

FEEDING SELECTIVITY OF DOVER SOLE, *MICROSTOMUS PACIFICUS*, OFF OREGON

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ABSTRACT

Factors influencing the selection of food by Dover sole were investigated by analyzing stomach contents of fish and serially sectioned box core samples for benthic invertebrates from two areas of high Dover sole abundance on the central Oregon continental shelf. At both locations (119 and 426 m depth), polychaetes and ophiuroids were more important than molluscs and crustaceans as food in terms of frequency of occurrence, weights, and numbers. Polychaetes and ophiuroids were generally positively selected at both locations; i.e., they were more common in fish stomachs than in box core samples. Molluscs were generally negatively selected at both locations. Crustaceans were positively selected at 426 m and consumed nonselectively at 119 m. The box core samples may, however, underestimate crustaceans and hence give artificially high values of electivity.

Significant changes in frequency of occurrence of principal prey taxa with fish size were observed for 27 principal prey taxa at 119 m and 7 prey taxa at 426 m. These changes indicate that composition of fish diet varies with fish size.

At the 119 m station, the larger the fish size at which a significant difference in prey frequency occurred, the larger the increase in electivity across the size interval. This implies increased selectivity by large fish. Body size of a prey taxon was positively correlated with fish length at which significant difference in prey frequency occurred: larger fish consumed larger prey. Mean depth of a prey taxon within the sediment was also positively correlated with the length of fish at which a significant increase in prey frequency occurred: larger fish consumed prey found deeper in sediment.

Few size-related changes in diet were found at the 426 m location. Environmental abundance of a preferred taxon, polychaetes, was lower at 426 m than at 119 m. Dover sole may therefore change feeding strategy from that of a specialized predator, whose feeding habits vary with its body size where polychaetes are abundant, to that of a generalist consuming more types and sizes where few polychaetes are available. Vertical distribution of prey within the sediment at 426 m was shallower than at 119 m; thus the advantage afforded large fish in removing deeply buried prey may be eliminated. Implications of results are discussed in terms of optimal foraging strategy.

The Dover sole, *Microstomus pacificus*, is a prominent member of the deepwater continental shelf community off Oregon (Pearcy 1978) and makes the largest contribution to total biomass of flatfishes landed commercially off the coast of Oregon (Demory et al.³). Yet the published literature on the trophic role of this species in deepwater continental shelf assemblages is sparse. Hagerman (1952) listed "small bivalves...scaphopods...sipunculids, polychaetes (*Nereis* sp.), nematodes, echinoids (sea urchins), ophiuroids (brittle stars),...gastropods (*Thais* sp.),...at times...

shrimp and other crustacean forms" as principal prey animals off California. Pearcy and Hancock (1978) included a list of 35 common polychaete species or taxa, 7 crustacean species or taxa, 9 mollusc species or taxa, and 2 echinoderm taxa consumed by Dover sole collected on the central Oregon continental shelf.

Although selectivity has long been considered an important aspect in resource partitioning within and among species, few studies have included a survey of available food items on which to base and compare feeding habit descriptions of benthic fishes. Early work by Steven (1930) described prey available and consumed by demersal fishes in the English Channel. Later, Jones (1952) related the Cumberland coast bottom fauna and food of flatfishes. More recently, Arntz (1978) described the benthic food web of the western Baltic, including food selection by the two most common demersal fish species found there (the cod, *Gadus*

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³Demory, R. L., M. J. Hosie, N. TenEyck, and B. O. Forsberg. 1976. Groundfish surveys on the continental shelf off Oregon, 1971-74. Oreg. Dep. Fish Wildl. Inf. Rep. 76-9, 7 p.

morhua, and the dab, *Limanda limanda*). Levings (1974) investigated seasonal changes in feeding and particle selection by winter flounder, *Pseudopleuronectes americanus*, and Moore and Moore (1976) studied various factors influencing the selection of food by the flounder *Platichthys flesus*. In North Pacific demersal communities, however, even the qualitative aspects of selectivity and the role of selectivity in trophic dynamics have yet to be estimated.

The objectives of this study are to: 1) describe the food habits of the Dover sole in an area of an active commercial fishery for this species off Oregon, 2) determine if the species is a selective feeder, and 3) determine how feeding habits are related to location of fish capture, size of fish, and size and depth of prey in the sediment.

METHODS AND MATERIALS

Samples of demersal fishes and benthic invertebrates were taken on the central continental shelf off Oregon in locations of high Dover sole abundance (Demory et al. footnote 3; Tyler⁴) (Figure 1). Station SG29 (lat. 44°05.0' N, long. 124°35.0' W) was located in Heceta Swale, the region east of Heceta Bank. The mean sampling depth was 119 m; the sediment is silty sand (Maloney 1965). Station SG10 (lat. 43°49.3' N, long. 124°50.0' W) was located south of Heceta Bank. The mean sampling depth was 426 m. The sediment is glauconitic sand; however, sediment distribution is patchy in this area (Bertrand 1971). Samples were taken over a limited area and time interval to reduce large-scale spatial and temporal variability (SG29: 41.6 km², 44 h; SG10: 34.21 km², 27 h; day and night 20-24 June 1976).

Benthic infauna was sampled at each station by two box corers: a 0.1 m² Bouma box corer (Bouma 1969) and a modified 0.25 m² Hessler-USNEL box corer (Hessler and Jumars 1974). The Hessler-USNEL box corer is designed to reduce pressure waves which often blow away small surface invertebrates before corer impact. Box cores provide the largest, deepest, and least disturbed sample of consistent surface area when compared with other commonly used sediment samplers (Word⁵). In

<45 min after retrieval of the core, core samples were extruded in 0.1 m² boxes and sectioned at 1 cm intervals for the first 10 cm, 2 cm intervals for the next 10 cm, and 4 cm intervals for the remainder of the core. These sections were then washed onto a 1 mm aperture sieve screen, and washed invertebrate samples were preserved in 4% unbuffered formaldehyde.

Beam trawl tows to sample Dover sole were made in the immediate area of box core sampling. A beam trawl with an effective trawling width of 2.72 m (Carey and Heyamoto 1972) and 3.8 cm stretched mesh lined with 1.3 cm mesh netting was towed at 3 kn for 30 min per haul at SG29 and 20 min at SG10. Fish were preserved in 8% (unbuffered) formaldehyde as soon as possible after the trawl was brought aboard. The body cavities of fish >12 cm were slit to allow rapid formaldehyde penetration into the coelom.

A total of four 0.1 m² box cores, eight 0.25 m² box cores, and 15 successful beam trawl tows were made at SG29. At SG10, nine 0.1 m² box cores and 10 successful beam trawl tows were made.

In the laboratory, invertebrates from box cores were transferred to 70% isopropyl alcohol, sorted into major taxa, and identified to species whenever possible. Dover sole were measured (standard length) and stomachs (from esophagus to constriction before pyloric caeca) were removed and transferred to 70% isopropyl alcohol. A total of 202 stomachs from SG29 and 63 stomachs from SG10 were processed. Stomach contents were sorted into phyla and identified to species whenever possible. Total lengths of polychaetes, aplousobranchs, and scaphopods were measured. Gastropod and pelecypod measurements were made along the longest axis and included shells. Crustaceans were measured from base of rostrum to point of flexure of abdomen. Since ophiuroids occurred as pieces, a single measurement of ophiuroid volume per stomach was made.

Dry weights of prey items were estimated using conversion factors. Shells, tubes, massive paleal setae (in the case of the polychaete *Pectinaria californiensis*), and posterior scutes (in the case of the polychaete *Sternaspis fossor*) were removed before individual items of known length were dried (36 h, 65° C). Items were weighed using an electrobalance or Mettler⁶ balance. Regression curves were fitted to sets of length-weight points

⁴A. V. Tyler, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, pers. commun. June 1976.

