Title	Summer diet and feeding strategy of Pacific cod (Gadus macrocephalus) inhabiting the southern coast of Hokkaido, Japan
Author(s)	Wang, Rongfu; Chimura, Masayuki; Sadayasu, Kazuhiro et al.
Citation	Marine biology research, 18(7-8), 435-447 https://doi.org/10.1080/17451000.2022.2147948
Issue Date	2023-12-05
Doc URL	https://hdl.handle.net/2115/90823
Rights	This is an Accepted Manuscript of an article published by Taylor & Francis in Marine biology research on 05 December 2022, available online: http://www.tandfonline.com/10.1080/17451000.2022.2147948.
Type	journal article
File Information	wang_et_al_2022.pdf

Summer diet and feeding strategy of Pacific cod (*Gadus macrocephalus*) inhabiting the southern coast of Hokkaido, Japan

Rongfu Wang[1], Masayuki Chimura[2], Kazuhiro Sadayasu[3], Mitsuhiro Ishino[2], Orio Yamamura[1]

[1]Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate City, 041-8611, Japan
[2]Fisheries Resources Institute, Japan Fisheries Research and Education Agency, 116 Katsurakoi, Kushiro, 085-0802, Japan
[3]Marine Fisheries Research and Development Center, Japan Fisheries Research and Education Agency, Shin-urashima-cho, Kanagawa-ku, Yokohama-City, 221-8529, Japan

Acknowledgments

We would like to thank the crew on board the Kaiyo-Maru No.5 for their assistance during the cruises. The specimens used in this study were collected during the stock assessment survey funded by the Japan Fisheries Agency (JFA). Orio Yamamura was funded by the JFA Project Promoting

Precise Stock Assessment. Rongfu Wang received funding from the China Scholarship Council (CSC).

Abstract

The ontogenetic and interannual variations in the diet and feeding strategy of Pacific cod (*Gadus macrocephalus*) were examined based on 1,302 specimens collected by a trawling net off the southern coast of Hokkaido from late June to early July during 2016–2020. The diet comprised 63 species (13 taxa). Fish was the most important prey, followed by decapod crustaceans. In 2016, walleye pollock (*Gadus chalcogrammus*) was the dominant fish prey species, while amphipods, decapods, and Japanese lanternfish (*Notoscopelus japonicus*) were prominent in the diet in 2017. Japanese sardine (*Sardinops melanostictus*) were more predominant during 2018–2020. An ontogenetic comparison of diet indicated that smaller individuals (≤ 400 mm standard length, SL) preyed mainly on small prey items, such as decapod crustaceans and polychaetes, whereas larger individuals (> 400 mm SL) preyed mainly on fish. Moreover, prey size exhibited a significant increasing trend with predator body length. These results suggest that Pacific cod has a flexible feeding strategy that differs by life stage. The updated information on predator–prey relationships provided herein improves our understanding of energy flow in the marine ecosystem and could facilitate ecosystem-based fishery management strategies.

Keywords

Pacific cod, stomach contents, diet composition, feeding strategy, Hokkaido

1 Introduction

Pacific cod (*Gadus macrocephalus*) is an important fishery resource with high ecological and economic value in marine ecosystems (Ueba et al. 2004; Savin 2007; Fissel et al. 2017). They are widely distributed throughout the North Pacific and feed on various fishes and invertebrates, particularly walleye pollock (*Gadus chalcogrammus*), Pacific herring (*Clupea pallasii*), shrimps, and crabs (Albers and Anderson 1985; Yamamura et al. 1993; Yang 2004; Poltev and Stominok 2008; Urban 2012; Gray et al. 2021). In turn, Pacific cod are consumed by upper-level predators, such as Steller sea lions (*Eumetopias jubatus* (Goto et al. 2017)) and beluga whales (*Delphinapterus leucas* (Quakenbush et al. 2015)). Thus, as an intermediate predator, Pacific cod play a critical role in maintaining trophic linkages in the food web.

In Japanese waters, Pacific cod is mainly distributed along the coast of the Sea of Japan, around the shores of Hokkaido (Mishima 1984), and off the northwestern coast of Honshu Island (Sakuma et al. 2019). In the marine ecosystem off the southern coast of Hokkaido, the catch of Pacific cod declined from over 29 thousand tons in 1987 to about 8.5 thousand tons in 2003, and then gradually increased to over 15 thousand tons after 2010 (Chimura et al. 2022). The fluctuations in the abundance of Pacific cod may induce variations in the predator-prey relationships. For example, the predation of Pacific cod may affect the stock abundance of pink shrimp (*Pandalus eous*) in the western Gulf of Alaska (Albers and Anderson 1985).

Elucidation of the feeding ecology of fish is crucial to understand the trophic relationships among species coexisting in the marine ecosystem, and for constructing food web models such as the Ecopath model (Polovina 1984), being widely used to analyze ecosystem trophic mass balance (Christensen and Walters 2004). A series of methods have been used to study fish feeding ecology. Stomach contents analysis permits a high degree of taxonomic clarity in the identification of prey (Hyslop 1980). This method has been widely used to determine the feeding ecology of many fish species, such as hairtail (*Trichiurus japonicus* (Mammel et al. 2022)), arrowtooth flounder (*Atheresthes stomias* (Draper 2022)), and rough scad (*Trachurus lathami* (Temperoni et al. 2021)). One shortcoming of this method is that it can only reflect a snapshot of the diet composition. In recent years, some chemical tracer methods have been used to examine fish feeding ecology, such as stable isotopes analysis (Jennings et al. 2002). This method traces dietary sources over a longer time period but the taxonomic resolution of prey items is relatively coarse (Hüne et al. 2018). In terms of Pacific cod, dominant prey items, including fish, crabs, and shrimps, usually stay in the stomach for a relatively long time due to their indigestible bones or carapaces. This makes it possible to examine the stomach contents of Pacific cod directly.

The feeding ecology of Pacific cod has attracted much attention, and has been examined in various marine ecosystems including the eastern Bering Sea (Suyehiro 1934; Lang et al. 2005), western Gulf of Alaska (Albers and Anderson 1985), and west coast of the Yellow Sea of Korea (Choi et al.

2019). On the southern coast of Hokkaido, however, only one relatively comprehensive study was performed, in the early 1990s (Yamamura et al. 1993). Oceanic conditions, such as water temperature and salinity may affect fish diets (Shehata et al. 2017). In recent years, anomalous oceanic conditions in summer during 2010–2016 (Miyama et al. 2021), and shifts in the abundance of some species, such as walleye pollock (Ishino et al. 2022) and Japanese sardine (*Sardinops melanostictus* (Furuichi et al. 2022)), have been observed off the southern coast of Hokkaido. In the context of these fluctuations in biotic and abiotic conditions in this marine ecosystem, it is necessary to conduct continuous observations of the feeding habits of Pacific cod. Therefore, the main objective of this study is to provide updated information on the feeding ecology of Pacific cod off the southern coast of Hokkaido. Furthermore, the results from this study will be useful for analyses of energy flow in the food web and provide information to make ecosystem-based fisheries management policies. To this end, the diet composition, ontogenetic and annual variations in diet, and feeding strategy of Pacific cod were examined via stomach contents analysis.

2 Material and methods

2.1 Field sampling

Pacific cod used for stomach contents analysis were collected from five cruises of the ocean research vessel Kaiyo Maru No. 5 during 2016–2020. Bottom trawl surveys were generally conducted from late June to early July along the southern coast of Hokkaido (Fig.1). A trawl net (50.65 m long with a cod end 11-mm mesh) was towed at a speed of 4.6–6.5 km/h at each station. The width and height of the net were 16.5 and 5.5 m, respectively. Fishing depth ranged from 50.3 to 477 m. Towing duration generally varied between 5 and 10 minutes, according to backscattering strength and sea floor roughness (monitored by an echosounder). On board, up to 20 Pacific cod individuals were randomly selected from the overall catch. Then, standard length (SL) and total weight were measured to the nearest 1 mm and 1 g, respectively. After dissection, stomachs, livers, and gonads were removed and weighed to within 0.1 g. The whole stomachs were frozen or preserved in 10% buffered formalin and then stored until further analysis. Thereafter, eviscerated weight was determined to the nearest 1 g. Longitude, latitude, and trawling depth were recorded at each trawling station. Data on water temperature and salinity, from the surface to bottom were collected using a conductivity, temperature and depth (CTD) profiler cast at predefined stations with a 1 m resolution (Fig.1).

2.2 Stomach contents analysis

In the laboratory, each stomach was opened and rinsed with water. Subsequently, food masses were examined and sorted based on morphological characteristics, under a stereomicroscope or macroscopically. All prey items were identified to the lowest possible taxonomic level and weighed to the nearest 0.01 g after draining off excess water by suction; those unable to be identified due to over-digestion were recorded as digested materials. In addition, the maximum lengths of intact prey items were measured to the nearest 0.01 mm using a vernier caliper.

