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Trophic Ecology of Alaska Plaice *Pleuronectes quadrituberculatus* (Pleuronectidae) in the Sea of Okhotsk and the Bering Sea

V. V. Napazakov

Pacific Fishery Research Center (TINRO-Center), Vladivostok, 690091 Russia

e-mail: napazakov@tinro.ru

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Abstract—The article contains the results of autecological studies of the Alaska plaice *Pleuronectes quadrituberculatus* in the Far East seas. It was found that its main food resources in different parts of the Sea of Okhotsk and the Bering Sea are worms and bivalves, while the proportion of other species is insignificant. All these worms and bivalves are the species of benthic infauna and onfauna. The trophic level is in the range from 3.39 to 4.13; its variability depends on the proportion of bivalves and polychaetes. We described the environmental conditions of the habitat of Alaska plaice: depth, temperature, and preferred types of soil. The adaptation of Alaska plaice to certain soil structure provides camouflage and easier access of food resources. Relatively nonselective consumption of polychaetes and bivalves provides A wider range of habitats.

Keywords: Alaska plaice, *Pleuronectes quadrituberculatus*, Sea of Okhotsk, Bering Sea, feeding, diet, trophic level, infauna, onfauna, benthos, trophodynamic indicators, ecosystem approach

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The Alaska plaice *Pleuronectes quadrituberculatus* inhabits the areas of the North Pacific Ocean from Peter the Great Gulf to the southern part of the Gulf of Anadyr and from the Bering Strait to southern Alaska as well as the shallow plateau of the Bering Sea. This is an elittoral (0–600 m) widely boreal species (Sheyko and Fedorov, 2000; Fadeev, 2005; *Promyslovye ryby...*, 2006). The population density is highest near the western coast of Kamchatka and in the Bering Sea (Fadeev, 2005). The Alaska plaice, as well as the yellowfin sole *Limanda aspera,* flathead sole *Hippoglossoides elassodon*, and Sakhalin sole *Limanda sakhalinensis* (Il'insky and Chetvergov, 2002), is one of the dominant species in terms of biomass in the benthic ichthyocenoses of the Sea of Okhotsk. The biomass of Alaska plaice on the shelf of western Kamchatka in 2005–2012 was 54653 t (9.8% of the total biomass of all flatfishes and 5.29% of all benthic fishes); this species is fourth after *Limanda sakhalinensis, L. aspera*, and *Hippoglossoides elassodon* (Terent'ev et al., 2013).

The diet of Alaska plaice has been studied in detail (Chuchukalo, 2006; D'yakov, 2011). However, the data on trophic ecological features and the environmental conditions of habitats in the range of this species need to be analyzed and summarized. The purposes of this study are to analyze the composition of food spectrum and its ontogenetic variability, to determine the trophic levels and trophic status, and to describe the environmental conditions of the habitat of Alaska plaice.

MATERIALS AND METHODS

The material for this study was collected in the Sea of Okhotsk in the Shelikhov Gulf (September 2004), on the shelf of western Kamchatka (June–July 2005, 2008, 2010), and in the western part of the Bering Sea (August–September 1998, October–November 2000). Trawling was performed by bottom trawl DT 27.1 with horizontal and vertical openings of 16 and 6 m, respectively. The total number of analyzed stomachs was 1035 (Table 1).

We measured the fork length (FL) and body weight of fishes. The content of stomachs was investigated by the quantitative-gravimetric method (*Metoicheskoe posobie...*, 1974; *Rukovodstvo...*, 1986). The composition of food was determined right after the collection of food samples; the components that could not be identified were fixed in formalin for further identification in laboratory conditions. We used the scale of digestion rate for investigating food components; the scale was created in the TINRO-Center (Chuchukalo and Napazakov, 1999).

