FEEDING HABITS OF DOVER SOLE, *MICROSTOMUS PACIFICUS*; REX SOLE, *GLYPTOCEPHALUS ZACHIRUS*; SLENDER SOLE, *LYOPSETTA EXILIS*; AND PACIFIC SANDDAB, *CITHARICHTHYS SORDIDUS*, IN A REGION OF DIVERSE SEDIMENTS AND BATHYMETRY OFF OREGON

WILLIAM G. PEARCY AND DANIL HANCOCK[1]

ABSTRACT

The feeding habits of the Dover sole and rex sole (mainly juveniles) and of slender sole and Pacific sanddab were investigated at seven stations on the continental shelf off central Oregon. Dover sole had a catholic diet, feeding on a large variety of infaunal and epifaunal invertebrates. The composition of the diet varied among stations of different depth and sediment type indicating opportunistic feeding. Pelecypoda were the most important prey on a weight basis at the shallow station (74 m) of well-sorted sand where they were the dominant macrofaunal invertebrate. Ophiuroids, sea pens, anemones, and pelecypods were the most important prey at 100-102 m stations of silty sand or sandy silt. Polychaetes composed over 90% of the diet at the deep stations (148-195 m) of clayey silt or silty sand. The average standing stocks per square meter of Dover sole caught in beam trawl collections and polychaetes in grab samples were positively correlated among stations.

Similarity of the food habits of Dover sole on the basis of food weight or frequency of occurrence was generally higher among stations of similar depth than of similar sediment texture. Similar trends were noted for assemblages of benthic fishes and invertebrates.

Dover sole collected during the winter had the highest percentage of empty stomachs, the fewest prey taxa, and often the lowest frequency of occurrence of prey taxa within a size group. Because seasonal variations were not observed in abundance of macrofaunal food in the sediments, availability of prey may change with season, or more likely, Dover sole feed more intensely and less selectively during summer.

Small (<150 mm standard length) rex sole fed mainly in amphipods and other crustaceans. Large (150-450 mm standard length) rex sole preyed chiefly on polychaetes. The diet of rex sole was less diverse than that of the Dover sole and overlap of diet between the two species was not large.

Both the Pacific sanddab, numerically the most common species of fish at the shallow sand station, and the slender sole, the most common species at the three deep, soft-sediment stations, preyed principally on pelagic crustaceans such as euphausiids, shrimps, and amphipods. Although the biomass of mollusks in the sediments was large at the shallow sand station, they were not consumed by Pacific sanddab. Fish were occasionally an important food for the sanddab.

The objectives of this study were: 1) to describe the food habits of the four species of flatfishes that are common in trawl catches on the central continental shelf off Oregon: Dover sole, *Microstomus pacificus*, rex sole, *Glyptocephalus zachirus*, slender sole, *Lyopsetta exilis*, and Pacific sanddab, *Citharichthys sordidus*; 2) to evaluate the possible effects of depth and sediment, size of fish, and season of capture on their food habits; and 3) to compare the biomass and composition of fish food from grab samples with feeding habits of fishes.

These species are among the most abundant flatfishes in demersal communities of this region of the Pacific Ocean (Alverson et al. 1964; Day and Pearcy 1968; Alton 1972; Demory and Hosie[2]). They dominated the fish catches at the stations where they were captured for this study (Pearcy 1978). In order to know more about the role of these fishes in their ecological communities, including competitive-predatory relationships, more data are required on their food habits.

Hagerman (1952) listed food items found in Dover sole caught in California waters. Pearcy and Vanderploeg (1973) listed general taxonomic groups preyed upon by Dover, rex, and slender soles and Pacific sanddab. Kravitz et al. (1977) gave a detailed account, including species of prey

[1]School of Oceanography, Oregon State University, Corvallis, OR 97331.

[2]Demory, R. L., and M. J. Hosie. 1975. Resource surveys on the continental shelf of Oregon. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Commer. Fish. Res. Dev. Act, Annu. Rep. July 1, 1974 to June 30, 1975, 9 p.

Manuscript accepted January 1978.
FISHERY BULLETIN: VOL. 76 NO. 3, 1978.

consumed by the rex sole and Pacific sanddab caught in a single collection off the central Oregon shelf. This study is, to our knowledge, the most complete study of the food habits of these four species.

METHODS

Fishes were collected during 115 tows with a 3-m beam trawl at seven stations on the continental shelf off central Oregon between August 1968 and August 1970. These stations are classified by four depth categories and the percentage of sand in the sediments in Figure 1. Details on methods and descriptions of the stations are given by Pearcy (1978).

All fishes were preserved at time of capture with Formalin,[3] and the body wall of large (>150-200 mm SL) fishes was incised to insure preservation of stomach contents. Fishes were identified and measured (standard length, SL) in the shore laboratory. Stomachs were removed from 326 Dover sole represented in the catches at all seven stations; and from 614 rex sole, 1,109 slender sole, and 723 Pacific sanddab captured at two or three stations where each of these species was most common.

Stomach contents were removed and empty stomachs were noted. Food organisms were identified to species when possible. Annelids, crustaceans, mollusks, echinoderms, coelenterates, and remaining taxa (major taxa) were weighed to the nearest 0.01 g (wet-preserved weight). Usually these weights were obtained for the contents of a single stomach, but when the contents were insufficient for accurate weighing, taxa from the stomach contents of several fish of the same species and size, and from the same tow, were combined and weighed together to constitute an observation. The number of observations for Dover, rex, and slender sole and Pacific sanddab were 325, 374, 607, and 392, respectively.

