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Food Habits and Ecological Interactions of Alaska Plaice, *Pleuronectes quadrituberculatus*, with Other Flatfish Species in the Eastern Bering Sea

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Food habits of Alaska plaice, *Pleuronectes quadrituberculatus*, and ecological interactions of this species with yellowfin sole, *Limanda aspera*, and rock sole, *Lepidopsetta bilineata*, in the eastern Bering Sea were studied. Alaska plaice mainly feed on polychaetes regardless of sex and size of fish. However, it was shown that food differed by sampling area. Feeding did not occur at night. Food competition seems to be negligible among the three shallow water flatfish species inhabiting the eastern Bering Sea due to differences in food spectra or spatial distribution.

Introduction

Alaska plaice, *Pleuronectes quadrituberculatus*, is a righteyed flounder of the family Pleuronectidae. It is the only member of the genus in the North Pacific Ocean. Alaska plaice range from the Gulf of Alaska to the Bering and Chukchi Seas and south in Asian waters to the Sea of Japan, including the Okhotsk Sea to as far south as Peter the Great Bay (Pertseva-Ostromova, 1961). They occur most commonly on the continental shelf of the eastern Bering Sea from depths less than 150*m* (Zhang, 1987). Alaska plaice are frequently encountered with yellowfin sole, and both species show a similar distribution in the eastern Bering Sea (Fadeev, 1965 ; Weber and Shippen, 1975 ; Bakkala et al., 1985).

Feeding is one of the most important functions of an animal. The basic functions of a fish-its growth, development, reproduction—all take place-at-the expense of the energy which enters the organism in the form of its food (Nikolsky, 1963).

Food habits of Alaska plaice in the eastern Bering Sea have been studied by some researchers. Moiseev (1953) reported that the main diet of Alaska plaice was echinoderms in spring and mollusks in summer. Skalkin (1963) found that major food items were benthic crustaceans, mollusks and polychaetes. Mineva (1964) also found bivalves, gastropods, polychaetes, amphipods and ophiuroide in the stomachs of Alaska plaice. According to Feder (1977, 1978), polychaetes, bivalves, amphipods and nemerteans were eaten by Alaska plaice in the Bering Sea. Recently, Allen (1984 a, 1984b) studied the food habits of Alaska plaice and classified the food items according to behavior of prey. Skalkin (1963) and Allen (1984a) also studied trophic interactions among Alaska plaice, yellowfin sole and rock sole which have a similar habitat.

The purpose of this study is to analyze stomach samples of Alaska plaice to describe food habits more thoroughly and to compare them with those of yellowfin sole and rock sole more quantitatively than previously.

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Materials and Methods

Specimens were collected in autumn 1982 and summer 1984 in the eastern Bering Sea aboard the *Miller Freeman*, a research vessel participating in the annual resource assessment survey conducted by the Resource Assessment and Conservation Engineering (RACE) Division of the NWAFC in Seattle, WA. U.S.A. Stomachs of Alaska plaice were taken from half-hour tows of an 83-112 Eastern otter trawl.

The samples were collected from standard resource assessment stations off Bristol Bay and in the vicinity of and southeast of the Pribilof Islands at bottom depths ranging from 24 to 27*m* (Fig. 1, Table 1). The stomach samples were taken from 99 Alaska plaice ranging in length from 22 to 48*cm*. Of 79 fish sexed, 37 were males and 42 females.

Specimens were divided into two size groups for data analysis : <30*cm* and $\geq$30*cm*, because the size at maturity was estimated at around 30*cm* in length (Zhang, 1987). Percent frequency of occurrence (%FO), percent of total stomach content weight (%W), percent of total stomach number (%N), and the index of relative importance (IRI = %FO(%N + %W)) (Pinkas et al., 1971) were calculated for major categories of food items by size group and sex and by sampling area.

