FEEDING ECOLOGY OF 0-AGE FLATFISHES AT A NURSERY GROUND ON THE OREGON COAST

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ABSTRACT

The food habits of 0-age English sole, *Parophrys vetulus*; butter sole, *Isopsetta isolepis*; speckled sanddab, *Citharichthys stigmaeus*; and sand sole, *Psettichthys melanostictus*; were investigated over a 2½-year period at a shallow nursery area (9-30 m) off the central Oregon coast. A total of 422 guts from recently metamorphosed fish (17-88 mm SL) were examined; only 16 were empty (4%). The greatest similarity in diets was between English and butter soles. Both species were benthophagous, feeding on a wide variety of prey, including palps of the polychaete *Magclona sacculata*, juvenile bivalves, siphons from tellinid clams, harpacticoid copepods, amphipods, cumaceans, and juvenile decapods. Speckled sanddabs fed equally on benthic prey (amphipods, cumaceans, decapods) and mysids, while sand sole almost exclusively ate mysids. The guts of all four species tended to be <25% full in the morning before 0900 h; stomach fullness gradually increased during the late morning and afternoon.

Food habits of English sole were a function of location of capture within the study area, season, and fish length. Juveniles <35 mm SL fed on small prey, e.g., polychaete palps, juvenile bivalves, tellinid clams, and harpacticoids, while larger individuals fed on larger prey, e.g., amphipods, cumaceans, and decapods. Diets of English sole <35 mm SL varied greatly both between seasons in the same year and between years. Spatially, the diets of English sole captured in trawls at the same depth and different depths were similar in January 1979 but highly variable in May 1979. These temporal and spatial differences in feeding are probably caused by seasonal changes in the abundance and spatial distributions of benthic prey.

Many juvenile flatfishes recruit to the sea floor in well-defined nursery areas following metamorphosis from pelagic larvae. The types and densities of food items present in such benthic regions potentially can affect growth and mortality of recently settled flatfish species (Paloheimo and Dickie 1966; Steele et al. 1970; Cushing and Harris 1973). In addition, whenever the nursery grounds of several species coincide or overlap, interspecific interactions originating from similarities in diet may also be a factor regulating growth and survival (e.g., Edwards and Steele 1968). Four species of pleuronectiform fishes—English sole, *Parophrys vetulus*; butter sole, *Isopsetta isolepis*; speckled sanddab, *Citharichthys stigmaeus*; and sand sole, *Psettichthys melanostictus*—utilize the shallow water of the open Oregon coast as a site of benthic recruitment and early growth. All but *C. stigmaeus* are important to the Oregon trawl fishery. English sole ranks among the top three commercial species based on annual landings.

In conjunction with a long-term research program designed to improve management of Oregon's multispecies demersal fishery (Pearcy et al. 1977; Richardson and Pearcy 1977; Pearcy and Hancock 1978; Laroche and Richardson 1979; Hayman and Tyler 1980), we examined the prey selected by recently settled individuals of these four species at one site over a 2½-yr period. Our specific goals were to describe the food habits of these fishes, to relate the temporal and spatial variability of the English sole diet to changes in prey abundance and distributions, and finally to compare the dietary and habitat overlap of English and butter soles.

MATERIALS AND METHODS

The area selected for this work was located off Moolach Beach on the open Oregon coast (Fig. 1). Situated between Yaquina Head and Cape Foulweather 10 km north of the nearest estuary, this site has been the focus of recent work on the recruitment and growth of juvenile pleuronectids (Laroche and Holton 1979; Rosenberg 1981; Krygier and Pearcy[2]) and the food habits of adult

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[2]Krygier, E., and W. G. Pearcy. Distribution, abundance, and growth of 0-age English sole in estuaries and along the coast of Oregon: the importance of estuarine nursery grounds.

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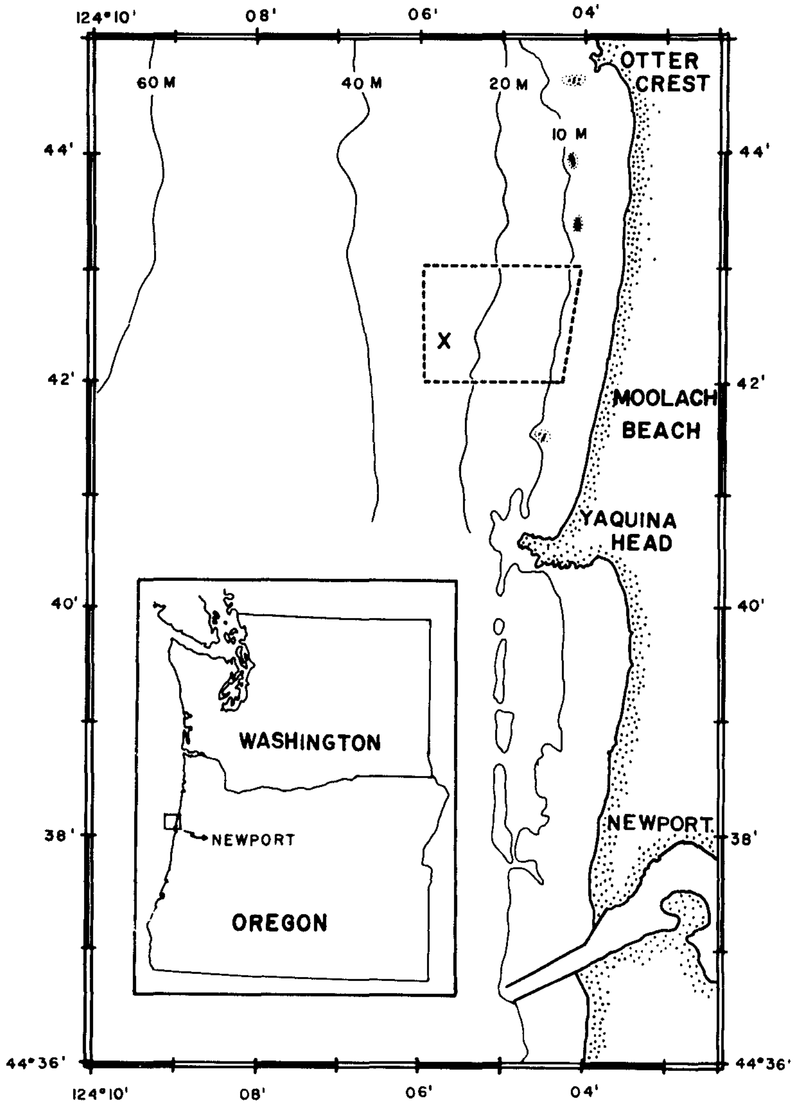