Results are reported as the a) percent that each major food taxa constitutes of the total wet weight of food found in stomachs for all seasons combined and for winter and summer seasons separately; and b) the frequency of occurrence (FO) of principal prey, i.e., species or taxa found in 5% or more of the observations for a species or size group of a species for all seasons combined.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

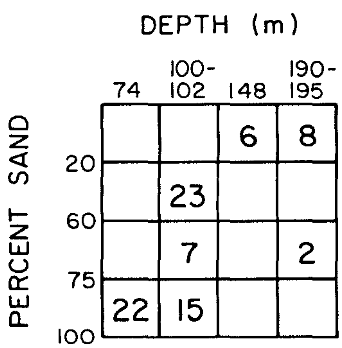

FIGURE 1.—Classification of the seven stations, each indicated by station number, according to depth of water and percent of sand (0-20, 20-60, 60-75, and 75-100%). The stations with similar sediment types but different depths are 6 and 8, 7 and 2, and 22 and 15. (See Pearcy 1978 for additional information.)

RESULTS

General Food Habits

Two general feeding types are indicated by differences in the weights of major food taxa (annelids, crustaceans, mollusks, echinoderms, coelenterates, and other taxa) found in the stomach contents of the four species (Table 1). Dover and rex soles fed largely (64%) on annelids, while slender sole and Pacific sanddab fed mainly on crustaceans (75%). Within these two apparent feeding types, differences occurred among the proportions of prey taxa of secondary importance. For example, crustaceans were more abundant in the diet of rex than Dover sole (31% vs. 11%), whereas mollusks were more abundant in Dover than in rex sole (18% vs. 1%). Annelids composed more of the stomach contents of slender sole than Pacific sanddab (15% vs. 7%).

Based on the average frequency of occurrence of principal prey (FO≥5%) from all sizes of fish and from all stations (Table 2), it is obvious that the food habits within these two feeding types (Dover sole-rex sole vs. slender sole-Pacific sanddab) are not as similar as shown by Table 1. Principal prey of Dover sole, for example, included 11 different identified polychaetes. Rex sole preyed mainly on three identified species of polychaetes. Only one principal prey species of polychaete was common to the diet of both Dover and rex soles. The shrimp *Pandalus jordani*, pelecypods, and ophiuroids were principal prey in the food of Dover but not rex sole, whereas crab larvae, cumaceans, and *Oiko-*

TABLE 1.—Percent by weight that major food taxa composed of the diet of the four flatfishes, all stations and seasons combined.

Taxa	Dover sole	Rex sole	Slender sole	Pacific sanddab
Annelida	64.4	64.8	15.6	7.2
Crustacea	11.2	31.0	75.6	74.8
Mollusks	18.3	1.4	0.7	0
Echinoderms	3.4	<0.1	<0.1	0
Coelenterates	2.6	0	0	0
Other taxa	0	2.8	8.2	18.0

TABLE 2.—Average frequency of occurrence of principal prey (those occurring in 5% or more of the observations) in the four species, all stations combined.

Prey	Rex sole	Dover sole	Slender sole	Pacific sanddab
Polychaeta:				
Sternaspis fossor	12	14		
Myriochele heeri		15		
Nothria geophiliformis	9			
Goniada brunnea	10			
Aricidea neoseucica		6		
Haploscoloplos elongatus		9		
Chaetozone setosa		6		
Terebellides stroemii		6		
Rhodine bitorquata		5		
Typosyllis hyalina		9		
Lumbrineris sp.		6		
Amphicteis sp.		5		
Glyceridae		5		
Unidentified	25	19	7	
Crustacea:				
Pandalus jordani		6	7	
Euphausia pacifica			9	7
Crab larvae or juvenile	7			13
Gammarid amphipods	29	24		
Copepods				12
Cumaceans	8			
Unidentified	16	12	21	24
Mollusca:				
Pelecypoda		12		
Echinodermata:				
Ophiuroidea		12		
Miscellaneous:				
Oikopleura spp.	7			
No. observations	347	325	607	392
No. fish	614	326	1,109	723

pleura were principal prey of rex but not Dover sole. Gammarid amphipods occurred frequently in stomachs of both rex and Dover soles; had they been identified to species, the overlap between the diets of the Dover and rex soles would appear even smaller. Overlap in the diets of Dover and rex soles of various size groups were also found to be small.

Gammarid amphipods, the major crustacean prey of Dover and rex soles, were not principal prey for slender sole and Pacific sanddab. Slender sole and Pacific sanddab fed largely on pelagic crustaceans, as indicated by the occurrence of euphausiids in stomachs of both species, by crab larvae and calanoid copepods in sanddab, and by *Pandalus jordani* in slender sole. Slender sole and Pacific sanddab are chiefly pelagic feeders. *Pandalus jordani* is known to migrate off the bottom at night (Pearcy 1970) and hence could have been consumed on the bottom or in midwater by slender sole. We have occasionally caught both slender sole and Pacific sanddab in midwater trawls at night. Barss[4] caught in midwater trawls at night Pacific sanddab that had been feeding heavily on northern anchovy, *Engraulis mordax*. The only good evidence for benthic feeding by either of these two species is the presence of annelids in their diets (Table 1).

Differences Among Stations

The proportions (by weight) of the major taxa in the diet of Dover sole were sometimes markedly different among stations (Table 3). Prey composition and availability may be functions of sediment and/or depth. Annelids constituted over 90% of the diet on a weight basis at the three deepest stations (2, 6, and 8), but <13% at the shallowest station (22) where the sediment was well-sorted sand. At this shallow station, mollusks and crustaceans were the major food items in the diet. Coelenterates (feeding polyps of sea pens and anemones) and echinoderms (brittlestars) were minor food taxa for Dover sole at all stations except Stations 15 and 23 (102 m depth), where together they composed over one-half the diet. The proportion of fish with food in their stomachs was also higher at these two stations than at any of the other stations.

