overnight over 1 N HCl to remove inorganic carbonates, oven-dried at 50 °C for 24 h, and then kept frozen at −20 °C until isotope analysis.

Samples of dominant zooplankton groups, copepods, and euphausiids were collected by obliquely towing a Bongo net (60 cm mouth diameter, 330 μm mesh), equipped with a flowmeter, at a depth of 100 m (Park et al., 2020). The zooplankton samples were preserved in 90% ethanol for taxonomic identification. Following transport to the laboratory, copepods and euphausiids were identified under a dissecting microscope.

All fish specimens were collected using a bottom trawl, which had a 6-seam net constructed of 120 mm (stretched) polyethylene mesh in the main body of the net, an 80 mm mesh in the intermediate part of the net, and a 60 mm mesh in the cod end with a 20 mm cod-end liner. The trawl was spread using a Jet 2 type; it had 5.14 m^2 quadrangle doors and weighed 1,990 kg. The fishing depth ranges averaged from 107.7 m to 167.1 m. All collected samples were sorted and identified to the species level, then their total lengths and weights were measured to the nearest 0.1 cm and 0.1 g, respectively. For isotope analysis, only the white muscle tissue of fish was used and was separated from the anterior dorsal regions using a knife. Squid and octopus muscle tissues were carefully dissected from the anterior mantle. All animal samples were freeze-dried, pulverized into a fine powder using a ball mill (MM200; Retsch GmbH, Haan, Germany), and then kept frozen (− 20 °C) until isotope analysis.

2.2.3. Stable isotope analyses

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

The differences in the lipid content among fish samples can result in bias in the interpretation of their $\delta^{13}C$ values (Sweeting et al., 2006). Thus, we used a lipid correction method proposed by (Post et al., 2007), in which the mass C:N ratios from the elemental fractions of fish tissues were assessed to determine whether the values were greater than 3.5, which may have indicated potential lipid bias. For C:N ratios greater than 3.5, lipid correction was performed as follows: $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C\colon N\ (ratios)$, where $\delta^{13}C_{untreated}$ and $\delta^{13}C_{normalized}$ are the measured and lipid-normalized values of the sample, respectively.

The trophic position (TP) of fish was calculated using the equation: $TP_i = (\delta^{15}N_i - \delta^{15}N_{baseline})/\Delta^{15}N + 2$, where $\delta^{15}N_i$ represents the mean $\delta^{15}N$ of the fish species, $\delta^{15}N_{baseline}$ is the mean $\delta^{15}N$ of the food web baseline, $\Delta^{15}N$ is the enrichment factor (3.4‰; (Post, 2002)) in $\delta^{15}N$ per TP, and 2 represents the baseline TP. The mean $\delta^{15}N$ value of calanoid copepods at each sampling site was used as the trophic baseline.

2.2.4. Data analyses

Prior to statistical analyses, all data were tested for normality and homogeneity of variance using the Shapiro–Wilk procedure and Levene's test, respectively, using IBM SPSS software (ver. 21.0, IBM Corp., Armonk, NY, USA). One-way analysis of variance (ANOVA), followed by Tukey's honest significant difference (HSD) multiple comparison post hoc test were used to distinguish significant differences in the $\delta^{13}C$ and $\delta^{15}N$ values of fish species among sampling sites and seasons. Significant differences in both the isotopic values of SPOM, zooplankton, and fish consumers among sampling sites and seasons were tested using a permutational multivariate analysis of variance (PERMANOVA). The PERMANOVA test was conducted using PRIMER version 6 (PRIMER-e, Auckland, New Zealand), with the PERMANOVA + PRIMER add-on (Anderson et al., 2008).

Isotopic niche parameters (total area; TA; and sample size-corrected standard ellipse area, SEAc) of fish assemblages were used to compare the trophic structure and trophic diversity among sampling sites and between seasons. This was done using the Stable Isotope Bayesian Ellipses in R (SIBER) package within R software. The TA values were assessed by a convex hull area encompassed by the points of all species in a $\delta^{13}C$–$\delta^{15}N$ bi-plot space, providing a measure of the total amount of isotopic niche space of consumers (Layman et al., 2007). The SEAc values were calculated as a quantification of the isotopic δspace to avoid problems because of small sample sizes (Jackson et al., 2011).

2.3 Results

2.3.1 Community structure of fish assemblages

The species number and abundance (individuals/km^2) of fish assemblages varied among the three sampling sites and between the two seasons, ranging from 12 (St. B in May) to 47 (St. C in May) and from 8996 (St. A in May) to 61051 (St. A in October), respectively (Table 2.2). At St. A and St. B of the East Sea during the two seasons, *Glyptocephalus stelleri* and *Gadus macrocephalus* generally dominated the fish assemblages, accounting for 75% and 71% of all individuals, respectively. In contrast, *Dentex tumifrons*, *Trachurus japonicus*, and *Zeus faber* at St. C of the South Sea were the most dominant species during the two seasons, accounting for 73% of all individuals. Univariate ecological indices of richness (*R*), evenness (*J*), and diversity (*H′*) varied widely among the three sampling sites and between the two seasons, ranging from 1.08 (St. B in May) to 4.72 (St. C in May), 0.44 (St. A in October) to 0.80 (St. A in May), and 1.31 (St. A in October) to 2.12 (St. C in May), respectively (Table 2.2).

Table 2.2. The species number and abundance (individuals/km^2) and univariate ecological indices (richness, *R*; evenness, *J*; diversity, *H'*) of fish assemblages collected at the St. A, St. B, and St. C during May and October 2020.

Species name	May			October		
	St. A	St. B	St. C	St. A	St. B	St. C
Total species number	16	12	47	19	19	36
Total individuals	8995	27906	17067	61053	13715	40800
Richness (*R*)	1.65	1.08	4.72	1.63	1.89	3.30
Evenness (*J*)	0.80	0.56	0.70	0.44	0.57	0.45
Diversity (*H'*)	2.21	1.40	2.69	1.31	1.67	1.62

2.3.2 Stable isotope values of SPOM and zooplankton

The $\delta^{13}C$ and $\delta^{15}N$ values of SPOM differed significantly among the sampling sites (PERMANOVA, pseudo-$F_{2,29} = 7.18$, $p = 0.004$) and between seasons (pseudo-$F_{1,29} = 15.70$, $p = 0.001$), ranging from –22.9 ± 0.3‰ (St. A in May) to –20.5 ± 0.1‰ (St. C in October) and from 4.6 ± 0.4‰ (St. B in May) to 5.8 ± 0.3‰ (St. C in October), respectively (Table 2.3). Similarly, significant differences in the isotopic values of zooplankton (both calanoid copepods and euphausiids) were observed among the sampling sites (pseudo-$F_{2,23} = 5.47$, $p = 0.012$; pseudo-$F_{2,23} = 15.25$, $p = 0.001$) and between seasons (pseudo-$F_{1,23} = 5.42$, $p = 0.029$ and pseudo-$F_{1,23} = 14.33$, $p = 0.001$), showing the lowest $\delta^{13}C$ at St. A in May and the highest at St. C in October for all cases. These overall mean $\delta^{13}C$ and $\delta^{15}N$ values varied between –22.0 ± 0.3‰ and –21.1 ± 0.4‰, and between 6.6 ± 0.4‰ to 7.4 ± 0.3‰ for copepods, and between –21.7 ± 0.3‰ and –20.4 ± 0.3‰ from 7.0 ± 0.4‰ to 8.1 ± 0.3‰ for euphausiids, respectively.

Table 2.3. δ^{13}C and δ^{15}N values of organic matter (SPOM, suspended particulate organic matter) and zooplankton (calanoid copepods and euphausiids) collected during May and October 2020 in the East Sea (St. A and St. B) and the South Sea (St. C). PERMANOVA test of δ^{13}C and δ^{15}N values for each potential food source between seasons and among sampling sites. Bold-face font indicates significance at $p < 0.05$. Data represent mean ± 1SD.

Potential food source	May					October				
		δ^{13}C		δ^{15}N			δ^{13}C		δ^{15}N	
	n	Mean	SD	Mean	SD	n	Mean	SD	Mean	SD
St. A										
SPOM	5	–22.9	0.4	4.7	0.8	5	–22.1	0.4	5.0	0.6
Copepods	4	–22.0	0.3	6.6	0.4	4	–21.7	0.3	7.0	0.4
Euphausiids	4	–21.7	0.3	7.0	0.4	4	–21.2	0.3	7.4	0.2
St. B										
SPOM	5	–22.5	0.4	4.6	0.4	5	–21.9	0.2	5.0	0.6
Copepods	4	–22.0	0.3	6.8	0.4	4	–21.6	0.4	7.2	0.3
Euphausiids	4	–21.7	0.3	7.1	0.2	4	–21.2	0.3	7.5	0.2
St. C										
SPOM	5	–22.5	0.8	5.1	0.9	5	–20.5	0.1	5.8	0.4
Copepods	4	–21.4	0.3	7.2	0.5	4	–21.1	0.4	7.4	0.3
Euphausiids	4	–20.9	0.4	7.7	0.3	4	–20.4	0.3	8.1	0.3

PERMANOVA test	Season		Site		Interaction	
	pseudo-*F*	*p*	pseudo-*F*	*p*	pseudo-*F*	*p*
SPOM	15.70	**0.001**	7.18	**0.004**	1.31	0.311
Copepods	5.42	**0.029**	5.47	**0.012**	0.21	0.896
Euphausiids	14.32	**0.001**	15.25	**0.001**	Negative	

2.3.3 Stable isotope values of fish assemblages

The $\delta^{13}C$ and $\delta^{15}N$ values of fish assemblages varied significantly between seasons (pseudo-$F_{1, 252} = 5.41$, $p = 0.010$) and among sites (pseudo-$F_{2, 252} = 18.98$, $p = 0.001$), whereas no significant effect of the interaction term of season × site (pseudo-$F_{2, 252} = 1.57$, $p = 0.200$) (Figure 2.2, and Tables 2.4 and 2.5) was observed. Additionally, the isotope values for fish consumers at the two sites within the East Sea significantly differed between seasons (pseudo-$F_{1, 129} = 5.06$, $p = 0.027$) and sites (pseudo-$F_{1, 129} = 5.46$, $p = 0.017$). No significant effect of the interaction term (site × season; pseudo-$F_{1, 129} = 1.54$, $p = 0.196$) was found in this case. The overall mean $\delta^{13}C$ values of fish consumers in May were significantly different among the three sites (Tukey's HSD test, $F_{2, 90} = 32.23$, $p < 0.01$; –21.2 ± 0.3‰ to –18.8‰, –21.4 ± 0.7‰ to –18.3‰, and –22.4‰ to –17.0 ± 0.2‰ at St. A, B, and C, respectively). In October, the $\delta^{13}C$ values were relatively higher at the C site (–19.9 ± 0.4‰ to –15.3‰) than at St. A and B (Tukey's HSD test, $F_{2, 161} = 23.91$, $p < 0.01$; –22.1‰ to –18.0‰ and –22.0 ± 0.6‰ compared to –18.0 ± 0.1‰, respectively). Similar ranges of $\delta^{15}N$ values were observed among the three sites in May (Tukey's HSD test, $F_{2, 90} = 1.01$, $p = 0.371$; 9.8 ± 0.1‰ to 12.9 ± 0.4‰, 10.5‰ to 13.6‰, and 7.4‰ to 13.2 ± 0.3‰ at St. A, B, and C, respectively) and October (Tukey's HSD test, $F_{2, 161} = 0.95$, $p = 0.389$; 9.9 ± 0.6‰ to 13.4 ± 0.4‰, 10.7 ± 0.4‰ to 13.3‰, and 9.3 ± 0.2‰ to 13.8‰ at St. A, B, and C, respectively).

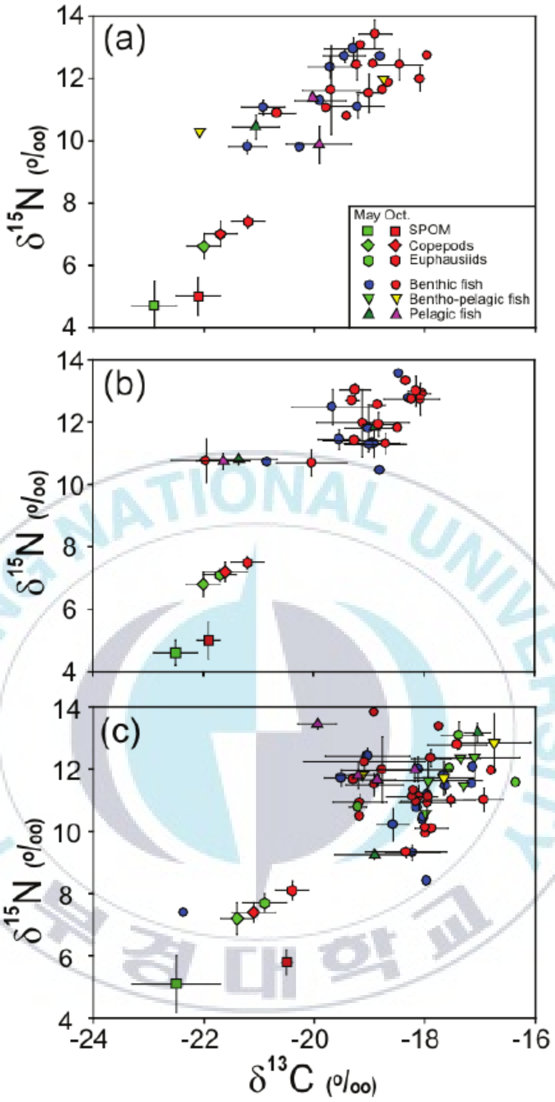


Figure 2.2. Dual isotope plots of $\delta^{13}C$ and $\delta^{15}N$ values of zooplankton (triangles, euphausiids; inverted triangles, copepods) and fish consumers (circles) and their potential food sources (squares, suspended particulate organic matter, SPOM) at the sampling sites (a, St. A; b, St. B; c, St. C) in May (blue colors) and October (green colors). Values are presented as mean $\delta^{13}C$ and $\delta^{15}N$ (‰ ± 1 SD). Species codes indicate the fish consumers listed in Tables 4 and 5.

Table 2.4. $\delta^{13}C$ and $\delta^{15}N$ values and trophic position (TP) of fish consumers collected at the St. A, St. B, and St. C during May 2020. Lower case codes indicate feeding modes (b, benthic feeder; bp, benthopelagic feeder; p, pelagic feeder). The lipid-correction was applied for the $\delta^{13}C$ of marked species (*). Data represent mean ± 1SD.

Species name	St. A						St. B						St. C					
	n	$\delta^{13}C$		$\delta^{15}N$		TP	n	$\delta^{13}C$		$\delta^{15}N$		TP	n	$\delta^{13}C$		$\delta^{15}N$		TP
		Mean	S.D.	Mean	S.D.			Mean	S.D.	Mean	S.D.			Mean	S.D.	Mean	S.D.	
Ammodytes personatus	3	–20.3	0.1	9.8	0.0	2.9												
Anisarchus macrops							2	–19.5	0.4	11.4	0.3	3.4						
Arctoscopus japonicus							1	–20.8		10.7		3.2						
Banjos banjos													1	–17.1		11.5		3.3
Caranx equula													3	–19.5	0.3	11.7	0.3	3.3
Chelidoperca hirundinacea													1	–18.0		10.4		2.9
Clupea pallasii	3	–21.1	0.4	10.4	0.4	3.1												
Coelorhynchus longissimus													1	–18.0		10.6		3.0
Conger myriaster													3	–19.0	0.8	12.4	0.3	3.5
Dasycottus setiger							3	–19.0	0.4	11.8	0.8	3.5						
Foetorepus altivelis													1	–18.0		8.4		2.4
Gadus macrocephalus	2	–19.7	0.4	12.4	0.3	3.7	4	–19.7	0.7	12.5	0.6	3.7						
Glyptocephalus stelleri	3	–19.2	0.5	11.1	0.4	3.3	3	–18.9	0.5	11.3	0.2	3.3						
Halieutaea stellata													1	–17.1		12.1		3.4
Hemilepidotus gilberti	1	–18.8		12.7		3.8	1	–18.5		13.6		4.0						
Hemitripterus villosus	3	–19.4	0.4	12.7	0.2	3.8												
Hippoglossoides dubius	3	–19.9	0.5	11.3	0.1	3.4	3	–18.9	0.5	11.3	0.4	3.3						
Hoplichthys giberti													2	–18.2	0.5	9.3	0.2	2.6
Icelus cataphractus							3	–19.0	0.1	11.3	0.2	3.3						
Laeops kitaharae													1	–22.4		7.4		2.1
Lepidotrigla microptera													1	–18.0		11.2		3.2
Limanda schrencki													1	–18.0		10.5		3.0
Malakichthys wakiyae													3	–18.9	0.7	9.2	0.1	2.6
Pagrus major													2	–18.1	0.1	12.0	0.4	3.4
Pampus argenteus													1	–17.3		11.5		3.3
Plectranthias kelloggi azumanus													1	–18.1		10.8		3.0
Pleurogrammus azonus	3	–21.2	0.3	9.8	0.2	2.9												
Podothecus thompsoni							1	–18.3		12.8		3.8						
Psenopsis anomala													2	–17.9	1.0	11.6	0.8	3.3
Pseudorhombus cinnamoneus													3	–18.6	0.3	10.2	0.5	2.9
Pseudorhombus pentophthalmus													2	–17.6	0.1	11.5	0.2	3.3

Table 2.4. Continued.