The trophic levels (T) were calculated by the following equation (Chassot et al., 2008):

$$T = 1 + \sum_{J=1}^{G} DC_{ij} T_j,$$

Table 1. Diet of Alaska plaice *Pleuronectes quadrituberculatus*

Region, date, name of ship	Size groups, cm						
	10.1–20.0	20.1–30.0	30.1–40.0	40.1–50.0	50.1–60.0	60.1–70.0	all groups
Sea of Okhotsk:							
—Shelikhov Gulf, Sept. 3–8, 2004, *Professor Kaganovsky*	–	–	–	6/1	15/1	2/1	23/3
—shelf of the western Kamchatka, July 2005, *Professor Kaganovsky*	–	83/5	82/8	40/3	–	–	205/16
—shelf of the western Kamchatka, July 2008, *Professor Kaganovsky*	–	60/5	141/8	24/5	–	–	225/18
—shelf of the western Kamchatka, June 27–Sept. 15, 2010, *Professor Kizevetter*	7/2	124/8	112/9	57/7	–	–	300/26
Western part of the Bering Sea:							
—Aug.–Sept. 1998, *Professor Kaganovsky*	–	–	10/2	18/4	10/2	–	38/8
—Oct.–Nov. 2000, *TINRO*	39/4	108/13	36/10	47/11	14/6	–	244/44
Total	46/6	375/31	381/37	192/31	39/9	2/1	1035/115

The number of stomachs is before the slash; the number of samples is after the slash.

where DC_{ij} is the share of a species (j) in the diet of consuming species (i), T_j is the mean trophic level of each species j, and G is the number of food components in the food samples of i (Gascuel and Pauly, 2009). The values of trophic levels were derived from the program TrophLab ver. June 2000 (Froese and Pauly, 2013). The importance of food components was assessed basing on their share in the total mass of food samples (%).

RESULTS AND DISCUSSION

Diet

Bering Sea. The diet of Alaska plaice with a *FL* of 30–60 cm in the western part of the Bering Sea in 1998 and 2000 mainly consisted of polychaetes (94–100% of food mass) (Tables 2, 3). The share of polychaetes in the diet of young fishes (*FL* = 10–20 cm) was 23%, while the same parameter for fishes with *FL* 20–30 cm reached 65%; i.e., the share of polychaetes increased with the age of fishes. Crustaceans were dominant in the diet of young fishes with *FL* ≤ 30 cm (up to 77%); their share in the diet of fishes with *FL* > 30 cm was 6% or less. Moreover, the diet of fishes with *FL* > 30 cm included bivalves, ophiuroids, sand dollars, and ascidians.

Sea of Okhotsk

According to a small amount of data (23 stomachs; Table 4), the diet of Alaska plaice with FL 40–70 cm in the Shelikhov Gulf in 2004 consisted of polychaetes (53.6) and bivalves (46.4%). Their proportion was almost equal, but the share of polychaetes decreased with the age of fishes, while the share of bivalves increased.

The diet of Alaska plaice with *FL* 20–50 cm on the shelf of western Kamchatka in 2005 mainly consisted of polychaetes (88.6%); the total share of worms (polychaetes and nemertines) was 89.9%. The share of bivalves in the diet of fishes with *FL* 20–30 and 30–40 cm was 27.1 and 8.0%, respectively; the share of sea anemones was 10.0 and 10.2%, respectively. The food samples also contained echinoderms and gammarids (Table 5).

The largest part of the diet of Alaska plaice with *FL* 20–50 cm on the shelf of western Kamchatka in 2008 consisted of polychaetes (54.4%; Table 6). The second dominant group was bivalves (37.3%); their share increased as the length of fishes increased. The diet also included amphipods (7.8), ophiuroids (0.2), caridean shrimps (0.1), and sea anemones (0.1%).

In 2010, polychaetes were dominant (70.8%) in the diet of Alaska plaice with *FL* 10–50 cm on the shelf of western Kamchatka. The second and third largest part of the diet consisted of bivalves (13.8) and echiurans (12.7%). The share of other components did not exceed 0.8% (Table 7).

According to Tables 2–7, the diet of Alaska plaice mainly consists of the species of benthic infauna and onfauna, while the species of epifauna have insignificant share. Dominant taxonomic groups in terms of both mass and number of species are polychaetes and bivalves (see Fig. 1). The share of amphipods and sea anemones is significantly lower.