FIGURE 1.—Location of study area. Dotted lines enclose area from which beam trawl samples were collected; "X" marks location of box core and Smith-McIntyre grab samples.

flatfishes (Wakefield[3]). Trawl samples collected from this area between May 1977 and September 1979 were utilized for our work. A 1.5 m beam trawl fitted with a recording odometer wheel and a 7 mm stretch mesh liner was employed for all but one of these collections. On one occasion, 22 March 1979, we obtained samples using a small otter trawl which also had a 7 mm stretch mesh liner. On each sampling date, 10-min tows covering about 750 m^2 surface area were made at several depths between the 9 and 30 m isobaths (0.9 and 2.7 km offshore, respectively). Fish were preserved in 10% buffered Formalin[4] immediately upon collection. No regurgitation of gut contents was observed. The daily time of sampling varied between 0830 and 1800 h.

From the 85 trawl collections obtained during this 29-mo period, we selected 31 for examination. Several criteria were used in choosing these samples. In keeping with an overall goal of the Pleuronectid Project to obtain detailed informa-

Unpubl. manuscr. School of Oceanography, Oregon State University, Corvallis, OR 97331.

[3]W. W. Wakefield. Feeding ecology within an assemblage of benthic fishes on the Oregon Continental Shelf. Unpubl. manuscr. School of Oceanography, Oregon State University, Corvallis, OR 97331.

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

tion on the most important commercial species, emphasis was placed on those trawls which contained English sole. Priority was also given to using samples which were collected between July 1978 and September 1979, since quantitative meiobenthic samples were also gathered from the study area during that period. We used selected trawl collections from 1977 and 1978 to investigate the between-year repeatability of trends noted in the 1979 data. Finally, only hauls containing specimens 70 mm SL and less were used.

In the laboratory a size range of juvenile flatfish was selected from each of the trawls chosen for study. Standard length of each specimen was recorded prior to removal of the gut. Both the stomach and intestinal tract were removed and opened under a dissecting microscope; gut contents were identified to the lowest possible taxon and counted. We used a subjective scale ranging between 0 and 4 to quantify the degree of gut fullness (0 = <5% full, 1 = 5-25% full, 2 = 25-50% full, 3 = 50-75% full, 4 = 75-100% full).

Quantitative data for each prey category were summarized in two ways. The frequency of prey occurrence, expressing the proportion of all fish sampled which had a given food item in their gut, was computed for each flatfish species within a trawl. The mean percent composition, based on numerical abundance, was determined also by averaging the percent composition of each individual fish gut for a given species within a trawl. When more than one trawl was examined from a sampling date, the frequency of occurrence and percent composition from the separate trawls were averaged to give an overall mean. Diversity (H') of prey consumed was computed using natural logarithms (Pielou 1969).

On two sampling dates, 29 May and 30 June 1979, English sole were captured at the study site and returned live to the laboratory along with sand collected from the same area using a 0.25 m^2 box core. Fish were placed in aquaria with the sediments, and their behavior was monitored over several days while they fed on naturally occurring prey in the sediments. Fresh seawater (12°C) was circulating continually through each aquarium. A photoperiod matching that experienced by the fish in the field was maintained using room lighting.

Quantitative meiobenthic samples were obtained from the study area at one site in 25 m of water (Fig. 1). Three replicate 0.25 m^2 box cores, positioned 30 m apart, were collected on each of six cruises between July 1978 and May 1979. Box cores were subsampled with at least three randomly placed clear plastic cores (1.9 cm internal diameter) which were in turn vertically partitioned into six depth increments (0-1 cm, 1-3 cm, 3-6 cm, 6-11 cm, 11-18 cm, and >18 cm). These plastic corers were also used to subsample Smith-McIntyre grabs collected on two cruises in July and September 1979 at the same site. Samples were preserved in 10% buffered Formalin and stained with rose bengal. The fauna was extracted from the sediments (well-sorted fine sand) by shaking and decanting followed by three rinses. A 38.5 μm sieve was used to retain the fauna. Harpacticoid copepods and nematodes were identified to species and enumerated.

RESULTS

The data for all four flatfish species are summarized in Table 1. A total of 422 guts from recently settled fish (17-88 mm SL) were examined, only 16 of which were empty (4%). The guts of an additional 40 late stage IV and early stage V *P. vetulus* larvae (sensu Shelbourne 1957) were also examined. These metamorphosing individuals, ranging in size from 16 to 18 mm SL, all had empty stomachs and intestinal tracts.

