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Trophic ecology of Pacific cod *Gadus macrocephalus* off the southern and northeastern coasts of Hokkaido

（北海道南岸および北東岸沖合におけるマダラ *Gadus macrocephalus* の栄養生態に関する研究）

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Abstract

Feeding habits and nutritional condition of Pacific cod *Gadus macrocephalus* were investigated based on the 1,893 specimens collected in the waters off the southern coast of Hokkaido (SCH) during 2016–2020 and off the northeastern coast of Hokkaido (NCH) during 2018–2020. The results of stomach contents analyses indicated that Pacific cod ingest a variety of prey species, comprising 60 and 45 species in SCH and NCH, respectively. Fish was the most important prey in SCH (95.3, %IRI; relative important index) and NCH (68.6, %IRI), respectively. The dominant fish prey were Japanese sardine *Sardinops melanostictus* in SCH (36.7, %IRI) and walleye pollock *Gadus chalcogrammus* in NCH (35.1, %IRI). Pacific cod also preyed highly on decapod crustaceans, mainly snow crab *Chionoecetes opilio* (44.2, %IRI) in NCH. In SCH, the predominance of walleye pollock in 2016 (48.5, %W; percentage of wet weight) was replaced by Japanese sardine in 2018-2020 (36.3–65%, %W). Such temporal and spatial variations in the diets suggest that Pacific cod is a generalist and opportunistic feeder. The variation of prey species was great in the cod measured 300–500 mm SL, whose main diet gradually shifted from decapods to fish as they grow. The stomach fullness index was higher in the individuals feeding on Japanese sardine (SCH) and walleye pollock (NCH). In SCH, the maximum length of Japanese sardine found in

a stomach was 220 mm SL, which is likely close to the asymptotic body length of the species. Walleye pollock ranging 37–390 mm and 55–331 mm SL were ingestible prey for Pacific cod in SCH and NCH, respectively. The results of quantile analysis indicated that SL of walleye pollock was positively correlated with SL of Pacific cod. The carapace width of snow crab consumed by Pacific cod in NCH ranged from 5.5 to 61.3 mm.

The nutritional condition of Pacific cod was evaluated by means of length–weight relationship (LWR), condition factor (CF), and hepatosomatic index (HSI). Pacific cod generally exhibit an isometric growth pattern in the areas investigated, as the slopes in the LWRs approximated the value of 3. CF ranged from 0.84 to 1.66 for Pacific cod in SCH and from 0.91 to 1.6 in NCH. HSI ranged from 0.26% to 12.83% for Pacific cod in SCH and from 0.85% to 15.76% in NCH. HSI was positively correlated with SL in all seasons surveyed. In SCH, HSI of Pacific cod with Japanese sardine in the stomachs was significantly high (1.58–11.27%). In NCH, Pacific cod those consumed snow crab usually had lower HSI values than those consumed other prey species. Female and male Pacific cod showed similar nutritional conditions in both areas. CF and HSI of mature Pacific cod were higher than immature individuals in NCH during autumn. Individuals sampled from shallow water had higher HSI in SCH, but those sampled in high temperature had higher HSI in NCH.

Results presented herein will advance our understanding of the trophic ecology of Pacific cod and enhance our ability to make ecosystem-based management strategies.

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Chapter 1 General introduction

1.1 Study region

The area off the southern coast of Hokkaido (SCH) is a productive fishing ground formed by the interactions between distinct currents, mainly subarctic Oyashio and the subtropical Kuroshio currents (Yasuda 2003). Many commercially important fish species inhabit this transition region, including Pacific cod *Gadus macrocephalus*, walleye pollock *Gadus chalcogrammus*, Japanese sardine *Sardinops melanostictus* and Pacific saury *Cololabis saira* (Sakurai 2007). The formation of the fishing grounds of the pelagic species depends strongly on oceanographic conditions (Kuroda and Yokouchi 2017). However, it has been widely reported that environmental conditions fluctuated in recent years in these areas. For example, the southward intrusion of the cold Oyashio water on the slope off the Hokkaido coast became weakened or even disappeared in some summers during 1993–2014 (Kuroda et al. 2015; Kuroda and Yokouchi 2017). Moreover, the sea surface temperature and salinity of the Oyashio region increased abruptly in summers during 2010–2016 (Miyama et al. 2021).

Interannual variations in oceanographic conditions might directly or indirectly regulate the distribution and abundance of marine organisms by

formulating different types of habitat (Taki 2007; Kasugai et al. 2016; Kuroda and Yokouchi 2017). Fish, especially during early life stages, are sensitive to the climatic changes (Houde 1987; Rijnsdorp et al. 2009). In the case of Pacific cod, the size and growth of the larvae were affected by the temperature fluctuations in the North Pacific (Laurel et al. 2008). Pacific cod stocks dramatically declined after the abnormal marine heatwave occurred in the Gulf of Alaska during 2014–2016 (Laurel and Rogers 2020). Experiments conducted under laboratory conditions had confirmed that accumulating temperature and salinity had profound impacts on the hatchability and development of Pacific cod larvae (Forrester and Alderdice 1966; Alderdice and Forrester 1971; Bian et al. 2016). Moreover, the optimal temperature range for the survival of the early life stages of Pacific cod was approximately 4–6 °C (Bian et al. 2016). Pacific cod juveniles were rarely found at temperatures higher than 12 °C in Mutsu Bay (Takatsu et al. 2001). Summer distribution of Pacific cod was correlated with near bottom temperature in the eastern Bering Sea (Burgos et al. 2013). Besides abiotic conditions, food availability is also an important factor affecting the spatial distribution of Pacific cod (Poltev 2007).

1.2 Pacific cod

Pacific cod are widely distributed throughout the North Pacific Ocean

(Ketchen 1961; Shimada and Kimura 1994; Kanno et al. 2001; Ueda et al. 2004; Savin 2007; Orlova et al. 2019). In Japanese waters, Pacific cod are 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). The fishery catch of Pacific cod in SCH ranged between 20–30 thousand tons during 1985–1999 and decreased to 8.6 thousand ton in 2003, and then returned to a level of 15–20 thousand tons during 2011–2020 (Chimura et al. 2022). In the waters off the northern coast of Hokkaido (NCH), the production of Pacific cod drastically increased from 0.9–4.5 thousand tons during 1985–2015 to 10.2 thousand ton in 2017, and has been kept at high levels at 7.4–9.2 thousand tons during 2018–2020 (Sakai et al. 2022).

In SCH, some fraction of Pacific cod migrate to Mutsu Bay, one of the most important spawning grounds, during December to March (Miura et al. 2019). After spawning, Pacific cod gradually expands northward for feeding with the increase in water temperature in the spawning ground (Takatsu et al. 2001). Larvae and juveniles fed mainly on copepod nauplii, crustacean eggs, calanoid copepods, and gammarid amphipods in Mutsu Bay (Takatsu et al. 1995). Off the eastern coast of Hokkaido, Pacific cod measured 167–902 mm in body length preyed mainly upon decapod crustaceans and fish (Yamamura et al. 1993). In turn, adult Pacific cod are consumed by upper-level predators, such as halibut (Burger and Gochfeld

2007), beluga whales *Delphinapterus leucas* (Quakenbush et al. 2015), and Steller sea lions *Eumetopias jubatus* (Goto et al. 2017; Tollit et al. 2017). Thus, as an intermediate predator, Pacific cod play a critical role in maintaining trophic linkages in the food web.

1.3 Trophic ecology

This study focuses on two aspects of trophic ecology of Pacific cod, feeding habits and nutritional condition. Information on the feeding habits of fish is imperative to understand predator-prey relationships, which can inform constructing food web models and ecosystem-based fishery management (Frisch et al. 2014; da Silveira et al. 2020). Moreover, trophic interactions might have profound influences on the distribution and abundance of prey species. For example, the southern boundary of geographic distribution of snow crab *Chionoecetes opilio* in the eastern Bering Sea was controlled by the northward expansions of Pacific cod (Orensanz et al. 2004). Predation pressure on pink shrimp *Pandalus borealis* by Pacific cod probably caused the rebuild failure of the shrimp stock in Pavlof Bay (Albers and Anderson 1985). The feeding habits of Pacific cod has been examined in various marine ecosystems, including eastern Bering Sea (Livingston 1989; Orensanz et al. 2004; Rohan and Buckley 2017), Gulf of Alaska (Jewett 1978; Albers and Anderson 1985; Yang 2004; Abookire et al. 2006; Urban and Vining 2008; Marsh et al.

2012), off eastern Hokkaido Island (Yamamura et al. 1993), Shelikhov Bay of the Sea of Okhotsk (Napazakov 2008), northern Kuril Islands and southern Kamchatka (Poltev and Stominok 2008), Southeast Sea of Korea (Lee et al. 2015), and west coast of Korea (Choi et al. 2019). Results from these studies indicate Pacific cod preyed mainly on decapods and fish, and ontogenetic and spatio-temporal variations in the diet composition do exist.

Nutritional condition is a powerful index to describe the dynamic interactions within organisms and between environment conditions. As such, nutritional condition of fish has frequently been used to evaluate habitat quality (Lloret et al. 2002), and predict stock biomass. For example, overwinter mortality is low in juvenile Atlantic cod with high nutritional condition (Geissinger et al. 2022). Decrease in the nutritional condition of Atlantic cod *Gadus morhua* synchronized with the collapse of stock in the northern Gulf of St. Lawrence (Lambert and Dutil 1997b). Moreover, nutritional condition is closely related to the development of gonad in Gadoid fishes (Kjesbu et al. 1991; Alonso-Fernández et al. 2008; Narimatsu et al. 2010; Jiang et al. 2012). Past study reported that nutritional condition of Atlantic cod peaked in November and dropped to low level between March to May, when spawning was completed, and then gradually recovered by intensive feeding in June (Jangaard et al. 1967). The highest nutritional condition of female pouting *Trisopeterus luscus* was observed prior to peak spawning, and decreased to a minimum at the end of

spawning season, May and June (Alonso-Fernández et al. 2008). Furthermore, Pacific cod exhibit a similar annual energy cycle with Atlantic cod (Smith et al. 1990). Positive relationships between nutritional condition and potential fecundity were observed in both Pacific and Atlantic cods (Kjesbu et al. 1991; Narimatsu et al. 2010). These results highlight the importance of conducting monthly observation on the nutritional condition when studying reproductive strategy.

To date, information on the trophic ecology is very limited for Pacific cod in SCH and NCH. This formed the motivation for a comprehensive study of the feeding habits and nutritional condition of Pacific cod in these two areas. Therefore, this study aims to examine whether the diet composition has changed in SCH and compare the diet composition between SCH and NCH. Moreover, this study aims to provide latest information on the nutritional condition of Pacific cod in SCH and NCH.

Chapter 2 Feeding habits of Pacific cod *Gadus macrocephalus* off the southern and northeastern coasts of Hokkaido

2.1 Introduction

Elucidation of feeding ecology of fish is crucial to understand the trophic relationships among species coexisting in a marine ecosystem, and for constructing the food web models such as the Ecopath model (Polovina 1984). A series of methods has been used to study fish feeding ecology. Stomach content analysis permits a high degree of taxonomic level 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).

The feeding ecology of Pacific cod has attracted much attention, and has been examined in various marine ecosystems. In SCH, however, only

one relatively comprehensive study has been 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. 2021) and Japanese sardine (Furuichi et al. 2022), have been observed in SCH. In the context of fluctuations in biotic and abiotic conditions in this marine ecosystem, it is necessary to conduct continuous observations on the feeding habits of Pacific cod. On the other hand, there is no information about the feeding habits of Pacific cod in NCH. Therefore, the main objective of this chapter is to provide updated and novel information on the feeding ecology of Pacific cod in SCH and NCH, respectively. 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 by means of stomach content analysis.

2.2 Materials and methods

2.2.1 Field sampling

In SCH, Pacific cod were collected during five cruises of the fishery

research vessel Kaiyo Maru No. 5 in the period 2016–2020, hired by Japan Fisheries Research and Education Agency. Bottom trawl surveys were generally conducted from late June to early July. 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. A total of 225 trawls were conducted at depth between 29.3 and 477 m (Fig. 2.1, Table S1). Towing duration generally varied between 5 and 10 minutes, according to backscattering strength and sea floor roughness (monitored by an echosounder). In NCH, Pacific cod specimens were collected from a total of 84 bottom trawls conducted during 2018–2020 (Fig. 2.1, Table S2) on board FRV Kaiyo Maru No. 5 hired by the same agency as in SCH. The specification of the trawling net and towing method was same as in SCH. The depths trawled ranged between 72 and 614 m. Towing duration generally lasted 30 minutes at each station.

On board, Pacific cod specimens were randomly selected from the overall catch. The number of Pacific cod selected from each station ranged from 1 to 33 (Fig. 2.2, Fig. 2.3). In SCH, 1,278 Pacific cod were collected from 146 stations. There was no Pacific cod in the catches from 79 stations (Table 2.1). In NCH, 615 Pacific cod were collected from 71 stations. No Pacific cod was found in the catches of 13 stations (Table 2.2). 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 the nearest 0.1 g. Sex was identified by the morphological characteristics of gonad. The whole stomachs were stored until further analysis by frozen or preserved in a 10% buffered formalin sea water solution. Thereafter, eviscerated weight was determined to the nearest 1 g, recorded as body weight (BW). Longitude, latitude, towing depth and water temperature at the depth of net mouth were recorded at each trawling station.
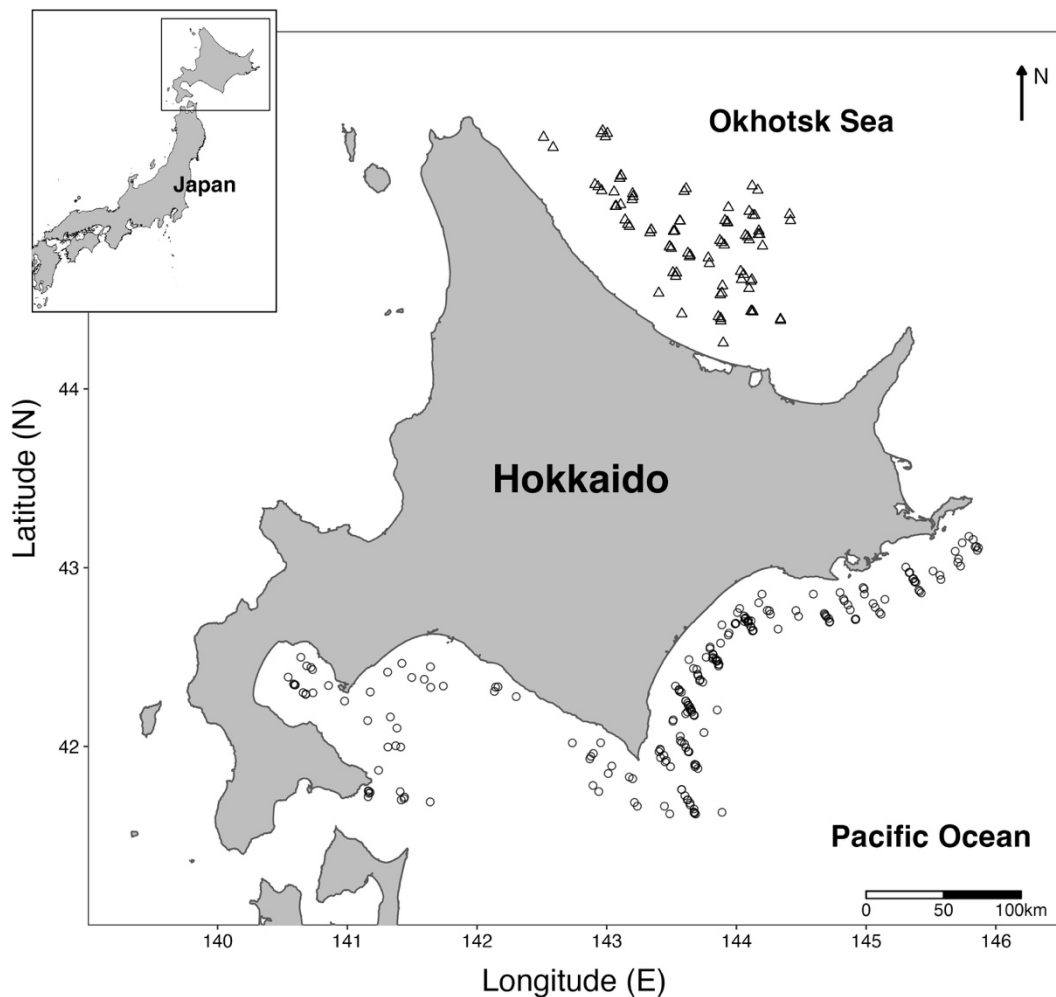
Fig. 2.1. Map showing the area surveyed and trawl locations off the southern (circles) and northeastern (triangles) coasts of Hokkaido.
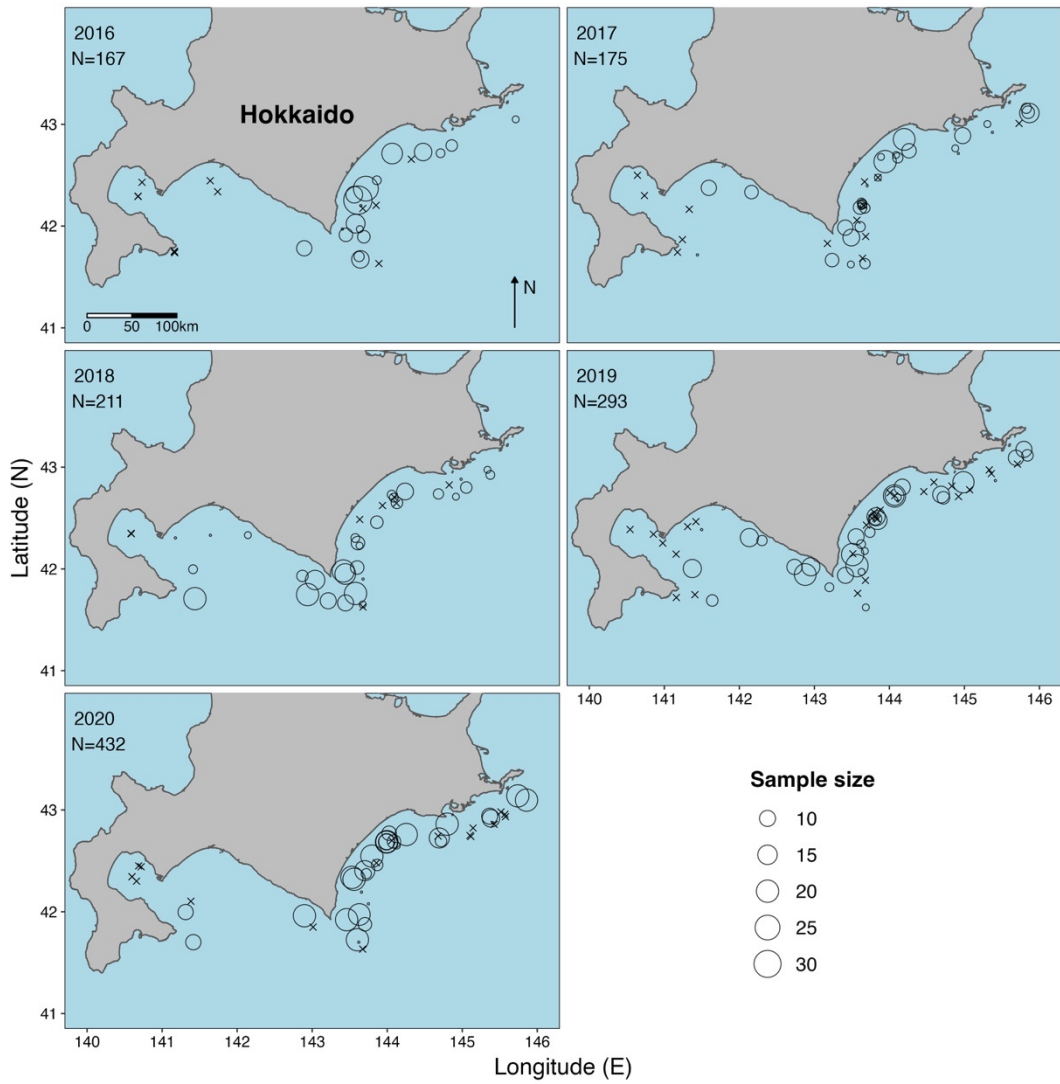
Fig. 2.2. Spatial distribution of the Pacific cod specimens off the southern coast of Hokkaido during 2016–2020. ×; no specimen was taken in that station.
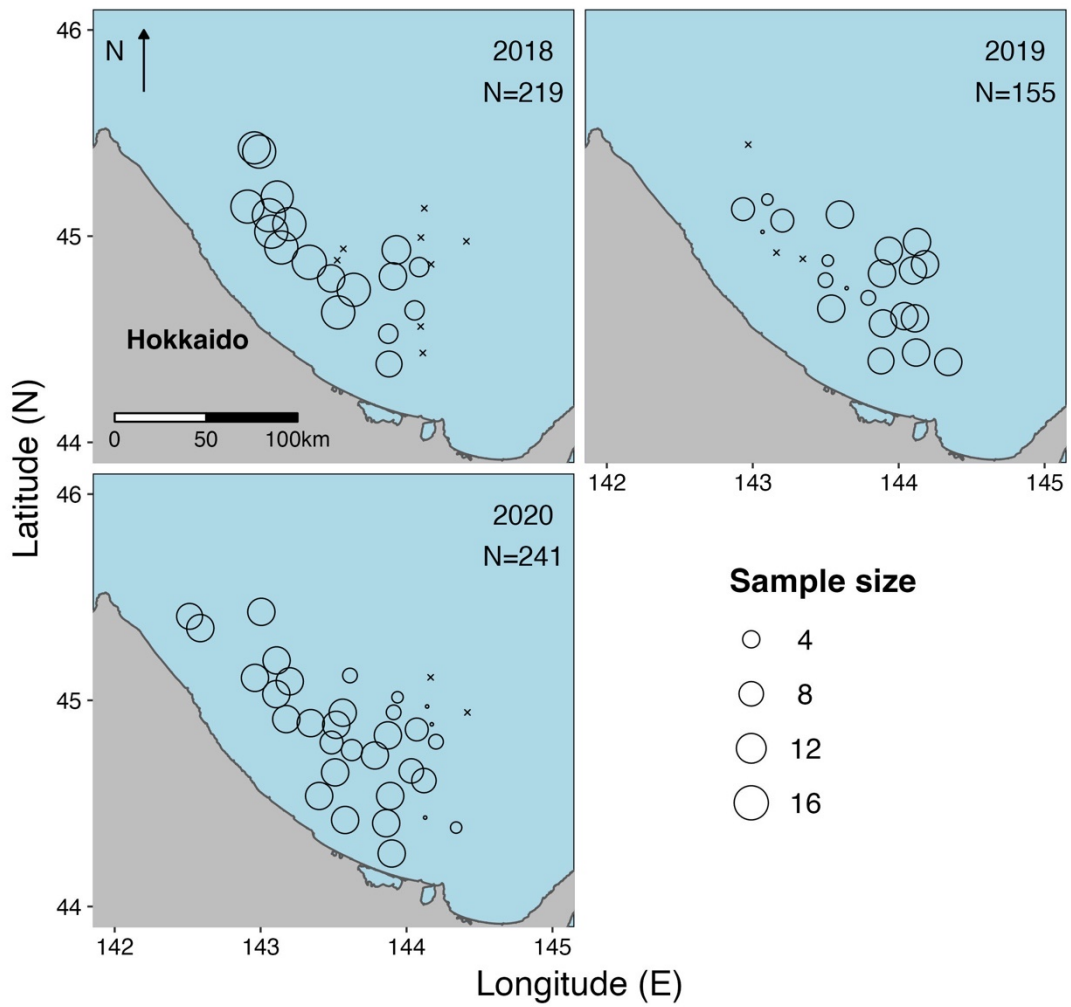
Fig. 2.3. Spatial distribution of the Pacific cod specimens off the northeastern coast of Hokkaido during 2018–2020. ×; indicate no specimen was taken in that station.

Table 2.1. Summary of the five cruises conducted off the southern coast of Hokkaido during 2016–2020. N, number of trawled stations, Nc, number of stations with Pacific cod, and number of Pacific cod specimens from each cruise.

Year	Duration	N	Nc	Cod
2016	Jun.15–Jul.7	30	18	167
2017	Jun.13–Jul.8	44	31	175
2018	Jun.14–Jul.8	38	30	211
2019	Jun.10–Jul.9	61	33	293
2020	Jun.11–Jul.7	52	34	432

Table 2.2. Summary of the three cruises conducted off the northeastern coast of Hokkaido during 2018–2020. N, number of trawled stations, Nc, number of stations with Pacific cod, and number of Pacific cod specimens from each cruise.

Year	Duration	N	Nc	Cod
2018	Apr.24–May.1	26	18	219
2019	Sep.30–Oct.10	24	21	155
2020	Apr.9–Apr.22	34	32	241

2.2.2 Stomach content 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 SL of Japanese sardine, walleye pollock and carapace width (CW) of snow crab were measured to the nearest 0.1 mm using a vernier caliper.

2.2.3 Diet characterization methods

Cumulative prey curves were 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 *specaccum* function in vegan 2.6.2 R package (Oksanen et al. 2020). A line was fitted through the final 10 data points. If the slope (k) of the fitted line was ≤0.05, the sample size was considered sufficient (Baremore et al. 2010). Empty stomachs and those only contained digested prey items were excluded from the calculation.

Stomach fullness index (SFI = wet weight of total stomach contents ×

100 / BW) was calculated to evaluate the feeding intensity. 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 × 100 / total weight of all prey) and frequency of occurrence ($\%F_i$ = number of stomachs containing prey i × 100 / total number of non-empty stomachs). However, the gravimetric method easily overemphasizes the contribution of even a single heavy prey (George and Hadley 1979). Therefore, the index of relative importance (IRI) was also calculated for each prey item i (IRI_i = $\%W_i$ × $\%F_i$) (Pinkas et al. 1971) and then standardized to a percentage value ($\%IRI$ = IRI / ΣIRI × 100) (Pinkas et al. 1971).

In this study, ontogenetic variation in diet composition of Pacific cod in SCH was investigated by grouping specimens into five body length categories [≤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 in SCH (Hattori et al. 1992a). Pacific cod collected in NCH were grouped into four SL classes, because only 14 specimens below 300 mm SL were available. To analyze the ontogenetic variation in feeding diversity, the number of prey species in each stomach was counted for all SL classes. Empty stomachs, and those containing only digested material, were not included in the diet analysis.