Our calculations showed that the trophic level of Alaska plaice varies in the range from 3.39 to 4.13

Table 2. Diet of Alaska plaice *Pleuronectes quadrituberculatus* in the Bering Sea in August–September 1998, % of total mass

Composition of food samples and other parameters	EG	Size groups, cm			
		30.1–40.0	40.1–50.0	50.1–60.0	all groups
Polychaeta		94.0	96.3	100	97.6
Nephtys sp.	Infauna	6.0	43.1	38.6	38.4
Maldanidae gen. sp.	"	88.0	53.2	61.4	59.2
Priapulida gen. sp.	"	–	1.5	–	0.8
Amphipoda		6.0	–	–	0.4
Melita formosa	Onfauna	6.0	–	–	0.4
Mollusca		–	2.2	–	1.2
Yoldia bartschi	Infauna	–	2.2	–	1.2
Number of stomachs/samples		10/2	18/4	10/2	38/8
Share of empty stomachs, %		20	22	20	
Mean stomach filling index, ‰		44	105	99	
Mean length (*FL*), cm		35	45	55	
Mean weight, g		796	1230	1752	
Trophic level (*T*)		3.88	3.56	3.61	3.60

Here and in Table 3–7, EG is ecological group.

(Tables 2–7). The size groups of this study usually have the third trophic level and sometimes the fourth; for example, Alaska plaices with *FL* 40–50 cm in 2004 mainly consumed *Golfingia marqaritacea* (Table 4). We did not observe any pattern in the changes in trophic levels during ontogeny; this corresponds with homogenous species composition of food samples obtained from all size groups of fishes. Obviously, the trophic level mainly depends on the proportion of bivalves and polychaetes.

Environmental Conditions of Habitats

The Alaska plaice is common at a depth of up to 600 m (Tuponogov and Kodolov, 2014). The depth is an integrated factor and is functionally associated with other abiotic elements of environment. Therefore, the bathymetric distribution of organisms can be limited by temperature, soil type, food resources, and other factors. All food samples were collected at a depth of 23–193 m, i.e., where the abundance of Alaska plaice is maximal (Fedorov, 2000; our data).

According to our measurements, bottom water temperature in the areas of collection varies in the range from –1.04 to 11.70°C. According to Fadeev (1987, 2005), the optimal temperature range for the Alaska plaice is the same (from –1 to +12°C); the maximal abundance of this species is observed at 3–4°C. The limiting effect of temperature on the distribution of Alaska plaice has already been observed.

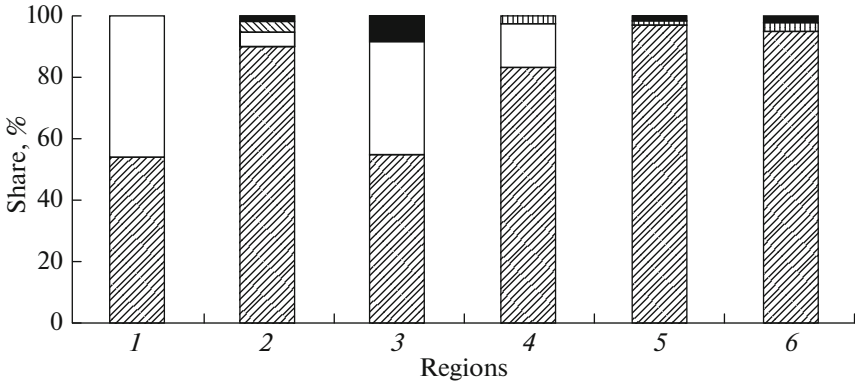

Fig. 1. Taxonomic composition of the diet of Alaska plaice *Pleuronectes quadrituberculatus* in some areas of (*1–4*) the Sea of Okhotsk and (*5, 6*) the Baring Sea: (*1*) Shelikhov Gulf (2004), (*2–4*) shelf of western Kamchatka (*2*—2005; *3*—2008; *4*—2010), (*5–6*) shelf of the western parts of the Bering Sea (*5*—1998; *6*—2000); (▨) polychaetes, (□) molluscc (▧) sea anemones, (■) amphipods, (▥) other species.