2.3 Diet characterization methods

A cumulative prey curve was generated to determine whether the sample size was sufficient to describe the diet composition of Pacific cod. Stomach content data were randomized and permuted 100 times. The mean number of cumulative prey species was plotted against the cumulative number of analyzed stomachs using the vegan 2.6.2 R package (Oksanen et al. 2020). A line was fitted through the final 10 data points. If the slope of the fitted line was ≤ 0.05, the sample size was considered sufficient (Baremore et al. 2009).

The contribution of each food item or category to the diet of Pacific cod was quantified as the percent wet weight ($\%W_i$ = weight of prey $i \times 100$ / total weight of all prey) and frequency of occurrence ($\%F_i$ = number of stomachs containing prey $i \times 100$ / total number of non-empty stomachs).

However, the gravimetric method easily overemphasize the contribution of single heavy prey items and underestimate those too small to be weighted (George and Hadley 1979). Therefore, the index of relative importance (IRI) was also calculated for each prey item *i* (IRI_i = $\%W_i \times \%F_i$) and then standardized to a percentage value, %IRI = IRI / ΣIRI × 100 (Pinkas et al. 1971).

In this study, ontogenetic variation in diet composition was investigated by grouping specimens into five SL classes [≤ 300 mm, 301–400 mm (age 2–3 years), 401–500 mm (age 3–4 years), 501–600 mm (age 4–5 years), and > 600 mm] based on the length–age relationship for Pacific cod inhabiting the area off the southern coast of Hokkaido (Hattori et al. 1992b). To analyze the ontogenetic variation in feeding diversity, the number of prey species in each stomach was counted for fish belonging to the five size groups. Dietary diversity was also assessed using the Shannon–Weiner index ($H = \Sigma P_i \times \log P_i$, where P_i is the gravimetric proportion of prey *i*), which was calculated for each SL class and each year. Empty stomachs, and those containing only digested material, were not included in the diet analysis.

2.4 Statistical analyses

2.4.1 Univariate analyses

Interannual variations in the SL of Pacific cod and walleye pollock consumed by Pacific cod were assessed using the nonparametric Kruskal–

Wallis test, followed by the Wilcoxon rank sum test. A Chi-square test was performed to determine if the proportion of Pacific cod that consumed a different number of prey species was significantly different among size classes. To examine the variation in prey size limit with the increase in Pacific cod SL, the relationship between prey size and Pacific cod SL was analyzed by quantile regression analysis using the quantreg 5.93 R package (Koenker 2022). The prey items with more than 10 length measurements were included in the quantile regression analysis. The significance of Pacific cod SL versus prey length relationships at the 10th and 90th quantiles was evaluated using 'summary' function with 'boot' method.

2.4.2 Multivariate analyses

To compliment the aforementioned analyses, constrained analysis of principal coordinates (CAP), also known as distance-based redundancy analysis, dbRDA (Legendre and Andersson 1999), was used to examine the variability in prey occurrence of Pacific cod. The CAP model was constructed using the vegan 2.6.2 R package (Oksanen et al. 2020). A Jaccard distance matrix was computed from prey presence/absence data. In the CAP model, continuous explanatory variables included longitude, latitude, temperature, salinity, trawling depth, and SL. Data on temperature and salinity at trawling depth were obtained from the nearest CTD station. All continuous variables were normalized. Year was included as a categorical variable. Multicollinearity between explanatory variables was evaluated by checking the variance inflation factor (VIF). A VIF value $\leq$

10 indicates that the independent variables are not significantly correlated. A forward selection procedure based on the adjusted R^2 statistic was used to identify the most parsimonious CAP model. The total variance explained by the constraints, and significance thereof, was evaluated using a permutation-based ANOVA test (999 permutations). Specimens with empty stomachs or containing only digested material, and those with missing values for any explanatory variable, were not included in the CAP model. All statistical analyses were performed using R 4.0.4 statistical software (R Core Team 2021). All graphs were plotted using the ggplot2 3.3.6 R package (Wickham 2016).

3 Results

3.1 Body size distribution of fish

A total of 1,302 Pacific cod specimens were collected from 150 stations for stomach contents analysis, including 50 (3.84%) empty stomachs (Fig. 1, Table 1). Pacific cod body length ranged from 127 to 977 mm SL. The Kruskal–Wallis test showed significant differences in SL among the five surveyed years ($\chi^2 = 175.66$, df = 4, $P < 0.05$). Specifically, Pacific cod SL was significantly smaller and larger in 2016 and 2020, respectively. No significant difference was detected among 2017, 2018, and 2019 (Wilcoxon rank sum test, $P > 0.05$).

3.2 Diet composition

The slope of the fitted line based on the final 10 points from cumulative prey curve (Fig. S1) was 0.02 (< defined 0.05), indicating that the sample size was sufficient to describe the diet composition of Pacific cod. Pacific cod fed on a wide variety of prey, comprising at least 63 species (13 taxonomical groups; Table 2). For all years combined, fish was the dominant prey category, with %IRI ranging from 57.5 in the 301–400 mm size class to 99.6 in the > 600 mm size class. Among the 30 fish species identified, the %IRI of walleye pollock was highest in the ≤ 300 and > 600 mm SL size classes, at 74.4 and 55.9, respectively. Japanese lanternfish

(*Notoscopelus japonicus*) and Japanese sardine accounted for 37.5 and 61.8 of %IRI in the 400–500 and 500–600 mm SL size classes, respectively. Decapod crustaceans also played an important role in the diet of Pacific cod, especially for the < 400 mm SL size class (14.2–24.1 %IRI). Polychaetes (10.5–39.7, %F), amphipods (11.2–55.2, %F), and decapod crustaceans (18.9–65.8, %F) frequently occurred in stomachs, although their overall contribution in terms of weight was rather limited (≤ 15.4%).

3.3 Ontogenetic and annual variation in diet

The diet composition of Pacific cod varied with SL (Fig. 2). Fish ≤ 400 mm SL preyed mainly on decapod crustaceans, polychaetes, and amphipods. The weight percentages of these prey items gradually decreased with increasing predator body length. Meanwhile, the proportion of fish in the diet increased. Individuals in the > 600 mm SL class fed almost entirely on fish, with %W ranging from 97.1 to 99.4 during 2017–2020. No fish prey was observed in the diet of Pacific cod ≤ 300 mm SL in 2020, when amphipods accounted for 94.7%. In addition, the weight percentages of Japanese sardine were higher in the > 400 mm SL size classes during 2018–2020 compared to 2016 and 2017. However, the situation was distinctly different in 2016. Fish was the most important prey category in all size classes, with walleye pollock being the predominant prey species. Additionally, the %W of fish was 86.3% in the smallest size class (≤ 300 mm SL) but only 55.3% in the > 600 mm SL class, which was far lower than in any other year. Moreover, the SL of consumed walleye pollock was significantly smaller in 2016 compared to other years ($\chi^2 = 85.25$, df = 4, $P < 0.05$), with an average value (± standard deviation) of 72.9 (± 27.3) mm SL.

3.4 Feeding strategy

Within the CAP model, there was no multicollinearity between explanatory variables (all VIF < 5). The most parsimonious CAP model included all variables except salinity, and explained about 10.8% of the total variance ($F_{9,\,1161} = 16.758$, $P < 0.01$). The first two constrained axes account for 77.3% of the explainable variance (Fig. 3). SL was highly correlated with CAP1. With an increase in Pacific cod SL, the occurrences of walleye pollock, Japanese sardine, and Japanese lanternfish increased, while the occurrences of amphipods, decapods, and polychaetes declined. Longitude, latitude, and depth had the greatest impact on CAP2. In general, Pacific cod consumed amphipods, Japanese sardine, and Japanese lanternfish in the shallow northeast area. By contrast, the consumption of decapods, cephalopods, and polychaetes tended to occur in the deep southwest area. Pacific cod consumed more Japanese sardine and Japanese lanternfish in 2020. Temperature was a significant predictor but had little impact on the ordination. Other prey items were located near the origin, indicating that the constraining variables had little influence on the occurrence of these prey types.

The proportion of Pacific cod that consumed a different number of prey species was significantly different between size classes ($\chi^2 = 120.43$, df = 28, $P < 0.01$). The proportions of Pacific cod that simultaneously consumed over four prey species were higher for 301–400 (29%) and 401–500 (32%) mm SL classes than the proportions for other size classes (≤ 300 mm, 11%; 501–600 mm, 12%; > 600 mm, 8%). Moreover, the lowest Shannon–

Weiner diversity index values were observed in the ≤ 300 mm class in 2016 and 2020, and in the > 600 mm class during 2017–2019 (Fig. 4).