Species name	St. A						St. B						St. C					
	n	$\delta^{13}C$		$\delta^{15}N$		TP	n	$\delta^{13}C$		$\delta^{15}N$		TP	n	$\delta^{13}C$		$\delta^{15}N$		TP
		Mean	S.D.	Mean	S.D.			Mean	S.D.	Mean	S.D.			Mean	S.D.	Mean	S.D.	
Scorpaenodes littoralis													1	–17.7		11.8		3.4
Sebastes owstoni	3	–20.9	0.4	11.1	0.2	3.3	1	–18.8		10.5		3.1						
Sphyraena pinguis													4	–17.0	0.2	13.2	0.3	3.8
Taurocottus bergi	3	–19.3	0.5	12.9	0.4	3.9												
Zenopsis nebulosa													2	–17.1	0.8	12.4	0.7	3.5
Zeus faber													2	–17.4	0.4	12.4	0.1	3.5
Euprymna morsei							1	–18.9		11.9		3.5						
Watasenia scintillans							2	–21.4	0.7	10.8	0.2	3.2						

Table 2.5. $\delta^{13}C$ and $\delta^{15}N$ values and trophic position (TP) of fish consumers collected at the St. A, St. B, and St. C during October 2020. Lower case codes indicate feeding modes (b, benthic feeder; bp, benthopelagic feeder; p, pelagic feeder). The lipid-correction was applied for the $\delta^{13}C$ of marked species (*). Data represent mean ± 1SD.

Species name	St. A						St. B						St. C					
	n	$\delta^{13}C$		$\delta^{15}N$		TP	n	$\delta^{13}C$		$\delta^{15}N$		TP	n	$\delta^{13}C$		$\delta^{15}N$		TP
		Mean	S.D.	Mean	S.D.			Mean	S.D.	Mean	S.D.			Mean	S.D.	Mean	S.D.	
Allolepis hollandi							2	–18.8	0.1	12.6	0.0	3.6						
Anoplagonus occidentalis	1	–19.8		11.1		3.2												
Argentina kagoshimae													6	–18.9	0.5	11.5	0.4	3.3
Ascoldia variegata	2	–18.9	0.3	13.4	0.4	3.9												
Aulopus japonicus													2	–18.2	0.3	11.0	0.0	3.1
Beringraja pulchra													1	–16.4		11.6		3.3
Caranx equula													4	–18.8	0.7	12.0	1.0	3.4
Ceratocottus diceraus diceraus	1	–18.0		12.7		3.7												
Chelidonichthys spinosus													1	–15.3		11.0		3.1
Chelidoperca hirundinacea													2	–18.1	0.0	11.1	0.4	3.2
Clupea pallasii	1	–20.0		11.4		3.3	4	–21.6	0.5	10.8	0.3	3.0						
Conger myriaster													2	–19.1	1.1	12.2	0.3	3.5
Cookeolus japonicus													1	–19.2		10.5		3.0
Cottiusculus gonez	1	–19.4		10.8		3.1	2	–19.3	0.6	11.4	0.0	3.2						
Dentex tumifrons													6	–17.9	0.4	12.3	0.3	3.5
Echelus uropterus													1	–16.8		11.9		3.4
Eopsetta grigorjewi													2	–17.5	0.4	11.0	0.2	3.1
Foetorepus altivelis													2	–18.3	0.7	9.3	0.2	2.6
Gadus macrocephalus	5	–19.7	0.5	11.6	1.4	3.4	5	–19.1	0.8	12.0	1.1	3.4						
Gymnocanthus herzensteini	2	–18.1	0.1	12.0	0.4	3.5	2	–18.1		12.7	0.5	3.6						
Hippoglossoides dubius							6	–18.7	0.4	11.3	0.3	3.2						
Hoplichthys giberti													2	–17.9	0.3	10.1	0.0	2.8
Hoplobrotula armata													1	–17.5		12.0		3.4
Hypsagonus quadricornis	1	–18.9		12.5		3.6												
Icelus cataphractus							6	–18.8	0.3	11.9	0.4	3.4						
Leiognathus nuchalis													2	–19.9	0.3	13.4	0.2	3.8
Lepidotrigla microptera													4	–18.2	0.5	11.1	0.2	3.2
Leptagonus leptorhynchus	3	–18.5	0.4	12.4	0.5	3.6	2	–18.0	0.1	12.9	0.0	3.7						
Liparis tessellatus							2	–20.0	0.6	10.7	0.4	3.0						
Lycodes nakamurae							2	–19.3	0.1	12.7	0.1	3.6						
Maurolicus muelleri							2	–22.0	0.6	10.8	0.7	3.0						
Monocentris japonica													1	–17.7		13.4		3.8
Ophius litulon													4	–17.4	0.5	12.8	0.2	3.6

Table 2.5. Continued.

Species name	St. A						St. B						St. C					
	n	$\delta^{13}C$		$\delta^{15}N$		TP	n	$\delta^{13}C$		$\delta^{15}N$		TP	n	$\delta^{13}C$		$\delta^{15}N$		TP
		Mean	S.D.	Mean	S.D.			Mean	S.D.	Mean	S.D.			Mean	S.D.	Mean	S.D.	
Petroschmidtia toyamensis							2	−18.2	0.5	12.7	0.1	3.6						
Podothecus thompsoni	4	−19.2	0.1	12.4	0.5	3.6	2	−18.1	0.1	13.0	0.5	3.7						
Psenopsis anomala													1	−19.1		11.8		3.4
Repomucenus ornatipinnis													1	−17.9		11.1		3.1
Saurida undosquamis													1	−18.9		13.8		3.9
Sebastes owstoni	2	−20.7	0.3	10.9	0.1	3.1												
Sebastiscus marmoratus													2	−16.9	0.4	11.0	0.4	3.1
Stichaeus grigorjewi							2	−19.2	0.3	13.0	0.2	3.7						
Synagrops philippinensis													4	−19.2	0.5	10.9	0.3	3.1
Synodus macrops													2	−18.2	0.1	11.3	0.0	3.2
Taurocottus bergi	1	−19.2		13.1		3.8	1	−18.3		13.3		3.8						
Thamnaconus modestus													2	−17.4	0.3	13.1	0.5	3.7
Trachurus japonicus													4	−19.2	0.4	11.8	0.4	3.4
Triglops jordani	1	−18.7		11.9		3.4	1	−18.5		11.8		3.4						
Upeneus japonicus													3	−18.4	0.9	11.2	0.6	3.2
Zalanyhias azumanus													1	−18.0		9.9		2.8
Zenopsis nebulosa													2	−17.7	0.5	11.7	0.5	3.3
Zeus faber													6	−16.7	0.7	12.8	0.9	3.7
Berryteuthis magister	1	−22.1		10.3		3.0												
Enteroctopus dofleini	4	−19.0	0.2	11.5	0.6	3.3												
Euprymna morsei	1	−18.7		12.0		3.5												
Loligo bleekeri													3	−19.2	0.2	10.8	0.1	3.1
Loligo beka													4	−18.2	0.7	12.0	0.4	3.4
Loligo japonica													2	−18.9	0.3	11.6	0.1	3.3
Octopus longispadiceus	1	−18.8		11.6		3.4												
Sepia esculenta													2	−18.0	0.0	10.1	0.1	2.9
Todarodes pacificus	4	−19.9	0.6	9.9	0.6	2.8												

2.3.4 Trophic positions and isotopic niche areas of fish assemblages

We calculated the TP value of each fish consumer based on the mean $\delta^{15}N$ value of calanoid copepods at each site in each season (Tables 2.4 and 2.5). In May, fish consumer TPs differed significantly among the three sites (Tukey's HSD test, $F_{2,\,90} = 4.31$, $p = 0.016$), ranging from 2.94 to 3.87, 3.08 to 3.99, and 2.05 to 3.76 at St. A, B, and C, respectively. In contrast, no significant differences were observed in the site TP values in October (Tukey's HSD test, $F_{2,\,162} = 1.22$, $p = 0.297$), which ranged from 2.84 to 3.89, 3.03 to 3.80, and 2.63 to 3.95 at St. A, B, and C, respectively.

The isotopic niche areas (‰^{2}) of fish assemblages at the three sites in the two seasons were estimated using the TA and SEAc values (Figure 2.3 and Table 2.5). In both seasons, the TA and SEAc values were relatively higher at the St. C (21.20 and 4.53 in May, and 17.92 and 3.03 in October, respectively) compared to those at St. A (6.13 and 2.35 in May, and 9.89 and 2.50 in October, respectively) and St. B (6.99 and 2.12 in May, and 7.54 and 2.56 in October, respectively).

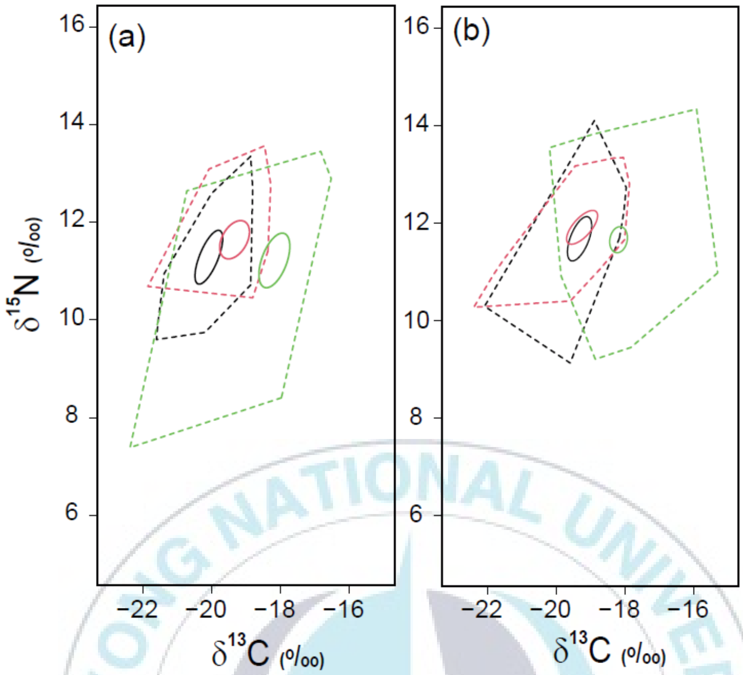


Figure 2.3. The isotopic niche areas (‰^{2}) of fish assemblages collected at the sampling sites (black lines, St. A; red lines, St. B; green lines, St. C) in May (a) and October (b) estimated as total area (TA, dotted line) and standard ellipse area (SEAc, solid line).

2.4 Discussion

The present study demonstrated the spatial and temporal variations in the trophic structure of fish assemblages in the East and South Seas of Korea by comparing their carbon and nitrogen stable isotope ratios and species compositions over two seasons. Our major results showed that the isotopic ratios of fish assemblages, with the food web base and dietary items, were spatially and seasonally variable. This reflects the regional-specific effects of oceanographic and geographical characteristics on the differences in the species composition and trophic structure between the two seas. Particularly, the presence of specific fish consumers due to differences in species composition may lead to spatial and seasonal variations in trophic structure reflecting the result of trophic niche indices. Information on the trophic dynamics of marine ecosystems under different environmental conditions can allow for a deeper understanding of climate-related changes in trophic diversity and community structure.

The fish communities in the East Sea and South Sea are generally known to have considerable differences in species composition and abundance, due to different environmental conditions (Jung et al., 2017). In the present study, the total composition and abundance of fish species collected from the sampling sites during the two seasons were similar to those previously reported in the East and South Seas of Korea (Han, 2003; Choi et al., 2012; Kang et al., 2014; Moon et al., 2015). In particular, clearly distinct dominant species between the two seas are among the most common characteristics of fisheries resources in Korean coastal waters, as reported in many studies (Han, 2003; Lee, 2011; Sohn et al., 2015; Song et al., 2019). The relatively high diversity of fish species in the South Sea (47 and 36 species recorded in May and

October, respectively) compared to those in the East Sea (12–16 and 19 species recorded in May and October, respectively) may be related to the unique environmental conditions created by complex interactions caused by the TWC input from the south and nutrient-enriched freshwater from major river systems of Seomjin, Nam, and Nakdong River (Moon et al., 2015). Also, fish communities in the East Sea are mostly comprised of resident and/or demersal fishes, such as the families Pleuronectidae and Cottidae, suggesting that certain biological characteristics occur only in the eastern coastal waters of the Korean peninsula rather than in the South Sea (Choi et al., 2012; Sohn et al., 2015).

Physical environmental changes may result in major temporal differences in the species composition and abundance of fish assemblages. The fish assemblages in the southern and eastern coastal waters of the Korean Peninsula may be substantially impacted by oceanographic conditions (e.g., seawater temperature and the thermal structure of the water mass) due to changes in the Kuroshio Current (Tian et al., 2006). In fact, (Kang et al., 2014) reported that the alteration in the oceanographic boundary of a thermal front could influence fish composition in mid-eastern coastal waters, related to the change in distribution of migratory pelagic species. Furthermore, the differences in seawater temperatures between the two seas may be the main factor causing the distinct species composition and abundance of fish assemblages. Because the range of seawater temperatures can directly or indirectly influence the life cycles (e.g., growth, reproduction, physiology, and behavior) of fish species, their spatial and seasonal variability may control the dynamics in fish communities and geographical inhabiting ranges (Stephens et al., 1988; Pankhurst and Munday, 2011). Thus, the spatial and seasonal variations in the composition and abundance of fish assemblages may be a feature of fish communities in Korean coastal waters, resulting from environmental changes in physical and trophic conditions affected by regional differences.

In the present study, despite the significant differences in the $\delta^{13}C$ and $\delta^{15}N$ of SPOM, little spatial and seasonal variations in the isotopic values were found in both cases (0.4–1.6‰ and 0.5–0.8‰, respectively). Spatial and seasonal variations in the $\delta^{13}C$ and $\delta^{15}N$ of SPOM may be influenced by changes in physical/chemical (e.g., water temperature and availability of dissolved inorganic carbon and nitrogen) and biological factors (e.g., phytoplankton taxonomic groups and their growth rates) under ambient environmental conditions (Cifuentes et al., 1988; Goering et al., 1990; Fry, 1990). Nevertheless, the $\delta^{13}C$ and $\delta^{15}N$ values of SPOM were consistent with previously reported ranges (–24 to –18‰ for $\delta^{13}C$ and 2–10‰ for $\delta^{15}N$) of general marine phytoplankton in coastal waters of the Korean peninsula and other temperate regions (Park et al., 2020; Fry and Sherr, 1984; Kang et al., 2009). The isotopic results suggest that organic matter derived from phytoplankton may be the most important source of the SPOM pool in both seas. In this respect, despite the statistical isotopic differences for zooplankton, their $\delta^{13}C$ and $\delta^{15}N$ values showed very similar patterns in spatial and seasonal variability (0.5–0.8‰ and 0.4–0.6 for copepods, and 0.8 and 0.6–0.7 for euphausiids, respectively) with those of SPOM as a food web baseline. Overall, our results suggest that the temporal isotopic trends of the trophic base line and lower trophic levels showed similar variability among the sampling sites during the two seasons.

Dual isotope plots for all sites in both seasons showed a notable pattern of increasing $\delta^{13}C$ and $\delta^{15}N$ values of fish species with increasing TPs due to the isotopic enrichment per trophic level. Regardless of sampling site, most fish species showed a continuum of $\delta^{13}C$ and $\delta^{15}N$ ranges along the TPs from the isotopic points of SPOM and zooplankton, suggesting that the trophic pathways may link phytoplankton-derived organic matter to fish assemblages. Additionally, based on the feeding zones classified by pelagic and benthic life patterns, demersal fishes generally exhibited higher $\delta^{13}C$ and $\delta^{15}N$ values than pelagic fishes. This result is consistent with those of several previous studies on greater ^{13}C- and ^{15}N-enrichments in benthic pathways than in pelagic pathways, suggesting the differentiation between benthic and pelagic food webs (Park et al., 2020; Davenport et al., 2002; Boyle et al., 2012). Indeed, such enriched ranges for $\delta^{13}C$ and $\delta^{15}N$ in fish species may be closely associated with the behavioral features of pelagic and benthic feeding strategies, and prey items along the trophic continuum, respectively. In terms of fish species trophic ecology, larger-sized individuals as predators or piscivores may generally tend to feed on large prey items, and thus are at the top of the $\delta^{13}C$–^{15}N dual isotope plot. In contrast, smaller fish species may feed mostly on invertebrates as preferred prey items compared to other fish individuals, reflecting their lower δ15N values. This size-dependent feeding pattern related to fish ecology of the present study is likely responsible for the position of fish species in the dual isotope plot, which reflects a general isotopic trend in common marine fish (Davenport et al., 2002; Galván et al., 2010).

Most fish species have a common characteristic of opportunistic feeding behavior, which is mainly influenced by ambient food availability (Elliott et al., 2007). In this regard, the spatial and seasonal patterns in the trophic structure of fish assemblages may be closely associated with the status of environmental conditions, which may lead to a dynamic utilization of available resources and diversity of prey items (Gay et al., 2017). Furthermore, the specific food web structure may be organized by a variety of trophic pathways involving many component species within the community. The spatial and seasonal variability in the species composition of communities may also be controlled by environmental factors (especially water temperature and food availability). Above all, because pelagic and migrating fish species may respond sensitively to ambient environmental conditions, the dynamics of pelagic trophic structures in coastal ecosystems can be clearly influenced by spatial and seasonal changes in species composition (Park et al., 2020). Therefore, the principal distinctions in the trophic structures of fish assemblages between the East Sea and the South Sea may be mainly induced by the differences in environmental factors, implying distinct prey availability for fish associated with the different oceanographic conditions discussed above.

