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Title	Seasonal change in daily ration of brown sole Pleuronectes herzensteini in the coastal waters of northern Niigata Prefecture, Japan
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Description	International Symposium on North Pacific Flatfish. 26-28 October 1994. Anchorage, Alaska, USA.
Relation	(Lowell Wakefield Fisheries Symposium)
Citation	Proceedings of the International Symposium on North Pacific Flatfish, 261-284
Issue Date	1995
Doc URL	https://hdl.handle.net/2115/38644
Rights	1995. Proceedings of the International Symposium on North Pacific Flatfish. Alaska Sea Grant College Program, University of Alaska Fairbanks.
Type	conference paper
File Information	takahashiII-7.pdf

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Proceedings of the International Symposium on North Pacific Flatfish
Alaska Sea Grant College Program AK-SG-95-04, 1995

Seasonal Change in Daily Ration of Brown Sole *Pleuronectes herzensteini* in the Coastal Waters of Northern Niigata Prefecture, Japan

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Abstract

Stomach contents of 2,407 brown sole *Pleuronectes herzensteini* collected from the Sea of Japan off northern Niigata Prefecture, Japan, during 1982-1985 were examined to estimate daily ration. Samples were collected throughout the 24-h day. Instantaneous evacuation rate *(R)* was estimated from the depletion of stomach contents (percent body weight) with time during the night for using Elliott and Persson's (1978) model. When the obvious feeding periodicity was not seen, R was estimated from the relationship between R and temperature *(T)* described by Durbin et al. (1983); $R = 0.043\, e^{0.115T}$. Gastric evacuation rates were used in conjunction with the field data to estimate the daily ration. Brown sole fed mainly on polychaetes through the year except April 1984. *Bregmaceros japonicus* (Pisces; Bregmacerotidae) was an important component of the diet in April 1984. Daily ration was high during the post-spawning season and highest in May (4.75% of body weight). In autumn and winter, the daily ration was low and was

lowest in February/March, just before the spawning season (0.48% of body weight). The seasonal variation of the daily ration seems to be closely related to physiological conditions. It is estimated that the annual ration was about 831.5% of body weight and about 8,870 metric tons of food were consumed by brown sole per year in this study area.

Introduction

Brown sole *Pleuronectes herzensteini* is an important commercial flatfish and one of the target species of stock enhancement studies (Aritaki and Yoseda 1994) in the coastal waters of Niigata Prefecture which is located in the northern part of Honshu Island. Brown sole inhabit the continental shelf area throughout the year (Tominaga et al. 1991). Tominaga and Nashida (1991) showed that brown sole ranked second in terms of both relative abundance (number/haul) and relative biomass (kg/haul) in experimental bottom trawl catches in this area. These results suggest that brown sole is a key member of the demersal fish community on the continental shelf.

The study of interspecific relationships for food is important in order to understand the role of brown sole in the demersal fish community. Previous studies provided a general description of the diet (Tominaga and Nashida 1991) and seasonal changes in feeding intensity expressed as stomach content index (Tominaga et al. 1991). However, the amount of food consumption was not estimated in these papers.

For better understanding of the relationship between brown sole and other demersal fishes, quantitative determination of the food is required. The quantity of food consumed by fish is commonly estimated on a daily basis. The daily ration model of Elliott and Persson (1978), which assumes an exponential gastric evacuation, is widely accepted as the most theoretically rigorous (Cochran 1979; Eggers 1979; Elliott 1979). The objective of this paper is to evaluate seasonal change in the daily food consumption of brown sole in the northern coastal waters of Niigata Prefecture. In addition, we discuss the annual food consumption of the brown sole population in this study area.

Materials and Methods

Sample collection and stomach content analysis

Six cruises were carried out in the areas where brown sole were densely distributed from May 1982 to February/March 1985 (Fig. 1),

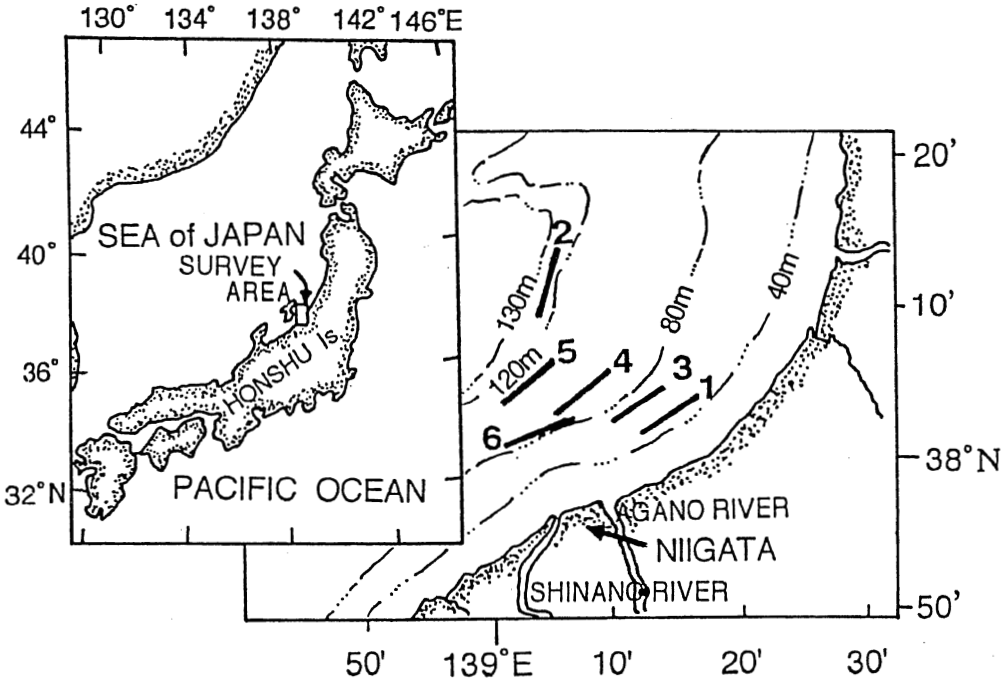

Figure 1. Map of the coastal waters of northern Niigata Prefecture showing locations of 24-hr. surveys in May 1982 (1), September 1983 (2), April 1984 (3), July 1984 (4), November 1984 (5), and February/March 1985 (6).

based on the results of the station surveys in this study area (Tominaga et al. 1991). Brown sole were caught by commercial fishing boats equipped with small otter trawls at 2-4 hour intervals over a 24-hr. period in each cruise (Table 1). Trawl nets were usually towed for an hour at speeds of about 3 knots on the bottom (Table 1). Fish were preserved in about 10% sea water formalin on board and carried to the laboratory.

Standard length of all captured brown sole were measured to the nearest millimeter and weights were taken to the nearest 0.1g. Stomachs were excised and preserved in 10% formalin for later analysis. The total stomach contents were weighed to the nearest milligram after blotting with filter paper and prey items were identified to the lowest possible taxonomic level and counted under the microscope. Wet weights of the prey items were recorded to the nearest milligram.