To illustrate the similarities of the food habits of Dover sole among these stations, we constructed a station-station matrix (Table 4) using an index (C_λ) that Horn (1966) recommended for comparing overlap in exploitation of alternative food sources

[4]Barss, W. H. (compiler). 1976. The Pacific sanddab. Oreg. Dep. Fish Wildl., Inf. Rep. 76-5, 5 p.

TABLE 3.—The average percentage composition of stomach contents of Dover sole on a weight basis at each of the stations.

Taxa	Station (depth in meters in parentheses) 22 (74)	7 (100)	15 (102)	23 (102)	6 (148)	2 (190)	8 (195)
Annelids	12.6	59.9	25.0	30.5	91.9	93.4	91.0
Crustaceans	29.6	14.1	3.3	3.1	3.7	3.5	6.5
Mollusks	57.9	23.7	13.5	12.4	3.0	2.2	0.3
Echinoderms	0	1.1	33.8	30.1	1.4	1.1	2.2
Coelenterates	0	1.2	24.3	23.8	0	0	0
Other taxa	0	0	0	0.1	0	0	0
No. fish examined	65	38	22	10	49	91	51
No. fish with stomach contents	28	19	20	10	22	61	32

TABLE 4.—Similarity (C_λ) in the diets of Dover sole at the seven stations based on the percentage of major taxa in their diets on a weight basis (below diagonal) and frequency of occurrence of principal polychaete prey (above diagonal). Stations are arranged by depth.

Stations	Frequency of occurrence 22	7	15	23	6	2	8
22		0.04	0	0	0.09	0.06	0
7	0.58		0.64	0.57	0.24	0.54	0.05
15	0.34	0.56		0.59	0.21	0.38	0
23	0.34	0.64	0.99		0.09	0.42	0
6	0.22	0.88	0.44	0.52		0.37	0.42
2	0.21	0.87	0.43	0.52	1.00		0.45
8	0.21	0.88	0.43	0.53	1.00	1.00	

within the same habitat. This measure of similarity varies from 0 to 1.0. The percentages by weight of the major taxa (lower half of Table 4) were identical at the three deepest (148-200 m) Stations: 2, 6, and 8. Stations 15 and 23, both located at 102 m depth, were also very similar. Station 7 at 100 m was fairly similar ($C_\lambda > 0.87$) to Stations 2, 6, and 8 located in deeper water. The percent of major taxa in the diet of Dover sole at the shallow, sand location (Station 22) was not very similar to any other station ($C_\lambda \leq 0.58$).

The frequency of occurrence of principal prey of Dover sole (Table 5) indicates fairly low similarity among different stations for species of polychaetes. Most species occurred at only one or two stations and the assemblage of polychaetes eaten by Dover sole appears to be different at each station. As one would expect, similarity is higher when higher taxa such as gammarid amphipods or pelecypods are considered as a group. For this reason comparisons of similarity among stations should be confined to prey identified to the same taxonomic level.

To examine differences in prey species among stations we calculated the overlap in diet (C_λ) based on polychaetes alone, the most common and speciose prey animals of Dover sole (and the food group that one of us (Hancock) was familiar with taxonomically). The range in overlap of diets based on frequency of occurrence of individual taxa of polychaetes at these stations (Table 5) was appreciably lower than that based on weight percentage of major taxa (upper half of Table 4). Stations 2, 6, and 8, which were very similar on the basis of the weight of major taxa in the Dover sole stomachs, overlapped only moderately on the basis of frequency of occurrence of polychaetes ($C_\lambda = 0.37 - 0.45$). Stations 15 and 23, similarly based on major taxa, were the most similar ($C_\lambda = 0.64$) stations based on frequency of occurrence of polychaetes. Station 23 was the next highest in

TABLE 5.—Frequency of occurrence of principal prey of Dover sole from the seven stations.

Taxa	Stn 22	7	23	15	6	2	8
Polychaeta:							
Sternaspis fossor		23	24	6		32	
Myriochele heeri		31	14	6	8	27	
Nothria geophiliformis					9	14	13
Chloeia pinnata						36	16
Melinna cristata						14	
Goniada brunnea		7			8	14	
Aricidea uschakowi		5			9		
Aricidea neosuecica		9			23		
Haploscoloplos leongatus					25	18	8
Owenia fusiformis		10				18	
Maldane sarsi		5	6				
Chaetozone setosa		8		6	8	9	
Terebellides stromenii		11	10				
Tharyx multifilis					6		8
Rhodine bitorquata		13					
Typosyllis hyalina		25		6			
Ammontrypane aulogaster							5
Nephtys cornuta							11
Anaitides groenlandica	10						
Lumbrineris sp.		12			6		
Ammontrypane spp.						9	
Amphitteis		9				18	
Aricidea spp.							5
Pherusa papillata		7					
Tharyx spp.					9		
Nephtys spp.		5		8		8	
Terebellidae						9	
Ampharetidae							5
Maldanidae						9	
Lumbrineridae					11		
Glyceridae		10	8				
Spinonidae	10	5			6	9	
Hemipodus borealis	10						
Laonice cirrata		6					
Megelona sp.		5					
Crustacea:							
Pandalus jordani	30	7	16			23	8
gammarid amphipod	70	22	22	24	14	45	26
copepod	20						
cumacean		7					8
Diastylis spp.							8
Valvifera spp.	10						
Ostracoda	10					14	5
unidentified crustacea							
Mollusca:							
Gastropoda		7					
Solenogasters spp.		7					8
Pelecypoda	20	20		10	16		8
Yoldia ensifera			8				
Lucina sp.						9	
Megacrenella columbiana		10		10			
Tellina salmonea	10						
Acila castrensis	10						
Echinodermata:							
Ophiuroidea		11	27	16		23	
sea pen			12				
Miscellaneous:							
Nematoda						18	
No. observations	10	91	51	49	64	22	38
No. fish	10	91	51	49	65	22	38

similarity with Stations 7 and 15. Thus, the polychaete prey of Dover sole were most similar among these three 100-102 m stations.