The 13 prey categories identified (Table 1, top) were placed into three broad groupings based on the size of individual food items and their typical location within the habitat. Small benthic prey were composed of palps from the surface deposit-feeding polychaete *Magelona sacculata*, juvenile bivalves (predominantly *Tellina modesta* and occasionally *Siliqua patula*), siphon tips cropped from tellinid clams, harpacticoid copepods (mainly *Halectinosoma* spp. and a few *Thompsonula hyaenae* and *Rhizothrix curvata*), free-living nematodes (*Theristus* sp. and *Mesacanthion* sp.), and tube feet from the sand dollar *Dendraster excentricus*. These food items were on the order of 0.5-1.5 mm long. Larger benthic prey were amphipods (predominantly *Ampelisca* spp. and *Eohaustoris* sp.), cumaceans, decapods (juvenile *Cancer magister*, pinnotherid crabs, and *Callianassa californiensis*), and polychaetes (*Nephtys* sp., *Glycinde armigera*, *Magelona sacculata*, *Thalenessa spinosa*, and *Spiophanes bombyx*). These prey were usually juveniles measuring 1.5-4 mm in their largest dimension. Species identifications were difficult for this latter group because of their immature status and tendency to fragment after being eaten. Examina-

TABLE 1.—Summary of data collected for English sole, *Parophrys vetulus*; butter sole, *Isopsetta isolepis*; speckled sanddab, are the number of fish out of the total examined which had empty guts. The two values listed for each prey category are average

Species and date	No. tows exam-ined	No. fish examined	Length range (mm)	Small benthic prey: *Magelona* palps	Juvenile bivalves	Tellinid siphons	Harpac-ticoid copepods	Nematodes	*Dendraster* tube feet
English sole									
12 May 1977	1	12 (1)	18-29	0.08 (0.64)	0.42 (0.91)	0.22 (0.73)	0.22 (0.82)	— (0.18)	
23 June 1977	1	16 (0)	19-48	0.01 (0.19)	— (0.19)	0.18 (0.56)	0.42 (0.69)	— (0.06)	
12 June 1978	1	3 (0)	22-24	0.04 (0.33)	0.88 (1.0)		0.04 (0.66)	0.02 (0.33)	
15 June 1978	1	5 (0)	20-25	0.59 (1.0)	0.17 (0.80)		0.14 (1.0)	0.05 (0.40)	
13 July 1978	2	14 (0)	19-46	0.46 (0.89)	0.24 (0.83)	0.08 (0.33)	0.18 (0.70)	— (0.06)	
25 July 1978	1	12 (0)	24-84	0.09 (0.75)	0.01 (0.08)		0.17 (0.42)	0.40 (0.67)	
5 Sept. 1978	1	3 (0)	45-58		1.0 (1.0)				
14 Nov. 1978	1	5 (0)	18-21	0.99 (1.0)					
23 Jan. 1979	4	24 (2)	17-34	0.72 (0.94)	0.05 (0.25)	— (0.06)	0.13 (0.52)		
22 Mar. 1979	2	20 (0)	19-35	0 02 (0.50)	0.80 (1.0)	0.02 (0.36)	0.14 (0.90)		
18 Apr. 1979	2	27 (1)	19-38	0.10 (0.50)	0.20 (0.73)	0.17 (0.61)	0.23 (0.67)	— (0.22)	
29 May 1979	4	37 (5)	18-42	0.07 (0.24)	0.20 (0.25)	0.24 (0.38)	0.20 (0.41)	0.05 (0.19)	
30 June 1979	2	23 (1)	18-61		0.01 (0.50)	— (0.09)	0.14 (0.75)		0.61 (0.75)
19 July 1979	3	10 (0)	27-62		0.20 (0.25)		0.30 (0.79)		
8 Aug. 1979	2	11 (0)	30-87		0.26 (0.19)	0.03 (0.06)	0.03 (0.19)		
24 Sept. 1979	2	13 (0)	46-82		0.02 (0.07)		0.10 (0.35)		
Total		235 (10)							
$\bar{x}$ 1979				0.11 (0.27)	0.22 (0.41)	0.06 (0.20)	0.16 (0.57)	0.01 (0.05)	0.08 (0.09)
Butter sole									
23 June 1977	1	6 (1)	18-23	0.01 (0.20)		0.25 (0.80)	0.47 (0.80)		
15 June 1978	1	16 (0)	19-30	0.62 (0.87)	0.13 (0.60)	0.01 (0.13)	0.01 (0.27)	0.05 (0.47)	
25 July 1978	1	16 (0)	22-31	0.44 (0.75)	0.06 (0.12)		0.24 (0.82)	0.13 (0.57)	
29 May 1979	3	14 (2)	17-35	0.04 (0.10)	0.15 (0.50)	0.25 (0.62)	0.17 (0.63)	0.11 (0.25)	
30 May 1979	1	4 (0)	49-60		0.03 (0.25)		0.03 (0.25)		
19 July 1979	3	7 (0)	21-88	— (0.08)	0.38 (0.58)		0.11 (0.33)		
8 Aug. 1979	4	9 (1)	24-34	0.02 (0.38)	0.43 (0.50)	— (0.13)	0.47 (0.58)		
Total		72 (4)							
$\bar{x}$ 1979				0.02 (0.12)	0.25 (0.46)	0.06 (0.19)	0.20 (0.45)	0.03 (0.06)	
Speckled sanddab									
23 June 1977	1	4 (0)	34-44			0.41 (0.75)	0.13 (0.25)		
25 July 1978	1	5 (0)	41-65						
22 Mar. 1979	1	10 (0)	29-39		0.08 (0.10)	0.01 (0.10)	0.10 (0.10)		
18 Apr. 1979	1	10 (0)	29-38						
29 May 1979	2	14 (0)	33-50	0.13 (0.13)					
30 June 1979	1	7 (0)	30-52						
19 July 1979	2	11 (1)	35-70						
24 Sept. 1979	3	15 (0)	38-70						
Total		76 (1)							
$\bar{x}$ 1979				0.02 (0.02)	0.01 (0.02)	— (0.02)	0.02 (0.02)		
Sand sole									
22 Jan. 1979	2	6 (0)	30-38						
18 Apr. 1979	1	3 (0)	29-55						
19 July 1979	2	6 (0)	29-50						
8 Aug. 1979	2	13 (0)	31-52						
24 Sept. 1979	2	11 (1)	30-48						
Total		39 (1)							
$\bar{x}$ 1979									

tion of the meiofaunal cores revealed that all the organisms classified as "benthic" occurred in the upper 1 cm of sediment. Prey items which were never found in benthic samples were defined as "pelagic" and consisted of mysids (mainly *Neomysis kadiakensis*), calanoid copepods (*Pseudocalanus* sp.), and veliger larvae. This distinction between benthic and pelagic organisms is somewhat arbitrary, since some of these species are mobile epibenthic forms which probably occur both in the sediments and the overlying water.