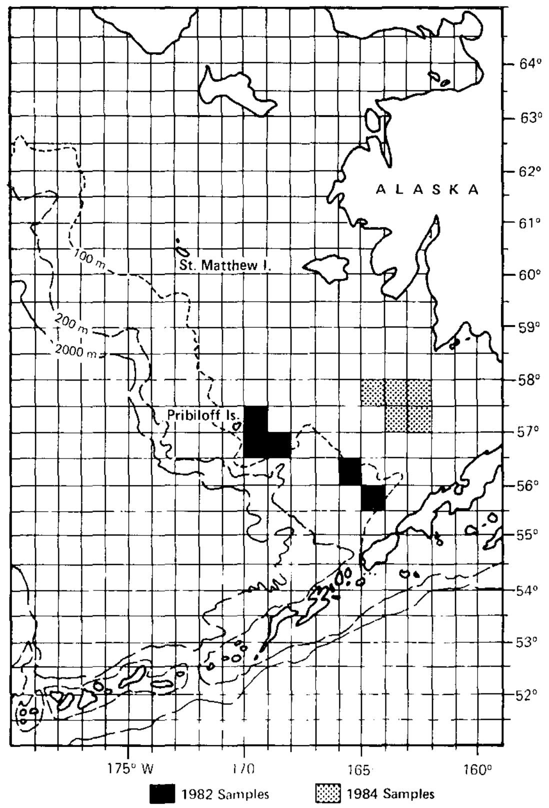

Fig. 1. Sampling locations for Alaska plaice stomachs collected in 1982 and 1984 in the eastern Bering Sea. Numbers in parentheses denote the number of stomachs collected.

Stomachs sampled were graded for fullness using a scale from 1 to 6 with 1 representing empty stomachs and 6 representing full stomachs. In order to define the time of active feeding, the fullness data were examined by four time periods : 2100 to 0000, 0300 to 0600, 0900 to 1200, and 1500 to 1800. An analysis of variance (ANOVA) was conducted for the null hypothesis that stomach fullness was the same in the 4 different time periods. If the hypothesis was rejected, the Tukey multiple comparison test (Zar, 1984) was carried out to determine which time period differed from the others.

Shannon-Wiener's diversity index (H′) was also calculated as

$$H' = -\sum_{i=1}^{s}(n_i/N)\ln(n_i/N)$$

where s = the total number of prey species ;

n_i = the number of indiciduals of the ith prey species ;

N = the total number of individuals.

In general, as the number of prey species increases so does the diversity index. But the index will also increase as the proportion of individuals per prey species becomes more constant. Thus, the diversity index measures two thing : prey species evenness and prey species richness. One cannot be sure which of these factors has caused any change in diversity (Gray, 1981). Prey evenness can be separated from the index by dividing the observed diversity value by the maximum possible value which would be obtained if each individual belonged to a different species. Thus, evenness (J′) was calculated as

$$J' = H'/H'(max)$$

where H′ = the Shannon-Wiener's diversity index and H′(max) = ln(s). Prey richness was also examined by the Margalef's index of species richness calculated as follows :

$$d' = (s-1)/\ln(N).$$

In the study of dietary overlap between species of

Table 1. Sampling location information and number of Alaska plaice stomachs collected at each station in the eastern Bering Sea during autumn 1982 and summer 1984