⁵Word, J. Q. 1977. An evaluation of benthic invertebrate sampling devices for investigating feeding habits of fish. In C. A. Simenstad and S. J. Lipovsky (editors), Proc. 1st Pac. NW. Tech. Workshop. Fish food habits studies, p. 43-55. Washington Sea Grant, Seattle. WSG-WO-77-2.

⁶Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

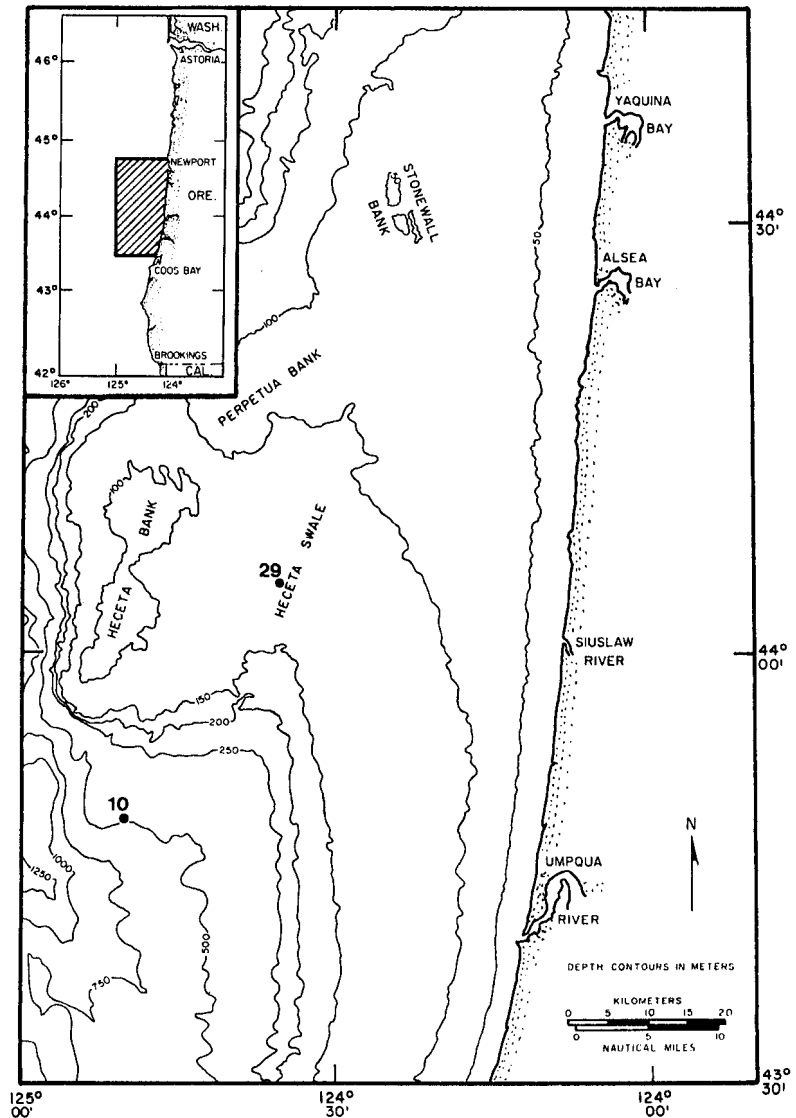


FIGURE 1.—Location of sampling stations on the central continental shelf off Oregon.

for gastropods, pelecypods, amphipods, cumaceans, and "noncylindrical" polychaetes (*Sternaspis fossor*); otherwise, a simple milligram per centimeter conversion factor was calculated for polychaetes, aplousobranchs, and scaphopods. For each prey taxon, at least 10% of the total number consumed or 20 individuals were dried and weighed. Although formaldehyde and particularly alcohol are known to leach out organic material from biological specimens and to reduce the weight of the organisms (Thorson 1957; Howmiller 1972), these estimates were assumed to be adequate for estimating relative importance of

prey taxa biomass. Dry weights of ophiuroids overestimate the food value of these animals compared with soft-bodied polychaetes. Therefore, ash-free dry weight estimations were made for all groups from conversion factors found in the literature and previous laboratory work for shell-free or tube-free weights (Richardson et al.⁷; Ruff⁸).

⁷Richardson, M. D., A. G. Carey, Jr., and W. H. Colgate. 1977. The effects of dredged material disposed on benthic assemblages off the mouth of the Columbia River. In Final report, Department of the Army Corps of Engineers, p. 59. Contracts DACW 57-75-C0137 and DACW 57-76-C-0092.

⁸R. E. Ruff, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. March 1978.

RESULTS

Feeding Habits of Dover Sole

Dover sole off the Oregon coast in midsummer fed most often on polychaetes, although a surprisingly large proportion of the diet consisted of ophiuroids (Table 1). At station SG29, polychaetes occurred in 97.3% of stomachs examined, and composed 43% of the total ash-free dry weight of stomach contents examined. Ophiuroids occurred in 63.0% of the stomachs, made up 41% of the

ash-free dry weight of stomach contents at that location. At station SG10, polychaetes occurred in 83.6% of the stomachs examined and constituted 11% of total ash-free dry weight of stomach contents examined, while ophiuroids occurred in 80% of those stomachs, composing 84% of ash-free dry weight of the diet at SG10; otherwise, crustaceans and molluscs made up <6% of biomass consumed.

The largest proportion of polychaete biomass consumed was derived from *Pectinaria californiensis* and members of the families Glyceridae (SG29: *Glycera capitata*, SG10: *Glycinde picta*),

TABLE 1.—Percentage of frequency of occurrence, numerical abundance, dry weight, and ash-free dry weight that polychaetes, molluscs, crustaceans, and ophiuroids composed in Dover sole stomachs at SG29 and SG10.

Taxon	Percent frequency of occurrence		Percentage of numerical total ¹		Percentage of total dry weight		Percentage of total ash-free dry weight	
	SG29	SG10	SG29	SG10	SG29	SG10	SG29	SG10
Polychaeta	97.3	83.6	84.7	57.7	22.3	3.6	42.7	10.5
Mollusca	68.6	69.1	9.1	15.4	6.0	1.0	14.5	3.5
Gastropoda	8.0	20.0	.4	2.3	.3	.3		
Pelecypoda	61.2	50.9	7.2	9.9	5.2	.5		
Scaphopoda	12.2	16.4	.7	1.5	.3	.1		
Aplacophora	16.9	14.5	.7	1.7	.2	.1		
Crustacea	62.2	83.6	6.2	26.9	.9	.8	1.5	2.1
Miscellaneous ²	15.3	18.2	.7	2.0	.5	.2		
Cumacea	26.6	47.3	1.5	5.5	.1	.2		
Amphipoda	48.9	76.4	3.9	19.4	.3	.4		
Ophiuroidea	63.0	80.0			70.8	94.6	41.4	84.0

¹Ophiuroids excluded from total, since this organism was nearly always found as uncountable fragments of arms.

²Includes Ostracoda, Copepoda, Pericarida, and Eucarida.

TABLE 2.—Frequency of occurrence of polychaete families in Dover sole, and percentage composition of polychaetes found in stomachs on numerical and dry weight bases at SG29 and SG10.