For diet analysis, percent frequency of occurrence (%F), percent of total number (%N), and percent of total weight (%W) of stomach contents were calculated for the entire data set for each cruise. Because of an insufficient number of specimens and similar diet

Table 1. Dates, time and number of *P. herzensteini* collected by whole-day and night surveys in the coastal waters of northern Niigata Prefecture from May 1982 to February 1985.

Date	Time of trawl tows		Number of individuals	Time interval of catches
	Start	Haul		
May 18 1982	06:04	07:02	01	2.00
May 18 1982	08:02	09:01	48	2.83
May 18 1982	10:55	11:44	49	3.17
May 18 1982	14:01	15:00	49	2.00
May 18 1982	16:02	17:00	50	1.83
May 18 1982	18:05	18:33	09	2.17
May 18 1982	20:07	21:02	31	4.00
May 19 1982	00:09	00:57	38	4.33
May 19 1982	04:23	05:11	44	1.67
May 19 1982	06:07	06:57	46	
Total			369	
Sep. 19 1983	04:02	05:02	57	1.92
Sep. 19 1983	05:59	06:50	59	1.92
Sep. 19 1983	08:03	08:42	52	2.00
Sep. 19 1983	09:59	10:42	55	2.00
Sep. 19 1983	12:03	12:45	54	2.00
Sep. 19 1983	13:59	14:43	59	4.00
Sep. 19 1983	17:59	18:43	99	2.00
Sep. 19 1983	20:00	20:41	60	2.00
Sep. 19 1983	22:00	22:42	60	2.00
Sep. 20 1983	00:00	00:43	59	2.00
Sep. 20 1983	02:00	02:43	60	
Total			674	
Apr. 7 1984	13:45	14:17	11	1.67
Apr. 7 1984	15:07	16:14	30	3.00
Apr. 7 1984	18:08	19:10	17	3.00
Apr. 7 1984	21:08	22:08	08	2.92
Apr. 8 1984	00:05	01:08	20	3.25
Apr. 8 1984	03:19	04:23	10	2.83
Apr. 8 1984	06:07	07:08	23	1.50
Total			119	

Table 1. (continued.)

Date	Time of trawl tows		Number of individuals	Time interval of catches
	Start	Haul		
Jul. 12 1984	04:05	05:05	19	2.93
Jul. 12 1984	07:00	08:03	17	3.13
Jul. 12 1984	10:08	11:11	14	2.93
Jul. 12 1984	13:05	14:05	09	1.95
Jul. 12 1984	15:12	15:52	28	2.07
Jul. 12 1984	17:06	18:07	06	2.42
Jul. 12 1984	19:30	20:33	37	2.53
Jul. 12 1984	22:01	23:06	59	3.25
Jul. 13 1984	01:05	02:22	51	2.73
Jul. 13 1984	04:01	05:04	41	
Total			281	
Nov. 29 1984	04:29	05:32	56	2.70
Nov. 29 1984	07:12	08:12	41	2.83
Nov. 29 1984	10:02	11:03	24	3.05
Nov. 29 1984	13:05	14:05	42	2.98
Nov. 29 1984	16:03	17:05	37	3.07
Nov. 29 1984	19:08	20:09	51	3.07
Nov. 29 1984	22:12	23:13	66	2.93
Nov. 30 1984	01:06	02:10	48	3.03
Nov. 30 1984	04:08	05:12	38	
Total			403	
Feb. 28 1985	04:06	05:07	81	3.03
Feb. 28 1985	07:03	08:05	79	2.95
Feb. 28 1985	10:10	10:52	94	2.87
Feb. 28 1985	13:03	13:43	31	3.07
Feb. 28 1985	16:06	16:48	38	3.02
Feb. 28 1985	19:07	19:48	59	3.07
Feb. 28 1985	22:10	22:54	60	2.90
Mar. 1 1985	01:02	01:50	60	3.25
Mar. 1 1985	04:17	05:05	62	
Total			564	

composition by fish size (Tominaga 1990), the data were not separated by predator size group for all analyses.

Daily ration

The daily ration of brown sole was estimated in terms of percent of body weight from the Elliott and Persson (1978)model:

$$C_t = \left(S_t - S_0 e^{-Rt}\right) Rt/(1-Rt); \quad (1)$$

where the consumption of food (C_t) during the time interval t_0 to t_1 from the average food amount in the stomach expressed as stomach content index (stomach content weight × 100/body weight) at time t_0 (S_0), the average stomach content index at time t_t (S_t) and the instantaneous evacuation rate (R). The estimates of C_t calculated for each time interval are then summed to give the total daily ration. Feeding is assumed constant within each time interval.

In the laboratory experiments to examine the feeding periodicity, brown sole fed on live polychaeta during hours of light but didn't feed during hours of dark (Tominaga 1990). It suggests that brown sole are day feeders. Assuming no feeding between sunset and sunrise, R was estimated from the depletion of stomach content index during the nights (including empty stomachs). Evacuation rate is therefore given by

$$S_{sr} = S_{ss} e^{-Rt'} \quad (2)$$

which, in its logarithmic form, is

$$\ln(S_{sr}) = \ln(S_{ss}) - Rt' \quad (3)$$

therefore,

$$R = (1/t')\ln(S_{ss}/S_{sr}) \quad (4)$$

where the instantaneous evacuation rate (R) is calculated from the average SCI of the sample collected shortly before or after sunset t_{ss} (S_{ss}), the average SCI shortly before or after sunrise t_{sr} (S_{sr}) and the time interval between t_{ss} and t_{sr} (t').

The clear depletion of SCI during night was not found in September, November, and February/March. R of three cruises could not be calculated from equation (4). Fortunately, Elliott (1972) found the general relationship between R and temperature (T) was exponential:

$$R = ae^{bT}. \quad (5)$$

In addition, Durbin et al. (1983) concluded that the slope *(b)* may be fairly constant for different prey types and both freshwater and marine fishes within their preferred temperature range (mean = 0.115), while the intercept *(a)* changes with prey type and can be estimated from gastric evacuation experiments. In this study, intercept was obtained from the data of the July cruise because the diet composition of brown sole collected in September, November, and February/March were similar to that in July. Bottom temperatures in the survey area were based on Naganuma and Ichihashi (1985).

Results

The stomach contents data from the sample collected at each tow were combined by cruise. The brown sole ranged in length from 92 mm to 266 mm with the majority (about 87% of the total number of specimens) between 110 mm to 190 mm BL. Fish from the May cruise were the smallest on average (mean = 129.4 mm, 95% C.I. = 1.45) and fish from the November cruise were the largest (mean = 156.6mm, 95% C.I. = 3.03). A total of 2,407 stomachs were analyzed. Of these, 963 (40.0%) stomachs were empty. The percentage of empty stomachs of brown sole collected from September, November, and February/March cruise were higher than those collected from April, May and July.

At least 39 different prey taxa were identified in the stomachs examined. Polychaetes were the most important food prey item throughout the year. Euphausiids and *Bregmaceros japonicus* (Pisces: Bregmacerotidae) were temporarily dominant by number and by weight, respectively. Bivalves also were temporally dominant numerically but considerably lower by weight.