Adequacy of the sample sizes used in determining food habits of the flatfish species was assessed using several techniques. The guts of 16 *Parophrys vetulus* (19-48 mm SL) and 16 *I. isolepis* (19-33 mm SL) were examined from each of two tows. These two species were selected because they fed on a much broader spectrum of prey than *Citharichthys stigmaeus* or *Psettichthys melanostictus* and hence are subject to greater sampling error. The cumulative number of prey categories encountered, expressed as a function of sample size, is shown in Figure 2. For both English sole and butter sole, after seven or eight fish had been examined, no new food categories were found. After examining only four fish, 75% of all food items had been collected. This qualitative consistency among guts is also reflected in the high frequency of occurrence (Table 1) for most prey. Quantitatively, the composition of gut

Citharichthys stigmaeus; and sand sole, *Psettichthys melanostictus*. Numbers in parentheses under the heading "No. fish examined" numerical percent composition and average frequency of occurrence (in parentheses). "—" indicates prey item <0.01.

Species and date	No. tows examined	No. fish examined	Length range (mm)	Large benthic prey: Amphipods	Large benthic prey: Cumacea	Large benthic prey: Decapods	Large benthic prey: Polychaetes	Pelagic prey: Mysids	Pelagic prey: Calanoid copepod	Pelagic prey: Veliger larvae
English sole										
12 May 1977	1	12 (1)	18-29	0.03 (0.27)		— (0.09)		0.01 (0.18)		
23 June 1977	1	16 (0)	19-48	0.15 (0.63)		0.24 (0.44)				
12 June 1978	1	3 (0)	22-24	0.01 (0.33)			0.01 (0.33)			
15 June 1978	1	5 (0)	20-25	0.02 (0.40)			0.04 (0.60)			
13 July 1978	2	14 (0)	19-46	0.02 (0.40)	0.01 (0.36)	0.02 (0.42)				
25 July 1978	1	12 (0)	24-84	0.18 (0.25)	0.04 (0.25)		0.03 (0.10)	0.04 (0.08)		
5 Sept. 1978	1	3 (0)	45-58							
14 Nov. 1978	1	5 (0)	18-21				0.01 (0.20)			
23 Jan. 1979	4	24 (2)	17-34	0.08 (0.52)	0.02 (0.14)			— (0.06)		
22 Mar. 1979	2	20 (0)	19-35	0.03 (0.60)	— (0.30)			— (0.10)		
18 Apr. 1979	2	27 (1)	19-38	0.25 (0.62)	0.04 (0.35)	— (0.03)		— (0.09)		
29 May 1979	4	37 (5)	18-42	0.03 (0.19)	0.03 (0.05)	0.17 (0.17)	0.02 (0.16)	— (0.13)		
30 June 1979	2	23 (1)	18-61	0.18 (0.54)	0.05 (0.25)	— (0.09)	— (0.09)			
19 July 1979	3	10 (0)	27-62	0.33 (0.70)	0.15 (0.50)	0.01 (0.08)				
8 Aug. 1979	2	11 (0)	30-87	0.45 (0.86)	0.21 (0.81)	0.01 (0.13)	— (0.33)	0.01 (0.06)		
24 Sept. 1979	2	13 (0)	46-82	0.29 (0.90)	0.41 (0.84)		0.18 (0.57)	— (0.09)		
Total		235 (10)								
x̄ 1979				0.21 (0.62)	0.11 (0.41)	0.02 (0.06)	0.03 (0.14)	— (0.07)		
Butter sole										
23 June 1977	1	6 (1)	18-23	0.07 (0.80)				0.20 (0.20)		
15 June 1978	1	16 (0)	19-30	0.02 (0.33)	0.01 (0.20)		0.16 (0.87)			
25 July 1978	1	16 (0)	22-31	0.03 (0.25)	0.05 (0.38)		0.05 (0.38)	— (0.06)		
29 May 1979	3	14 (2)	17-35	0.04 (0.21)	0.03 (0.16)		0.03 (0.16)	0.05 (0.33)		
30 May 1979	1	4 (0)	49-60	0.32 (1.0)	0.26 (1.0)	0.29 (1.0)	0.07 (0.25)			
19 July 1979	3	7 (0)	21-88	0.21 (0.58)	0.04 (0.17)	0.18 (0.33)		0.08 (0.08)		
8 Aug. 1979	4	9 (1)	24-34	0.07 (0.54)	0.01 (0.63)			— (0.13)		
Total		72 (4)								
x̄ 1979				0.16 (0.58)	0.09 (0.49)	0.12 (0.33)	0.03 (0.10)	0.03 (0.14)		
Speckled sanddab										
23 June 1977	1	4 (0)	34-44	0.20 (0.50)	0.13 (0.25)	0.11 (0.25)		0.03 (0.25)		
25 July 1978	1	5 (0)	41-65					1.0 (1.0)		
22 Mar. 1979	1	10 (0)	29-39	0.08 (0.30)	0.01 (0.10)			0.72 (0.80)		
18 Apr. 1979	1	10 (0)	29-38	0.20 (0.20)	0.52 (0.60)	0.03 (0.10)		0.25 (0.30)		
29 May 1979	2	14 (0)	33-50	0.25 (0.43)		0.30 (0.53)		0.32 (0.53)		
30 June 1979	1	7 (0)	30-52	0.03 (0.57)	— (0.05)	0.01 (0.29)		0.96 (1.0)		
19 July 1979	2	11 (1)	35-70	0.04 (0.20)				0.96 (1.0)		
24 Sept. 1979	3	15 (0)	38-70	0.14 (0.52)	0.08 (0.25)	0.20 (0.52)		0.59 (0.86)		
Total		76 (1)								
x̄ 1979				0.12 (0.37)	0.10 (0.17)	0.09 (0.24)		0.63 (0.75)		
Sand sole										
22 Jan. 1979	2	6 (0)	30-38					1.0 (1.0)		
18 Apr. 1979	1	3 (0)	29-55					1.0 (1.0)		
19 July 1979	2	6 (0)	29-50					1.0 (1.0)		
8 Aug. 1979	2	13 (0)	31-52			0.03 (0.17)		— (0.13)	0.69 (0.80)	0.28 (0.40)
24 Sept. 1979	2	11 (1)	30-48					1.0 (1.0)		
Total		39 (1)								
x̄ 1979						0.01 (0.03)		0.80 (0.83)	0.14 (0.13)	0.06 (0.08)