Quantile regression analysis indicated that prey length was positively correlated with Pacific cod SL at the 10th quantile (*t* = 20.11, $P < 0.001$) and 90th quantile (*t* = 10.07, $P < 0.001$) (Fig. 5). A total of 656 prey items were measured: 150 walleye pollock; 159 Japanese sardine; 148 Japanese lanternfish and 199 other prey (mainly decapods). The size range of walleye pollock, Japanese sardine and Japanese lanternfish was 37.1–428.3 mm, 112.8–220 mm, and 105.5–183.5 mm, respectively. Decapods primarily influenced the Pacific cod versus prey size relationship at the 10th quantile.

4 Discussion

It has been over 20 years since the last study was conducted on the diet of Pacific cod along the southern coast of Hokkaido (Yamamura et al. 1993). In the present study, we found significant interannual differences in the SL of Pacific cod. The differences in SL were related to the age composition of the population. It has been reported that the estimated abundance of age 1–2 Pacific cod accounted for over 80% of the population in 2016 and less than 65% in 2020, while the proportions for other years (2017–2019) ranged between 70–80% (Chimura et al. 2022). Laboratory experiments about thermal sensitivity have demonstrated the growth of juvenile Pacific cod was positively correlated with water temperature in the range of 2–11°C (Hurst et al. 2010). During our surveys, the temperature range was 1.5–11.1°C in 2016, while it was mainly between 1 and 8.2°C during 2017–2020. Given the optimal temperature range for growth in the laboratory and the temperature ranges in our field study, it is likely that the favourable thermal condition contributed to the high recruitment of Pacific cod in 2016. A representative sample with sufficient specimens is required to describe the diet composition of fish by the means of stomach contents analysis. In the present study, the Pacific cod SL covered a wider range than in the previous study (Yamamura et al. 1993), which included 336 Pacific cod ranging from 167 to 902 mm SL. Moreover, the sample size was sufficient to describe the diet of Pacific cod, as indicated by the cumulative prey curve reaching asymptote. Compared to Yamamura et al. (1993), our study has a more representative sample size and length range offering a better representation of the Pacific cod population off the southern coast of Hokkaido.

We found that the feeding intensity of Pacific cod was relatively high in summer. Among the 1,302 stomachs analyzed, 1,252 (96.2%) contained at least one prey item, similar to the percentage obtained in the previous study conducted off the eastern Hokkaido (94.1%) (Yamamura et al. 1993). High feeding intensity in summer may be related to the reproductive cycle of this species. From April to August, female individuals mature from the yolkless to yolk vesicle phase (Hattori et al. 1992a). The adult Pacific cod prepare for spawning by frequent predation. Meanwhile, small Pacific cod may feed actively to sustain energetic demands for fast growth, which could contribute to a smaller chance of being preyed upon by size-selective predators in the ecosystem. Consistent with previous study (Yamamura et al. 1993), we also found that walleye pollock was a predominant prey for Pacific cod. High feeding intensity of Pacific cod may impose a negative impact on the recruitment of walleye pollock. Along the southern coast of Hokkaido, walleye pollock spawned around the mouth of Funka Bay (Nakatani 1988), and juveniles migrated into south-eastern coast of Hokkaido for feeding during their first summer (Nishimura et al. 2002). This increased geographic overlap between Pacific cod and juvenile walleye pollock. In the present study, the standard length of walleye pollock consumed by Pacific cod mainly ranged from 59.6 (0.1 quantile) to 298.9 mm (0.9 quantile) SL. It has been reported that walleye pollock grew to 303.7–385.1 mm in fork length at age 3 in the western Gulf of Alaska (Hughes and Hirschhorn 1979). The mean total length of walleye pollock larvae reached over 60 mm in July in Funka Bay (Nakatani 1988). Therefore, we speculate that walleye pollock from larvae phase to about age 3 were available prey for Pacific cod in our investigated area.

In the present study, the diet of Pacific cod comprised at least 63 prey species, with fish and decapod crustaceans as predominant prey categories. This result was similar to the former study, which identified 70 prey taxa (Yamamura et al. 1993). However, only 25 species were found in the stomachs of Pacific cod caught from the western coastal of Korea (Choi et al. 2019). The diet of Pacific cod inhabiting the Kuril–Kamchatka region included 99 species (Poltev and Stominok 2008). Regional differences in the number of prey species utilized by Pacific cod suggest that their diet composition is determined by food availability in the habitat. In our study, there were spatial variations in the diet of Pacific cod. Japanese sardine was more likely to be consumed in the shallow northwest area, while decapods, polychaetes, cephalopods, and walleye pollock were frequently part of the diet of Pacific cod collected in the deep southeast area. This was likely related to the spatial distribution of prey species. Japanese sardine migrates into the Doto region for feeding (Watanabe et al. 1995), which may increase the geographic overlap with Pacific cod. The feeding ecology of Pacific cod has been studied in various areas. In the eastern Bering Sea, crabs, sand-dwelling worms, walleye pollock, and several flatfishes were frequently consumed by Pacific cod (Suyehiro 1934; Lang et al. 2005). In

Pavlof Bay, western Gulf of Alaska, pink shrimp frequently occurred in the stomachs of Pacific cod (Albers and Anderson 1985). On the eastern coast of the northern Kuril Islands and southern Kamchatka, fish were the most important prey, followed by cephalopods and fishery discards (Poltev and Stominok 2008). On the west coast of the Yellow Sea of Korea, fish and carid shrimps were the predominant prey for Pacific cod (Choi et al. 2019).

We examined diet composition over several years (2016–2020). In 2016, the diet composition was distinct compared to other years. Walleye pollock played an important role in Pacific cod diets, especially the smallest size class (≤ 300 mm). This interannual variation in feeding strategy may be related to fluctuations in food abundance. The estimated walleye pollock recruitment was higher in 2016 than the other surveyed years (Ishino et al. 2022). The higher recruitment may have been related to the relatively high water temperature recorded in 2016, because it has been confirmed that sea surface temperature is positively correlated with walleye pollock recruitment (Funamoto et al. 2013). Furthermore, the SL of walleye pollock consumed in 2016 was significantly smaller compared to other years, similar to Pacific cod. Combined with the result of quantile regression analysis, the phenomenon of small walleye pollock frequently being used by small Pacific cod indicates size-dependent feeding habits. Increasing prey size with Pacific cod size has also occurred in the eastern Bering Sea, where the carapace width of snow crab (*Chionoecetes opilio*) in stomachs increased with Pacific cod size (Burgos et al. 2013). Notably, a pelagic fish, the Japanese sardine, played a more important role in the diet of Pacific cod between 2018 and 2020 than in the previous study (Yamamura et al. 1993). This may be related to the fact that the biomass and recruitment of walleye pollock stock have been decreasing since the 1990s, and fluctuated in recent years (Ishino et al. 2022), while the stock of Japanese sardine has tended to increase in the western North Pacific (Niino et al. 2021; Furuichi et al. 2022). Japanese lanternfish undergo diel vertical migration (Watanabe et al. 1999), and thus may be more vulnerable to Pacific cod at certain times.

In the early 1990s, threadfin hakeling (*Laemonema longipes*) was a more important prey species than Japanese sardine for Pacific cod ≥ 601 mm SL (Yamamura et al. 1993). This species, however, did not appear in the present study. The reason for this phenomenon is unclear, but is probably related to the fluctuations in the abundance of prey species. The abundance of Japanese sardine has increased in recent years (Niino et al. 2021; Furuichi et al. 2022). In the present study, Pacific cod ≥ 600 mm SL tended to prey on the abundant pelagic Japanese sardine. This may reduce the spatial overlap between Pacific cod and demersal threadfin hakeling. Moreover, in the Pacific waters around northern Japan, the fatness of Japanese sardine was relatively high during summer (Kawabata et al. 2011). This result reflects Pacific cod are likely able to actively select optimal prey species in the habitat. The feeding selectivity of two gadoid species, Atlantic cod (*Gadus morhua* (Rowlands et al. 2008)) and walleye pollock (Adams et al. 2007), have been reported. However, the prey selectivity of

Pacific cod requires further confirmation. Compared to the previous study conducted off the eastern Hokkaido (Yamamura et al. 1993), the diet composition of Pacific cod has changed. These variations are noteworthy because the diet data is critical for constructing food web models, such as Ecopath (Polovina 1984; Lima et al. 2020).

Taken together with previous studies conducted in the North Pacific (Albers and Anderson 1985; Yamamura et al. 1993; Poltev and Stominok 2008; Choi et al. 2019), spatiotemporal and ontogenetic variations in the diet of Pacific cod exist, but fish and decapod crustaceans were always the most important prey items. Moreover, some small prey species, such as euphausiids and echinoderms, were also found in the stomachs of Pacific cod > 500 mm SL in the present study, confirming that Pacific cod is an opportunistic predator off the southern coast of Hokkaido.