2.2.4 Statistical analyses

Generalized linear models (GLMs) with Gamma error distribution and log-link function were used to check whether there was significant difference in SL and BW of Pacific cod between years or sexes. In the dataset of the NCH, a fish weighted 12,313 g were identified as an outlier and excluded from the statistical analysis as this observation had too much leverage on the model fit. GLMs with Gamma error distribution and log-link function were also used to examine the effects of year and sex on the SFI. Another categorical variable, named prey, was also introduced into GLMs. This variable divided the cod specimens into four groups on the basis of consuming prey: walleye pollock, Japanese sardine, and snow crab (see below).

Chi-square test was used to determine whether the sex ratio deviated from 1:1 in each surveyed year and whether it varied between years. Chi-square test was also 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 the prey size limit of main prey species 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 significance of Pacific cod SL versus prey length relationships at the 10th and 90th quantiles was evaluated using 'boot' method. All statistical

analyses were performed using R 4.2.0 statistical software (R Core Team 2022). All graphs were plotted using the ggplot2 3.3.6 R package (Wickham 2016). Statistical significance was set at the level of $P<0.05$.

2.3 Results

2.3.1 Sex ratio and body size

In SCH, the sex of 1,263 Pacific cod was identified. The result of Chi-square test indicated that the sex ratio was not significantly different from 1:1 (Table 2.3) and there was no significant difference in the sex ratio among years ($\chi^2 = 2.79$, $df = 4$, $P>0.05$). SL and BW of Pacific cod ranged from 160 to 977 mm and from 40 to 10,035 g, respectively (Fig. 2.4). The results from GLMs indicated there were significant differences in SL and BW among the five years surveyed ($P<0.001$) while no significant difference was found between sexes ($P>0.05$) (Table 2.4). Specifically, the SL and BW of Pacific cod were significantly smaller and larger in 2016 and 2020, respectively. No significant difference was detected among 2017, 2018, and 2019 ($P>0.05$).

In NCH, sex data were available for all of the 615 specimens. The result of the Chi-square test indicated that the sex ratio was not significantly different from 1:1 (Table 2.5) and there was no significant difference in the sex ratio among years ($\chi^2 = 0.58$, $df = 2$, $P>0.05$). SL and BW of Pacific cod ranged from 248 to 933 mm and from 152 to 12,313 g,

respectively (Fig. 2.5). GLMs indicated SL and BW of Pacific cod collected in 2019 were significantly different from those in 2018 and 2020 (Table 2.6). There was no significant sexual difference in SL or BW (Table 2.6).

Table 2.3. Summary of the Chi-square test for the sex ratio of Pacific cod collected off the southern coast of Hokkaido.

Year	Female	Male	Ratio	chi	*df*	*P*
2016	74	93	0.80	2.16	1	0.14
2017	83	91	0.91	0.37	1	0.54
2018	106	105	1.01	0.00	1	0.95
2019	145	134	1.08	0.23	1	0.63
2020	216	216	1.00	0.00	1	1.00

Table 2.4. Summary of generalized linear models explaining the standard length (SL) and body weight (BW) of Pacific cod collected off the southern coast of Hokkaido. SE; standard error.

Variables	Model for SL				Model for BW			
	Estimates	SE	*t* value	*P*	Estimates	SE	*t* value	*P*
Intercept	5.84	0.03	198.02	**<0.001**	6.47	0.10	64.59	**<0.001**
Year (2017)	0.19	0.04	4.54	**<0.001**	0.38	0.14	2.70	**0.007**
Year (2018)	0.23	0.04	5.74	**<0.001**	0.60	0.14	4.37	**<0.001**
Year (2019)	0.22	0.04	5.78	**<0.001**	0.51	0.13	3.92	**<0.001**
Year (2020)	0.29	0.04	8.24	**<0.001**	0.70	0.12	5.85	**<0.001**
Sex (Female)	-0.04	0.04	-0.95	0.341	-0.17	0.15	-1.15	0.252
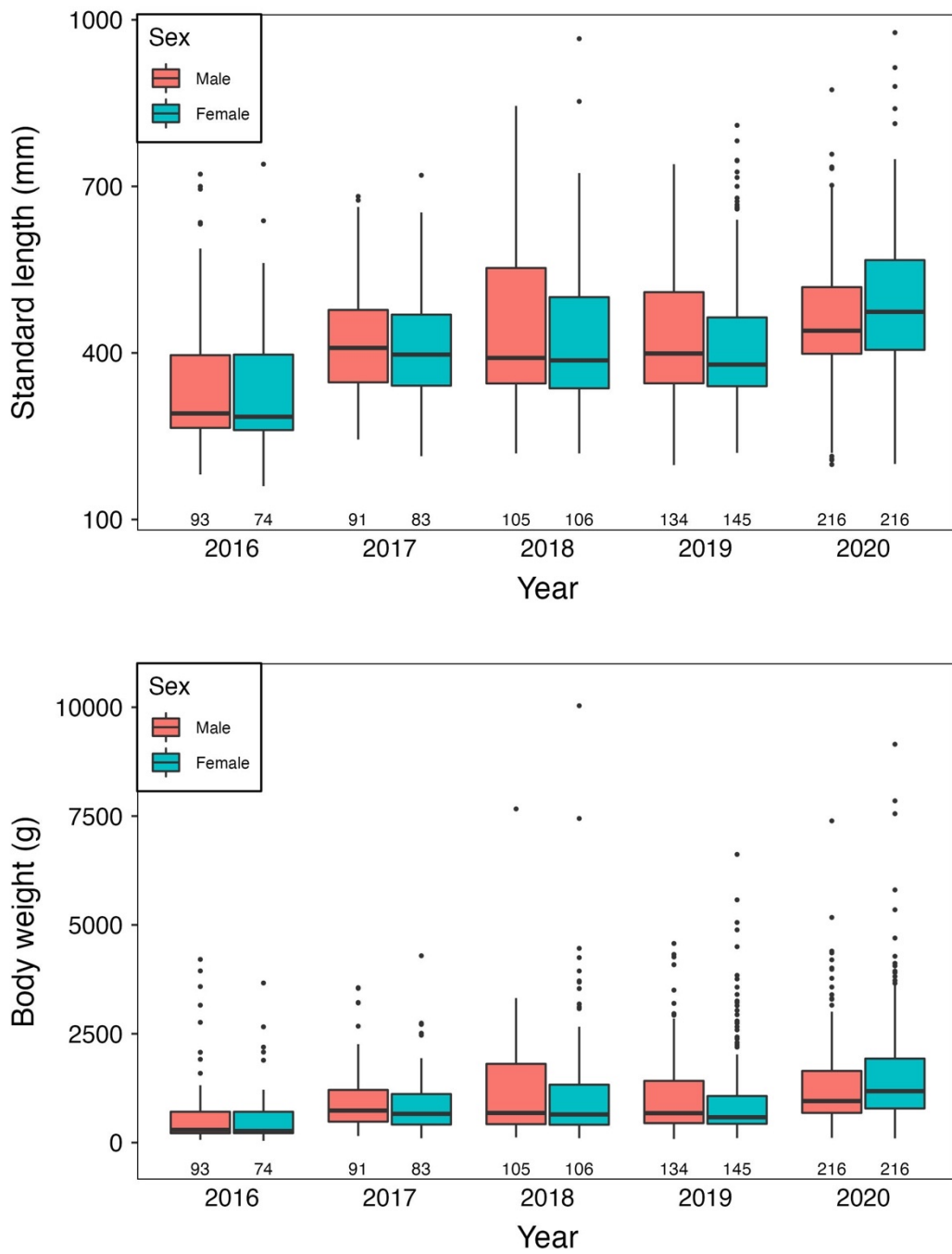
Fig. 2.4. Boxplot of standard length and body weight of Pacific cod collected off the southern coast of Hokkaido. The bottom numbers represent the sample size. The bold line represents the median. The lower and upper hinges correspond to the first and third quartiles. The upper and lower whiskers extend to the largest and smallest value with 1.5 times the interquartile range.

Table 2.5. Summary of the Chi-square test for the sex ratio of Pacific cod collected off the northeastern coast of Hokkaido.

Year	Female	Male	Ratio	chi	*df*	*P*
2018	103	116	0.89	0.77	1	0.38
2019	79	76	1.04	0.06	1	0.81
2020	116	125	0.93	0.34	1	0.56

Table 2.6. Summary of generalized linear models explaining the standard length (SL) and body weight (BW) of Pacific cod collected off the northeastern coast of Hokkaido. SE; standard error.

Variables	Model for SL				Model for BW			
	Estimates	SE	*t* value	*P*	Estimates	SE	*t* value	*P*
Intercept	6.26	0.02	275.38	**<0.001**	7.47	0.07	102.17	**<0.001**
Year (2019)	-0.19	0.04	-5.16	**<0.001**	-0.33	0.12	-2.84	**0.005**
Year (2020)	-0.01	0.03	-0.37	0.712	0.04	0.10	0.39	0.698
Sex (Female)	-0.00	0.03	-0.13	0.896	0.04	0.11	0.41	0.680
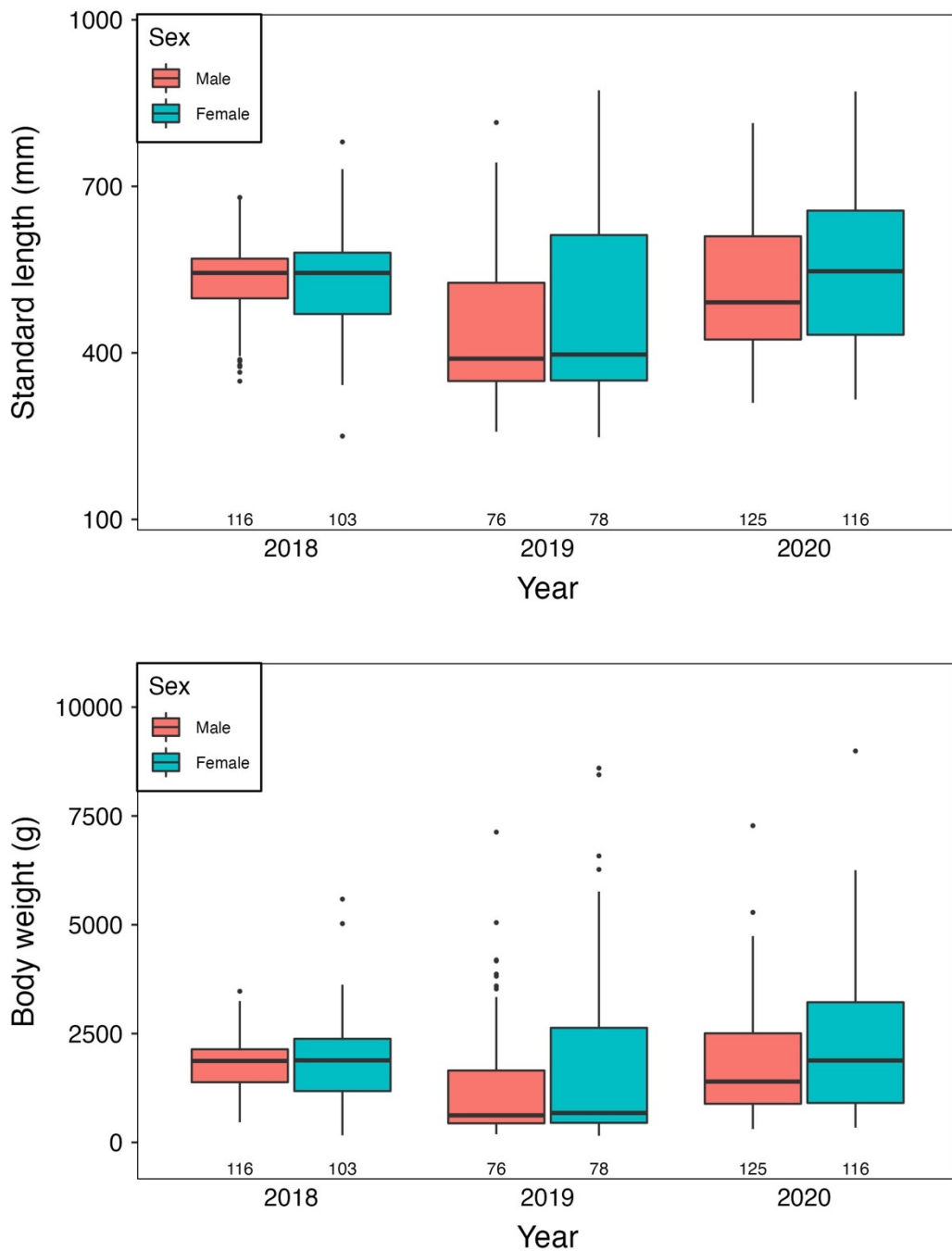
Fig. 2.5. Boxplot of standard length and body weight of Pacific cod collected off the northeastern coast of Hokkaido. A Pacific cod collected in 2019 (933 mm standard length, 12313 g total weight) was not shown in the figures. The bottom numbers represent the sample size. The bold line represents the median. The lower and upper hinges correspond to the first and third quartiles. The upper and lower whiskers extend to the largest and smallest value with 1.5 times the interquartile range.

2.3.2 Diet composition

In SCH, the slopes of the fitted lines based on the final 10 points from cumulative prey curves were ≤0.05 in all years, except 2017 (k = 0.06), indicating that the sample size was generally sufficient to describe the diet composition of Pacific cod (Fig. 2.6). Pacific cod fed on a wide variety of prey species, comprising 13 taxa (Table 2.7) and at least 60 species (Fig. S1, Table S3). Prey species composition varied among the years. Specifically, 15 species occurred in all surveyed years, four and nine species occurred in four and three years, and other species occurred in a single or two years (Fig. S1).

For all of the five years combined, 46 (3.6%) stomachs were empty. Fish was the most dominant prey category (95.3, %IRI). Among the fish species identified, Japanese sardine showed the highest %IRI (36.7%), followed by walleye pollock (30.9%) and Japanese lanternfish *Notoscopelus japonicus* (15.2%). The %IRI of other fish species were lower than 0.05%. Decapod crustaceans was also an important prey category for Pacific cod in SCH. Although they accounted for as much as 2.8% in terms of weight, decapod crustaceans occurred in 47.6% of stomachs examined. The %IRI for other prey taxa were less than 1%. Moreover, amphipods (37.9, %F), polychaetes (29.1, %F), cephalopods (12.8, %F) and euphausiids (10, %F) occurred from the stomachs frequently, although their overall contribution in terms of weight was rather

limited.

In NCH, the slopes of the lines fitted based on the final 10 points from cumulative prey curves (Fig. 2.7) were ≤0.05 in 2018 and 2020, indicating that the sample size was sufficient to describe the diet composition of Pacific cod during spring in the area investigated. In contrast, the slope was 0.06, which was slightly larger than 0.05 for specimens collected in 2019 (Fig. 2.7). In this area, the diet of Pacific cod included 13 taxa (Table 2.8) represented by at least 45 species (Fig. S2, Table S4). The number of species occurring in all of the years surveyed was 16, and 19 species occurred in a single year (Fig. S2).

Of the 615 stomachs from NCH, 16 (2.6%) were empty. For all years combined, fish was the most dominant prey category (68.6, %IRI), followed by decapod crustaceans (28.7, %IRI) and cephalopods (2, %IRI). There was no prey category of which %IRI value exceeded 1% (Table 2.8). Among the identified fish species, the %IRI of walleye pollock was 35.1%, which was substantially higher than other fish species (Table S4). The relatively high importance of snow crab is a noticeable feeding peculiarity for Pacific cod in this area (44.2, %IRI). Snow crab occurred in 42.7% of stomachs examined and accounted for 19.4% in terms of weight. Amphipods (31.7, %F), euphausiids (18.9, %F) and polychaetes (12.5, %F) also occurred frequently in the stomachs of Pacific cod, although their overall contribution in terms of weight was rather trivial.
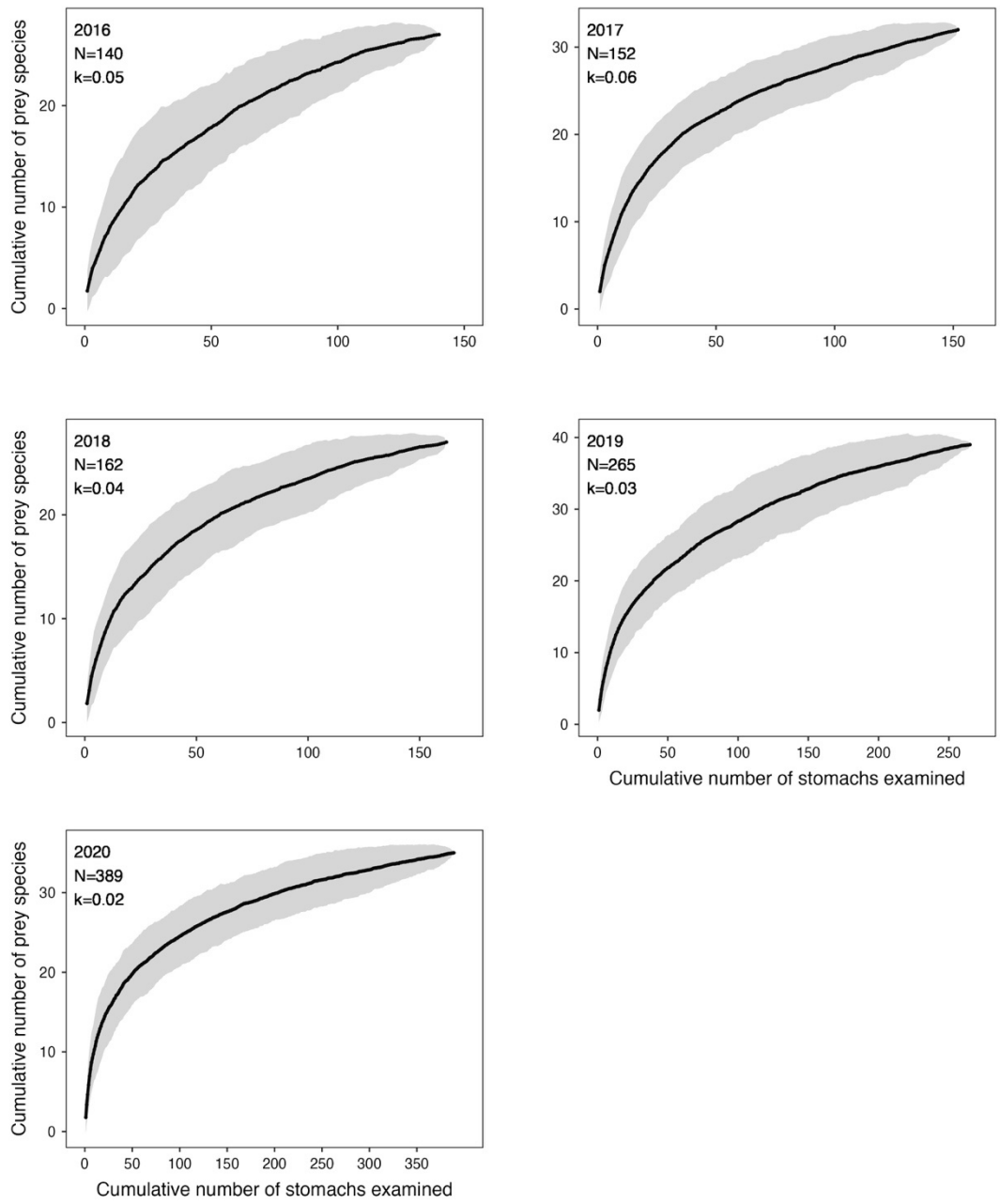
Fig. 2.6. Cumulative prey curves for Pacific cod collected in different years off the southern coast of Hokkaido, generated by a total of 100 permutations using *specaccum* function. Grey shades indicate 95% confidence intervals.

Table 2.7. Prey taxa composition of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. For finer taxonomic resolution, refer to Table S3. %W; wet weight composition, %F; frequency of occurrence, %IRI; percent index of relative importance. +: <0.01.

Prey taxa	%W	%F	%IRI
Coelenterata	0.17	0.24	+
Polychaeta	1.65	29.08	0.85
Echiuroidea	0.79	4.20	0.06
Gastropoda	0.24	3.88	0.02
Bivalvia	0.05	4.85	+
Cephalopoda	3.32	12.76	0.75
Mysidacea	0.01	0.40	+
Isopoda	0.03	2.91	+
Amphipoda	0.97	37.88	0.65
Euphausiidae	0.32	10.02	0.06
Decapoda	2.79	47.58	2.34
Echinodermata	0.10	6.38	0.01
Pisces	89.47	60.42	95.27
Digested matter	0.09	3.80	0.01
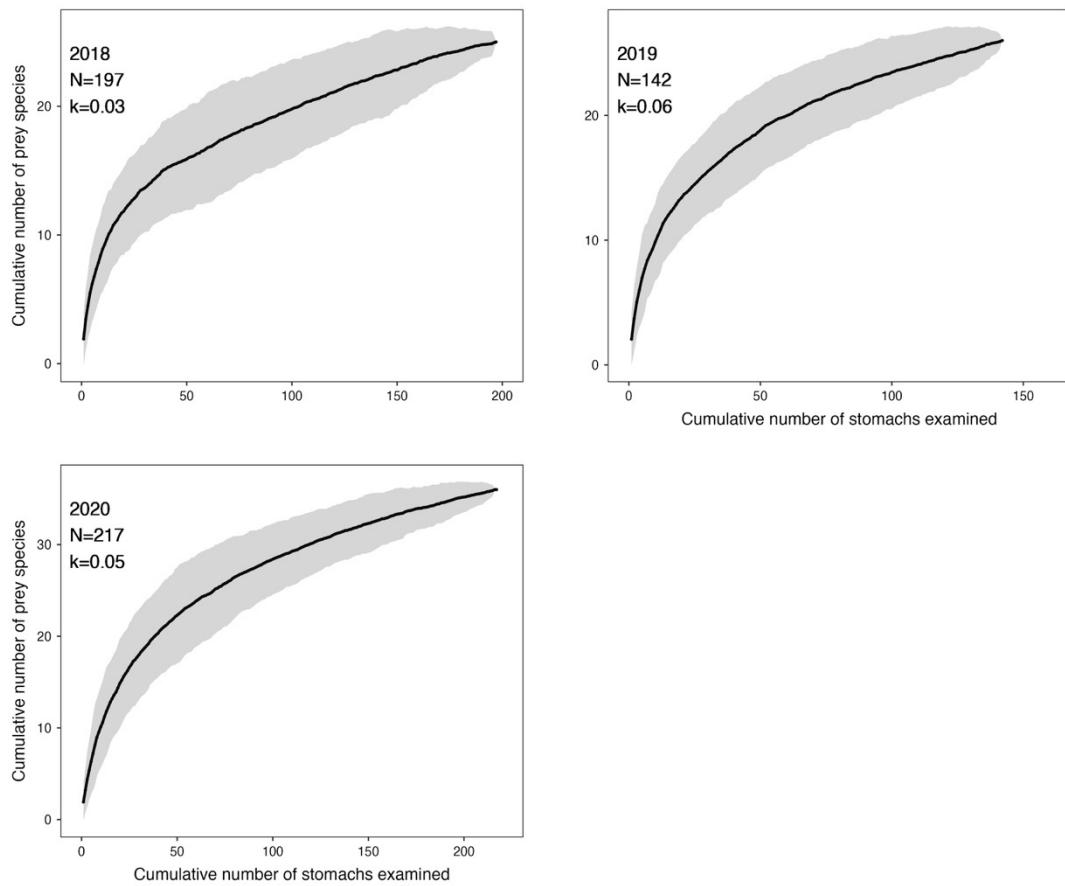
Fig. 2.7. Cumulative prey curves for Pacific cod collected in different years off the northeastern coast of Hokkaido, generated by a total of 100 permutations using *specaccum* function. Grey shades indicate 95% confidence intervals.

Table 2.8. Prey taxa composition of Pacific cod collected off the northeastern coast of Hokkaido during 2018–2020. For finer taxonomic resolution, refer to Table S4. %W; wet weight composition, %F; frequency of occurrence, %IRI; percent index of relative importance. +; indicate <0.01.

Prey taxa	%W	%F	%IRI
Coelentrata	0.03	0.17	+
Polychaeta	0.46	12.52	0.10
Echiuroidea	3.74	2.50	0.16
Gastropoda	0.05	1.50	+
Bivalvia	0.01	1.67	+
Cephalopoda	8.45	13.86	2.01
Mysidacea	0.01	0.33	+
Isopoda	0.03	0.67	+
Amphipoda	0.41	31.72	0.22
Euphausiidae	0.60	18.86	0.19
Decapoda	25.14	66.44	28.68
Echinodermata	0.02	1.34	+
Pisces	60.91	65.61	68.62
Digested matter	0.14	2.67	0.01

2.3.3 Ontogenetic and interannual variations in diet

In SCH, the proportion of Pacific cod that consumed different number of prey species were different among size classes (χ^2 = 112.79, *df* = 12, *P*<0.001). The proportions of stomachs simultaneously included four or more prey species were higher in 301–400 mm and 401–500 mm SL classes (28.5% and 31.8%, respectively) than the proportions in other size classes (≤300 mm, 10.3%; 501–600 mm, 10.9%; >600 mm, 7.4%; Fig. 2.8).

The dietary composition of Pacific cod varied with SL classes (Fig. 2.9). Pacific cod of ≤400 mm SL preyed mainly on decapod crustaceans, polychaetes, and amphipods. The weight percentages of these prey items gradually decreased with increasing body length, while, that of fish increased. Individuals in the >600 mm SL class fed almost exclusively on fish, with %W ranging from 96.9 to 99.4 during 2017–2020. No fish was observed in the diet of Pacific cod ≤300 mm SL in 2020, when amphipods accounted for 92.5%. In addition, %W (Fig. 2.9) and %F (Fig. 2.10) of Japanese sardine were higher in the >400 mm SL classes during 2018–2020 compared to 2016 and 2017. Generally, walleye pollock occurred more frequently from the stomachs of cod with larger body lengths (Fig. 2.10). However, this was not in 2016 when fish was the most important prey in all size classes, with walleye pollock being predominant. 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 that in any other year.