Haul	Date	Time	Depth (*m*)	Bottom temp(°C)	Latitude (°N)	Longitude (°W)	No. * stomach
Autumn 1982							
21	09/29	0300	50	4.3	55 59.48	164 34.30	1(0)
23	09/29	2100	47	2.7	56 19.96	165 11.94	3(0)
24	09/30	0100	50	3.9	55 20.46	165 47.38	3(0)
27	09/30	2100	57	3.9	56 40.07	168 15.62	3(1)
29	10/01	0300	54	4.2	56 40.60	168 54.93	3(0)
30	10/01	0600	42	5.8	56 42.18	169 31.63	1(1)
31	10/01	2200	32	6.3	57 00.60	169 33.32	1(1)
Subtotal							15(3)
Summer 1984							
69	09/03	1200	25	7.6	57 44.01	162 15.40	3(0)
70	09/03	1500	27	5.8	57 35.59	162 24.04	3(0)
71	09/03	1800	27	5.1	57 27.35	162 30.24	3(1)
72	09/03	2100	28	4.5	57 19.78	162 39.69	3(0)
73	09/04	2400	32	3.1	57 10.46	162 49.62	3(1)
74	09/04	0300	31	2.9	57 14.35	163 05.35	3(1)
75	09/04	0600	26	4.1	57 23.64	162 56.96	3(0)
76	09/04	0900	27	5.2	57 31.10	162 49.22	3(0)
77	09/04	1200	24	6.7	57 39.14	162 37.04	3(0)
78	09/04	1500	24	7.6	57 49.04	162 28.85	3(0)
79	09/04	1800	24	7.4	57 53.31	162 43.33	3(0)
80	09/04	2100	25	5.5	57 44.27	162 54.20	3(1)
81	09/04	2400	27	5.6	57 36.35	163 04.18	3(0)
82	09/05	0300	29	4.5	57 29.74	163 10.01	3(0)
83	09/05	0600	31	2.8	57 18.74	163 20.69	3(2)
84	09/05	0900	31	2.6	57 23.06	163 37.53	3(0)
85	09/05	1200	27	4.4	57 32.01	163 30.14	3(0)
87	09/05	1800	25	6.6	57 49.56	163 11.63	3(1)
88	09/05	2100	24	7.5	57 56.46	163 03.17	3(0)
89	09/05	2400	24	8.0	58 01.62	163 21.00	3(0)
90	09/06	0300	26	6.6	57 54.37	163 28.95	3(0)
91	09/06	0600	27	5.4	57 45.90	163 35.88	3(2)
92	09/06	0900	28	3.6	57 36.42	163 45.88	3(0)
93	09/06	1200	30	2.2	57 27.23	163 53.79	3(0)
94	09/06	1500	30	2.3	57 31.95	163 09.12	3(0)
95	09/06	1800	29	3.6	57 40.26	163 59.50	3(0)
96	09/06	2100	27	5.7	57 49.64	163 53.29	3(0)
97	09/06	2400	26	8.2	57 58.88	163 45.84	3(0)
Subtotal							84(9)
Total							99(12)

* Numbers of empty stomachs are given in parentheses.

the three flatfish, Schoener's (1970) index was chosen because it was found to measure overlap accurately over most of the range of potential overlap (Cailliet and Barry, 1979 ; Linton et al., 1981). Schoener's index (C(x,y)) is calculated as

$$C(x,y) = 1.0 - (\sum | P(x,i) - P(y,i) |)/2$$

where P (x,i) and P (y,i) are the estimated proportions by weight of prey i in the diets of species x and y, respectively. The index ranges from 0 which indicates no dietary overlap to a maximum overlap of 1 when all prey items are found in equal proportions.

Results

Of the 99 Alska plaice stomachs sampled 12 (12%) were empty. All the empty stomachs were collected from 1800 to 0600 and five of these were collected at 0600 (Table 1). Stomach fullness was highest in the 1500~1800 collections with a mean index of 4.333 and lowest during 0300~0600 with a mean index of 2.913 (Table 2). The ANOVA to test if feeding was the same in the four time periods showed that the hypothesis was rejected at $\alpha=0.01$ ($0.005<P<0.01$) (Table 3). The tukey multiple comparison test showed that feeding was significantly lower during 0300~0600 than during the other time periods. Feeding did not differ significantly among the other three time periods (Table 3).

A total of 26 prey species representing 9 phyla were found in the 87 stomachs of Alaska plaice containing food (Table 4). In general, the pattern of food consumption was very similar for the two size groups of Alaska plaice. Polychaetes were the most important prey (75.2% for fish≥30*cm* and 63.3% for fish <30 *cm*). Of these Nephtyidae was the dominant polychaete consumed. Other important items were unidentified polychaetes, and polychaetes other than Nephtyidae (36.3%), amphipods (6.7%) and echiurids (5.7%) for the≥30*cm* group and sipunculid (21.7%), unidentified polychaetes and polychaetes other than Nephtyidae (15.2%), and amphipods (11.6%) for the <30 *cm* group. Prey fish were found in the stomachs of only the ≥30*cm* group with extremely small amounts. Miscellaneous food items included Echinodermata, Protozoa, and Coelenterata.

