Diets of walleye pollock *Theragra chalcogramma* in the Doto area, northern Japan: ontogenetic and seasonal variations

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ABSTRACT: Seasonal, ontogenetic and bathymetric variations of diet were examined for walleye pollock *Theragra chalcogramma* based on a total of 6666 fish collected off the southeastern coast of Hokkaido Island, northern Japan (Doto area) during 1989 to 2000. Walleye pollock depended exclusively (>99%) on pelagic prey and showed a clear ontogenetic dietary shift: smaller fish depended mainly upon mesozooplankton such as *Neocalanus cristatus* and *Euphausia pacifica*, and larger fish preyed upon pollock (cannibalism), myctophids *Diaphus theta* and firefly squid *Watasenia scintillans*. Seasonal variation was also evident. Smaller pollock depended mainly upon *N. cristatus* during spring then shifted gradually to *E. pacifica* during other seasons. For larger pollock, major prey shifted from pollock (cannibalism) during spring to micronekton during other seasons. Bathymetric variation was less pronounced, with cannibalism and *Themisto* spp. being more important in the shallow area (≤150 m). Feeding intensity, measured as stomach content index, was generally higher during spring and summer than autumn and winter, but showed incidentally high values during winter, suggesting sporadic but intense feeding opportunities. Fish condition fell during winter and then recovered rapidly during May and June. Recovery coincided with superabundance of *N. cristatus* during blooming, so that this species is essential for the recovery of pollock from wintering and spawning.

KEY WORDS: *Theragra chalcogramma* · Food habits · Seasonality · Feeding intensity · Condition

INTRODUCTION

The nutrition of high latitude fishes varies seasonally. These fishes generally feed during the productive spring and summer in order to endure (and compensate for) the less productive winter. This cycle reflects seasonal variation of the physical environment and resulting prey availability (MacKinnon 1972, Dygert 1990, Robards et al. 1999). Prey for various fishes exhibit an intense decline during winter resulting in occasional starvation mortality of the fishes (Adams et al. 1982, Henderson et al. 1988). Fish diets also vary ontogenetically due to changes in gape morphology,

swimming ability, feeding tactics and distribution (e.g. Eggold & Motta 1992). Maximum prey size increases with fish growth whereas minimum prey size increases only slightly with fish growth. This results in an 'asymmetric predator–prey size distribution' (Scharf et al. 2000). Such variation would facilitate ontogenetically different responses in a spectrum of available prey and further determine the pattern of resource use in a community (Hyndes et al. 1997).

Walleye pollock *Theragra chalcogramma* is a key species of the subarctic North Pacific, which is distributed from the coast of Korea through the northwestern coast of the USA (Bailey et al. 1999). Besides being an important prey for demersal fishes, marine mammals and seabirds (Springer 1992, Livingston 1993, Mito et al. 1999), it also supports the largest single-species

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fisheries in the world (Anonymous 2000). Due to their predominance, pollock has the potential to impact entire ecosystems (Springer 1992). Although numerous studies have been made on the feeding habits of post-settlement pollock (Takahashi & Yamaguchi 1972, Bailey & Dunn 1979, Clausen 1983, Maeda 1986, Dwyer et al. 1987, Grover 1991, Yoshida 1994, Merati & Brodeur 1996, 1998, Kooka et al. 1997), most of them covered only limited seasons and fish sizes. The studies made by Dwyer et al. (1987) and Mito et al. (1999) in the Bering Sea were exceptionally comprehensive describing geographical, seasonal and ontogenetic variations of pollock diet. They revealed that pollock depends primarily upon pelagic prey and shift gradually from zooplankton to fishes during growth. However, they identified the prey only to the major taxonomic levels.

The southeastern coast of Hokkaido Island, northern Japan (Doto area, Fig. 1) is the major feeding ground of the Japan Pacific population of walleye pollock (JPP). The spawning of JPP occurs mainly during January and February in the area of Funka Bay (Maeda 1986). As age-0 pollock grow to 85 mm in total length, a substantial part of age-0 pollock settle during late summer and early autumn in the Doto area (Miyake et al. 1996), where they winter and reside for years. Although cross- and along-shore migrations of the Doto pollock have been observed regularly even to the southern Kuril Islands and northeastern coast of the main island of Japan, their residence in the Doto area is considered to be stable based on the results of tagging experiments and hydroacoustic surveys (Maeda 1986, S. Honda unpubl. data). The Doto area is strongly influenced by the Oyashio current, which causes conspicuous seasonal and interannual variabilities in physical and biological environments (Kono & Kawasaki 1997, Saito et al. 1998, Mackas & Tsuda 1999). These vari-
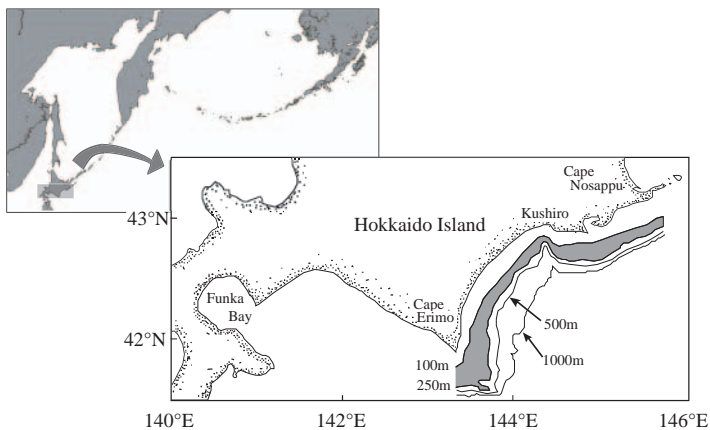

Fig. 1. Map showing the area studied relative to the North Pacific (inset) and the area of sample collection (shaded area). Some fish samples were collected outside of the depth range

abilities clearly affect food habits and the resulting condition of pollock, as has been observed in other areas (Smith et al. 1988, Paul et al. 1998, Willette et al. 1999), and further results in variations in winter survival of juveniles and reproductive potential of spawning adults (Harris et al. 1986, Sogard 1997, Marshall et al. 1999). In the present study, we examined seasonal and ontogenetic variations of diets and feeding condition of pollock collected in the Doto area over 10 yr as well as clarifying the key prey determining the condition of pollock.