Family	Percent frequency of occurrence		Percentage of numerical total of polychaetes		Percentage of total dry weight of polychaetes	
	SG29	SG10	SG29	SG10	SG29	SG10
Ampharetidae	19.1	34.5	2.0	8.5	1.5	2.5
Apistobranchidae	18.1	1.8	1.3	.2	.1	.1
Arenicolidae	.5	0	.1	0	<.1	.1
Capitellidae	52.7	30.9	7.7	7.6	1.8	1.7
Chaetopteridae	2.7	0	<.1	0	<.1	0
Cirratulidae	26.1	18.2	2.1	5.0	.6	1.6
Cossuridae	33.5	0	4.4	0	.2	0
Flabelligeridae	5.9	3.6	.4	.9	3.6	2.4
Glyceridae	43.6	18.2	3.7	4.0	11.3	14.1
Goniadidae	3.2	14.5	.2	1.2	.8	6.5
Lumbrineridae	81.4	23.6	19.2	4.3	4.5	1.6
Magelonidae	6.4	5.5	.3	.7	.4	1.0
Maldanidae	39.9	21.8	4.3	4.0	4.5	3.2
Nephtyidae	34.6	60.0	3.4	24.6	.5	2.8
Nereidae	1.1	0	<.1	0	<.1	0
Onuphidae	13.8	3.6	.9	.7	3.7	.5
Opheliidae	1.6	25.5	<.1	5.2	.5	7.4
Orbiniidae	4.3	0.0	.2	0	<.1	0
Oweniidae	56.9	14.5	8.8	1.7	.8	.1
Paraonidae	78.7	45.5	24.1	14.7	4.0	5.5
Pectinariidae	11.7	18.2	1.1	3.1	20.9	29.2
Phyllodocidae	17.0	7.3	1.1	2.8	.1	.6
Polynoidae	.5	0	<.1	0	<.1	0
Sabelliidae	.5	3.6	<.1	.5	<.1	.1
Sigalionidae	23.9	29.1	1.6	4.0	.3	2.6
Sphaerodoridae	.5	0	<.1	0	<.1	0
Spionidae	51.6	9.1	5.9	1.4	4.7	1.4
Sternaspidae	32.4	5.5	2.1	.9	12.1	4.5
Syllidae	6.9	7.3	.3	.7	<.1	0
Terebellidae	31.9	16.4	3.8	3.1	22.7	10.5

Terebellidae (SG29: *Pista disjuncta*), Sternaspidae (SG29: *Sternaspis fossor*), and Opheliidae (SG10: *Travisia foetida*). Most frequently consumed polychaete species were generally smaller bodied, including lumbrinerid (primarily at SG29), nephtyd (primarily at SG10), paraonid, and capitellid polychaetes (Table 2). Principal prey species are listed in Tables 3 (SG29) and 4 (SG10).

Pelecypods were the most frequently consumed molluscs, constituting most of the mollusc biomass eaten (Table 1). *Macoma* spp., *Adontorhina cyclia*, and *Axinopsida serricata* were most important at SG29 and *Crenella decussata*, *Huxleyia munita*, and *Odontogena borealis* were common at SG10. Among crustaceans, amphipods (SG29: *Harpiniopsis excavata*, *H. fulgens*; SG10: *Melphidippa*

amorita, *Ampelisca macrocephala*, *Nicipe tumida*) occurred more frequently and in larger numbers than cumaceans, and were consumed more often than molluscs at the deeper station.

Changes in Diet with Predator Length

A chi-square test (Tyler⁹) was used to determine the dependency of diet on fish size, based on differences in frequency of occurrence of prey items consumed by predators belonging to different length intervals. The chi-square test showed many size-related variations in the diet of Dover sole taken at SG29 but few in the diet at SG10. At

⁹Tyler, A. V. 1969. Computer programs for analysis of feeding heterogeneities related to predator body size. Fish. Res. Board Can. Tech. Rep. 121, 49 p.

TABLE 3.—SG29: Changes in selectivity with fish size considered by principal prey taxa. Range of fish size is divided to maximize heterogeneity between size intervals for each principal prey taxon as described in text.

Taxon	For fish < length (cm)	Ivlev index of electivity	Chi-square value	Significance ¹	For fish ≥ length (cm)	Ivlev index of electivity	Chi-square value	Significance ¹
1 Polychaeta:								
2 Ampharetidae ²	31	0.45	8.646	***	31	-0.33	2.060	NS
3 Apistobranchidae: <i>Apistobranchus ornatus</i>	21	-1.00	.688	NS	21	.59	7.286	**
4 Capitellidae: <i>Decamastus gracilis</i>	29	-.05	1.957	NS	29	.15	2.086	NS
5 Cirratulidae: <i>Tharyx</i> spp. ³					11	-.13	3.034	NS
6 Cossuridae: <i>Cossura</i> sp.	29	.52	11.762	***	29	.72	42.421	***
7 Glyceridae: <i>Glycera capitata</i>	37	-.12	1.781	NS	37	.55	18.297	***
8 <i>Glycinde picta</i>					11	.69	11.073	***
9 Lumbrineridae: <i>Lumbrineris latreilli</i>					11	.68	149.112	***
10 <i>Ninoe gemma</i>	32	-.76	33.946	***	32	-.20	1.858	NS
11 Maldanidae ²	33	-.64	206.469	***	33	-.18	12.331	***
12 Nephtyidae: <i>Nephtys</i> sp.	33	.67	25.046	***	33	.54	7.781	**
13 Onuphidae: <i>Nothria</i> spp. ⁴	35	-.62	17.607	***	35	.50	10.411	***
14 Oweniidae: <i>Myriochele heeri</i>	33	.15	.540	NS	33	-.48	5.548	*
15 <i>M. oculata</i>	33	-.17	17.364	***	33	-.60	37.979	***
16 Paraonidae ²	21	.42	15.575	***	21	.60	179.784	***
17 <i>Aedicira antennata</i> ⁵	24							
18 <i>Aricidea ramosa</i>	21	.66	22.164	***	21	.73	86.711	***
19 <i>Paraonis gracilis</i> ⁵	21							
20 Pectinariidae: <i>Pectinaria californiensis</i>	34	-.38	.851	NS	34	.91	59.486	***
21 Phyllocooidae: <i>Anaitides groenlandica</i> ⁶	29	.28	.127	NS	29	.66	5.983	*
22 Sigalionidae ²	24	.77	2.343	NS	24	.93	21.043	***
23 Spionidae: <i>Prionospio</i> spp. ³					11	.12	.144	NS
24 <i>Spiophanes</i> spp. ³	26	-.35	9.185	***	26	.08	.129	NS
25 <i>S. berkeleyorum</i>	27	-.47	17.738	***	27	-.19	5.501	*
26 Sternaspidae: <i>Sternaspis fossor</i>	21	-1.00	2.775	NS	21	.22	1.613	NS
27 Terebellidae: <i>Pista cristata</i>	35	.19	0.625	NS	35	.79	66.159	***
28 <i>Terebellides stroemii</i>	28	-.70	13.772	***	28	-.13	1.180	NS
Mollusca:								
29 Pelecypoda (unidentifiable, nonprincipal) ⁷					11	-.81	668.332	***
30 "A-type" ⁸	33	-.55	195.445	***	33	-.95	137.863	***
31 <i>Macoma</i> spp. ³					11	-.47	50.222	***
32 Scaphopoda	28	-.86	80.797	***	28	-.68	70.064	***
33 Aplacophora					11	.09	.002	NS
Crustacea:								
34 Cumacea: <i>Eudorella pacifica</i>	35	-.07	.859	NS	35	-.72	8.243	***
35 Amphipoda: <i>Harpiniopsis excavata</i> ⁹					11			
36 <i>H. fulgens</i> ⁹	36	.38	6.935	**	36	-.01	.001	NS
37 Ophiuroidea ¹⁰	28	.92	37.430	***	28	.93	41.757	***

¹NS = not significant; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

²All members of family pooled.

³All members of genus pooled (species identifications not possible).

⁴Members of two species pooled based on taxonomic uncertainty (*Nothria elegans* and *N. iridescens*).

⁵No members of this genus present in box core.

⁶All members of genus pooled (species identifications tentative or uncertain).

⁷All nonprincipal or unidentifiable pelecypods found in fish compared with all pelecypods found in box core.

⁸*Axinopsida serricata* and *Adontorhina cyclia* pooled.

⁹No members of this genus present in box cores, value for *Harpiniopsis fulgens* represents all Phoxocephalidae, pooled.

¹⁰Based on frequency of occurrence in fish compared with numbers of ophiuroids found in box core.

TABLE 4.—SG10: Changes in selectivity with fish size considered by principal prey taxon. Range of fish size is divided to maximize heterogeneity between size intervals for each principal prey taxon as described in text.