In NCH, although the result of chi-square test was not significant (χ^2 = 9.66, df = 9, P>0.05), the proportion of stomachs included four or more prey species was highest (25.7%) in the ≤400 mm SL class. Meanwhile, the proportion of stomachs containing only one prey species was highest (27.6%) in the >600 mm SL class (Fig. 2.8).

The importance of prey species for Pacific cod varied among years and SL classes. Generally, the %W of fish increased with SL in all three years (Fig. 2.9). In 2018 and 2020, %W of fish ranged from 28 to 52% and from 56 to 71% for ≤500 mm and >500 mm SL cod, respectively. In 2019, Pacific cod >500 mm preyed almost entirely on fish (>85, %W). Walleye pollock occurred in 111 stomachs (50.7, %F, Fig. 2.11), and accounted 44.8% weight of stomach contents in 2018 (Fig. 2.9). The %F of walleye pollock decreased to 15.3% and 13.1% in 2019 and 2020, respectively. Meanwhile, Pacific herring *Clupea pallasi* accounted for a high percentage of weight in 2020, especially in the class of >600 mm (28.4%, %W). Snow crab occurred in 47.2% and 48.5% of the stomachs in 2018 and 2020, respectively and occurred less frequently in 2019 (27.3, %FO) (Fig. 2.11). Similarly, %W of snow crab was much higher in 2018 (21.3%) and 2020 (22.6%) than that in 2019 (4.9%) (Fig. 2.9).
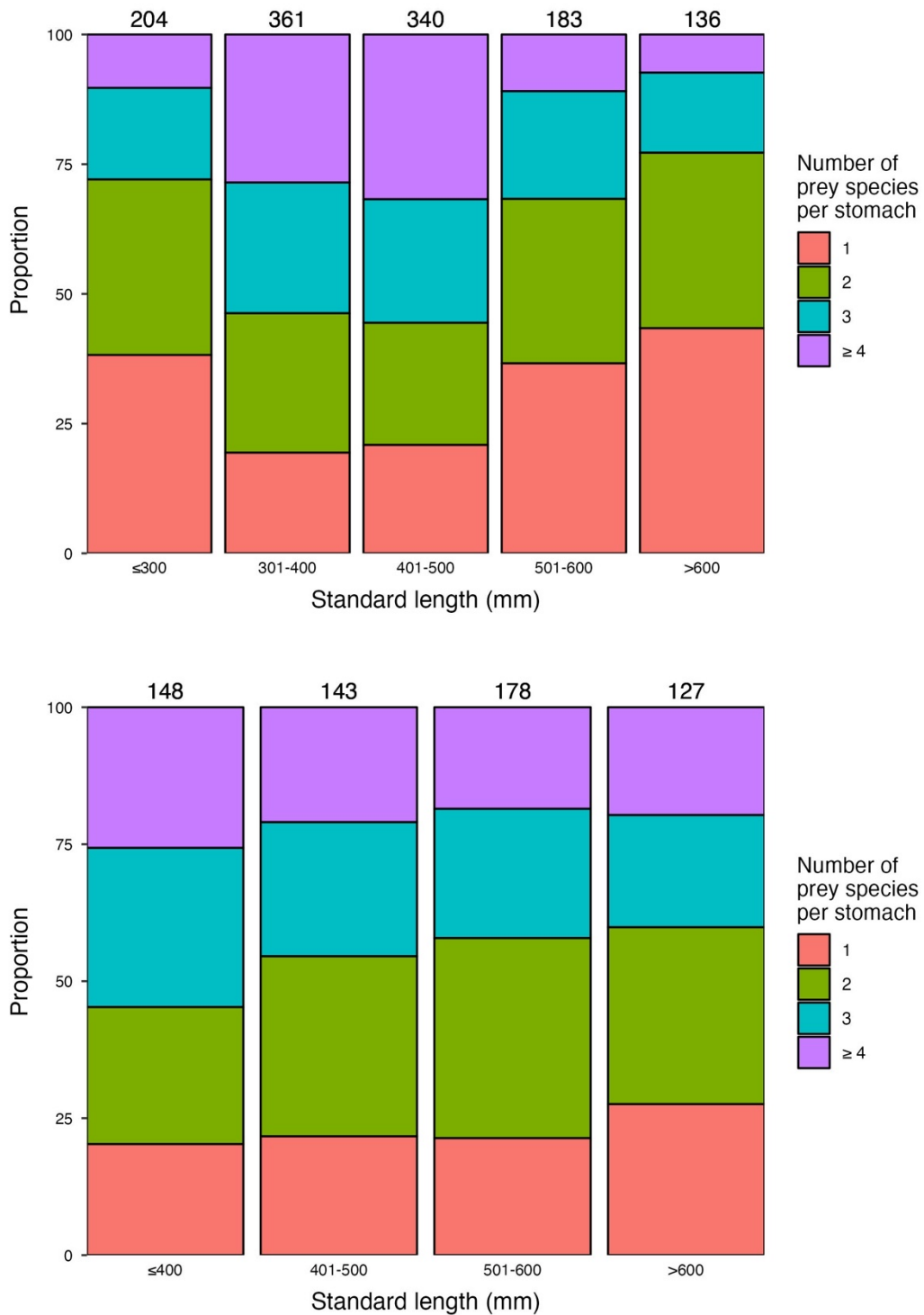
Fig. 2.8. Proportions of Pacific cod with different number of prey species in stomachs collected off the southern coast (upper) and off the northeastern coast (bottom) of Hokkaido.
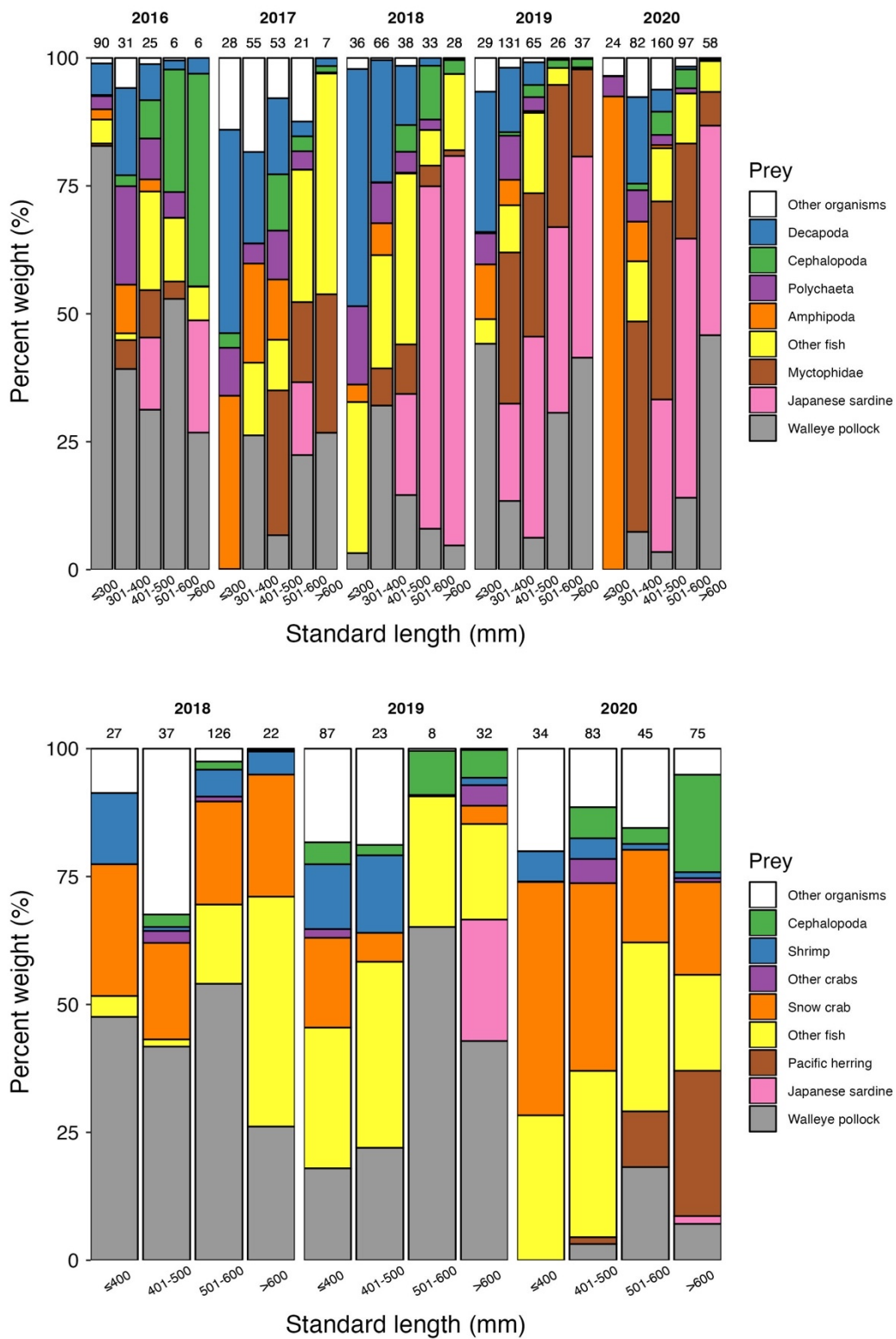
Fig. 2.9. Percent wet weight composition of prey in the diet of Pacific cod collected off the southern coast of Hokkaido during 2016–2020 (upper) and the northeastern coast of Hokkaido during 2018–2020 (bottom). The numerals above the bars indicate the number of stomachs examined.
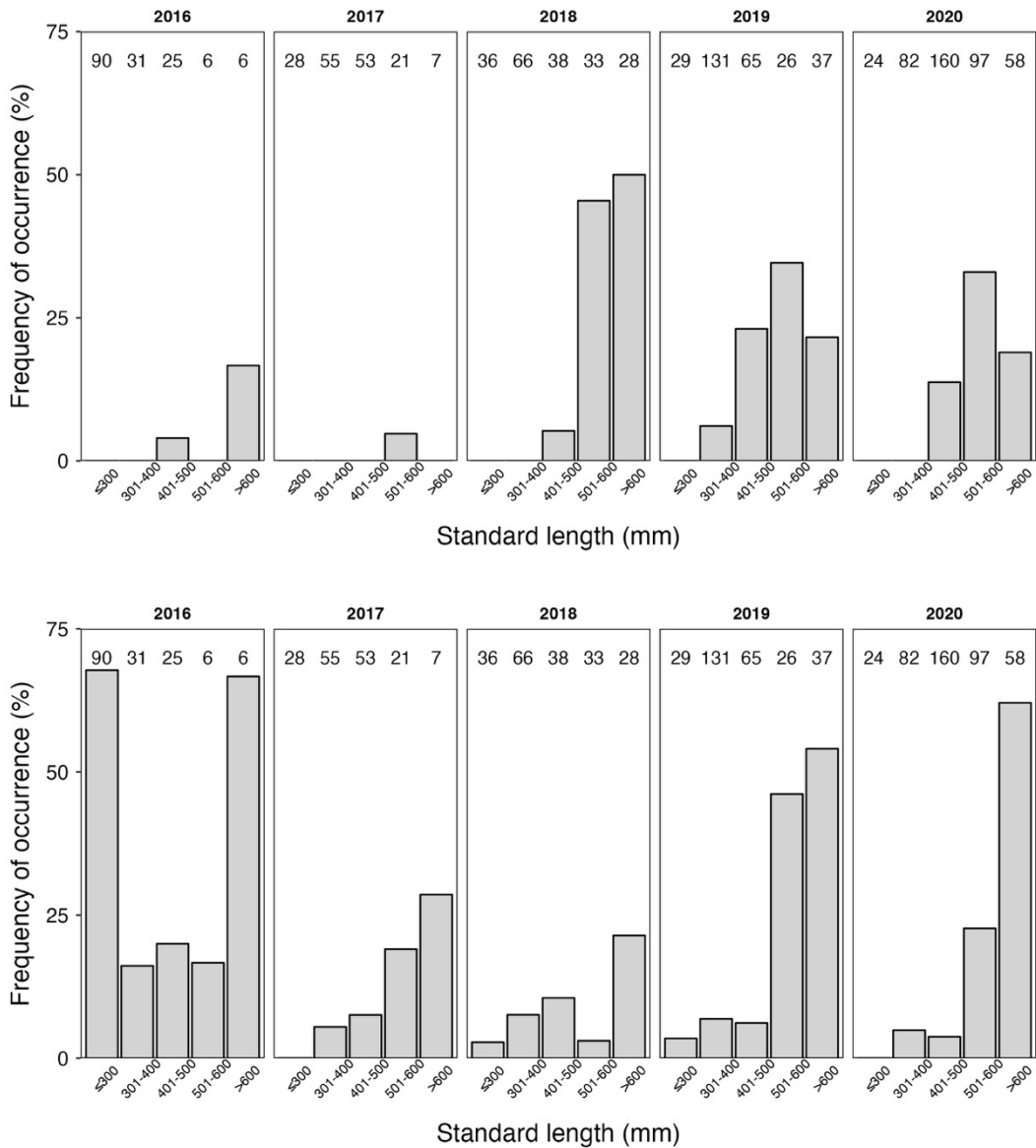
Fig. 2.10. Frequency of occurrence of Japanese sardine (upper) and walleye pollock (bottom) in the stomachs of Pacific cod collected off the southern coast of Hokkaido during 2016–2020.
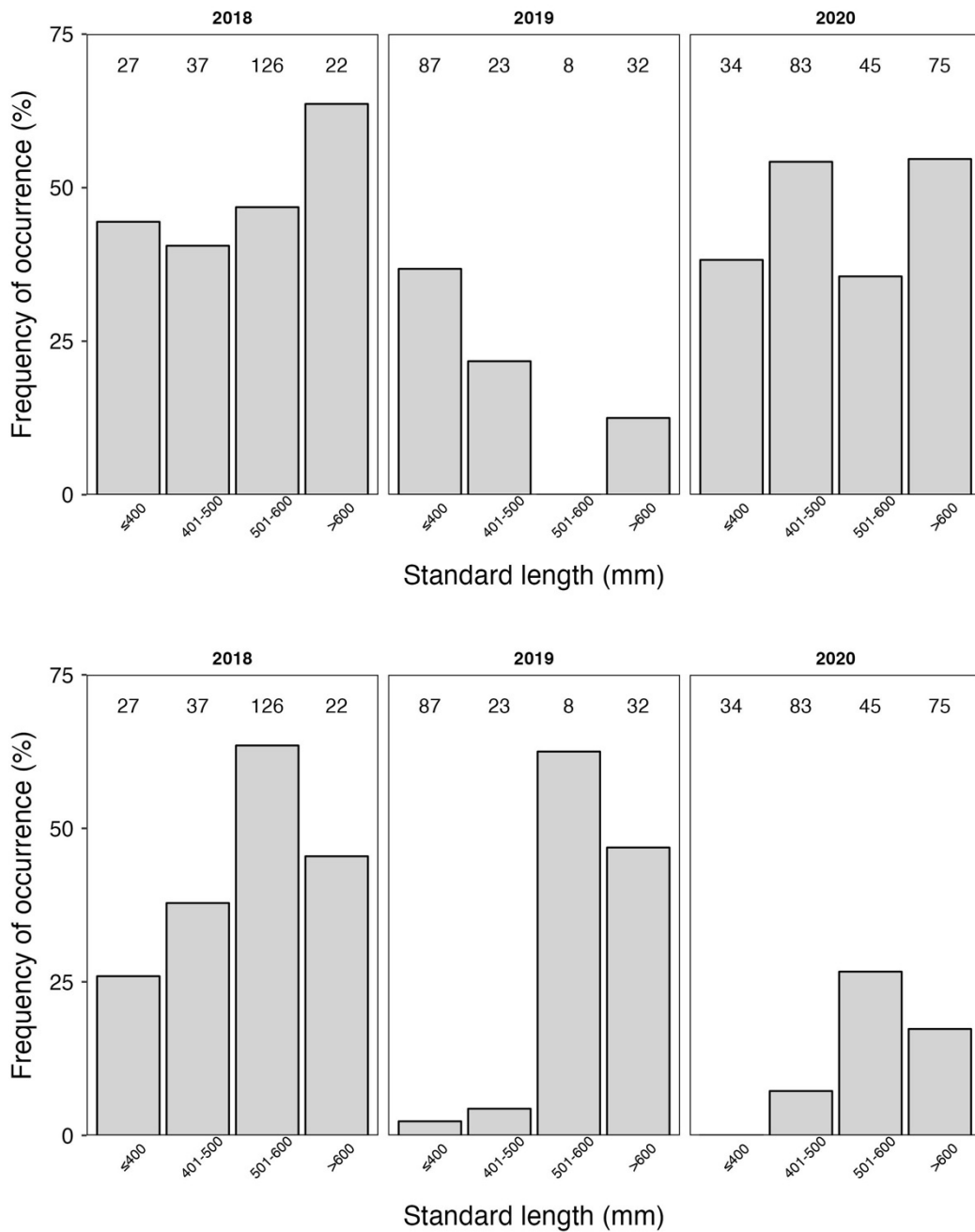
Fig. 2.11. Frequency of occurrence of snow crab (upper) and walleye pollock (bottom) in the stomachs of Pacific cod collected off the northeastern coast of Hokkaido during 2018–2020.

2.3.4 Feeding intensity

The SFI of the 1,232 Pacific cod collected in SCH ranged from 0.001 to 30.58%, varying significantly among years but not between sexes (Table 2.9, Fig. 2.12). Specifically, the SFI of Pacific cod collected during 2018–2020 was significantly higher than that in 2016 and 2017. Diet had a significant effect on SFI; SFI of Pacific cod consuming Japanese sardine was higher than those consuming walleye pollock. Pacific cod consuming other prey items had the lowest SFI among the four groups.

In NCH, SFI of the 599 Pacific cod ranged from 0.001% to 21.07%, showing no significant sexual difference (Table 2.10, Fig. 2.13). SFI was significantly higher in 2020 than in 2018 and 2019. Pacific cod those consumed walleye pollock and snow crab had higher SFI values in 2018-2019 and 2020, respectively.

Table 2.9. Summary of generalized linear model explaining the SFI of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. "Both" indicates the individuals consuming Japanese sardine and walleye pollock. SE; standard error.

Variables	Estimates	SE	*t* value	*P*
Intercept	0.12	0.11	1.11	0.267
Year (2017)	0.26	0.14	1.80	0.071
Year (2018)	0.33	0.14	2.40	**0.017**
Year (2019)	0.64	0.13	5.05	**<0.001**
Year (2020)	0.65	0.12	5.45	**<0.001**
Sex (Female)	0.01	0.07	0.12	0.905
Japanese sardine	1.60	0.12	13.30	**<0.001**
Walleye pollock	1.03	0.10	10.29	**<0.001**
Both	1.54	0.33	4.69	**<0.001**
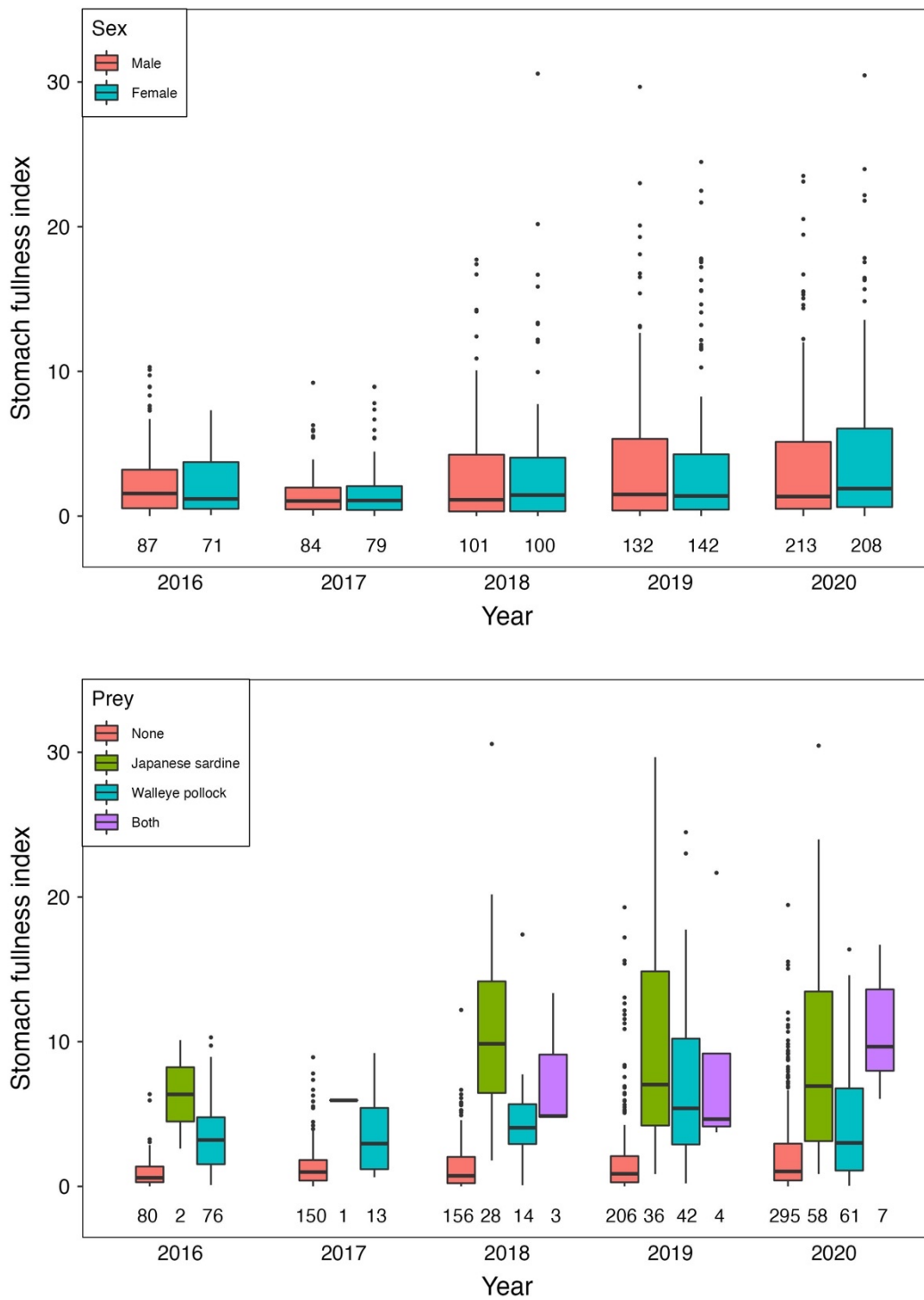
Fig. 2.12. Boxplots of the stomach fullness index of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. The bottom numbers represent the sample size. The bold lines represent the median. The lower and upper hinges correspond to the first and third quartiles. The upper and lower whiskers extend to the largest and smallest value with 1.5 times the interquartile range.

Table 2.10. Summary of generalized linear model explaining the SFI of Pacific cod collected off the northeastern coast of Hokkaido during 2018–2020. "Both" indicates the individuals consuming snow crab and walleye pollock. SE; standard error.

Variables	Estimates	SE	*t* value	*P*
Intercept	0.35	0.11	3.12	**0.002**
Year (2019)	-0.03	0.12	-0.23	0.821
Year (2020)	0.83	0.11	7.81	**<0.001**
Sex (Female)	0.06	0.08	0.72	0.470
Snow crab	0.16	0.10	1.59	0.112
Walleye pollock	0.77	0.13	5.91	**<0.001**
Both	0.56	0.16	3.62	**<0.001**
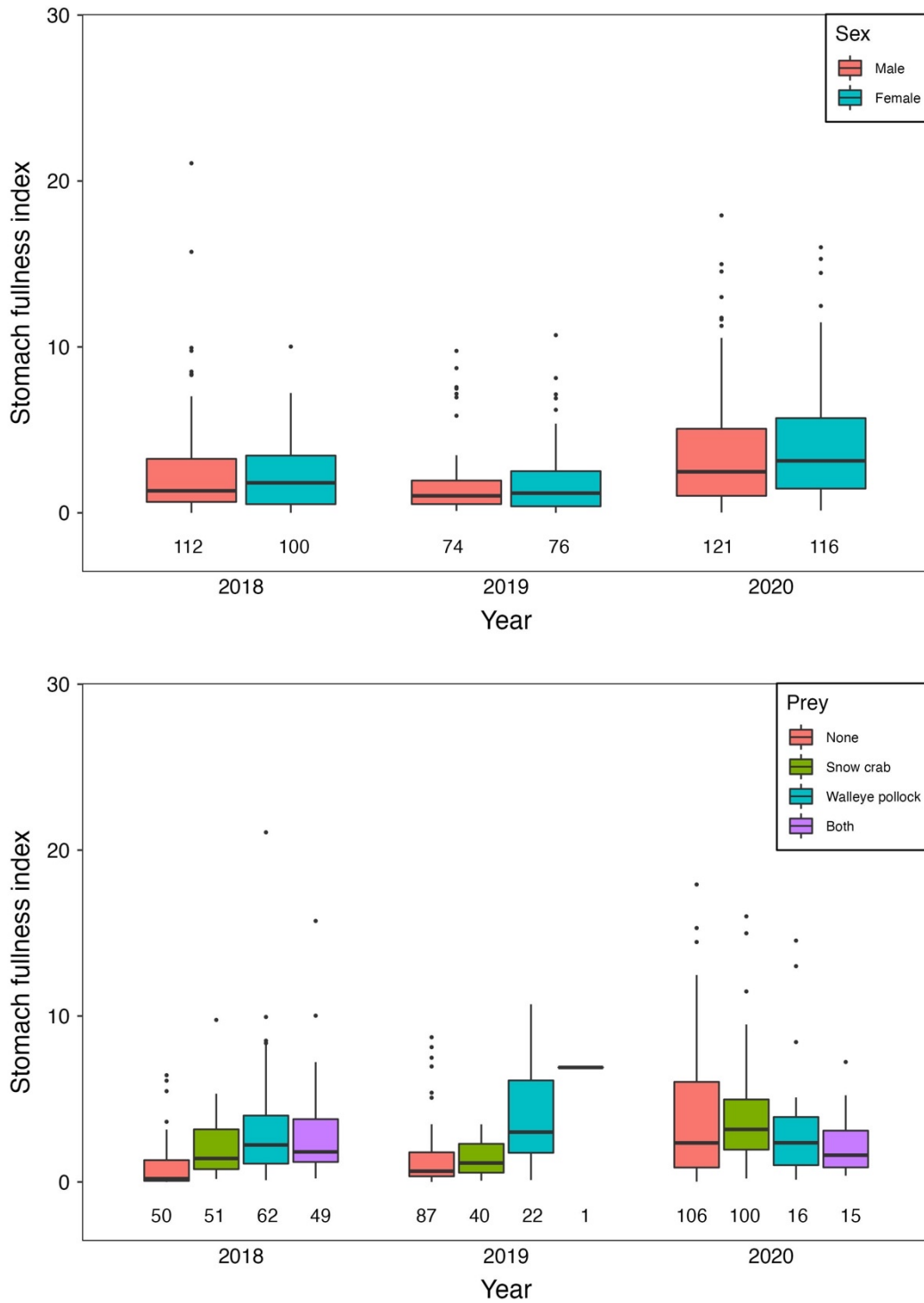
Fig. 2.13. Boxplots of the stomach fullness index of Pacific cod collected off the northeastern coast of Hokkaido during 2018–2020. The bottom numbers represent the sample size. The bold line represents the median. The lower and upper hinges correspond to the first and third quartiles. The upper and lower whiskers extend to the largest and smallest value with 1.5 times the interquartile range.