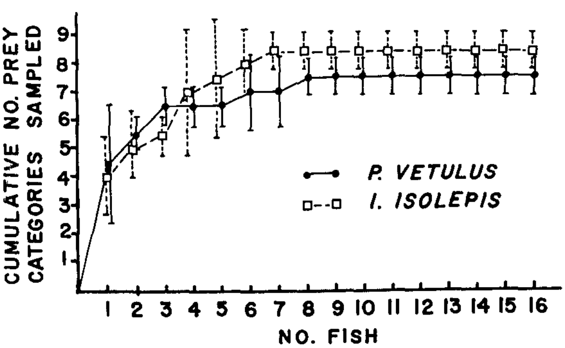

FIGURE 2.—Cumulative number of prey categories sampled as a function of sample size for *Parophrys vetulus* and *Isopsetta isolepis*. Each data point represents the mean of two separate trawl collections. Vertical bars are ±1 standard deviation.

contents varied little among individuals of a species within a trawl. For each species studied, food items from fish caught in the same trawl tended to have the same rank order of numerical abundance. This consistency of results was statistically significant; the null hypothesis of independence among prey rankings was rejected (Friedman's nonparametric randomized block ANOVA, $P<0.005$; Gibbons 1971). On several sampling dates the number of fishes available for study was small, e.g., *Parophrys vetulus* on 5 September 1978 (three fish), *I. isolepis* on 30 May 1979 (four fish). The small within-sample variability of these species, however, indicates that such small sample sizes will not unduly bias determination of the major food items consumed.

As is apparent from Table 1, *P. vetulus* feeds on a wide variety of benthic animals. Juvenile bivalves, harpacticoid copepods, *Magelona* palps, and amphipods are particularly abundant in English sole guts. On most sampling dates, the frequency of occurrence of these four prey in the diet of English sole was high, although typically only one or two items dominated the diet numerically. Occasionally a food item which was usually rare became a major component in the guts of English sole, such as free-living nematodes on 25 July 1978 or echinoid tube feet on 30 June 1979. The diet of *I. isolepis* was very similar to that of *P. vetulus*, with the exception that butter sole fed to a greater extent on mysids and decapods. *Citharichthys stigmaeus* fed equally on large epibenthic crustaceans (amphipods, decapods, cumaceans) and pelagic prey. Polychaetes were totally lacking in the diet. *Psettichthys melanostictus* consumed mysids almost exclusively; only on 8 August 1979 were other pelagic prey found in the guts of this species. Average *H'* diversity of food consumed per sampling date in 1979 was 1.38 for English sole, 1.47 for butter sole, 0.81 for speckled sanddabs, and 0.14 for sand sole. The similarity in diets of these four species was compared by computing the percent similarity index (PSI; Whittaker 1960) based on the average 1979 proportions of prey consumed by each species (Table 2). Two of these paired comparisons, *Parophrys vetulus-I. isolepis* and *C. stigmaeus-Psettichthys melanostictus*, indicate similarities exceeding 50%. In the case of the speckled sanddab and the sand sole, this dietary overlap is based on their common utilization of one food category, mysids. English and butter soles share a wide variety of prey which were consumed in very similar proportions, e.g., 29 May 1979.

Observations of 20-25 mm *Parophrys vetulus* feeding in laboratory aquaria revealed two basic types of foraging behavior. In the first, fish remained motionless on the bottom and then periodically lunged forward 1-2 cm, striking at objects located on the surface of the sediment. In the second, fish slowly raised their heads above the bottom then rapidly thrust forward, causing the upper few millimeters of sediment to billow into suspension. *Parophrys vetulus* would then strike in rapid succession at small objects presumably temporarily displaced from the bottom. Neither type of behavior predominated; both were detected in all of the individuals observed. After monitoring these responses for several hours, fish were sacrificed and the guts examined. Harpacticoid copepods dominated the diet of these fish.

Shifts in prey preference as a function of fish size (age) were observed in English sole. The average diets of all *P. vetulus* less than and greater than 35 mm SL were computed using the 1979 data and then compared (Table 3). The dramatic difference in prey of these two size classes is apparent. Smaller fish (17-35 mm SL) consumed small prey almost exclusively, while larger fish (35-82 mm SL) only occasionally ingested these small items, choosing instead amphipods and cumaceans. *Isopsetta isolepis* showed a similar shift in the preferred size of prey as standard length increased from 30 to 40 mm. Fourteen butter sole (17-35 mm SL) caught on 29 May 1979 fed predominantly on small food items, while the gut contents of four larger fish (49-60 mm SL) caught 1 d later were composed of amphipods, cumaceans, and decapods (Table 1). A similar distinction was found in fish collected on 19 July 1979. Neither *C. stigmaeus* nor *Psettichthys melanostictus* altered the taxonomic composition of their diet within the size ranges of fish we examined, although, as with English and butter soles, larger fish ate larger prey.