Diet composition by season

Polychaetes were the most abundant taxa in all numeric indicators (%N, %W, %F) in July, September, November, and February/March (Table 2). Of all polychaetes, sigalionids were the most common important prey item (%N 1.8-17.5%, %W 39.4-69.0%, %F 26.4-37.2%). Sigalionids are big worms, so most of them found in the stomachs were the anterior part of body. Other important polychaetes were different by month. In July *Euchone* sp. was more abundant in terms of %N (80%) and %F (73.4%) than sigalionids. *Euchone* sp. was a small food organism (mostly 0.01 g/individual), and less by weight than sigalionids. *Nothria* sp. was the third-ranking taxon in terms of %W. In

Table 2. Prey item found in stomachs of *Pleuronectes herzensteini* collected in the northern coastal waters of Niigata Prefecture from May 1982 to February/March 1985. N% = percent by number, W% = percent by weight, F% = percent frequency of occurrence.

	February/March			April			May			July			September			November		
Prey item	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%
Polychaetes	78.6	90.0	92.3	39.6	10.7	77.2	80.7	42.7	83.1	91.5	93.7	93.7	51.5	97.8	69.1	79.9	72.2	93.9
Errantia total	39.3	72.9	64.4	5.2	7.5	53.5	8.2	19.6	41.1	8.4	57.1	73.8	19.5	76.9	49.5	26.3	58.1	48.6
Aphroditidae	0.1	0.1	0.3	0.0	0.0	0.9	1.2	0.6	8.3	0.1	0.0	1.7	0.1	0.0	0.3			
Sigalionidae	17.5	56.8	37.2	0.6	3.5	14.0				1.8	39.4	30.8	9.8	69.0	29.6	13.2	48.9	26.4
Euralia sp.	1.5	4.4	3.7	0.0	0.0	0.9	0.5	0.5	3.5	0.1	0.0	1.7	0.6	0.1	2.3			
Syllidae							0.0	0.0	0.3				0.3	0.0	1.0	0.3		0.7
Nereidae	0.3	0.1	0.6	0.0	0.1	0.0	0.0	0.0	0.3				0.1	0.0	0.3			
Nephtys sp.	9.7	0.1	19.5	1.5	0.0	24.6	1.0	0.2	9.3	1.4	0.3	25.3	3.4	0.1	11.4	0.9	0.0	2.0
Glyceridae	0.3	0.0	0.6				0.5	0.1	3.5	0.0	0.6	1.3				1.3	0.0	2.7
Goniadidae	6.3	5.4	14.2	0.1	0.4	3.5	0.8	0.1	6.1	0.6	4.2	11.8	1.5	0.7	7.5	1.6	0.2	3.4
Eunicidae							0.0	0.0	0.3				1.1	5.7	3.9	0.9	0.8	2.0
Nothria sp.	1.8	0.5	4.3	2.7	2.7	26.3	0.2	0.2	1.3	3.9	10.6	32.9	1.4	0.6	4.6	5.6	1.8	11.5
Lumbrinereidae	1.7	5.4	4.0	0.2	0.7	4.4	0.9	0.3	6.4	0.5	1.7	11.8	1.3	0.7	4.6	1.6	6.2	3.4
Other Errantia	0.1	0.0	0.3				2.9	17.7	20.1	0.0	0.3	1.3	0.1	0.0	0.3	0.9	0.2	2.0
Sedentaria total	39.0	17.0	58.2	34.4	3.2	68.4	72.3	23.0	74.8	83.0	35.8	81.9	30.9	19.2	50.2	53.6	14.1	68.2
Orbiniidae	0.8	0.2	1.9	0.0	0.0	0.9	0.0	0.0	0.3	0.0	0.0	0.4				0.9	0.3	2.0
Spionidae	10.2	0.2	22.6	0.3	0.0	4.4	2.4	0.1	11.5	0.2	0.0	4.2	3.8	0.1	11.1	2.5	0.1	4.7
Magelona sp.							0.9	0.1	3.2									
Cirratulidae	2.9	1.7	10.2	0.2	0.3	6.1				0.2	2.0	5.9	2.6	6.3	9.4	6.9	4.5	13.5
Frabelligeridae	0.1	0.2	0.3	0.0	0.0	0.9	0.1	0.0	0.6	0.0	0.1	0.8	0.3	0.9	1.0	0.9	0.2	2.0
Scalibregmidae				0.0	0.0	0.9	0.1	0.0	0.6							0.6	0.3	1.4
Opheliidae	0.8	0.1	1.9				6.9	3.8	25.2	0.3	0.1	5.9	12.3	0.7	16.9	3.4	0.3	7.4
Capitellidae	0.3	0.0	0.6				25.0	5.3	48.6	0.1	0.1	1.7	1.4	0.1	4.6	2.2	0.0	4.7
Arenicolidae	0.4	0.1	0.9				0.0	0.3	0.3				0.2	0.3	0.7			
Maldanidae	4.3	0.2	10.5	0.3	0.1	7.9	1.4	0.3	10.2	0.6	0.3	14.8	5.5	7.6	16.9	6.0	4.9	12.8

Table 2. *(continued.)*

Prey item	February/March			April			May			July			September			November		
	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%
Sedentaria (continued)																		
Pectinariidae							0.2	0.1	1.6									
Sternaspis scutata	2.4	0.1	4.3	0.1	0.0	2.6	18.2	2.7	51.1	0.2	0.1	4.6				0.3	0.0	0.7
Ampharetidae	1.7	0.1	3.7	0.4	0.1	8.8	9.8	1.1	23.6	1.0	1.6	16.9	1.9	0.2	4.9	20.7	1.7	24.3
Terebellidae	6.5	13.1	14.2	0.1	0.2	2.6	2.3	9.0	12.5	0.5	2.2	10.1				2.8	1.0	6.1
Euchone sp.	7.5	0.8	15.8	32.7	2.4	68.4	4.7	0.2	17.9	80.0	29.1	73.4	1.5	0.1	4.6	5.6	0.6	10.8
Unidentified polychaetes	0.4	0.1	0.9				0.2	0.1	1.6	0.1	0.9	2.1	1.0	1.7	3.6			
Crustacea	9.2	2.2	16.7	50.0	28.0	78.1	4.1	2.8	22.7	6.7	1.7	54.4	17.5	0.8	25.7	6.9	0.4	12.2
Gammaridea	5.5	0.1	9.3	0.7	0.0	12.3	2.8	0.1	15.7	5.1	0.9	40.1	5.3	0.1	10.1	1.9	0.0	2.7
Mysids	0.1		0.3				0.1	0.0	1.0	0.0		0.4	0.5	0.0	2.0	0.6	0.0	1.4
Maclura	1.4	1.9	3.4	0.2	0.3	5.3	0.8	2.5	5.8	0.0	0.3	0.8	2.3	0.4	7.8	1.6	0.2	3.4
Brachyura	1.7	0.2	3.4	0.3	0.0	5.3	0.1	0.1	1.0	0.4	0.5	9.7	0.6	0.1	2.3	0.3	0.2	0.7
Cumacea	0.4	0.0	0.9	0.1	0.0	0.9				1.2	0.2	21.9	8.7	0.2	10.1	1.9	0.0	4.1
Euphausia pacifica				48.6	27.6	72.8												
Other crustacea	0.1	0.0	0.3	0.1	0.0	2.6	0.3	0.1	1.9				0.1	0.0	0.3	0.6	0.0	1.4
Sipunculoidea	0.3	0.0	0.6	0.0	0.0	0.9	0.7	0.0	4.2	0.0	0.0	0.8	0.2	0.2	0.7			
Mollusca	4.9	3.2	11.5	0.4	0.2	8.8	4.1	2.5	21.7	1.2	1.5	6.8	31.9	0.6	27.7	2.2	0.1	4.1
Bivalvia	1.3	0.3	3.1				0.4	0.1	1.6	0.9	0.1	3.0	31.2	0.6	26.1	1.9	0.0	3.4
Anaspidea	3.2	0.7	7.7	0.4	0.2	8.8	3.7	2.4	20.4	0.1	1.4	3.8				0.3	0.0	0.7
Other Mollusca	0.4	2.2	0.9							0.2	0.0	0.4	0.7	0.0	1.6			
Actinaria							0.8	0.3	4.2									
Ophiuroidea	3.3	0.3	8.0	0.2	0.0	4.4	0.5	0.2	3.5	0.2	0.2	3.8	6.0	0.5	21.2	5.3	0.1	11.5