2.3.5 Predator–prey size relationship

In SCH, SL of 139 Pacific cod with Japanese sardine in stomachs ranged from 328 to 874 mm. SL range of 159 intact Japanese sardine found in the stomachs of 53 Pacific cod was 113–220 mm (Fig. 2.14). The results of quantile regression analysis indicated that the size relationship was neither significant at 10th quantile ($t = 1.48$, $P>0.05$) nor 90th quantile ($t = 0.57$, $P>0.05$). SL of 220 Pacific cod with walleye pollock in stomachs ranged from 181 to 977 mm. SL range of 149 intact walleye pollock found in the stomachs of 101 Pacific cod was 37–390 mm. SL of walleye pollock was positively correlated with Pacific cod SL at 90th quantile ($t = 10.62$, $P<0.001$), while the relationship was not significant at 10th quantile ($t = 0.82$, $P>0.05$.

In NCH, SL of 256 Pacific cod with snow crab in stomachs ranged from 258 to 814 mm. CW of 273 intact snow crab found in the stomachs of 119 Pacific cod ranged from 5.5 to 61.3 mm. Quantile regression analysis indicated that CW of snow crab was significantly correlated with Pacific cod SL at 10th quantile ($t = 4.9$, $P<0.001$), while the relationship was not significant at 90th quantile ($t = 1.43$, $P>0.05$; Fig. 2.15). SL of 165 Pacific cod with walleye pollock in stomachs ranged from 349 to 873 mm. SL range of 81 intact walleye pollock found in the stomachs of 67 Pacific cod was 55–331 mm. SL of walleye pollock was positively correlated with Pacific cod SL at both 10th quantile ($t = 2.19$, $P<0.05$) and 90th quantile (t

$= 2.44$, $P<0.05$).
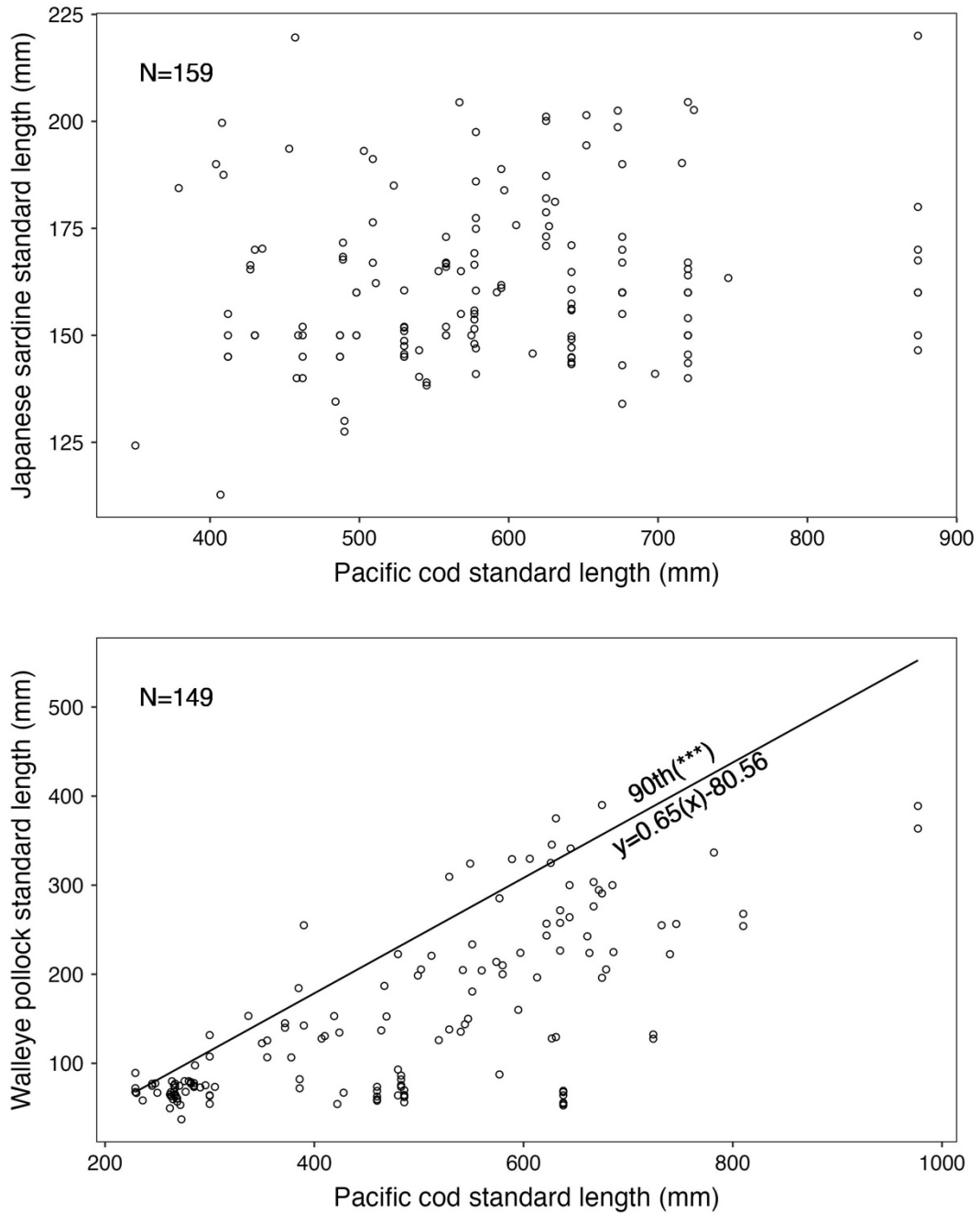
Fig. 2.14. Prey size (upper; Japanese sardine, bottom; walleye pollock) against the standard length of Pacific cod collected off the southern coast of Hokkaido. Solid line indicates significant quantile regression relationship (***; $P<0.001$).
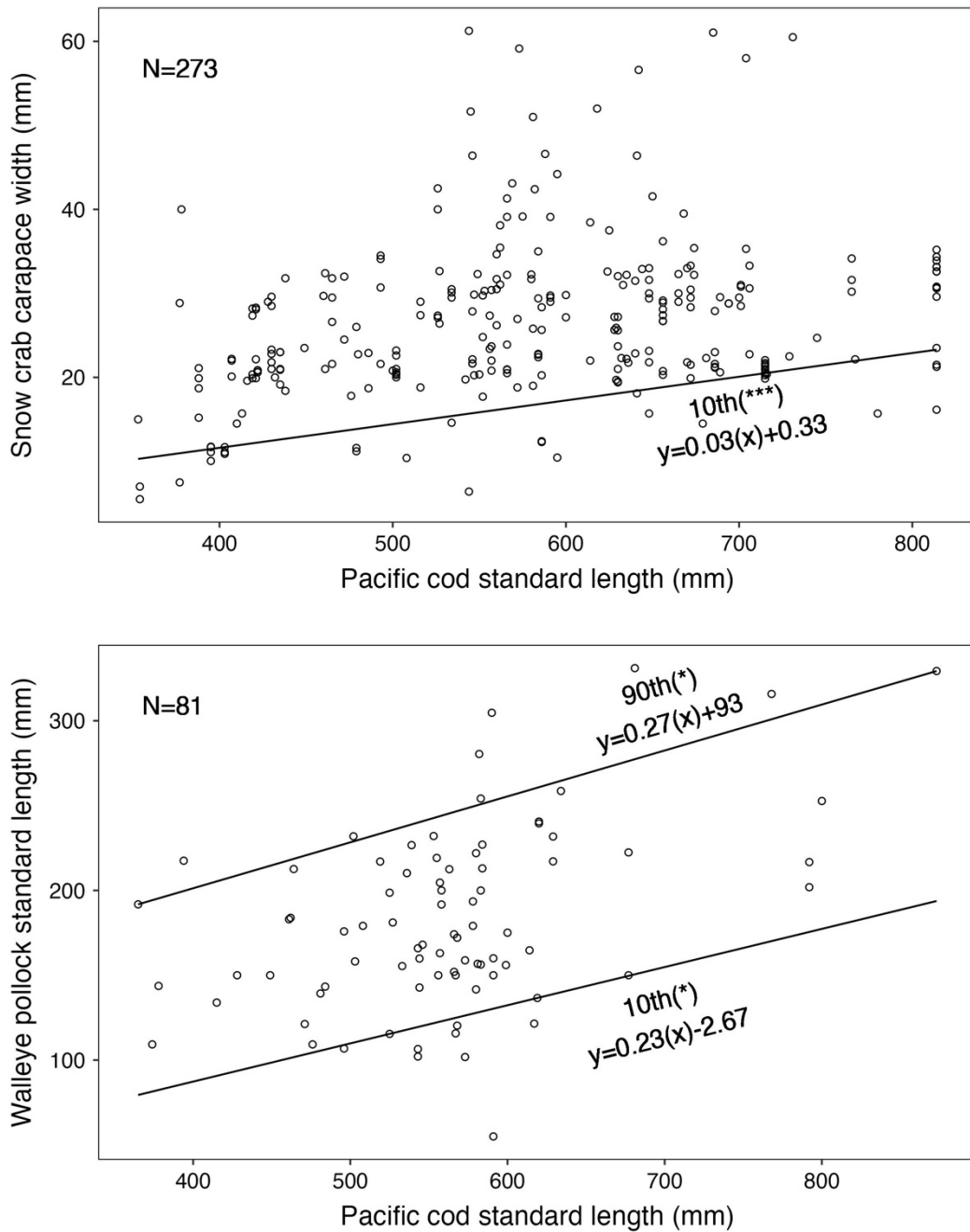
Fig. 2.15. Prey size (upper; snow crab, bottom; walleye pollock) against the standard length of Pacific cod collected off the northeastern coast of Hokkaido. Solid lines indicate significant quantile regression relationships (*; $P<0.05$, ***; $P<0.001$).

2.4　Discussion

In SCH, the significant differences in SL between years 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 65% in 2020, while the proportions for other years (2017–2019) ranged between 70–80% (Chimura et al. 2022). An experiment has demonstrated the growth of juvenile Pacific cod was positively corelated with water temperature in the range of 2–11°C (Hurst et al. 2010). During the period investigated, the highest sea bottom temperature was observed in 2016. This is coincident with the reported marine heatwave occurred in summer in 2010–2016 (Miyama et al. 2021). Therefore, the high recruitment of Pacific cod in 2016 is probably related to the favorable thermal condition. In NCH, the SL and BW of Pacific cod collected during autumn were significantly smaller than those collected in spring reflecting the higher proportion of 300–400 mm SL (age 2) fish in the autumn. This indicates most age 2 fish recruited to the area surveyed.

It has been over 20 years since the last study (Yamamura et al. 1993), was conducted on the diet of Pacific cod off eastern Hokkaido. A representative sample with sufficient specimen is required to describe the diet composition of fish by means of stomach content 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. On the other hand, the sample size was sufficient to describe the diet of Pacific cod, as indicated by the cumulative prey curves. Therefore, the description of Pacific cod diet is more representative in our study.

Most of the Pacific cod specimens contained at least one prey item in their stomachs (96.4% and 97.4% in SCH and NCH, respectively), indicating the feeding intensity of Pacific cod was rather high during the period surveyed. The low ratio of empty stomachs was also reported in the previous study conducted off eastern Hokkaido (Yamamura et al. 1993). In SCH, the SFI of Pacific cod with Japanese sardine in the stomachs were higher than those ingesting other prey. Japanese sardine have a schooling behavior, which likely made it possible for Pacific cod to ingest more amount of prey. In NCH, although both %F and %W of walleye pollock declined in 2020, the SFI was significantly higher than in 2018 and 2019. This result can be partly explained by the occurrence of more fish species in the stomachs collected in 2020, especially Pacific herring. This fish may play a similar role in the diet as Japanese sardine in SCH. The reason for the abrupt decrease of walleye pollock in 2020 has remained not very clear. It could have been related to the recruitment dynamics of walleye pollock in NCH, as the prey pollock comprised mainly age-1 cohort inferring from its body length (Fig. 2.15; Hamatsu et al. 2021).

The intensive feeding may be related to the reproductive cycle of

Pacific cod. From April to August, female individuals mature from the yolkless to yolk vesicle phase (Hattori et al. 1992b). The adult Pacific cod accumulate energy for spawning by frequent predation. Meanwhile, small Pacific cod may feed actively to sustain energetic demands for fast growth, which could contribute to avoid being preyed upon by size-selective predators in the ecosystem (Sogard 1997). On the other hand, high feeding intensity of Pacific cod may impose a negative impact on the recruitment of walleye pollock. As previous study documented (Yamamura et al. 1993), we also found that walleye pollock was a predominant prey for Pacific cod. Along SCH, walleye pollock spawned around the mouth of Funka Bay (Nakatani 1988), and juveniles migrated into southeastern 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 SL of walleye pollock consumed by Pacific cod mainly ranged from 59.6 (0.1 quantile) to 298.9 mm (0.9 quantile) SL in SCH and from 115.8 (0.1 quantile) to 240.6 mm (0.9 quantile) SL in NCH. It has been reported that walleye pollock grew to 303.7–385.1 mm and about 300–350 mm in fork length at age 3 in the western Gulf of Alaska (Hughes and Hirschhorn 1979) and southern Okhotsk Sea (Hamatsu et al. 2021). The mean total length of walleye pollock juveniles reached over 60 mm in July in Funka Bay (Nakatani 1988). Therefore, it can be speculated that walleye pollock from juvenile

stage to about age 3 were available prey for Pacific cod in the areas surveyed.

The feeding ecology of Pacific cod has been studied in various areas. In the eastern Bering Sea, crabs, sand-dwelling worms, walleye pollock, and flatfishes were frequently consumed by Pacific cod (Suyehiro 1934; Lang et al. 2005). In Pavlof Bay, western Gulf of Alaska, pink shrimp (*Pandalus borealis*) frequently occurred in the stomachs of Pacific cod (Albers and Anderson 1985). Off 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). Together, the findings of these stomach contents studies suggest that Pacific cod feed on a wide variety of organisms, with fish, crab, and shrimp being the dominant prey items. In this study, the diet of Pacific cod comprised at least 60 and 45 prey species in SCH and NCH, respectively, with fish and decapod crustaceans as predominant prey categories. These results were similar to the former study, which identified 70 prey species (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 highly determined by food availability in the habitat.

In the present study, we examined diet composition of Pacific cod in SCH 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 ($\leq$ 300 mm). The SL of walleye pollock consumed in 2016 was significantly smaller compared to other years, similar to Pacific cod. This phenomenon of small walleye pollock frequently being used by small Pacific cod indicates size-dependent predation on walleye pollock. A pelagic fish, Japanese sardine, played a more important role in the diet of Pacific cod between 2018 and 2020 than that 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. 2021), while the stock of Japanese sardine has tended to increase in the western North Pacific (Niino et al. 2021; Furuichi et al. 2022).

In the early 1990s, threadfin hakeling *Laemonema longipes* was a more important prey species than Japanese sardine for Pacific cod $\geq$601 mm SL off the eastern coast of Hokkaido (Yamamura et al. 1993). This species, however, did not appear in the stomachs collected in SCH. 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 threadfin hakeling which inhabit upper slope zone (Yamamura and Nobetsu 2012). This result reflects Pacific cod are able to actively select optimal prey species in the habitat. Compared to the previous study conducted off eastern Hokkaido (Yamamura et al. 1993), the diet composition of Pacific cod has changed. This variation is noteworthy because the diet data is critical for constructing food web models (Polovina 1984; Lima et al. 2020).

Snow crab was a major dietary component for Pacific cod in NCH. Snow crab was also found from the stomachs of Pacific cod in the eastern Bering Sea (Livingston 1989; Orensanz et al. 2004; Burgos et al. 2013), and off the northern Kuril Islands and southern Kamchatka (Poltev and Stominok 2008). In the present study, snow crab ranged between 18 (0.1 quantile) and 36 (0.9 quantile) mm CW were most vulnerable to predation by Pacific cod. Similarly, most of snow crab consumed by Pacific cod were <35 mm in the eastern Bering Sea (Livingston 1989; Orensanz et al. 2004). Snow crab grew to 24 and 39 mm CW at the end of age 1 and 2, respectively (Lang et al. 2003). In NCH, CW at which 50 percent of snow crab had finished the terminal molt was estimated at 106.0 mm for males and 63.4 mm for females (Yanagimoto et al. 2004). Therefore, it seems that

Pacific cod mainly consumed young snow crabs, belonging to age 1–2 groups. Large-sized snow crab tends to be consumed by large fish. The nonsignificant relationship between size of Pacific cod and snow crab at 0.9^{th} quantile indicates there is an upper size limit of snow crab can be consumed by Pacific cod. In NCH, snow crab >60 mm accounted high proportion of the population in the depth range between 150–200 m (Yanagimoto et al. 2004). However, these large snow crabs were virtually absent in the Pacific cod stomachs. According to these results, it is reasonable to infer that the observed maximum CW, 61.3 mm is likely close to the upper size limit of snow crab consumed by Pacific cod. The upper size limit of snow crab is likely induced by their morphometric characteristic. Large snow crabs may be too wide to be swallowed by Pacific cod when they extend pereiopods. This phenomenon also occurred in Atlantic cod (Chabot et al. 2008). Moreover, the angle of attack and molting status were important factors affecting predation successfully on large snow crab by Atlantic cod (Robichaud et al. 1991; Chabot et al. 2008). Therefore, larger snow crab occasionally appeared in the stomachs of large-sized Pacific cod.

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 do 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 even in the stomachs of Pacific cod >500 mm SL in the present study, confirming that Pacific cod is an opportunistic predator.

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 changes in swimming performance and gape size (e.g., Yamamura et al. 2002; Temperoni et al. 2021). In this study, the diet of Pacific cod shifted gradually from decapods to fish after reaching ~400–500 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 (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. 2006). Small organisms are important for small-sized predators because they are digested more rapidly than large ones (Sikora et al. 1972) and are easier to catch. 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 show that Pacific cod had a more opportunistic and generalized feeding strategy at about age 2–3 (~300–500 mm) than in other phases. The food spectrum of smaller fish is usually limited by the gape size and swimming ability (Ingram and De Silva 2007; Temperoni et al. 2021). This limit probably occurs in Pacific cod as well. In this study, smaller-sized Pacific cod mainly consumed decapod crustaceans and other benthic organisms. Larger individuals fed mainly on fish, and occasionally on small prey items such as polychaetes and decapod crustaceans. Moreover, the upper size limit for the main prey species, walleye pollock, increased significantly with predator's body length. The feeding strategy that prey size increase with predator size is common in piscivorous fishes (e.g., Scharf et al. 2000; Dörner et al. 2007; Holt et al. 2019), and could mitigate intraspecific competition for food among different body size classes, when food availability is limited.

Chapter 3 Nutritional condition of Pacific cod *Gadus macrocephalus* off the southern and northeastern coasts of Hokkaido

3.1 Introduction

Nutritional condition of fish, as a measure of energy reserves, is impacted by a series of factors, including habitat, season, depth, water temperature, food availability, and aquatic pollution (Le Cren 1951; Hossain et al. 2006; Hattori et al. 2009; Singh and Srivastava 2015). Therefore, nutritional condition of fish can be used to evaluate the potential for reproduction and survival of the population, and further reflect the quality of habitat (Pedersen and Jobling 1989; Lambert and Dutil 2000; Lloret et al. 2002; Hattori et al. 2009). In benthic and demersal fishes, the nutritional condition is usually assessed by length-weight relationship (LWR), condition factor (CF), and hepatosomatic index (HSI) (Jangaard et al. 1967; Lambert and Dutil 1997a; Lloret et al. 2002; Froese 2006; Hattori et al. 2009).

LWR not only provides information on the life history of fish (Nieto-Navarro et al. 2010) , but also facilitate valuable convert of length data into weight estimates, which is a critical step in fish biomass estimates (Froese 1998). LWR is usually characterized by the equation, $W = aL^b$, where W is weight, L is length (Kzys 1928; Froese 1998). The value of exponent b

represents growth pattern of fish. The LWR of Pacific cod has been evaluated in some areas, including Port Townsend Bay, northwestern USA (Willim and Bruce 1977; Bruce et al. 1978), eastern Bering Sea (Wespestad et al. 1982), Gulf of Alaska (Smith et al. 1990), and waters off the Pacific coast of northern Honshu, Japan (Ueda et al. 2006).

In terms of energy cycling, Pacific cod is similar to Atlantic cod (Smith et al. 1990). Previous study has confirmed that CF and HSI can be used as indicators of the energy reserves of Atlantic cod (Lambert and Dutil 1997a). On the basic assumption that heavier weight at a given length corresponds to a better condition. CF based on the data of length and weight has been widely used to evaluate the state of well-being or fatness of fish (Raeisi et al. 2011). In the case of Pacific cod, the potential fecundity is highly correlated with the CF in the North Pacific off Japan (Narimatsu et al. 2010). Additionally, HSI has commonly been used to assess the nutritional condition of fish, because liver is main organ for lipid reserves in many demersal fishes, including Pacific cod, Atlantic cod, and saithe *Pollachius virens* (Jensen 1979; Holdway and Beamish 1984; Lambert and Dutil 1997a; Shulman and Love 1999; Jiang et al. 2012; Copeman et al. 2017; Goldstein et al. 2021). These two simple indices provide a feasible method to compare seasonal and interannual variations in nutritional condition within and between populations (Lambert and Dutil 1997a).

Although CF and HSI are important biological indicators, there has

been relatively limit information on the nutritional condition of Pacific cod in SCH and NCH. Therefore, the aim of this chapter was to carry out the first comprehensive description on the nutritional condition of Pacific cod inhabit these two areas by evaluating the morphometric indices (LWR and CF) and physiological index (HSI). Furthermore, the difference in the nutritional condition between immature and mature Pacific cod was also examined for the specimens collected in NCH in the autumn of 2019.

3.2 Materials and methods

3.2.1 Field sampling

Sampling process is same with that documented in 2.2.1.

3.2.2 Nutritional indices

LWR was examined with a linear regression equation $\log \mathrm{BW} = \log a + b \log \mathrm{SL}$. In the model, $\log a$ is the intercept, regression coefficient b is an exponent which could reflect growth pattern. It indicates equal growth of height, length, and width when b equal to three (isometric growth). Conversely, allometric growth prioritizes width and height (positive growth, $b>3$) or length (negative growth, $b<3$). The reproductive condition of Pacific cod collected in NCH during autumn was determined by the gonadosomatic index (GSI). In order to distinguish the interannual and seasonal effect on the nutritional condition, Pacific cod collected in NCH

were divided into two groups, spring specimens (2018 and 2020) and autumn specimens (2019). CF, expressed as Fulton's condition factor, HSI, and GSI were calculated using the following equations:

$$CF = BW \times 10^5 / SL^3$$

$$HSI \, (\%) = LW \times 100 / BW$$

$$GSI \, (\%) = GW \times 100 / BW,$$

where LW and GW are wet weights of liver and gonad, respectively.

3.2.3　Statistical analyses

LWRs were evaluated for Pacific cod collected from both areas by the linear regression model. Year and sex were also introduced into the models as categorical variables. To examine the effects of year and sex on the CF and HSI, GLMs with Gamma error distribution and log-link function were used, as the distribution of response variables were skewed with occasional high values. According to the result of stomach content analysis, Japanese sardine and walleye pollock were two of the most important prey items in the diet of Pacific cod from the SCH. Snow crab and walleye pollock were two of the most important prey items in the diet of Pacific cod in NCH. Therefore, an additional categorical variable, named prey, was also introduced into the GLMs, which divided Pacific cod into four groups on the basis of diet composition (see below). The effect of reproductive condition (immature or mature) on the CF and HSI was evaluated by GLM

for the Pacific cod collected in NCH in 2019. Pairwise comparisons for significant predict variables were conducted using *glht* function implemented in the multcomp 1.4-19 R package (Hothorn et al. 2008).

Generalized additive models (GAMs) with Gamma error distribution and log-link function were used to evaluate the effects of continuous variables on the nutritional condition. The response variable was CF or HSI. Latitude, towing depth (defined as the bottom depth where the trawling net was set), water temperature at the depth of trawl mouth, and SL were incorporated into the model as predictors. Significant explanatory variables were included in the model. The model with the lowest Akaike's information corrected criterion (AICc) value was selected as the final model. GAMs were constructed using *gam* function implemented in the mgcv 1.8-40 R package. The process of model selection were conducted by *dredge* function in MuMIn 1.46.0 R package (Bartoń 2022). Specimens with missing values of any explainable variable were excluded from the model constructing. All statistical analyses were performed using R 4.2.0 statistical software (R Core Team 2022). Graphs were plotted using the ggplot2 3.3.6 R package (Wickham 2016). Statistical significance was set at the level of *P*<0.05.

3.3 Results

3.3.1 Length-weight relationship

In SCH, there was no significant difference in LWR between sexes (t = -0.58, P>0.05). The relationship was significantly different among years. Therefore, the LWR was further fitted for each year (Fig. 3.1). All LWRs were significant with determination (r^2) values being greater than 0.99. The estimated coefficients for SL ranged from 2.89 to 3.09, and were significantly different from 3 in 2016, 2018, and 2020 (Fig. 3.1).