Spatial and seasonal variability in the ecological and trophic niches of consumer species have been investigated using the isotopic niche parameters of TA and SEAc, allowing for the identification of intra- and interspecific competition for prey items, and spatiotemporal shifts in food web structure (Park et al., 2020; Layman et al., 2007; Rigolet et al., 2015). The ranges of isotopic niche areas are important for estimating the diversity of trophic pathways within a complicated ecosystem (Rigolet et al., 2015). In our study, during both seasons, the TA and SEAc of fish assemblages in the South Sea exhibited wider ranges than those in the East Sea. Such spatial differences in the isotopic niche areas may mostly result from the different environmental conditions and/or species compositions that can alter the trophic relationships within the community (Cherel et al., 2007; Włodarska-Kowalczuk et al., 2019). Our results also suggest that the spatial differences in the TA and SEAc may be associated with the regional distinction in the fish community interacting with different environmental conditions. In general, regional environmental differences, due to longitudinal and latitudinal changes in physical and chemical factors, are likely to alter the community components from low trophic organisms to top predators, and may therefore reflect the regional isotopic variation in the different prey-consumer relationships (Włodarska-Kowalczuk et al., 2019; Kingsbury et al., 2020). As a result, the site differences in the isotopic niche parameters are likely due to differences in the species composition of fish assemblages adapting to ambient environmental conditions with different levels of food availability.

In conclusion, our isotopic investigation of fish assemblages showed spatial differences in the food web structure and species composition between the East and South Seas of the Korean peninsula. Additionally, the difference in the isotopic niche parameters between the two seas suggests the distinction of trophic diversity of fish assemblages, coupled with the relative differences in abundance and population size of component species. Overall, our isotopic evidence implies that spatial and temporal variations in fish communities in response to changing environmental conditions (especially ocean warming) can alter the trophic relationships among species and the food web structure. Further long-term studies considering top-down and bottom-up trophic processes, based on community compositions of fish assemblages and their stable isotope ratios, are needed to better understand the functioning of coastal ecosystems under globally changing climate.

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

3.1 Introduction

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

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

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

The objective of this study was to describe the trophic ecology of the largehead hairtail in the South Sea of Korea. We explored changes in the dietary composition and TP of largehead hairtail across ontogeny and seasons based on stable isotope analysis and supplementary stomach content data. A combination of stable isotope and stomach content analyses has rarely been applied to this species (Hamaoka et al., 2014). In addition, most studies have investigated the feeding characteristics of *T. lepturus*, whereas information on the trophic ecology of *T. japonicus* is very limited (Mammel et al., 2022). To the best of our knowledge, this is the first study to identify the trophic ecology of the largehead hairtail that may play an important role in the marine food web of Korean coastal waters.

3.2 Materials and methods

3.2.1 Study Sites

Field surveys were performed on the continental shelf of the South Sea of the Korean Peninsula (Northern East China Sea, 33° 49´N, 127° 13´E) (Figure 3.1). The water temperature and salinity levels in the sampling site were obtained using a CTD (SBE 911 Plus, Seabird Electronics Inc., Bellevue, WA, USA). The sampling site had low tidal amplitude (less than 30 cm) and water depth of approximately 94–102 m. All specimens of largehead hairtail *T. japonicus* (a total of 422 individuals) and other fish were collected during February, May, August, and November 2021. Sampling was conducted using a trawl net (12 cm mesh in the main body, 8 cm mesh in the intermediate part, and 6 cm mesh in the cod end with a 2 cm cod end liner of the net) from a research vessel (R/V Tamgu 22) for over 30 min at 3 knots. The fishing depth for sampling ranged from 91.1 m to 98.2 m. The total length and weight of each individual was measured on board to the nearest 0.1 cm and 0.1 g, respectively. The collected fish samples were stored in a deep freezer (−60 °C) and transported to the laboratory. For the collection of dominant zooplankton groups, sampling was conducted through oblique towing on each occasion using a Bongo net (2.0 m^2 mouth opening, 500 μm mesh) equipped with a flowmeter. The collected zooplankton samples were frozen in 1 L polyethylene bottles in a deep freezer (−60 °C) for laboratory processing.

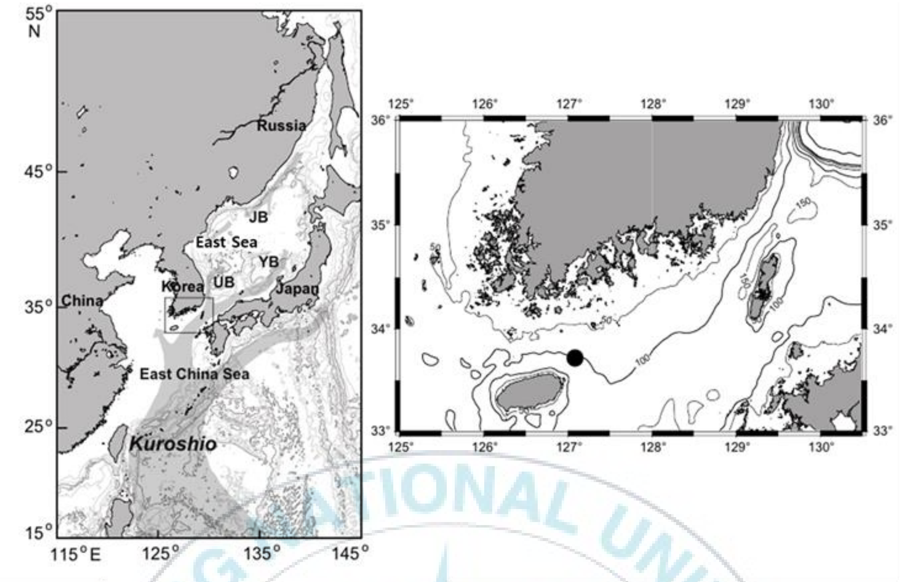


Figure 3.1. Map of the sampling area in the South Sea of Korea. Filled circle indicates the sampling site collected for zooplankton, large-head hairtail (*Trichiurus japonicus*), and other fishes.

3.2.2 Laboratory processing

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

3.2.3 Stomach content analysis

In the laboratory, the preserved stomach contents were identified to the lowest possible taxonomic level under a stereomicroscope (LEICA 12; Wetzlar, Germany). The wet weight of each food item was measured to the nearest 0.1 mg using an analytical balance (ME204TE/00; Mettler Toledo, Greifensee, Switzerland). Fresh and partially digested prey were used to reduce bias in the stomach content analysis. Food components were estimated by the percent frequency of occurrence (%F, number of stomachs in which a particular food item occurred as a percentage of the total number of stomachs examined), percent numerical frequency (%N) of each prey item to the total number of identifiable food items, and percent wet weight (%W) of each prey item to the total wet weight of the identifiable food items. An index of relative importance (IRI) for all food components was calculated for each prey type [$IRI = (\%N + \%W) \times \%F$] and expressed as a percentage (%IRI) as follows: $\%IRI = IRIi / \sum_{i=1}^{n} IRIi \; 100$ (Pinkas et al., 1971), where n is the total number of food components categorized as class levels. Size-related dietary changes were examined by dividing the largehead specimens into three size classes: <10 cm, 10–15 cm, and ≥15 cm, based on their anal lengths (ALs).

3.2.4 Stable isotope analysis

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

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

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

3.2.5 Data analysis

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

3.3 Results

3.3.1 Environmental conditions

The surface water temperature was lowest (16.2 °C) in February and highest

(27.6 °C) in August (Table 3.1). In contrast, during the four seasons, the bottom layer water temperature did not change much, ranging from 15.2 °C in August to 15.9 °C in February. The salinities in the surface layer varied between 30.6 in August and 34.8 in February. In the bottom layer, it was fairly constant (34.4 in August and 34.8 in February). Chlorophyll *a* concentrations of the surface water ranged from 0.8 μg/L in August to 1.2 μg/L in November.

Table 3.1. The environmental conditions (water temperature, salinity, and chlorophyll *a*) at the surface and bottom layers of the sampling site in the South Sea of Korea during February, May, August, and November 2021.

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

3.3.2 Dietary compositions

Of the 747 largehead hairtail stomachs sampled, 322 (43.1%) were empty. A total of 14 prey taxa groups were identified based on class (Figure 3.2). The diet of the largehead hairtail (based on IRI, %) consisted mainly of Pisces (1.6% in May to 84.8% in February) and Euphausiacea (3.0% in February to 93.0% in May) over the four seasons. The minor components of the stomach contents were Macrura (1.6% in May to 26.8% in November) and Amphipoda (0.1% in February to 7.4% in August). Size-related stomach compositions also showed that Pisces and Euphausiacea were preferred by the three AL groups (10 cm, 10–15 cm, and > 15 cm). While the small and mid-groups of largehead hairtails represented 5.5–93.4% and 22.1–94.6% for Pisces and 0–24.7% and 1.0–69.5% for Euphausiacea, respectively; the preferred prey composition of their largest group was 4.3 to 92.5% for Euphausiacea and 2.4 to 81.3% for Pisces.

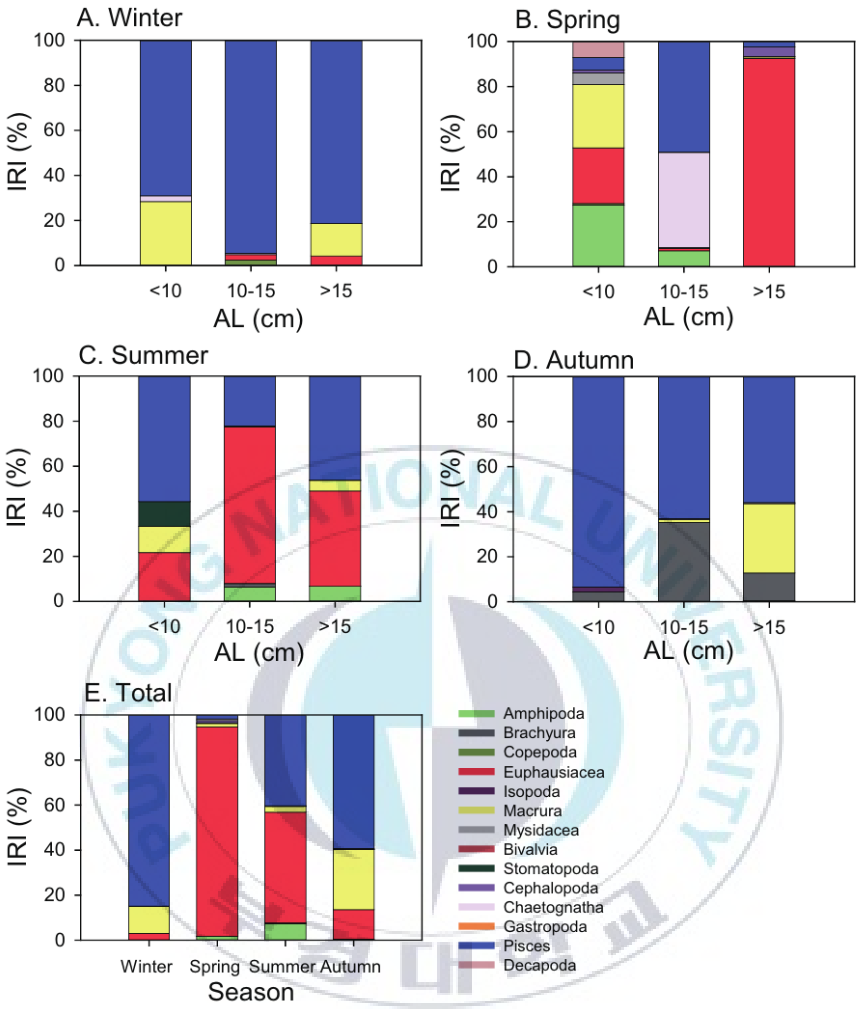


Figure 3.2. Size-related (anal length, AL; 10 cm, 10–15 cm, and > 15 cm) and total (E) compositions of the stomach contents of large-head hairtail (*Trichiurus japonicus*) by the index of relative importance (%IRI) expressed as a percentage of the sum of the IRI values in the South Sea of Korea during winter (A, February), spring (B, May), summer (C, August), and autumn (D, November) 2021.

3.3.3 Stable isotope ratios

3.3.3.1 Zooplankton

The δ^{13}C and δ^{15}N values of both zooplankton groups (calanoid copepods and euphausiids) differed significantly among the four seasons (PERMANOVA, pseudo-$F_{3, 48}$ = 12.29, p = 0.001 and pseudo-$F_{3, 35}$ = 9.36, p = 0.001, respectively) (Table 3.2). The mean δ^{13}C and δ^{15}N values of copepods ranged from −22.5 ± 0.5‰ (November) to −20.2 ± 1.2‰ (February) and from 6.4 ± 0.5‰ (February) to 8.0 ± 0.9‰ (August), respectively. The euphausiids showed mean δ^{13}C and δ^{15}N values of −21.3 ± 0.9‰ (May) to −20.4 ± 1.0‰ (February) and 6.1 ± 0.6‰ (November) to 8.5 ± 0.9‰ (August), respectively.

Table 3.2. $\delta^{13}C$ and $\delta^{15}N$ values of zooplankton (calanoid copepods and euphausiids) collected during February, May, August, and November 2021 in the South Sea of Korea. PERMANOVA test of $\delta^{13}C$ and $\delta^{15}N$ values for each zooplankton among seasons. Bold-face font indicates significance at $p < 0.05$. Data represent mean ± 1SD.

Zooplankton	February					May					August					September					PERMANOVA	
		$\delta^{13}C$		$\delta^{15}N$			$\delta^{13}C$		$\delta^{15}N$			$\delta^{13}C$		$\delta^{15}N$			$\delta^{13}C$		$\delta^{15}N$		pseudo-*F*	*p*
	n	Mean	SD	Mean	SD	n	Mean	SD	Mean	SD	n	Mean	SD	Mean	SD	n	Mean	SD	Mean	SD		
Copepods	12	–20.2	1.2	6.4	0.5	18	–22.1	1.1	7.4	0.5	10	–21.3	1.0	8.0	0.9	9	–22.5	0.5	7.5	0.6	12.29	**0.001**
Euphausiids	7	–20.4	1.0	7.1	0.8	13	–21.3	1.1	6.7	0.6	8	–20.5	0.8	8.5	1.0	8	–21.2	0.4	6.1	0.6	9.36	**0.001**

3.3.3.2 Largehead hairtail

Largehead hairtails of 18 (August) to 37 (November) individuals were prepared for stable isotope analysis during the four seasons (Figure 3.3). Seasonal variations were observed in $\delta^{13}C$ and $\delta^{15}N$ values of the largehead hairtail (pseudo-$F_{3,94} = 9.03$, $p = 0.001$). The $\delta^{13}C$ values of largehead hairtail ranged from −19.8 ± 0.8‰ (May) to −18.2 ± 0.3‰ (August), whereas the $\delta^{15}N$ values varied between 10.8 ± 0.7‰ (May) and 11.3 ± 1.2‰ (February). The TPs of largehead hairtails, calculated based on the lowest $\delta^{15}N$ values of zooplankton, showed significant differences among seasons (Tukey's HSD test, $p < 0.01$), ranging from 2.8 ± 0.2 in August to 3.5 ± 0.2 in November.

There were significant differences in the mean ALs of analyzed largehead hairtails among seasons (one-way ANOVA, $p = 0.001$), ranging from 11.6 ± 4.0 cm (5.8 to 19.3 cm in February) to 17.9 ± 7.3 cm (6.8 to 28.4 cm in May). The $\delta^{13}C$ values in May decreased significantly with AL ($r^2 = 0.594$, $p < 0.001$), whereas there were no significant correlations between ALs and $\delta^{13}C$ in February, August, and November ($r^2 = 0.033$, $p = 0.461$; $r^2 = 0.002$, $p = 0.929$; $r^2 = 0.006$, $p = 0.147$, respectively; Figure 3.4). In contrast, significant positive relationships were found between ALs and $\delta^{15}N$ in May, August, and November ($r^2 = 0.441$, $p = 0.002$; $r^2 = 0.244$, $p = 0.033$; $r^2 = 0.420$, $p < 0.001$, respectively). However, in February, there was no significant relationship between the AL and $\delta^{15}N$ ($r^2 = 0.115$, $p = 0.148$).