MATERIALS AND METHODS

Fish specimens included in the present study were sampled in the Doto area bounded by Capes Erimo and Nosappu and the isobathes of 100 to 250 m (Fig. 1). Although the depths sampled ranged from 41 to 540 m, the greatest portion (72.8%) of specimens was collected from 100 to 250 m. The samples were obtained from 1989 to 1992 and from 1995 to 2000. Fish were sampled mainly by bottom (N = 3160) and midwater (N = 2297) trawling and hook-and-line fishing (N = 70) operated by research vessels, while some were caught by commercial bottom trawling (N = 710) and gillnet (N = 429). The number of fish specimens were classified by year, month, depth of capture and fish size (Table 1). The time of commercial fishing operations was unavailable although it occurred mostly during daytime. Fish were measured and weighed to the nearest 1 mm standard length (SL) and 5 g, respectively, on board or in the laboratory, after which they were dissected and their stomachs fixed in a 10% formalin-seawater solution. In the laboratory, stomachs were cut open and food items were sorted to the lowest possible taxon. When unnaturally intact prey such as fish with complete scales was found, they were regarded as ingested in the net and excluded from the analysis. Each prey item was dried at 52°C in a drying oven for 24 h and in a desiccator for 36 to 48 h, and then weighed to the nearest 1 mg. The data are divided according to predator 10 cm size class and season (Spring, April to June; Summer, July to September, etc.). Diets were also analyzed by depth stratum (shallow, ≤150 m; deep, >150 m in bottom depths).

To examine the seasonal variation of feeding intensity, stomach content index (SCI) was calculated as follows:

$$SCI = (SCW/BW) \times 10^3$$

where SCW is dry weight (g) of stomach contents and BW is body weight. SCI was averaged for each 10 cm size class and month. Subsamples representing ≥30 fish specimens were included. Fish condition was cal-

Table 1. *Theragra chalcogramma*. Number of specimens, the stomachs of which were examined in this study

| | Shallow waters (<150 m) | | | | Deep waters (>150 m) | | | | |
	<200	201−300	301−400	>400	<200	201−300	301−400	>400	Total
Spring (Apr – Jun)	273	159	211	87	133	97	444	247	1651
Summer (Jul – Sep)	284	6	0	0	95	173	237	151	946
Autumn (Oct – Dec)	292	187	134	36	391	557	279	142	2018
Winter (Jan – Mar)	114	157	100	64	144	423	491	558	2051
Total	963	509	445	187	763	1250	1451	1098	6666

culated to examine the seasonal variation of nutritional accumulation. Although BW of pollock specimens for stomach contents analysis was measured, no measurement was available for gonads. Therefore, it was inevitably affected by hydration of gonad during maturation, and the nourishment would be biased toward overestimate during autumn and winter if BW was used for examining fish condition. We therefore calculated the following condition factor index (CF) based on a total of 24 771 market-size specimens collected during 1984 to 1997:

$$CF = [(GutW + LW) / SL] \times 10^6$$

where GutW is gutted weight (g) and LW is liver weight. LW was included since absorbed energy is initially stored in the liver as somatic tissue energy in pollock (Maeda 1986, Smith et al. 1988). Few specimens ≤200 mm SL had been available in the market, so the sample was divided into 'large' (>400 mm) and 'small' (≤400 mm) size classes, and the index was calculated for the each month. The importance of various food taxa was represented in terms of dry weight composition and frequency of occurrence. The diet was compared between different predator size classes, seasons, depth strata and fishing gears. In the comparison for fishing gear, specimens were divided into 'midwater' (collected by midwater trawling) and 'bottom' (collected by bottom trawling and bottom gillnet) samples.

RESULTS

Overall diet

The body size of 6666 fish examined for stomach contents ranged from 68 to 681 mm SL. Of these, 899 (13.5%) had empty stomachs. The diet of walleye pollock varied widely with fish size, and was predominated by pelagic organisms such as zooplankton, mesopelagic and pelagic fishes, whereas benthic animals represented <1% in all of the size classes (Table 2). The prey items varied widely, representing over 80 taxa, but several major categories such as copepods, amphipods, euphausiids, decapod cephalo-

pods and osteichthys made up the bulk of the diet (>96% in all size classes). Of the 6 species of decapod cephalopods identified, firefly squid *Watasenia scintillans* was most important, making up 20.1% in DW composition of the 201 to 300 mm size class. Most of the other squids identified were gonatiids, but a benthic sepiorid *Rossia pacifica* was found in a 621 mm SL pollock. Larger species such as *Berryteuthis magister* and Japanese common squid *Todarodes pacificus* were also identified, but they were not found as whole bodies, but as fragments of posterior (head and tentacles) or anterior (fin) parts. This suggests scavenging by pollock on leftovers discarded by predatory (or cannibalistic) squids, as reported for brown hakeling *Physiculus maximowiczi* by Kitagawa et al. (1992). The importance of copepods was higher in smaller pollock, constituting 42.4% of ≤200 mm fish diet. *Neocalanus cristatus* was predominant representing >83% of the copepods identified in each size class. Other species such as *Neocalanus plumchrus/flemingeri* and *Eucalanus bungii* represented <1%. Euphausiids were the most important prey for ≤400 mm size classes; of the 7 species identified, *Euphausia pacifica* was most important representing 76.1 to 90.0% of identifiable euphausiids. Other commonly occurring euphausiids were *Thysanoessa inermis* and *T. longipes.* Hyperiids, represented mainly by *Themisto* sp. were less important compared with copepods and euphausiids constituting 4.7% of the diet of >400 mm fish. At least 10 species of decapod crustaceans, including natant and carid shrimps and hermit crabs, were identified; however, they were of limited importance (<1.2%). A total of 27 fish taxa were identified and became more diverse and important in pollock of larger size. Most of the fish identified were mesopelagic species such as bathylagids, gonostomatids, myctophids and macrourids. Of these, myctophids were predominant with *Diaphus theta* being the most common. Walleye pollock (i.e. cannibalism) was an important prey item for the largest size class accounting for 23.9% of total diet. As presented in Yamamura et al. (2001), most of the cannibalized prey were age-1 pollock. The epipelagic fishes Japanese anchovy *Engraulis japonicus* and saury *Cololabis saira* were less important.