Knowledge of the ontogenetic variation in fish diet helps clarify intraspecific food resource utilization tactics in the ecosystem. It is common for the diet composition of fish to change with increasing body size, mainly due to superior swimming performance and hunting ability (e.g., Yamamura et al. 2002; Temperoni et al. 2021). In this study, the diet of Pacific cod tended to gradually shift from decapods to fish after reaching ~400 mm SL. Poltev and Stominok (2008) reported that the dominant prey shifted from crustaceans to fish when the body length of Pacific cod reached ~36–45 cm. On the other hand, copepods were the predominant prey for Pacific cod juveniles in Mutsu Bay, Japan (Takatsu et al. 2002). Juveniles (42–110 mm fork length) mainly fed on small calanoid copepods, mysids, and gammarid amphipods near Kodiak, Alaska (Abookire et al. 2007). Small organisms, such as amphipods and decapod crustaceans, are likely to be important for Pacific cod < 400 mm SL because they are digested more rapidly than large ones (Sikora et al. 1972). Accordingly, the predominant prey taxa of Pacific cod may vary from small gammarids and copepods during the juvenile phase (< 100 mm SL) to decapods (100–400 mm SL), before shifting to fish at about age 3 (> 400 mm SL).

The results regarding the proportions of stomachs including more prey species and variations in the Shannon–Weiner diversity index across SL classes further confirm that Pacific cod had a more opportunistic and generalized feeding strategy at about age 3 (~400 mm) than in other phases. The food spectrum of smaller fish is usually limited by the mouth gape size and swimming ability (Ingram and De Silva 2007; Temperoni et al. 2021). This limit probably also occurred in Pacific cod. Also, in support of ontogenetic dietary shifts, prey size increased significantly with Pacific cod SL. This feeding strategy is not uncommon in fish (e.g., Scharf et al. 2000; Dörner et al. 2007; Holt et al. 2019), and could mitigate intraspecific competition for food between size classes, when food availability is limited.

In conclusion, off the southern coast of Hokkaido, Pacific cod fed actively during summer and there were temporal and spatial variations in the diet composition. Japanese sardine played a more important role in their diet, and threadfin hakeling did not appear in the diet in recent years. Consistent with previous study (Yamamura et al. 1993), our data indicate that the diet of Pacific cod shifts through ontogeny. More specifically, the feeding habits varied significantly at about age 3 (~400 mm). However, we only collected Pacific cod specimens during summer; seasonal variations in the diet of Pacific cod inhabiting the southern coast of Hokkaido require further examination. Variations in the diet composition are likely related to the prey abundance and climate changes in the habitat. This research could inform food web models, as it provides updated information on the diet composition of Pacific cod. Furthermore, these results suggest the importance of continuous monitoring of the feeding ecology of ecologically important species in the context of environment changes. Be aware of changes in energy flow in the food web will enhance our ability to understand the mechanisms driving population dynamics and implement more sustainable fisheries management.

References

Abookire AA, Duffy-Anderson JT, Jump CM. 2007. Habitat associations and diet of young-of-the-year Pacific cod (*Gadus macrocephalus*) near Kodiak, Alaska. Marine Biology. 150:713–726. doi:10.1007/s00227-006-0391-4

Adams CF, Pinchuk AI, Coyle KO. 2007. Seasonal changes in the diet composition and prey selection of walleye pollock (*Theragra chalcogramma*) in the northern Gulf of Alaska. Fisheries Research. 84:378–389. doi:10.1016/j.fishres.2006.11.032

Albers WD, Anderson PJ. 1985. Diet of Pacific cod, *Gadus macrocephalus*, and predation on the northern pink shrimp, *Pandalus borealis*, in Pavlof Bay, Alaska. Fishery Bulletin. 83:601–610

Baremore IE, Murie DJ, Carlson JK. 2009. Seasonal and size-related differences in diet of the atlantic angel shark *Squatina dumeril* in the northeastern Gulf of Mexico. Aquatic Biology. 8:125–136. doi:10.3354/ab00214

Burgos J, Ernst B, Armstrong D, Orensanz JM. 2013. Fluctuations in range and abundance of snow crab (*Chionoecetes opilio*) from the eastern bering sea: What role for pacific cod (*Gadus macrocephalus*) predation? Bulletin of Marine Science. 89:57–81. doi:10.5343/bms.2011.1137

Chimura M, Sakai O, Chiba satoru N, Hamatsu T. 2022. Stock assessment and evaluation for Pacific cod (fiscal year 2021). Marine fisheries stock assessment and evaluation for Japanese waters. Japan Fisheries Agency and Japan Fisheries Research and Education Agency, Tokyo. 1–25

Choi D hyek, Sohn M ho, Kim MJ, Lee S jong. 2019. Feeding Habits of Pacific cod (*Gadus macrocephalus*) in the West Coast of Yellow Sea of Korea. Korean Journal of Ichthyology. 31:77–82. doi:10.35399/ISK.31.2.2

Christensen V, Walters CJ. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling. 172:109–139. doi:10.1016/j.ecolmodel.2003.09.003

Dörner H, Hülsmann S, Hölker F, Skov C, Wagner A. 2007. Size-dependent predator-prey relationships between pikeperch and their prey fish. Ecology of Freshwater Fish. 16:307–314. doi:10.1111/j.1600-0633.2006.00223.x

Draper DL. 2022. Food habit variability of arrowtooth flounder (*Atheresthes stomias*) along the U.S. west coast. Fisheries Research. 248:106205. doi:10.1016/j.fishres.2021.106205

Fissel B, Dalton M, Felthoven R, et al. 2017. Economic status of the groundfish fisheries off Alaska, 2016. Stock Assessment and Fishery Evaluation Report for the Groundfish Fisheries of the Gulf of Alaska and Bering Sea/Aleutian Islands Area. 1–488

Funamoto T, Yamamura O, Kono T, Hamatsu T, Nishimura A. 2013. Abiotic and biotic factors affecting recruitment variability of walleye pollock (*Theragra chalcogramma*) off the Pacific coast of Hokkaido, Japan. Fisheries Oceanography. 22:193–206. doi:10.1111/fog.12015

Furuichi S, Yukami R, Kamimura Y, Nishijima S, Watanabe R. 2022. Stock assessment and evaluation for Japanese sardine (fiscal year 2021), in Marine Fisheries Stock Assessment and Evaluation for Japanese Waters (fiscal year 2021/2022). Fisheries Agency and Fisheries Research and Education Agency of Japan. 1–50

George EL, Hadley WF. 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieui*) young of the year. Transactions of the American Fisheries Society. 108:253–261. doi:10.1577/1548-8659(1979)108<253:fahpbr>2.0.co;2

Goto Y, Wada A, Hoshino N, Takashima T, Mitsuhashi M, Hattori K, Yamamura O. 2017. Diets of Steller sea lions off the coast of Hokkaido, Japan: An inter-decadal and geographic comparison. Marine Ecology. 38:1–22. doi:10.1111/maec.12477

Gray BP, Bishop MA, Powers S. 2021. Winter variability in the diets of groundfish inhabiting a subarctic sound with a focus on Pacific herring and walleye pollock piscivory. Deep-Sea Research Part II: Topical Studies in Oceanography. 194:104984. doi:10.1016/j.dsr2.2021.104984

Hattori T, Sakurai Y, Shimazaki K. 1992a. Maturation and reproductive cycle of female Pacific cod in waters adjacent to the southern coast of

Hokkaido, Japan. Nippon Suisan Gakkaishi. 58:2245–2252. doi:10.2331/suisan.58.2245

Hattori T, Yasunori S, Kenji S. 1992b. Age determination by sectioning of otoliths and growth pattern of Pacific Cod. Nippon Suisan Gakkaishi. 58:1203–1210. doi:10.2331/suisan.58.1203

Holt RE, Bogstad B, Durant JM, Dolgov A V, Ottersen G. 2019. Barents Sea cod (*Gadus morhua*) diet composition: long-term interannual, seasonal, and ontogenetic patterns. ICES Journal of Marine Science. 76:1641–1652. doi:10.1093/icesjms/fsz082

Hughes SE, Hirschhorn G. 1979. Biology of walleye pollock, *Theraga chalcogramma*, in the western Gulf of Alaska, 1973-75. Fishery Bulletin. 77:263–274

Hüne M, Davis E, Murcia S, Gutiérrez D, Haro D. 2018. Trophic relationships of a subtidal fish assemblage in the Francisco Coloane Coastal Marine Protected Area, southern Chilean Patagonia. Polar Research. 37:. doi:10.1080/17518369.2018.1435107

Hurst TP, Laurel BJ, Ciannelli L. 2010. Ontogenetic patterns and temperature-dependent growth rates in early life stages of pacific cod (*Gadus macrocephalus*). Fishery Bulletin. 108:382–392