Taxon	For fish >length (cm)	Ivlev index of electivity	Chi-square value	Significance ¹
Polychaeta:				
Ampharetidae ²	24	0.57	11.875	***
Capitellidae: <i>Decamastus gracilis</i> ³	24	-.22	4.777	*
Cirratulidae: <i>Tharyx</i> sp. ⁴	24	.89	11.436	***
Glyceridae: <i>Glycinde</i> sp.	28	.59	3.320	NS
Lumbrineridae: <i>Lumbrineris</i> sp. ⁴	24	.77	8.518	***
Maldanidae ²	24	-.32	5.788	*
Nephtyidae: <i>Nephtys</i> sp.	24	.98	91.741	***
Opheliidae: <i>Travisia</i> sp. ⁴	24	.91	15.763	***
Paraonidae ²	24	.45	13.691	***
Pectinariidae: <i>Pectinaria californiensis</i> ⁵	24	.41	1.823	NS
Sigalionidae ²	24	.68	6.778	**
Mollusca:				
Pelecypoda (unidentifiable, nonprincipal)	24	-.35	14.176	***
<i>Huxleyia munita</i>	24	-.84	110.067	***
<i>Crenella decussata</i>	24	-.78	171.609	***
<i>Odontogena borealis</i>	25	-.81	61.853	***
Gastropoda: pteropoda ⁶	24			
Scaphopoda	24	-.39	5.516	*
Aplacophora	26	.28	.756	NS
Crustacea:				
Amphipoda: <i>Melphidippa amorita</i> ⁶				
<i>Nicipe tumida</i> ⁶				
<i>Metopa</i> sp.				
<i>Ampelisca macrocephala</i>	24	.77	8.518	***
Cumacea: <i>Campylaspis</i> sp. ⁴	24	.79	14.800	***
Ophiuroidea ⁷	24	.25	3.764	NS

¹NS = not significant; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

²All members of the same family pooled.

³Positive identification of species difficult for this species, pooled with *Mediomastus californiensis*.

⁴Species not found in box core, calculation based on numbers of representatives of same genus.

⁵Species pooled with *Pectinaria belgica*.

⁶No representative of genus in box core—no electivity values calculated.

⁷Based on frequency of occurrence in fish compared with numbers of ophiuroids found in box core.

SG29, out of 35 principal prey taxa (taxa occurring in at least 10% of stomachs containing food), 27 showed significant changes in frequency of occurrence. Five types of prey frequency patterns were apparent for these 27 prey over the size range of fish sampled, 11-42 cm. Examples are shown in Figure 2.

The first prey pattern, typified by the polychaete *Decamastus gracilis* (I), reflects prey which occurred at low frequencies in diets of small-sized fish (11-20 cm) and at increasing frequency in diets in intermediate-sized fish (21-30 cm), and which remained approximately constant at that same frequency in the diets of large-sized fish (30-42 cm) (Figure 2). Other taxa for which this pattern existed include the Ophiuroidea; polychaetes *Aedicira antennata*, *Spiophanes berkeleyorum*, the Sigalionidae, *Ninoe gemmea*, *Spiophanes* sp.; and the Scaphopoda, many of which are sessile or motile outside of tubes and surface feeders.

The second prey pattern describes taxa which occurred at relatively high frequency in diets of small-sized fish and occurred at decreased frequency in diets of intermediate- and large-sized fish; e.g., the small tubed polychaetes *Myriochele oculata* (II) and *M. heeri*, the amphipod *Harpiropsis fulgens*, and small ampharetid

polychaetes. The cumacean *Eudorella pacifica*, pelecypod group *Adontorhina cyclia-Axinopsida serricata*, and polychaete *Nephtys* sp. also occurred often in diets of intermediate-sized fish, but occurred at low frequency in diets of large-sized fish.

The third prey pattern is depicted by a hump-shaped curve, in which case a prey taxon occurred at low frequencies in diets of small- and large-sized fish but at relatively high frequencies in diets of intermediate-sized fish. Many principal prey taxa belong to this category, including the polychaetes *Anaitides groenlandica* (III), *Aricidea ramosa*, *Sternaspis fessor*, *Paraonis gracilis*, *Apistobranchus ornatus*, *Cossura* sp., and *Terebellides stroemii*.

The fourth prey pattern reflects increasing prey frequency with increasing fish size. Prey taxa following this pattern included many larger tubed, surface and subsurface feeding polychaetes: *Nothria elegans* (IV), *Pectinaria californiensis*, *Glycera capitata*, *Pista cristata*, and the Maldanidae.

The fifth prey pattern includes prey whose frequency of occurrence in diets did not change significantly over the entire size range of fish sampled; e.g., polychaetes *Lumbrineris latreilli* (V),

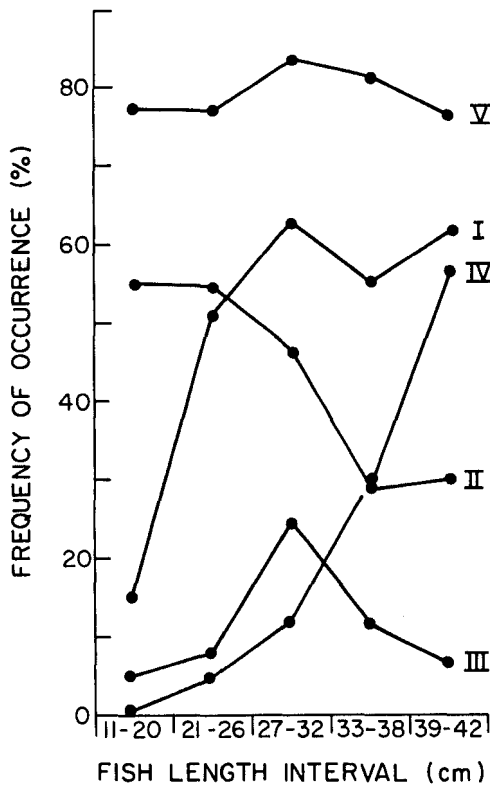


FIGURE 2.—Five patterns of change in the frequency of occurrence of prey for different sizes of Dover sole at SG29. Curve shape I typified by *Decamastus gracilis*, shape II by *Myriochele oculata*, shape III by *Anaitides groenlandica*, and shape IV by *Nothria elegans*.

Glycinde picta, *Prionospio* sp., *Tharyx* sp., the amphipod *Harpiniopsis excavata*, the Aplacophora, unidentifiable Pelecypoda, and *Macoma* sp.

At SG10, 19 out of the 26 principal prey species showed no significant change in frequency of occurrence over the range of fish sampled (24-43 cm). The frequency of occurrence of *Melphidippa amorita*, an amphipod, increased significantly in fishes 32 cm or longer. Occurrence of two amphipod taxa, *Nicipe tumida* and *Metopa* sp., decreased significantly in fish 32-33 cm or larger. In the case of the four remaining taxa, the series of chi-square tests produced intervals across which frequency of occurrence changed gradually, rather than defining a well-marked break in frequency at one particular length. *Glycinde picta*, a tubeless, subsurface deposit feeding polychaete, increased in frequency in fish 28-29 cm or longer. *Odontogena borealis*, a small bivalve, increased over the 25-32 cm fish size interval. Aplacophorans increased in

frequency in 26-27 cm fish and longer, and Ophiuroidea increased in the 30-32 cm interval.

Selectivity

A chi-square test of 2×2 contingency tables was used to test the null hypothesis that the relative abundance of a taxon among items consumed is dependent on the relative abundance of the taxon in the environment. Ivlev's (1961) index of electivity

$$E = (r_i - p_i)/(r_i + p_i),$$

where r_i = percentage of ration composed of a given prey taxon i and p_i = percentage of food complex in environment composed of prey taxon i , was used to determine whether selection was positive or negative. Overall trends in selectivity by major taxa for all fish from each station are shown in Table 5. Ophiuroids were the most highly selected food taxon at SG29. The calculations of electivity indices and chi-square values for this taxon were based on number of occurrences rather than number of individuals consumed, and hence underestimated the importance of ophiuroids. Ophiuroids were removed from the data sets for subsequent calculations so that estimations for other taxa were unbiased by this representation. Polychaetes were selected food of fish at both locations. Chi-square values were larger for polychaetes than any other positively selected taxon. Molluscs, especially pelecypods and

TABLE 5.—Summary of selectivity considered by major taxa at stations SG29 and SG10 for Dover sole of all sizes.