There was no significant sexual difference in LWR (t = -0.81, P>0.05) for Pacific cod collected in NCH in 2018 and 2020. The estimated slope of SL for Pacific cod in 2018 was slightly but significantly higher than that in 2020 (t = -3.76, P<0.05) (Fig. 3.2). Both b values were not significantly different from 3. No significant sexual difference was found in LWR of Pacific cod collected in NCH in 2019 (t = 0.24, P >0.05). The estimated b value was 3.2, which was significantly higher than 3 (95% confidence interval: 3.16-3.24, r^2 = 0.99).
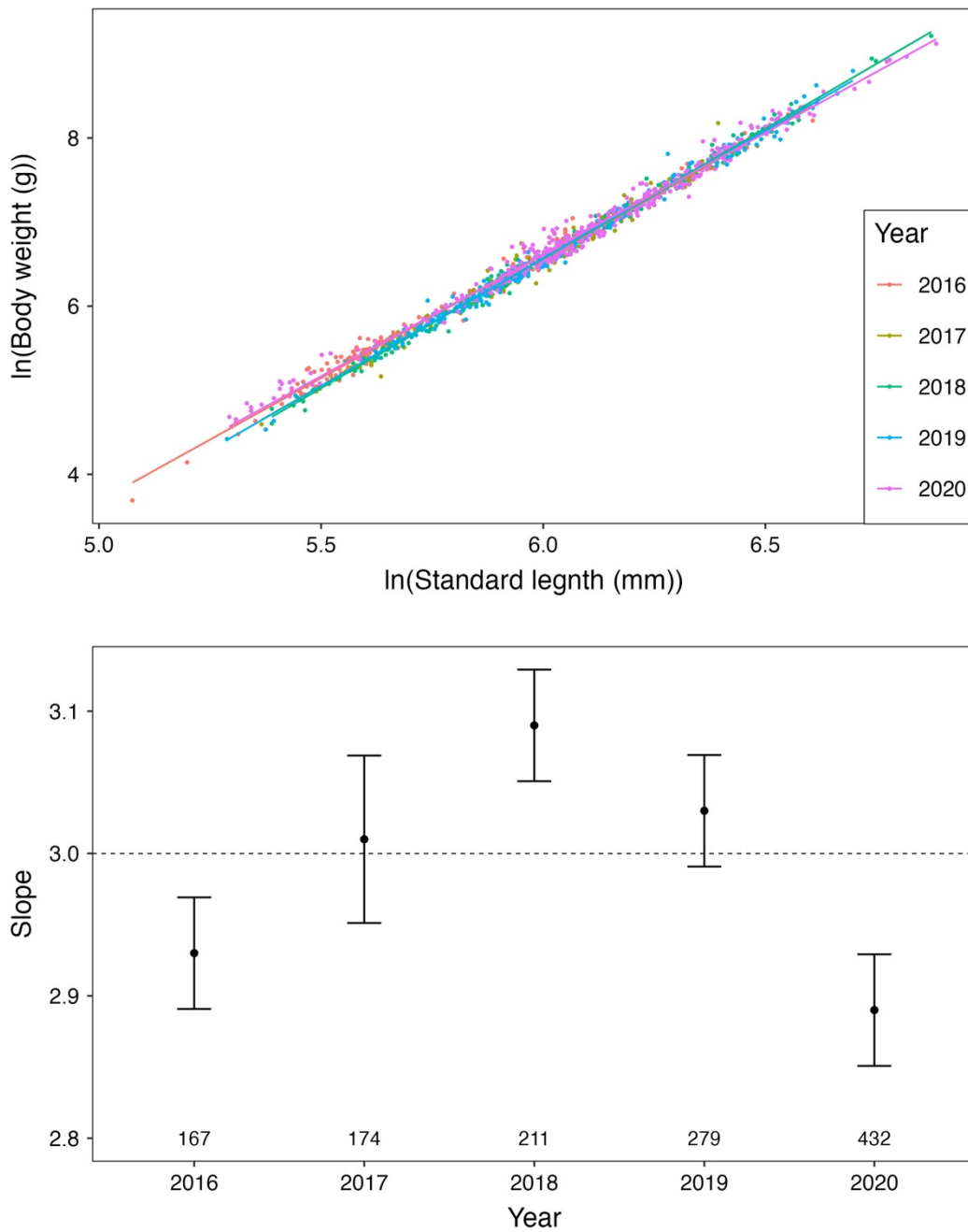
Fig. 3.1. Length-weight relationships (upper) and the estimated coefficients for the effect of SL in the LWRs (bottom) for Pacific cod collected off the southern coast of Hokkaido during 2016–2020. The numerals at the bottom of the lower panel represent the sample size in each year. Error bars represent 95% confidence interval.
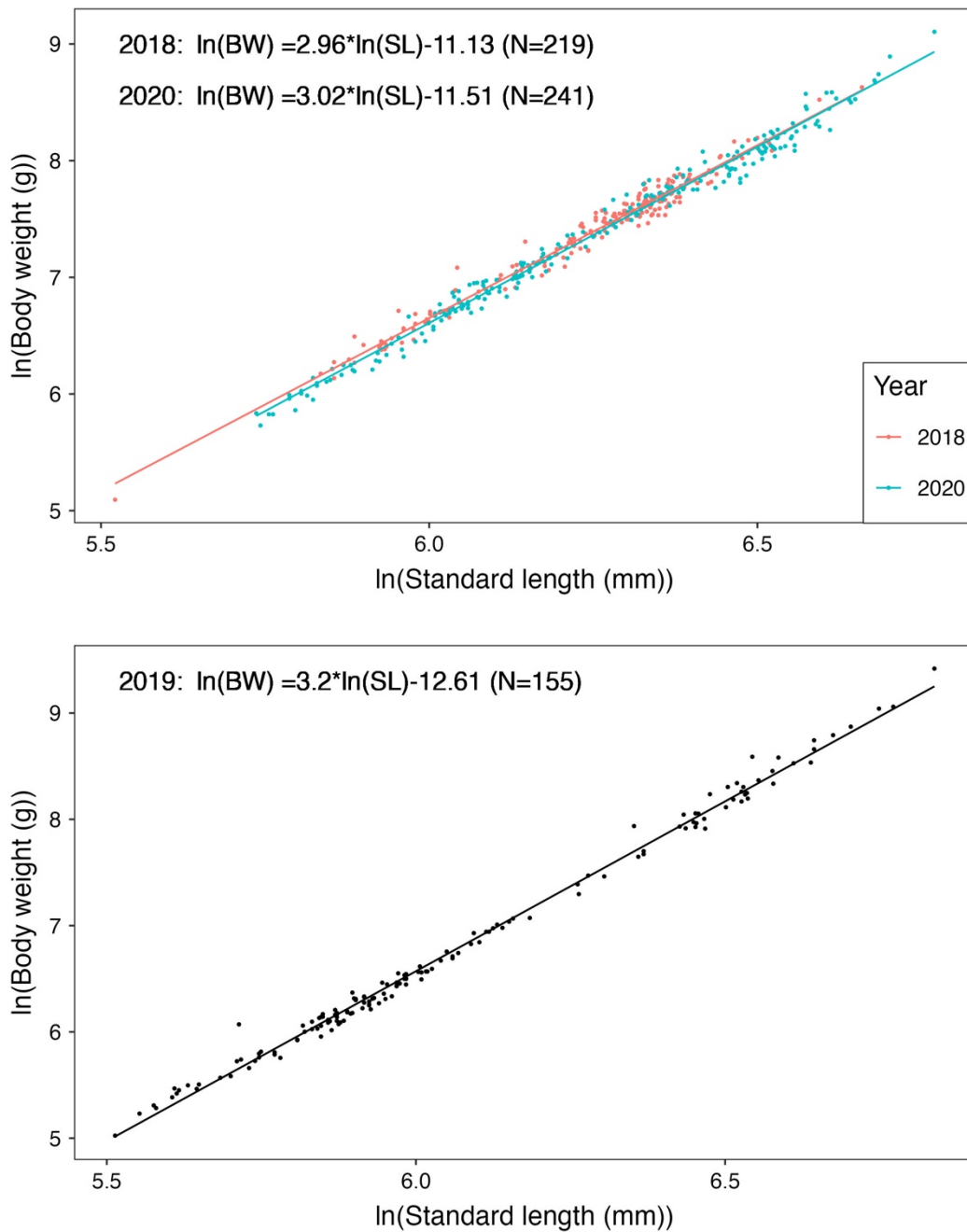
Fig. 3.2. Length-weight relationships of Pacific cod collected off the NCH in 2018 and 2020 (upper), and 2019 (bottom). N; the number of Pacific cod specimens.

3.3.2 Condition factor

In SCH, the CF of 1,217 Pacific cod was calculated and ranged from 0.84 to 1.66. GLM revealed that prey and sex had no significant effect on CF (Table 3.1, Fig. 3.3). CFs in 2016 and 2020 were significantly higher than that in the other three years (Table 3.1, Fig. 3.3). All of the candidates of variables were included in the final GAM model and explained 10.5 % of total variance (Table 3.2). Generally, Pacific cod collected near 42.4 °N, at 3.5 °C and shallower depths (<150 m) had relatively high CF (Fig. 3.4). Additionally, small- (<400 mm SL) and large-sized (>600 mm SL) fish had better condition during summer (Fig. 3.4).

In NCH, CF ranged from 0.91 to 1.6 for Pacific cod collected in 2018 and 2020. There was no significant difference in CF between sexes and among prey groups (Table 3.3, Fig. 3.5). CF was significantly higher in Pacific cod caught in 2018 than that in 2020 (Table 3.3, Fig. 3.5). Latitude and water temperature were included in the final GAM and explained 8.1% of total variance (Table 3.4). Specifically, CF was negatively related to latitude, and positively correlated with temperature (Fig. 3.6). In 2019, the CF ranged from 0.93 to 1.6. There was also no significant sexual difference in CF (Table 3.5). CF of Pacific cod with walleye pollock in their stomachs was significantly higher than other groups (Table 3.5). Bottom temperature and SL were included in the final GAM and explained 50.3% of total variance (Table 3.6). CF was positively correlated with bottom temperature

and SL (Fig. 3.7).

Table 3.1. Summary of generalized linear model explaining the condition factor of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. SE; standard error.

Variables	Estimates	SE	t value	P
Intercept	0.14	0.01	17.48	**<0.001**
Year (2017)	-0.06	0.01	-5.89	**<0.001**
Year (2018)	-0.05	0.01	-5.58	**<0.001**
Year (2019)	-0.06	0.01	-6.34	**<0.001**
Year (2020)	-0.02	0.01	-2.49	**0.013**
Japanese sardine	-0.00	0.01	-0.48	0.629
Walleye pollock	0.01	0.01	1.19	0.235
Both	-0.00	0.02	-0.01	0.996
Sex (Female)	-0.00	0.01	-0.39	0.697

Table 3.2. Summary of generalized additive model explaining the condition factor of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. edf; estimated degrees of freedom.

Variables	edf	F	P
Latitude	1.97	21.44	**<0.001**
Temperature	1.95	11.15	**<0.001**
Depth	2.73	11.73	**<0.001**
Standard length	1.92	5.86	**<0.001**
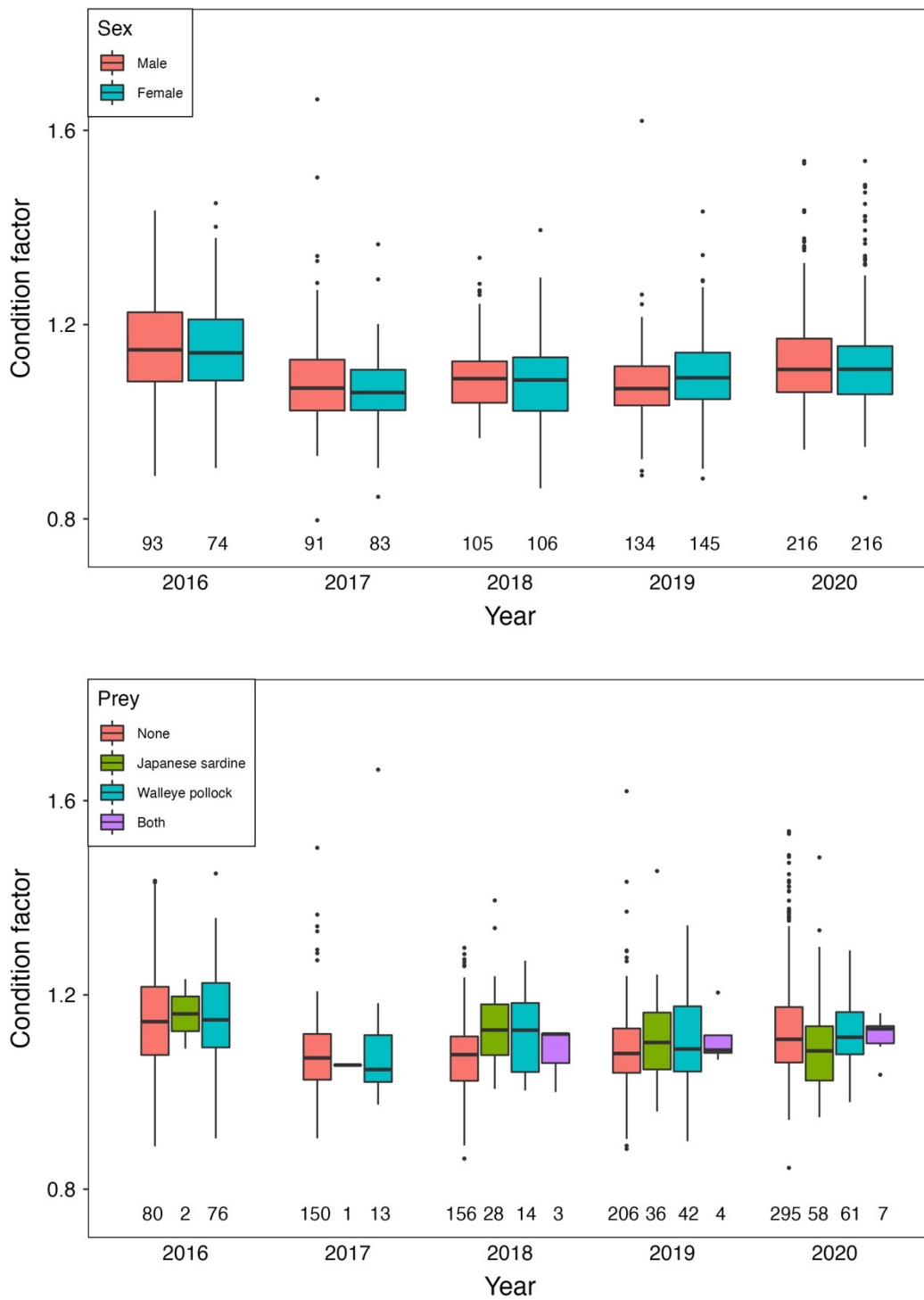
Fig. 3.3. Boxplots of the condition factor of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. The numbers at the bottom of each panel represent sample size. The bold lines represent the median, the lower and upper hinges correspond to the first and third quartiles, and the upper and lower whiskers extend to the largest and smallest value with 1.5 times the interquartile range.
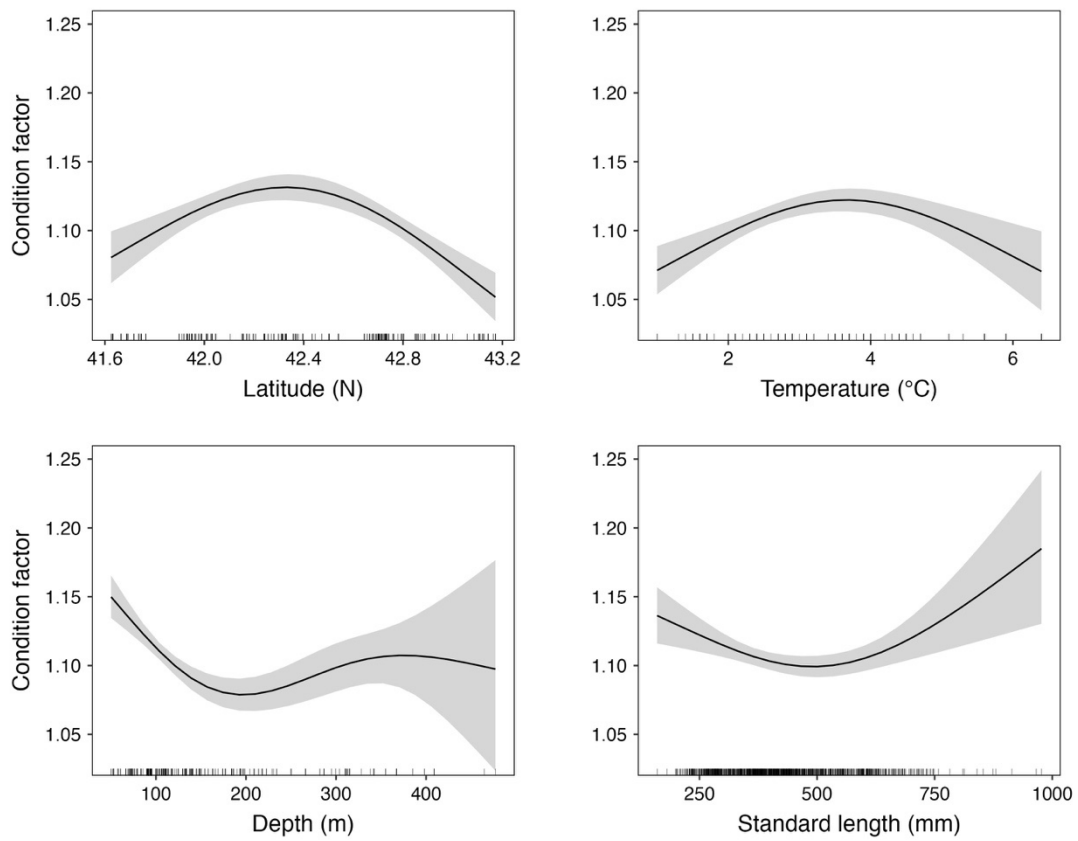
Fig. 3.4. Partial plots from the final generalized additive model showing the influence of covariates on the condition factor of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. Response curves are given by the solid lines and 95% confidence interval by the shaded areas.

Table 3.3. Summary of generalized linear model explaining the condition factor of Pacific cod collected off the northeastern coast of Hokkaido in 2018 and 2020. SE; standard error.

Variables	Estimates	SE	*t* value	*P*
Intercept	0.15	0.01	16.59	**<0.001**
Year (2020)	-0.02	0.01	-2.70	**0.007**
Snow crab	-0.01	0.01	-0.99	0.321
Walleye pollock	0.01	0.01	0.88	0.378
Both	0.01	0.01	0.62	0.535
Sex (Female)	0.01	0.01	0.86	0.392

Table 3.4. Summary of generalized additive model explaining the condition factor of Pacific cod collected off the northeastern coast of Hokkaido in 2018 and 2020. edf; estimated degrees of freedom.

Variables	edf	*F*	*P*
Latitude	1.00	26.83	**<0.001**
Temperature	1.00	16.69	**<0.001**

Table 3.5. Summary of generalized linear model explaining the condition factor of Pacific cod collected off the northeastern coast of Hokkaido in 2019. SE; standard error.

Variables	Estimates	SE	*t* value	*P*
Intercept	0.07	0.01	5.25	**<0.001**
Snow crab	0.00	0.02	0.17	0.862
Walleye pollock	0.11	0.02	4.58	**<0.001**
Both	0.00	0.10	0.01	0.989
Sex (Female)	0.02	0.02	1.51	0.132

Table 3.6. Summary of generalized additive model explaining the condition factor of Pacific cod collected off the northeastern coast of Hokkaido in 2019. edf; estimated degrees of freedom.

Variables	edf	*F*	*P*
Standard length	1.72	57.43	**<0.001**
Temperature	1.68	6.15	**<0.01**
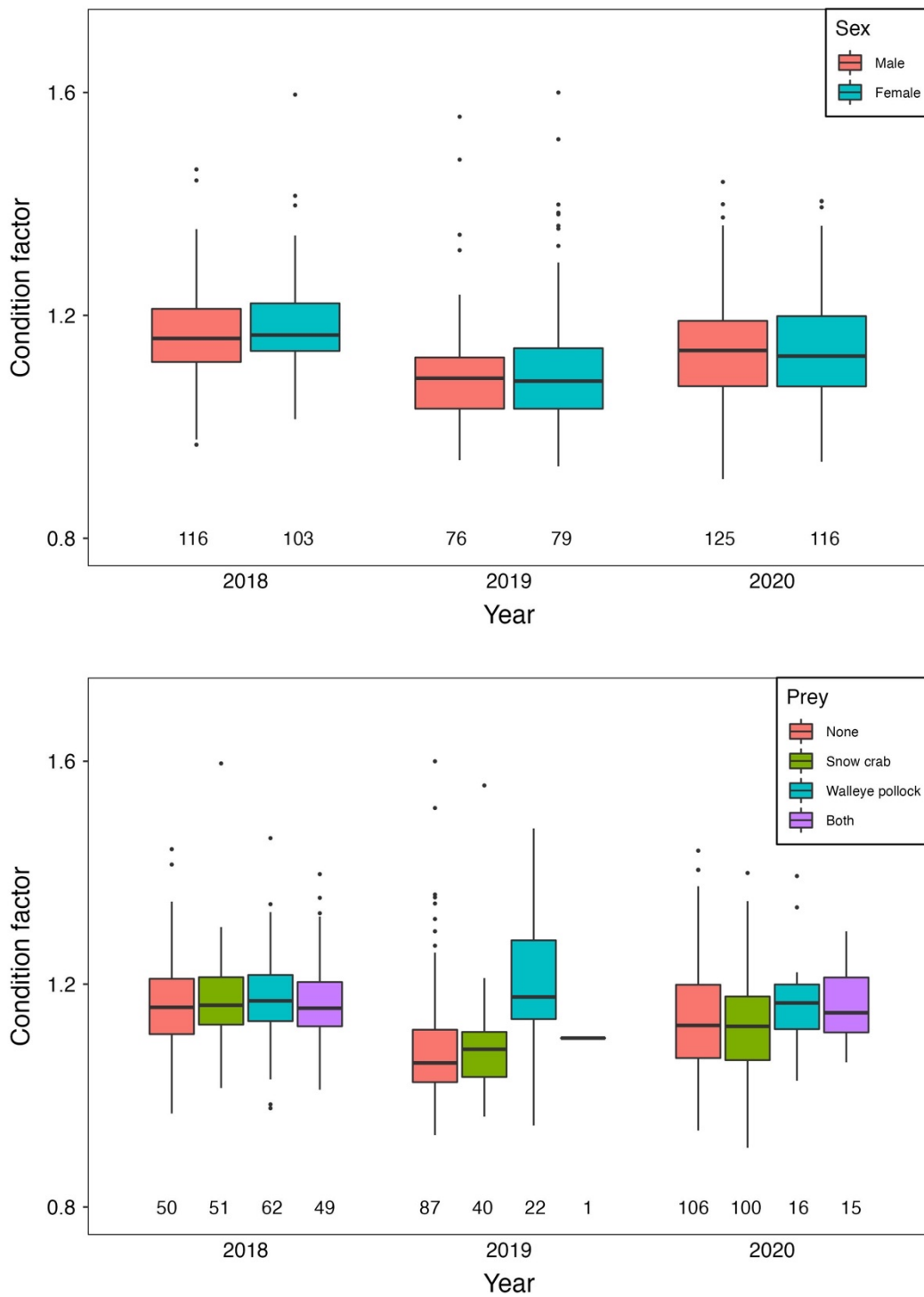
Fig. 3.5. Boxplots of the condition factor of Pacific cod collected off the northeastern coast of Hokkaido during 2018–2020. The numbers at the bottom of each plot represent the sample size. The bold lines represent the median, the lower and upper hinges correspond to the first and third quartiles, and the upper and lower whiskers extend to the largest and smallest value with 1.5 times the interquartile range.
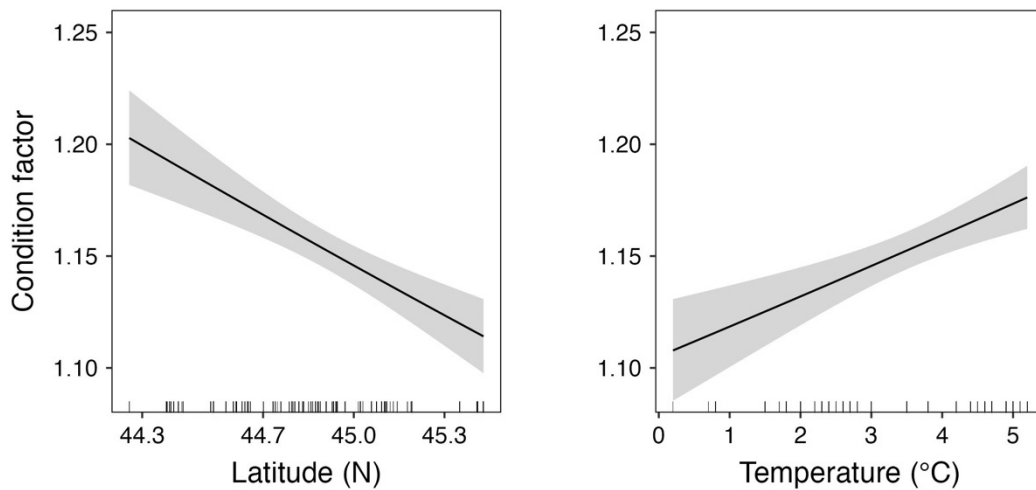
Fig. 3.6. Partial plots from the final generalized additive model showing the influence of covariates on the condition factor of Pacific cod collected off the northeastern coast of Hokkaido during in 2018 and 2020. Response curves are given by the solid lines and 95% confidence interval by the shaded areas.
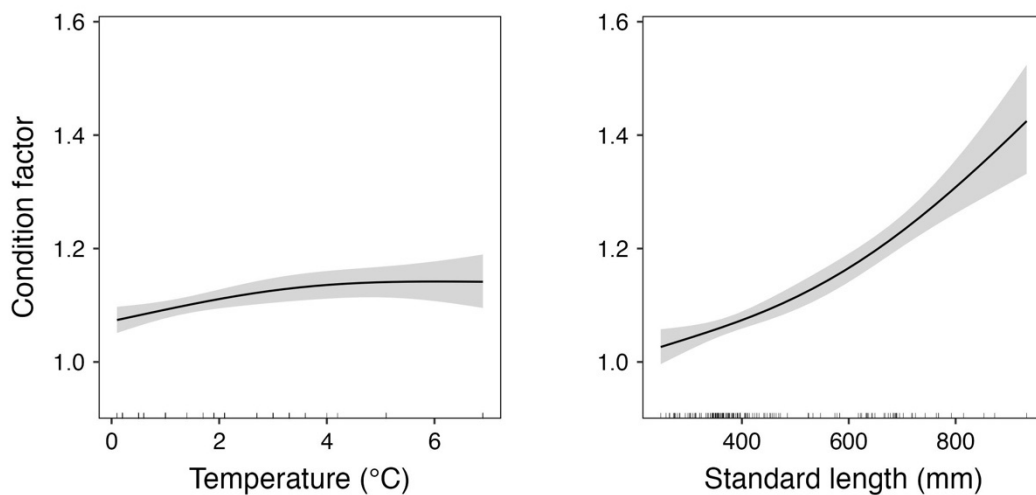
Fig. 3.7. Partial plots from the final generalized additive model showing the influence of covariates on the condition factor of Pacific cod collected off the northeastern coast of Hokkaido during in 2019. Response curves are given by the solid lines and 95% confidence interval by the shaded areas.