Table 3. Diet of Alaska plaice *Pleuronectes quadrituberculatus* in the Bering Sea, Oct. 29–Nov. 25, 2000, % of total mass

Composition of food samples and other parameters	EG	Size groups, cm					
		10.1–20.0	20.1–30.0	30.1–40.0	40.1–50.0	50.1–60.0	all groups
Polychaeta		23.0	64.9	94.5	95.8	98.5	94.5
Nephtys sp.	Infauna	–	2.9	1.1	20.3	10.9	14.4
Nereis sp.	Onfauna	–	–	8.2	6.8	–	5.0
Ophelina acuminata	Infauna	–	–	–	1.1	–	0.6
Polychaeta gen. sp.	"	23.0	38.3	69.2	42.7	80.1	55.1
Echiurus sp.	Onfauna	–	23.7	16.0	24.9	7.5	19.4
Mollusca		–	–	1.9	1.2	–	0.9
Bivalvia gen. sp.	Infauna	–	–	–	0.6	–	0.3
Gastropoda gen. sp.	"	–	–	–	+	–	+
Macoma sp.	"	–	–	–	0.4	–	0.2
Nuculana sp.	"	–	–	–	0.2	–	0.1
Yoldia sp.	"	–	–	1.9	–	–	0.3
Ophiuroidea gen. sp.	Onfauna	–	–	–	1.4	–	0.8
Crustacea		77.0	34.2	2.8	1.6	0.3	3.3
Amphipoda gen. sp.	"	77.0	34.2	1.8	0.3	0.3	2.4
Anonyx sarsi	"	–	–	1.0	0.7	–	0.5
Chionoecetes opilio	"	–	–	–	0.3	–	0.2
Hyas coarctatus	"	–	–	–	0.3	–	0.2
Isopoda gen. sp.	"	–	–	+	–	–	+
Echinodermata		–	0.9	0.8	–	–	0.2
Echinarachnius parma	"	–	0.9	0.8	–	–	0.2
Ascidiacea		–	–	–	–	1.2	0.3
Boltenia ovifera	Epifauna	–	–	–	–	1.2	0.3
Number of stomachs/samples		39/4	108/13	36/10	47/11	14/6	244/44
Share of empty stomachs, %		89.7	75.0	22.2	19.1	7.1	
Mean stomach filling index, ‰		3.3	29	91	117	99	
Mean length (*FL*), cm		17.8	24.8	35.1	44.6	54.3	
Mean weight, g		86	212	605	1235	2394	
Trophic level (*T*)		3.90	3.70	3.76	3.70	3.83	3.74

Here and in Table 7: "+" designates <0.05.

According to Mikulich (1954), negative temperatures near the southern coast of southern Sakhalin serves as a barrier for migration outside the range of 40–100 m for all species of Pleuronectidae, although there are available food resources. According to the data of trawling in 1982–2006, all species of Pleuronectidae, including the Alaska plaice, do not inhabit waters with a temperature below 2°C in the eastern parts of the Bering Sea (Spencer, 2008). In cold summers, cold water masses (<2°C) in the eastern parts of the Bering Sea are spread to the middle shelf (50–100 m), thus serving as the barriers that limit the distribution of Pleuronectidae species on the inner shelf (up to 50 m) and stimulate the competition for food resources (Stabeno et al., 2012; Yeung et al., 2013).

Benthic sediments and soils have a significant effect on the distribution of benthic species in seas and oceans, since some animal and plant species use soil as a substrate, while others use its organic matter as food (Nevesskaya, 1998). The habitat of Alaska plaice, as well as of other pleuronectids, consists of benthic sediments with certain granulometric properties. For example, McConnaughey and Smith (2000) concluded that the texture of benthic sediments is the main factor that determines the quality of habitats of benthophagous pleuronectids. According to their data, Alaska plaices are mainly common on sand-silty soils. Such soils are an indispensable environmental factor for pleuronectids due to several properties. The morphological structure of scales of the eyed side pro-

Table 4. Diet of Alaska plaice *Pleuronectes quadrituberculatus* in the Shelikhov Gulf in September 2004, % of total mass

Composition of food samples and other parameters	EG	Size groups, cm			
		40.1–50.0	50.1–60.0	60.1–70.0	all groups
Polychaeta		86.8	50.7	30.1	53.6
Golfingia marqaritacea	Onfauna	86.8	50.7	30.1	53.6
Mollusca		13.2	49.3	69.9	46.4
Megayoldia thraciaeformis	Infauna	13.2	12.7	45.8	15.8
Macoma moesta	"	–	36.6	24.1	30.6
Number of stomachs/samples		6/1	15/1	2/1	23/3
Share of empty stomachs, %		33.33	6.67	0	
Mean stomach filling index, ‰		119	183	138	
Mean length (*FL*), cm		47.9	54.4	61	
Mean weight, g		1688	2581	3000	
Trophic level (*T*)		4.13	3.66	3.39	3.70