The guts of all four species were generally <25% full in the morning before 0900 h. Stomach fullness gradually increased during the late morning and afternoon. The correlation between

TABLE 2.—Percent similarity of prey consumed by English sole, *Parophrys vetulus*; butter sole, *Isopsetta isolepis*; speckled sanddab, *Citharichthys stigmaeus*; and sand sole, *Psettichthys melanostictus*, based on the average 1979 diets shown in Table 1.

Species	*I. isolepis*	*C. stigmaeus*	*P. melanostictus*
P. vetulus	0.77	0.29	0.01
I. isolepis	—	0.39	0.05
C. stigmaeus	—	—	0.64

TABLE 3.—Mean numerical proportions of dominant prey items in the guts of *Parophrys vetulus* less than and greater than 35 mm SL.

	SL <35 mm	SL >35 mm
Small benthic prey		
Magelona palps	0.28	0.03
Juvenile bivalves	0.29	0.01
Tellinid siphons	0.13	0.01
Harpacticoid copepods	0.16	0.08
Total	0.86	0.13
Large benthic prey		
Amphipods	0.08	0.46
Cumaceans	0.03	0.30
Decapods	0.01	0.04
Polychaetes	0.0	0.06
Total	0.12	0.86

the time of capture (ranging between 0830 and 1800 h) and average gut fullness for English sole was significant; $r = 0.49$, $P = 0.05$. On 22 March 1979 two otter trawl hauls were made, one at 1000 and another at 1800 h. Guts of 10 English sole ranging in size between 19 and 35 mm SL were examined from both trawls. The diets of both groups of fish were the same, but the fish collected at 1800 h had an order of magnitude more food items in their guts than the earlier collection: 90% full, 198±56 SD items, vs. 10% full, 18±17 SD items. *Isopsetta isolepis*, *C. stigmaeus*, and *P. melanostictus* showed similar daily trends.

Sufficient numbers of English sole of the same size were collected on 23 January and 29 May 1979 to compare the similarity of diets within and between replicate trawls. The PSI was used to quantify the proportion of food items found in common for each possible pair of fish collected on a sampling date. Mean similarity values were then obtained by averaging the PSI values for the fish within the same trawl and for fish collected in different trawls. Comparing replicate samples obtained at the same depth (Table 4), the average PSI for fish guts within the same trawl in both January and May, as well as the mean PSI between fish in different trawls in January, were approximately the same, 50%. The similarity between two trawls at the same depth in May, though, is very low (3%). Table 4 (bottom) also shows a comparison of within-trawl and between-trawl similarity, where trawls were collected at different depths (20 m and 30 m). Again the within-trawl affinities are high in both January and May, as is the between-tow similarity in January. The average PSI in May for fish from different depths is low. The increased between-trawl variability in food habits noted on 29 May was a general feature observed in all late spring and early summer replicate collections of *Parophrys vetulus*. For example, on 13 July 1978, trawls were made at 15 m and 20 m. *Magelona* palps numerically comprised 72% of the English sole diet at 15 m but only 19% at 20 m, while juvenile bivalves and harpacticoid copepods combined to form 19% of the prey consumed at 15 m and 63% at 20 m.

TABLE 4.—Average percent similarity of index of *Parophrys vetulus* diets within and between replicate trawls on 23 January and 29 May 1979.

	Replicates at same depth		Replicates at different depths	
	Within trawl	Between trawl	Within trawl	Between trawl
23 January 1979				
20 m	53%	53%		
20 m and 30 m			71%	66%
29 May 1979				
10 m	50%	3%		
20 m and 30 m			65%	12%

The diet of recently settled English sole changed continually among sampling months. Comparing similar-sized fish (17-35 mm SL) caught in 1979 (Fig. 3) reveals that dominant food items on a numerical basis varied from *Magelona* palps (November 1978, January 1979), juvenile bivalves (March 1979), bivalve siphons (April and May 1979), to juvenile bivalves and harpacticoid copepods (July 1979). Examination of samples collected in 1977 and 1978 showed that the sequence of changes noted in 1979 does not repeat each year. *Magelona* palps, which in 1979 were never a dominant item in the diet of *P. vetulus* after January, were numerically the most abundant food on two sampling dates in the summer of 1978. Other between-year differences exist, e.g., 5 September 1978 and 24 September 1979, but it is impossible to determine whether these differences are real or a result of spatial variability in diet combined with insufficient sampling.

The apparent increased equitability of prey items shown in Figure 3 for April and May relative to January and March does not indicate that spring and summer diets of individual fish are more diverse than in winter. Instead, the difference is an artifact of the spatial variability previously noted, being generated by averaging the data for all fish caught in different tows. The average dietary diversity (H') of an individual fish on 23 January 1979 (0.43±0.35 SD, $n = 24$) was not significantly different from that on 29 May 1979 (0.37±0.41 SD, $n = 32$).

The only seasonal data currently available on the abundance of benthic organisms at Moolach Beach are for nematodes and harpacticoid copepods. Nematodes are very abundant ($\bar{x} = 1{,}050 \cdot 10\ \text{cm}^{-2}$), but quantitatively, with the exception of one sampling date, are not significant in the diet of the fish species we studied. Harpacticoids are important in the diets of English and butter soles, yet are not abundant at the study site. Their average density for the eight sampling dates between July 1978 and September 1979 was 12.2 ± 4.0 SE $\cdot 10\ \text{cm}^{-2}$. Only the larger species found in the 0-1 cm depth increment were present in fish guts. *Halectinosoma* spp. comprised more than 80% of all harpacticoid prey.