3.3.3　Hepatosomatic index

In SCH, HSI of 1,259 Pacific cod ranged from 0.26% to 12.83%. HSI varied with year, but not with sex (Table 3.7). Pacific cod collected in 2016 showed significantly lower HSI than in other years (Table 3.7, Fig. 3.8). The HSI of Pacific cod consuming Japanese sardine was significantly higher than those consuming walleye pollock. Pacific cod consuming neither walleye pollock nor Japanese sardine had the lowest HSI among the four predefined groups (Table 3.7, Fig. 3.8). All explanatory variables were included in the final GAM for HSI, and 45.6% of the variability in HSI was explained (Table 3.8). HSI was inversely related to latitude and depth, and positively correlated with SL (Fig. 3.9). HSI peaked at ca. 4 °C and decreased towards 6 °C (Fig. 3.9).

In NCH, the range of HSI was 0.91–12.38% for 460 Pacific cod collected in 2018 and 2020. HSI of Pacific cod collected in 2018 was significantly higher than that in 2020 (Table 3.9, Fig. 3.10). HSI of Pacific cod with snow crab in stomachs was significantly lower than those consumed walleye pollock or other prey items (Table 3.9, Fig. 3.10). Bottom temperature and SL were included in the final GAM, and explained 46.4% of the variation in HSI (Table 3.10). HSI was positively correlated with bottom temperature and SL (Fig. 3.11). In 2019, HSI of 155 Pacific cod was calculated, ranging from 0.85 to 15.76%. There was no significant difference in HSI between sexes (Table 3.11). Pacific cod with walleye

pollock in the stomachs had remarkably higher HSI than other groups (Table 3.11, Fig. 3.10). The final GAM accounted for 83.1% of the variation in HSI, with latitude, bottom temperature, and SL being significant variables (Table 3.12). HSI peaked at about 3 °C and was positively correlated with latitude and SL (Fig. 3.12).

Table 3.7. Summary of generalized linear model explaining the hepatosomatic index of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. SE, standard error.

Variables	Estimates	SE	*t* value	*P*
Intercept	0.92	0.04	21.95	**<0.001**
Year (2017)	0.26	0.05	4.92	**<0.001**
Year (2018)	0.45	0.05	8.84	**<0.001**
Year (2019)	0.37	0.05	7.90	**<0.001**
Year (2020)	0.52	0.04	11.76	**<0.001**
Japanese sardine	0.46	0.05	9.92	**<0.001**
Walleye pollock	0.31	0.04	8.17	**<0.001**
Both	0.46	0.13	3.65	**<0.001**
Sex (Female)	-0.00	0.03	-0.05	0.959

Table 3.8. Summary of generalized additive model explaining the hepatosomatic index of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. edf; estimated degrees of freedom.

Variables	edf	*F*	*P*
Latitude	1.00	12.55	**<0.001**
Temperature	1.93	11.48	**<0.001**
Depth	1.77	9.35	**<0.001**
Standard length	1.00	810.63	**<0.001**
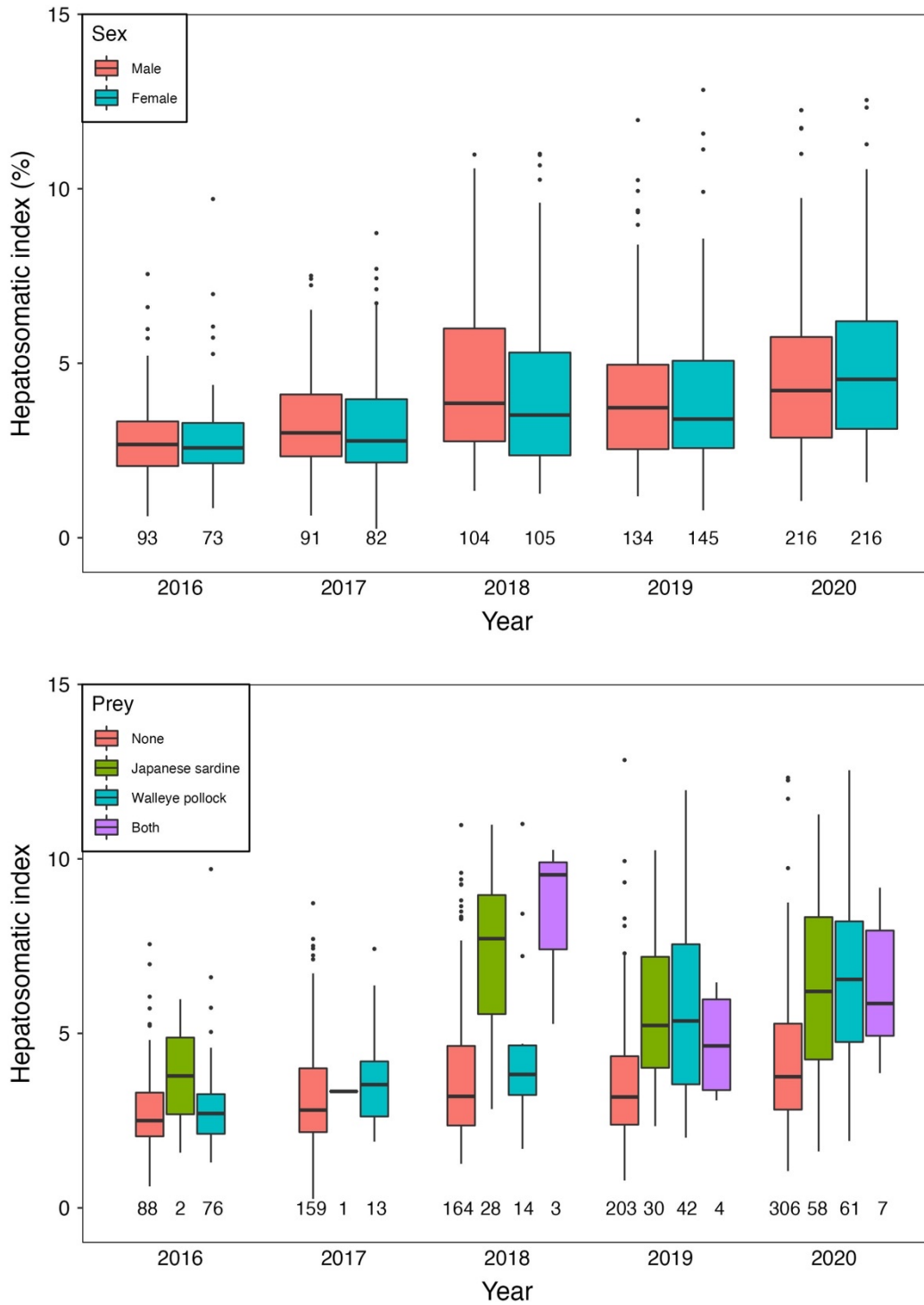
Fig. 3.8. Boxplots of the hepatosomatic index of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. The numbers at the bottom of each panel represent the sample size. The bold lines represent the median, the lower and upper hinges correspond to the first and third quartiles, and the upper and lower whiskers extend to the largest and smallest value with 1.5 times the interquartile range.

70
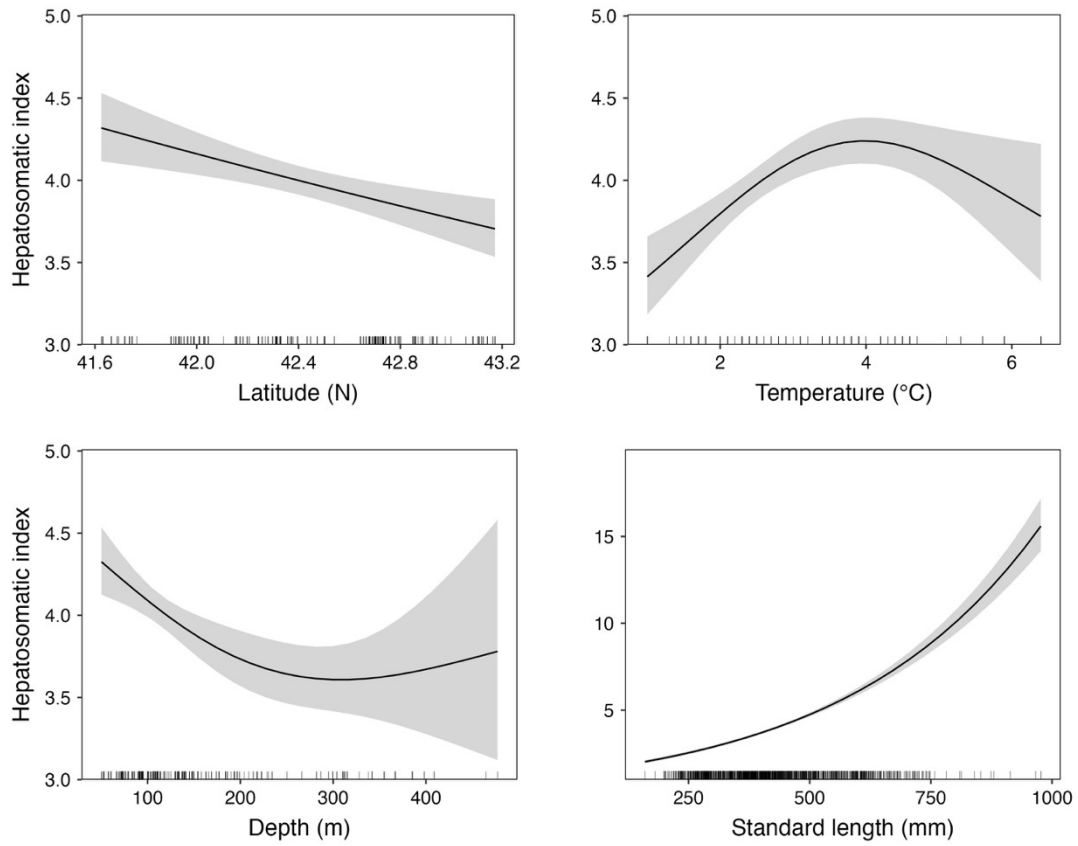
Fig. 3.9. Partial plots from the final generalized additive model showing the influence of covariates on hepatosomatic index of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. Response curves are shown by solid lines and shaded areas show 95% confidence intervals.

Table 3.9. Summary of generalized linear model explaining the hepatosomatic index of Pacific cod collected off the northeastern coast of Hokkaido in 2018 and 2020. SE; standard error.

Variables	Estimates	SE	*t* value	*P*
Intercept	1.87	0.04	44.34	**<0.001**
Year (2020)	-0.30	0.04	-7.70	**<0.001**
Snow crab	-0.12	0.04	-2.81	**0.005**
Walleye pollock	0.05	0.05	0.85	0.396
Both	0.02	0.06	0.39	0.696
Sex (Female)	0.07	0.04	2.04	**0.041**

Table 3.10. Summary of generalized additive model explaining the hepatosomatic index of Pacific cod collected off the northeastern coast of Hokkaido in 2018 and 2020. edf; estimated degrees of freedom.

Variables	edf	*F*	*P*
Temperature	1.57	60.87	**<0.001**
Standard length	1.96	176.59	**<0.001**

Table 3.11. Summary of generalized linear model explaining the hepatosomatic index of Pacific cod collected off the northeastern coast of Hokkaido in 2019. SE; standard error.

Variables	Estimates	SE	*t* value	*P*
Intercept	1.28	0.10	12.71	**<0.001**
Snow crab	-0.27	0.14	-1.94	0.053
Walleye pollock	0.56	0.17	3.23	**0.001**
Both	0.72	0.74	0.98	0.326
Sex (Female)	0.22	0.12	1.88	0.060

Table 3.12. Summary of generalized additive model explaining the hepatosomatic index of Pacific cod collected off the northeastern coast of Hokkaido in 2019. edf; estimated degrees of freedom.

Variables	edf	*F*	*P*
Latitude	1.81	5.51	**<0.01**
Temperature	1.94	11.79	**<0.001**
Standard length	1.55	285.76	**<0.001**
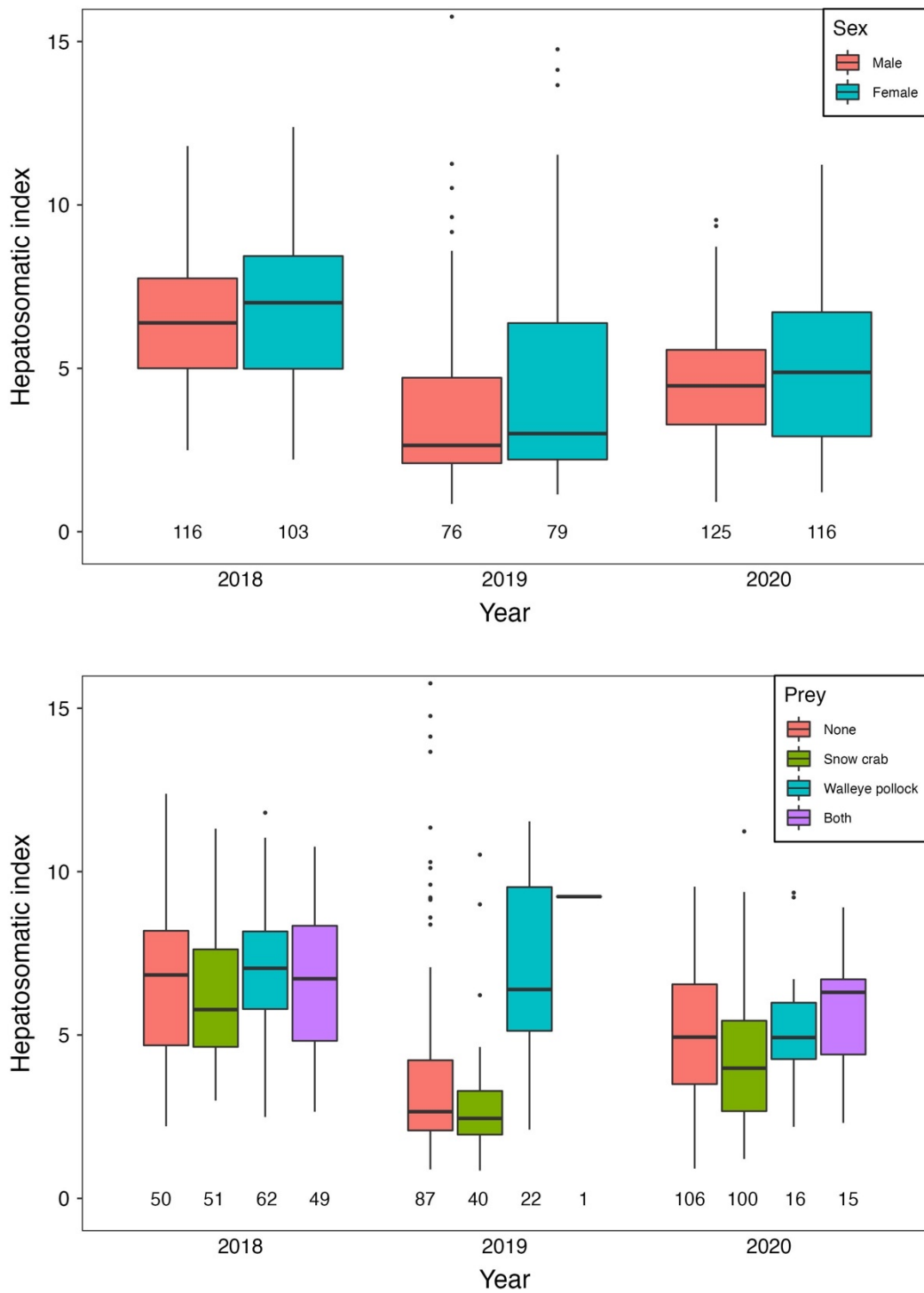
Fig. 3.10. Boxplots of the hepatosomatic index of Pacific cod collected off the northeastern coast of Hokkaido during 2018–2020. The numbers at the bottom of each panel represent the sample size. The bold lines represent the median, the lower and upper hinges correspond to the first and third quartiles, and the upper and lower whiskers extend to the largest and smallest value with 1.5 times the interquartile range.
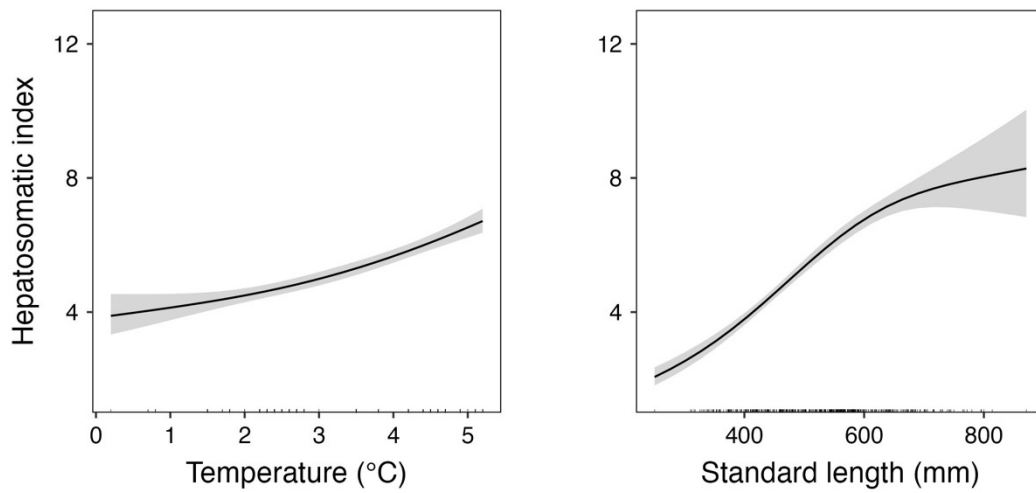
Fig. 3.11. Partial plots from the final generalized additive model showing the influence of covariates on the hepatosomatic index of Pacific cod collected off the northeastern coast of Hokkaido in 2018 and 2020. Response curves are shown by solid lines and shaded areas show 95% confidence intervals.
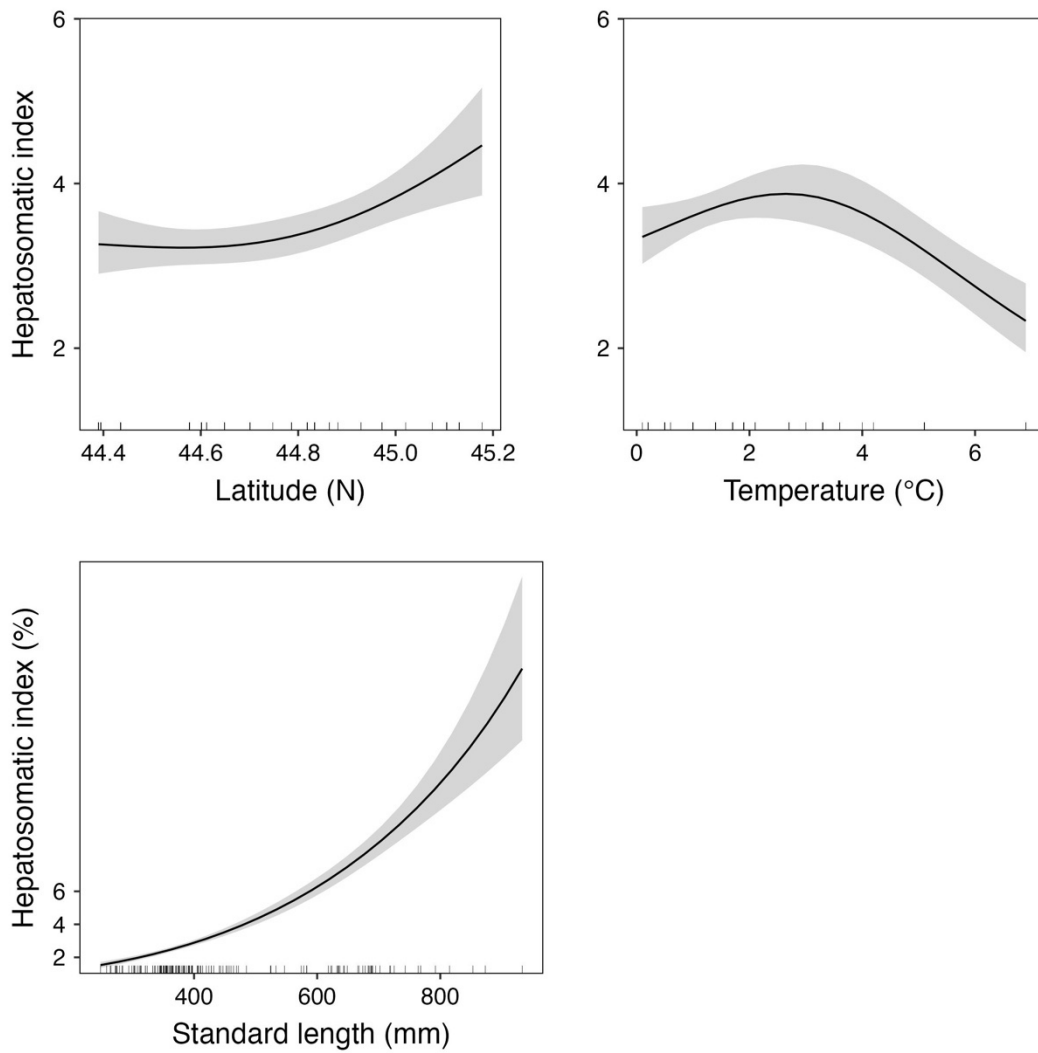
Fig. 3.12. Partial plots from the final generalized additive model showing the influence of covariates on the hepatosomatic index of Pacific cod collected off the northeastern coast of Hokkaido in 2019. Response curves are shown by solid lines and shaded areas show 95% confidence intervals.

3.3.4 Gonadosomatic index

In NCH, among the 76 male Pacific cod collected in 2019, GSI remarkably increased from 0.65% to 7.23% in a Pacific cod measured 533 mm (Fig. 3.13). In this study, 18 male Pacific cod with GSI values ranged from 7.23% to 37.1% (16.2 ± 7.48%, mean ± standard deviation) were assumed to be mature individuals. Other fish with GSI value ≤0.65% were assumed to be immature. SL of immature male fish ranged from 158 to 578 mm (Fig. 3.13). Among the 79 female Pacific cod collected in 2019, GSI remarkably increased from 1.47% to 3.58% in a Pacific cod measured 622 mm (Fig. 3.13). Female Pacific cod with GSI values ranged from 3.58% to 8.66% (5.58 ± 1.25%, mean ± standard deviation) were assumed to be mature individuals. Other 58 female fish with GSI value ≤1.47% were assumed to be immature. SL of these immature fish ranged from 248 to 583 mm (Fig. 3.13).

Both CF and HSI were significantly higher in mature Pacific cod than immature individuals (Table 3.13, Fig. 3.14). Among mature Pacific cod, CF and HSI were significantly higher in females than males (Fig. 3.14).
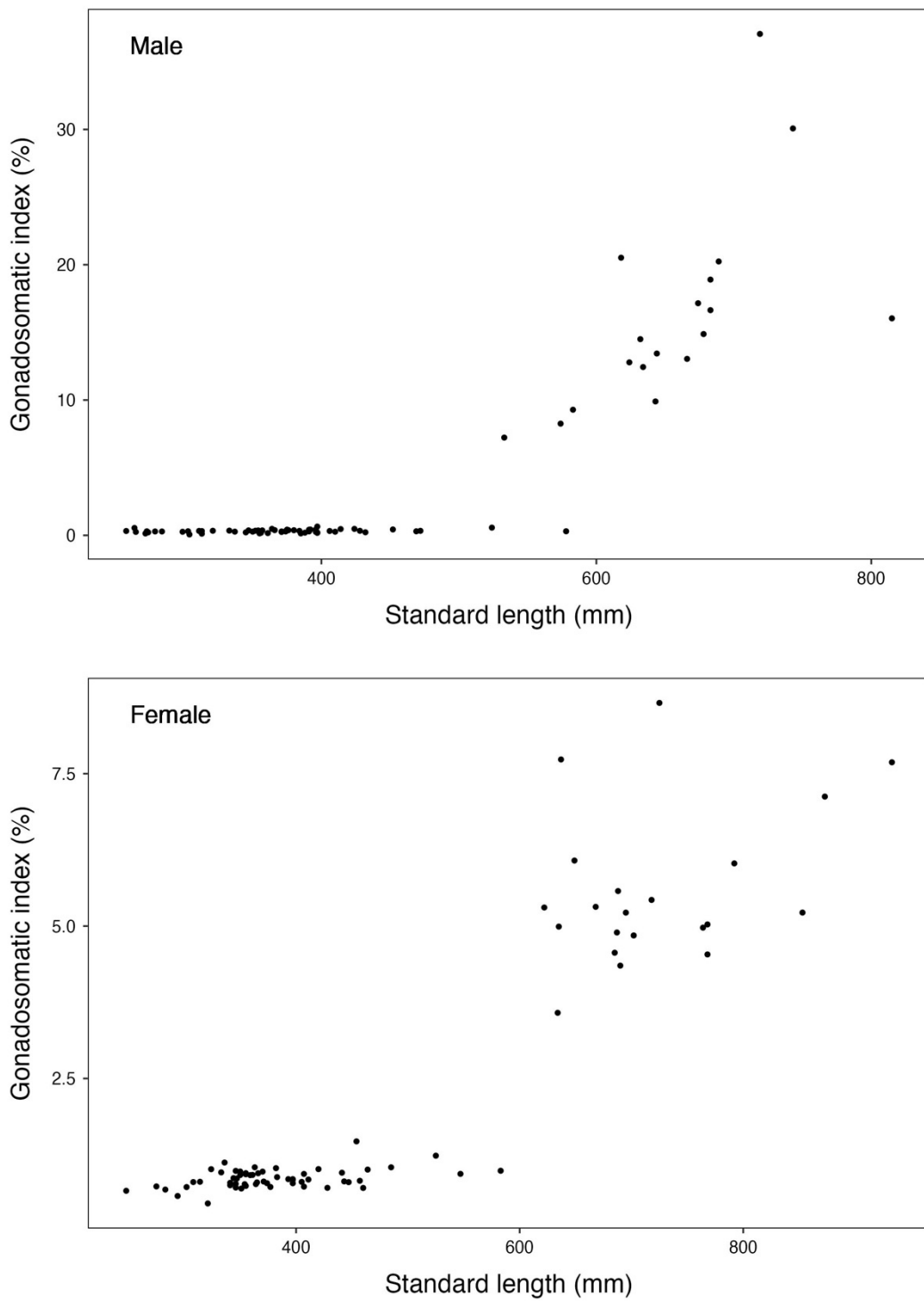
Fig. 3.13. Relationship between gonadosomatic index and standard length of Pacific cod collected off the northeastern coast of Hokkaido in 2019.