Hyslop EJ. 1980. Stomach contents analysis—a review of methods and their application. Journal of Fish Biology. 17:411–429. doi:10.1111/j.1095-8649.1980.tb02775.x

Ingram BA, De Silva SS. 2007. Diet composition and preference of juvenile Murray cod, trout cod and Macquarie perch (Percichthyidae) reared in fertilised earthen ponds. Aquaculture. 271:260–270. doi:10.1016/j.aquaculture.2007.06.012

Ishino M, Sakai O, Chimura M, Kawamura M, Chiba satoru N, Narimatsu Y, Hamatsu T. 2022. Stock assessment and evaluation for walleye pollock (fiscal year 2021). Marine fisheries stock assessment and evaluation for Japanese waters. Japan Fisheries Agency and Japan Fisheries Research and Education Agency, Tokyo. 1–59

Jennings S, Warr KJ, Mackinson S. 2002. Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. Marine Ecology Progress Series. 240:11–20. doi:10.3354/meps240011

Kawabata A, Yamaguchi H, Kubota S, Nakagami M. 2011. Growth and fatness of 1975-2002 year classes of Japanese sardine in the Pacific waters around northern Japan. Fisheries Science. 77:291–299. doi:10.1007/s12562-011-0326-y

Koenker R. 2022. quantreg: Quantile Regression. R package version 5.88. https://CRAN.R-project.org/package=quantreg

Lang GM, Livingston PA, Dodd KA. 2005. Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1997 through 2001. NOAA Technical Memorandum NMFS-AFSC. 158:i–xvi, 1–230

Legendre P, Andersson MJ. 1999. Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. Ecological Monographs. 69:1–24. doi:10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2

Lima MAL, Doria CR, Carvalho AR, Angelini R. 2020. Fisheries and trophic structure of a large tropical river under impoundment. Ecological Indicators. 113:106162. doi:10.1016/j.ecolind.2020.106162

Mammel M, Wang Y-C, Lan Y-C, Hsu C-M, Lee M-A, Liao C-H. 2022. Ontogenetic diet shifts and feeding dynamics of *Trichiurus japonicus* Temminck & Schlegel, 1844, off Guishan Island, Southern East China Sea. Regional Studies in Marine Science. 49:102104. doi:10.1016/j.rsma.2021.102104

Mishima S. 1984. Stock assessment and biological aspects of Pacific cod (*Gadus macrocephalus* TILESIUS) in Japanese Waters. Bull Int North Pacific Fish Commission. 42:180–188

Miyama T, Minobe S, Goto H. 2021. Marine heatwave of sea surface temperature of the Oyashio region in summer in 2010–2016. Frontiers in Marine Science. 7:1–12. doi:10.3389/fmars.2020.576240

Nakatani T. 1988. Studies on the early life history of walleye pollock *Theragra chalcogramma* in Funka Bay and vicinity, Hokkaido. MEMOIRS OF THE FACULTY OF FISHERIES HOKKAIDO UNIVERSITY. 35:1–46

Niino Y, Furuichi S, Kamimura Y, Yukami R. 2021. Spatiotemporal spawning patterns and early growth of Japanese sardine in the western North Pacific during the recent stock increase. Fisheries Oceanography. 30:643–652. doi:10.1111/fog.12542

Nishimura A, Hamatsu T, Yabuki K, Shida O. 2002. Recruitment fluctuation and biological responses of walleye pollock in the Pacific coast of Hokkaido. Fisheries science. 68:206–209. doi:10.2331/fishsci.68.sup1_206

Oksanen J, Blanchet FG, Friendly M, et al. 2020. vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Pinkas L, Oliphant S, Iverson ILK. 1971. Food habits of albacore, bluefin tuna and bonito in California waters. Fish Bulletin. 152:1–105

Polovina JJ. 1984. Model of a coral reef ecosystem. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs. 3:23–27. doi:10.1007/bf00306137

Poltev YN, Stominok DY. 2008. Feeding habits the Pacific cod *Gadus macrocephalus* in oceanic waters of the Northern Kuril Islands and Southeast Kamchatka. Russian Journal of Marine Biology. 34:316–324. doi:10.1134/S1063074008050088

Quakenbush LT, Suydam RS, Bryan AL, Lowry LF, Frost KJ, Mahoney BA. 2015. Diet of beluga whales, *Delphinapterus leucas*, in Alaska from stomach contents, March-November. Marine Fisheries Review. 77:70–84. doi:10.7755/MFR.77.1.7

R Core Team. 2021. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. URL https://www.R-project.org/

Rowlands WL, Dickey-Collas M, Geffen AJ, Nash RDM. 2008. Diet overlap and prey selection through metamorphosis in Irish Sea cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*). Canadian Journal of Fisheries and Aquatic Sciences. 65:1297–1306. doi:10.1139/F08-041

Sakuma K, Yoshikawa A, Goto T, Fujiwara K, Ueda Y. 2019. Delineating management units for Pacific cod (*Gadus macrocephalus*) in the Sea of Japan. Estuarine, Coastal and Shelf Science. 229:106401. doi:10.1016/j.ecss.2019.106401

Savin AB. 2007. Seasonal migrations of pacific cod *Gadus macrocephalus* (Gadidae) off the eastern coast of Kamchatka. Journal of Ichthyology. 47:620–630. doi:10.1134/S0032945207080085

Scharf FS, Juanes F, Rountree RA. 2000. Predator size - Prey size relationships of marine fish predators: Interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Marine Ecology Progress Series. 208:229–248. doi:10.3354/meps208229

Shehata S, Ghanem M, Ragab A. 2017. Effect of some environmental factors on the food and feeding habits of the Cichlid fish, Tilapia zillii, inhabiting Lake Qarun, Egypt. Egyptian Academic Journal of Biological Sciences, B Zoology. 9:55–70

Sikora WB, Heard RW, Dahlberg MD. 1972. The occurrence and food habits of two species of hake, *Urophycis regius* and *U. floridanus* in Georgia Estuaries. Transactions of the American Fisheries Society. 101:513–525. doi:10.1577/1548-8659(1972)101<513:toafho>2.0.co;2

Suyehiro Y. 1934. Studies on the digestive system and the feeding habit of the important fishes of the North Pacific. I. The cods, *Gadus macroccphalus* Tilbsius and *Theragra chalcogramma* (Pallas). Nippon Suisan Gakkaishi. 3:8–16. doi:10.2331/suisan.3.8

Takatsu T, Nakatani T, Miyamoto T, Kooka K, Takahashi T. 2002. Spatial distribution and feeding habits of Pacific cod (*Gadus macrocephalus*) larvae in Mutsu Bay, Japan. Fisheries Oceanography. 11:90–101. doi:10.1046/j.1365-2419.2002.00193.x

Temperoni B, Barbini SA, Orlando P, Buratti CC. 2021. Ontogenetic diet shifts of rough scad *Trachurus lathami* in the North Patagonian shelf (south-west Atlantic Ocean). Journal of Fish Biology. 99:1832–1842. doi:10.1111/jfb.14884

Ueba Y, Kanno Y, Matsuishi T. 2004. Weight-based virtual population analysis of Pacific cod *Gadus macrocephalus* off the Pacific coast of southern Hokkaido, Japan. Fisheries Science. 70:829–838. doi:10.1111/j.1444-2906.2004.00876.x

Urban D. 2012. Food habits of Pacific cod and walleye pollock in the northern Gulf of Alaska. Marine Ecology Progress Series. 469:215–222. doi:10.3354/meps10135

Watanabe H, Moku M, Kawaguchi K, Ishimaru K, Ohno A. 1999. Diel vertical migration of myctophid fishes (Family myctophidae) in the transitional waters of the western North Pacific. Fisheries Oceanography. 8:115–127. doi:10.1046/j.1365-2419.1999.00103.x

Watanabe Y, Zenitani H, Kimura R. 1995. Population decline of the Japanese sardine *Sardinops melanostictus* owing to recruitment failures. Canadian Journal of Fisheries and Aquatic Sciences. 52:1609–1616. doi:10.1139/f95-154

Wickham H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York

Yamamura O, Honda S, Shida O, Hamatsu T. 2002. Diets of walleye pollock *Theragra chalcogramma* in the Doto area, northern Japan: Ontogenetic and seasonal variations. Marine Ecology Progress Series. 238:187–198. doi:10.3354/meps238187

Yamamura O, Watanabe K, Shimazaki K. 1993. Feeding habits of pacific cod, *Gadus Macrocephalus*, off eastern Hokkaido, north Japan. Proceedings of the NIPR Symposium on Polar Biology. 6:44–54. doi:10.15094/00005184

Yang MS. 2004. Diet changes of Pacific cod (*Gadus macrocephalus*) in Pavlof Bay associated with climate changes in the Gulf of Alaska between 1980 and 1995. Fishery Bulletin. 102:400–405

Table 1

Table 1. Number of sampling stations (N_S), sample size (N, with number of empty stomachs in parentheses), standard length (SL, mm; range), and mean ± standard deviation (SD) SL of Pacific cod.