Station	Taxon	Ivlev index of electivity	Chi-square value	Significance ¹
SG29	Polychaeta	0.13	243.451	***
	Mollusca:			
	Pelecypoda	-.49	248.739	***
	Gastropoda	-.43	6.015	**
	Scaphopoda	-.75	112.448	***
	Aplacophora	.09	.105	NS
	Crustacea:			
	Amphipoda	.08	.839	NS
	Cumacea	-.10	.766	NS
	Ophiuroidea	.92	40.724	***
SG10	Polychaeta	.33	117.446	***
	Mollusca:			
	Pelecypoda	-.72	425.683	***
	Gastropoda	.50	4.061	*
	Scaphopoda	-.39	4.602	*
	Aplacophora	.28	1.039	NS
	Crustacea:			
	Amphipoda	.69	79.629	***
	Cumacea	.67	20.771	***
	Ophiuroidea	.25	3.764	NS

¹NS = not significant; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

scaphopods, were the least often selected food at both locations. Aplacophoran molluscs, however, were neither significantly selected nor rejected. At SG29, the numerical proportions of crustaceans (amphipods and cumaceans) in stomachs and box core samples were nearly equal. At SG10, however, these crustaceans appeared highly selected.

Among polychaetes at SG29, the most highly selected prey species were *Glycinde picta* and *Lumbrineris latreilli* (in fish of all sizes, i.e., >11 cm), Sigalionidae (especially in fish >21 cm), *Aricidea ramosa* (in fish of all sizes, but especially those >21 cm), *Cossura* sp. (in fish of all sizes, but especially those >29 cm), *Pectinaria californiensis* (in fish >34 cm), and *Pista cristata* (in fish >35 cm) (Table 3). No principal mollusc taxa were selected, with the exception of aplacophorans, which appeared to be neither significantly selected nor ignored. The cumacean *Eudorella pacifica* was negatively selected by fish >34 cm. The phoxocephalid amphipod species *Harpiniopsis excavata* and *H. fulgens* were not present in box cores, indicating high selectivity by fish or inadequate box core sampling. If values for all phoxocephalids were pooled, it appeared that the family was selected positively by fish <36 cm.

Changes in electivity related to fish size and

prey taxa are shown in Figure 3. Values of E were calculated for each principal prey taxon found at SG29 within three fish size intervals (11-21, 22-31, and 32-42 cm). The patterns of changes in electivity with fish size are similar to the patterns found for changes in frequency of occurrence of prey with fish size in Figure 2. In one pattern, electivity of a prey taxon was low by small fish, higher by intermediate fish, and remained constant by large fish relative to intermediate values (Figure 3A). Taxa belonging to this category included the polychaetes *Anaitides groenlandica* (21), *Sternaspis fossor* (26), *Prionospio* spp. (23), *Spiophanes* spp. (24), and *Terebellides stroemii* (28); and the Scaphopoda (32). In the second pattern (Figure 3B), electivity of prey taxa decreased with fish size. Taxa in this category included the polychaetes *Myriochele oculata* (15), *M. heeri* (14), and Ampharetidae (2); phoxocephalid amphipods; the cumacean *Eudorella pacifica* (34); and the combined pelecypod group *Adontorhina cyclia-Axinopsida serricata* (30). In the third category (Figure 3C), electivity was highest by intermediate-sized fish, and lower for larger and smaller fish. Taxa following this pattern included the polychaetes *Cossura* sp. (6), *Tharyx* sp. (5), and *Apistobranchus ornatus* (3). In the fourth

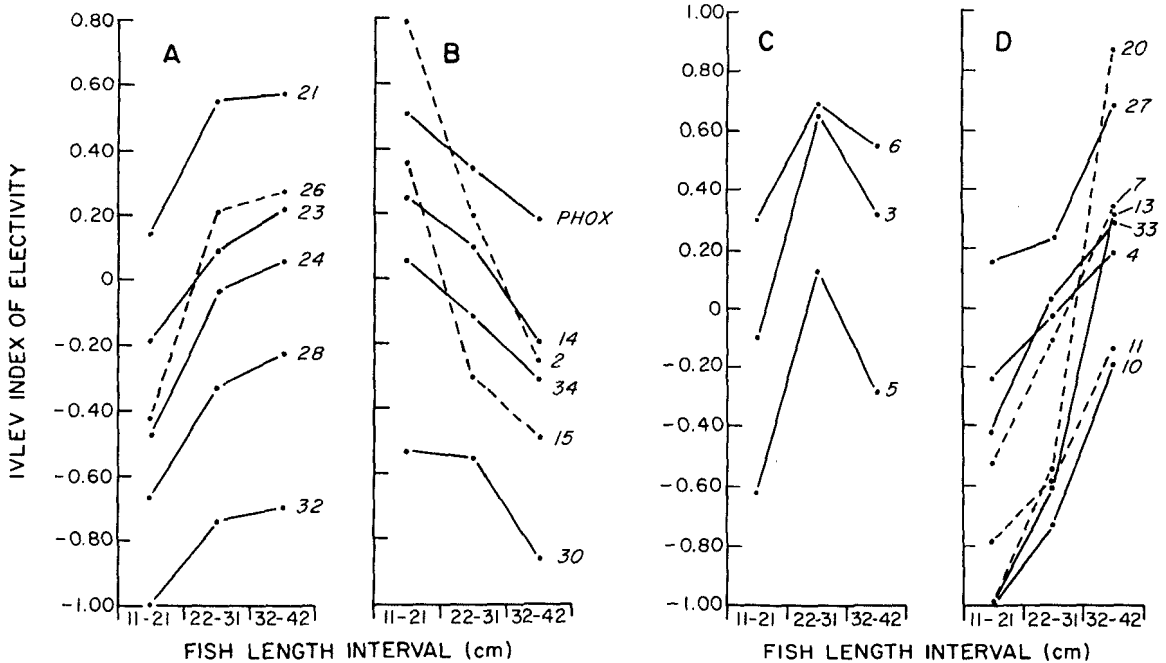


FIGURE 3.—Changes in Ivlev indices of electivity with fish length at SG29. Numbers designate taxa of prey in Table 3. Phox = Phoxocephalidae. Taxa with similar patterns of change are grouped as Figures A, B, C, and D.

category (Figure 3D), electivity increased among all three size categories of fish. This pattern existed for the large-bodied, tubed polychaetes *Pectinaria californiensis* (20), *Pista cristata* (27), *Nothria* sp. (13), and Maldanidae (11), the large-bodied, tubeless polychaete *Glycera capitata* (7); two small-bodied, tubeless polychaetes *Decamastus gracilis* (4) and *Ninoe gemmea* (10); and the aplacophoran molluscs (33). In a fifth pattern (not shown), electivity of a prey taxon did not change significantly with fish size. The polychaetes *Lumbrineris latreilli*, *Glycinde picta*, the Paraonidae, and the Sigalionidae followed this pattern, as did the molluscan genus *Macoma*. Taxa belonging to each category of electivity patterns were not necessarily identical to taxa belonging to each analogous category of frequency of occurrence patterns, since the index of electivity of a prey taxon was based on proportion of numerical abundances of the prey taxon in the diet, rather than on frequency of occurrence.

Among polychaetes at SG10, the most highly selected prey taxa were *Nephtys* sp. and *Tharyx* sp. by fish of all sizes (Table 4). No specimens of *Travisia foetida* or *Lumbrineris latreilli* were found in the core samples so the values shown in Table 4 were based on pooling of the taxa at the generic level. Once again, all principal molluscan taxa were negatively selected, with the exception of aplacophorans (no significant selection) and pteropods, which were not found in core samples. If values for all cumaceans of genus *Campylaspis* were pooled, the taxon appeared positively selected; however, no species common to both fish and box core were found. In the case of amphipods, three of the four principal taxa were not represented in box core samples. The fourth, *Ampelisca macrocephala*, appeared positively selected based on these samples.