Table 3.13. Summary of generalized linear models explaining condition factor (CF) and hepatosomatic index (HSI) of Pacific cod collected off the northeastern coast of Hokkaido in 2019. SE, standard error.

Variables	Model for CF				Model for HSI			
	Estimates	SE	t value	P	Estimates	SE	t value	P
Intercept	0.06	0.01	5.70	**<0.001**	0.90	0.05	18.76	**<0.001**
Mature	0.15	0.01	10.40	**<0.001**	1.22	0.07	16.75	**<0.001**
Female	0.01	0.01	0.89	0.376	0.14	0.06	2.26	**0.024**
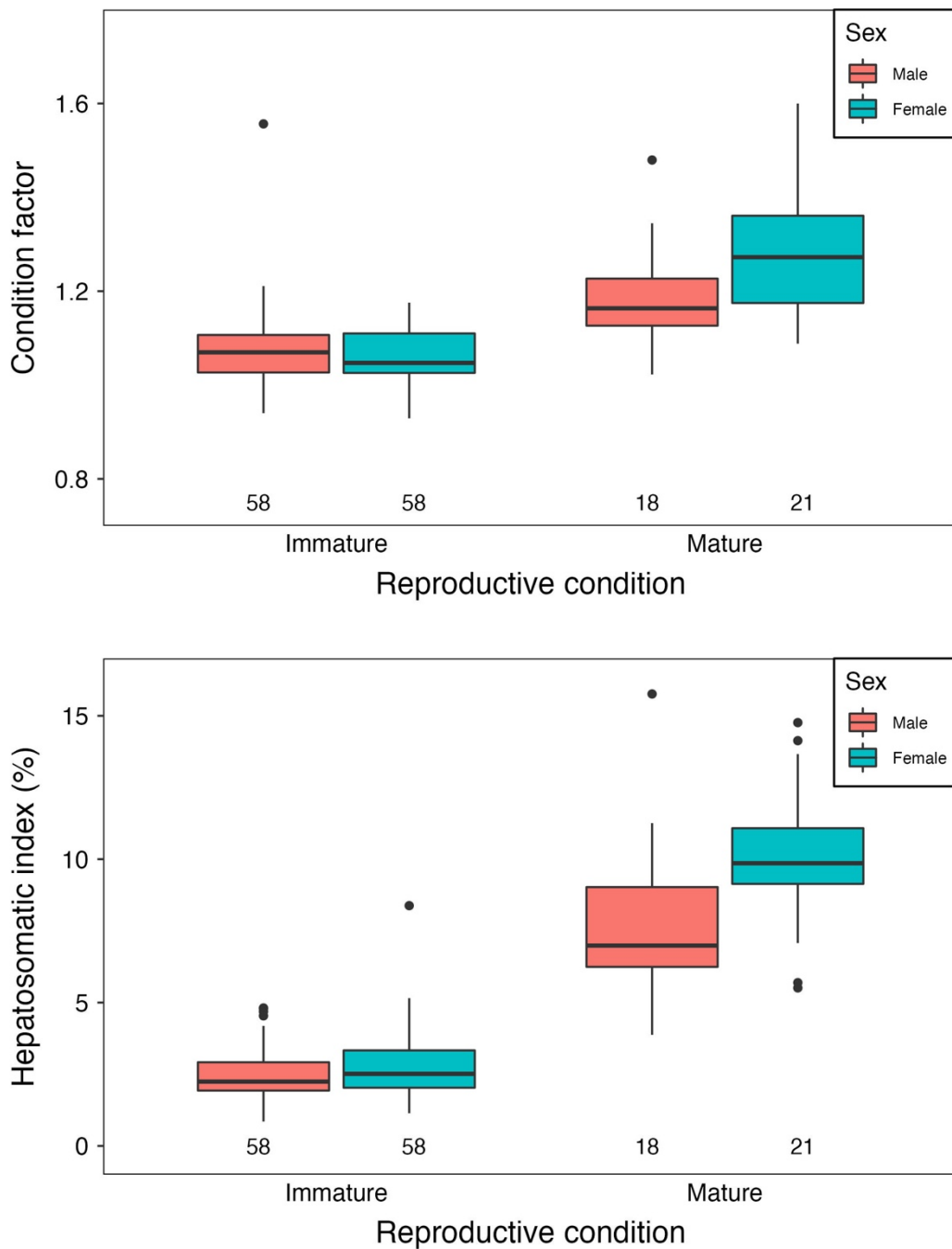
Fig. 3.14. Boxplots of the condition factor and hepatosomatic index of Pacific cod collected off the northeastern coast of Hokkaido in 2019. The numbers at the bottom of each panel represent the sample size. The bold lines represent the median, the lower and upper hinges correspond to the first and third quartiles, and the upper and lower whiskers extend to the largest and smallest value with 1.5 times the interquartile range.

3.4　Discussion

According to the results of LWRs, the estimated b values fluctuated around 3, indicating Pacific cod generally exhibit isometric growth pattern in SCH in summer and in NCH in spring. Similar growth pattern was also observed in the Pacific cod in Port Townsend Bay, northwest USA (Willim and Bruce 1977; Bruce et al. 1978) and in the eastern Bering Sea (Wespestad et al. 1982). In NCH, the estimated b for the Pacific cod collected in autumn was significantly higher than that in the spring, indicating a positive allometric growth pattern in autumn. Similarly, in the waters off the Pacific coast of northern Honshu, the estimated b for Pacific cod was higher in October ($b = 3.26$) than that in February ($b = 3.17$) (Ueda et al. 2006). Pacific cod expend about 30–31% of prespawning stored energy during the spawning season (Smith et al. 1990). Seasonal variations in the growth pattern suggest Pacific cod have recovered from energy depleted condition and accumulated energy for the following overwintering and reproductivity in October. Moreover, female and male fish might undergo synchronous changes in the LWRs throughout the year, because there was no sexual difference in LWRs in all surveyed seasons in both areas.

Although the nutritional condition was affected by a number of factors, the ranges of CF and HSI remained relatively stable in the seasons surveyed. The biomass of Pacific cod in SCH and NCH have increased in

recent years (Chimura et al. 2022; Sakai et al. 2022). These facts suggest that the abiotic and biotic conditions in both areas are suitable for Pacific cod. CF was not affected by the diet composition in SCH in summer and in NCH in spring. Meanwhile, the HSI of Pacific cod with Japanese sardine in the stomachs was significantly higher than those consumed other prey items. Conversely, the HSI of Pacific cod with snow crab in the stomachs in NCH in spring was lower than other fish groups. On the other hand, the fraction of variations in CF explained by the factors included in the final GAMs were relatively limited (8.1–50.3%), while GAMs performed on HSI showed better performance explaining 45.6–83.1% fractions of total variation. In general, CF reflects fish nutritional condition over longer time period when compared with HSI which is more sensitive to environmental conditions in short time period, including the availability of preferable food (Lambert and Dutil 1997a). For instance, a feeding experiment conducted on Atlantic cod showed that fish fed with herring stored more lipids in liver than those fed with squid (Black and Love 1986). These results coincide with the abovementioned relationship between HSI and CF.

The difference in the HSI among the prey groups suggests that Japanese sardine would be a nutritionally better prey for Pacific cod in SCH. In contrast, snow crab should be a less nutritional prey contributing less to the energy accumulation for Pacific cod in NCH, although it occurred frequently in the stomachs. This could be explained by the

different biological and physiological characteristics of prey species. Japanese sardine is nutritionally rich prey containing much lipids (Walker 1996), while snow crab is uneasy to be digested due to the hard exoskeleton (Couturier et al. 2013). In the present study, HSI increased with SL in all investigated seasons. Similarly, larger Atlantic cod generally have higher fat content in liver (Jangaard et al. 1967). The positive relationship between HSI and SL might derive from the diet composition, as fish prey occurred more frequently in the diet of larger Pacific cod.

There was no significant sexual difference in CF and HSI in all surveyed seasons. This result suggests that both sexes of Pacific cod were in similar nutritional condition, although they might undergo different physical development, including the seasonal cycle in gonad development. Similar results were also found in Atlantic cod in the northern Gulf of St. Lawrence stock (Lambert and Dutil 1997b).

In NCH, nutritional condition was lower in the Pacific cod collected in the autumn than that in the spring. However, in the Gulf of Alaska, the CF and HSI of Pacific cod was usually lower during April to July relative to autumn and winter (Smith et al. 1990). The results of GAMs indicated that HSI was positively correlated with SL. Therefore, the seasonal difference in the nutritional condition is possibly related to the higher proportion of small-sized cod in the specimens in the autumn. On the other hand, as was described in the previous study, seasonal patterns in the

nutritional condition is also associated with maturation and spawning (Lambert and Dutil 1997a). Therefore, in the present study, the development of the gonad was also examined.

It has been reported that Pacific cod had already made the decision of whether to spawn in the next reproductive season in October off the northeastern Honshu (Narimatsu et al. 2010). Moreover, in that study, female Pacific cod, caught between October and December, with GSI value less than 2.2 and larger than 2.6 were determined to be immature and mature, respectively. GSI was bimodally distributed for the Pacific cod caught in NCH in the autumn of 2019. The remarkable increase in GSI along SL makes it possible to divide specimens roughly into the two separate groups, immature and mature group. The average GSI of mature female Pacific cod (5.58 ± 1.25, mean ± standard deviation) was close to the range of 4.68–6.73, which was observed in the population in SCH during autumn (Hattori et al. 1992b). In NCH, Pacific cod grow to about 600 mm SL at the age of 5–6 year (Kaga et al. 2020). Taken together with the relationship between GSI and SL, it can be concluded that almost all Pacific cod mature when SL attain about 550 mm (age 5) in males and 650 mm (age 6) in females in NCH. Similar results were also reported in the previous studies, which documented that 100% sexual maturation in Pacific cod occurred at the ages >5 and 6–7 in the Tohoku region and Japan Sea, respectively (Narimatsu 2010; Vdovin 2019). The phenomenon that

male Pacific cod mature earlier than female was also found in the waters of the northern Kuril Islands and the southern part of Kamchatka, where almost all fish matured when males reach a length of 61–70 cm and females 65–75 cm (Poltev 2008). Male Pacific cod also matured earlier than females in Strait of Georgia waters and in the northern Hecate Strait (Ketchen 1961).

In NCH, nutritional condition of Pacific cod was positively correlated with SL during autumn. Meanwhile, large-sized Pacific cod usually had high GSI. Therefore, Pacific cod in better nutritional condition tend to has higher GSI. CF also positively affects the potential fecundity of Pacific cod population in Tohoku region and in the Gulf of Alaska (Smith et al. 1990; Narimatsu et al. 2010). Poor conditioned Atlantic cod reduce reproductive investment to limit somatic energy losses (Lambert and Dutil 2000). This phenomenon is probably because that low-conditioned female fish would reduce reproductive investment in order to keep enough energy reserves for the wintering.

Chapter 4 General discussion

Overall, this work has provided updated information on the diet composition of Pacific cod in SCH. The feeding habits of Pacific cod in NCH was firstly documented. Moreover, the nutritional condition of Pacific cod in these two areas was evaluated from morphometric and physiological perspectives. Information from this study has advanced our understanding of the trophic ecology of Pacific cod, and can be used to inform ecosystem mass balance models, stock assessments, and evaluate the habitat suitability.

In chapter 2, feeding habits of Pacific cod were examined by means of stomach content analysis. The diet of Pacific cod consisted of at least 60 prey species in SCH and 45 species in NCH. The broad food spectra indicate Pacific cod is a generalist feeder. Generally, the main diet shifted from decapod crustaceans to fish at about age 3 (400–500 mm SL). Previous studies performed on the feeding ecology of Pacific cod in the North Pacific have shown that there are temporal and spatial variations in the diet composition of Pacific cod (Suyehiro 1934; Albers and Anderson 1985; Lang et al. 2005; Poltev and Stominok 2008; Choi et al. 2019). These variations also exist in the areas investigated. Moreover, factors affecting the nutritional condition of Pacific cod are partly different between SCH and NCH. These results suggest Pacific cod are able to adapt various

ecosystems.

Although many species occurred in the stomachs, results of stomach contents analysis have revealed that Pacific cod tend to feed mainly on limited prey species in the areas investigated (walleye pollock and Japanese sardine in SCH; walleye pollock and snow crab in NCH). Walleye pollock played important roles in the diet of Pacific cod in both areas surveyed. Moreover, the size of walleye pollock found in the stomachs increased with the body size of Pacific cod. Walleye pollock from juvenile to about age 3 can be used by Pacific cod. Japanese sardine gradually became main prey for Pacific cod in SCH during 2018–2020. The SL of intact Japanese sardine found in the stomachs ranged from 112.75 to 220 mm. The upper size limit of Japanese sardine consumed by Pacific cod is likely close to the asymptotic body length, suggesting Japanese sardine from juvenile to adult stage are available prey for Pacific cod. The relatively high consumption of snow crab is a noticeable feeding peculiarity for Pacific cod in NCH. Most of the consumed snow crab located in the size range of 18–36 mm CW, indicating Pacific cod mainly preyed upon young snow crab. The intensive predation on these three species may exert a negative impact on the recruitment of these populations. However, results provided here are not insufficient to elaborate the interspecific relationships between Pacific cod and main prey species populations. Data on the biomass of main prey species is critical for further

understanding of the complex bottom-up and top-down interactions, which will inform the ecosystem-based fishery management. Therefore, these data are recommended to collect in the future surveys. The feeding intensity was relatively high during surveyed seasons and affected by the main prey species. The SFI of Pacific cod was usually high when fed Japanese sardine and/or walleye pollock. The diet information presented herein can be used to inform ecological models, such as the Ecopath model (Polovina 1984).

In chapter 3, the nutritional condition of Pacific cod was evaluated by LWR, CF, and HSI. The results of LWRs indicate Pacific cod generally exhibit isometric growth pattern in the areas investigated. The relatively stable nutritional condition, combined with the increased stock biomass (Chimura et al. 2022; Sakai et al. 2022), suggest both areas are possibly suitable habitats for Pacific cod. Diet significantly affect the HSI but not CF, indicating CF might reflect the nutritional condition over longer time period than HSI. The HSI of Pacific cod with Japanese sardine in the stomachs was significantly high. In contrast, Pacific cod consumed snow crab usually had lower HSI values. These results indicate the nutrient rich fish, Japanese sardine, is a better prey species. Meanwhile, snow crab is not optimal prey for Pacific cod from the digestibility and availability perspective. The high proportion of snow crab in the diet is likely due to the high abundance in the habitat. On the other hand, snow crab is usually easier to be caught than fish. This result indicates there may be a tradeoff

between nutrient rich prey and abundant prey in the prey selection.

Generally, Large size Pacific cod tend to have a better nutritional condition. This is probably due to the higher proportion of fish in the diet of large-sized Pacific cod. Female and male Pacific cod were in similar nutritional condition, although they might undergo different physical development, including the seasonal cycle in gonad development. In NCH, almost all Pacific cod matured when SL attained about 550 mm (age 5) in males and 650 mm (age 6) in females. Both CF and HSI were significantly higher in mature Pacific cod than immature individuals. The potential fecundity of female Pacific cod seems to be positively correlated with CF. However, the sample size of mature Pacific cod was too small to conduct statistical analysis. Therefore, more specimens are needed to explore relationships between nutritional condition and fecundity. This information might provide a simple and efficient method for monitoring and predicting the Pacific cod population dynamics.

In spite of the trophic ecology of Pacific cod has been studied in detail based on the data collected in this study, some aspects are deserved to be further examined in the future studies. Firstly, other chemical tracer methods, such as stable isotopes analysis (Jennings et al. 2002), should be introduced to examine feeding habits of Pacific cod as a complementary method, because stomach content analysis used here only provides a snapshot of the diet composition. Secondly, variances in the CF explained

by the factors included in the final GAMs were limited, indicating there are probably some other factors affecting the nutritional condition of Pacific cod, but was not taken in to the model. Thirdly, monthly sampling throughout year will help to evaluate annual variation in the relationship between nutritional condition and reproductive characteristics. Finally, it is strongly recommended to conduct continuous surveys to assess changes in the trophic ecology of Pacific cod.

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Appendix

Fig. S1. Prey species occurred from the stomachs of Pacific cod collected in different years (2016–2020) off the southern coast of Hokkaido. The colors of the bars indicate the number of years that the prey occurred (red; 5, darkgreen;4, green;3, blue;2, pink;1). Total number of prey species in each year is indicated in parentheses at bottom of each column.
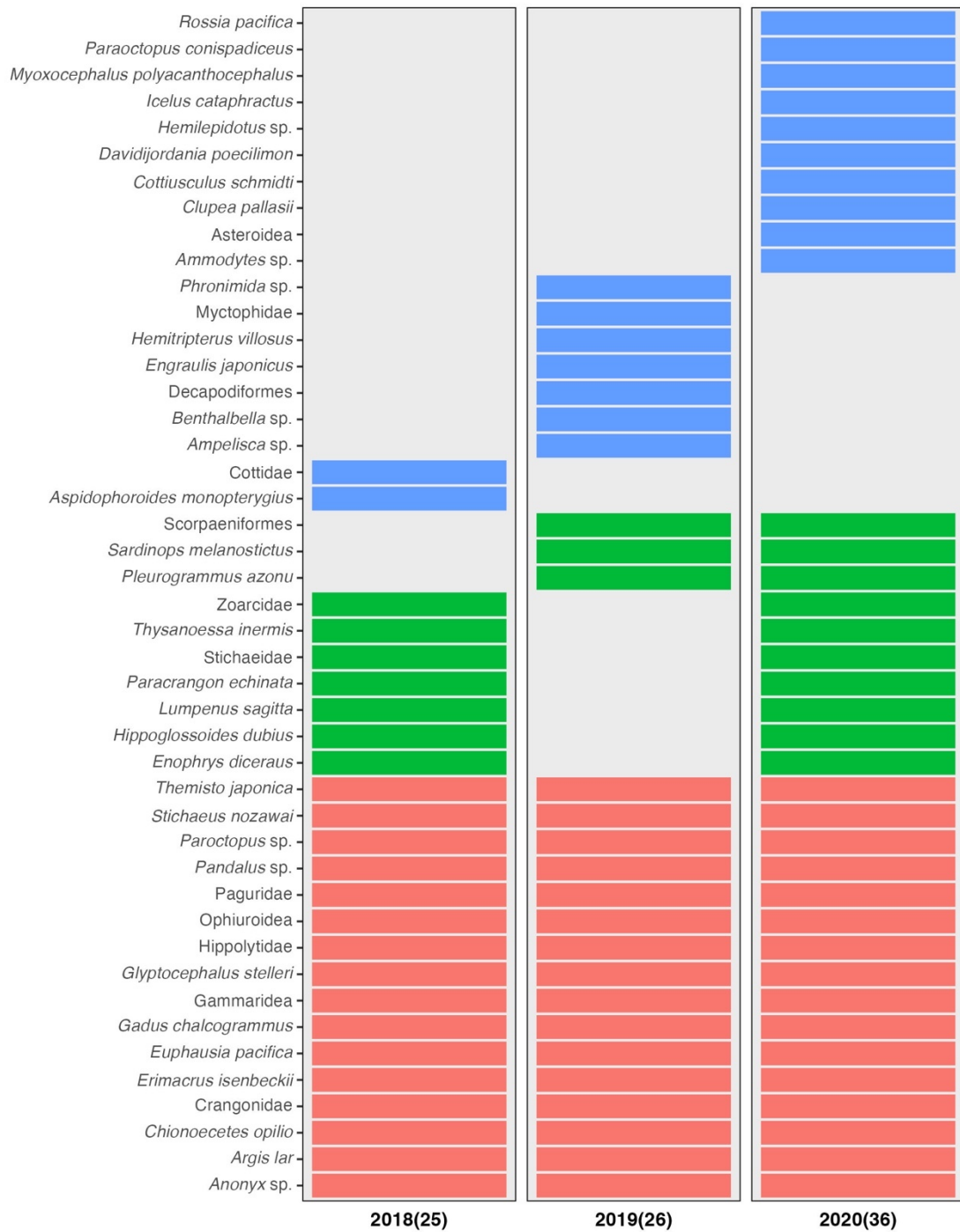
Fig. S2. Prey species occurred from the stomachs of Pacific cod collected in different years (2018–2020) off the northeastern coast of Hokkaido. The colors of the bars indicate the number of years that the prey occurred (red; 3, green; 2, blue; 1). Total number of prey species in each year is indicated in parentheses at bottom of each column.

Table S1. Number of Pacific cod specimens collected from each station conducted off the southern coast of Hokkaido during 2016–2020.

Year	Station	Longitude	Latitude	Depth	Cod
2016	MT-1	141.17	41.74	136.17	0
2016	MT-2	141.16	41.75	118.33	0
2016	MT-3	141.16	41.75	115.11	0
2016	MT-4	140.73	42.43	62.56	0
2016	MT-5	140.68	42.29	80.35	0
2016	MT-6	140.68	42.29	78.54	0
2016	MT-7	141.64	42.45	86.29	0
2016	MT-8	141.74	42.34		0
2016	MT-9	142.89	41.78	57.47	9
2016	MT-10	143.64	41.67	338.47	12
2016	MT-11	143.62	41.70	236.76	4
2016	MT-12	143.40	41.97	83.70	1
2016	MT-13	143.45	41.91	118.66	7
2016	MT-14	143.89	41.63	962.88	0
2016	MT-15	143.69	41.90	338.27	6
2016	MT-16	143.63	41.97	205.19	2
2016	MT-17	143.58	42.02	150.01	14
2016	MT-18	143.68	42.17	308.16	0
2016	MT-19	143.65	42.20	204.27	1
2016	MT-20	143.56	42.31	85.68	11
2016	MT-21	143.61	42.26	129.66	33
2016	MT-22	143.85	42.20	830.88	0
2016	MT-23	143.72	42.37	134.99	25
2016	MT-24	143.86	42.45	246.10	3
2016	MT-25	144.07	42.71	119.51	17
2016	MT-26	144.32	42.66	941.27	0
2016	MT-27	144.48	42.73	136.34	12
2016	MT-28	145.71	43.05	106.08	2
2016	MT-29	144.86	42.79	119.87	5
2016	MT-30	144.71	42.72	164.21	3
2017	MT-1	141.18	41.74	146.59	0
2017	MT-2	140.74	42.30	66.40	0
2017	MT-3	141.44	41.72	318.00	1
2017	MT-4	141.24	41.87	233.94	0
2017	MT-5	140.64	42.50	67.15	0
2017	MT-6	141.33	42.16	360.85	0
2017	MT-7	141.59	42.38	366.16	9

Year	Station	Longitude	Latitude	Depth	Cod
2017	MT-8	142.16	42.33	70.55	7
2017	MT-9	143.17	41.83	63.20	0
2017	MT-10	143.24	41.67	148.31	7
2017	MT-11	143.49	41.62	253.75	2
2017	MT-14	143.64	41.68	286.59	0
2017	MT-15	143.68	41.63	205.89	4
2017	MT-16	143.49	41.89	130.65	11
2017	MT-17	143.41	41.98	83.05	9
2017	MT-18	143.68	41.90	379.83	0
2017	MT-19	143.57	42.06	138.56	0
2017	MT-20	143.61	41.99	196.77	4
2017	MT-21	143.65	42.20	216.08	0
2017	MT-22	143.64	42.21	171.93	3
2017	MT-23	143.67	42.18	297.52	4
2017	MT-24	143.63	42.23	139.18	3
2017	MT-25	143.67	42.44	85.31	0
2017	MT-26	143.70	42.40	124.24	1
2017	MT-27	143.85	42.48	142.44	0
2017	MT-28	143.85	42.48	140.99	2
2017	MT-29	143.89	42.68	58.20	2
2017	MT-30	143.94	42.63	102.26	20
2017	MT-31	144.11	42.67	306.25	4
2017	MT-32	144.09	42.70	173.60	2
2017	MT-33	144.26	42.74	373.32	8
2017	MT-34	144.20	42.85	73.15	19
2017	MT-35	144.92	42.71	197.03	1
2017	MT-36	144.88	42.76	136.17	2
2017	MT-37	144.98	42.89	79.88	10
2017	MT-38	145.37	42.92	113.77	1
2017	MT-39	145.31	43.00	59.64	2
2017	MT-40	145.85	43.12	116.24	6
2017	MT-41	145.87	43.11	125.89	15
2017	MT-42	145.82	43.16	91.53	4
2017	MT-43	145.73	43.01	118.23	0
2017	MT-44	143.64	42.22	165.86	3
2017	MT-45	143.61	42.18	138.59	7
2017	MT-46	143.62	42.19	148.63	2
2018	MT-1	140.59	42.35	92.94	0
2018	MT-2	140.59	42.34	92.42	0
2018	MT-3	141.44	41.71	305.86	20