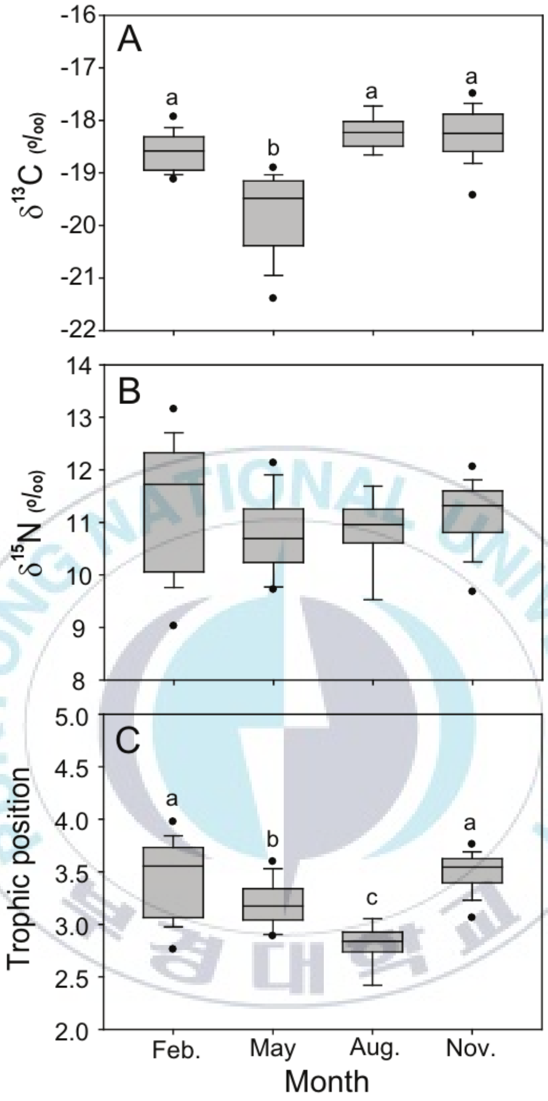


Figure 3.3. $\delta^{13}C$ (A), $\delta^{15}N$ (B), and trophic position (TP, C) values of large-head hairtail (*Trichiurus japonicus*) collected in the South Sea of Korea during February (Feb.), May, August (Aug.), and November (Nov.) 2021. One-way ANOVA and mean values of $\delta^{13}C$, $\delta^{15}N$, and TP values for large-head hairtail among four months.

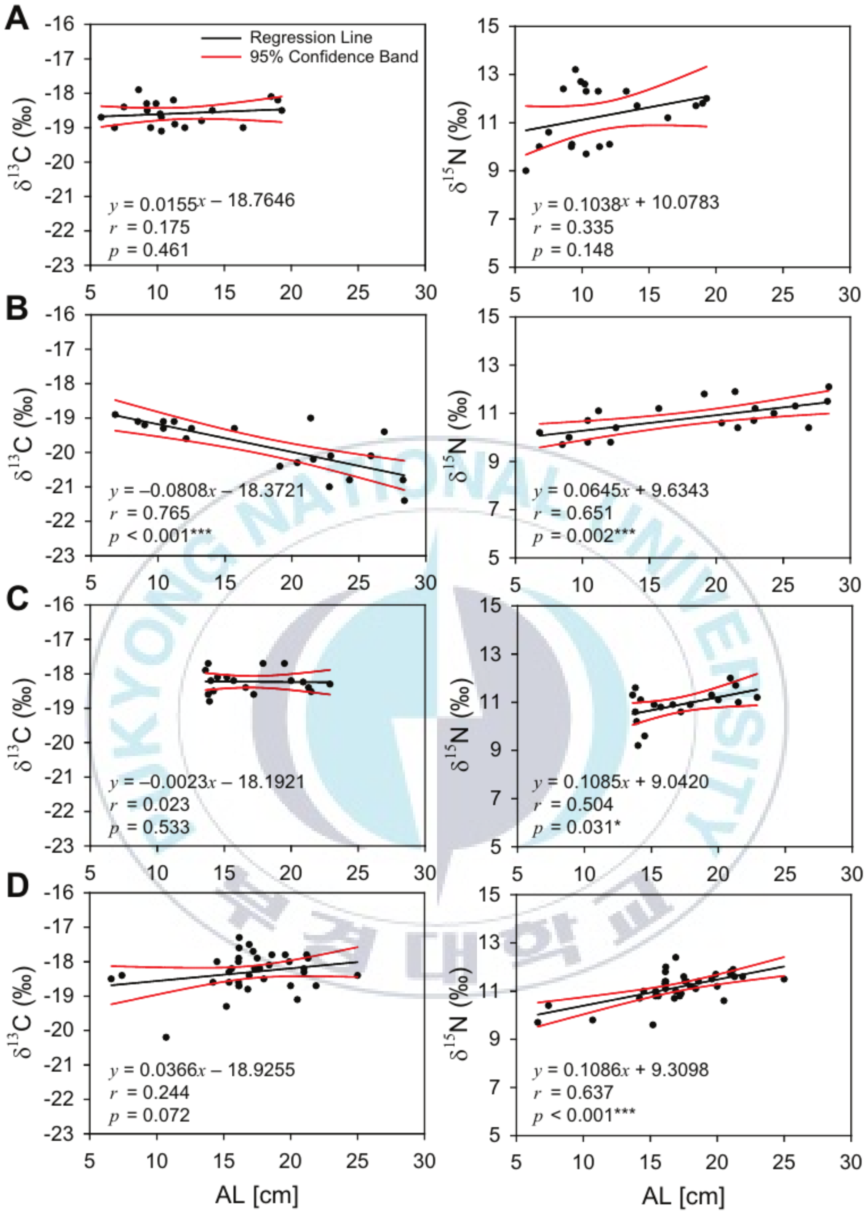


Figure 3.4. Regression relationships between δ^{13}C – anal length (cm, left) and δ^{15}N – anal length (cm, right) of large-head hairtail (*Trichiurus japonicus*) collected in the South Sea of Korea during February (A), May (B), August (C), and November (D) 2021.

3.3.3.3 Dual isotope plot for largehead hairtail and other fish consumers

Dual isotope plots for all fish consumers showed variable ranges of δ^{13}C and δ^{15}N values (Figure 3.5 and Table 3.3), which were significantly different among the seasons (PERMANOVA, pseudo-$F_{3,\ 179}$ = 7.52, p = 0.001). The range of δ^{13}C values of fish consumers during February (–21.8‰ to –16.6 ± 0.4‰) and May (–20.8‰ to –17.3 ± 0.3‰) were broader than those during August (–19.4‰ to –17.4 ± 0.2‰) and November (–18.6 ± 0.4‰ to –16.6 ± 0.2‰). Similarly, relatively wide ranges were observed for δ^{15}N values during February (8.8‰ to 13.8 ± 0.7‰) and May (9.5‰ to 13.3 ± 0.4‰) compared with those during August (9.6‰ to 12.3 ± 0.2‰) and November (10.1‰ to 12.6 ± 0.3‰). The mean TP values of fish consumers (except for largehead hairtail) differed significantly among seasons (Tukey's HSD test, $p < 0.01$), ranging from 2.90 ± 0.2 in August (2.46 − 3.27) to 3.59 ± 0.2 in November (3.20 − 3.93). Overall, the largehead hairtails showed intermediate δ^{13}C and δ^{15}N positions in the dual isotope plots during all seasons.

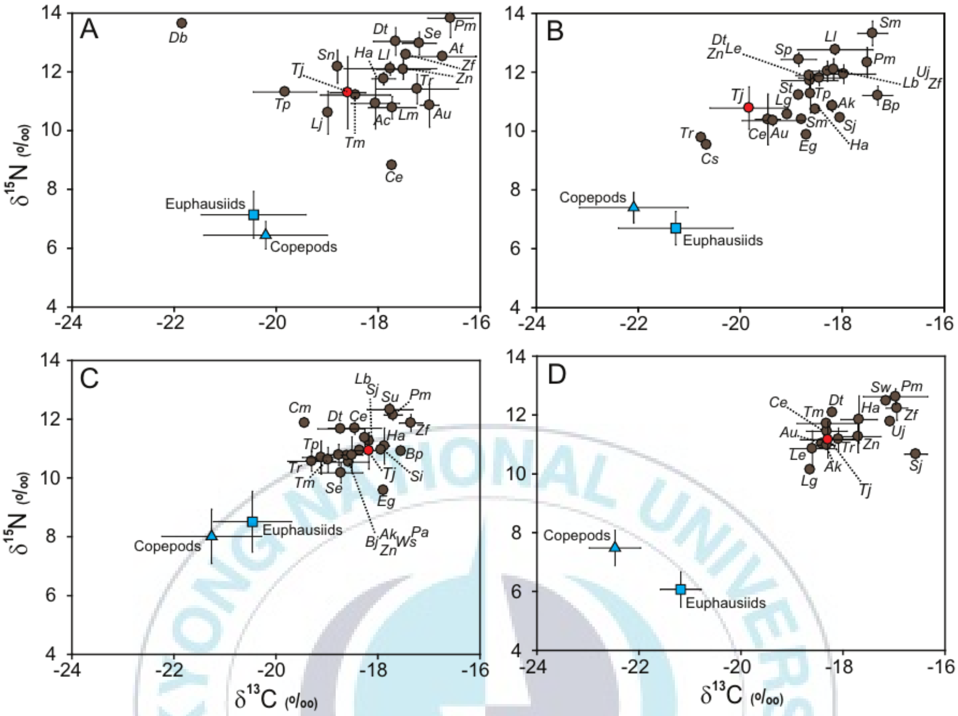


Figure 3.5. Dual isotope plots of $\delta^{13}C$ and $\delta^{15}N$ values of zooplankton (blue squares, euphausiids; blue triangles, copepods), large-head hairtail (red circles, *Trichiurus japonicus*), and other fishes (gray circles) in the South Sea of Korea during February (A), May (B), August (C), and November (D) 2021. Values are presented as mean $\delta^{13}C$ and $\delta^{15}N$ (‰ ± 1 SD).

Table 3.3. $\delta^{13}C$ and $\delta^{15}N$ values and trophic position (TP) of large-head hairtail *Trichiurus japonicus* and other fish consumers collected during February, May, August, and November 2021 in the South Sea of Korea. Data represent mean ± 1SD.

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

Table 3.3. Continued.

Month	Species name	Code	n	$\delta^{13}C$		$\delta^{15}N$		TP
				Mean	S.D.	Mean	S.D.	
August	***Trichiurus japonicus***	Tj	18	−18.2	0.3	10.9	0.6	2.82
	Argentina kagoshimae	Ak	1	−18.6		10.8		2.81
	Beringraja pulchra	Bp	1	−17.5		10.9		2.85
	Branchiostegus japonicus	Bj	3	−18.8	0.2	10.8	0.4	2.82
	Caranx equula	Ce	3	−18.5	0.5	11.7	0.2	3.08
	Conger myriaster	Cm	1	−19.4		11.9		3.13
	Dentex tumifrons	Dt	3	−18.7	0.4	11.7	0.1	3.08
	Eopsetta grigorjewi	Eg	1	−17.9		9.6		2.46
	Hoplobrotula armata	Ha	3	−17.9	0.1	11.1	0.6	2.90
	Loligo bleekeri	Lb	3	−18.3	0.1	11.4	0.3	2.99
	Pagrus major	Pm	3	−17.7	0.2	12.1	0.2	3.21
	Psenopsis anomala	Pa	1	−18.4		10.9		2.86
	Saurida undosquamis	Su	3	−17.8	0.4	12.3	0.2	3.27
	Scorpaena izensis	Si	1	−17.9		11.0		2.87
	Sepia esculenta	Se	3	−18.7	0.4	10.2	0.3	2.64
	Sepiella japonica	Sj	1	−18.2		11.3		2.95
	Thamnaconus modestus	Tm	3	−19.0	0.1	10.6	0.4	2.77
	Todarodes pacificus	Tp	3	−19.1	0.4	10.7	0.6	2.79
	Trachurus japonicus	Tr	3	−19.3	0.5	10.6	0.3	2.75
	Watasenia scintillans	Ws	3	−18.5	0.2	10.8	0.6	2.81
	Zenopsis nebulosa	Zn	3	−18.6	0.4	10.5	0.0	2.74
	Zeus faber	Zf	3	−17.4	0.2	11.9	0.3	3.13
November	***Trichiurus japonicus***	Tj	37	−18.3	0.5	11.2	0.6	3.50
	Argentina kagoshimae	Ak	3	−18.3	0.2	11.0	0.0	3.44
	Aulopus japonicus	Au	1	−18.4		11.0		3.46
	Caranx equula	Ce	3	−18.3	0.4	11.4	0.2	3.58
	Dentex tumifrons	Dt	3	−18.2	0.0	12.1	0.1	3.77
	Hoplobrotula armata	Ha	3	−17.7	0.4	11.8	0.8	3.70
	Lepidotrigla guentheri	Lg	1	−18.6		10.1		3.20
	Loligo edulis	Le	3	−18.6	0.4	10.9	0.6	3.41
	Pagrus major	Pm	5	−17.0	0.6	12.6	0.3	3.93
	Saurida wanieso	Sw	1	−17.2		12.5		3.89
	Scomber japonicus	Sj	3	−16.6	0.2	10.7	0.1	3.35
	Thamnaconus modestus	Tm	3	−18.3	0.6	11.7	0.0	3.66
	Trachurus japonicus	Tr	3	−18.1	0.3	11.2	0.4	3.50
	Upeneus japonicus	Uj	1	−17.1		11.8		3.68
	Zenopsis nebulosa	Zn	6	−17.7	0.4	11.3	0.6	3.53
	Zeus faber	Zf	10	−16.9	0.2	12.2	0.4	3.81

3.4 Discussion

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

3.4.1 Seasonal effects on the dietary compositions of largehead hairtail

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

In this study, stable isotope analysis revealed seasonal changes in the feeding ecology of largehead hairtail. Significant seasonal differences in the δ^{13}C and δ^{15}N values of the largehead hairtail suggest that its diet is flexible. Hairtails and largehead hairtails inhabiting the East Asian Marginal Seas are generally known to exhibit different spatiotemporal feeding habits due to differences in reliance on pelagic and benthic production, mainly through consuming pelagic and benthic fishes and *Eupausia pacifica* (Yan et al., 2011; Hamaoka et al., 2014). Several studies have reported that consumer species commonly discriminate isotopically between benthic and pelagic food webs, as shown by a higher number of ^{13}C- and ^{15}N-enriched benthic species than pelagic feeders (Davenport and Bax, 2002; Boyle et al., 2012; Park et al., 2020). Benthic consumers may display an increasing tendency of δ^{13}C and δ^{15}N values with increasing depth due to the biogeochemical process of sinking phytoplankton-derived organic matter as the basal nutritional source supporting benthic food webs (Polunin et al, 2001; Park et al., 2018). The relatively lower $\delta^{13}C$ values of the largehead hairtail in spring compared with those in other seasons were closely related to the higher reliance on pelagic production. These results were supported by the increased contribution of Euphausiacea to the diet of hairtails, as estimated by stomach content analysis. Furthermore, although hairtails are generally known as top predators, their relatively lower $\delta^{15}N$ values than those of other carnivorous fishes were likely related to the higher contribution of pelagic sources to their diets. Dual isotope plots of fish consumers showed that hairtails had intermediate positions between pelagic and benthic fishes and was more ^{13}C and ^{15}N-depleted than other large carnivorous fishes. Thus, these results suggest that largehead hairtails may feed on both pelagic and benthic dietary sources and dietary items with a pelagic source affinity (Le Loc'h et al., 2008).

3.4.2 Size-related dietary compositions of largehead hairtail

Our isotopic results revealed a significant positive relationship between ALs and $\delta^{15}N$ values of largehead hairtails, coinciding with higher $\delta^{15}N$ values in larger individuals, except in February. Since higher $\delta^{15}N$ values of carnivorous consumers are closely related to larger and higher TP dietary items, such ontogenetic dietary shifts are likely to be a general trend in the feeding characteristics of common fish species (Link and Garrison, 2002; Graham et al., 2007). The ecological function of increasing fish body and mouth size can allow individuals to capture a wider range of prey sizes and types for energy optimization (Gerking, 1994). Studies of the hairtail species *T. margarites*, *T. lepturus*, and *T. japonicus* show that with growth-related increasing body length, noticeable ontogenetic dietary changes have been observed by increasing the consumption of larger prey items (Yan et al., 2011; Mammel et al., 2022).

However, except in May, the $\delta^{13}C$ values of largehead hairtails in our study did not reflect isotopic changes with body size. This result suggests that they may feed on similar dietary sources among size classes and that their dietary overlap may be relatively high. Although many fish species tend to have the potential for resource and trophic niche partitioning because of differences in their size-dependent distribution depths and feeding behaviors, no correlations in the $\delta^{13}C$ values among size classes of largehead hairtails were inconsistent with the stable isotope and/or stomach content results indicated by several previous studies (Pinnegar and Polunin, 2000; Bode et al., 2004; Collins et al., 2005; Park et al., 2018). This tendency may increase intraspecific competition and cannibalism of feeding behavior for largehead hairtails, with no size-dependent patterns in resource use. Cannibalism has been reported as a general phenomenon in the hairtail species in coastal waters to efficiently control population stock and species abundance (Lin et al., 2005; Yan et al., 2012; Mammel et al., 2022). However, in our study, such cannibalism was not observed in any size class during the stomach contents analysis of largehead hairtails (Chiou et al., 2006).

Interestingly, the significant negative correlation between the size and $\delta^{13}C$ of largehead hairtails in May could disagree with the observations of common fishes that can feed on a variety of food types through opportunistic strategies by enhanced prey-catchability with growth (Le Loc'h et al., 2008; Boyle et al., 2012). Moreover, for some fish species, larger individuals may generally inhabit deeper waters than smaller individuals, to divide habitats and dietary resources (Adin and Mueter, 2007; Park et al., 2018). The enhanced swimming ability of largeheads with growth may allow large individuals to feed on pelagic fishes rather than on dominant zooplankton groups (Yan et al., 2011). However, the high contribution (approximately 93%) of Euphausiacea to the diet of the largest group (AL, > 15 cm) in May, observed by stomach content analysis, may support our isotopic results. Such a large proportion of Euphausiacea as a food source for largehead hairtails may result in a relationship that has lower $\delta^{13}C$ values compared with the smaller groups and other benthic/benthopelagic feeders. In addition, the relatively high contribution and low diversity of Euphausiacea as a dietary source during a specific season can be explained by food availability due to their dense patch distribution (Martins et al., 2005), leading to a tight connection between pelagic prey sources and large individuals. Thus, despite the seasonal variability of prey composition and isotope values for largehead hairtails, Euphausiacea may be its most important dietary component in the South Sea of Korea.