Table 2. *Theragra chalcogramma*. Dry weight percent composition (W) and percent frequency of occurrence (F) of prey items in the diet of different size classes. F was calculated based on the number of stomachs containing food: +: <0.01%; [a]: benthic organisms; [b]: mesopelagic fish

Size class (mm)	≤200 mm		201–300 mm		301–400 mm		>400 mm	
	W	F	W	F	W	F	W	F
Protozoa: Radiolaria	+	0.06	–	–	–	–	+	0.08
Ctenophora	–	–	+	0.11	+	+	+	0.16
Annelida: Polychaeta	0.04	0.34	0.06	1.20	0.05	0.05	0.03	1.09
Chaetognatha: *Sagitta* sp.	0.50	4.46	0.22	4.12	0.52	0.52	0.20	4.28
Mollusca								
Buccinidae	–	–	+	0.06	–	–	0.01	0.08
Limacinidae	0.02	0.17	0.01	0.23	0.02	0.02	0.07	0.39
Decapod Cephalopoda								
Unidentified	–	–	0.10	0.34	0.08	0.08	0.17	2.02
Rossia pacifica[a]	–	–	–	–	–	–	0.03	0.08
Watasenia scintillans	1.22	0.17	20.10	3.89	13.95	14.06	1.47	1.40
Gonatidae (unid.)	–	–	–	–	0.04	0.04	0.23	1.25
Berryteuthis magister	–	–	–	–	–	–	0.51	0.08
Gonatus onyx	–	–	+	0.06	0.17	0.17	0.26	0.86
Gonatopsis makko	–	–	–	–	0.99	1.00	–	–
Gonatopsis sp.	–	–	–	–	–	–	0.26	0.23
Todarodes pacificus	–	–	–	–	0.07	0.07	0.04	0.08
Arthropoda								
Ostracoda	+	0.06	+	0.06	–	–	–	–
Copepoda								
Unidentified	31.31	31.79	6.47	11.45	2.57	2.51	1.32	4.98
Neocalanus cristatus	9.24	5.77	5.10	4.81	9.92	9.99	2.62	10.66
N. plumchrus / flemingeri	0.89	1.89	–	–	+	+	–	–
Eucalanus bungii	0.63	2.46	0.09	1.26	0.06	0.06	0.00	0.08
Metridia sp.	0.32	0.29	+	0.11	–	–	–	–
Euchaeta sp.	0.03	0.91	+	0.74	0.01	0.01	0.05	1.95
Candacia sp.	+	0.34	0.01	2.23	+	+	+	1.63
Total Copepoda	42.42		11.68		12.57		4.00	
Mysidacea (unid.)	+	0.06	+	0.06	0.05	0.05	0.11	1.09
Meterithrops microphthalma	+	0.11	0.09	0.34	0.11	0.11	0.17	1.95
Neomysis sp.	0.16	3.54	+	0.06	–	–	–	–
Ianiridea	+	0.06	–	–	–	–	–	–
Gammaridea (total)	0.28		0.12		0.23		0.21	
Unidentified	0.03	1.03	0.07	1.20	0.04	0.04	+	0.54
Ampelisca sp.	0.24	1.60	0.04	0.52	0.19	0.19	0.13	2.02
Bibris sp.	+	0.34	–	–	+	+	+	0.08
Anonyx sp.	+	0.06	+	0.11	+	+	0.07	0.47
Cyphocaris challengeri	–	–	+	0.40	+	+	+	0.23
Hyperiidea								
Unidentified	0.03	0.23	+	0.06	0.01	0.01	+	0.16
Themisto japonica/pacifica	1.19	10.12	1.41	18.79	1.74	1.75	4.74	29.88
Primno sp.	–	–	+	0.06	+	+	+	0.47
Phronima sp.	–	–	–	–	–	–	+	0.08
Phronima atlantica	–	–	–	–	–	–	+	0.08
Vibilia sp.	+	0.06	–	–	+	+	+	0.16
Total Hyperiidea	1.22		1.42	1.75		4.75		
Euphausiacea								
Unidentified	6.33	9.49	1.87	8.48	3.38	3.37	4.64	12.76
Euphausia pacifica	40.47	49.34	34.46	63.34	24.15	24.26	13.25	46.23
E. pacifica (juvenile/furcilia)	0.32	4.63	0.60	4.52	0.09	0.09	0.12	0.78
Thysanoessa sp.	–	–	–	–	0.10	0.10	0.08	0.23
Th. inermis	2.83	2.46	1.63	4.24	1.25	1.25	0.97	6.93
Th. longipes	1.12	1.33	2.82	2.84	3.50	3.52	2.87	8.64
Th. macrura	–	–	–	–	0.01	0.01	+	0.08
Th. rashi	–	–	0.01	0.06	0.02	0.02	0.11	0.16
Th. spinifera	–	–	+	0.06	+	+	–	–
Tessarabrachion oculatum	0.22	0.69	0.28	2.52	0.08	0.08	0.01	0.62
Total Euphausiacea	51.29		41.68		32.58		22.04	

