PREDATION ON *CAPITELLA* SPP. BY SMALL-MOUTHED PLEURONECTIDS IN PUGET SOUND, WASHINGTON[1]

D. SCOTT BECKER[2] AND KENNETH K. CHEW[3]

ABSTRACT

This study examined the predation patterns of three flatfishes (English sole, Dover sole, and rex sole) on the opportunistic polychaetes *Capitella* spp. in disturbed soft-bottom habitats of Puget Sound, Washington. Sampling was conducted throughout the diel cycle during May and June 1981. All three fishes exhibited some degree of selective predation on *Capitella* spp. based on both number and size of these prey. Numerical dietary contribution by *Capitella* spp. was greatest at night for all three fishes, suggesting that these polychaetes become more accessible to predators at night. Predation on *Capitella* spp. allowed English sole to alter their normal diurnal feeding chronology and forage successfully at night. This study supports the hypothesis that some demersal fishes can exploit opportunistic prey in disturbed habitats.

The composition of soft-bottom marine benthic invertebrate assemblages can be altered by a variety of natural and anthropogenic disturbances, including salinity reduction (Boesch et al. 1981), storm-induced surge (Rees et al. 1977), hypoxia (Santos and Simon 1980), dredge-spoil dumping (Rhoads et al. 1978), sewage disposal (Pearson and Rosenberg 1978), and oil spills (Sanders et al. 1980). To predict the effects of these events on demersal fishes, predator-prey relationships between benthic invertebrates and their piscine predators must be understood. Unfortunately, this kind of information is rare for marine ecosystems (Mills 1975).

Frequently, benthic invertebrate assemblages in disturbed habitats are dominated by one or more opportunistic species (e.g., Grassle and Grassle 1974; McCall 1977; Pearson and Rosenberg 1978; Rhoads et al. 1978). These opportunists are adapted to rapidly colonize disturbed environments and often attain exceptionally high population densities. Because many of these species reside at or near the sediment-water interface, they represent a potential food bonanza to bottom-feeding demersal fishes. When fishes encounter such an abundant and accessible food source, it seems likely that those species capable of modifying their foraging behavior to fully exploit this windfall will do so. Such opportunistic predation on temporally or spatially variable superabundant prey has been found for a variety of fishes (e.g., Nilsson 1960; Ivlev 1961; Zaret and Rand 1971; Murdoch et al. 1975), and is one prediction of optimal foraging theory (review in Pyke et al. 1977).

As an example of how a group of demersal fishes responds to a disturbed soft-bottom habitat dominated by opportunistic benthic invertebrates, we describe the foraging patterns of three flatfishes (Pleuronectidae) in Puget Sound, WA on *Capitella* spp., a well-known group of opportunistic polychaetes (Grassle and Grassle 1974; Pearson and Rosenberg 1978). The flatfishes targeted for study were English sole, *Parophrys vetulus*; Dover sole, *Microstomus pacificus*; and rex sole, *Glyptocephalus zachirus*. These fishes belong to the small-mouthed subgroup of pleuronectids identified by Moiseev (1953) and, as such, prey primarily upon small infaunal and epifaunal benthic invertebrates. These species also form a major component of demersal fish assemblages in Puget Sound (Miller et al. 1977; Wingert and Miller 1979; Becker 1984), as well as in most nearshore areas along the west coasts of the United States and Canada (e.g., Alverson et al. 1964; Day and Pearcy 1968; Hart 1973; Allen 1982).

MATERIALS AND METHODS

Field Sampling

The study was conducted on the delta of the

[1]Contribution No. 723, School of Fisheries, University of Washington, Seattle, WA 98195.

[2]School of Fisheries, University of Washington, Seattle, WA 98195; present address: Tetra Tech, Inc., 11820 Northup, Bellevue, WA 98005.

[3]School of Fisheries, University of Washington, Seattle, WA 98195.

Manuscript accepted March 1987.
FISHERY BULLETIN: VOL. 85, NO. 3, 1987.

Puyallup River, in Puget Sound's Commencement Bay (Fig. 1). This dynamic area receives a variety of anthropogenic and natural discharges. For example, the river discharges approximately 5,500 kg/year of sediments in a seasonally variable manner (Dexter et al. 1981). In addition, the City of Tacoma releases primary-treated sewage into the river at an annual flow rate of 0.9 m^3/second (20.5 MGD) approximately 2.4 km upstream from the river mouth (Tetra Tech 1981). A preliminary survey conducted by the authors showed that benthic invertebrate assemblages throughout much of the delta were dominated numerically by *Capitella* spp.

Field sampling was conducted from 26 May to 3 June 1981. All three target species have spawned by this time (Hart 1973) and, as typical of most adult pleuronectids, are presumably feeding intensely to replenish the energy used previously for migration, overwintering, and spawning (e.g., Moiseev 1953; Roff 1982).