Seasonally, *Halectinosoma* ranged in abundance from a mean of 6.8 · 10 cm^{-2} between May and September ($n = 5$) to zero from October to March ($n = 3$). Their period of maximum density coincides with their maximum occurrence in the diet of 17-35 mm SL English sole (Fig. 3).

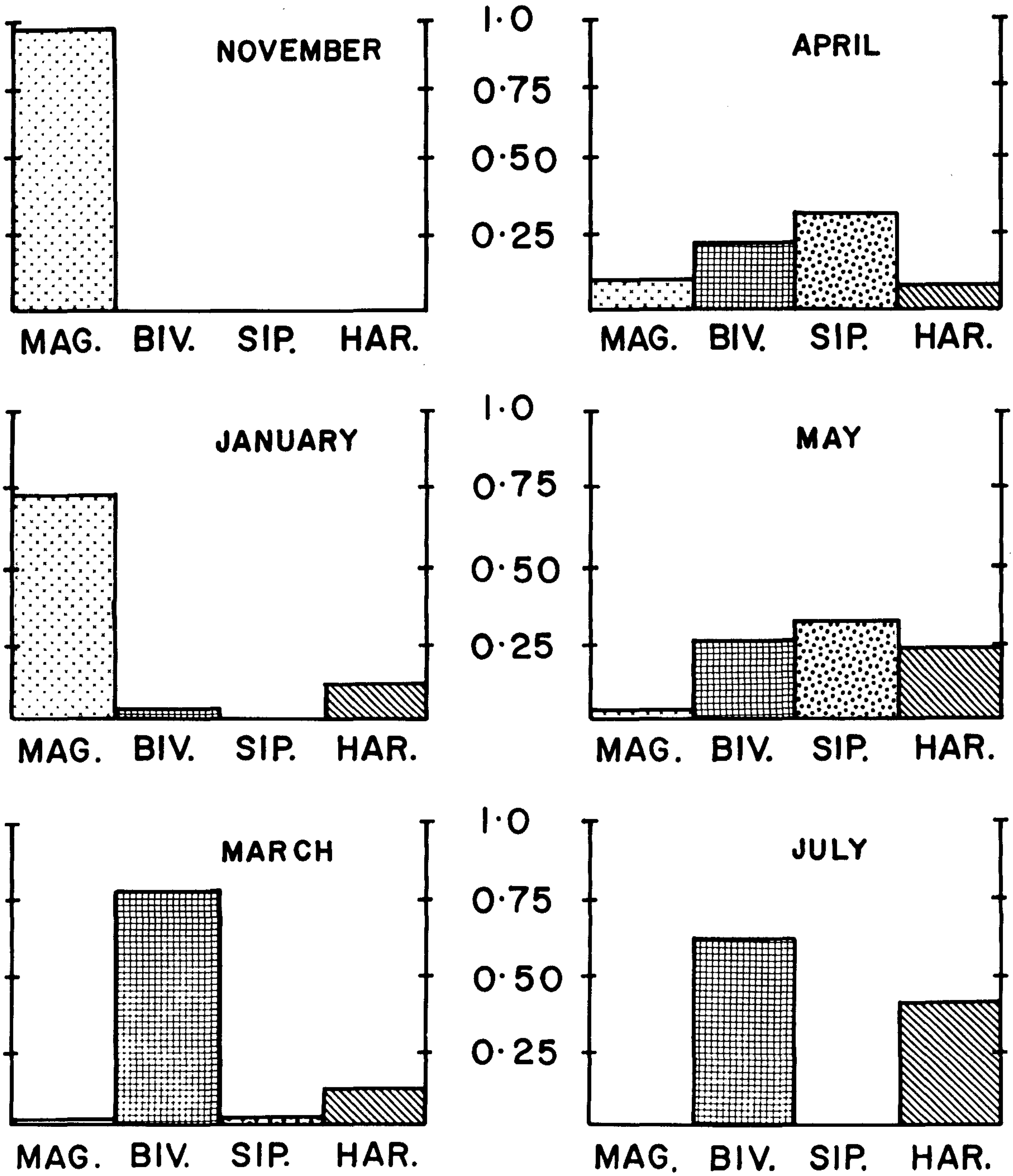

FIGURE 3.—Seasonal change in food habits of *Parophrys vetulus* <35 mm SL between November 1978 and July 1979. Vertical bars indicate average proportion of *Magelona* palps (Mag.), juvenile bivalves (Biv.), clam siphons (Sip.), and harpacticoid copepods (Har.) in the diet.

DISCUSSION

The diet of recently settled English sole is a function of size, location of capture, and season (Tables 1, 3, 4). Both the within-year and between-year differences in diet noted for *P. vetulus* are similar to changes documented for other pleuronectid species (Macer 1967; Edwards and Steele 1968) and are probably related to temporal changes in density of prey organisms. Steele et al. (1970) concluded that variations in predation on *Tellina* siphons and polychaetes by young plaice, *Pleuronectes platessa*, were a result of changes in both the absolute and relative abundances of these prey over time. The observed relationship between seasonal changes in harpacticoid copepod abundance and the utilization of these prey as food by English sole is the only direct evidence we have to support this contention. However, the juvenile bivalves (*Tellina* and *Siliqua*) consumed by *Parophrys vetulus* were all young of the year which are known to have temporally variable recruitment (Jones[5]), suggesting that seasonal availability of this food item is also not constant. Moreover, Oliver et al. (1980) seasonally sampled the nearshore macrobenthos in a region of Monterey Bay, Calif., which was very similar to Moolach Beach in terms of physical environment and fauna present. Their results indicate that the abundance of amphipods and such polychaetes as *Magelona sacculata* vary both within and between years. English sole at Moolach Beach probably alter their diet over time in accordance with similar temporal changes in the density of these larger prey species, but additional benthic data obtained concurrently with fish collections are necessary to substantiate this conclusion.