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

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

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

IV. Feeding ecology of common squid *Todarodes pacificus* in the South Sea of Korea determined through stable isotope and stomach content analyses

4.1 Introduction

Squids, which are widely distributed throughout most marine systems worldwide, comprise approximately 300 species characterized by pronounced differences in biological and ecological traits and habitat preferences (Clarke, 1996; Navarro et al., 2013). In general, squids are ecologically important organisms in marine communities, within which they constitute a predominant group, owing to their high biomass, and represent a major prey resource for marine predators, including fishes, seabirds, and mammals (Clarke, 1996; Lordan et al., 1998). Squids are active predators that feed on a diverse range of prey types, including zooplankton, crustaceans, cephalopods, and fishes, which they capture via different predatory behaviors, ambushing, stalking, and pursuit, and can thereby play an important role in marine food webs (Takai et al., 2000; Cherel and Hobson, 2005; Ibáñez et al., 2008; Leite et al., 2009; Ibáñez et al., 2021). Most squids are characterized by high feeding rates, which are necessary in maintaining the high metabolic and growth rates associated with their short lifespans of approximately 1 or 2 years (Boyle and Rodhouse, 2006). Given their ecological characteristics, squids have attracted considerable attention as potential beneficiaries in the future changing oceans and/or indicators of the impacts of climate change on marine systems (Dawe et al., 2000; Coll et al., 2013; Stewart et al., 2014). Consequently, it is important to understand the ecological roles played by squid populations in marine systems, particularly their feeding ecology, dietary composition, ontogenetic dietary changes, and feeding behaviors.

The common squid *Todarodes pacificus* (Ommastrephidae) is among the predominant species comprising epipelagic communities in the South and East Seas of Korea and the East China Sea (Hwang et al., 2012; Sakurai et al., 2013). In Korean waters, the total catch of *T. pacificus* as a warm-water species underwent a rapid increase after the late 1980s, which is assumed to be associated with the general response of marine ecosystems to shifts in the climatic regime (Jung et al., 2017). Furthermore, this squid is a commercially important species, accounting for more than 10% of the total catch obtained by the Korean fishery industry (KOSIS, 2019). It is a generalist predator that typically feeds on zooplankton and small pelagic fish (Lee et al., 2019). Similar to other Ommastrephidae squids, *T. pacificus* undergoes ontogenetic dietary changes from crustaceans (e.g., copepods, amphipods, and euphausiids) in juveniles (< 50 mm mantle length, ML) to crustaceans and fish in middle-sized individuals (50–99 mm ML), fish in adult-sized individuals (100–150 mm ML), and fish and squid in the largest individuals (> 150 mm ML), as assessed via stomach content analyses (Sakurai et al., 2013; Uchikawa and Kidokoro, 2014). *T. pacificus* exhibits a wide prey spectrum, including cannibalism, which varies among regions and is dependent on the availability of the prey (Sakurai et al., 2013). Nevertheless, despite the acknowledged ecological importance of *T. pacificus*, studies of its feeding ecology are notably limited. Given its increasing commercial value as a fishery resource, information on the trophic ecology of the common squid is essential for successful fishery management and conservation in rapidly changing oceanic environments.

A stomach content analysis has conventionally been used to assess the feeding ecology and quantify the dietary composition of marine organisms, including cephalopods (Ibáñez et al., 2021; Nixon, 1987; Buckland et al., 2017). However, given several limitations associated with digested, unidentifiable, or absent dietary items in the stomachs of consumers and differences in digestibility dietary components, this approach may present problems with respect to identification, quantification, and interpretation (Ibáñez et al., 2008; Deb, 1997; Wang et al., 2022). To overcome such drawbacks, an analysis of the stable isotopes of carbon and nitrogen has been used as a complementary approach for analyzing the stomach contents to identify assimilated dietary items among available food sources and determine the structure of food webs in marine ecosystems (Davenport and Bax, 2002; Layman et al., 2012; Park et al., 2020). Carbon stable isotope ratios ($\delta^{13}C$) generally increase from the diet to consumer at an enrichment of approximately 1.0‰ and have been used to infer dietary sources (DeNiro and Epstein, 1978). In contrast, nitrogen stable isotope ratios ($\delta^{15}N$) can significantly increase by 2–4‰ from prey to predator, thereby generally providing information on the trophic position (TP) of the consumer species (Minagawa and Wada, 1984; Post, 2002). Recently, the combined application of stable isotope and stomach content analyses has been successfully adopted to provide insights into the feeding habits and ontogenetic dietary shifts of various fish species and cephalopods (Ruiz-Cooley et al., 2006; Santos et al., 2013; Merten et al., 2017; Park et al., 2018).

In this study, based on a combined analysis of stable isotopes and stomach contents, we sought to assess the trophic ecology of *T. pacificus* in the South Sea of Korea, which, as the predominant species, may play a significant ecological role in the marine food web of coastal waters. Specifically, to assess dietary composition, TP, and ontogenetic dietary shifts, we analyzed $\delta^{13}C$ and $\delta^{15}N$ concentrations in the muscle tissues of common squid and the stomach contents of specimens in different body size classes during different seasons in the South Sea of Korea. As a primary approach for common squid collected in Korean coastal waters and a useful tool for investigating the dietary characteristics of cephalopods, a combination of stable isotope and stomach content analyses can be expected to reflect the trophic role of common squid in the marine food web and its feeding ecology during ontogeny.

4.2 Materials and methods

4.2.1 Study area and sample collection

For the study, we collected samples at four sampling sites in the subtidal zone off the southern part of the Korean Peninsula (#104: 34° 25´ N, 127° 75´ E; #106: 34° 25´N, 128° 75´E; #111: 33° 75´N, 128° 75´E; #224: 33° 75´N, 127° 25´E) in February, May, and August 2021 (Figure 4.1). The water depth at the sampling sites ranged from 83 to 123 m, with a low tidal amplitude less than 30 cm. Samples of all fish and zooplankton species were collected from the Tamgu 20 (885 t) and Tamgu 22 (1,458 t) research vessels of the Fisheries Resources Research Center of the National Institute of Fisheries Science (NIFS). Fish samples were collected by trawl surveys (12 cm mesh in the main body, 8 cm mesh in the intermediate part, and 6 cm mesh in the cod end with a 2 cm cod end liner), and zooplankton samples were collected using a Bongo net (2.0 m^2

mouth opening, 500 μm mesh). For fish samples, biological parameters, including total length (to the nearest 0.1 cm) and biomass (to the nearest 0.1 g) of each individual were gauged onboard. All collected fish and zooplankton samples were initially stored in a freezer (−20 °C) and then transported to the laboratory for processing.

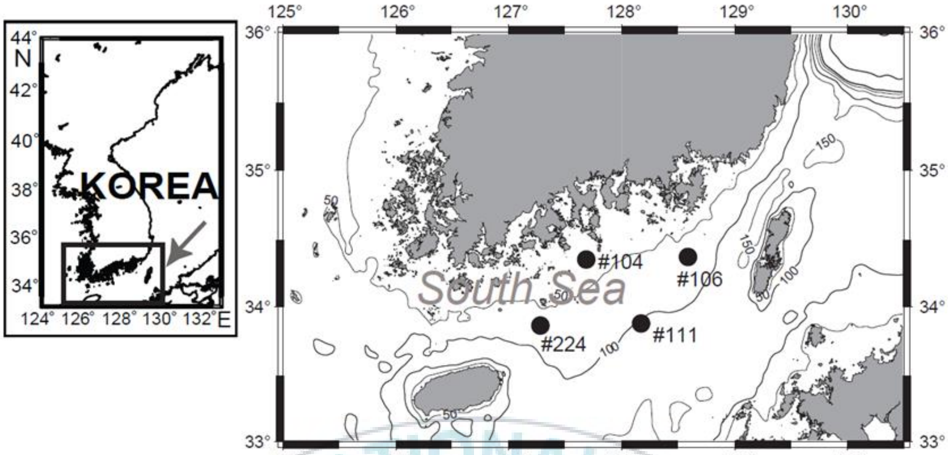


Figure 4.1. Map of the sampling areas in the southern sea of Korea. Filled circles indicate the four sampling sites (#104, #106, #111, and #224) at which zooplankton, common squid *Todarodes pacificus* and other fish consumers were collected.

4.2.2 Sample processing

In the laboratory, all sampled fish and common squid were dissected, and muscle tissues were collected from the anterior dorsal parts for stable isotope analysis. Whole body samples were prepared for the stable isotope analysis of dominant zooplankton, including copepods and euphausiids. All prepared samples were freeze-dried, ground into a homogenous powder using a ball mill, and stored in a vacuum desiccator until further analyses. Common squid stomach samples were collected and individually preserved in 10% formalin for further analyses, as described below.

4.2.3 Stomach content analysis

During the sampling period, a total of 701 *T. pacificus* individuals were collected; among which, the stomachs of 233 were sampled for content analysis. Each stomach sample was examined using LEICA L2 stereomicroscope (Leica Microsystems, Wetzlar, Germany), and prey items were counted and categorized to the lowest possible taxonomic level. The wet weight of each item was measured to the nearest 0.0001 g using an analytical balance (ME204TE/00; Mettler Toledo, Greifensee, Switzerland). Given the uncertainty and biases associated with the estimates of cephalopod dietary compositions obtained using the index of relative importance (IRI), we applied a ranking index (RI) in this study (Ibáñez et al., 2008; Ibáñez et al., 2021). Food items in the stomachs of common squids were assessed based on the percentage frequency of occurrence (%*F*), which is the number of stomachs in which a particular food item occurs (as a percentage of the total number of examined stomachs), and percentage wet weight (%*W*) of each food item to the total wet weight of the identifiable food items.

RI values were estimated for all food items of each prey type [$RI = \%W \times \%F$] and expressed as a percentage (%RI) as follows: $\%RI = RIi/\sum_{i=1}^{n} RIi\ 100$ (Hobson, 1974), where n is the total number of food items categorized as class levels. Size-related ontogenetic dietary changes in common squids were examined using the three size classes: <10, 10–20, and ≥20 cm ML.

4.2.4 Stable isotope analyses

Small quantities (0.5–1.0 mg) of the powered samples were weighed into tin combustion capsules. All encapsulated samples were combusted at high temperature (1,020 °C) using a CNSOH elemental analyzer (EA Isolink, Bremen, Germany), and the resulting gas was analyzed for carbon and nitrogen stable isotope ratios using a continuous-flow isotope ratio mass spectrometer (CF-IRMS: DELTA V PLUS, Bremen, Germany). The carbon and nitrogen isotope ratios are expressed in delta (δ) notation as a difference from the respective conventional standard (Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen) as follows: $\delta X\ (‰) = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 10^3$, where X is ^{13}C or ^{15}N, and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. To calibrate the analyzed isotope values, we obtained the international standard values of sucrose (ANU $C_{12}H_{22}O_{11}$; NIST, Gaithersburg, MD, USA) and ammonium sulfate ($[NH_4]_2SO_4$; NIST) after measuring each group of 10 samples. The analytical reproducibility, based on 20 urea replicates, was within 0.11‰ and 0.15‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Lipids are generally highly abundant in fish, which can lead to a bias in $\delta^{13}C$ values estimates. If the mass ratio of carbon to nitrogen (C/N) for fish species exceeded 3.5, it is considered to be attributable to a reduction in the $\delta^{13}C$ value owing to ^{12}C enrichment, and in this case, we applied lipid correction (non-lipid extracted) according to Post et al. (Post et al., 2007). The lipid correction formula for non-lipid extracted samples was as follows: $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C{:}N\ (ratios)$, where $\delta^{13}C_{untreated}$ and $\delta^{13}C_{normalized}$ are the measured and lipid correction δ^{13}C values of the non-lipid extracted sample, respectively.

The TP values of consumer species were calculated according to the following formula: $TP_i = (\delta^{15}N_i - \delta^{15}N_{baseline})/\Delta^{15}N + 2$, where $\delta^{15}N_i$ represents the δ^{15}N value of each target consumer, $\delta^{15}N_{baseline}$ is the mean δ^{15}N of baseline organisms (copepod group) selected in this study, $\Delta^{15}N$ is the nitrogen enrichment factor of 3.4‰ in δ^{15}N, and 2 represents the baseline TP (Minagawa and Wada, 1984; Post, 2002).

4.2.5 Data analyses

All data were initially assessed for normality (Shapiro–Wilk test) and homogeneity of variance (Levene's test) prior to further statistical analyses using the R software (R Core Team, Vienna, Austria, 2016). A permutational multivariate analysis of variance (PERMANOVA) using PRIMER version 6 + PRIMER add-on (PRIMER-e, Auckland, New Zealand) was used to compare seasonal differences in the δ^{13}C and δ^{15}N values of common squid and other consumer species (zooplankton and fish). A one-way analysis of variance (ANOVA, San Francisco, CA, USA) with Tukey's honest significant difference (HSD) multiple-comparison *post hoc* test in R software was performed to compare stable isotope and TP values of consumer species and MLs of common squids. A linear regression analysis was performed using the R software to assess the size-based trophic relationship between ML and stable isotope values (δ^{13}C and $\delta^{15}N$) in common squid. Moreover, dietary compositions were assessed based on a detrended correspondence analysis (DCA) using the R program, which visually depicts the relationship between samples and species in a reduced space (Ibáñez et al., 2021; Jongman et al., 1995).

4.3 Results

4.3.1 Dietary compositions: relative importance (RI)

Among the stomachs of the 701 common squids was examined; 468 stomachs were found to be empty, whereas the contents of the remaining stomachs comprised prey from eight groups, as examined based on class (Figure 4.2). Regardless of season, Pisces (37.9% in August to 94.0% in February) and Cephalopoda (6.0% in February to 61.0% in August) contributed the largest proportions of the stomach contents of common squid. An analysis of size-related stomach contents based on ML (<10, 10–20, and >20 cm) also revealed major components of Pisces and Cephalopoda to be the major constituents. However, among squids in the ML <10 cm group, the stomach contents of specimens collected in August comprised primarily Crustacea (95.5%), whereas Pisces and Cephalopoda were found to be minor components (2.3 and 2.2%, respectively).

The arrangement of *T. pacificus* and its dietary items based on DCA ordination yielded eigenvalues of $\lambda_1 = 0.928$, $\lambda_2 = 0.221$, and $\lambda_3 = 0.138$ for the first composition gradients (Figure 4.3). The smallest individuals of common squid collected in August were associated with Crustacea, whereas the other groups were plotted in the vicinity of Pisces in February, that of Stomatopoda and Salpida in May, and that of Brachyura in August.

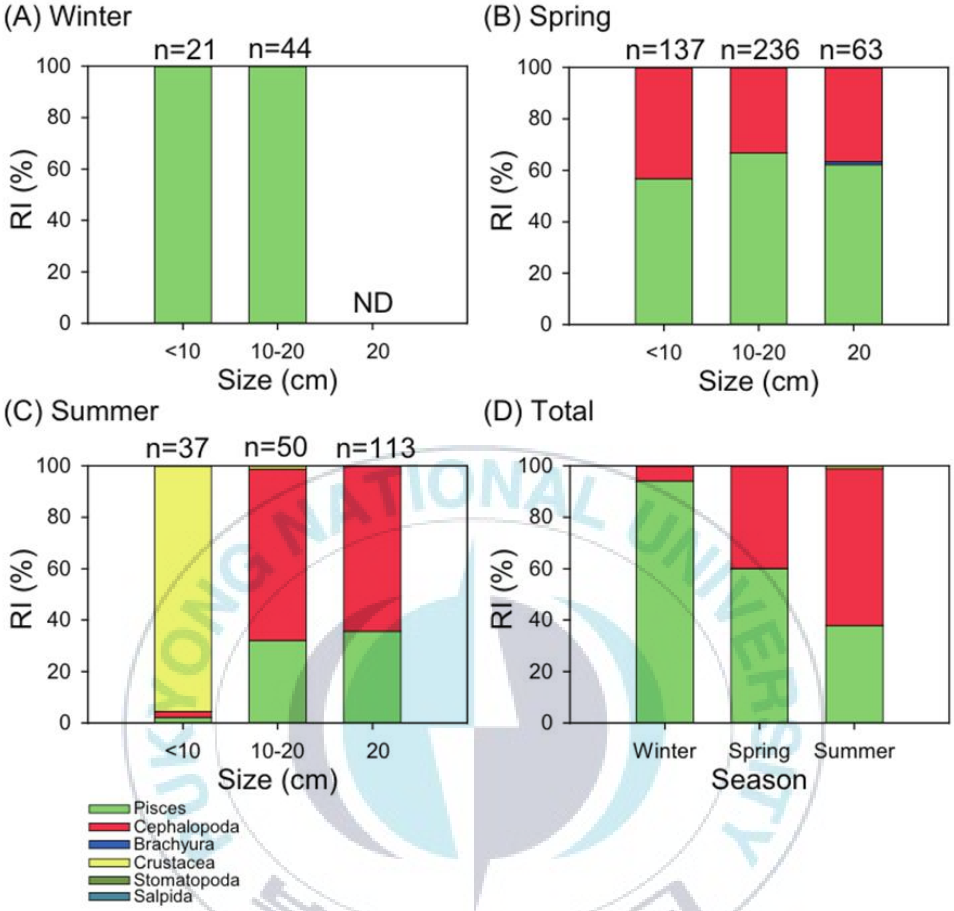


Figure 4.2. Size-related (mantle length, ML; three size classes, <10 cm, 10–20 cm, and >20 cm) and total (D) compositions of the stomach contents of common squid *Todarodes pacificus* based on the ranking index (%RI) expressed as a percentage of the sum of the RI values in the South Sea of Korea during February (winter, (A)), May (spring, (B)), and August (summer, (C)) 2021.