Sampling was conducted along two 300 m transects located at a depth of 32 ± 2 m (Fig. 1). This depth corresponds to the upper boundary of the

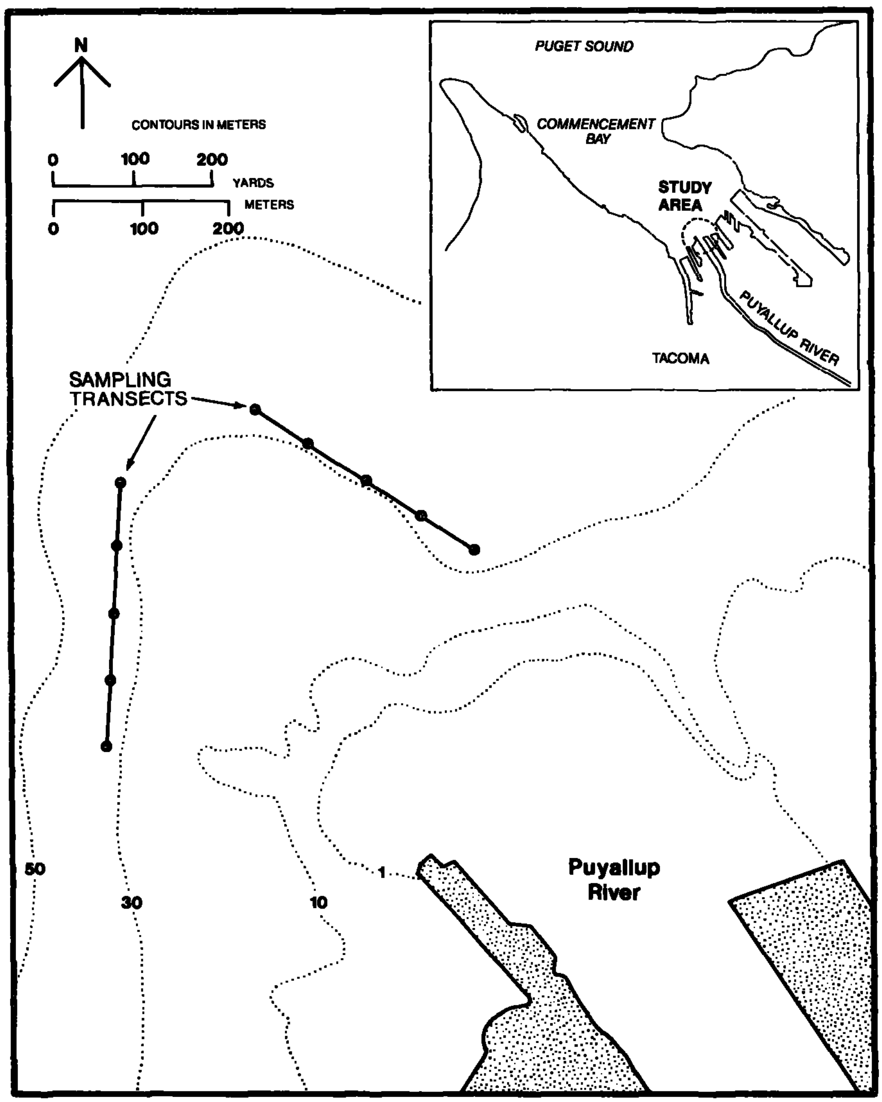

FIGURE 1.—Locations of sampling transects and benthic sampling points (i.e., large dots) along each transect.

intermediate faunal zone (i.e., 30-70 m depth) identified for Puget Sound demersal fish assemblages by Wingert and Miller (1979). All three target species are sufficiently abundant in this depth zone to allow a quantitative food habits analysis to be conducted. Data from both transects were pooled prior to analysis.

Fishes were collected using a 7.6 m (headrope) otter trawl having a body mesh size of 3.2 cm (stretched) and a cod-end liner mesh size of 0.8 cm (stretched). Trawling was conducted along both transects at a constant vessel speed of approximately 2.5 kn. All positioning was achieved using the LORAN-C navigation system. To assess diel variations in feeding behavior, hauls were made along each transect during four periods of the diel cycle: morning (0900-1030 h), afternoon (1300-1500 h), evening (1900-2030 h), and night (2330-0100 h). Each transect was sampled twice during each time period, yielding eight hauls per transect or a total of 16 hauls for the study.

At sea, the stomach contents of the target species were fixed by injecting, using a 50 cc syringe, a 10% solution of buffered formalin into the body cavity of each individual. These fishes were then brought to the laboratory and stored at 4°C.