The Shannon-Wiener index indicates that diversity and evenness of diets was similar between sexes, somewhat different between size groups, and very different between sampling areas (Table 5). However, the index of richness was quite different both between size groups and between sampling areas.

Prey importance by size group, sex and sampling area is shown in Figure 2 based on the index of relative importance (IRI). The combined sample shows that polychaetes were the most important prey in terms of weight and amphipods in terms of number. The overlap in diets between size groups and sexes

Table 2. Stomach fullness of Alaska plaice by time period

Time period	Mean	SD	Sample size
2100 to 0000	4.167	1.704	30
0300 to 0600	2.913	1.443	23
0900 to 1200	4.143	1.315	21
1500 to 1800	4.333	1.713	21

Stomach fullness was categorized as : 1(empty), 2(trace of prey organisms), 3(25% full), 4(50% full), 5(75% full), and 6(100% full)

Table 3. Results of ANOVA to test for diurnal differences in stomach fullness and the Tukey multiple comparison test (Zar 1984) to determine the differences in stomach fullness by time period

ANOVA test

Ho : u1=u2=u3=u4

SOURCE	DF	SS	MS	F
FACTOR	3	29.72	9.91	4.04
ERROR	91	223.23	2.45	
TOTAL	94	252.95		

$F(3,91,0.05)=2.71$, $F(3,91,0.01)=4.01$

Conclusion : significant at $\alpha=0.01$ ($0.005<p<0.01$)