Merely because a taxon is positively selected does not mean it plays an especially important role in diet. For example, frequency of occurrence, biomass contribution, and numerical abundance of gastropods in diets of fish at SG10 were small compared with other taxa. Yet this taxon was positively selected (Table 5). Conversely, even though a taxon is negatively selected, it may still play an important role in diets. Positive selection may also be an artifact of the environmental sampling device. Crustaceans appear highly selected at SG10 (Table 5), but this may be partly due to the inefficiency of the box corer in sampling motile epifauna relative to infauna.

A significant positive correlation was found between prey size (weight/length) of 16 prey and the length of fish at which that prey began to significantly increase in frequency ($r = 0.540$, $P < 0.05$) (Figure 4). Large prey were consumed by large fish. Prey which decreased in frequency were generally small-bodied polychaetes (Ampharetidae, *Nephtys* sp., *Myriochele heeri*, *M. oculata*), amphipods, and cumaceans. In the case of the five prey taxa which showed no significant change in frequency in fish of different sizes (Aplacophora, *Glycinde picta*, *Prionospio* sp., *Tharyx* sp., and *Lumbrineris latreilli*) some other criteria for inclusion in diet may have been more important than size.

When prey frequency increased with increased size of Dover sole at SG29, predator selectivity also appeared to increase. From the iterative chi-square tests described earlier, a fish length was found which divided the total fish size range into (usually) two length intervals of statistically homogeneous prey frequency for each prey taxon. A value of E was calculated for each interval, and the difference in values between the two intervals was determined for each applicable prey taxon. This difference was then plotted against the fish

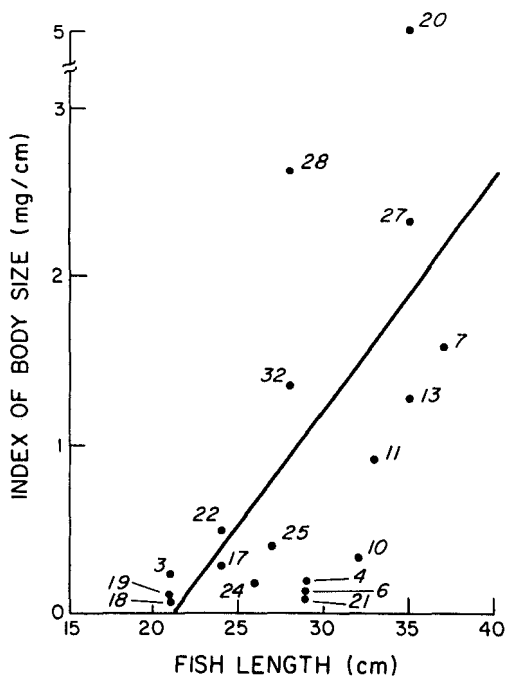


FIGURE 4.—Body size of prey vs. fish length at which frequency of prey increased significantly. Numbers designate prey taxa (see Table 3).

length which separated the two intervals of statistical homogeneity for that prey. (Prey species which were not present over the entire range of fish sampled were not included, e.g., *Apistobrachius ornatus* and *Sternapis fossor*.) For example, the value of E for the polychaete *Glycera capitata* for fish <37 cm was -0.12. For fish 37 cm or larger, the value of E rose to 0.55; the difference, 0.67, was associated with a division point of 37 cm. Although the resulting relationship (Figure 5) may not be amenable to tests of statistical significance, a positive trend exists. Prey which showed an increase in frequency in larger fishes also showed a greater increase in electivity by these larger fish.

Nonparametric ranking statistics were used to test the possible effects of prey mobility, feeding method, and protective structures (polychaete tubes) on size-related increases in prey frequency. The rank for each prey was determined by the fish length at which the prey showed a significant increase in frequency (Table 3). For each test, prey were assigned to categories based on characteristics as described in published literature (Barnes 1968; Smith and Carlton 1975; Jumars and

Fauchald 1977) or as described by workers familiar with local fauna (Jones et al.¹⁰). A lack of difference between summed ranks for each category would imply that the distributions of different prey types (motile, discretely motile, or sessile, in this example) were the same over all fish sizes at which any prey frequency increased; e.g., a prey taxon which was found at higher frequency in fish >21 cm was just as likely to be motile or sessile as one which was found at higher frequencies in fish 35 cm or longer.

The results of these nonparametric tests (Table 6) show that no one motility type predominated in prey taxa frequent in either small or large fish sizes. Feeding locale, a possible indicator of exposure of a taxon to predation at the sediment surface, was not significant in explaining size-related variations in prey frequency. Feeding type, which is related to both degree of exposure and motility, also showed no trend when ranked over fish lengths. The only statistically significant relationship appeared when ranks for 11 tubed polychaetes were compared with ranks for 7 untubed polychaetes. Tubed taxa generally had a higher rank than untubed taxa. This implied that large fish selected tubed more often than untubed polychaetes. However, three of the four polychaete taxa which decreased in frequency in larger fish (Table 3) have tubes. Thus, the presence or absence of tubes in polychaetes did not always appear to be an important criterion for variation in prey frequency with fish size.

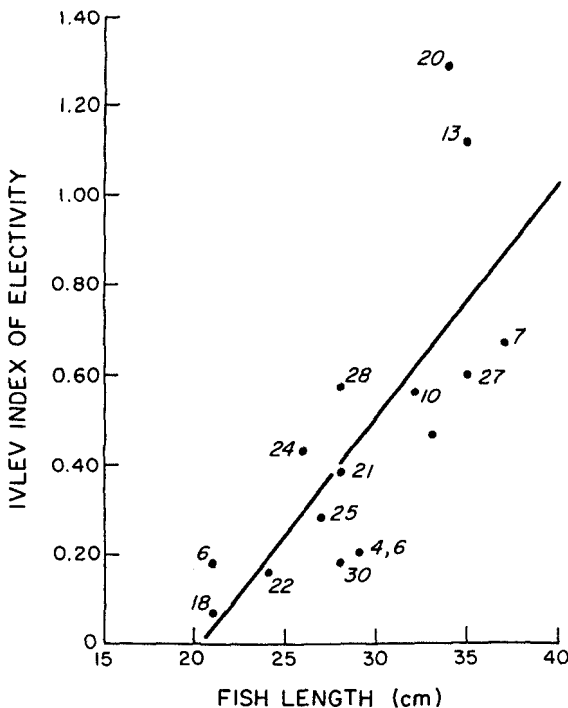


FIGURE 5.—Increase in the Ivlev electivity of prey vs. length of fish at which frequency of that prey increased significantly. Numbers designate prey taxa (see Table 3).

¹⁰H. Jones, G. Bilyard, and K. Jefferts, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. March 1978.

TABLE 6.—Results of nonparametric tests of effects of prey characteristics on fish size related increases of prey frequency. Prey are ranked by fish size at which prey frequency increased.

Test and categories	Value of test statistic	Critical value for significance ¹
Prey motility:		
Motile	$^2H = 0.029$	$\chi^2 = 5.991$
Discretely motile	NS	df = 2
Sessile		
Feeding mechanism:		
Tentaculate	$^2H = 3.508$	$\chi^2 = 5.991$
Burrowing (deposit feeder)	NS	df = 2
Carnivorous (raptorial)		
Protective structures:		
Tubed polychaetes	$^3U_S = 58$	$U_S = 58$
Untubed polychaetes	"	$n_1 = 11, n_2 = 7$
Feeding locale:		
Surface	$^3U_S = 57$	$U_S = 72$
Subsurface	NS	$n_1 = 11, n_2 = 9$

¹Significant at 95% confidence level.