Benthic invertebrates along each transect were sampled within 2 days of trawling. Organisms were collected using a 0.1 m^2 van Veen bottom grab, sieved through a 1.0 mm mesh screen, fixed with a 10% solution of buffered formalin, and transferred to 70% ethanol for storage. A single grab sample was taken during daytime at each of five sampling points positioned at approximately equal distances along each transect (Fig. 1).

Laboratory Analysis

Within 5 days of sampling, the total length (TL) of each fish was measured to the nearest 1.0 mm. The body cavity was then opened and the stomach was removed by severing the esophagus and pylorus. Stomachs were stored in 70% ethanol prior to analysis.

For food habits analysis, stomachs were subsampled from the total pool of available stomachs. To minimize within-species variation as a result of size-dependent foraging patterns (e.g., Gabriel and Pearcy 1981), only individuals within an 80 mm length range were selected for analysis. The ranges used for English sole, Dover sole, and rex sole were 240-320, 200-280, and 210-290 mm TL, respectively. Each length range bracketed the median length observed for each species.

Identifications of all invertebrates in stomachs and benthic samples were made using a dissecting microscope. Sizes of all *Capitella* spp. were estimated using the width of the fifth setiger (cf. Tsutsumi and Kikuchi 1984). This measurement was used instead of body length because many of these polychaetes were fragmented during grab sampling or ingestion by the fishes. Setiger widths were measured to the nearest 0.1 mm using an ocular micrometer.

The dietary contribution of *Capitella* spp. to the total stomach contents of each target species was estimated using percentages based on numerical proportions. In addition, the total number of prey per stomach (i.e., *Capitella* spp. plus all other organisms) was used as an index of feeding intensity for each species.

Statistical Analysis

Nonrandom predation on *Capitella* spp. (i.e., selection) was tested by comparing the numerical proportions of these polychaetes in the stomachs of the fishes with the proportion found in the benthos using a 2 × 2 contingency formulation and the chi-square criterion (Pearre 1982). Direction of selection was determined by inspecting the relative proportions of prey in the stomachs and benthos. Nonrandom size selection of *Capitella* spp. was tested by comparing the size distributions of these polychaetes in the stomachs of the fishes with the size distribution found in the benthos using the Mann-Whitney U-test. In both of these analyses, four comparisons (i.e., one for each time period) for each species were made with a single set of benthic observations. Because these four comparisons lacked independence, significance levels were adjusted conservatively using Bonferroni's technique (Miller 1981).

To examine how the foraging patterns of English sole differed between habitats where benthic assemblages were dominated by *Capitella* spp. and habitats where assemblages did not include these polychaetes, the values of feeding intensity (i.e., numbers of prey per stomach) found in the present study were compared with those obtained at six other sites in Puget Sound by Becker (1984). These six sites were located at depths between 12 and 32 m, and fishes were sampled and processed using methods identical to those described for the present study. Values of feeding intensity were compared during each period of the diel cycle using the Mann-Whitney U-test. Similar analyses could not be conducted for Dover sole and rex sole because these fishes were not sufficiently abundant at the six additional sites.

RESULTS

Prey Selection

Throughout the diel cycle, the numerical proportion of *Capitella* spp. in the diets of all three fishes exceeded the proportion of these polychaetes in the benthos (Table 1). Selection of *Capitella* spp. was highly significant ($P < 0.001$) during all four time periods for English sole and rex sole, and during morning and night for Dover sole. Selection was significant at $P < 0.01$ during evening for Dover sole, but not significant ($P > 0.05$) during afternoon for this species.

TABLE 1.—Comparisons of proportions of *Capitella* spp. in fish stomachs with the proportion in the benthos using a 2 × 2 contingency test. $^{**}P < 0.01$, $^{***}P < 0.001$, ns = $P > 0.05$ (experimentwise).

	Number of *Capitella* spp./Total number of prey[1,2]			
Species	Morning	Afternoon	Evening	Night
English sole	508/1,464*** (50)	425/1,029*** (40)	1,072/1,596*** (32)	1,904/2,592*** (56)
Dover sole	329/861*** (35)	114/416 ns (21)	200/612** (36)	218/461*** (36)
Rex sole	456/526*** (16)	272/412*** (18)	209/276*** (15)	603/671*** (19)

[1]Number of stomachs examined is given in parentheses.
[2]Proportion of *Capitella* spp. in the benthos was 904/3,517.

Percent numerical contribution by *Capitella* spp. to the total diet varied considerably among the three fishes (Fig. 2). Rex sole showed the greatest preference for these polychaetes, including them in 66-90% of the diet throughout the diel cycle. By contrast, Dover sole exhibited the least preference for *Capitella* spp., including them in only 27-47% of the diet. English sole showed moderate preference for these polychaetes, including them in 35-73% of the diet. Diel variation of feeding intensity closely paralleled dietary contributions of *Capitella* spp. for English sole and rex sole, with both variables peaking at night (Fig. 2). For Dover sole, however, these two variables followed substantially different diel trends, with percent dietary contribution of *Capitella* spp. reaching its maximum and feeding intensity dropping to its minimum at night.