Table 2. *(continued.)* Prey item found in stomachs of *Pleuronectes herzensteini* collected in the northern coastal waters of Niigata Prefecture from May 1982 to February/March 1985. N% = percent by number, W% = percent by weight, F% = percent frequency of occurrence.

	February/March			April			May			July			September			November		
Prey item	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%
Teleosts																		
Bregmaceros japonicus	0.6	2.2	1.5	8.8	61.0	75.4	0.5	2.9	3.5				0.1	0.5	0.3			
Sardinops melanostictus	0.1	0.3	0.3				4.2	47.2	30.4									
Other Pisces	0.5	1.3	1.2							0.0	0.0	0.4						
Other food organisms	2.4	0.1	1.9	1.0	0.1	7.9	3.8	4.3	21.1	0.2	2.8	5.5	1.2	2.4	3.6	5.6	27.2	12.2
Total	782	101		2919	184		2242	94.5		6100	91.8		1100	80.9		319	73.5	
Total stomachs with food			323			114			314			237			307			148
No. of empties			241			5			55			44			367			255
Percent of empties			42.7			4.2			14.9			15.7			54.5			63.3

September sigalionids alone comprised 69% by weight of the prey in the stomach. Ophelids accounted for 12.3% of all individuals in the stomachs examined, but only 0.7% by weight. Eunicids, cirratulids, and maldanids were relatively abundant by weight. Bivalves indicates 31.9% and 27.7% in terms of %N and %F, respectively, but comprised only 0.6% of total weight. In November ampharetids were present in 24.3% of the stomachs and the percentage of unidentified food organisms was extraordinarily high by weight (27.2%). In February/March terebellids occupied a relatively large portion by weight (13.1%).

In April, frequency of occurrence of polychaetes was 77.2% but they contributed only 10.7% by weight (Table 2). *Bregmaceros japonicus* was the most abundant species by weight (61.0%), followed by *Euphausia pacifica* (27.6%). Frequency of occurrence of *B. japonicus* and *E. pacifica* were 75.4% and 72.8%, respectively. Since *B. japonicus* was collected by a standard-type Smith-McIntyre grab in our benthos research survey, it seems reasonable to suppose that they occur in or on the bottom sediment like a polychaete annelid. *E. pacifica* was also an important species and occurred in the stomachs only in April. A diurnal vertical migration of *E. pacifica* was reported by Terazaki (1981) and Ebisawa (1994). Ebisawa (1994) collected *E. pacifica* 60 cm above the bottom by sledge net during daytime. Thus, epibenthic animals were also available food organisms for brown sole.

In May polychaetes were the dominant prey taxa by percentage of total number (80.7%) and frequency of occurrence (83.1%). However, they were the second-ranking taxa by weight (42.7%). Sardine, *Sardinops melanostictus,* was the highest percentage by weight (47.2%). Sardine in the stomach was identified by the shape of the pyloric appendage. Brown sole did not feed on the whole body of the sardine but a part of the body, especially the gut. In 1981 and 1982, a large number of dead sardine were observed in the study area. If this had not occurred, polychaetes might have been the dominant prey taxa by weight.

Estimate of instantaneous evacuation rate *(R)*

The average SCIs of brown sole collected in April, May, and July were high during daytime (Fig. 2). They had a tendency to decline during the night, while the percentage of empty stomachs gradually increased after sunset (Fig. 3). The average SCI of the samples taken on the February/March, September, and November cruises were constantly low throughout the whole day and clear depletions of SCI were