Because stomachs of the other flounders were examined for only two or three stations, few station comparisons could be made. As with Dover sole, the percentage of major taxa in the diets of rex sole at Stations 2, 6, and 7 were similar, and food habits were almost identical at Stations 2 and

TABLE 6.—The average percent by weight that major taxa composed of the diet of rex sole, slender sole, and Pacific sanddab at Stations 7, 6, and 2.

	Rex sole			Slender sole			Pacific sanddab	
Taxa	Stn.7	6	2	7	6	2	7	6
Annelida	58.7	69.7	64.5	1.2	18.5	13.1	8.2	0.1
Crustaceans	39.2	24.8	29.6	92.2	72.3	77.8	71.3	99.9
Mollusks	2.1	1.0	0.5	0.9	0.8	0	0	0
Echinoderms	0	0	0	0	0	0	0	0
Coelenterates	0	0	0	0	0	0	0	0
Other taxa	0	4.5	5.5	5.8	8.5	9.1	20.5	0
No. fish examined	376	210	28	68	844	197	690	33
No. fish with stomach contents	262	160	25	35	403	83	478	13

6 (Table 6). A larger percentage of crustaceans (and the lowest percentage of annelids) was found at Station 7 than at 2 or 6 for both rex and slender soles. But crustaceans were more abundant in the diet of sanddab at Station 6 than at Station 7. Fishes (included as other taxa) were an appreciable part of the sanddab diet at Station 7. Again, differences in availability of food taxa apparently occurred among stations for the same predator species, and different trends in the importance of food taxa are evident for different species of fish at the same stations.

The principal prey were most similar for rex sole at Stations 2 and 6, as were the major taxa by weight. The polychaete *Nothria geophiliformis* and the larvacean *Oikopleura* occurred in over 5% of the observations only at these two stations. It is curious that the planktonic *Oikopleura* was so frequent in the diet of this primarily benthophagus fish. Other prey common at all these stations included the polychaete *Goniada brunnea*, unidentified polychaetes, gammarid amphipods, and cumaceans.

Pandalus jordani was a principal prey species for slender sole at Stations 6 and 7 but not at Station 2. The shrimp *Spirontocaris bispinosa* and unidentified fish were found in over 5% of the fish only at Station 6. Copepods were common only at Station 7.

Euphausia pacifica was a principal prey for Pacific sanddab at Stations 6 and 7. *Pandalus jordani* occurred in 26% of the fish at Station 6, but was uncommon at Station 7. Decapod crab larvae and copepods, on the other hand, were common prey only at Station 7.

Variations With Seasons or Size of Fish

Changes in the relative proportions of the major taxa of food consumed by different sizes of the four species of flatfishes are shown for "summer" (May-September) and "winter" (October-April) in Figures 2-5. Because food habits as well as sizes of fishes vary among stations (Tables 3, 6; Pearcy 1978), geographic effects are confounded in these figures.

Annelids usually dominated the diet of all size groups of these juvenile Dover sole during both seasons (Figure 2). Crustaceans appeared to decrease in importance with increasing size of fish during the winter season, but reached peaks in the summer. Mollusks (*Solegasters* spp., *Yoldia ensifera*, and unidentified pelecypods) attained peaks in the diet of intermediate-sized (200-300 mm) Dover sole, and echinoderms (mainly ophiuroids) attained a peak at a larger size of fish.

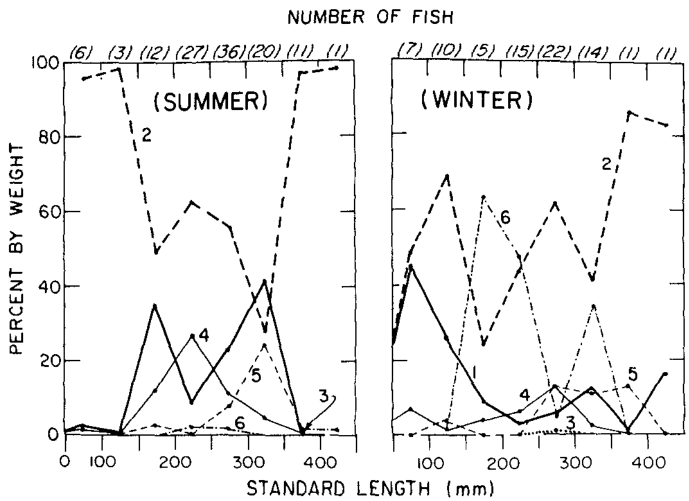

FIGURE 2.—The percent by wet weight of the major food taxa for different length groups of Dover sole for summer and winter. 1 = crustaceans, 2 = annelids, 3 = other taxa, 4 = mollusks, 5 = echinoderms, and 6 = coelenterates.

The largest difference between seasons was for coelenterates. Anemones and the feeding polyps of sea pens were unimportant constituents of the food during the summer (<2% of diet by weight) but were sometimes a major food >30% by weight) during the winter. Anemones and sea pens are probably available as prey during both seasons but for some reason only consumed in significant quantities during the winter.

Seasonal differences in the intensity of feeding were also indicated by the higher frequency of empty stomachs in winter than in summer (Table 7). The number of principal prey occurring in the diet of Dover sole was consistently larger during summer than winter regardless of fish size. Although the smaller number of stomachs with contents during the winter reduces sample size, and hence the number of taxa found, the frequency of occurrence of many of the individual taxa of polychaetes, crustaceans, and mollusks (taxa listed in Table 5) was higher in summer than winter. Bertrand (1971) found no evidence for seasonal variations in the numbers or biomass of infauna sampled with grabs at these stations. Therefore a more diverse assemblage of prey was probably available to Dover sole during the summer or fish were usually less selective during the summer than during the winter. The summer is the season of most active growth of Dover sole (Demory 1972) when intraspecific and possibly interspecific competition for food may be most intense. Decreased prey selectivity is known to occur under conditions of low food abundance or availability (Ivlev 1961; Schoener 1971).