Year	N_S	N	SL (mm)	Mean SL (mm) ± SD
2016	18	168 (9)	127–740	366.4 ± 113.0
2017	34	192 (15)	214–764	425.0 ± 115.1
2018	31	212 (10)	219–966	432.0 ± 136.0
2019	33	298 (5)	198–810	422.9 ± 121.4
2020	34	432 (11)	199–977	474.3 ± 121.2

Table 2

Table 2. Diet composition of 1,252 Pacific cod specimens collected off the southern coast of Hokkaido, showing percentage of weight (%W), frequency of occurrence (%F) and percentage of index of relative importance (IRI%). SL, standard length; +, <0.01.

Size classes in SL	**≤300 mm**			**301–400 mm**			**401–500 mm**			**501–600 mm**			**>600 mm**		
	%W	**%F**	**%IRI**	**%W**	**%F**	**%IRI**	**%W**	**%F**	**%IRI**	**%W**	**%F**	**%IRI**	**%W**	**%F**	**%IRI**
Coelenterata							**0.05**	**0.29**	**+**	**0.55**	**1.07**	**0.01**			
Actiniaria							0.05	0.29	+						
Hydrozoa										0.55	1.07	0.02			
Polychaeta	**4.84**	**29.33**	**3.48**	**7.58**	**39.67**	**7.14**	**3.19**	**32.37**	**1.68**	**1.17**	**17.11**	**0.25**	**0.13**	**10.49**	**0.02**
Aphroditidae				0.26	1.09	0.02	0.17	1.16	0.01				0.01	0.70	+
Polynoidae				0.17	0.54	0.01									
Polychaeta (digested)	4.84	29.33	5.77	7.14	38.04	20.79	3.02	31.50	6.49	1.17	17.11	0.84	0.13	9.79	0.04
Echiuroidea (digested)	**0.58**	**0.48**	**0.01**	**3.32**	**5.16**	**0.41**	**2.33**	**6.94**	**0.26**	**0.21**	**4.28**	**0.01**			
Gastropoda	**0.19**	**0.96**	**+**	**0.32**	**3.53**	**0.03**	**0.82**	**7.51**	**0.10**	**0.08**	**3.21**	**+**	**0.04**	**1.40**	**+**
Buccinidae	0.06	0.48	+	0.13	1.09	0.01	0.20	2.02	0.03	+	0.53	+			
Notaspidea	0.13	0.48	+	0.03	0.54	+									
Gastropoda (digested)				0.16	1.90	0.02	0.62	5.49	0.23	0.07	2.67	0.01	0.04	1.40	+

Bivalvia (digested)	**0.03**	**4.81**	**+**	**0.18**	**7.61**	**0.03**	**0.14**	**5.78**	**0.01**	**0.02**	**1.60**	**+**	**+**	**0.70**	**+**
Cephalopoda	**0.36**	**4.81**	**0.04**	**0.76**	**9.24**	**0.17**	**4.61**	**17.92**	**1.35**	**4.98**	**16.58**	**1.03**	**1.88**	**16.78**	**0.34**
Decapodiformes				0.26	1.09	0.02	0.38	2.02	0.05	0.50	0.53	0.01			
Gonatidae							0.07	0.87	+						
Paroctopus sp.	0.06	0.48	+	0.37	2.72	0.08	4.05	7.51	2.08	3.73	8.56	1.34	1.74	4.90	0.29
Rossia pacifica	0.13	0.48	+												
Cephalopoda (digested)	0.17	3.85	0.03	0.13	5.43	0.05	0.11	7.51	0.06	0.75	7.49	0.24	0.14	11.89	0.06
Mysidacea (digested)	**0.49**	**0.96**	**0.01**	**0.08**	**0.82**	**+**									
Isopoda	**0.41**	**8.17**	**0.08**	**0.12**	**2.99**	**0.01**	**0.06**	**2.02**	**+**	**+**	**0.53**	**+**	**+**	**0.70**	**+**
Anthuridea				0.02	0.54	+									
Ianiridae				+	0.54	+									
Isopoda (digested)	0.41	8.17	0.14	0.09	1.90	0.01	0.06	2.02	0.01	+	0.53	+	+	0.70	+
Amphipoda	**9.84**	**45.67**	**11.03**	**7.88**	**55.16**	**10.32**	**1.57**	**37.86**	**0.97**	**0.03**	**17.11**	**0.01**	**0.01**	**11.19**	**+**
Ampelisca sp.	4.24	17.31	2.99	2.73	20.38	4.26	0.28	8.67	0.17	0.01	4.81	+	+	3.50	+
Anonyx sp.	3.05	14.90	1.85	1.84	28.53	4.01	0.39	21.68	0.57	0.02	8.56	0.01	0.01	6.99	+
Gammaridea	2.37	17.31	1.67	3.18	16.03	3.91	0.90	8.38	0.51	+	3.74	+	+	2.10	+
Phronima atlantica				+	0.27	+									
Themisto japonica	0.18	4.33	0.03	0.12	4.89	0.05	0.01	3.18	+	+	1.07	+	+	0.70	+
Euphausiidae	**0.75**	**8.65**	**0.16**	**0.97**	**10.60**	**0.25**	**0.41**	**11.56**	**0.08**	**0.51**	**11.76**	**0.07**	**0.02**	**6.99**	**+**
Euphausia pacifica	0.12	4.33	0.02	0.59	5.71	0.26	0.18	8.09	0.10	+	5.35	+	+	4.20	+
Thysanoessa inermis	0.20	1.44	0.01	0.31	1.90	0.05	0.22	1.73	0.03	0.45	3.74	0.07	+	1.40	+

Euphausiidae (digested)	0.43	2.88	0.05	0.08	2.99	0.02	0.01	1.73	+	0.06	2.67	0.01	0.02	1.40	+
Decapoda	**14.65**	**39.42**	**14.18**	**15.42**	**65.76**	**24.09**	**5.92**	**54.62**	**5.27**	**0.76**	**28.88**	**0.27**	**0.20**	**18.88**	**0.04**
Hippolytidae	0.23	4.33	0.04	0.51	7.07	0.28	0.04	3.76	0.01	+	0.53	+	+	0.70	+
Pandalus sp.	0.56	0.96	0.02	0.47	1.36	0.05	0.23	3.47	0.05	0.07	2.67	0.01	0.01	2.10	+
Crangonidae	8.42	25.96	8.89	6.47	48.37	23.94	1.74	35.55	4.23	0.22	17.11	0.16	0.06	10.49	0.02
Argis lar	3.41	6.25	0.87	3.15	5.71	1.38	2.63	10.69	1.92	0.24	2.14	0.02			
Paracrangon echinata				0.03	0.27	+	0.05	0.58	+						
Paguridae	0.38	0.96	0.01	0.32	1.90	0.05	0.38	2.89	0.07	0.12	1.60	0.01			
Elassochirus cavimanus	0.56	0.48	0.01	2.74	2.72	0.57	0.20	2.02	0.03						
Pagurus trigonocheirus	0.50	0.96	0.02	0.58	2.45	0.11									
Erimacrus isenbeckii	0.11	0.48	+	0.18	1.09	0.02	0.03	0.87	+	0.06	1.60	+	0.04	0.70	+
Chionoecetes opilio				0.19	1.63	0.02	0.24	2.02	0.03	0.02	0.53	+			
crabs (digested)	+	0.48	+	0.16	1.09	0.01	0.12	2.02	0.02				0.07	0.70	+
shrimp (digested)	0.48	4.81	0.09	0.61	11.41	0.54	0.25	4.05	0.07	0.03	4.81	0.01	0.01	4.20	+
Echinodermata	**0.07**	**0.48**	**+**	**0.20**	**6.25**	**0.03**	**0.34**	**11.85**	**0.07**	**0.04**	**4.81**	**+**	**+**	**3.50**	**+**
Asteroidea							0.07	0.29	+						
Ophiuroidea	0.07	0.48	+	0.20	6.25	0.10	0.28	11.56	0.22	0.04	4.81	0.01	+	3.50	+
Pisces	**67.54**	**42.79**	**70.96**	**62.72**	**38.59**	**57.47**	**80.47**	**68.79**	**90.21**	**91.63**	**86.10**	**98.34**	**97.61**	**93.71**	**99.59**
Sardinops melanostictus				9.88	2.45	1.85	26.72	11.56	21.08	48.17	30.48	61.78	46.86	23.78	37.71
Diaphus kuroshio	0.31	0.48	0.01	0.28	0.54	0.01									
Diaphus theta										0.03	0.53	+			