Table 5. Diet of Alaska plaice *Pleuronectes quadrituberculatus* in the Sea of Okhotsk in June–July 2005, % of total mass

Composition of food samples and other parameters	EG	Size groups, cm			
		20.1–30.0	30.1–40.0	40.1–50.0	all groups
Nemertea gen. sp.	Onfauna	–	4.3	0.2	1.3
Polychaeta		61.3	74.9	97.9	88.6
Polychaeta gen. sp.	Infauna	50.9	13.4	–	7.9
Nephthys sp.	"	–	45.7	97.0	74.9
Travisia forbesii	"	10.4	10.0	–	3.6
Echiurus sp.	Onfauna	–	5.8	0.9	2.2
Mollusca		27.1	8.7	1.2	5.4
Bivalvia gen. sp.	Infauna	27.1	8.0	0.3	4.6
Yoldia bartschi	"	–	–	0.9	0.6
Yoldia sp.	"	–	0.7	–	0.2
Ophiuroidea gen. sp.	Onfauna	1.6	0.2	–	0.2
Echinodermata		–	–	0.5	0.3
Chiridota sp.	Infauna	–	–	0.5	0.3
Gammaridea		–	1.8	0.2	0.7
Anonyx sarsi	Onfauna	–	1.0	–	0.3
Gammaridea gen. spp.	"	–	0.8	0.2	0.4
Actiniaria gen. sp.	Epifauna	10.0	10.1	–	3.5
Number of stomachs/samples		83/5	82/8	40/3	205/16
Share of empty stomachs, %		27.7	22.9	0	
Mean stomach filling index, ‰		51	69	154	
Mean length (*FL*), cm		26.7	35.6	43.5	
Mean weight, g		263	651	1413	
Trophic level (*T*)		3.56	3.68	3.88	3.80

Table 6. Diet of Alaska plaice *Pleuronectes quadrituberculatus* in the Sea of Okhotsk in July 2008, % of total mass

Composition of food samples and other parameters	EG	Size groups, cm			
		20.1–30.0	30.1–40.0	40.1–50.0	all groups
Polychaetes		50.8	57.4	44.2	54.4
Polychaeta gen. sp.	Infauna	45.6	51.9	44.2	51.4
Echiurus sp.	Onfauna	5.2	5.5	–	3.0
Mollusca		3.5	33.4	55.3	37.4
Bivalvia gen. sp.	Infauna	3.3	20.2	3.0	13.9
Yoldia sp.	"	–	1.1	8.5	3.1
Yoldia myalis	"	–	7.3	43.9	18.1
Yoldia bartschi	"	–	4.8	–	2.3
Macoma moesta	"	0.2	–	–	+
Ophiuroidea gen. sp.	Onfauna	–	0.3	–	0.2
Amphipoda		45.7	8.7	–	7.8
Gammaridea gen. spp.	"	45.7	8.6	–	7.8
Ampelisca macrocephala	"	–	0.1	–	+
Caridea gen. sp.	"	–	–	0.5	0.1
Actiniaria gen. sp.	Epifauna	–	0.2	–	0.1
Number of stomachs/samples		60/5	141/8	24/5	225/18
Share of empty stomachs, %		20	9.9	0	
Mean stomach filling index, ‰		34	71	94	
Mean length (FL), cm		24.9	34.3	42.9	
Mean weight, g		341	559	1157	
Trophic level (T)		3.64	3.51	3.42	3.50