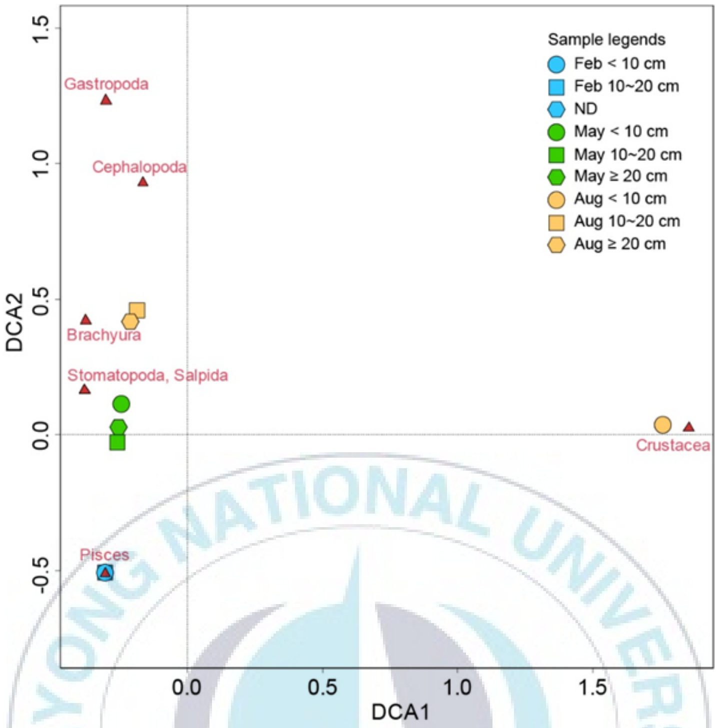


Figure 4.3. Bi-plot of detrended correspondence analysis (DCA) derived from consumer species and their dietary compositions in a reduced space. Red triangles represent prey items. Circles, squares, and hexagons represent common squid *Todarodes pacificus* in the South Sea of Korea during February (blue), May (green), and August (yellow) 2021.

4.3.2 Stable isotope ratios

4.3.2.1 Common squid

The $\delta^{13}C$ and $\delta^{15}N$ values of common squid were found to differ significantly among the three seasons (PERMANOVA: pseudo-$F_{2, 95} = 8.01$, $p = 0.002$). The $\delta^{13}C$ values being higher in August (−18.9‰ ± 0.6‰) than in February (−19.3‰ ± 0.8‰) and May (−19.5‰ ± 0.7‰) (Tukey's HSD test: each $p < 0.01$). Whereas $\delta^{15}N$ values were higher in February (11.3‰ ± 0.6‰) than in May (10.4‰ ± 0.7‰) and August (10.8‰ ± 1.0‰) (Tukey's HSD test: each $p < 0.01$). The TP values of common squid were higher in February than in May and August (Tukey's HSD test: each $p < 0.01$), ranging from 2.9 ± 0.3 (August) to 3.4 ± 0.2 (February).

In contrast, we detected no significant differences in the ML of common squid in the three seasons (one-way ANOVA: $p = 0.232$), ranging from 16.8 ± 4.0 cm (6.9–23.7 cm in May) to 18.6 ± 4.6 cm (8.6–23.5 cm in February). Furthermore, in February and May, no significant correlations were found between the MLs and isotopic values ($\delta^{13}C$: $r = 0.096$, $p = 0.689$ and $r = 0.260$, $p = 0.060$, respectively; $\delta^{15}N$: $r = 0.399$, $p = 0.081$ and $r = 0.086$, $p = 0.540$, respectively) (Figure 4.4). However, in August, ML was significantly correlated with both isotopic values ($\delta^{13}C$: $r = 0.556$, $p = 0.006$; $\delta^{15}N$: $r = 0.839$, $p < 0.001$).

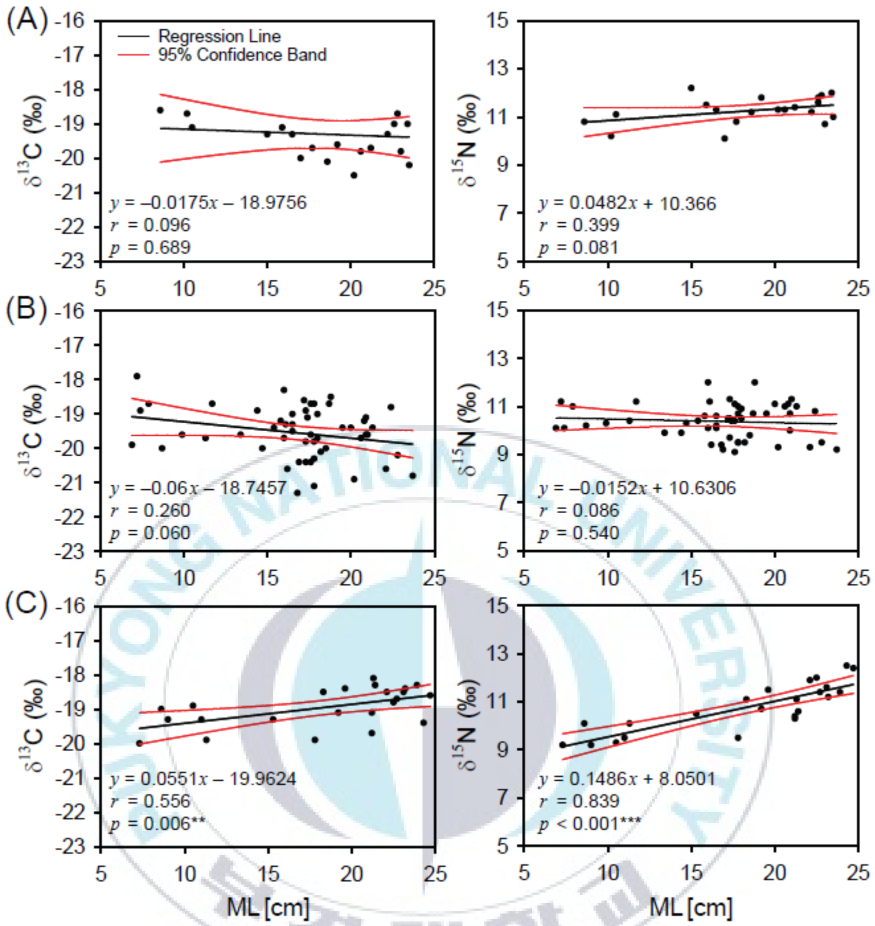


Figure 4.4. Regression relationships between $\delta^{13}C$ – mantle length (cm, left) and $\delta^{15}N$ – mantle length (cm, right) of common squid *Todarodes pacificus* collected in the South Sea of Korea during February (winter, (A)), May (spring, (B)), and August (summer, (C)) 2021.

4.3.2.2 Zooplankton and other fish consumers

Significant differences were detected among the sampling periods with respect to the $\delta^{13}C$ and $\delta^{15}N$ values of the two zooplankton groups copepods and euphausiids (PERMANOVA: pseudo-$F_{2, 29} = 13.22$, $p = 0.001$ and pseudo-$F_{2, 19} = 5.43$, $p = 0.003$, respectively) (Table 4.1). For copepods, we obtained $\delta^{13}C$ and $\delta^{15}N$ values of −22.2‰ ± 0.9‰ (May) to −20.1‰ ± 1.0‰ (February) and 6.5‰ ± 0.4‰ (February) to 8.2‰ ± 0.3‰ (August), respectively. Comparatively, the $\delta^{13}C$ and $\delta^{15}N$ values of euphausiids ranged from −21.3‰ ± 1.1‰ (August) to −20.2‰ ± 1.0‰ (February) and from 6.9‰ ± 0.9‰ (February) to 7.8‰ ± 0.7‰ (August), respectively.

With the exception of those of common squid, the $\delta^{13}C$ and $\delta^{15}N$ values of all fish consumers differed significantly among the sampling periods (PERMANOVA: pseudo-$F_{2, 87} = 8.87$, $p = 0.001$). The mean $\delta^{13}C$ values of fish were relatively high in February (–19.4‰ ± 0.5‰ to –16.4‰ ± 0.1‰) and August (–19.1‰ ± 0.8‰ to –17.9 ‰) compared with those in May (–20.1‰ ± 0.8‰ to –17.1‰ ± 0.8‰) (Figure 4.5, and Tables 4.2, 4.3 and 4.4). In contrast, fish had lower $\delta^{15}N$ values in August (8.9‰–11.9‰) than in February (9.3‰–14.9‰ ± 0.5‰) and May (8.5‰–13.1‰ ± 0.6‰). The mean TP values of fish were significantly higher in February (3.72 ± 0.50) than in May (3.10 ± 0.33) and August (2.84 ± 0.27; Tukey’s HSD test: each $p < 0.01$).

Table 4.1. Mean $\delta^{13}C$ and $\delta^{15}N$ values of the zooplankton groups calanoid copepods and euphausiids sampled during February, May, and August 2021 in the South Sea of Korea (#104, #106, #111, and #224). PERMANOVA test of $\delta^{13}C$ and $\delta^{15}N$ values for each zooplankton among seasons. Bold-face font indicates significance at $p < 0.05$. Data represent mean ± 1SD.

Zooplankton group	**February**					**May**					**August**					**PERMANOVA**	
		$\delta^{13}C$		$\delta^{15}N$			$\delta^{13}C$		$\delta^{15}N$			$\delta^{13}C$		$\delta^{15}N$		pseudo-*F*	*p*
	n	Mean	SD	Mean	SD	n	Mean	SD	Mean	SD	n	Mean	SD	Mean	SD		
Copepods	10	–20.1	1.0	6.5	0.4	12	–22.2	0.9	7.3	0.4	7	–20.2	0.5	8.2	0.3	13.22	**0.001**
Euphausiids	5	–20.2	1.0	6.9	0.9	10	–21.1	0.8	6.9	0.4	4	–21.3	1.1	7.8	0.7	5.43	**0.003**

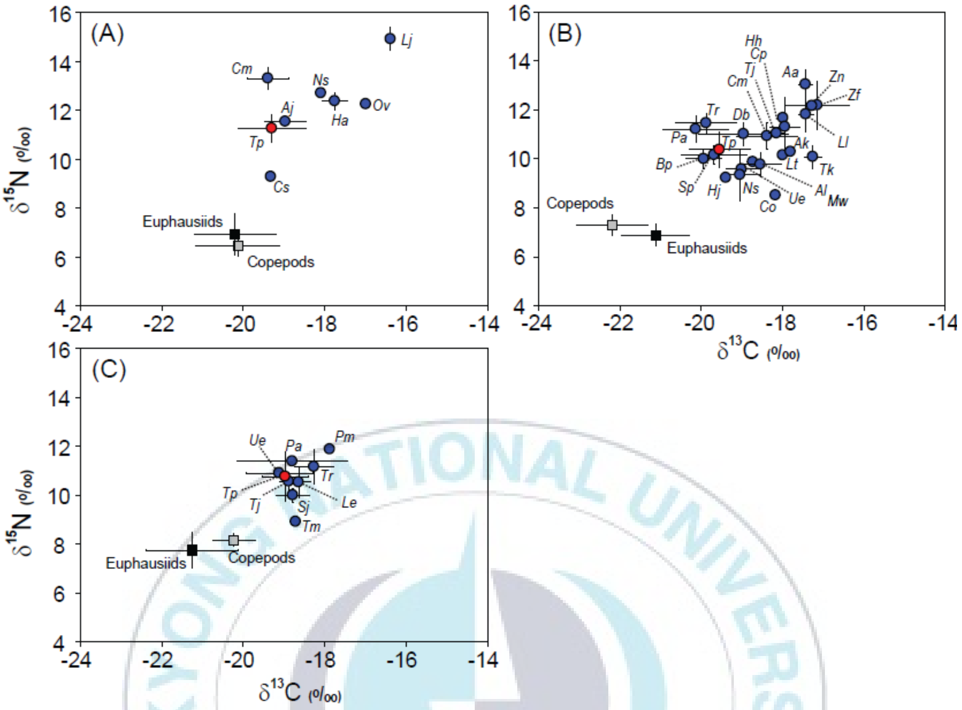


Figure 4.5. Dual isotope plots of δ^{13}C and δ^{15}N values of zooplankton (black squares, euphausiids; gray squares, copepods), common squid *Todarodes pacificus* (red circles), and other fishes (blue circles) in the South Sea of Korea during February (winter, (A)), May (spring, (B)), and August (summer, (C)) 2021. Values are presented as mean δ^{13}C and δ^{15}N (‰ ± 1 SD). Species codes are presented in Tables 4.2, 4.3, and 4.4.

Table 4.2. Mean $\delta^{13}C$ and $\delta^{15}N$ values and trophic position (TP) of common squid *Todarodes pacificus* and other fish consumers collected in February 2021 in the South Sea of Korea (#104, #106, #111, and #224). Data represent means ± 1SD.

Month	**Species name**	**Code**	**n**	$\delta^{13}C$		$\delta^{15}N$		TP
				Mean	S.D.	Mean	S.D.	
February	*Todarodes pacificus*	Tp	**20**	-19.3	0.8	11.3	0.6	3.41
	Acropoma japonicum	Aj	3	-19.0	0.5	11.5	0.2	3.48
	Champsodon snyderi	Cs	1	-19.3		9.3		2.82
	Conger myriaster	Cm	2	-19.4	0.5	13.3	0.4	4.00
	Hoplobrotula armata	Ha	3	-17.8	0.3	12.4	0.4	3.73
	Lateolabrax japonicus	Lj	3	-16.4	0.1	14.9	0.5	4.47
	Niphon spinosus	Ns	1	-18.1		12.7		3.82
	Octopus vulgaris	Ov	1	-17.0		12.2		3.69

Table 4.3. Mean $\delta^{13}C$ and $\delta^{15}N$ values and trophic position (TP) of common squid *Todarodes pacificus* and other fish consumers collected in May 2021 in the South Sea of Korea (#104, #106, #111, and #224). Data represent means ± 1SD.

Month	**Species name**	**Code**	**n**	$\delta^{13}C$		$\delta^{15}N$		TP
				Mean	S.D.	Mean	S.D.	
May	*Todarodes pacificus*	Tp	53	-19.5	0.7	10.4	0.7	3.03
	Apogon lineatus	Al	3	-18.7	0.2	9.9	0.1	2.87
	Argentina kagoshimae	Ak	2	-17.8	0.0	10.3	0.1	3.00
	Argyrosomus argentatus	Aa	2	-17.4	0.2	13.0	0.6	3.81
	Benthosema pterotum	Bp	3	-19.9	0.4	10.0	0.4	2.91
	Cleisthenes pinetorum	Cp	3	-17.9	0.4	11.3	1.2	3.30
	Coelorinchus multispinulosus	Co	1	-18.2		8.5		2.47
	Conger myriaster	Cm	3	-18.4	0.8	10.9	0.6	3.19
	Doederleinia berycoides	Db	3	-19.0	1.1	11.0	0.5	3.21
	Helicolenus hilgendorfi	Hh	1	-18.0		11.7		3.40
	Hyperoglyphe japonica	Hj	1	-19.4		9.2		2.68
	Liparis tanakae	Lt	1	-18.0		10.1		2.96
	Lophius litulon	Ll	3	-17.4	0.2	11.8	0.7	3.45
	Malakichthys wakiyae	Mw	3	-18.5	0.5	9.8	0.5	2.84
	Neobythites sivicola	Ns	3	-19.0	0.5	9.3	1.1	2.72

Table 4.3. Continued.

Month	Species name	Code	n	$\delta^{13}C$		$\delta^{15}N$		TP
				Mean	S.D.	Mean	S.D.	
May	*Psenopsis anomala*	Pa	3	-20.1	0.8	11.2	0.5	3.27
	Synagrops philippinensis	Sp	3	-19.7	0.8	10.2	0.4	2.96
	Tanakius kitaharae	Tk	3	-17.3	0.2	10.1	0.5	2.94
	Trachurus japonicus	Tj	3	-18.1	0.2	11.0	0.2	3.22
	Trichiurus japonicus	Tr	3	-19.9	0.7	11.5	0.4	3.34
	Uroteuthis edulis	Ue	3	-19.0	0.4	9.6	0.2	2.79
	Zenopsis nebulosa	Zn	1	-17.3		12.2		3.55
	Zeus faber	Zf	3	-17.1	0.8	12.2	1.0	3.56

Table 4.4. Mean $\delta^{13}C$ and $\delta^{15}N$ values and trophic position (TP) of common squid *Todarodes pacificus* and other fish consumers collected in August 2021 in the South Sea of Korea (#104, #106, #111, and #224). Data represent means ± 1SD.