Year	Station	Longitude	Latitude	Depth	Cod
2018	MT-4	141.18	42.30	85.30	1
2018	MT-5	141.41	42.00	356.88	3
2018	MT-6	141.64	42.33	463.91	1
2018	MT-7	142.14	42.33	76.23	2
2018	MT-8	142.87	41.93	109.70	5
2018	MT-9	142.94	41.75	142.71	20
2018	MT-10	143.04	41.89	66.33	15
2018	MT-11	143.21	41.69	138.41	10
2018	MT-12	143.44	41.67	179.83	10
2018	MT-13	143.68	41.63	199.19	0
2018	MT-14	143.67	41.65	301.50	2
2018	MT-15	143.58	41.76	159.20	20
2018	MT-16	143.44	41.95	107.40	17
2018	MT-17	143.41	41.98	85.10	20
2018	MT-18	143.68	41.90	363.07	1
2018	MT-19	143.60	42.01	182.98	7
2018	MT-20	143.63	42.23	142.81	2
2018	MT-21	143.61	42.25	129.60	7
2018	MT-22	143.57	42.30	95.15	3
2018	MT-23	143.63	42.49	48.90	0
2018	MT-24	143.86	42.46	222.16	6
2018	MT-25	143.94	42.62	103.95	0
2018	MT-26	144.06	42.73	109.07	3
2018	MT-27	144.24	42.76	289.56	11
2018	MT-28	144.12	42.65	415.61	0
2018	MT-29	144.13	42.65	414.47	5
2018	MT-30	144.09	42.70	168.99	0
2018	MT-31	144.09	42.70	166.10	3
2018	MT-32	144.68	42.74	142.56	4
2018	MT-33	144.92	42.71	196.86	2
2018	MT-34	144.83	42.83	102.85	0
2018	MT-35	144.99	42.88	83.33	1
2018	MT-36	145.05	42.80	126.26	5
2018	MT-37	145.34	42.97	77.19	2
2018	MT-38	145.38	42.92	111.19	3
2019	MT-1	141.16	41.72	151.45	0
2019	MT-2	141.37	42.00	343.96	13
2019	MT-3	140.98	42.25	66.43	0
2019	MT-4	141.16	42.15	121.38	0
2019	MT-5	141.41	41.75	280.00	0

Year	Station	Longitude	Latitude	Depth	Cod
2019	MT-6	141.31	42.42	88.04	0
2019	MT-7	140.54	42.39	95.35	0
2019	MT-8	140.85	42.34	44.52	0
2019	MT-9	141.50	42.39	327.57	1
2019	MT-10	141.42	42.47	84.76	0
2019	MT-11	142.13	42.31	99.26	13
2019	MT-12	142.30	42.28	72.72	4
2019	MT-13	142.74	42.02	125.12	9
2019	MT-14	142.88	41.95	104.84	19
2019	MT-15	142.95	42.02	75.10	13
2019	MT-16	143.67	42.18	301.84	2
2019	MT-17	143.62	42.24	135.97	3
2019	MT-18	143.56	42.32	81.70	10
2019	MT-19	143.74	42.36	173.73	4
2019	MT-20	143.69	42.43	98.00	0
2019	MT-21	143.84	42.49	124.82	0
2019	MT-22	143.82	42.52	99.04	0
2019	MT-23	143.82	42.51	104.15	13
2019	MT-24	143.84	42.48	133.80	14
2019	MT-25	143.81	42.49	111.76	6
2019	MT-26	143.82	42.50	111.10	0
2019	MT-27	143.80	42.56	78.71	0
2019	MT-28	143.77	42.50	97.99	0
2019	MT-29	143.88	42.58	96.01	0
2019	MT-30	143.51	42.15	108.81	0
2019	MT-31	144.17	42.80	113.98	10
2019	MT-32	144.11	42.67	315.89	1
2019	MT-33	144.01	42.75	71.17	0
2019	MT-34	144.11	42.70	216.65	2
2019	MT-35	143.68	41.89	360.90	0
2019	MT-36	143.63	41.97	199.62	2
2019	MT-37	143.57	42.03	141.52	20
2019	MT-38	143.51	42.14	109.16	20
2019	MT-39	141.64	41.69	264.42	5
2019	MT-40	143.69	41.62	204.43	2
2019	MT-41	143.58	41.76	158.56	0
2019	MT-42	143.41	41.94	96.96	10
2019	MT-43	143.20	41.82	68.97	3
2019	MT-44	144.46	42.76	129.89	0
2019	MT-45	144.72	42.70	185.03	6

Year	Station	Longitude	Latitude	Depth	Cod
2019	MT-46	144.69	42.73	148.18	11
2019	MT-47	144.59	42.85	83.70	0
2019	MT-48	144.92	42.71	200.59	0
2019	MT-49	144.83	42.81	106.90	0
2019	MT-50	145.07	42.78	142.60	0
2019	MT-51	144.99	42.85	98.24	18
2019	MT-52	145.41	42.87	179.39	1
2019	MT-53	145.36	42.94	100.74	0
2019	MT-54	145.33	42.97	76.34	0
2019	MT-55	145.79	43.17	76.27	10
2019	MT-56	145.84	43.12	112.74	5
2019	MT-57	145.69	43.09	87.13	9
2019	MT-58	145.71	43.03	112.64	0
2019	MT-59	144.07	42.72	117.38	14
2019	MT-60	144.07	42.72	117.75	20
2019	MT-61	144.07	42.72	117.65	0
2020	MT-1	141.42	41.70	296.54	9
2020	MT-2	141.31	42.00	288.76	9
2020	MT-3	140.72	42.44	63.58	0
2020	MT-4	140.69	42.45	67.54	0
2020	MT-5	140.66	42.30	80.16	0
2020	MT-6	140.60	42.34	89.36	0
2020	MT-7	140.60	42.34	89.48	0
2020	MT-8	141.38	42.10	400.18	0
2020	MT-9	143.01	41.85	80.59	0
2020	MT-10	142.90	41.96	97.55	20
2020	MT-11	143.67	41.63	209.72	0
2020	MT-12	143.60	41.73	155.22	20
2020	MT-13	143.62	41.70	233.23	1
2020	MT-14	143.46	41.92	120.50	20
2020	MT-15	143.70	41.88	393.00	7
2020	MT-16	143.63	41.97	199.54	19
2020	MT-17	143.99	42.69	100.10	20
2020	MT-18	143.99	42.69	101.30	10
2020	MT-19	143.99	42.69	101.30	20
2020	MT-20	144.00	42.69	100.30	20
2020	MT-21	143.99	42.69	100.50	19
2020	MT-22	143.99	42.69	100.00	10
2020	MT-23	143.75	42.08	471.45	1
2020	MT-24	143.66	42.19	239.82	1

Year	Station	Longitude	Latitude	Depth	Cod
2020	MT-25	143.53	42.34	61.99	20
2020	MT-26	143.56	42.32	79.23	20
2020	MT-27	143.72	42.37	136.90	4
2020	MT-28	143.70	42.40	118.85	16
2020	MT-29	143.86	42.48	154.20	0
2020	MT-30	143.87	42.46	229.30	5
2020	MT-31	143.80	42.55	80.77	20
2020	MT-32	144.13	42.65	406.32	2
2020	MT-33	144.09	42.69	203.11	7
2020	MT-34	144.06	42.70	126.26	0
2020	MT-35	144.03	42.77	65.31	8
2020	MT-36	144.25	42.76	316.30	20
2020	MT-37	144.80	42.86	81.80	20
2020	MT-38	144.72	42.70	190.64	5
2020	MT-39	144.69	42.73	154.89	16
2020	MT-40	144.68	42.74	134.09	0
2020	MT-41	145.12	42.74	374.54	0
2020	MT-42	145.10	42.75	189.45	0
2020	MT-43	145.15	42.82	134.74	0
2020	MT-44	145.43	42.86	382.01	0
2020	MT-45	145.37	42.94	101.48	10
2020	MT-46	145.38	42.92	117.42	12
2020	MT-47	145.41	42.88	199.68	1
2020	MT-48	145.58	42.93	194.69	0
2020	MT-49	145.57	42.96	122.70	0
2020	MT-50	145.52	42.98	100.46	0
2020	MT-51	145.74	43.14	80.73	20
2020	MT-52	145.86	43.10	125.41	20

Note, depth of 'MT-18' in 2016 was not available.

Table S2. Number of Pacific cod specimens collected from each station conducted off the northeastern coast of Hokkaido during 2018–2020.

Year	Station	Longitude	Latitude	Depth	Cod
2018	A1	142.96	45.43	118	14
2018	A1P	142.99	45.41	118	15
2018	A2	143.11	45.19	125	14
2018	A3	142.91	45.14	126	15
2018	A3P	143.06	45.10	130	15
2018	A4	143.20	45.06	135	15
2018	A5	143.07	45.02	131	15
2018	B1	143.14	44.95	132	15
2018	B2	143.33	44.87	139	16
2018	B3	143.53	44.63	129	15
2018	B4	143.88	44.38	154	9
2018	B5	143.48	44.80	145	10
2018	C2	143.93	44.93	185	11
2018	C3	143.53	44.88	153	0
2018	C3P	143.57	44.94	158	0
2018	C4	144.09	44.85	191	5
2018	D1	143.91	44.80	170	10
2018	D2	143.64	44.74	149	15
2018	D3	144.06	44.64	197	5
2018	D4	143.88	44.53	165	5
2018	E1	144.10	44.99	213	0
2018	E2	144.17	44.86	207	0
2018	E3	144.10	44.56	208	0
2018	E4	144.11	44.43	221	0
2018	G1	144.12	45.13	482	0
2018	G2	144.41	44.98	614	0
2019	A1	142.97	45.44	118	0
2019	A2	143.10	45.18	124	2
2019	A3	142.93	45.13	127.26	7
2019	A4	143.20	45.08	133.09	7
2019	A5	143.07	45.02	131.79	1
2019	B1	143.16	44.92	133.66	0
2019	B2	143.34	44.89	140.69	0
2019	B3	143.54	44.65	130.67	10
2019	B4	143.88	44.40	157.72	9
2019	B5	143.50	44.79	146.17	3
2019	C1	143.60	45.10	160.66	10

Year	Station	Longitude	Latitude	Depth	Cod
2019	C2	143.93	44.93	184.1	10
2019	C3	143.51	44.88	150.11	2
2019	C4	144.10	44.83	191.38	10
2019	D1	143.89	44.82	169.6	10
2019	D2	143.64	44.75	148.95	1
2019	D3	144.04	44.61	193.57	10
2019	D4	143.89	44.58	166.15	10
2019	D5	143.79	44.70	158.67	3
2019	E1	144.13	44.97	213.69	10
2019	E2	144.18	44.86	210.15	10
2019	E3	144.11	44.60	215.54	10
2019	E4	144.12	44.44	225.2	10
2019	G4	144.34	44.39	338.03	10
2020	A1	143.00	45.43	118	10
2020	A2	143.11	45.19	123	10
2020	A3	142.96	45.11	126	10
2020	A4	143.20	45.09	132	10
2020	A5	143.11	45.03	132	10
2020	B1	143.18	44.91	132	10
2020	B2	143.34	44.89	138	10
2020	B3	143.51	44.65	127	10
2020	B4	143.86	44.40	154	10
2020	B5	143.49	44.80	143	7
2020	C1	143.61	45.12	160	3
2020	C2	143.91	44.94	183	3
2020	C3	143.52	44.88	150	10
2020	C3P	143.56	44.94	157	10
2020	C4	144.07	44.86	187	7
2020	C5	143.94	45.02	202	2
2020	D1	143.87	44.83	167	10
2020	D2	143.63	44.76	146	6
2020	D3	144.03	44.66	190	8
2020	D4	143.89	44.54	164	10
2020	D5	143.78	44.73	157	10
2020	E1	144.14	44.97	217	1
2020	E2	144.17	44.88	210	1
2020	E3	144.12	44.61	221	8
2020	E4	144.13	44.43	229	1
2020	E5	144.20	44.80	199	3
2020	G1	144.16	45.11	469	0

Year	Station	Longitude	Latitude	Depth	Cod
2020	G2	144.42	44.94	495	0
2020	G4	144.34	44.38	310	2
2020	SA1	142.51	45.41	73	9
2020	SA2	142.59	45.35	83	10
2020	SB3	143.40	44.54	73	10
2020	SB4	143.58	44.42	77	10
2020	SB5	143.90	44.26	72.08	10

Table S3. Prey species composition of Pacific cod collected off the southern coast of Hokkaido during 2016–2020. %W; percentage of wet weight, %F; frequency of occurrence, %IRI; percentage of index of relative importance.

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
Actiniaria							0.05	0.29	+						
Hydrozoa										0.56	1.09	0.03			
Aphroditidae				0.27	1.1	0.02	0.17	1.17	0.01				0.01	0.74	+
Polynoidae				0.18	0.55	0.01									
unidentified Polychaeta	4.85	28.99	5.68	7.33	35.62	20.5	3.12	30.5	6.54	1.17	15.85	0.78	0.13	9.56	0.04
unidentified Echiuroidea	0.58	0.48	0.01	3.41	5.21	1.4	2.42	7.04	1.17	0.21	4.37	0.04			
Buccinidae				0.14	1.1	0.01	0.2	2.05	0.03	+	0.55	+			
Notaspidea	0.13	0.48	+	0.03	0.55	+									
unidentified Gastropoda				0.16	1.92	0.02	0.64	5.57	0.25	0.07	2.73	0.01	0.04	1.47	+
unidentified Bivalvia	0.02	4.35	+	0.19	7.4	0.11	0.15	5.87	0.06	0.02	1.64	+			
Decapodiformes				0.27	1.1	0.02	0.39	2.05	0.05	0.5	0.55	0.01			
Gonatidae							0.08	0.88	+						
Paroctopus sp.	0.06	0.48	+	0.38	2.74	0.08	4.21	7.33	2.12	3.74	7.65	1.2	1.83	5.15	0.34
Rossia pacifica	0.14	0.48	+												
unidentified Cephalopoda	0.15	3.38	0.02	0.13	5.48	0.06	0.12	7.62	0.06	0.75	7.65	0.24	0.11	11.76	0.05

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
unidentified Mysidacea	0.5	0.97	0.02	0.09	0.82	0.01									
Anthuridea				0.02	0.55	+									
Ianiridae				+	0.55	+									
unidentified Isopoda	0.42	8.21	0.14	0.1	1.92	0.02	0.06	1.76	0.01	+	0.55	+	+	0.74	+
Ampelisca sp.	4.3	17.39	3.02	2.79	18.9	4.14	0.29	8.8	0.18	0.01	4.92	+	+	3.68	+
Anonyx sp.	1.9	14.49	1.11	1.89	27.12	4.02	0.33	20.53	0.47	0.02	7.65	0.01	0.01	7.35	+
Gammaridea	2.4	16.91	1.64	3.27	16.16	4.15	0.93	8.5	0.54	+	3.28	+	+	1.47	+
Phronima atlantica				+	0.27	+									
Themisto japonica	0.18	4.35	0.03	0.12	4.93	0.05	0.01	3.23	+	+	1.09	+	+	0.74	+
Euphausia pacifica	0.12	4.35	0.02	0.6	5.75	0.27	0.18	7.92	0.1	+	4.92	+	+	4.41	+
Thysanoessa inermis	0.2	1.45	0.01	0.32	1.92	0.05	0.23	1.76	0.03	0.45	3.83	0.07	+	1.47	+
unidentified Euphausiidae	0.43	2.9	0.05	0.08	2.74	0.02	0.01	1.47	+	0.06	2.19	0.01	0.02	1.47	+
Hippolytidae	0.23	4.35	0.04	0.53	7.12	0.3	0.04	3.81	0.01	+	0.55	+	+	0.74	+
Pandalus sp.	0.57	0.97	0.02	0.48	1.37	0.05	0.24	3.52	0.06	0.07	2.73	0.01	0.01	2.21	+
Crangonidae	8.53	26.09	8.99	6.64	45.48	23.71	1.8	34.6	4.28	0.22	16.39	0.15	0.06	11.03	0.02
Argis lar	3.46	6.28	0.88	3.23	5.75	1.46	2.69	10.56	1.95	0.24	2.19	0.02			
Paracrangon echinata				0.03	0.27	+	0.05	0.59	+						
Paguridae	0.39	0.97	0.02	0.33	1.92	0.05	0.39	2.93	0.08	0.12	1.64	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
Elassochirus cavimanus	0.57	0.48	0.01	2.82	2.74	0.61	0.21	2.05	0.03						
Pagurus trigonocheirus	0.5	0.97	0.02	0.6	2.47	0.12									
Erimacrus isenbeckii	0.12	0.48	+	0.19	1.1	0.02	0.03	0.88	+	0.06	1.64	+	0.05	0.74	+
Chionoecetes opilio				0.2	1.64	0.03	0.25	2.05	0.04	0.02	0.55	+			
unidentified crabs	+	0.48	+	0.17	1.1	0.01	0.13	2.05	0.02				0.07	0.74	+
unidentified shrimp	0.49	4.83	0.1	0.63	11.23	0.56	0.26	4.11	0.07	0.03	4.92	0.01	0.01	4.41	+
Asteroidea							0.07	0.29	+						
Ophiuroidea	0.07	0.48	+	0.21	6.3	0.1	0.29	11.73	0.23	0.04	4.92	0.01	+	3.68	+
Sardinops melanostictus				8.39	2.19	1.44	27.75	11.73	22.38	48.31	31.15	63.07	49.31	23.53	41.73
Diaphus kuroshio	0.32	0.48	0.01	0.29	0.55	0.01									
Diaphus theta										0.03	0.55	+			
Notoscopelus japonicus				24.78	6.85	13.33	30.01	18.48	38.13	17.15	17.49	12.57	8.47	17.65	5.38
Myctophidae				0.06	0.27	+	1.02	0.88	0.06	0.07	0.55	+			
Gadus chalcogrammus	61.19	30.43	75.22	16.74	7.12	9.36	6.77	6.16	2.87	17.58	21.31	15.7	32.04	44.85	51.68
Acantholumpenus mackayi													1.21	0.74	0.03
Arctoscopus japonicus													0.4	0.74	0.01
Ammodytes sp.	1.01	0.48	0.02							0.46	0.55	0.01			
Cottiusculus schmidti				0.2	0.82	0.01	0.3	1.47	0.03						

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
Cryptacanthoides bergi							1.22	1.17	0.1	0.63	1.09	0.03			
Davidijordania poecilimon				0.07	0.55	+	0.08	0.59	+				0.28	0.74	0.01
Lumpenus sagitta							1.43	1.47	0.14	0.94	1.64	0.06	0.19	1.47	0.01
Stichaeidae				0.11	0.27	+	0.29	0.59	0.01						
Stichaeus nozawai										1.14	1.09	0.05	1.45	1.47	0.08
Zoarcidae				0.05	0.27	+	0.04	0.29	+						
Scomber sp.													2.06	0.74	0.05
Aspidophoroides monopterygius							0.01	0.29	+						
Cottidae							0.32	0.29	0.01				0.03	0.74	+
Hemilepidotus sp.													0.86	0.74	0.02
Hemitripterus villosus							0.02	0.29	+						
Icelus cataphractus				1.05	0.55	0.05	0.61	0.59	0.02	0.16	0.55	+			
Myoxocephalus polyacanthocephalus							0.02	0.29	+						
Podothecus thompsoni				0.03	0.27	+									
Sarritor leptorhynchus							0.19	1.17	0.02						
Scorpaeniformes	0.03	0.48	+				0.66	0.88	0.04				0.09	0.74	+
Tilesina gibbosa							0.04	0.29	+						
Triglops jordani				0.83	0.55	0.04									

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
Glyptocephalus stelleri										0.01	0.55	+	0.18	2.21	0.01
unidentified Pisces	5.87	12.08	2.86	9.15	18.9	13.58	9.08	28.45	17.76	5.15	27.32	5.9	0.97	14.71	0.51
Digested matter	0.26	4.83	0.05	0.45	6.03	0.21	0.09	2.93	0.02	0.01	1.64	+	0.08	1.47	+

Table S4. Prey species composition of Pacific cod collected off the northeastern coast of Hokkaido during 2018–2020. %W; percentage of wet weight, %F; frequency of occurrence, %IRI; percentage index of relative importance.

Size classes in SL	≤400 mm			401–500 mm			501–600 mm			>600 mm		
	%W	%F	%IRI	%W	%F	%IRI	%W	%F	%IRI	%W	%F	%IRI
unidentified Coelentrata										0.05	0.78	+
unidentified Polychaeta	4.93	25.68	6.71	1.01	14.69	0.78	0.28	7.26	0.06	0.01	2.33	+
unidentified Echiuroidea				5.59	4.2	1.23	5.09	2.23	0.35	2.84	3.88	0.6
unidentified Gastropoda	0.07	2.7	0.01	0.32	2.8	0.05	+	0.56	+			
unidentified Bivalvia	+	2.03	+	+	0.7	+	0.02	2.79	+	+	0.78	+
Decapodiformes	0.08	1.35	0.01									
Paraoctopus conispadiceus										11.12	3.1	1.86
Paroctopus sp.	1.53	2.03	0.16	4.92	6.99	1.8	2.16	5.03	0.34	2.08	12.4	1.39
Rossia pacifica				0.04	0.7	+	0.02	0.56	+			
unidentified Cephalopoda	0.04	7.43	0.02	0.17	7.69	0.07	0.36	6.7	0.08	0.01	2.33	+
unidentified Mysidacea	0.02	0.68	+	0.09	0.7	+						
unidentified Isopoda	0.65	2.7	0.09									
Ampelisca sp.	0.11	6.08	0.04	0.03	1.4	+						
Anonyx sp.	3.1	36.49	5.99	0.85	33.57	1.49	0.13	20.67	0.08	0.03	11.63	0.02
Gammaridea	0.09	4.73	0.02	0.01	1.4	+	+	1.68	+			

Size classes in SL	≤400 mm			401–500 mm			501–600 mm			>600 mm		
	%W	%F	%IRI	%W	%F	%IRI	%W	%F	%IRI	%W	%F	%IRI
Phronimida sp.	0.09	3.38	0.02	0.04	2.1	+	+	0.56	+			
Themisto japonica	0.57	13.51	0.41	0.3	8.39	0.13						
Euphausia pacifica	1.07	14.19	0.8	0.44	7.69	0.18	0.18	8.94	0.05	0.01	3.1	+
Thysanoessa inermis	0.54	2.7	0.08	1.67	8.39	0.73	0.38	6.7	0.08	+	1.55	+
unidentified Euphausiidae	0.11	2.7	0.02	0.12	7.69	0.05	0.11	7.26	0.02	+	2.33	+
Hippolytidae	0.01	0.68	+	0.01	1.4	+	0.01	0.56	+			
Pandalus sp.	4.03	10.14	2.17	2.56	7.69	1.03	2.61	11.17	0.91	1.49	14.73	1.19
Crangonidae	4.59	25	6.08	1.05	12.59	0.69	0.22	8.94	0.06	0.08	7.75	0.03
Argis lar	0.58	2.7	0.08	0.44	2.1	0.05	0.49	4.47	0.07	0.09	3.88	0.02
Paracrangon echinata	0.74	0.68	0.03	0.05	0.7	+	0.13	1.12	+			
Paguridae	0.05	1.35	+	0.43	0.7	0.02	0.36	0.56	0.01			
Erimacrus isenbeckii	0.33	1.35	0.02	3.54	6.99	1.29	0.08	0.56	+	0.77	3.1	0.13
Chionoecetes opilio	30.74	36.49	59.44	31.25	44.06	71.94	18.24	39.66	22.57	15.9	41.09	35.31
unidentified shrimp	0.2	10.14	0.11	0.08	7.69	0.03	0.07	7.82	0.02	0.08	4.65	0.02
unidentified crabs	4.1	2.03	0.44	5.19	0.7	0.19	0.84	1.68	0.04	0.87	3.88	0.18
Ophiuroidea	0.08	2.03	0.01	0.02	0.7	+	+	0.56	+	0.01	1.55	+
Asteroidea				0.08	0.7	+						
Sardinops melanostictus										6.05	3.88	1.27

Size classes in SL	≤400 mm			401–500 mm			501–600 mm			>600 mm		
	%W	%F	%IRI	%W	%F	%IRI	%W	%F	%IRI	%W	%F	%IRI
Engraulis japonicus	0.65	0.68	0.02									
Clupea pallasii				0.98	0.7	0.04	3.79	1.12	0.13	17.91	11.63	11.26
Benthalbella sp.				1.8	0.7	0.07						
Myctophidae										0.12	0.78	0.01
Gadus chalcogrammus	16.69	6.08	5.38	11.65	13.99	8.52	42.22	52.51	69.18	17.72	26.36	25.25
Ammodytes sp.	3.21	2.03	0.35	8.07	2.1	0.89						
Davidijordania poecilimon				0.14	0.7	0.01	0.12	0.56	+			
Lumpenus sagitta				1.14	1.4	0.08	0.38	1.12	0.01	0.43	0.78	0.02
Stichaeidae							2.51	1.68	0.13	0.14	0.78	0.01
Stichaeus nozawai				4.13	0.7	0.15	1.84	1.68	0.1	1.66	2.33	0.21
Zoarcidae							0.66	1.12	0.02	0.85	2.33	0.11
Cottidae							0.14	0.56	+			
Hemilepidotus sp.										0.7	0.78	0.03
Hemitripterus villosus				0.1	0.7	+						
Myoxocephalus polyacanthocephalus	0.76	0.68	0.03									
Cottiusculus schmidti	1.54	2.7	0.22									
Icelus cataphractus										0.29	0.78	0.01
Enophrys diceraus	2.69	4.05	0.58				0.04	0.56	+			

Size classes in SL	≤400 mm			401–500 mm			501–600 mm			>600 mm		
	%W	%F	%IRI	%W	%F	%IRI	%W	%F	%IRI	%W	%F	%IRI
Scorpaeniformes	0.54	0.68	0.02	0.02	0.7	+	0.39	1.12	0.01	0.6	2.33	0.08
Aspidophoroides monopterygius				0.08	0.7	+						
Pleurogrammus azonu	4.6	1.35	0.33	3.37	1.4	0.25	1.12	1.12	0.04	1.14	0.78	0.05
Glyptocephalus stelleri	1.31	2.7	0.19	0.7	4.2	0.15	2.42	7.82	0.59	3.56	7.75	1.49
Hippoglossoides dubius				1.14	0.7	0.04	5.23	3.35	0.55	2.5	3.1	0.42
unidentified Pisces	7.74	22.97	9.42	6.3	24.48	8.06	7.33	19.55	4.47	10.82	32.56	19.04
Digested matter	1.83	7.43	0.72	0.08	1.4	0.01	0.01	0.56	+	0.08	1.55	0.01