vides higher friction rate and, as a result, aggregation of smaller sediment particles on the body of fishes (Spinner et al., 2016). Obviously, the adaptation to certain soil structure is important for masking. On the other hand, the adaptation of Alaska plaice to sand-silty soils is caused by the presence of food resources, which consist of emphitonic species (inhabiting soft soils: Railkin, 2015); according to our data, such species are the main component of diet for Alaska plaice. Another important feature of the diet is nonselective consumption of polychaetes and bivalves. For example, Yeung et al. (2013) reported that the composition of diet of benthophagous pleuronectids correlates with the species composition of infauna invertebrates of habitats. Such spatial correlation between the composition of polychaetes in the stomachs of pleuronectids and in infauna has already been observed by other authors (Cabral et al., 2002; Yeung et al., 2010). This behavioral feature of the Alaska plaice could be used for prediction. Thus, the inclusion of abundance rates for the main species consumed by two sympatric pleuronectids, *Solea solea* and *S. senegalensis*, as variables to the model used for estimating the suitability of habitats was found to be necessary for accurate prognosis (Vinagre et al., 2006). Soft soils, such as sand, silt, and clay (pelites and aleurites), in Far East seas are mainly inhabited by bivalves and polychaetes, which can move and feed in such soils and are usually detritophagous (Tsikhon-Lukanina, 1987; Zhirkov, 2010). According to the data of Shuntov (2001), bivalves, polychaetes, and echinoderms account for 60–85% of macrozoobenthic biomass in the lower sublittoral zone of Far East seas and for 33–80% of the lower sublittoral zone of Far East seas and for 33–80% of the Sea of Japan. The share of bivalves on the shelf of the Sea of Okhotsk is 22.8%, while the share of polychaetes is 10.0%; their total share is approximately one third of the total zoobenthic biomass (Nadtochy et al., 2007).

Based on the literature data on the diet of pleuronectids in Far East seas, it was concluded that the Alaska plaice, as well as halibuts, speckled flounder *Mezopsetta punctatissima*, marbled flounder *Pseudopleuronectes yokohamae*, starry flounder *Platichthys stellatus,* and blackfin flounder *Glyptocephalus stelleri,* are most conservative species with lowest lability in terms of the main food resources (Dyakov, 2011). Our data correspond with this finding. We concluded that this results from the adaptation of Alaska plaice to the consumption of species inhabiting soft soils.

Thus, the main food resources for Alaska plaice in different regions of the Sea of Okhotsk and the Bering

Table 7. Diet of Alaska plaice *Pleuronectes quadrituberculatus* in the Sea of Okhotsk in July 2010, % of total mass

Composition of food samples and other parameters	EG	Size groups, cm				
		10.1–20.0	20.1–30.0	30.1–40.0	40.1–50.0	all groups
Nemertea gen. sp.	Onfauna	–	0.6	–	–	+
Polychaeta		100	87.1	79.2	85.0	83.5
Ampharetidae gen. sp.	"	–	–	–	0.5	0.3
Glycera capitata	Infauna	100	4.7	–	–	0.5
Lumbrineris sp.	"	–	14.7	–	–	1.2
Nephtys paradoxa	"	–	–	–	13.5	8.3
Nephtys sp.	"	–	4.9	11.0	0.5	4.1
Nereis sp.	Onfauna	–	–	–	0.7	0.4
Nicomache lumbricalis	Infauna	–	–	–	0.1	0.1
Polychaeta gen. sp.	"	–	46.3	36.9	61.7	52.7
Scalibregma inflatum	"	–	5.1	–	–	0.4
Travisia forbesii	"	–	7.3	6.1	0.6	2.8
Echiuridae gen. sp.	Onfauna	–	–	–	0.6	0.4
Urechis unicinctus	"	–	4.1	25.2	6.8	12.3
Sipuncula gen. sp.	"	–	0.6	1.9	–	0.6
Priapulida gen. sp.	"	–	–	–	0.4	0.2
Mollusca		–	8.0	17.0	13.0	13.8
Bivalvia gen. sp.	Infauna	–	8.0	12.7	–	4.6
Mya sp.	"	–	–	–	4.3	2.6
Yoldia bartschi	"	–	–	–	8.1	4.9
Yoldia sp.	"	–	–	4.3	0.6	1.7
Echinodermata		–	1.5	1.1	+	0.5
Echinarachnius parma	Onfauna	–	1.5	1.1	+	0.5
Ophiuroidea gen. sp.	"	–	0.7	0.5	0.9	0.8
Amphipoda		–	1.5	0.3	–	0.2
Anonyx sarsi	"	–	0.6	–	–	+
Gammaridea gen. sp.	"	–	0.9	0.3	–	0.2
Ascidiacea	Epifauna	–	–	–	0.7	0.4
Number of stomachs/samples		7/2	124/8	112/9	57/7	300/26
Share of empty stomachs, %		57.1	42.7	17.0	10.5	
Mean stomach filling index, ‰		31	39	69	114	
Mean length (*FL*), cm		18.5	24.9	34.3	43.7	
Mean weight, g		85	253	586	1269	
Trophic level (*T*)		4.3	3.8	3.42	3.59	3.56