Tukey test

K=4, MS error=2.45, DF error=91, q(91, 4, 0.05)=3.70,

2.913	4.143	4.167	4.333

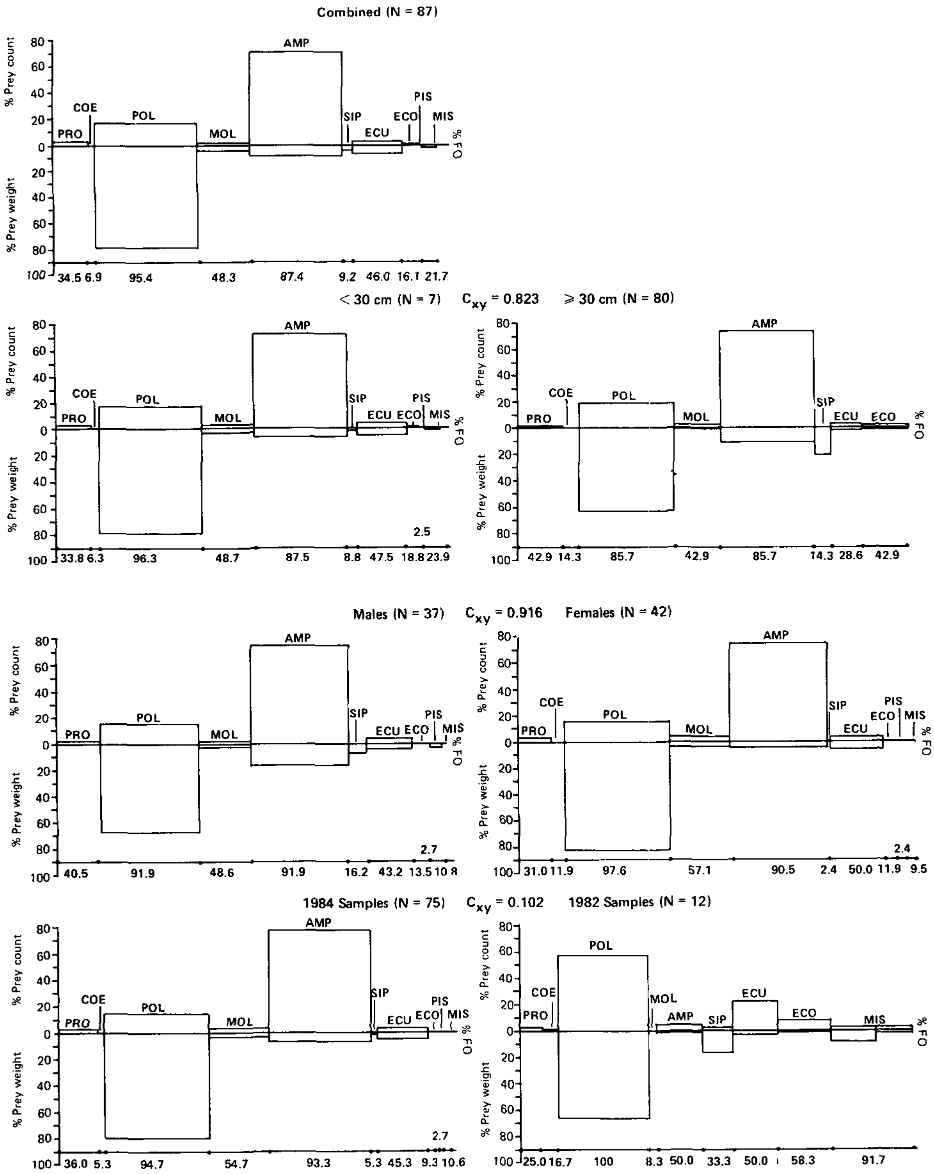

Fig. 2. Indices of relative importance of major prey items in the diets of Alaska plaice by size group, sex and sampling area in the eastern Bering Sea. (C(x,y), Schoener's index of diet overlap ; %FO, percent frequency of occurrence ; %N, percentage of prey number ; %W, percentage of total stomach content weight ; PRO, Protozoa ; COE, Coelenterata ; POL, Polychaeta ; MOL, Mollusca ; AMP, Amphipoda ; SIP, Sipuncula ; ECU, Echiura ; ECO, Echinodermata ; PIS, Pisces ; MIS, miscellaneous).

based on Schoener's overlap index was high (C(x,y)= 0.823 and 0.916, respectively).

The compositions of prey species in the two sampling areas were quite different, however (Fig. 2). In the 1982 samples, from southeast of the Pribilof Islands there was only one dominant prey (polychaetes), both in terms of numbers (greater than 50%) but also in terms of weight (greater than 60%). On the other

Table 4. Percentages by weight of prey items in the stomachs of two size groups of Alaska plaice collected in the eastern Bering Sea in autumn 1982 and summer 1984

	Predator size group (*cm*)	
Prey item	< 30	≥ 30
Protozoa	0.06	0.11
Coelenterata	0.01	0.03
Annelida		
Polychaeta	63.32	75.23
Nephtyidae	48.10	38.96
Polynoidae	6.57	2.08
Maldanidae	1.52	4.64
Others	7.13	29.55
Others	0.00	4.04
Mollusca		
Gastropoda (Snails)	0.88	0.98
Bivalvia (Clams)	0.02	2.63
Others	0.02	0.08
Arthropoda		
Amphipoda	11.61	6.65
Others	0.02	0.08
Sipuncula	21.74	2.66
Echiura	1.27	5.74
Echinodermata	1.08	0.25
Vertebrata		
Pisces	0.00	0.02
Others	0.00	1.54

Table 5. Results of the Shannon-Wiener index of diversity for Alaska plaice diets in the eastern Bering Sea (H′ represents diversity, J′ evenness, and d′ richness)

Sex, size group and area of samples	H′	J′	d′
Combined samples	0.735	0.375	24.875
Males	0.672	0.394	15.095
Females	0.631	0.373	14.580
‹30 *cm*	0.560	0.411	8.487
≥ 30 *cm*	0.739	0.379	24.615
Pribiloff Is.	1.432	0.823	22.284
Bristol Bay	0.602	0.349	14.487