²H: result from Kruskal-Wallis test (3 categories) (Sokal and Rohlf 1969).

³U_S: result from Wilcoxon two sample test (2 categories) (Sokal and Rohlf 1969).

The mean depth of a prey taxon within the sediment was significantly related to fish size at which frequency of that prey increased (Figure 6, $r = 0.542$, $P < 0.05$). Prey which were important to large fish were usually found deeper in the sediment. Prey occurring frequently in small fish were found near the sediment surface. Prey which occurred at statistically equal frequencies for all-sized fish were generally found within the top 4 cm of the core sample, e.g., *Lumbrineris latreilli*, which was consumed in large numbers by fish of all sizes. Prey which decreased in occurrence in larger fish were often concentrated near the surface, with a mean depth distribution of 2 cm. Although the relationship between depth of prey in sediment and index of body prey was not significant (Figure 7) ($r = 0.220$), few large-bodied principal prey taxa had a mean depth in the sediment < 4 cm.

At SG10, few prey taxa changed significantly in frequency of occurrence over the range of fish sizes sampled. The mean depth of a taxon within the sediment was rarely > 4 cm, and usually < 3 cm, regardless of prey body size. The depth range of all

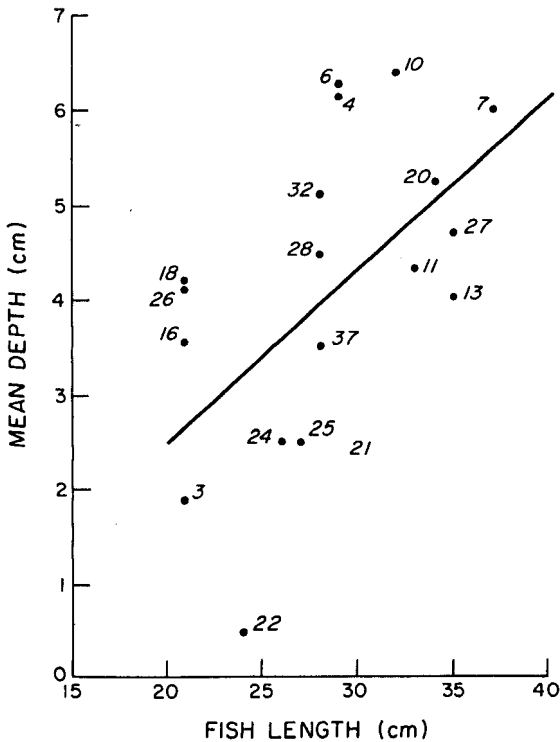


FIGURE 6.—Mean depth of prey in the sediment vs. fish length at which frequency of prey increased significantly. Numbers designate prey taxa (see Table 3).

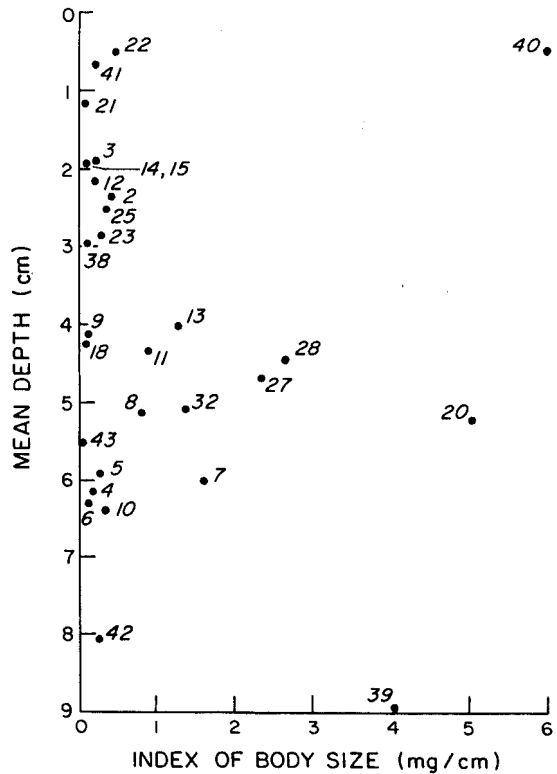


FIGURE 7.—Mean depth of prey in the sediment vs. index of prey body size. Numbers designate prey taxa (see Table 3. Nonprincipal prey: 38 = *Aricidea neosuecica*, 39 = *Laonice cirrata*, 40 = *Pherusa papillata*, 41 = *Polydora socialis*, 42 = *Spiochaetopterus costarum*, 43 = *Haploscoloplos elongatus*).

invertebrates at this station was generally shallower than at SG29.

Prey Abundance Patterns

Prey abundance also varied with location. Although the total density of individuals per square meter was slightly higher at SG10 than SG29, the density of polychaetes, a preferred taxon, averaged 886 individuals/m² at SG29 and only 397 individuals/m² at SG10 (Table 7). Most principal polychaete taxa were found in lower densities at SG10 than SG29. The density of pelecypod molluscs, a negatively selected (avoided) taxon, was several times higher at SG10 than SG29, 861 and 297 individuals/m², respectively.

DISCUSSION

How similar is the Dover sole to the hypothetical

TABLE 7.—Major taxon composition of 19 box core¹ samples containing 154 species taken at SG29 (119 m deep) and 8 box core samples containing 97 species taken at SG10 (426 m deep).

Taxon	SG29		SG10		Bertrand 1971 ²
	No./m ²	Percent	No./m ²	Percent	
Polychaetes	886.4	65.5	396.8	26.9	30.1%
Molluscs	388.5	28.7	928.5	62.9	
Pelecypods	296.6	21.9	861.1	58.3	59.2%
Gastropods	14.2	1.0	7.9	.5	1.2%
Scaphopods	66.0	4.9	45.6	3.1	1.2%
Aplacophorans	8.4	10.6	13.9	.9	0%
Other	3.3	.2			
Crustacea	73.5	5.4	61.5	4.2	4.4%
Amphipods	45.9	3.4	45.6	3.1	
Cumaceans	25.9	1.9	15.9	1.1	
Other	1.7	.1			
Echinoderms	.8	<.1	51.6	3.5	2.3%
Ophiuroids	.8	<.1	47.6	3.2	
Miscellaneous	3.3	.2	9.6	2.0	.9%
Individuals	1,352.5	n = 1,619	1,476.2	n = 744	343

¹Effective sampling area is 0.063 m².

²Values found for the same location.

optimal forager that 1) prefers more profitable prey, i.e., prey whose ratio of food value to predator search and handling time is highest, 2) feeds more selectively when profitable prey are common, and 3) ignores unprofitable prey whose addition to the diet lowers the net energy intake per time spent searching and handling (Pyke et al. 1977; Krebs 1978)?

The Dover sole is not a simple opportunistic feeder, consuming all available prey in proportion to their occurrence in the environment. Since the percentage contribution of a major taxon in the diet and in the environment (as reflected by box core samples) was often significantly different, the Dover sole can be termed a selective feeder. For example, polychaetes and ophiuroids played a more important role in the diet than molluscs and crustaceans, despite the fact that polychaetes and ophiuroids were not always most abundant in box core samples. Moreover, trends in selectivity of major taxa were qualitatively similar at both locations despite different abundances of prey. Polychaetes and ophiuroids were always positively selected, occurring more often in the diet than in the environment. Even though density of pelecypod molluscs at SG10 was three times greater than at SG29, the contribution of molluscs to total diet was lower at SG10 than SG29. This general consistency of diet between these two locations in the face of varying abundances of prey, species composition, depth of benthic macrofauna within the sediment, and depth of the station itself does not support a hypothesis of the Dover sole as a simple opportunistic feeder.