Table 2 (continued)

| Size class (mm)	≤200 mm		201–300 mm		301–400 mm		>400 mm	
	W	F	W	F	W	F	W	F
Decapod Crustacea								
Unidentified	0.02	0.11	+	0.06	–	–	+	0.23
Unidentified zoea	+	0.29	–	–	–	–	–	–
Acanthephyra sp.	–	–	–	–	–	–	0.01	0.08
Bentheogennema borealis	–	–	–	–	+	+	0.01	0.16
Sergestes similis	0.14	0.06	0.15	0.69	0.83	0.84	0.11	1.71
Hippolytidae sp.	0.03	0.06	–	–	–	–	0.01	0.16
Pandalus borealis[a]	–	–	–	–	0.02	0.02	–	–
Crangonidae (unid.)[a]	0.04	0.74	0.01	0.11	+	+	+	0.08
Neocrangon sp.[a]	0.15	0.11	–	–	–	–	–	–
Neocrangon communis[a]	0.30	0.23	0.36	0.92	0.18	0.18	0.61	3.19
Argis sp.[a]	–	–	–	–	0.02	0.02	–	–
A. lar[a]	–	–	–	–	0.09	0.09	0.06	0.31
Paguridea (unid.)[a]	–	–	+	0.11	–	–	–	–
Pagurus trigonocheirus[a]	0.04	0.06	–	–	0.02	0.02	–	–
Brachyura (megalopae)	+	0.11	+	0.11	–	–	–	–
Total decapod Crustacea	0.73		0.53		1.16		0.82	
Cumacea	0.22	2.52	0.02	1.78	+	+	+	0.08
Echinodermata: Ophiuroidea[a]	–	–	–	–	+	+	+	0.08
Protochordata: *Oikopleura* sp.	1.69	3.83	1.53	3.44	0.76	0.77	0.98	2.65
Vertebrata								
Osteichthys								
Unidentified	–	–	0.62	1.20	2.15	2.17	1.41	4.28
Unidentified larvae	–	–	–	–	+	+	–	–
Engraulis japonicus	–	–	0.01	0.06	2.78	2.76	3.94	0.93
Bathylagidae sp.[b]	–	–	0.15	0.06	–	–	0.01	0.16
Leuroglossus schmidti[b]	0.01	0.11	0.10	0.23	0.88	0.89	0.81	2.02
L. schmidti (larvae)[b]	0.02	0.17	–	–	+	+	+	0.16
Bathylagus sp.[b]	–	–	–	–	–	–	0.41	0.23
B. ochotensis[b]	–	–	0.24	0.06	0.08	0.08	0.32	0.39
B. milleri[b]	–	–	–	–	–	–	0.20	0.08
B. pacificus[b]	–	–	–	–	–	–	0.14	0.16
Maurolicus muelleri[b]	–	–	+	0.06	–	–	–	–
Gonostoma gracile[b]	–	–	–	–	0.22	0.22	0.09	0.23
Cyclothone alba[b]	–	–	+	0.11	+	+	+	0.23
Vinciguerria nimbaria[b]	–	–	–	–	–	–	0.03	0.16
Chauliodus sp.[b]	–	–	–	–	–	–	0.03	0.08
Tactostoma macropus[b]	–	–	–	–	+	+	–	–
Myctophidae (total)	–		17.81		19.87		29.46	
Myctophidae sp.[b]	–	–	3.15	0.86	6.46	6.51	13.10	5.60
Lampanyctus sp.[b]	–	–	–	–	+	+	–	–
L. jordani[b]	–	–	–	–	0.77	0.77	3.11	0.78
L. regalis[b]	–	–	–	–	0.19	0.19	3.74	0.70
Diaphus sp.[b]	–	–	0.33	0.11	0.05	0.05	0.05	0.08
D. theta[b]	–	–	13.32	2.29	10.91	10.99	7.17	3.42
Myctophum sp.[b]	–	–	–	–	0.92	0.93	0.03	0.08
M. asperum[b]	–	–	0.25	0.06	0.19	0.19	–	–
Tarletonbeania taylori[b]	–	–	–	–	+	+	+	0.08
Protomyctophum thompsoni[b]	–	–	+	0.17	–	–	0.15	0.08
Stenobrachius leucopsarus[b]	–	–	–	–	0.01	0.01	0.10	0.23
Symbolophorus californiensis[b]	–	–	–	–	0.21	0.21	2.01	0.47
Ceratoscoperus warmingi[b]	–	–	0.76	0.11	0.15	0.15	–	–
Paralepidiidae sp.[b]	–	–	–	–	–	–	0.58	0.23
Benthalbella sp. (larvae)[b]	–	–	–	–	+	+	0.61	0.08
Theragra chalcogramma	–	–	3.15	0.52	8.31	8.37	23.88	5.29
Macrouridae sp.[b]	–	–	–	–	0.04	0.04	–	–
Lumpenus sagitta[a]	–	–	–	–	–	–	0.11	0.08
Cololabis saira	–	–	– –	–	–	1.33	0.31	
Total fish	0.04		21.98		34.24		63.37	
Unidentified gelatinous matter	0.02	0.06	0.02	0.34	+	+	0.02	0.78
Unidentified digested matter	0.14	0.86	0.32	2.41	0.53	0.53	0.25	2.26
No. of stomachs examined	1726		1746		1884		1285	
No. of stomachs containing food	1427 (82.7%)		1509 (86.4%)		1731 (91.9%)		1076 (83.7%)	
Total DW of food examined	89.9		362.8		1619.2		1836.0	
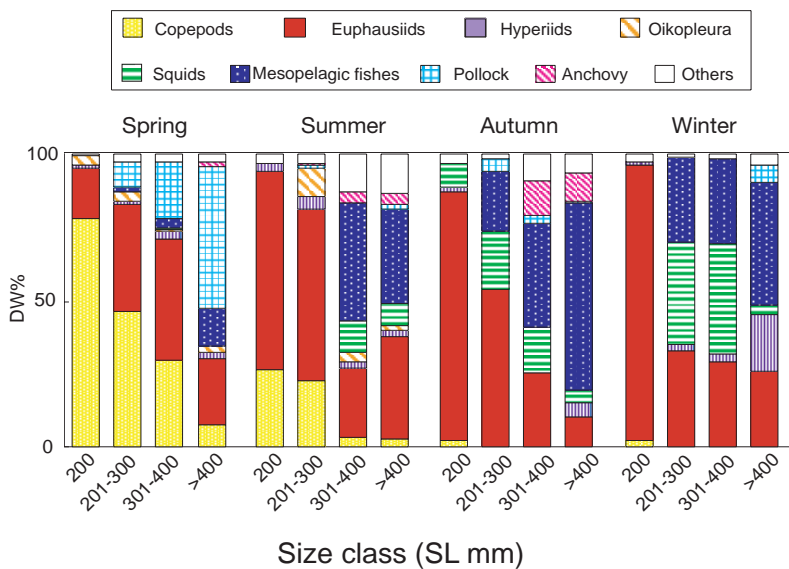
Fig. 2. *Theragra chalcogramma*. Dry weight prey composition by fish size and season based on samples collected during 1989 to 2000 in the Doto area. Season is defined as: spring, April to June; summer, July to September, etc.