Notoscopelus japonicus				24.14	6.79	12.55	29.23	18.79	37.47	17.24	17.65	12.80	8.83	17.48	5.23
Myctophidae				0.06	0.27	+	0.99	0.87	0.06	0.07	0.53	+			
Gadus chalcogrammus	60.40	30.29	74.42	16.31	7.07	8.82	9.63	6.94	4.56	17.58	21.93	16.22	33.71	48.95	55.86
Acantholumpenus mackayi													1.15	0.70	0.03
Arctoscopus japonicus													0.38	0.70	0.01
Ammodytes sp.	1.00	0.48	0.02							0.45	0.53	0.01			
Cottiusculus schmidti				0.19	0.82	0.01	0.29	1.45	0.03						
Cryptacanthoides bergi							1.17	1.16	0.09	0.63	1.07	0.03			
Davidijordania poecilimon				0.07	0.54	+	0.11	0.87	0.01				0.27	0.70	0.01
Lumpenus sagitta							1.38	1.45	0.14	0.94	1.60	0.06	0.18	1.40	0.01
Stichaeidae				0.11	0.27	+	0.28	0.58	0.01						
Stichaeus nozawai										1.14	1.07	0.05	1.37	1.40	0.07
Zoarcidae				0.05	0.27	+	0.04	0.29	+						
Auxis sp.													0.77	0.70	0.02
Scomber sp.													1.95	0.70	0.05
Aspidophoroides monopterygius							0.01	0.29	+						
Cottidae							0.31	0.29	0.01				0.03	0.70	+
Hemilepidotus sp.													0.82	0.70	0.02
Hemitripterus villosus							0.02	0.29	+						
Icelus cataphractus				1.02	0.54	0.04	0.59	0.58	0.02	0.16	0.53	+			
Myoxocephalus polyacanthocephalus							0.02	0.29	+						

Podothecus thompsoni				0.03	0.27	+									
Sarritor leptorhynchus							0.18	1.16	0.01						
Scorpaeniformes	0.03	0.48	+				0.64	0.87	0.04				0.08	0.70	+
Tilesina gibbosa							0.04	0.29	+						
Triglops jordani				0.81	0.54	0.03									
Glyptocephalus stelleri										0.01	0.53	+	0.17	2.10	0.01
Pisces (digested)	5.79	12.50	2.95	9.77	19.29	14.42	8.84	30.35	18.31	5.22	28.34	6.23	1.03	16.08	0.56
Digested matter	**0.26**	**4.81**	**0.03**	**0.44**	**5.98**	**0.06**	**0.09**	**3.18**	**+**	**0.01**	**1.60**	**+**	**0.09**	**2.10**	**+**

Figure captions

Figure 1. Sampling area and spatial distribution of trawl stations (colored points) and CTD stations (black points) off the southern coast of Hokkaido.

Figure 2. Percent wet weight of food items in the diet of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. The number of examined stomachs is shown above each bin. Other organisms include Coelenterata, Echiuroidea, Gastropoda, Bivalvia, Mysidacea, Isopoda, Euphausiidae, Echinodermata.

Figure 3. Constrained analysis of principal coordinates (CAP) triplot showing the influence of the selected constraints on prey occurrence in the diet of Pacific cod. The gray dots represent stomachs. The dominant prey taxa (> 10, %F) are labeled by name and a solid red triangle. Other prey taxa (< 10, %F) are represented by open triangles, including bivalves, Echinodermata, Echiuroidea, euphausiids, gastropods, and isopods. The blue arrows and dots represent continuous explanatory variables and the categorical variable “year”, respectively. The length of the vector is proportional to the importance to the ordination. The amount of constrained variance explained by each axis is given in parentheses after the axis label.

Figure 4. Shannon–Weiner diversity index of the prey species of Pacific cod grouped by body size class and years of sampling year.

Figure 5. Scatterplot and regression lines at the 10th and 90th quantiles for the relationship between prey size and standard length of Pacific cod. Others include Gammaridea, Hippolytidae, Crangonidae, *Lumpenus sagitta*, and *Cryptacanthoides bergi*.

Figure. 1

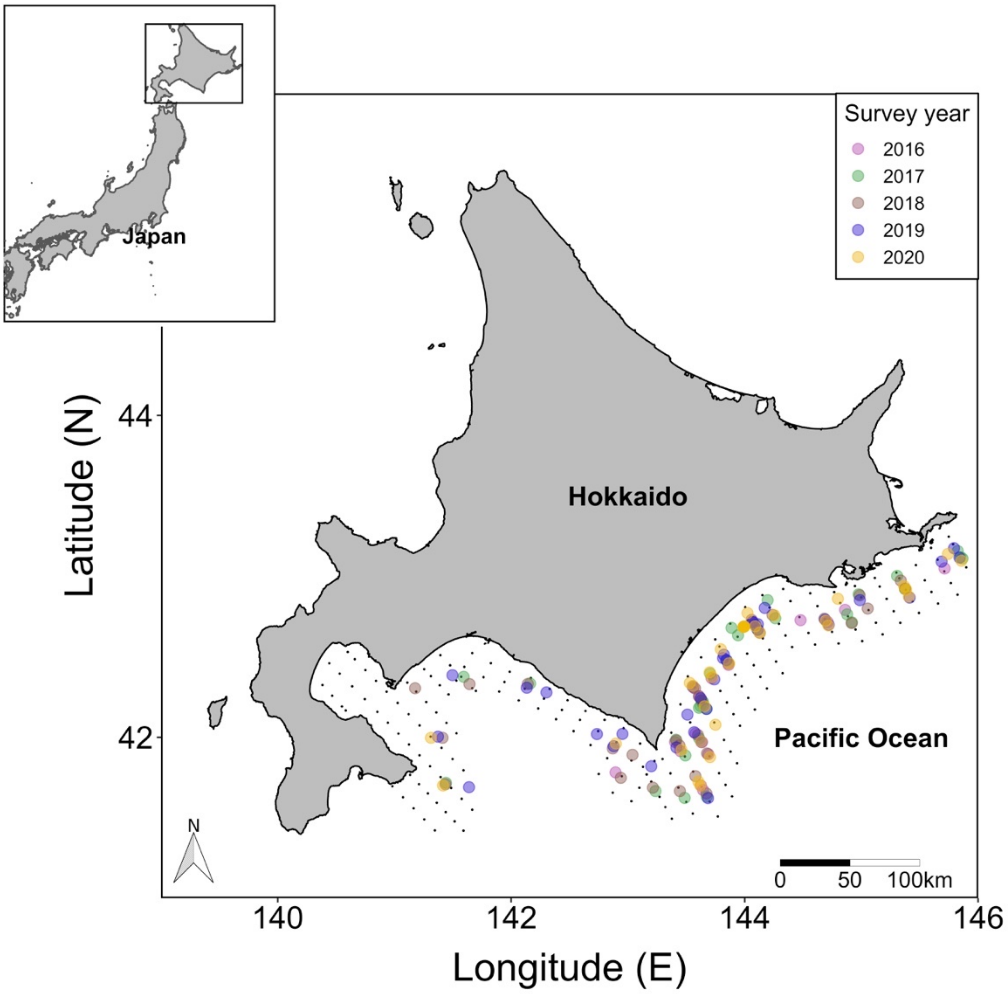

Figure 1. Sampling area and spatial distribution of trawl stations (colored points) and CTD stations (black points) off the southern coast of Hokkaido.

Figure. 2

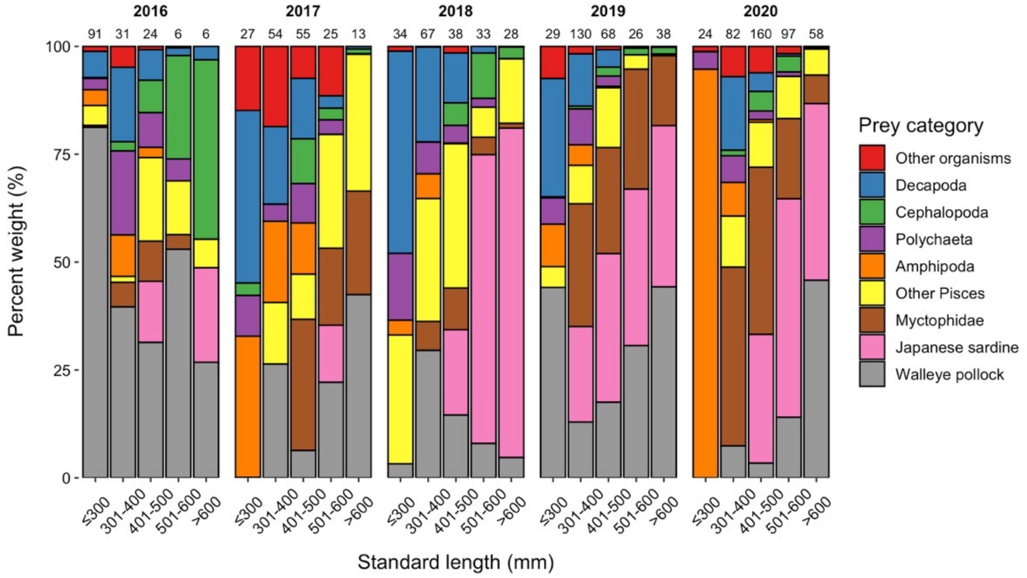

Figure 2. Percent wet weight of food items in the diet of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. The number of examined stomachs is shown above each bin. Other organisms include Coelenterata, Echiuroidea, Gastropoda, Bivalvia, Mysidacea, Isopoda, Euphausiidae, Echinodermata.