The most profitable prey for a Dover sole in

terms of food value (gram-calorie per gram dry weight) are first, molluscs and crustaceans; second, polychaetes; and third, ophiuroids (Brawn et al. 1968; Cummins and Wuycheck 1971; Tyler 1973). However, most observations of calories per gram dry weight were made for shell-free molluscs while polychaete weights included tubes. This is probably why values for *Lumbrineris fragilis*, an un-tubed polychaete, are comparable with those for pelecypods (= 4,500 g cal/g dry weight) and greater than those for amphipods (e.g., 4,050 g cal/g dry weight), while those for tubed polychaetes (e.g., *Pherusa plumosa*, *Pectinaria hyperborea*) are lower (2,200-3,500 g cal/dry weight). Ophiuroids generally have lowest food values (2,100 g cal/g dry weight) of the four major prey taxa consumed (Brawn et al. 1968; Cummins and Wuycheck 1971). Thus, an optimal diet based only on maximum caloric value per gram of food ingested would consist principally of crustaceans, followed by molluscs and polychaetes, and lastly of ophiuroids. However, observed diets of all sizes of Dover sole consisted primarily of ophiuroids and polychaetes, with relatively few molluscs and crustaceans. Thus, food value alone does not explain the diet of Dover sole.

The second factor determining profitability of prey, the relative expense of acquiring and digesting different prey, may play a more important role than food value in structuring the diet of Dover sole. Although no quantitative observations of feeding behavior in terms of search and handling costs have been made, some inferences can be made based on knowledge of environmental conditions and morphological features. Crustaceans were not major components of the diet, perhaps because 1) crustaceans such as amphipods may be difficult to detect in dim or turbid bottom water, 2) energy expended in pursuit of agile swimming prey may be greater than that derived from their digestion, or 3) jaw morphology may make capture of swimming crustacea difficult (Yazdani 1969, based on *Microstomus kitt*).

Molluscs may also require expenses in acquisition or digestion beyond their energetic benefits. They may be more difficult to detect and less efficiently digested than polychaetes and ophiuroids. Because the shell is not digested, digestion of molluscs such as pelecypods must take place slowly through the apertures of the shell. Calcium from the shell may also raise pH in the gut, thereby reducing efficiency of gastric enzymes. The optimal pH level for enzymes found in the stomachs of

plaice, *Pleuronectes platessa*, lies between 1.5 and 2.5; and stomach enzyme activity in plaice may cease at pH levels above 5.5 (Bayliss 1935). However, optimal pH levels in Dover sole stomachs and effects of food on local pH levels are unknown.

Relatively indigestible, low caloric ophiuroid arms were surprisingly abundant in the stomachs of Dover sole. Rae (1956) reported frequent occurrences (up to 30% of stomachs sampled) of ophiuroids in the guts of lemon sole, *Microstomus kitt*. Ophiuroids may be easy to capture and readily available. Alternatively, they could provide some required nutrient unavailable in other food sources. Finally, different rates of stomach evacuation and digestion could affect our results. The importance of ophiuroids may be easily overestimated because ophiuroids may remain in the stomach longer than the soft-bodied polychaetes, small molluscs, or crustaceans. Their arms were frequently tangled in a bulky, inflexible mass which may move slowly through the digestive tract. If a stomach contained only one or two food items, ophiuroid arms were usually present. Less digestible food items in the diet of fishes often have slower gastric evacuation rates (Fänge and Grove 1979). This would result in a longer "residence time" for ophiuroids than other prey taxa and suggests that the diet of Dover sole is principally composed of polychaetes. De Groot (1971) categorized *M. pacificus* as a polychaete-mollusc (echinoderm) feeder, characterized by a small esophagus and stomach and complicated intestinal loop, an adaptation characteristic of flatfishes which feed on polychaetes which are often contaminated with indigestible items, e.g., tubes.

On first inspection, it appears that Dover sole do not feed more selectively on energetically more profitable prey when these prey types are more common. For example, the value of E of polychaetes at SG29 was lower than at SG10 (0.13 vs. 0.33, Table 5) while the abundance of polychaetes at SG29 was higher than at SG10 (886 vs. 396/m²; 66% vs. 27% of the total numbers of benthic animals in the box cores (Table 7)). However, the frequency of occurrence of principal prey often changed with fish size at SG29, indicating prey selection, whereas most prey species occurred at statistically equal frequencies over the entire size range of fish sampled at SG10.

These size-related changes in selectivity at the two locations may be related to availability or energetic advantage of the prey. Prey body size was significantly correlated with size of fish at

which a prey increased in importance in diet at SG29 (Figure 4). Large fish were apparently more successful than small fish at capturing large prey. Small fish may be limited to smaller, slower moving or weaker prey by mouth size or body strength. These predator-prey size relationships are consistent with those observed by Schoener (1971) for *Anolis* lizards: as predator size increased, average prey size increased. Ross (1978) also reported that mean size of prey increased with fish size for the leopard sea robin *Prionotus scitulis*, >90 mm.

Depth of prey in sediment is also significantly correlated with size of fish at which a prey species begins to occur more significantly (SG29; Figure 6). Although prey depth and prey body size were not statistically correlated, the small-bodied prey found deep in the sediment were usually not the same species which increased in frequency in larger fish. Thus, large fish apparently are physically capable of extracting large-bodied, deeply buried prey from sediment while smaller fish are not. Learning as well as extraction capability may be important in successful extraction of large polychaetes.

Since the distribution of prey species was shallower at SG10 than at SG29, the physical advantage afforded large fish in the exploitation of prey buried deep in the sediments may be eliminated at SG10. When depths of species common to both stations were compared, nearly all species were found closer to the surface at SG10, although the differences are not often statistically significant because of small sample size at SG10.

Two potential instances of increased selectivity in the face of increased abundance of a profitable or preferred prey are suggested in this study. First, the abundance of polychaetes, a preferred taxon, was lower at SG10 than SG29 (Table 7). Few significant changes in the frequency of occurrence of prey occurred with fish size at SG10 where large fish may have had to consume any polychaete encountered, regardless of size and/or location, to meet their energetic requirements. In other words, the energetic advantage arising from size-selective specialization may disappear as abundance of preferred food items decreases, as found for bluegills by Werner and Hall (1974).

Second, size-related availability results in differing effective prey densities to larger vs. smaller fish at SG29. As fish size increases, a wider range of prey may become available and so prey densities are effectively higher for larger fish. Selectivity increases with fish size (Figure 5). Since body size

of prey is also correlated with fish size, it can again be concluded that selectivity increases with an increase in densities of profitable prey.

Even though large fish at SG29 strongly selected large-bodied prey, some small-bodied prey showed no statistically significant change in frequency over the entire size range of fish. These small prey may still be "profitable" to capture by large fish. Large fish at SG29 generally consumed a wider variety of prey than small fish. The number of large-sized prey species which increased in frequency with fish size was greater than the number of small-sized species which decreased with fish length. Thus, although large-size fish consumed large-sized prey more often than small fish, they also consumed a larger range of prey sizes than did small fish.

SUMMARY

1. Dover sole off the Oregon coast in midsummer of 1976 were polychaete-ophiuroid-mollusc feeders, according to analysis of stomach contents. Polychaetes and ophiuroids were more important than molluscs and crustaceans as food in terms of frequency of occurrence, weight, and numbers.

2. Dover sole were selective feeders. Polychaetes and ophiuroids were positively selected and composed higher proportions of fish diets than of box core samples from the same location. Molluscs were not generally selected. Crustaceans were selected (SG29) or nonselectively consumed (SG10).

3. Dependency of diet on fish size varied with location. Dover sole sampled in a region of high polychaete abundance (SG29) showed size-related changes in diet. Dover sole sampled in a region of relatively low polychaete abundance (SG10) showed few size-related changes in diet.

4. When size-related changes in diet were observed, prey body size was positively correlated with predator length at which the prey taxon showed a significant increase in frequency of occurrence.

5. Consumption of polychaetes by Dover sole was a function of depth of prey taxon within the sediment and size of the fish consuming the prey. The mean depth of a prey taxon within the sediment was positively correlated with the predator length at which the prey taxon showed a significant increase in frequency of occurrence (SG29). Where polychaetes were distributed closer to the surface, few size-related changes were observed.

ACKNOWLEDGMENTS

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