Comparison of diet by depth and fishing gear

Pollock showed broadly similar seasonal and ontogenetic patterns of diet in the shallow and deep strata (Fig. 3). However, the occurrences of some prey taxa differed clearly by depth. During spring, copepods showed similar ontogenetic patterns in both strata. Cannibalism was more important in the shallow area, whereas euphausiids were more important in the deep area. During summer, no sufficient fish specimens >200 mm were available in the shallow area due to offshore distribution reflecting seasonally raised water temperature. Therefore, the comparison was possible only for pollock ≤200 mm, which mainly consisted of newly recruited age-0 fish. In both strata, pollock ≤200 mm showed similar diets which consisted mainly of euphausiids and copepods, but the proportion of copepods was higher in the deep stratum (35.1%) than in the shallow (15.1%).

Seasonal variation of diet

Pollock showed substantially different diets both by season and fish size (Fig. 2). During spring, copepods (mainly *Neocalanus cristatus*) were predominant for smaller pollock, and replaced gradually by euphausiids as fish grew. Walleye pollock (cannibalism) was the most important prey (48.1%) for pollock >400 mm. During summer, the euphausiids increased their importance as part of the copepods in the diet for pollock ≤300 mm. *Oikopleura* was a characteristic summer prey contributing 9.7% of diet in 201 to 300 mm pollock. Although *Oikopleura* from stomachs were unidentifiable due to advanced digestive stages, *O. labradoriensis* appeared to be present, which is abundant in the Oyashio waters (N. Shiga, Hokkaido University, pers. comm.). For larger pollock (>300 mm), mesopelagic fish and squids were important. Although the greatest portion of the overall diet was represented by northern species, southern species such as anchovy and saury also occurred during summer and autumn. In autumn, copepods were almost replaced by euphausiids. Squids became more common prey in larger size classes, whereas mesopelagic fish were predominant in pollock >300 mm. During winter, euphausiids were still an exclusively predominant prey for pollock ≤200 mm; whereas mesopelagic fish and squids were also important in pollock of 201 to 400 mm size classes. Euphausiids and mesopelagic fish were predominant prey for pollock >400 mm.
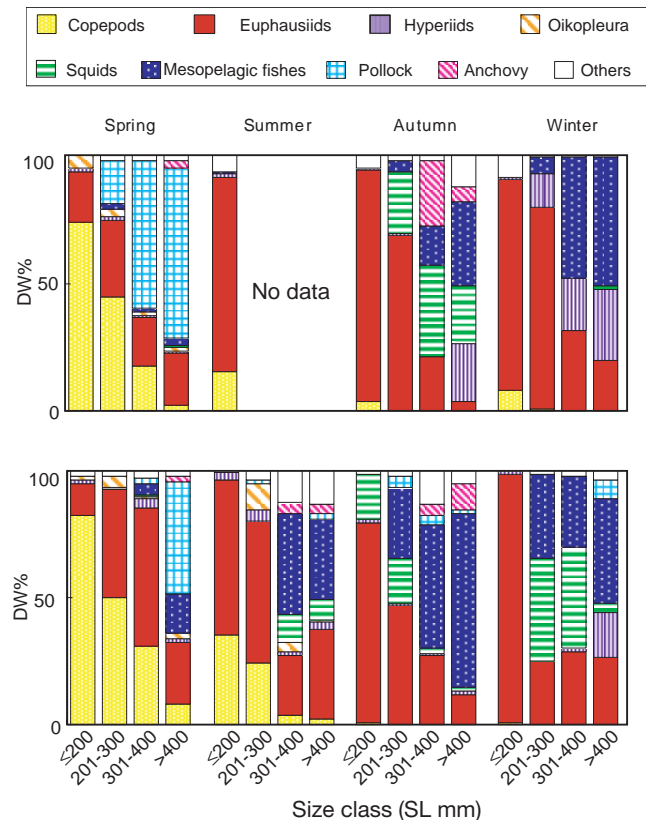