Table 6. Results of Schoener's index (C(x,y) of diet overlap (Schoener, 1970) between Alaska plaice, yellowfin sole and rock sole of the eastern Bering Sea

	Alaska plaice	Yellowfin sole	Rock sole
By the lowest possible taxonomic level			
Alaska plaice	–	0.127	0.299
Yellowfin sole		–	0.154
Rock sole			–
By the phylum level			
Alaska plaice	–	0.313	0.787
Yellowfin sole		–	0.517
Rock sole			–

Values were calculated for the lowest possible prey taxonomic level and at the phylum level in Table 4.

hand, two prey items were dominant in the 1984 samples from outer Bristol Bay. They were polychaetes in terms of weight (about 80%) and amphipods in terms of numbers(greater than 70%). The Schoener's overlap index was very low (C(x,y)=0.102) for samples from these two areas.

In order to examine diet overlap among Alaska plaice, yellowfin sole and rock sole, which are considered shallow water flatfish, 1982 samples for the three species were used for the analyses because they were collected from the same time period and area (see Fig. 1).

Schoener's (1970) index of dietary overlap was also used to compare the similarity of diets between Alaska plaice, yellowfin sole, and rock sole for two taxonomic levels of prey. One for the lowest possible taxonomic level and the other for the phylum level (Table 6). The values indicated that diet overlap between the three species was less than 0.3 for the lowest possible taxonomic level, but as high as 0.8 at the phylum level.

Figure 3 shows prey importance of these three species of shallow water flatfish in the eastern Bering Sea. Schoener's index of diet overlap was the highest between Alaska plaice and rock sole ; it was only C (x,y)=0.299 at the lowest possible taxonomic level but was relatively high (C(x,y)=0.787) at the phylum

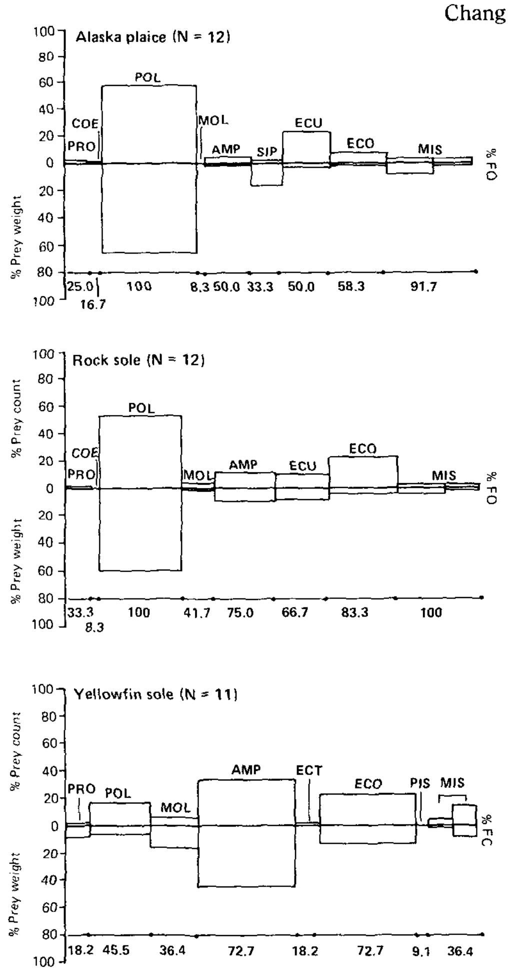

Fig. 3. Indices of relative importance of major prey items in the diets of Alaska plaice, yellowfin sole and rock sole in the eastern Bering Sea. (%FO, percent frequency of occurrence ; %N, percentage of prey number ; %W, percentage of total stomach content weight ; PRO ; Protozoa ; COE, Coelenterata ; POL, Polychaeta ; MOL, Mollusca ; AMP, Amphipoda ; SIP, Sipuncula ; ECU, Echiura ; ECO, Echinodermata ; PIS, Pisces ; MIS, Miscellaneous).

level. The most important common prey of the two species was polychaetes. However, the second most important prey was Echiura for Alaska plaice, while for rock sole amphipods, Echiura and Echinodermata were equally important as the second most abundant prey. The diet of yellowfin sole was quite different from these other two species. The most important prey of yellowfin sole was amphipods while Echinodermata was the second most important prey item.