Although the magnitudes of percent dietary contribution by *Capitella* spp. differed among the three fishes, several similarities existed in the diel variation of these values (Fig. 2). Minimum dietary contributions were found during morning (English sole) or afternoon (Dover sole and rex sole), whereas maximum contributions were found at night (all three fishes).

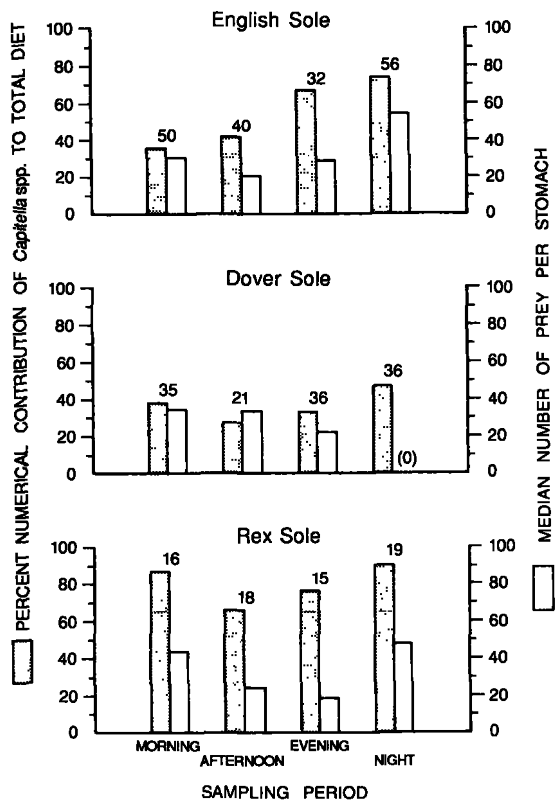

FIGURE 2.—Diel predation patterns of the target species. Number of stomachs examined is presented above each pair of bars.

Prey Size Selection

Median size of *Capitella* spp. in stomachs exceeded the median size of these polychaetes in the benthos during all four time periods for English sole and rex sole, and during morning, afternoon, and night for Dover sole (Fig. 3). Median prey size for Dover sole during evening was approximately equal to median size of *Capitella* spp. in the benthos. Size differences of *Capitella* spp. between diets and the benthos were highly significant ($P < 0.001$) during all four time periods for rex sole, during morning, afternoon, and night for English sole, and during morning and afternoon for Dover sole. Size differences were significant at