The marked differences between summer and winter spatial variability in English sole diets (Table 4) are thought to be related to changes in both the abundance and spatial distribution of prey. During the winter, intense storm activity along the Oregon coast produces large waves which continually disturb and mix the sediments of the inner continental shelf (Komar et al. 1972). The meiobenthos has been shown to become randomly distributed during these periods within small areas (1 m^2) and only slightly aggregated on larger scales (Hogue 1982). Small benthic prey fed upon by 0-age English sole would most likely be affected by this vigorous physical mixing in much the same way as the meiofauna. As a result, English sole feeding at either the same depth or different depths may consume similar prey in the winter (Table 4, January) because prey organisms are more evenly distributed within the study area compared to other times of the year. Such a distribution, when coupled with the numerical dominance of one food item, would increase the similarity of food items available for consumption throughout the region. During the late spring and summer the physical disruption of sediment is minimized and the spatial distribution of the meiofauna becomes increasingly aggregated (Hogue 1982). Distinct differences in the species composition and abundance of nematodes and harpacticoids have been found at locations only 250 m apart. During this period there is little similarity in diets of English sole from replicate trawls (Table 4, May). In the spring and summer, *P. vetulus* may be opportunistically exploiting different prey which are densely aggregated in different sectors of the Moolach Beach site.

Seasonal changes in the spatial distribution of prey items may also alter the rate at which prey are consumed. Experiments with fish feeding in aquaria (Ivlev 1961) have shown that an increase in the degree of aggregation of food sources has the same effect on the rate of food consumption as an increase in the concentration of food. Results of Tinbergen et al. (1967) suggest similar relationships between the spatial distribution of prey and predation. Fish commencing their benthic feeding in the late spring and summer at Moolach Beach may benefit energetically from the increased aggregation of benthic organisms during this period relative to that found during the winter.

The consumption of parts of macrobenthic organisms, e.g., *Magelona* palps and tellinid clam siphons, rather than whole individuals by English sole <35 mm in length is probably related to the maximum size of food items capable of being captured and ingested by these fish. We measured the mouth size of 30 mm *P. vetulus* and found that prey greater than about 2 mm in their largest dimension are too large to be consumed by such small fish. Siphons and palps are apparently the only portion of larger prey which are available for ingestion by fish <35 mm SL. As fish grow larger than 35 mm, small food items are neglected in favor of polychaetes, amphipods, and cumaceans which yield far more en-

[5]H. R. Jones, School of Oceanography, Oregon State Univ., Corvallis, OR 97331, pers. commun.

ergy per individual item. Two fortuitous consequences of this size-dependent predation may be important. First, the dietary overlap between small juveniles and larger fish is minimized, thus conserving food stocks for recently settled individuals. Second, both siphons and palps are capable of being regenerated. By consuming only parts of benthic organisms, food sources are not destroyed and may be cropped again in later months by other individuals following regeneration. This may be particularly important in the case of English sole because juveniles are continuously recruited to the bottom over a 9-mo period (Krygier and Pearcy footnote 2).

The four pleuronectiform fishes we studied form a trophic continuum, ranging from generalists feeding upon numerous benthic prey (*P. vetulus*) to specialists relying on a few pelagic food items (*Psettichthys melanostictus*). *Isopsetta isolepis* and *C. stigmaeus* are intermediate in their position on the continuum. Few published results exist with which to compare ours. Cailliet et al. (1979) investigated the food habits of *Parophrys vetulus, C. stigmaeus,* and *Psettichthys melanostictus* at an ocean station in Monterey Bay. The fish they examined were all larger than the ones for which we have data, but the same basic trends emerge. They found that English sole was a generalist, eating a wide variety of benthic food items; sand sole relied almost totally on mobile crustaceans for food; and speckled sanddab fed on pelagic and epibenthic crustacea and occasional infaunal worms and molluscs. Wakefield (footnote 3) has studied the adult food habits of these three species as well as those of *I. isolepis* collected at the Moolach Beach site. Although the specific food items ingested differ for recently settled juveniles and adults at this site, the basic modes of feeding, e.g., infaunal generalist or pelagic specialist, remained unchanged at Moolach Beach as the youngest juveniles mature to adults.

The greatest similarity among diets is between those of *Parophrys vetulus* and *I. isolepis*. Both of these benthophagous species have similar mouths with small, asymmetrical jaws and small incisor teeth. Both complete metamorphosis and commence benthic feeding at the same size (18-20 mm SL). Qualitatively there is no difference in their diet, although quantitatively butter sole occasionally feed more heavily on mysids. Comparing fish of the same size (17-35 mm SL) on 29 May 1979, *P. vetulus* and *I. isolepis* fed on the same prey items in the same proportions. If food should be limiting for these two species, then in the absence of subsequent shifts in food preference the potential exists for competitive interaction. While observing the feeding behavior of *P. vetulus* in the laboratory, several butter sole were placed in the aquaria along with the English sole. *Isopsetta isolepis* were observed to bite the fins of *P. vetulus* and pursue them around the tank. These were casual observations which were only replicated over a 2-d period. Should this aggressive behavior be substantiated by further work, then interference competition between *P. vetulus* and *I. isolepis* in the Moolach Beach area seems likely. On the whole, however, English and butter soles do not settle at the same time or place. *Parophrys vetulus* has a protracted benthic recruitment period, settling to the bottom between November and July in estuarine and coastal waters <30 m deep (Krygier and Pearcy footnote 2). *Isopsetta isolepis*, on the other hand, has a restricted settling period (May-August) yet occurs over a broader depth range (9-60 m) (Krygier and Pearcy footnote 2). If interspecific interactions were occuring between English and butter soles, it is likely that they would be limited to regions of overlap like Moolach Beach in the summer months.

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