Discussion

The diet of fishes is related to their digestive morphology and mouth structure. Their sensory organs are adapted to seek out food, their buccal cavity to seize preys and their intestine to digest it. Fishes have evolved organs to seek out food according to the characteristics of their feeding behavior (Nikolsky, 1963). For example, Stickney et al. (1974) found that the size of the mouth relative to body length was correlated with the size of food organisms in bothid flounders of Georgia coastal waters of the United States. Symmetry of the jaws also plays a important role in the mode of feeding. Species with symmetrical jaws generally take free-swimming food, while those with asymmetrical jaws are mainly bottom feeders (Yazdani, 1969). Flatfishes that feed on polychaetes and mollusks typically have smaller stomachs, larger intestines, and smaller gill rakers with fewer teeth than flatfishes that feed on other species (DeGroot, 1971 ; Tyler, 1973). The mouth of Alaska plaice is small, the jaws and dentition are better developed on the blind side (i.e., asymmetrical). These morphological adaptations correlate with the preponderance of benthic invertebrates in their diets.

Stomach fullness was lowest after midnight (0300 to 0600) (Table 2), suggesting that feeding does not occur at night. Stomach fullness was greatest in the afternoon (1500 to 1800) and thus feeding seems to be active during daytime.

The main food items of Alaska plaice were obviously polychates and amphipods in this study, regardless of sex and size. However, it was shown that food differed by area (Tables 4 and 5, Fig. 2).

Skalkin (1963) found that major food items of Alaska plaice were benthic crustaceans, mollusks, and polychaetes. All three major food types were not usually found in stomach contents at any one time. Rather, the diet often consisted of polychaetes and mollusks or only one of the three groups. No single polychaete species dominated by weight or incidence. Three species of mollusks were important in the diet ; *Serripes groenlandicus* in shallow water of the southeastern Bering Sea and *Yoldia hyperborea* and *Y. johanni* at depths near 50*m*. A fourth species, *Gomphina fluctuosa*, appeared with the other three species in shallower waters.

Mineva (1964) examined 190 stomachs of Alaska plaice in the eastern Bering Sea and found bivalves such as *Yoldia hyperborea, Y. johanni*, and *Macoma calcarea*, gastropods such as *Cylichna alba*, polychaetes such as *Sternaspia scutata*, and *Scalibregma* sp., Nephtyidae, Terebellidae, amphipods, and ophiuroids to be important. Polychaetes, bivalves, amphipods, and nemerteans were eaten by Alaska plaice in other Bering Sea studies (Feder, 1977 ; 1978).

Differences in food habits of Alaska plaice by fish size and sex were not substantial in the present study. Skalkin (1963) and Mineva (1964) also showed that adult Alaska plaice appeared to consume the same food items regardless of size of plaice. However, diet may not remain constant but vary seasonally, by life history stage and with changes in the composition and availability of the food organisms.

Moiseev (1953) found the diet to vary seasonally with echinoderms being important in spring and mollusks and polychaetes during summer. According to Moiseev (1953) and Mineva (1964), Alaska plaice eat little and may hibernate in the winter. Intensive post-spawning feeding has been observed in June and July (Skalkin, 1963). Seasonal variations in the diet may reflect seasonal bathymetric migrations during which they encounter different dominant fauna. The present study also reflected differences in diet by sampling area.