The number of principal prey taxa generally increased with size of Dover sole (Table 7). This trend may be related to sample size (number of stomachs with food) and to the ability of large fish to consume a larger range of prey sizes than small fish. The less diverse diet of small fish resulted from ingestion of only a few species of polychaetes.

TABLE 7.—Frequency of empty stomachs (no. empty stomachs/ no. fish) and the number of principal taxa (occurring in 5% or more of at least 10 observations) of prey for different sizes of Dover sole collected during summer and winter seasons.

Standard length (mm)	Frequency of empty stomachs		Number of taxa	
	Summer	Winter	Summer	Winter
51-100	6/12	15/22	9	4
101-150	—	19/29	—	8
151-200	4/16	10/15	24	12
210-250	7/34	19/34	25	18
251-300	11/47	20/42	37	17
301-350	4/24	7/21	21	15
351-400	5/16	—	41	—

Those prey types eaten by a broad size range (50-400 mm SL) of Dover sole include: *Myrochele heeri*, *Typosyllis hyalina*, *Lumbrineris* sp., Glyceridae, gammarid amphipods, pelecypods, *Megacrenella columbiana*, ophiuroids, unidentified polychaetes, and unidentified crustaceans.

Annelids and crustaceans were the major food items for rex sole (Figure 3). (Most of the rex sole represented here are juveniles.) Annelids increased in importance with an increase in the sizes of rex sole, up to 150-250 mm. This increase was associated with a decrease in the proportion by weight of crustaceans, the dominant food item for small rex sole during both seasons. Euphausiids, decapod crab larvae, copepods, and ostracods were only found as principal prey of rex sole of <200 mm. Mollusks formed only a minor portion of the diet. Differences in the FO of principal prey were not pronounced. Some polychaetes (*Sternaspis fossor*, *Myriochele heerie*, *Nothria geophiliformis*, and *Choelia pinnata*) were found more frequently in large (220-300 mm SL) rex sole.

Some seasonal differences in the diet of rex sole were evident. Euphausiids were principal prey only during the summer. Cumaceans and *Oikopleura* were more common during the winter. Principal prey that were commonly ingested by all or most size groups during both seasons were: *Sternaspis fossor*, *Goniada brunnea*, unidentified polychaetes, gammarid amphipods, and uniden-

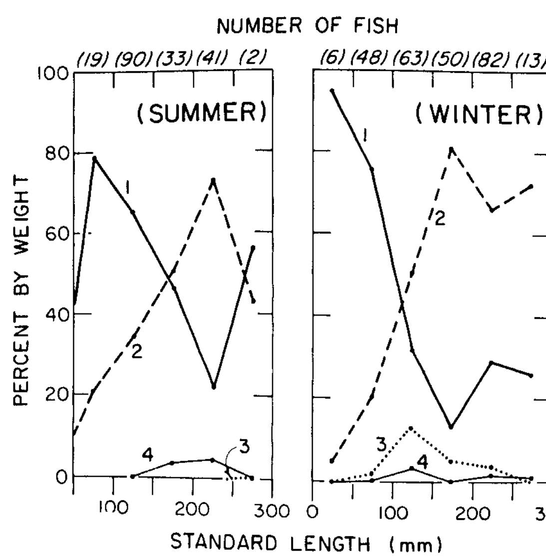

FIGURE 3.—The percent by wet weight of the major food taxa for different length groups of rex sole for summer and winter. 1 = crustaceans, 2 = annelids, 3 = other taxa, and 4 = mollusks.

tified crustaceans. Kravitz et al. (1977) listed *Nothria* spp. as frequently occurring polychaetes and *Ampelisca macrocephala*, *Hippomedon wecomus*, *Paraphoxus epistomus*(?), and *P. obtusidens* as frequently occurring amphipod prey for rex sole.

Crustaceans composed the bulk of the diet of all sizes of slender sole during both seasons (Figure 4). Annelids and "other taxa" were most important in the diet of intermediate-sized (101-200 mm) slender sole during either summer or winter. Pelagic crustaceans such as copepods, euphausiids, and crab larvae occurred frequently in the diet of small (<150 mm) slender sole, whereas polychaetes, the shrimps *P. jordani* and *S. bispinosa*, and fishes were important for large slender sole (>150 mm). Again, a larger number of principal prey taxa occurred during the summer than winter.

Crustaceans also were the most important taxa in the diet of the Pacific sanddab, except for five 201-250 mm individuals during the summer, when fishes composed 95% of the food by weight (Figure 5). Kravitz et al. (1977) found that all *C. sordidus* (90-377 mm total length) collected in May off Oregon had been feeding intensively on northern anchovy. Barss (see footnote 4) reported that sanddab eat small fishes, squids, and octopuses.

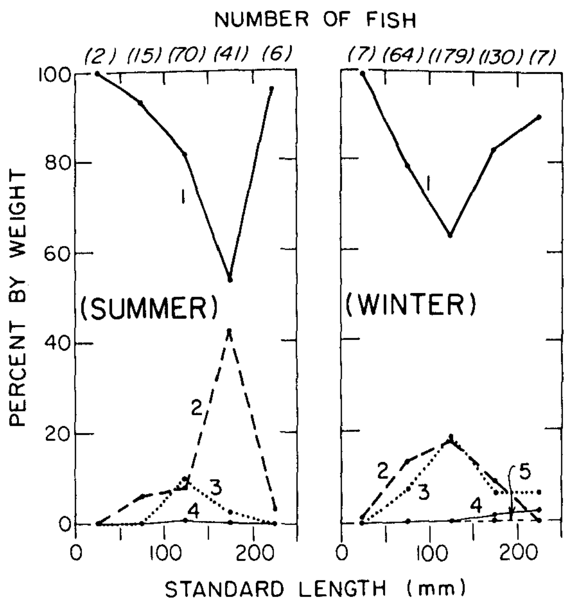

FIGURE 4.—The percent by wet weight of the major food taxa for different length groups of slender sole for summer and winter. 1 = crustaceans, 2 = annelids, 3 = other taxa, 4 = mollusks, and 5 = echinoderms.