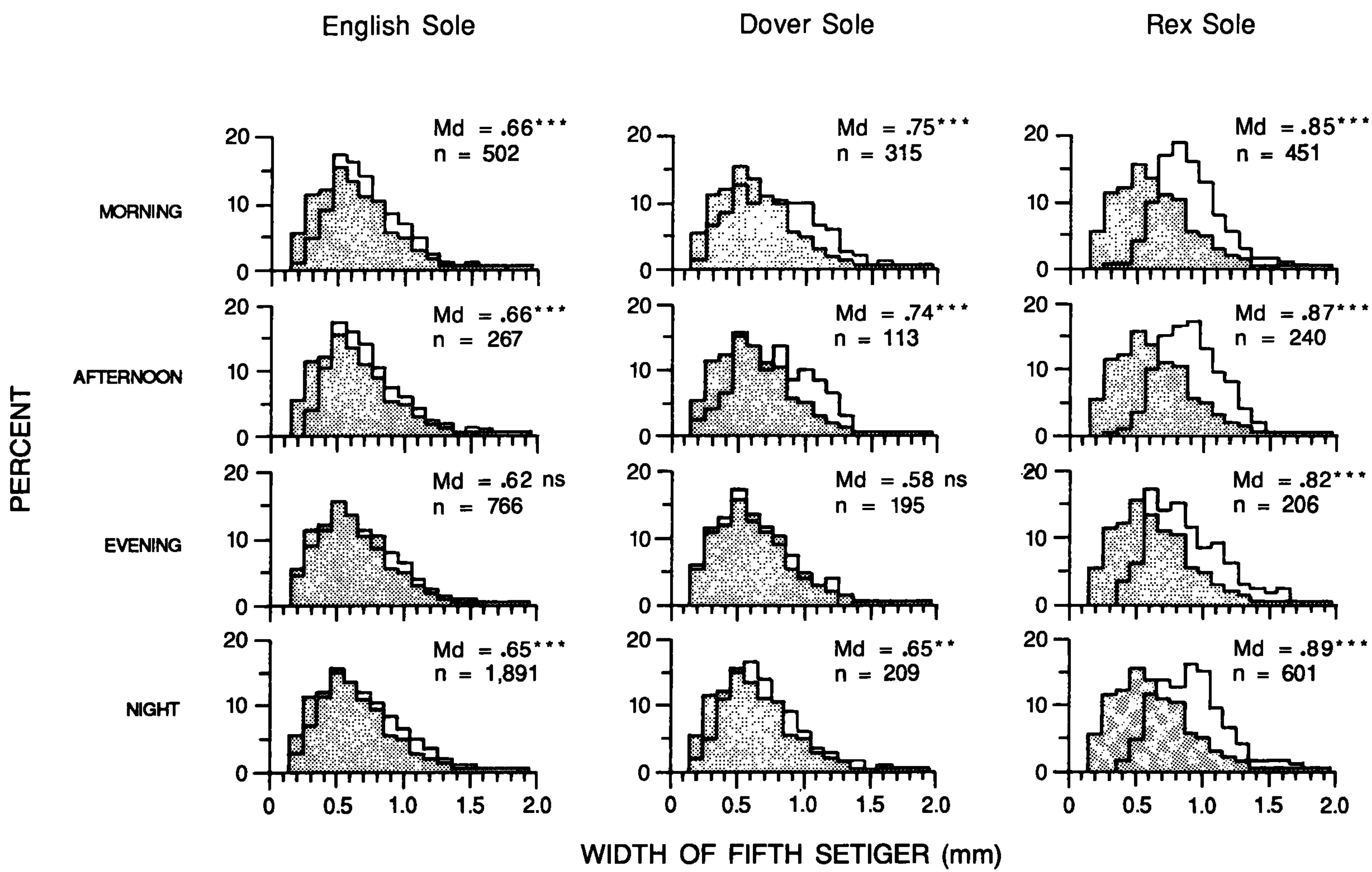

FIGURE 3.—Comparisons of size distributions of *Capitella* spp. in fish stomachs (i.e., open distributions) with the size distribution in the benthos (i.e., stippled distribution) using the Mann-Whitney U-test. Median size (Md) and sample size (n) are given with each distribution from the stomachs. Median size in the benthos was 0.59 mm and sample size was 898 individuals. $^{**}P < 0.01$, $^{***}P < 0.001$, ns = $P > 0.05$ (experimentwise).

$P < 0.01$ during night for Dover sole. No significant size differences ($P > 0.05$) were found during evening for English sole and Dover sole.

Of the three fishes, rex sole selected the largest *Capitella* spp. during every time period, with median size ranging from 0.82 to 0.89 mm throughout the diel cycle. Median size of *Capitella* spp. selected by English sole and Dover sole ranged from 0.62 to 0.66 mm and 0.58 to 0.75 mm, respectively.

Habitat Comparisons

Differences in number of prey per stomach between English sole captured in habitats where *Capitella* spp. were present and conspecifics captured in habitats where these polychaetes were absent were highly significant ($P < 0.001$) at night, but not significant ($P > 0.05$) during morning, afternoon, and evening (Fig. 4). The diel trends of feeding intensity in the two habitats were strikingly different. Where *Capitella* spp. were present, feeding intensity increased from afternoon to evening, and then peaked at night (median = 53.5 prey per stomach). By contrast, in habitats where *Capitella* spp. were absent, feeding intensity declined from afternoon to evening,

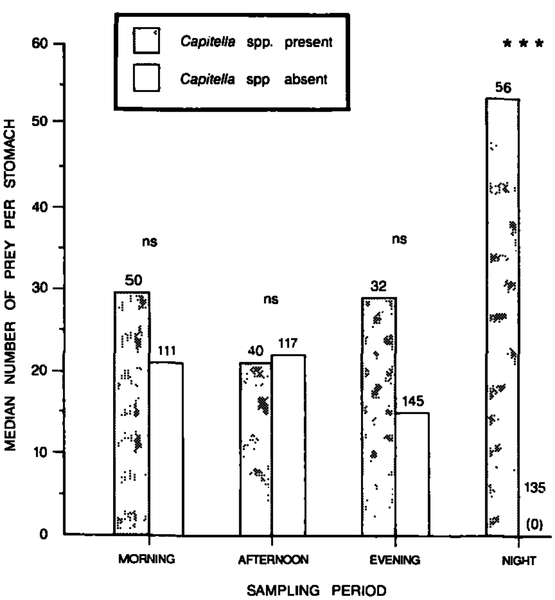

FIGURE 4.—Comparisons of values of feeding intensity for English sole between habitats with and without *Capitella* spp. using the Mann-Whitney U-test. Number of stomachs examined is presented above each bar. Significance level is given above each pair of bars. ***$P < 0.001$, ns = $P > 0.05$.

and reached a minimum (median = 0 prey per stomach) at night.