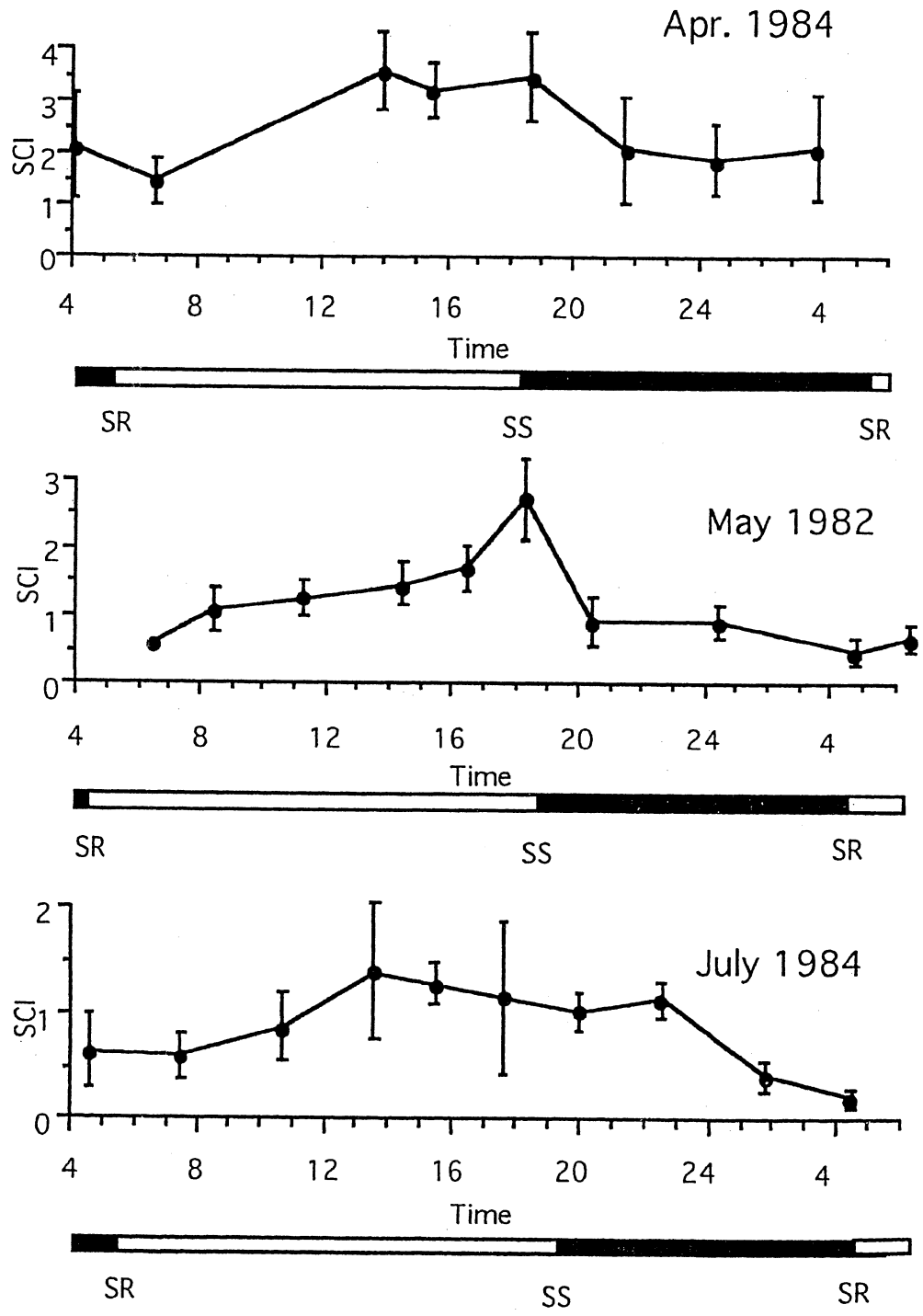

Figure 2. Diel changes in average stomach content index (SCI) of P. herzensteini in April 1984, May 1982, and July 1984. Vertical lines indicate 95% confidence interval. SR: sunrise, SS: sunset

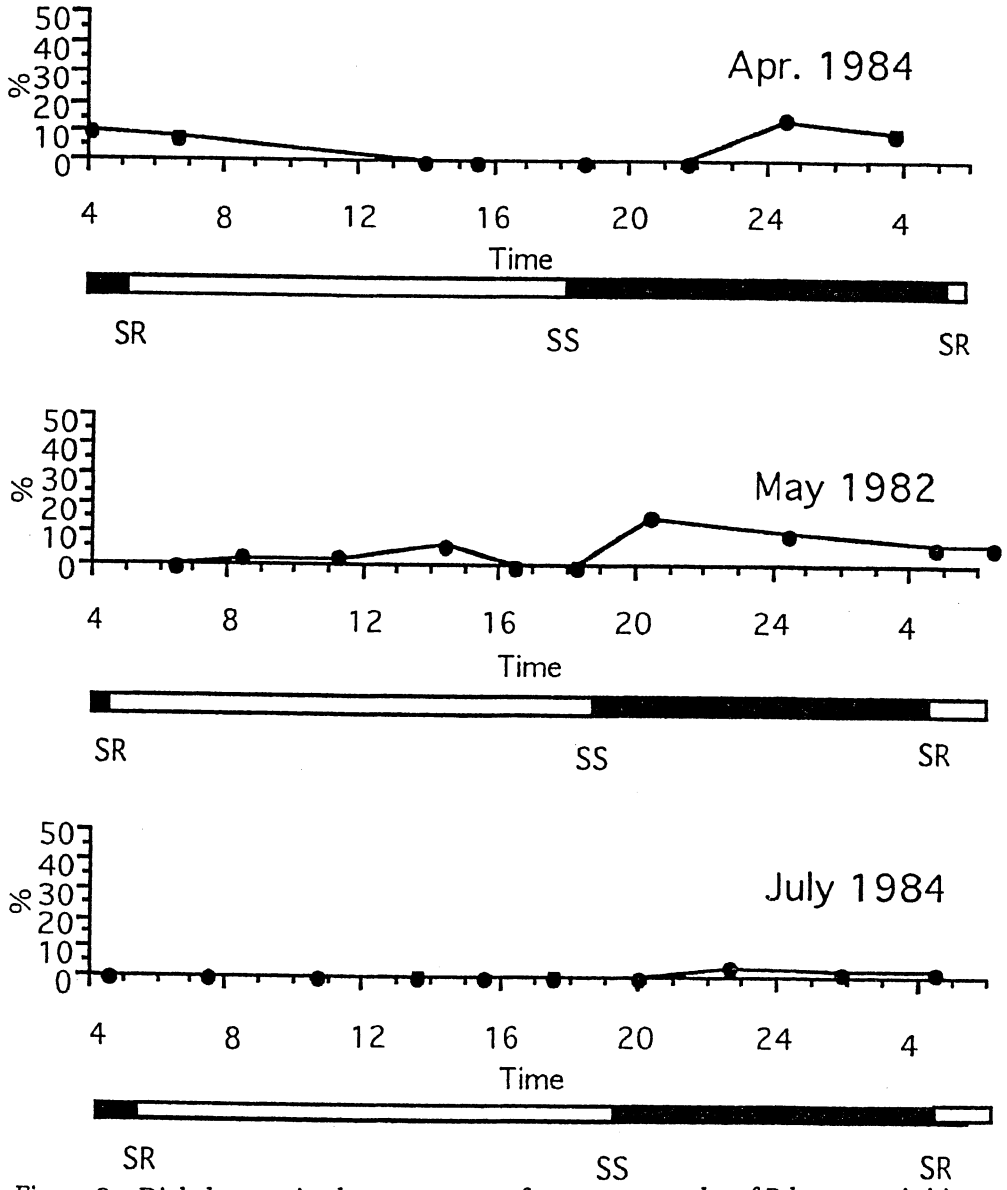

Figure 3. Diel changes in the percentage of empty stomachs of P. herzensteini in April 1984, May 1982, and July 1984. SR: sunrise, SS: sunset