Month	**Species name**	**Code**	**n**	$\delta^{13}C$ Mean	$\delta^{13}C$ S.D.	$\delta^{15}N$ Mean	$\delta^{15}N$ S.D.	TP
August	*Todarodes pacificus*	Tp	23	-19.0	0.6	10.8	1.0	2.89
	Loligo edulis budo	Le	3	-18.6	0.3	10.5	0.6	2.80
	Pagrus major	Pm	1	-17.9		11.9		3.20
	Psenopsis anomala	Pa	2	-18.8	1.3	11.4	0.1	3.05
	Scomber japonicus	Sj	4	-18.8	0.4	10.0	0.3	2.65
	Thamnaconus modestus	Tm	1	-18.7		8.9		2.33
	Trachurus japonicus	Tj	3	-18.9	0.2	10.6	0.4	2.81
	Trichiurus japonicus	Tr	3	-18.3	0.5	11.2	0.7	2.99
	Uroteuthis edulis	Ue	3	-19.1	0.8	10.9	0.1	2.91

4.4 Discussion

The feeding ecology of marine species is generally influenced by environmental conditions, food availability, trophic interactions, and species competition (Navarro et al., 2013; Fry and Sherr, 1984; Juanes et al., 2022). In the present study, we adopted the combined application of stomach content and stable isotope analyses to explain the feeding ecology of common squid, *T. pacificus*, along the southern coast of Korea, from seasonal and size-related ontogenetic feeding perspectives. Collectively, the findings of the study revealed temporal and size-related patterns among common squid, indicating that theses cephalopods are opportunistic carnivores based on seasonal differences in their dietary composition and ontogenetic dietary shifts during the sampling periods. Such information on seasonal dietary changes and ontogenetic variation in the common squid provides further insight into how changes in environmental conditions and prey availability may affect the trophic ecology of this commercially important species.

The results of the present study revealed seasonal dietary shifts in the diets of common squid in terms of prey composition, of which the main groups, based on a stomach content analysis, were Pisces (37.9–94.0%) and Cephalopoda (6.0–61.0%) throughout the three sampling periods, with gradual increase in the proportion of dietary items from Pisces to Cephalopoda from winter to summer. Similarly, the DCA results indicated a seasonal variability in the dietary composition of common squid and dietary changes relative to ML. Although the potential effects of body size were considered, we observed that dietary trends were similar across sampling periods. Such seasonal shifts in the dietary items consumed by common squid may be associated with the change in regional food availability, as indicated by the wide regional seasonal variation in the feeding spectrum (Sakurai et al., 2013). In general, most omnivore and carnivore consumers in marine ecosystems tend to be characterized by dietary plasticity, that is, feeding on a variety of prey, depending on food availability and environmental conditions (Park et al., 2020; Henriques et al., 2017; Szczepanek et al., 2021). Many squid species, including *T. pacificus*, actively feed on zooplankton, cephalopods, and small fish, and may also engage in cannibalism (Ibáñez et al., 2008; Leite et al., 2009; Ibáñez et al., 2021). However, despite the dietary opportunism of *T. pacificus*, the stomach contents observed in the present study showed relatively little seasonal variation and low prey diversity, compared with the results of previous studies (Sakurai et al., 2013; Uchikawa and Kidokoro, 2014), which we suspect could be due to the geographical differences in the abundance and availability of potential prey to *T. pacificus*.

A stomach content analysis revealed very similar patterns in dietary prey composition among common squid of the three different size classes in February and May, which indicated high intraspecific feeding competition with no size-related dietary shift. Although marine fishes typically undergo ontogenetic changes that entail partitioning of dietary resources, our results indicated an absence of ontogenetic size-related dietary shifts in prey composition during winter and spring. Compared with those of the other two size classes, the common squid of size group ML <10 cm showed a rather obvious distinction in dietary composition in August with respect to the high proportion of Crustacea (95.5%) in the diet. In this regard, numerous studies have reported that marine fishes and cephalopods undergo ontogenetic dietary shifts that are characterized by changes in size-specific prey-predator relationships (Wang et al., 2022; Park et al., 2018; Juanes et al., 2002). Consistent with the findings of the present study, Uchikawa and Kidoroko detected a clear size-related dietary change in *T. pacificus*, in which small individuals fed mainly on crustaceans, whereas larger individuals shifted to a more fish-based diets (Uchikawa and Kidoroko, 2014). Such ontogenetic shifts in the diets of marine consumers are assumed to be associated with their higher predatory ability and improved swimming capacity with increasing body growth (Lundvall et al., 1999; Boyle et al., 2012). Growth and morphological changes in *T. pacificus* may result in higher swimming performance, and thus a higher proportions of fish in their diets (Uchikawa and Kidokoro, 2014; Christensen, 1996). However, the feeding characteristics of *T. pacificus* observed during only one specific season (i.e., summer) may be an effect of seasonal changes in prey availability, as opportunistic consumers generally tend to achieve energy optimization by reducing intra- and/or interspecific food competition (Griffiths, 1975; Park et al., 2017). Thus, size-related changes in common squid diets that occur only during summer may be closely associated with prey availability and environmental conditions in the foraging area rather than with an enhancement in predation capacity.

The stable isotope data obtained in this study revealed isotopic variation over the sampling periods, thereby indicating a seasonal shift in dietary sources, and thus a change in TP values, as observed based on stomach content analysis. As discussed above, most squid can rapidly adjust their feeding strategies in response to changes in seasonal and annual prey availability (Wang et al., 2022; Hunsicker et al., 2010). This may be supported by seasonal isotopic variability, which reflects the temporal changes in the feeding ecology of *T. pacificus*. In the present study, we established that the relatively high $\delta^{15}N$ values of *T. pacificus* in February compared to those obtained in other seasons may be associated with the high proportion of fish in their diets, with respect to the generally high TP of fish species. In August, despite a reduction in the contribution of dietary fish to the composition of common squid tissue, the relatively high $\delta^{13}C$ values compared to those in other months may be associated with seasonal variability in the trophic baseline (i.e., phytoplankton-derived organic matter) in sampling regions with different prey compositions (Kang et al., 2009). In marine ecosystems, $\delta^{13}C$ values of phytoplankton-derived organic matter generally reflect spatial and temporal variation in marine particles, including phytoplankton, under different ambient conditions, and thereby contribute the $\delta^{13}C$ values of higher TP consumers along food chains (Fry and Sherr, 1984). The $\delta^{13}C$ values of common squid (−19.5 to −18.9‰) obtained in the present study may reflect a tendency of trophic connections of general pelagic system with two zooplankton groups, indicating a linkage between *T. pacificus* and phytoplankton-derived organic matter (Park et al., 2020). Accordingly, seasonal changes in the isotopic composition of the common squid are considered to be indicative of the variability of dietary items and isotopic baseline sources corresponding to changes in seasonal environmental conditions.

The $\delta^{13}C$ and $\delta^{15}N$ dual-isotope plots shown in Figure 4.5 indicate discrimination between pelagic and benthic feeders along the $\delta^{13}C$ axis. Compared with the benthic-feeding demersal fish, pelagic feeders, such as the common squid, are generally characterized by relatively low $\delta^{13}C$ and $\delta^{15}N$ values (Park et al., 2020; Park et al., 2018). Consistently, our findings in the present study revealed the relatively low $\delta^{13}C$

and $\delta^{15}N$ values of common squid, indicating that the isotopic niche of this species is closer to that of the zooplankton groups copepods and euphausiids regardless of the season. Moreover, the distribution and migration of *T. pacificus* are significantly influenced by physical conditions (e.g., water temperature), which can play an important role in altering seasonal patterns in marine fish food webs (Sakurai et al., 2013; Park et al., 2020).

The TP estimations obtained for common squid and other consumers based on the $\delta^{15}N$ values of zooplankton have revealed temporal variation resulting from a seasonal difference in the $\delta^{15}N$ values of food web baselines (Park et al., 2020). The relatively high $\delta^{15}N$ values of zooplankton recorded in August compared with those obtained in February may have contributed to the low TP estimates obtained for consumers during summer. The high $\delta^{15}N$ values of phytoplankton-derived organic matter as an isotopic baseline during summer can probably be attributed to the proliferation of phytoplankton influenced by excessive nutrient input associated with heavy monsoonal rainfall, which is consistent with previous observations in the southern coastal waters of Korea (Kang et al., 2009). Similar to the temporal variability of common squid $\delta^{13}C$, seasonal differences in the TP values of these squid may result from the variability of zooplankton $\delta^{15}N$ influenced by phytoplankton dynamics associated with regional oceanographic conditions.

In the present study, significant positive correlations between ML and both $\delta^{13}C$ and $\delta^{15}N$ values of common squid were detected only in summer, thereby indicating clear size-dependent shifts in ontogenetic dietary composition, which is consistent with our observations of seasonal dietary changes based on the stomach content analysis

(Figure 4.2). The high contribution of Crustacea (more than 95%) to the diet of the smallest common squids (ML <10 cm) in August may have led to lower δ^{13}C and δ^{15}N values compared with those of larger individuals and thereby to positive isotopic gradients with increasing body size. Such relationships between size and isotopic values of cephalopods and fish species have been reported in several studies and may be indicative of a general size-related pattern in ontogenetic dietary shifts (Merten et al., 2017; Park et al., 2018; Graham et al., 2007). Similarly, an increase in the higher δ^{15}N values of common squid with increasing with ML is assumed to reflect an increase in the consumption of larger and trophically higher prey items (e.g., fish and cephalopods) during summer.

In contrast, the lack of size-related isotopic relationships of common squid during winter and spring indicates a high dietary overlap among the specimens in the three assessed size classes associated with the consumption of similar diets. This lack of size-related patterns in resource use by common squid as observed in the current study may result in heightened intraspecific competition, as indicated by the composition of stomach contents. Overall, the observed seasonal patterns in size-related isotopic distributions of common squid may be explained in terms of the temporal variability of the major dietary components for specific size classes associated with the seasonally changing availability of food in the region.

In conclusion, our combined application of stomach content and stable isotope analyses in this study revealed seasonal differences in the dietary composition and ontogenetic dietary patterns of common squid in the South Sea of Korea. Our observations indicate that the feeding strategy adopted by these squid changes with seasonal availability of prey in this region. In particular, although, we detected no apparent size-related dietary changes during winter or spring, there was a clear ontogenetic dietary shift from crustaceans to cephalopods and fishes during summer, thereby indicating temporal variability in feeding strategies in response to the availability of prey. Collectively, the findings of this study advance our understanding of the feeding ecology of *T. pacificus*, thereby providing valuable information that will contribute to refining the ecological-based fishery management of this commercially important species.

V. Conclusions

The trophic variability of fish assemblages inhabiting coastal marine ecosystems in Korea under different environmental conditions was investigated in 2020 and 2021 in this study. Through the combined use of stable isotopes and stomach content analyses, this dissertation study specifically revealed the feeding ecology of largehead hairtail (*Trichiurus japonicus*) and common squid (*Todarodes pacificus*), which are economically valuable species in fisheries industries along the southern coast of Korea. Generally, the feeding ecology of marine species is influenced by environmental conditions, food availability, trophic interactions, and competition (Navarro et al., 2013; Fry and Sherr, 1984; Juanes et al., 2022). The results showed that the isotopic ratios of fish assemblages with the food web base were spatially and seasonally variable in the spring and autumn of 2020. This reflects the regional-specific differences in oceanographic characteristics and species composition between the South and East Seas. In particular, the presence of specific fish consumers due to differences in species composition may lead to spatial and seasonal variations in the trophic structure, resulting from changes in trophic niche indices. The total species composition, abundance, and range of $\delta^{13}C$ and $\delta^{15}N$ values of fish species collected from the sampling sites were similar to those previously reported in the East and South Seas of Korea (Han, 2003; Lee, 2011; Choi et al., 2012; Kang et al., 2014; Moon et al., 2015; Sohn et al., 2015; Park et al., 2020). In this study, the major diets of largehead hairtail were Pisces (1.6–84.8%) and Euphausiacea (3.0–93.0%) over the four seasons. Furthermore, the prey composition of common squid (*Todarodes pacificus*) was Pisces (37.9–94.0%) and Cephalopoda (6.0–61.0%) throughout the three sampling periods

(Figure 5.1). The results of this study revealed seasonal shifts in the diets of these two species using stable isotope and stomach content analyses. The specific conclusions of this dissertation are as follows;

In Chapter 2, our isotopic investigation of fish assemblages showed spatial differences in the food web structure and species composition between the East and South Seas of the Korean peninsula, implying the occurrence of different environmental conditions. Additionally, the difference in the isotopic niche parameters between the two seas suggests the distinction of trophic diversity of fish assemblages, coupled with the relative differences in abundance and population size of component species. Overall, our isotopic evidence implies that spatial and temporal variations in fish communities in response to changing environmental conditions (especially ocean warming) can alter the trophic relationships among species and the food web structure. Further long-term studies considering top-down and bottom-up trophic processes, based on community compositions of fish assemblages and their stable isotope ratios, are needed to better understand the functioning of coastal ecosystems under global climate change.

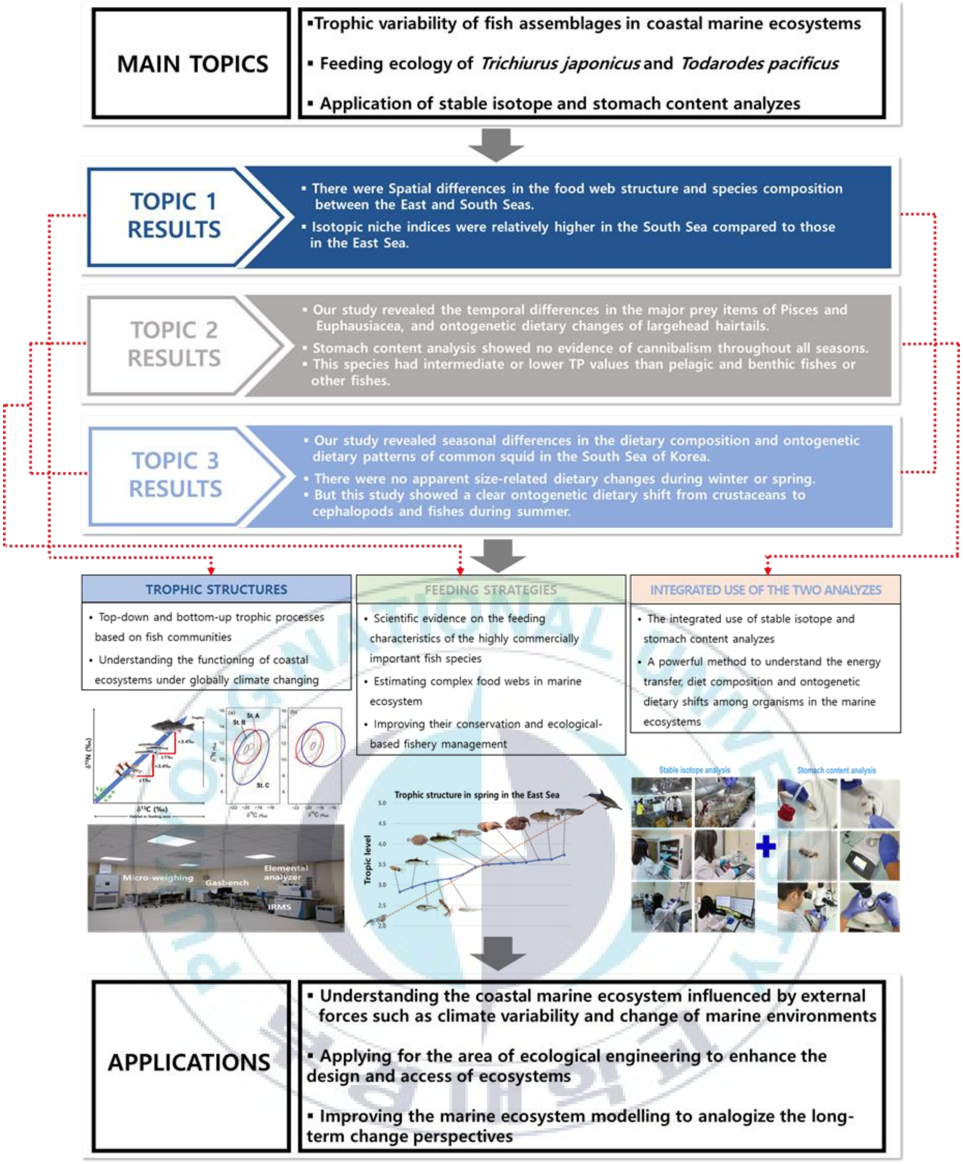
In Chapter 3, our study revealed the seasonal and size-related patterns in the feeding strategy and dietary composition of largehead hairtails in the South Sea of Korea, exhibiting temporal contrasting differences in the major prey items of Pisces and Euphausiacea, and ontogenetic dietary changes through the combination of stomach and stable isotope analyses. The feeding ecology of largeheads may be opportunistic carnivorous feeding on available dietary species. Stomach content analysis showed no evidence of cannibalism throughout all seasons. Our isotopic results showed greater ^{13}C- and ^{15}N-depleted signatures in largehead hairtails than in other large carnivorous fishes, suggesting a high consumption of dietary items with pelagic source affinity. Similarly, this species had intermediate or lower TP values than pelagic and benthic fishes or other fishes. Overall, our study provides scientific evidence on the feeding characteristics of the highly commercially important fish species largehead hairtails in the western North Pacific, which improves our understanding of their conservation and ecological-based management.