Fig. 3. *Theragra chalcogramma*. Diets for different fish size and season in shallow (≤150 m; top) and deep (>150 m; bottom) waters represented as dry weight percentage composition. Subsamples with ≥30 fish specimens were included. Depths refer to maximum bottom depth at sampling
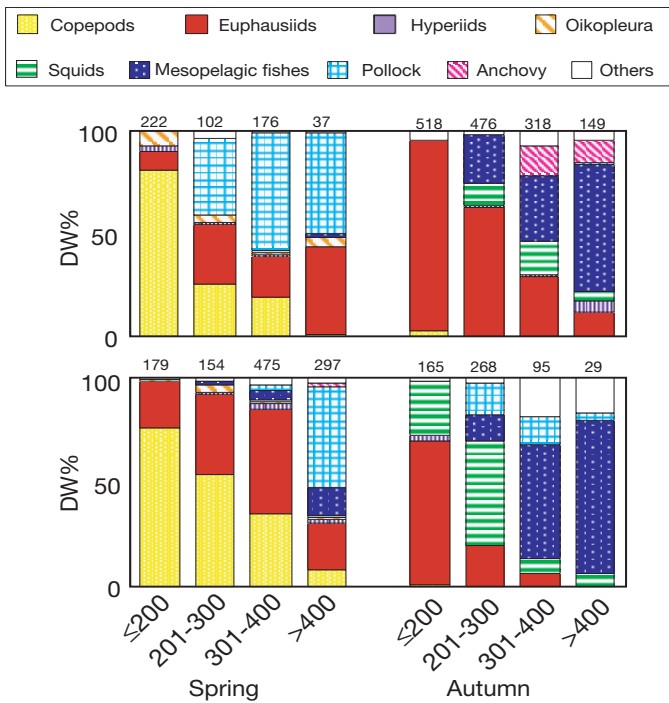
Fig. 4. *Theragra chalcogramma.* Diets for fish caught by different fishing gears: midwater trawl (top) and bottom trawl and gill net (bottom)

From autumn through winter, remarkable differences by depth were found in the predominance of micronekton and hyperiids. During autumn, squids were more important than mesopelagic fish whereas the opposite was true in the deep stratum. However, squids were found only in the deep area during winter. Hyperiids were more important in the shallow area during autumn and winter.

For the comparison between fishing gears (Fig. 4), sufficient specimens were available from spring and autumn. During spring, cannibalism occurred more commonly in the midwater whereas copepods and euphausiids were less important. However, cannibalism during autumn occurred only in the bottom layer. Squids were also more important in the bottom layer, while euphausiids were less important. Anchovy was found only in the midwater samples.

Feeding intensity and condition

In general, the SCI for pollock >200 mm showed minima during winter and increased during spring, and then decreased gradually during summer and autumn (Fig. 5). However, 201 to 400 mm pollock showed incidental maxima during January. These high values were due to intense feeding on micronekton;
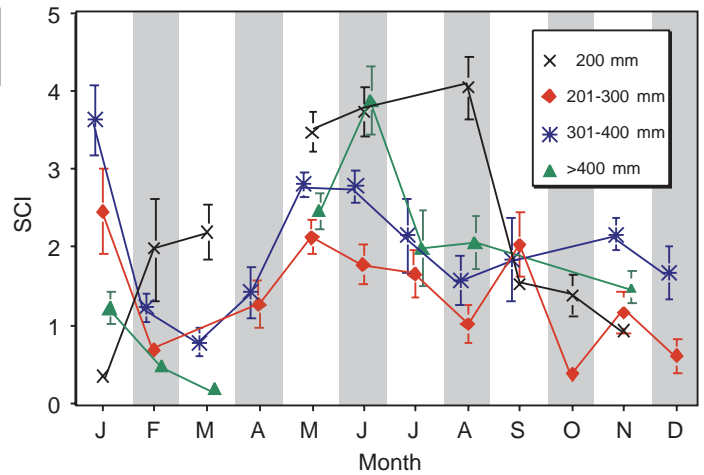
Fig. 5. *Theragra chalcogramma.* Monthly variation of mean (±1 SD) stomach contents index (SCI) for different size classes (SL, mm) in the Doto area. Subsamples represent ≥30 fish

squids and mesopelagic fishes accounted for 41.9 and 29.9% in 201 to 300 mm pollock, and 51.7 and 32.6% in 301 to 400 mm pollock, respectively. The smallest size class of pollock showed somewhat different seasonal cycle of SCI compared with larger size classes. In the case of the smallest size pollock, there was a minimum during January which then increased through August and decreased abruptly during September and continued to decrease through January. The seasonal cycles of CF were similar between fish size classes (Fig. 6). In both size classes, CF was minimal during spring (April and May) and then increased abruptly through June (≤400 mm) or July (>400 mm). Whereas pollock ≤400 mm showed a continuous decrease from August through April, CF in pollock >400 mm continued to increase from August through December.
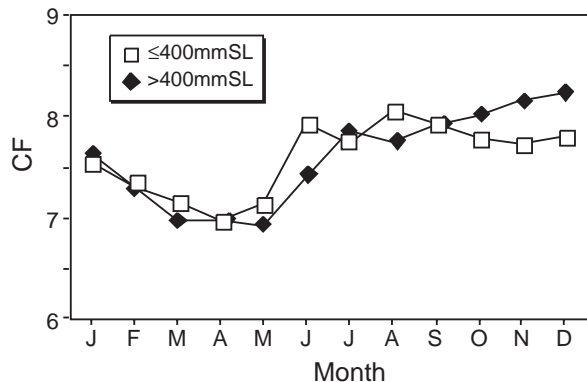

Fig. 6. *Theragra chalcogramma.* Monthly variation of mean condition factor (CF) for different size classes of fish in the Doto area based on ca 25 000 market specimens collected during 1984 to 1997. For definition of CF, see text

DISCUSSION

Potential sources of error

In the present study, feeding periodicity was not examined since the greatest portion of the specimens was sampled during daytime. The prey of pollock are generally diurnal vertical migrants along with pollock itself (e.g. Bailey 1989, Taki et al. 1996, Watanabe et al. 1999); therefore, pollock diet and feeding condition would vary by time of day. However, the relatively slow gastric evacuation rate of pollock (Dwyer et al. 1987, Yoshida 1994) and the low percentage of unidentifiable stomach contents found in the present study suggest a minimal bias due to daytime sampling. Variation of diet by sampling location has been found by previous authors (Dwyer et al. 1987, Mito et al. 1999) and was attributed to local differences in prey availability. Although fish specimens were sampled from a relatively narrow geographic range in the present study, local variation of prey distribution was probable in some occasions. For instance, warm core eddies shed by the Kuroshio extension can occasionally persist for months in the Doto area (Uehara et al. 1997). Such eddies create a distinct thermal and prey environment (e.g. Hattori 1993), and result in different diets and feeding performances of pollock. Furthermore, the shelf canyon situated off Kushiro (Fig. 1) seems to have a substantial influence on the physical and biological environments (Greene et al. 1988, Allen et al. 2001). To take these variations into consideration, samplings of finer spatial and temporal scales are required. Fish diet also varies interannually due to the variations in abundance and distribution of both predator and prey, as has been reported in other areas (Brodeur & Pearcy 1992, Tanasichuk 1999). Therefore, the feeding habits presented here are given as an average over a decade, rather than a snapshot for a specific period.