DISCUSSION

Although *Capitella* spp. accounted for only 25.7% of benthic individuals, their importance as prey to English sole, Dover sole, and rex sole was substantial. All three fishes exhibited significant ($P < 0.05$) numerical and size selection of these polychaetes during all or most of the diel cycle. Based on literature accounts of the food habits of these fishes, the observed importance of *Capitella* spp. as prey could not have been predicted directly.

Most historical accounts of the food habits of the three fishes do not identify *Capitella* spp. as prey (e.g., Hagerman 1952; Kravitz et al. 1977; Hulberg and Oliver 1978; Pearcy and Hancock 1978; Gabriel and Pearcy 1981; Allen 1982; Hogue and Carey 1982). However, most of these studies were conducted in areas where *Capitella* spp. generally would not be expected to occur in large numbers in the benthos (i.e., the continental shelf off Oregon and California). At least two studies have found that one or more of these fishes consume *Capitella* spp. Cross et al. (1984) examined the food habits of English sole (n = 13) and Dover sole (n = 38) in areas influenced by sewage discharges off Los Angeles, CA. Although *C. capitata* numerically accounted for 40-95% of benthic assemblages, the dietary contributions by this polychaete were small (i.e., 0% for English sole and <10% for Dover sole). Toole (1980) found that *C. capitata* was a major prey item of juvenile English sole (66-102 mm TL, n = 45) captured on an intertidal sand flat in Humbolt Bay, CA. However, because benthic assemblages were not sampled, it is unknown whether these fish were preying nonrandomly on *C. capitata*.

Of the three fishes sampled in the present study, rex sole exhibited the greatest degree of selective predation on *Capitella* spp. This species was the only one to nonrandomly select *Capitella* spp. based on both prey number and prey size throughout the diel cycle. In addition, rex sole selected the largest *Capitella* spp. of the three fishes, and included these polychaetes in the largest percentage of total diet during all four time periods. The observed peak in feeding intensity at night agrees with past descriptions of rex sole as a nocturnal forager (Kravitz et al. 1977; Allen 1982; Becker 1984). The concomitant peak in percent dietary contribution of *Capitella* spp. at night indicates that when rex sole were feeding most intensely, selection of *Capitella* spp. was at its highest level.

Dover sole was the least selective of the three fishes with respect to predation on *Capitella* spp. This species did not exhibit selective predation based on prey number during afternoon, nor based on prey size during evening. In addition, the percent dietary contribution by *Capitella* spp. for Dover sole was the smallest of the three fishes during three of the four time periods. The observed minimum level of feeding intensity at night is consistent with the description of Dover sole as a diurnal forager (Allen 1982; Becker 1984). The nighttime peak in percent dietary contribution by *Capitella* spp. suggests that even though this fish normally does not forage at night, *Capitella* spp. could be captured quite successfully relative to other benthic invertebrates.

English sole was intermediate between rex sole and Dover sole with respect to degree of selective predation on *Capitella* spp. Although this species selectively consumed these polychaetes based on prey number throughout the diel cycle, prey size selection was not observed during evening. In addition, dietary contribution by *Capitella* spp. for English sole was the smallest of the three fishes during morning, but intermediate in magnitude during the remainder of the diel cycle. The observed peak in feeding intensity at night is contradictory to the description of English sole as a diurnal forager (Allen 1982; Hogue and Carey 1982; Becker 1984). Because dietary contribution of *Capitella* spp. peaked at a high level of 73% at night, much of the ability of English sole to forage at night resulted from predation on these polychaetes. The influence of *Capitella* spp. on nocturnal foraging by English sole was confirmed by the comparison of diel variation of feeding intensity in habitats with and without *Capitella* spp.

The observed diel variations of predation on *Capitella* spp. could have resulted from behavioral differences of either the fishes or the polychaetes. Because the fishes were sampled throughout the diel cycle, much of the variation due to the predators was accounted for. However, because diel variation in behavior of *Capitella* spp. could not be evaluated using the sampling methods employed in this study, variation in prey availability is unknown. However, at least one pattern is suggested. Because dietary contribution by *Capitella* spp. peaked at night for all three fishes, these polychaetes may become more active at the sediment surface and thus more vulnerable to predation at night. The ability of English sole to alter its normal diurnal feeding chronology to forage primarily on *Capitella* spp. at night further suggests that these polychaetes become more accessible at night. Levinton (1971) found that the bivalve *Macoma tenta* foraged primarily at night and suggested that this periodicity was used, in part, to avoid diurnal predators (primarily winter flounder, *Pseudopleuronectes americanus*). Although this defense mechanism may succeed with obligate diurnal predators, it would not be effective in avoiding nocturnal predators (e.g., rex sole) or species capable of modifying their normal diurnal feeding chronology (e.g., English sole).