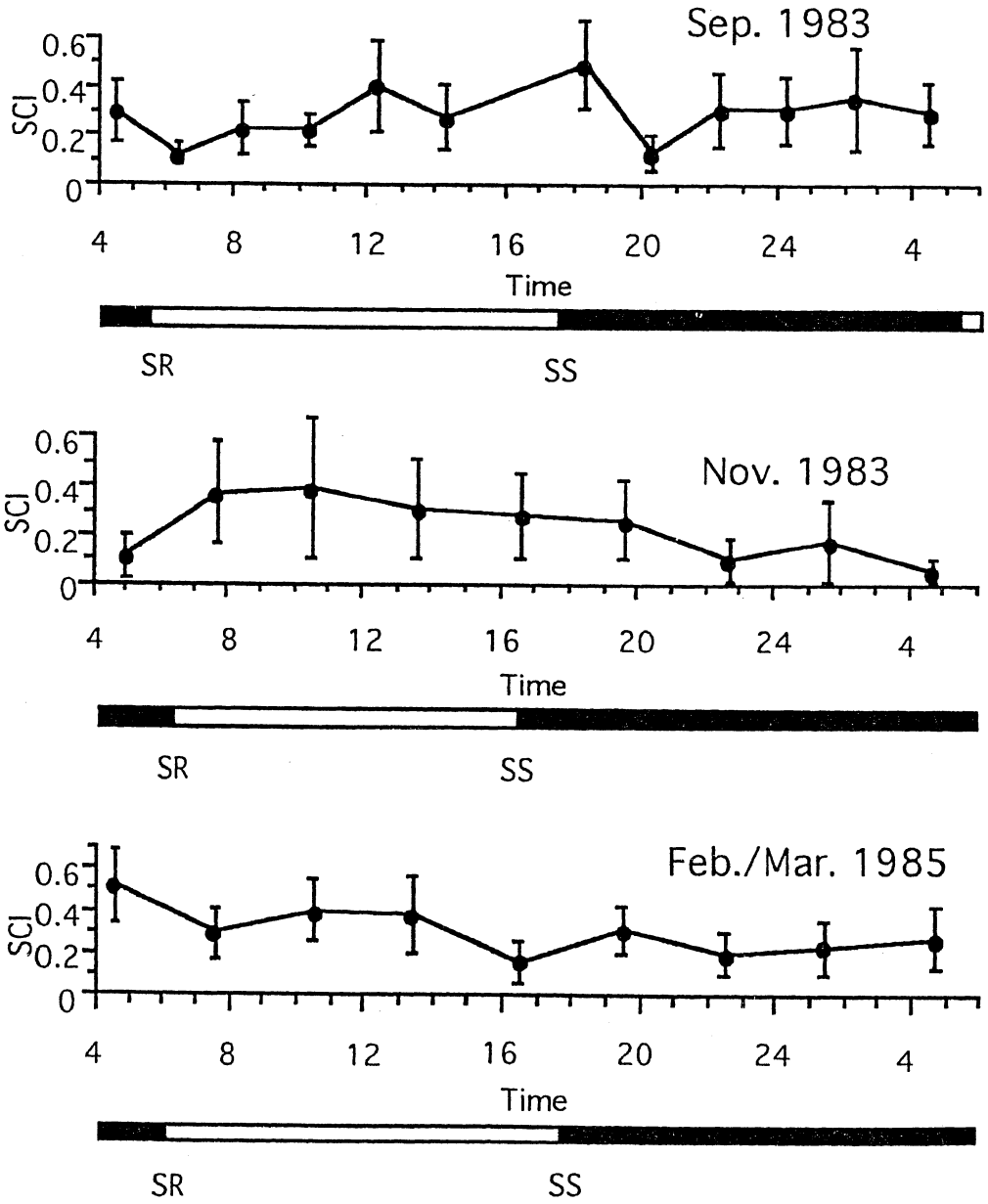

Figure 4. Diel changes in average stomach content index (SCI) of P. herzensteini in September 1983, November 1984, and February/March 1985. Vertical lines indicate 95% confidence interval. SR: sunrise, SS: sunset

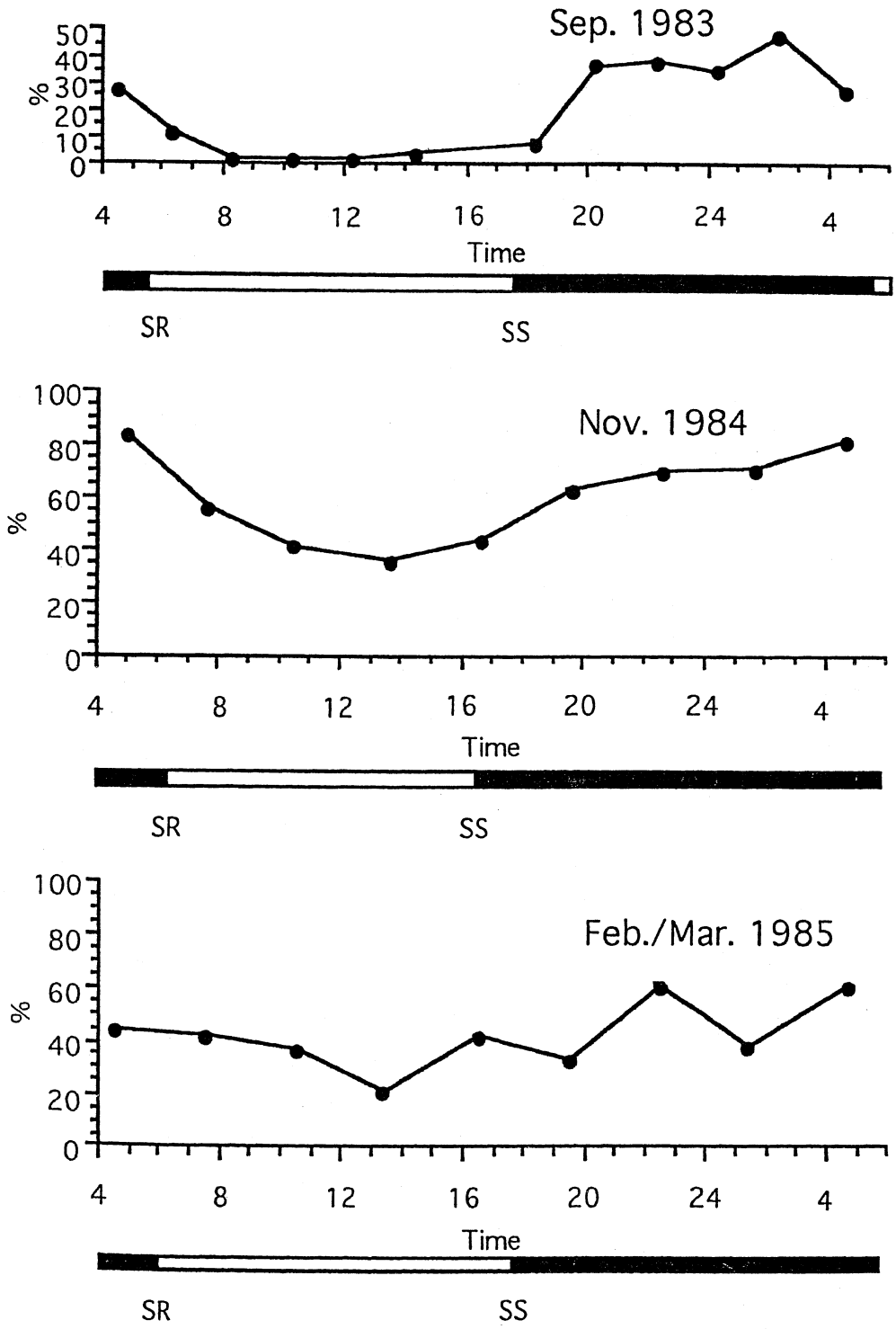

Figure 5. Diel changes in the percentage of empty stomachs of P. herzensteini in September 1983, November 1984, and February/March 1985. SR: sunrise, SS: sunset

Table 3. Instantaneous evacuation rate *(R)*, stomach content index at shortly before or after sunset *(S_{ss})*, one at shortly before or after sunrise *(S_{sr})* and time intervals between the two tows in April 1984, May 1982, and July 1984.