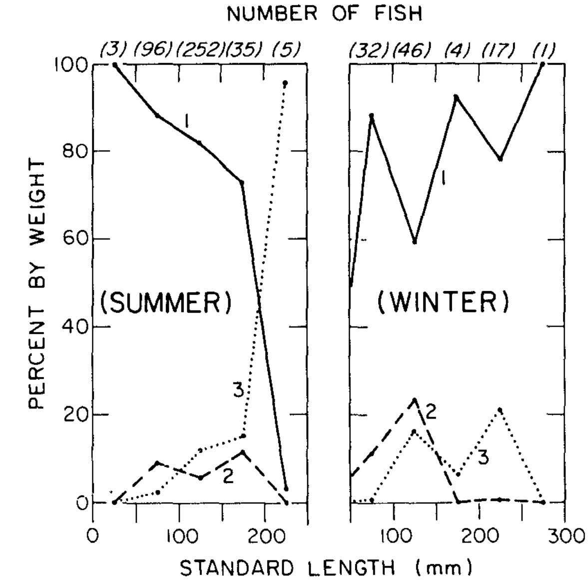

FIGURE 5.—The percent by wet weight of the major food taxa for different length groups of Pacific sanddab for summer and winter. 1 = crustaceans, 2 = annelids, and 3 = other taxa.

Crustaceans were the predominant prey during both seasons and for most sizes of sanddab. Euphausiids, copepods, and cumaceans occurred more frequently in small than large individuals. *Pandalus jordani*, crangonids, and fishes were most common in the diet of large Pacific sanddab.

DISCUSSION

The four common flatfishes caught in this study compose two generalized feeding types. Dover and rex soles feed almost exclusively on benthic invertebrates, mainly polychaetes and amphipods, while slender sole and Pacific sanddab prey mainly on pelagic crustaceans. The food habits of these two types are related to mouth structure and digestive morphology. Flatfishes that feed on benthos usually have asymmetrical jaws, small stomachs, and long intestines, whereas pelagic feeders have longer, symmetrical jaws with sharp teeth and long serrated gill rakers, adaptations for grasping and retaining animals that swim in midwater (Hatanaka et al. 1954; Groot 1971). Dover and rex soles belong to the benthos-feeding type and sanddab and slender sole to the pelagic-feeding type. Kravitz et al. (1977) also recognized these two feeding types among five flatfishes off

Oregon, and included rex sole as a benthophagus species and Pacific sanddab as a piscivorous-pelagic feeder.

Rae (1956, 1969) studied the feeding habits of the lemon sole, *Microstomus kitt*, and the witch, *Glyptocephalus cynoglossus*, off Scotland. Some of his results are remarkably similar to ours for the congeneric Dover sole, *M. pacificus*, and rex sole, *G. zachirus*. Both the witch and lemon sole, like the Dover and rex soles, feed predominantly on polychaetes. Crustaceans were next in importance followed by other phyla such as mollusks, echinoderms, and coelenterates. Ophiuroids and anthozoans were also eaten by both lemon sole and the witch. These similarities in diets indicate common feeding specializations within pleuronectid genera.

Although the major food of the lemon sole and witch were very similar, these two species, like the Dover and rex soles, preyed on different families or different genera of the same family so that food overlap, and presumably competition, are rare (Rae 1956, 1969). As pointed out by Rae, these differences in feeding habits reflect behaviorial differences of the fishes as well as differences in the composition of the benthic communities of which these fishes are a part. The habitats of the lemon sole and witch often differ, the lemon sole preferring hard, rocky bottoms, and the witch soft, muddy bottoms.

Both the lemon sole and witch fed most heavily during the summer. Regional differences were also marked. Polychaetes decreased in importance as prey for the witch in shallow water (<100 m), as they did in our study for Dover sole (Table 3). Rae (1939, 1956) also believed that differences in the types and quantities of food available between one area and another resulted in different growth rates of lemon sole. Sedentary polychaetes were most common as prey in areas of rapid growth.

One of the objectives of this study was to learn if differences in the availability of prey for flatfishes occurred and how it may be related to sediment types and water depth at our stations. The composition of prey of Dover sole clearly varies among stations. Polychaetes were the main food at the three deepest stations; echinoderms, coelenterates, and polychaetes were similar on a weight basis at the two 102-m stations; polychaetes, followed by mollusks, were most important at the 100-m station; and mollusks and crustaceans were most abundant at the 74-m station (Table 3). Based on the percentage by weight of major food taxa, higher similarities occurred among stations at similar depths rather than with similar sediment types: Stations 15 and 23 at 102 m and the deep stations 6, 2, and 8 at at 148-195 m (Table 4). Sediment texture at Stations 15 and 23 were dissimilar. (See Figure 1 for summary of depth and sediments for the stations.) Although Station 2 had an average sediment texture that differed from Stations 6 and 8, a thin layer of silt overlaid coarse sand at Station 2, hence the surface sediment of Stations 6, 2, and 8 were probably more similar than indicated in Figure 1.