From an applied standpoint, results of this study have several implications regarding the concept of disturbance management described by Rhoads et al. (1978). Those authors suggested that by properly managing habitat disturbance (i.e., dredge-spoil disposal in their case), benthic invertebrate assemblages can be maintained in the early successional stages when they are dominated by pioneering species, including opportunists such as *Capitella* spp. Because productivity of these early successional stages generally exceeds that of later stages, Rhoads et al. (1978) hypothesized that benthic assemblages dominated by pioneering species represent an enhanced food resource for demersal fishes. The observed importance of *Capitella* spp. as prey for the three fishes considered in the present study supports this hypothesis. For example, all three fishes selectively preyed upon *Capitella* spp. throughout all or most of the diel cycle, and English sole was able to modify its normal diurnal feeding chronology to prey primarily on these polychaetes at night.

Although the hypothesis of Rhoads et al. (1978) is supported by the present study, enhancing the productivity of a food resource may not be beneficial to demersal fishes if the nutritional quality of their diet is reduced in the process. For example, a variety of fish diseases have been attributed, in part, to dietary deficiencies or imbalances of specific nutrients (reviews in National Research Council 1977, 1981). In addition, the toxicity of chemical contaminants to fishes may be enhanced as a result of improper diets (e.g., Mehrle et al. 1977). Although *Capitella* spp. accounted for only 25.7% of the benthic invertebrates sampled in the present study, the dietary contributions of these polychaetes generally were much greater, especially for rex sole. Given the influence of a balanced diet on fish health, it is possible that prolonged dietary restriction to one or several opportunistic prey could compromise the health of the fishes.

In summary, all three fishes exhibited some degree of selective predation on *Capitella* spp. based on both number and size of these prey. Dietary contribution by these polychaetes was greatest at night for all three fishes, suggesting that *Capitella* spp. may become more accessible to predators at night. Predation on *Capitella* spp. allowed English sole to alter its normal diurnal feeding behavior and forage successfully at night. Finally, this study supports the hypothesis that some demersal fishes can exploit opportunistic prey in disturbed habitats.

ACKNOWLEDGMENTS

We thank M. J. Allen, J. N. Cross, and E. W. Hogue for their comments on the manuscript. This study was supported by the Office of Marine Pollution Assessment of the National Oceanic and Atmospheric Administration (Contract NA80RAD00050). A. J. Mearns was the Project Officer. This study is part of a dissertation submitted to the School of Fisheries of the University of Washington (Seattle, USA) in partial fulfillment of a Ph.D. degree for D. S. Becker.

LITERATURE CITED

ALLEN, M. J.
1982. Functional structure of soft-bottom fish communities of the Southern California Shelf. Ph.D. Thesis, Univ. California, San Diego, 577 p.

ALVERSON, D. L., A. T. PRUTER, AND L. L. RONHOLT.
1964. A study of demersal fishes and fisheries of the northwestern Pacific Ocean. H. R. MacMillan Lect. Fish., Inst. Fish., Univ. Br. Columbia, Vancouver, 199 p.

BECKER, D. S.
1984. Resource partitioning by small-mouthed pleuronectids in Puget Sound, Washington. Ph.D. Thesis, Univ. Washington, Seattle, 139 p.

BOESCH, D. F., R. J. DIAZ, AND R. W. VIRNSTEIN.
1981. Effects of Tropical Storm Agnes on soft-bottom macrobenthic communities of the James and York estuaries and the Lower Chesapeake Bay. Chesapeake Sci. 17:246-259.

CROSS, J. N., J. RONEY, AND G. S. KLEPPEL.
1984. Fish food habits along a pollution gradient. Calif. Fish Game 71:28-39.

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

DEXTER, R. N., D. E. ANDERSON, E. A. QUINLAN, L. S. GOLDSTEIN, R. M. STICKLAND, S. P. PAVLOU, J. R. CLAYTON, R. M. KOCAN, AND M. LANDOLT.
1981. A summary of knowledge of Puget Sound related to chemical contaminants. U.S. Dep. Commer., NOAA Tech. Memo. OMPA-13, Boulder, CO, 435 p.

GABRIEL, W. L., AND W. G. PEARCY.
1981. Feeding selectivity of Dover sole, *Microstomus pacificus*, off Oregon. Fish. Bull., U.S. 79: 749-763.

GRASSLE, J. F., AND J. P. GRASSLE.
1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. J. Mar. Res. 32:253-284.

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

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

HOGUE, E. W., AND A. G. CAREY.
1982. Feeding ecology of 0-age flatfishes at a nursery ground on the Oregon coast. Fish. Bull., U.S. 80:555-565.