Month	R	S_{ss}	S_{st}	T'
April	0.073	3.49	1.45	12.0
May	0.166	2.73	0.48	10.5
July	0.192	1.04	0.22	8.5

Table 4. Instantaneous evacuation rate *(R)* calculated by $R = 0.043\, e^{0.115T}$, and water temperature *(T)* of September 1984, November 1984, and February/March 1985.

Month	R	T
September	0.242	15
November	0.242	15
February/March	0.108	08

not seen during the night (Fig. 4), although the percentage of empty stomachs gradually increased during the night (Fig. 5).

Instantaneous evacuation rate *(R)* for the samples of April, May, and July (Table 3) was estimated by using equation (4). The evacuation rate estimate of July was the highest (0.192), followed by May (0.166) and April (0.073). R for the remaining three months (Table 4) was calculated by equation (5). In the equation, slope *(b)* was approximated by 0.115 (Durbin et al. 1983). As the diet composition of brown sole collected in September, Nqvember, and February/March were similar to that in July, intercept ($a = 0.043$) was calculated with R (0.192) and bottom temperatures (13°C) in the survey area (Naganuma and Ichihashi 1985) of July. The R-temperature *(T)* relationship was described as follows:

$$R = 0.043\, e^{0.115T} \tag{6}$$

Instantaneous evacuation rates of September, November, and February/March calculated by substituting the bottom temperature at

each month into T in equation (6) were 0.242 (T = 15°C), 0.242 (T = 15°C), and 0.108 (T = 8°C), respectively.

Daily ration

The average stomach content index, which included fish with empty stomachs, was used to estimate the average food consumption for each time interval (C_t) during the day with equation (1). The estimates of food consumption per unit time (hour) were sometimes negative as well as positive (Table 5). Daily rations were obtained by summing the amount of food consumption during each interval, including negative values.

In April, May, and July, food consumption per unit time was comparably high during daytime and fluctuated considerably with some negative values (Table 5). In the other three months, food consumption per unit time was low throughout 24 hours and clear feeding periodicity was not seen.

The daily ration began to increase in April (4.43% BW), and reached peak in May (4.75% BW) (Fig. 6). It was relatively high until July and then gradually decreased. The minimum value (0.48% BW) of the daily ration was found in February/March, at the mid-spawning season. The annual ration of brown sole obtained from the area surrounded by yearly change in daily ration in Fig. 6 was 831.5% BW.

Discussion

In the present study, the Elliott and Persson (1978) model was used to determine the daily food consumption of brown sole. This model requires two assumptions: (1) the rate of food consumption is constant within the time interval between samplings, and (2) the rate of gastric evacuation (R) is exponential.

Elliott and Persson (1978) showed that even if feeding is not constant, the first assumption is satisfied by collecting samples at intervals within 3 hours. In this study, although the sampling interval was sometimes over 3 hours, this assumption was almost satisfied.

By assuming that the stomach content index exponentially decreased during nighttime, R was obtained in this study. In the previous studies, some models assumed a linear gastric evacuation (Bajkov 1935; Hunt 1960; Seaburg and Moyle 1964; Kitchell and Windell 1968; Swenson and Smith 1973; Daan 1973; Brodeur 1984), others use a square root (Jobling 1981; Brodeur 1984; Tomiyama et al. 1985), or exponential model (Aoyama 1957; Mochizuki and Ishiwata

Table 5. Estimated average amount (C_t) of food ingested and that per hour during time intervals (t) of catch in April 1984, May 1982, July 1984, September 1983, November 1984, and February/March 1985.

Time	t	C_t	C_t/t	Time	t	C_t	C_t/t
April 1984				September 1983			
03:50-06:40	2.83	-0.301	-0.106	04:30-06:25	1.92	-0.086	-0.045
06:40-14:00	7.34	3.528	0.481	06:25-08:20	1.92	0.182	0.095
14:00-15:40	1.67	0.065	0.039	08:20-10:20	2.00	0.101	0.051
15:40-18:40	3.00	0.999	0.333	10:20-12:20	2.00	0.320	0.160
18:40-21:40	3.00	-0.806	-0.269	12:20-14:20	2.00	0.029	0.015
21:40-00:35	2.92	0.256	0.088	14:20-18:20	4.00	0.581	0.145
00:35-03:50	3.25	0.685	0.211	18:20-20:20	2.00	-0.217	-0.109
Total		4.425		20:20-22:20	2.00	0.281	0.140
				22:20-0020	2.00	0.135	0.068
May 1982				00:20-02:20	2.00	0.202	0.101
06:30-08:30	2.00	0.787	0.393	02:20-04:30	2.17	0.105	0.049
08:30-11:20	2.83	0.717	0.253	Total		1.236	
11:20-14:30	3.17	0.920	0.290				
14:30-16:30	2.00	0.720	0.360	November 1984			
16:30-18:20	1.83	1.745	0.954	05:00-07:42	2.70	0.409	0.152
18:20-20:30	2.17	-1.160	-0.535	07:42-10:32	2.83	0.270	0.096
20:30-00:30	4.00	0.618	0.154	10:32-13:35	3.05	0.149	0.049
00:30-04:50	4.33	0.038	0.009	13:35-16:34	2.98	0.170	0.057
04:50-06:30	1.67	0.362	0.217	16:34-19:38	3.07	0.167	0.055
Total		4.746		19:38-22:42	3.07	-0.046	-0.015
				22:42-01:38	2.93	0.168	0.057
July 1984				01:38-04:40	3.03	-0.048	-0.016
04:35-07:31	2.93	0.286	0.098	Total		1.241	
07:31-10:39	3.13	0.696	0.222				
10:39-13:35	2.93	1.147	0.391	February/March 1985			
13:35-15:32	1.95	0.363	0.186	04:36-07:34	3.03	-0.096	-0.032
15:32-17:36	2.07	0.318	0.154	07:34-10:31	2.95	0.206	0.070
17:36-20:01	2.42	0.352	0.145	10:31-13:23	2.87	0.098	0.034
20:01-22:33	2.53	0.601	0.237	13:23-16:27	3.07	-0.138	-0.045
22:33-01:48	3.25	-0.289	-0.089	16:27-19:28	3.02	0.225	0.075
01:48-04:32	2.73	-0.040	-0.015	19:28-22:32	3.07	-0.034	-0.011
Total		3.434		22:32-01:26	2.90	0.089	0.031
				01:26-04:41	3.25	0.129	0.040
				Total		0.480	