Figure. 3

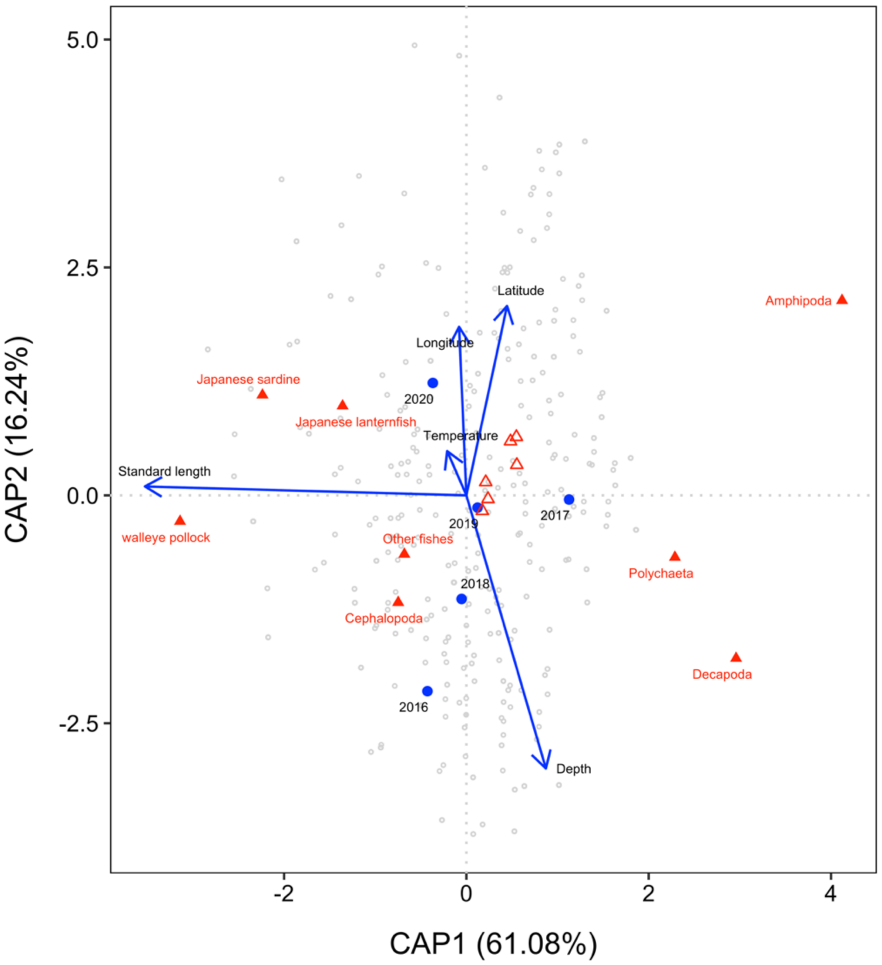

Figure 3. Constrained analysis of principal coordinates (CAP) triplot showing the influence of the selected constraints on prey occurrence in the diet of Pacific cod. The gray dots represent stomachs. The dominant prey taxa (> 10, %F) are labeled by name and a solid red triangle. Other prey taxa (< 10, %F) are represented by open triangles, including bivalves, Echinodermata, Echiuroidea, euphausiids, gastropods, and isopods. The blue arrows and dots represent continuous explanatory variables and the categorical variable "year", respectively. The length of the vector is proportional to the importance to the ordination. The amount of constrained variance explained by each axis is given in parentheses after the axis label.

Figure. 4

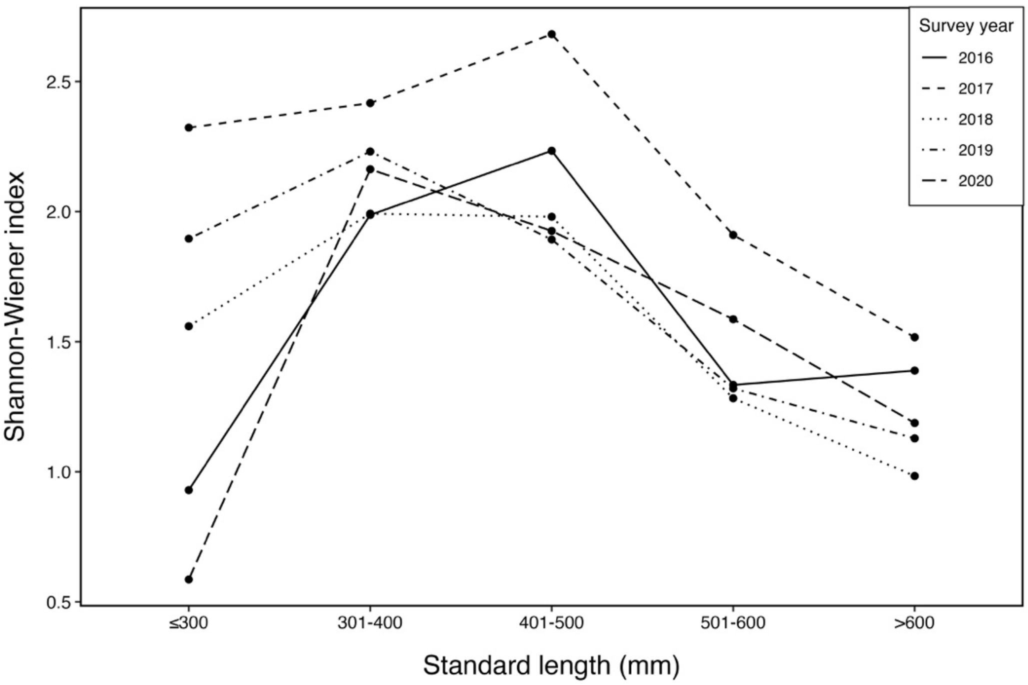

Figure 4. Shannon–Weiner diversity index of the prey species of Pacific cod grouped by body size class and years of sampling year.

Figure. 5

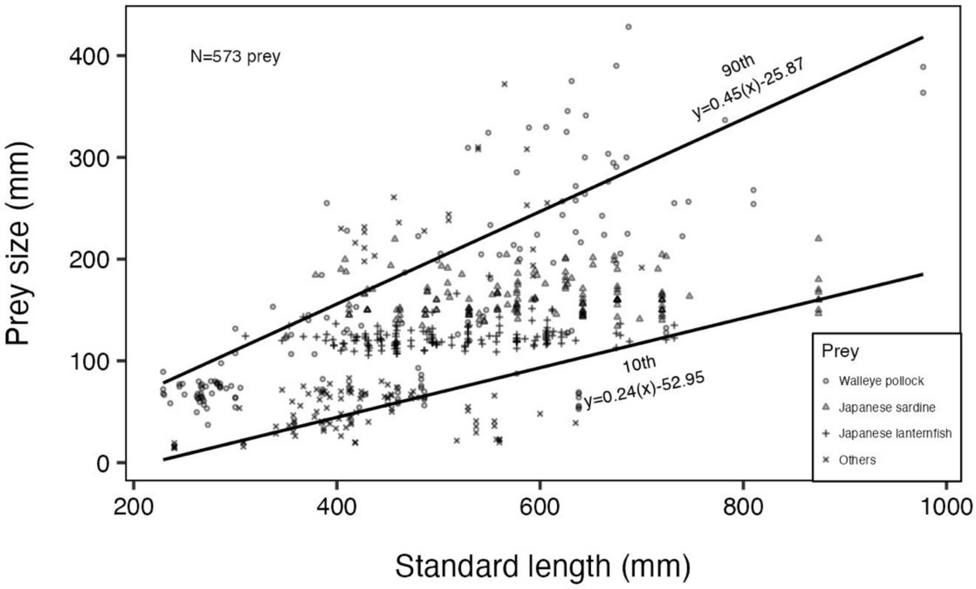

Figure 5. Scatterplot and regression lines at the 10th and 90th quantiles for the relationship between prey size and standard length of Pacific cod. Others include Gammaridea, Hippolytidae, Crangonidae, *Lumpenus sagitta*, and *Cryptacanthoides bergi*.