Sea are polychaetes and bivalves. All of them are the species of benthic infauna and onfauna or emphitone; the nonselective consumption of such species provides wider range of habitats limited by the type of soils. The trophic level is usually three; its variability depends on the proportion of bivalves and polychaetes.

REFERENCES

Cabral, H.N., Lopes, M., and Loeper, R., Trophic niche overlap between flatfishes in a nursery area on the Portuguese coast, *Sci. Mar.*, 2002, vol. 66, no. 3, pp. 293–300.

Chassot, E., Rouyer, T., Trenkel, V.M., and Gascuel, D., Investigating trophic level variability in Celtic Sea fish predators, *J. Fish Biol.*, 2008, vol. 73, no. 4, pp. 763–781.

Chuchukalo, V.I., *Pitanie i pishchevye otnosheniya nektona i nektobentosa v dal'nevostochnykh moryakh* (Deeding and Food Relationships of Nekton and Nektobenthos in the Far Eastern Seas), Vladivostok: TINRO-Tsentr, 2006.

Chuchukalo, V.I. and Napazakov, V.V., Determination of the diurnal food diet and digestion rate in raptorial and benthos-feeding fishes, *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 1999, vol. 126, pp. 160–171.

D'yakov, Yu.P., Feeding of Far Eastern flounders (Pleuronectiformes), *Issled. Vodn. Biol. Resur. Kamchat. Sev.-Zap. Chasti Tikhogo Okeana*, 2011, no. 21, pp. 5–72.

Fadeev, N.S., *Severotikhookeanskie kambaly (rasprostranenie i biologiya)* (North Pacific Flounders: Distribution and Biology*)*, Moscow: Agropromizdat, 1987.

Fadeev, N.S., *Spravochnik po biologii i promyslu ryb severnoi chasti Tikhogo okeana* (Handbook on Biology of Fishes and Fishery in the Northern Part of Pacific Ocean), Vladivostok: TINRO-Tsentr, 2005.

Fedorov, V.V., Species composition, distribution, and the depths of the fish-like species and fishes of northern Kurile Islands, in *Promyslovo-biologicheskie issledovaniya ryb v tikhookeanskikh vodakh Kuril'skikh ostrovov i prilegayushchikh raionov Okhotskogo i Beringova morei v 1992–1998 gg.* (Commercial and Biological Studies of Fishes in Pacific Waters of Kurile Islands and Adjacent Areas of the Okhotsk and Bering Seas in 1992–1998), Moscow: VNIRO, 2000, pp. 7–41.

FishBase, Version 08.2013, Froese, R. and Pauly, D., Eds., 2013. http://www.fishbase.org.

Gascuel, D. and Pauly, D., EcoTroph: modeling marine ecosystem functioning and impact of fishing, *Ecol. Model.*, 2009, vol. 220, no. 21, pp. 2885–2898.

Il'inskii, E.N. and Chetvergov, A.V., Modern status of reserves and distribution of flounders in the Sea of Okhotsk, *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2002, vol. 130, pp. 1104–1121.

McConnaughey, R.A. and Smith, K.R., Associations between flatfish abundance and surficial sediments in the eastern Bering Sea, *Can. J. Fish. Aquat. Sci.*, 2000, vol. 57, pp. 2410–2419.

Metoicheskoe posobie po izucheniyu pitaniya i pishchevykh otnoshenii ryb v estestvennykh usloviyakh (Handbook on Analysis of Nutrition and Food Relationships of Fishes in Natural Conditions), Moscow: Nauka, 1974.

Mikulich, L.V., Feeding of flounders at the southern coasts of Sakhalin and Southern Kurile Islands, *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 1954, vol. 39, pp. 136–224.