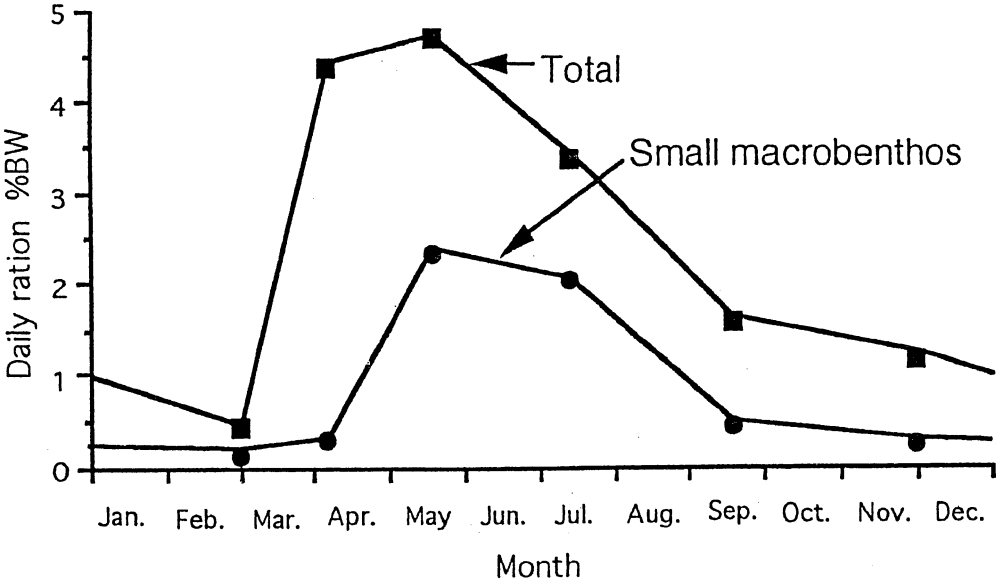

Figure 6. Seasonal change in daily ration (% of wet body weight) of P. herzensteini (solid square and solid line) and daily amount of small macrobenthos consumed by P. herzensteini (solid circle and solid line) in the coastal waters of northern Niigata Prefecture.

1970; Tyler 1970; Elliott 1972; Kiorboe 1978; Ishiwata 1978; Lane et al. 1979; Koshiishi 1980; Macdonald et al. 1982; Huebner and Langton 1982; Brodeur 1984; Tomiyama et al. 1985; Nashida and Tominaga 1987). Of these three models, when the gastric evacuation rate is small enough, a square root model and an exponential model closely resemble each other (Tomiyama et al. 1985). Therefore, gastric evacuation models were classified into two types of models except for fish with large R value, like larvae or juveniles.

Persson (1986) reanalyzed several studies on food evacuation of fishes in his review and concluded the exponential model is generally the most appropriate. Although Jobling (1981) concluded that the majority of gastric evacuation studies showed that the application of the square root model in general provided the better fit to the data, his later study (Jobling 1986) showed that the exponential evacuation model generally gave a better description of the rate of food evacuation, when fish were fed on relatively small and easily digestible low-energy prey. Exponential models have been applied to the gastric evacuation rate of pleuronectiformes fishes (Kiorboe 1978; Huebner and Langton 1982; Macdonald et al. 1982; Nashida and Tominaga 1985). In the present paper, although the instantaneous evacuation

rate was estimated by assuming that the stomach content index decreased exponentially, the prey items of brown sole were small and easily digestible and application of the exponential model was thought to be reasonable.

The instantaneous evacuation rate *(R)* is calculated by equation (4). When the exponential model is applied to the gastric evacuation rate, stomach content weight decreases rapidly during the first few hours and afterward it gradually diminished. Therefore, the stomach content index of brown sole collected during the first few hours after sunset varied widely. This variation of SCI decreased with time during the night. This is the reason why we used the S_{ss} and S_{sr} to estimate R.

The daily ration increased from mid-spawning season and peaked (4.75% BW) in May. Then it decreased gradually to the lowest value (0.48% BW) in February/March. Tominaga et al. (1991) showed the period May to July to be an active feeding season and that of August to December to be an inactive one. The present study supports the results of seasonal variation of feeding intensity by Tominaga et al. (1991).

In the laboratory study of the temperature-daily ration relationship of brown sole (Takahashi et al. 1987), at temperatures below 18-19°C, the daily ration (% wet body weight/day) increased with increasing temperature and began to decrease remarkably at about 19°C. The highest daily ration (6.8-11.4% BW) of brown sole was seen at temperatures of 17.8-19.0°C and the brown sole cease to feed at temperatures below 0.7°C. The daily rations in the laboratory were 6.0 to 7.2% BW at temperatures (10-13°C) of the active feeding season in the study area, and were relatively high compared with daily ration estimates in the field. The reason for this seemed to be due to more abundant and bigger food items in the laboratory.

The temperatures of the study area in the inactive feeding season were from 13-17.5°C. Even at 13°C, the daily ration in the laboratory was approximately over four times (7.2% BW) as much as that estimated in the field during this season. This suggests that physiological conditions affect the feeding intensity of brown sole as Takahashi et al. (1982) and Tominaga et al. (1991) stated.

The annual ration of brown sole was estimated to be 831.5% BW. For the brown sole in the coastal waters of Niigata Prefecture, a biomass of 1,482.5 metric tons and an abundance of 82,624,000 were calculated by cohort analysis (Niigata Prefectural Fisheries Experimental Station 1987). Estimated population biomass of brown sole in this study area was about 1,067 metric tons on the basis of the ratio of commercial catch amount in this study area to the total amount of

commercial catch in Niigata Prefecture. Therefore, it was estimated that brown sole consumed about 8,872 metric tons of animals distributed in this study area annually.

Brown sole fed exclusively on polychaetes except for spring. In spring, polychaetes were not the most dominant in their stomachs but still important food items. Hayashi (1988) showed that polychaetes were the most abundant and the largest biomass of the small macrobenthos community (less than 1 g in wet weight but larger than 1 mm in size) in this study area. Hayashi (1987) estimated that the annual production of small macrobenthos in this study area was about 40,000 metric tons. Judging from the observation that brown sole feed only during daylight in the laboratory (Tominaga 1990), they must use vision in their search for food. Brown sole easily search for and eat polychaetes which have head and/or feeding appendages, or they move on the bottom but can't feed on polychaetes inhabiting the deep layer of bottom sediment. Hayashi (1987) also estimated the production of small macrobenthos in 0-2 cm of bottom sediment to be about 15,000 metric tons. It seems reasonable to suppose that the amount of available small macrobenthos is about 15,000 metric tons.

The annual amount of small macrobenthos consumed by brown sole is estimated to be about 416% BW (Fig. 6) on the basis of wet weight percent in the stomachs, and it is calculated that brown sole consume about 4,440 metric tons of small macrobenthos. This value is equivalent to about 30% of the annual production of available small macrobenthos. In addition to small macrobenthos, brown sole cut and eat parts of Sigalionids which are larger than 1 g in wet weight. Moreover, they took euphausids, small fish, *B. japonicus,* and/or dead sardine in their active feeding season. Therefore, food availability for brown sole is thought to be sufficiently high.

There is no abundant fish that feeds mainly on polychaetes in this study area, except for brown sole (Tominaga and Nashida 1991). This is advantageous to brown sole. Brown sole consumed about 80% of the annual ration from April to September. They feed on various food organisms besides polychaetes and were distributed widely during this period (Tominaga et al. 1991). This might reduce intraspecific competition for food.

In the present study, the annual ration was estimated from the daily rations of different years. Therefore, it was at best only an approximation. By conducting both field experiments throughout the year and laboratory experiments, we might get better estimates of the annual ration of brown sole.

Acknowledgments

We wish to thank Mr. H. Kitazawa and Mr. S. Miyazaki, captains of the fishing boats, for their assistance in collecting materials.

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