The occurrence of individual species of polychaetes consumed by Dover sole is probably a more sensitive indicator of station differences than the biomass of major taxa. Stations 7, 15, and 23, at 100-102 m, but with different sediment types, were most similar in polychaete prey. Stations 2, 6, and 8 in deep water, at 148-195 m were again similar. Thus, these similarities in prey for these two groups of stations seem to be correlated with depth. However, polychaete prey at Station 2 (190 m) was similar to that of Station 7 (100 m), which had similar sediment type, as well as that at Stations 15 and 23 (102 m) with different sediments. Stations 22 and 15 with similar sediment types, but at different depths, had low similarity of polychaete prey.

Based on 82 species of mollusks, cumaceans, and ophiuroids sampled in 0.1-m^2 Smith-McIntyre grabs, Bertrand (1971) calculated the similarity of the fauna among the same seven stations included in this study. He also found that Stations 2, 6, and 8 formed a deep-water group of high similarity. Stations 7 and 23 (at 100-102 m) were similar, as were Stations 7 and 8, with different depths and sediment types. Gunther (1972) also calculated similarities among these same stations based on living benthic foraminifera and found that strong faunal affinities crossed depth and sediment boundaries. Again, Stations 2, 6, and 8 formed one group. Stations 2 and 7, and 15 and 22, station pairs based on sediments, were not very similar.

Similarities among the fishes caught were also strong among Stations 2, 6, and 8. The remaining stations (7, 15, 22, and 23) formed another group of high affiinity (Pearcy 1978). These two species associations agree with those described by Day and Pearcy (1968) for the continental shelf off central Oregon. They found a shallow (42-73 m) water association on a sand bottom dominated by Pacific sanddab and English sole, *Parophrys vetulus*, and an association at 119-159 m on a silty-sand bottom dominated by slender sole and rex sole.

Shallow-water and deep-water associations are therefore evident at these stations, based on previous studies of benthic invertebrates and vertebrates, as well as the composition of the diet of Dover sole in this study. Because surface sediments were fairly similar at our three deep stations, sediment vs. depth effects could not be separated here. The lack of precise similarities of sediment types for station pairs also weakens this part of our study. Nevertheless, stations with the most similar sediment types often had low similarity of benthic fauna. We conclude that depth-related factors may have greater influence than sediment type on the composition of benthic fishes, fish food, and invertebrate fauna within the boundaries of our study area. This conclusion must be tempered, however, by the realization that other sediment parameters besides texture and percent organic matter may be important, and we simply did not study the proper sediment characteristics. We agree with Peterson (1918): "It is clear then that the character of the bottom is of fundamental importance for the presence or absence of epifauna. Nevertheless, the succession of the various types of epifauna and of the communities belonging to the level bottom cannot be explained by the character of the bottom alone."

Bertrand (1971) estimated the "edible" biomass of infauna (>1.0 mm) for demersal fishes (i.e., all infauna less holothurians, echinoids, echiurids, and burrowing anemones) at these stations from 0.1-m² Smith-McIntyre grab samples taken on the same cruises. He detected no seasonal variations in the wet or ash-free dry weight of this biomass fraction. The ash-free dry weights per square meter for polychaetes, mollusks, and crustaceans given by Bertrand for the seven stations are shown in Table 8. Crustacean biomass was consistently low at all stations, probably because of the ineffectiveness of the grab to sample epibenthic and motile amphipods, major food items of Dover and rex soles. There was no direct or consistent relationship between the biomass per square meter of

TABLE 8.—Ash-free dry weights in grams per square meter of macro-infaunal fish food at the seven stations (from Bertrand 1971).

Taxa	Stn 22	7	23	15	6	2	8
Polychaetes	0.04	0.17	0.30	0.08	0.17	0.14	0.19
Mollusks	4.50	1.10	1.74	2.09	0.20	0.16	0.07
Crustaceans	0.006	0.005	0.001	0.004	0.008	0.004	0.003
Total	4.55	1.28	2.04	2.17	0.38	0.30	0.26

"edible" fish food and the biomass of all fish or Dover sole. Stations with similar standing stocks of infaunal food had widely different standing stocks of benthic fishes.

Station 22, the beach sand station—with the lowest organic carbon in the sediment of all stations—supported a fairly low biomass of fish, but the largest biomass of edible fish food, 4.55 g/m², and the largest biomass of invertebrate macrobenthos. Conversely, Wigley and McIntyre (1964) found the largest biomass in finer sediments off Massachusetts, and Lie and Kisker (1970) found that the shallow-water sand communities off Washington had a lower average standing stock of infauna than deeper communities on the shelf. The large biomass at Station 22 is composed primarily of the bivalves *Acila castrensis* and secondarily of *Tellina salmonea*. Both of these mollusks were principal prey of Dover sole only at Station 22 (Table 5). Although the frequency of occurrence of these two mollusks in Dover sole stomachs was only 10%, mollusks composed 58% by weight of the food of Dover sole at this station. Thus Dover sole are versatile predators, changing their diets opportunistically in response to changes of prey availability.

The dominant fish at Station 22 was Pacific sanddab, primarily a pelagic feeder. Mollusks were not principal prey. *Acila* and other burrowing animals are unavailable as food for fishes adapted for pelagic feeding, illustrating a basic reason for the lack of any direct relationships between edible fish food and fish biomass.