Skalkin (1963) stated that the degree of food similarity between Alaska plaice and yellowfin sole caught in the same trawl was more than 50%. Polychaetes were especially evident in both species. However, it is difficult to identify species of polychaetes because they are partly digested in fish stomachs and it is unknown whether the same species of polychaete was consumed by Alaska plaice and yellowfin sole in Skalkin's (1963) study. Skalkin also found an unusually high degree of food similarity between Alaska plaice and rock sole involving polychaetes. He thought this to be a rare occurrence, however, since he believed rock sole prefer polychaetes and Alaska plaice usually consume mainly molluskas. Differences between studies may be due to small samples and lack of sampling over broad areas and time periods.

Allen (1984b) has hypothesized that ecological segregation among species of fish resulted from differences in foraging behavior and spatial distribution. He believed that competitive species have the same spatial distribution (habitat) and foraging behavior (niche), while non-competitive species have either different feeding behavior or spatial distribution. My findings for the three flatfish species studied would tend to support this hypothesis. Schoener's index of diet overlap was highest between Alaska plaice and rock sole whick have the most dissimilar distribution and lowest for Alaska plaice and yellowfin sole which have the most similar distribution.

Allen (1984a) stated that even though Alaska plaice, yellowfin sole, and rock sole have similar habitats, they have differences in shapes of their mouths which results in different foraging behavior. Alaska plaice have only a few teeth on the anterior portion of the jaws on the eyed side, whereas the jaws of the other species are more completely toothed. Alaska plaice and rock sole both have a more pointed snout and a head that is indented at the level of the upper eye, giving them a better downward field of vision than yellowfin sole. Rock sole and Alaska plaice are benthic foragers whereas yellowfin sole feed to a greater extent somewhat above the bottom. Allen (1984a) characterized the foraging behavior of the three species as follows : Alaska plaice are benthivores and more specifically stalkers and are adapted for extracting polychaetes from the sediment ; yellowfin sole are benthopelagivore and more specifically active searcher-pursuers ; rock sole are benthivores and more specifically searcher-stalkers and are adapted for excavating and extracting.

Recurrent group analyses (Fager, 1957, 1963 ; Fager and Longhurst 1968) have been used to demonstrate fish species associations within the demersal community of the eastern Bering Sea (Kihara, 1976 ; Mito, 1977 ; Pereyra et al., 1976 ; Smith and Bakkala, 1982 ; Kihara 1983). The procedure identifies species relationships on the basis of co-occurrence within samples. When joint occurrences are equal to or exceed 0.50, the species are considered to show affinity.

These five studies showed wide variation in the species that co-occurred with Alaska plaice. This variation might arise from differences in areas, time periods, and years of surveys from which the data were analyzed. However, certain species co-occurred more

Table 7. Species associated with Alaska plaice as in dicated by recurrent group analysis

Authority	Season	Years of study	Species showing affinity with Alaska plaice
Kihara (1976)	Summer	1966-71, 1974	Yellowfin sole
			Rock sole
			Flathead sole
			Pacific cod
			Walleye pollock
			Cottidae
			Agonidae
Mito (1977)	Winter	1972	Yellowfin sole
		1974-75	Rock sole
			Yellow Irish Lord
			Plain sculpin
Pereyra et al. (1976)	Summer	1975	Yellowfin sole
			Pacific herring
Bakkala and Smith (1978)	Spring	1976	Yellowfin sole
			Pacific herring
			Sturgeon poacher
			Capelin
Kihara (1983)	Summer	1966-71, 1973-77	Yellowfin sole
			Rok sole
			Flathead sole
			Pacific halibut
			Pacific herring
			Walleye pollock
			Pacific cod
			Cottidae
			Agonidae

consistently with Alaska plaice than others (Table 7). Yellowfin sole were found to co-occur in all studies, rock sole and Pacific herring in three studies, and flathead sole, Pacific cod, walleye pollock, Agonidae and Cottidae in two studies.

In conclusion, food competition seems to be negligible among the shallow water flatfish species inhabiting the eastern Bering Sea due to differences in food spectra or spatial distribution. One might hypothesize that the abundance and distribution of Alaska plaice is less than that of yellowfin sole because Alaska plaice are more specialized and less generalized in terms of their food habits.

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