Nadtochii, V.A., Budnikova, L.L., and Bezrukov, R.G., The results of benthic bonification in Russian waters of the Far Eastern seas: composition and quantitative distribution (Bering Sea), *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2007, vol. 153, pp. 264–282.

Nevesskaya, L.A., *Etapy razvitiya bentosa fanerozoiskikh morei. Paleozoi* (Development Stages of the Benthos from Phanerozoic Seas. Paleozoic Period), Moscow: Nauka, 1998.

Promyslovye ryby Rossii (Commercial Fish Species of Russia)*, Gritsenko, O.F., et al.*, Moscow: VNIRO, 2006, vol. 2.

Railkin, A.I., Classification of the general ecological groups of the sea hydrobionts, *Nauch. Al'm., Biol. Nauki*, 2015, no. 7 (9), pp. 989–991.

Rukovodstvo po izucheniyu pitaniya ryb (Manual on Analysis of Fish Feeding), Vladivostok: Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr., 1986.

Sheiko, B.A. and Fedorov, V.V., Fish-like species and fishes, in *Katalog pozvonochnykh Kamchatki i sopredel'nykh akvatorii* (Catalogue of Vertebrates of Kamchatka and Adjacent Marine Basins), Petropavlovsk-Kamchatskii: Kamchat. Pechat. Dvor, 2000, ch. 1, pp. 7–69.

Shuntov, V.P., *Biologiya dal'nevostochnykh morei Rossii* (Biology of Far Eastern Russian Seas), Vladivostok: TINRO-Tsentra, 2001, vol. 1.

Spencer, P.D., Density-independent and density-dependent factors affecting temporal changes in spatial distributions of eastern Bering Sea flatfish, *Fish. Oceanogr.*, 2008, vol. 17, no. 5, pp. 396–410.

Spinner, M., Kortmann, M., Traini, C., and Gorb, S.N., Key role of scale morphology in flatfishes (Pleuronectiformes) in the ability to keep sand, *Sci. Rep.*, 2016, vol. 6, no. 26308. doi 10.1038/srep26308

Stabeno, P.J., Kachel, N.B., Moore, S.E., et al., Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem, *Deep Sea Res., Part II*, 2012, vols. 65–70, pp. 31–45.

Terent'ev, D.A., Mikhalyutin, E.A., and Matveev, A.A., Modern resources, long-term dynamics of distribution and size structure of mass commercial fish species on the self of western coast of Kamchatka during summer, *Issled. Vodn. Biol. Resur. Kamchat. Sev.-Zap. Chasti Tikhogo Okeana*, 2013, no. 30, pp. 5–27.

Tsikhon-Lukanina, E.A., *Trofologiya vodnykh mollyuskov* (Trophology of Aquatic Mollusks), Moscow: Nauka, 1987.

Tuponogov, V.N. and Kodolov, L.S., *Polevoi opredelitel' promyslovykh i massovykh vidov ryb dal'nevostochnykh morei Rossii* (Field Guide for Identification of Commercial and Mass Fish Species from Far Eastern Seas of Russia), Vladivostok: Russkii Ostrov, 2014.

Vinagre, C., Fonseca, V., Cabral, H., and Costa, M.J., Habitat suitability index models for the juvenile soles, *Solea solea* and *Solea senegalensis*, in the Tagus estuary: defining variables for species management, *Fish. Res.*, 2006, vol. 82, pp. 140–149.

Yeung, C., Yang, M.S., and McConnaughey, R.A., Polychaete assemblages in the southeastern Bering Sea: linkage with groundfish distribution and diet, *J. Mar. Biol. Ass. U.K.*, 2010, vol. 90, no. 5, pp. 903–917.

Yeung, C., Yang, M.S., Jewett, S.C., and Naidu, A.S., Polychaete assemblage as surrogate for prey availability in assessing southeastern Bering Sea flatfish habitat, *J. Sea Res.*, 2013, vol. 76, pp. 211–221.

Zhirkov, I.A., *Zhizn' na dne. Biogeografiya i bioekologiya bentosa* (Life at the Bottom: Biogeography and Bioecology of Benthos), Moscow: KMK, 2010.

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