In Chapter 4, our combined application of stomach content and stable isotope analyses in this study revealed seasonal differences in the dietary composition and ontogenetic dietary patterns of common squid in the South Sea of Korea. Our observations indicate that the feeding strategy adopted by these squid changes with seasonal availability of prey in this region. In particular, although, we detected no apparent size-related dietary changes during winter or spring, there was a clear ontogenetic dietary shift from crustaceans to cephalopods and fishes during summer, thereby indicating temporal variability in feeding strategies in response to the availability of prey. Collectively, the findings of this study advance our understanding of the feeding ecology of *T. pacificus*, thereby providing valuable information that will contribute to refining the ecological-based fishery management of this commercially important species.

In conclusion, this research confirmed that the integrated use of stable isotopes and stomach content analyses is a powerful method for understanding energy transfer, diet composition, and ontogenetic dietary shifts among organisms in marine ecosystems. Such differences in food-web characteristics among sites are likely due to the specific environmental effects on the differences in species compositions and their trophic relationships. Therefore, this result will help estimate complex food webs in marine ecosystems and in improving effective fishery resource management for sustainable use at the ecosystem level (Figure 5.2).

Nevertheless, in this study, it was difficult to analyze the ecological characterization of fish species and food web structure more accurately because of the lack of data on the abundance of primary food sources (sediment-derived organic matter and macrobenthic organisms) and their stable isotopic values. In addition, the field survey in this study was not performed in the Yellow Sea in western Korea during this research period. Therefore, additional studies are required to support these findings. More accurate and detailed clues can be found regarding the energy transfer among organisms in marine food webs in various environments using DNA barcoding and fatty acid analyses.

This dissertation presents valuable results and a new approach to understanding coastal marine ecosystems and studying the impact of external forces, such as climate variability and changes in marine environments, in the future. This study can be used in various ecological engineering studies in the future. For example, they can be actively used in ecosystem utilization, artificial ecosystem creation, ecosystem restoration, ecological biological harvesting, and clean production technology development. Therefore, it is necessary to develop an upgraded methodology and analysis method. However, it is considered that these have been covered by the most timely analysis at this point. Furthermore, these methods can be used to improve marine ecosystem modeling to analogize long-term change perspectives.



- Trophic variability of fish assemblages in coastal marine ecosystems
- Feeding ecology of *Trichiurus japonicus* and *Todarodes pacificus*
- Application of stable isotope and stomach content analyzes

- There were Spatial differences in the food web structure and species composition between the East and South Seas.
- Isotopic niche indices were relatively higher in the South Sea compared to those in the East Sea.

- Our study revealed the temporal differences in the major prey items of Pisces and Euphausiacea, and ontogenetic dietary changes of largehead hairtails.
- Stomach content analysis showed no evidence of cannibalism throughout all seasons.
- This species had intermediate or lower TP values than pelagic and benthic fishes or other fishes.

- Our study revealed seasonal differences in the dietary composition and ontogenetic dietary patterns of common squid in the South Sea of Korea.
- There were no apparent size-related dietary changes during winter or spring.
- But this study showed a clear ontogenetic dietary shift from crustaceans to cephalopods and fishes during summer.

- Top-down and bottom-up trophic processes based on fish communities
- Understanding the functioning of coastal ecosystems under globally climate changing

- Scientific evidence on the feeding characteristics of the highly commercially important fish species
- Estimating complex food webs in marine ecosystem
- Improving their conservation and ecological-based fishery management

- The integrated use of stable isotope and stomach content analyzes
- A powerful method to understand the energy transfer, diet composition and ontogenetic dietary shifts among organisms in the marine ecosystems

- Understanding the coastal marine ecosystem influenced by external forces such as climate variability and change of marine environments
- Applying for the area of ecological engineering to enhance the design and access of ecosystems
- Improving the marine ecosystem modelling to analogize the long-term change perspectives

Figure 5.1. Schematic diagram of the main topics, results, and applications of this study.

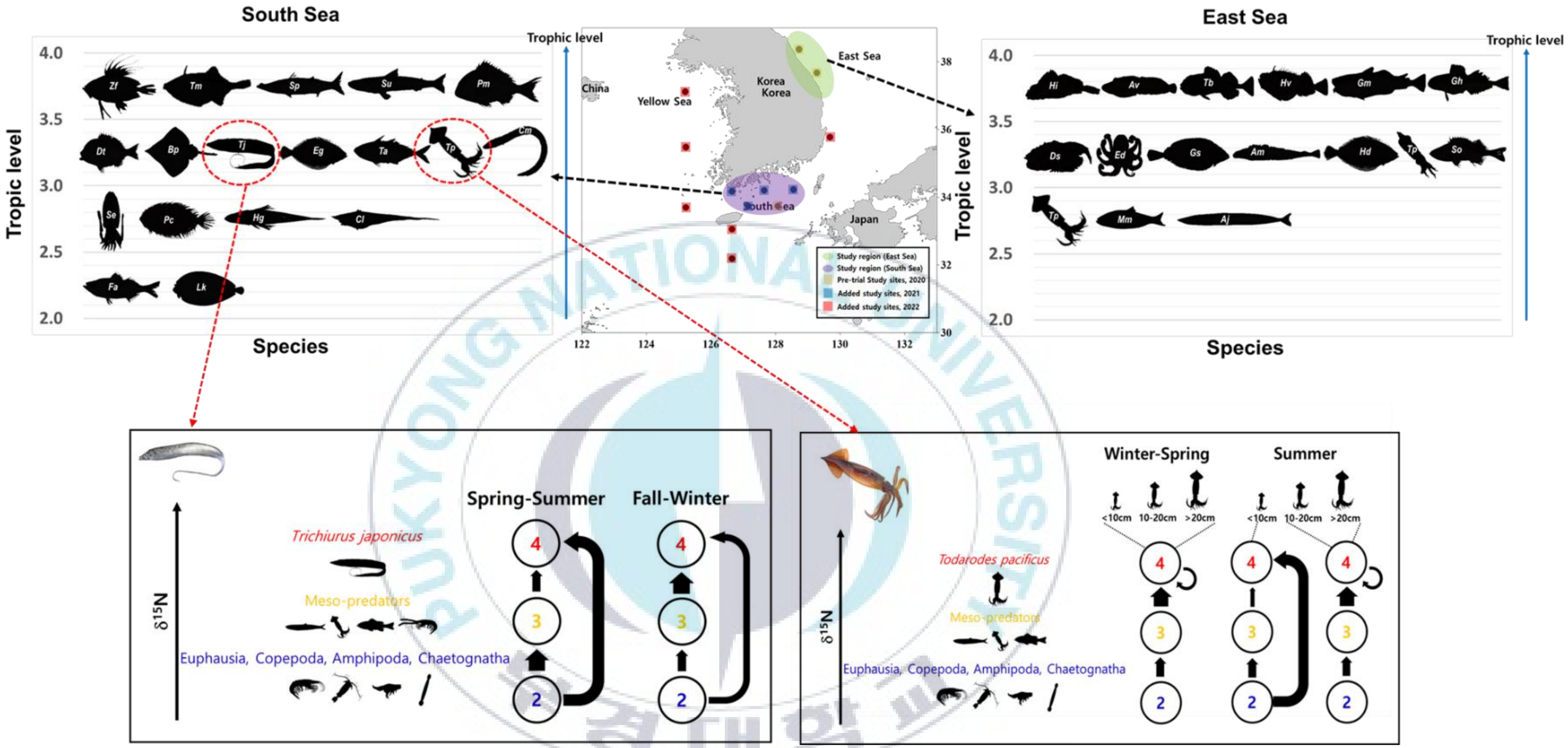


Figure 5.2. Schematic diagram of the integrated results of this study. The relative contribution is indicated by the thickness of the filled arrow. Species codes are presented in Tables 3.3, 4.2, 4.3, and 4.4.

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VII. Appendixes

Appendix 1. $\delta^{13}C$ and $\delta^{15}N$ values of organic matter (SPOM, suspended particulate organic matter) and zooplankton (calanoid copepods and euphausiids) collected during May and October 2020 in the East Sea (St. A and St. B) and the South Sea (St. C). ANOVA test of $\delta^{13}C$ and $\delta^{15}N$ values for each potential food source between seasons and among sampling sites. Bold-face font indicates significance at $p < 0.05$. Data represent mean ± 1SD.

ANOVA test		Season		Site		Interaction	
		pseudo-*F*	*p*	pseudo-*F*	*p*	pseudo-*F*	*p*
SPOM	$\delta^{13}C$	71.084	**0.000**	20.228	**0.000**	9.127	**0.001**
	$\delta^{15}N$	5.159	**0.032**	4.173	**0.028**	0.531	0.595
Copepods	$\delta^{13}C$	6.816	**0.018**	7.942	**0.003**	0.076	0.927
	$\delta^{15}N$	4.343	0.052	3.599	**0.048**	0.355	0.706
Euphausiids	$\delta^{13}C$	15.177	**0.001**	15.554	**0.000**	0.035	0.966
	$\delta^{15}N$	11.073	**0.004**	13.136	**0.000**	0.001	0.999

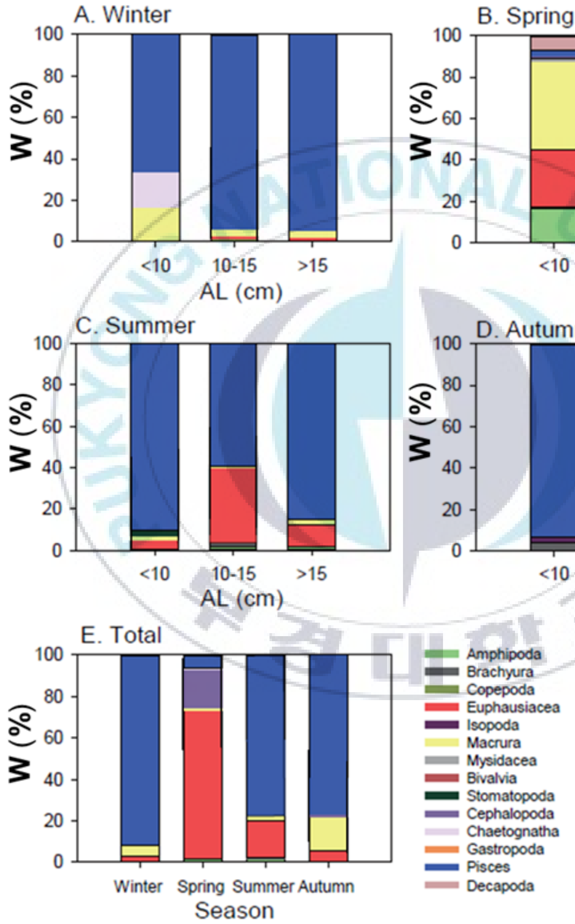
Appendix 2. $\delta^{13}C$ and $\delta^{15}N$ values of zooplankton (calanoid copepods and euphausiids) collected during February, May, August, and November 2021 in the South Sea of Korea. ANOVA test of $\delta^{13}C$ and $\delta^{15}N$ values for each zooplankton among seasons. Bold-face font indicates significance at $p < 0.05$. Data represent mean ± 1SD.

Zooplankton group		ANOVA test	
		pseudo-F	*p*
Copepods	$\delta^{13}C$	7.937	**0.000**
	$\delta^{15}N$	15.626	**0.000**
Euphausiids	$\delta^{13}C$	1.653	0.197
	$\delta^{15}N$	16.367	**0.000**

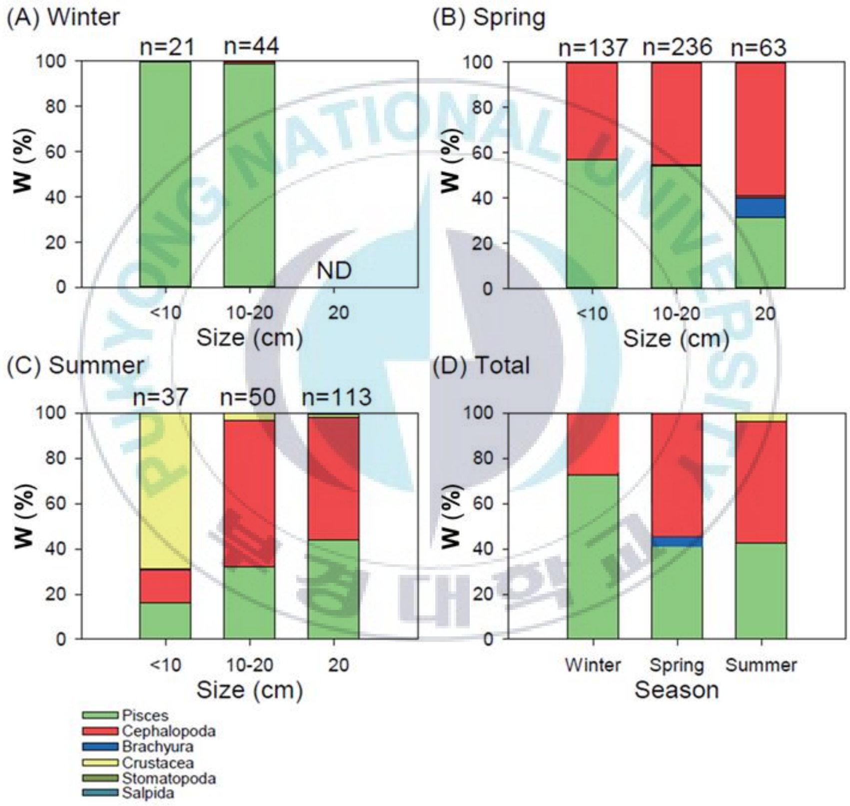
Appendix 3. Mean $\delta^{13}C$ and $\delta^{15}N$ values of the zooplankton groups calanoid copepods and euphausiids, collected during February, May, and August 2021 in the South Sea of Korea (#104, #106, #111, and #224). ANOVA test of $\delta^{13}C$ and $\delta^{15}N$ values for each zooplankton among seasons. Bold-face font indicates significance at $p < 0.05$. Data represent mean ± 1SD.

Zooplankton group		ANOVA test	
		pseudo-*F*	*p*
Copepods	$\delta^{13}C$	12.246	**0.000**
	$\delta^{15}N$	15.343	**0.000**
Euphausiids	$\delta^{13}C$	2.633	0.103
	$\delta^{15}N$	8.369	**0.003**

Appendix 4. Size-related (anal length, AL; 10 cm, 10–15 cm, and > 15 cm) and total (E) compositions of the stomach contents of large-head hairtail (*Trichiurus japonicus*) expressed as a percentage wet weight (%W) in the South Sea of Korea during winter (A, February), spring (B, May), summer (C, August), and autumn (D, November) 2021.



Appendix 5. Size-related (mantle length, ML; three size classes, <10 cm, 10–20 cm, and >20 cm) and total (D) compositions of the stomach contents of common squid *Todarodes pacificus* expressed as a percentage wet weight (%W) in the South Sea of Korea during February (winter, (A)), May (spring, (B)), and August (summer, (C)) 2021.



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Publications

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Presentations

1. **Shin, D. et al.**, “The importance of benthos: community dynamics of macroinvertebrates in invasive seagrass ecosystems caused by climate change”, 2013, 4th interdisciplinary summer school on geoengineering, Boston, USA, Poster presentation.

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5. **Shin, D. et al.**, "Stable isotopes reveal trophic structures among coastal habitats in the *Halophila*-invaded seagrass ecosystems.", 2016, KOFFST International Conference 2016, Pusan, South Korea, Poster presentation.

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9. **Shin, D. et al.**, "Species composition and seasonal variations of seaweeds and fishes in coastal waters of Oryukdo, Busan: A study of methods for managing Marine Protected Areas", 2018, Busan young innovator BTIS, Pusan, South Korea, Poster presentation.

10. **Shin, D. et al.**, "Distribution of common squid, *Todarodes pacificus*, paralavae in the southwestern part of the East Sea in Summer and Autumn, 2015", 2018, Fall Conference of Society of Ecological Engineering of Korea, Pusan, South Korea, Oral presentation.

11. **Song, S. et al.**, "The seasonal variation of anchovy (*Engraulis japonicus*) catch and long-term prediction by RCP climate change scenarios.", 2019, KOFFST International Conference 2019, Pusan, South Korea, Poster presentation.

12. **Park, H. J. et al.**, "Seasonal variation in trophic structure of fish assemblages in the South Sea and the East Sea, Korea.", 2021, Fall Conference of Society of Society of Oceanography of Korea, Jeju, South Korea, Poster presentation.

13. **Shin, D. et al.**, "Diet and resource partitioning of large-head hairtail *Trichiurus japonicus* in the southern sea of Korea: Application of stable isotope and gut content analyses.", 2022, Spring Conference of Society of Ichthyology of Korea, Seoul, South Korea, Oral presentation.

14. **Shin, D. et al.**, "Trophic ecology of fishes in Korean waters: A stable

isotope study.", 2022, R.O.K-U.S. Bilateral Meeting on Fisheries Science 2022, Busan, South Korea, Oral presentation.

15. **Shin, D. et al.**, "Trophic ecology of common squid *Todarodes pacificus* in the South Sea of Korea as determined by stable isotope and stomach content analyses.", 2022, KOFFST International Conference 2022, Busan, South Korea, Poster presentation.

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17. **Shin, D. et al.**, "Characterization of trophic structure of cetaceans in Korean waters using C and N stable isotope analysis.", 2022, The First Conservation Medicine Workshop on Marine Mammals, Ulsan, South Korea, Oral presentation.

Certificates & Training

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