The average biomass of Dover sole was directly related to the biomass of their principal food, polychaetes, at the seven stations (Figure 6). Station 22, where Dover sole consumed principally mollusks, had the lowest biomass of both polychaetes and Dover sole; intermediate values of biomass of both fish and food are found at the three deep stations (2, 6, 8). The three stations at about 100 m (2, 7, and 15) differed markedly in standing stocks of both polychaetes and Dover sole. This positive correlation ($r = 0.73$) of standing stocks of predator and prey implies that Dover sole selected habitats within our study area where their prinicpal preferred food was most abundant regardless of depth and bottom type. Of more fundamental interest is the fact that standing stocks of polychaetes may indicate the amount of food available to Dover sole, and perhaps the production rates of polychaetes at the different stations. Similar direct relationships between standing

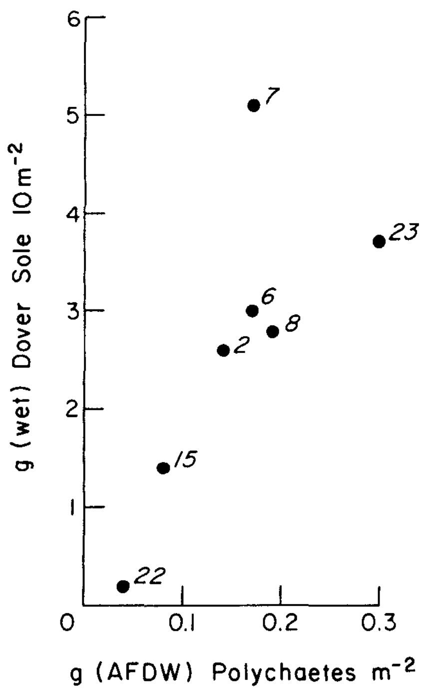

FIGURE 6.—The relationship between average standing stocks of prey (grams ash-free dry weight of polychaetes per square meter) and predator (grams wet weight of Dover sole per 10 m^2) at the seven stations.

stocks of predator and prey have been elucidated by Brocksen et al. (1970) for the biomass of phytoplankton and zooplankton and for zooplankton and sockeye salmon among ecosystems with different productivities. This is the first example, to our knowledge, of such a relationship for the marine benthos.

ACKNOWLEDGMENTS

This research was sponsored by the Oregon State University Sea Grant College Program, supported by NOAA Office of Sea Grant, U.S. Department of Commerce, Grant 04-5-158-2. We thank John Dickinson, Gail Breed, and anonymous reviewers for helpful comments on the manuscript.

LITERATURE CITED

ALTON, M. S.
1972. Characteristics of the demersal fish fauna inhabiting the outer continental shelf and slope off the northern Oregon coast. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, p. 583-634. Univ. Wash. Press, Seattle.

ALVERSON, D. L., A. T. PRUTER, AND L. L. RONHOLT.
1964. A study of demersal fishes and fisheries of the northeastern Pacific Ocean. H. R. MacMillan Lect. Fish., Inst. Fish. Univ. B.C., Vancouver, 190 p.

BERTRAND, G. A.
1971. A comparative study of the infauna of the central Oregon continental shelf. Ph.D. Thesis, Oregon State Univ., Corvallis, 113 p.

BROCKSEN, R. W., G. E. DAVIS, AND C. E. WARREN.
1970. Analysis of trophic processes on the basis of density-dependent functions. *In* J. H. Steele (editor), Marine food chains, p. 468-498. Univ. Calif. Press, Berkeley and Los Ang.

DAY, D. S., AND W. G. PEARCY.
1968. Species associations of benthic fishes on the continental shelf and slope off Oregon. J. Fish. Res. Board Can. 25:2665-2675.

DEMORY, R. L.
1972. Scales as a means of aging Dover sole (*Microstomus pacificus*). J. Fish. Res. Board Can. 29:1647-1650.

GROOT, S. J. DE.
1971. On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes). Neth. J. Sea Res. 5:121-196.

GUNTHER, F. J.
1972. Statistical foraminiferal ecology from seasonal samples, central Oregon continental shelf. Ph.D. Thesis, Oregon State Univ., Corvallis, 128 p.

HAGERMAN, F. B.
1952. The biology of the Dover sole, *Microstomus pacificus* (Lockington). Calif. Dep. Fish Game, Fish Bull. 85, 48 p.

HATANAKA, M., M. KOSAKA, Y. SATO, K. YAMAKI, AND K. FUKUI.
1954. Interspecific relations concerning the predacious habits among the benthic fish. Tohoku J. Agric. Res. 5:177-189.

HORN, H. S.
1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100:419-424.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, 302 p.

KRAVITZ, M. J., W. G. PEARCY, AND M. P. GUIN.
1977. Food of five species of coocurring flatfishes on Oregon's continental shelf. Fish. Bull., U.S. 74:984-990.

LIE, U., AND D. S. KISKER.
1970. Species composition and structure of benthic infauna communities off the coast of Washington. J. Fish. Res. Board Can. 27:2273-2285.

PEARCY, W. G.
1970. Vertical migration of the ocean shrimp, *Pandalus jordani*: A feeding and dispersal mechanism. Calif. Fish Game 56:125-129.
1978. Distribution and abundance of small flatfishes and other demersal fishes in a region of diverse sediments and bathymetry off Oregon. Fish. Bull., U.S. 76:629-640.

PEARCY, W. G., AND H. A. VANDERPLOEG.
1973. Radioecology of benthic fishes off Oregon. *In* Radioactive contamination of the marine environment, p. 245-260. Int. At. Energy Agency, Vienna.

PETERSEN, C. G. J.
1918. The sea bottom and its production of fish-food. Rep. Dan. Biol. Stn. 25, 62 p.

RAE, B. B.
1939. Factors in the growth of lemon soles. Scott. Home Dep. Fish. Div., Sci. Invest. 1939(3), 18 p.
1956. The food and feeding habits of the lemon sole. Scott. Home Dep., Mar. Res. 1956(3), 32 p.
1969. The food of the witch. Dep. Agric. Fish. Scotl., Mar. Res. 1969(2), 23 p.

SCHOENER, T. W.
1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2:369-404.

WIGLEY, R. L., AND A. D. MCINTYRE.
1964. Some quantitative comparisons of offshore meiobenthos and machrobenthos south of Martha's Vineyard. Limnol. Oceanogr. 9:485-493.