Food habits and their seasonal variation

Pollock diet showed extensive variabilities both by fish size and season, reflecting changes in prey catchability as well as co-occurrence of predator and prey (Eggers 1982, Persson et al. 1996, Scharf et al. 2000). Further, it suggests that walleye pollock is an opportunistic feeder as has been shown for other gadids (e.g. Hop et al. 1993, Yamamura et al. 1993). Pollock depended (almost) exclusively (>99%) on pelagic prey, which agrees well with its protruded lower jaw. However, ingestions of fair amounts of benthic animals by pollock have been reported from the eastern Bering Sea (EBS) (Dwyer et al. 1987, Mito et al. 1999). Given

the opportunistic nature of pollock feeding, the difference would be due to prey abundance. The seasonal and ontogenetic pattern found in the Doto area resemble those found in the EBS; copepods were the most important prey for smaller pollock during spring and summer (Dwyer et al. 1987, Mito et al. 1999). Although no species identification was available in their studies, Yoshida (1994) pointed out that the copepods ingested by pollock in the central Bering Sea were dominated by *Neocalanus cristatus* (*Calanus* in his text) and *N. plumchrus*. However, Grover (1991) reported that the summer diet of age-1 pollock (131 to 220 mm TL) in the EBS was represented exclusively by *Calanus marshallae* and euphausiid furcilia and juveniles. Similarly, species composition of euphausiids in pollock diet also seems distinct in the EBS when compared to the Doto area; for example, whereas *Euphausia pacifica* was important in the Doto area, *Thysanoessa* spp. was predominant in the Bering Sea, reflecting the geographical difference in species composition of euphausiids (Coyle et al. 1992, O. Yamamura unpubl. data). The most notable difference between these areas was the occurrence of cannibalism. Although age-0 pollock were cannibalized heavily during autumn and winter in the EBS, they represented only slight fractions in the diet of adult pollock in the Doto area. Instead, age-1 pollock were consumed during spring. The different seasonality and the age composition of the prey are due to the homogeneous thermal structure of the water column in the Doto area during spring (Yamamura et al. 2001). The water column is well stratified from summer through winter, providing thermal refuges for juveniles. However, the weak stratification during spring increases encounters with adults resulting in an increased incidence of cannibalism. In the Doto area, the occurrence of cannibalism was found to be density dependent; age-1 pollock were cannibalized more heavily in the year following strong recruitment. Yamamura et al. (2001) hypothesized that the 'overflow' of age-1 fish from the shelf waters during periods of high abundance would result in increased co-occurrence with adult fish and consequent cannibalism.

Spring diet differed distinctively from the other seasons with *Neocalanus cristatus* and cannibalism being predominant. The importance of copepods in the spring diet of pollock has been reported widely in previous studies (Bailey & Dunn 1979, Dwyer et al. 1987, Mito et al. 1999, Willette et al. 1999). The occurrence of copepods in pollock diet synchronized well with the annual life cycle of *N. cristatus* in the Doto area. From April to July, when chlorophyll concentration is high, *N. cristatus* is distributed between the thermocline (20 to 80 m) and 250 m depth, developing from copepodite stage 1 (C1) to C5. Then they migrate into deep layers where they diapause during summer (Kobari & Ikeda

1999). This vertical distribution overlaps with that of pollock during spring (S. Honda unpubl. data) and results in its importance in the pollock diet. Other predominant copepods in the Doto area, *Neocalanus plumchrus/flemingeri* and *Eucalanus bungii*, showed only slight occurrences from pollock stomach analyses. They partition habitat with each other, with *N. plumchrus/flemingeri* in the mixed layer and *E. bungii* below the thermocline (Mackas et al. 1993, Tsuda & Sugisaki 1995). Accordingly, the small contribution of *N. plumchrus/flemingeri* in pollock diet was ascribable to the limited vertical overlap. As for *E. bungii*, its extremely transparent body likely avoided predation as has been reported for other copepods, in spite of the high degree of vertical overlap with pollock (Hays et al. 1994, Tsuda et al. 1998).

Euphausiids were an important prey item for pollock throughout. In the Doto area, euphausiids showed the highest abundance of 30 g wet wt m^{-2} (WWT) during June and then decreased gradually to 2 g WWT during February (O. Yamamura unpubl. data). However, the predominance of euphausiids was lowest in pollock diet during spring. This inconsistency was perhaps due to the superabundance of *Neocalanus cristatus* during spring, which exceeded 50 g WWT (A. Tsuda pers. comm.). From summer through winter, euphausiids remained to be the most predominant prey for pollock ≤200 mm although decreased abundance has been observed during this period. Two factors are probable for the steady dependence of pollock ≤200 mm upon euphausiids: (1) they cannot shift to micronekton as larger pollock did, due to size constraints; and (2) higher abundance or denser patches of euphausiids were encountered by pollock ≤200 mm inhabiting specific environments. Although detailed distribution of euphausiids during winter has been unavailable, ≤200 mm pollock attained moderate prey ingestion (SCI > 2.0) during February and March although they showed a near-0 value during January (Fig. 5). These results suggest that juvenile pollock were distributed in a different environment compared with older fish. Further studies on winter distribution of pollock and euphausiids are needed since these prey seem crucial for winter survival of juveniles.

The southern epipelagic fishes (i.e. anchovy and saury) were ingested mainly during summer and autumn as a result of their northward migration into the subarctic area (Novikov 1986, Pearcy et al. 1996, Mihara 2000). Although pollock and anchovy co-occur because anchovy is often found at depths as deep as 150 m (S. Honda unpubl. data), natural encounters with saury were improbable as saury is distributed above the thermocline (Wada & Kitakata 1982). Yamamura (1997) found saury in stomachs of demersal fishes including pollock off Sendai Bay. He concluded that the saury was not preyed upon, but was discarded by stick-held dip net fleets and was then scavenged by the fishes. This fishery also operates in the Doto area during summer and autumn. It is therefore suggested that the saury were discarded by the fleets, then scavenged by pollock. Micronekton, represented mainly by firefly squid and myctophids, was important for larger pollock except during spring, when cannibalism was important instead. This result suggests low availability of micronekton during spring along with a lack of thermal refuge for conspecific prey. However, we cannot draw a conclusion since quantitative data on seasonal abundance of micronekton in the Doto area is still wanting.

Comparison by depth and fishing gear

The importance of copepods and euphausiids showed differences by depth and fishing gear, with higher contribution in the shallow area and midwater. The differences were more obvious in larger pollock, whereas smaller individuals showed relatively steady diets over different depths and layers. Therefore, the differences were probably not due to different availability of mesozooplankton between depths and layers, but due to an ontogenetic difference in catchability of alternative prey. However, hyperiids represented mainly by *Themisto* spp. occurred more frequently in the shallow stratum. This seems to reflect the relation of *Themisto* spp. to the Kuroshio extension water, since the water mixes the upper layer of the Doto area from summer through winter (Kono 1997). The incidence of cannibalism was more frequent in the shallow area and in the midwater during spring. These results reflect the preference of age-1 pollock for shallow stratum (Watanabe et al. 1993). After comparing body sizes of cannibals and their prey by depths, Yamamura et al. (2001) suggested that deep-water adult pollock venture into shallow waters to cannibalize on juveniles. The present result suggests that the vertical overlap between cannibals and prey is also an important condition for the incidence of cannibalism. During autumn, cannibalism occurred only in the bottom layer of the deep area. Although we have no plausible explanation, the fact that greater numbers of potential prey < 200 mm have been sampled in the midwater (see Fig. 4) suggests that the present result was not derived from prey pollock distribution but from some other factor(s).

Squids, represented mainly by firefly squid, occurred in both of the shallow and deep strata during autumn, but only in the deep stratum during winter. This implies cross-shore movement of firefly squid in relation to physical environment and/or reproduction

(Yamamura & Inada 2001). The importance of meso-pelagic fish was generally higher in the deep stratum, with an exception for pollock >300 mm during winter. The occurrence of mesopelagic fish from the shallow area was curious since deep scattering layers representing aggregations of micronekton have been observed only in the areas with >150 m bottom depths (S. Honda unpubl. data). Plausible explanations for the occurrence in the shallow area are: (1) mesopelagic fish were advected to the shallow area as they ascended during nighttime (Perissinotto & McQuaid 1992); and (2) pollock containing mesopelagic fish in their stomachs were sampled after moving into the shallow area from the deep area. Detailed data on distribution of mesopelagic fishes is needed to draw a conclusion.

Implications for the seasonal cycle

The condition of pollock decreased steadily during winter, although moderate to high SCI values were observed (Figs. 4 & 5). Since the maturation of pollock generally occurs as they grow >400 mm SL (Hamatsu et al. 1993), the decrease of SCI in pollock ≤400 mm represents the expenditure of energy reserves under reduced food availability, whereas the transformation of energy to gonad maturation was probable for fish >400 mm. Decrease of condition during winter has been frequently reported in high latitude fishes (e.g. Griffiths & Kirkwood 1995, Paul & Paul 1998) and it has a potential to cause size-selective mortality in juveniles (Sogard 1997). The SCI of pollock >400 mm continued to decrease during winter, reaching almost 0 during March. This decrease was partly due to compression of the abdominal cavity as a result of maturation since the spawning of walleye pollock occurs during early spring (Maeda 1986, Hamatsu & Yabuki 1995). On the contrary, fish ≤200 mm showed relatively high values of SCI during February and March. Since smaller fish exhaust stored energy more quickly than larger fish, due to both fewer reserves and a higher metabolic rate (Paul 1986), smaller fish need to ingest food more frequently than larger fish. In a laboratory experiment, >80% of overwintering juvenile pollock endured starvation for >200 d at a temperature of 0.5°C (Sogard & Olla 2000). However, water temperature during winter tends to be higher (~3°C) in the Doto area (Kono & Kawasaki 1997, Saito et al. 1998). Juveniles therefore need to feed continuously to support their metabolic demand (Paul et al. 1998), using *Euphausia pacifica* during February and March. Given the necessity of feeding during winter, the availability of *E. pacifica* seems critical for winter survival of juvenile pollock.

Pollock showed a rapid recovery of feeding condition during May. Since juveniles fed mainly on *Neocalanus cristatus* and adults cannibalized on juveniles, both juveniles and adults recovered utilizing *N. cristatus* directly and indirectly, respectively. It is therefore considered that *N. cristatus* plays an important role in transmitting primary production immediately to recovering pollock. Variations in the duration of *Neocalanus* 'bloom' associated with the degree of stratification of the surface caused dietary shifts in pollock in Prince Williams Sound (Willette et al. 1999). In addition, in the Oyashio area, spring bloom is determined by the vertical stability of the water column (Yoshimori et al. 1995) and is subjected to temporal variability (Kasai et al. 1997). It is therefore suggested that climatic variability has a potential to delay the timing of *N. cristatus* 'bloom' as has been reported in the NE Pacific (Mackas et al. 1998) and would therefore seriously affect the survival of wintering juvenile pollock by extending the starvation period.

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