HULBERG, L. W., AND J. S. OLIVER.
1978. Prey availability and the diets of two co-occuring flatfish. *In* S. J. Lipovski and C. A. Simenstad (editors), Fish food habits studies, p. 29-36. Wash. Sea Grant, Univ. Wash., Seattle.

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

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

LEVINTON, J. S.
1971. Control of Tellinacean (Mollusca: Bivalvia) feeding behavior by predation. Limnol. Oceanogr. 16:660-662.

MCCALL, P. L.
1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res. 35:221-266.

MEHRLE, P. M., F. L. MAYER, AND W. W. JOHNSON.
1977. Diet quality in fish toxicology: effects on acute and chronic toxicity. *In* F. L. Mayer and J. L. Hamelink (editors), Aquatic toxicology and hazard evaluation, p. 269-280. American Society for Testing and Materials, Philadelphia, PA.

MILLER, B. S., B. B. MCCAIN, R. C. WINGERT, S. F. BORTON, K. V. PIERCE, AND D. T. GRIGGS.
1977. Ecological and disease studies of demersal fishes in Puget Sound near Metro-operated sewage treatment plants and in the Duwamish River. Univ. Wash., Fish. Res. Inst., FRI-UW-7721, 164 p.

MILLER, R. G.
1981. Simultaneous statistical inference. Springer-Verlag, N.Y., 299 p.

MILLS, E. L.
1975. Benthic organisms and the structure of marine ecosystems. J. Fish. Res. Board Can. 32:1657-1663.

MOISEEV, P. A.
1953. Cod and flounder of the Far Eastern Seas. Fish Res. Board Can. Transl. Ser., No. 119, 576 p.

MURDOCH, W. M., S. AVERY, AND M. E. B. SMYTH.
1975. Switching in predatory fish. Ecology 56:1094 1105.

NATIONAL RESEARCH COUNCIL.
1977. Nutrient requirements of warmwater fishes. Natl. Acad. Sci., Wash., DC, 78 p.
1981. Nutrient requirements of coldwater fishes. Natl.

Acad. Press, Wash., DC, 63 p.

NILSSON, N. A.
1960. Seasonal fluctuations in the food segregation of trout, char, and whitefish in 14 north-Swedish lakes. Inst. Freshwater Res., Drottningholm 41:185-205.

PEARCY, W. G., AND D. HANCOCK.
1978. Feeding habits of Dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*; slender sole, *Lyopsetta exilis*; and Pacific sanddab, *Citharichthys sordidus*, in a region of diverse sediments and bathymetry off Oregon. Fish. Bull., U.S. 76:641-651.

PEARRE, S.
1982. Estimating prey preference by predators: use of various indices, and a proposal of another based on chi square. Can. J. Fish. Aquat. Sci. 39:914-923.

PEARSON, T. H., AND R. ROSENBERG.
1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Ann. Rev. 16:229-311.

PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV.
1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52:137-154.

REES, E. I. S., A. NICHOLAIDOU, AND P. LASKARIDOU.
1977. The effects of storms on the dynamics of shallow water benthic associations. *In* B. F. Keegan, P. O. Ceidigh, and P. J. S. Boaden (editors), Biology of benthic organisms, p. 465-477. Pergamon Press, N.Y.

RHOADS, D. C., P. L. MCCALL, AND J. Y. YINGST.
1978. Disturbance and production on the estuarine seafloor. Am. Sci. 66:577-586.

ROFF, D. A.
1982. Reproductive strategies in flatfish: a first synthesis. Can. J. Fish. Aquat. Sci. 39:1686-1698.

SANDERS, H. L., J. F. GRASSLE, G. R. HAMPSON, L. S. MORSE, S. GARNER-PRICE, AND C. C. JONES.
1980. Anatomy of an oil spill: long-term effects from the grounding of the barge *Florida* off West Falmouth, Massachusetts. J. Mar. Res. 38:265-380.

SANTOS, S. L., AND J. L. SIMON.
1980. Response of soft-bottom benthos to annual catastrophic disturbance in a South Florida estuary. Mar. Ecol. Prog. Ser. 3:347-355.

TETRA TECH.
1981. Technical evaluation of City of Tacoma Central Treatment Plant Section 301(h) application for modification of the requirements of secondary treatment. Report prepared for U.S. Environmental Protection Agency, Washington, DC, 299 p.

TOOLE, C. L.
1980. Intertidal recruitment and feeding in relation to optimal utilization of nursery areas by juvenile English sole (*Parophrys vetulus*: Pleuronectidae). Environ. Biol. Fish. 5:383-390.

TSUTSUMI, H., AND T. KIKUCHI.
1984. Study of the life history of *Capitella capitata* (Polychaeta: Capitellidae) in Amakusa, South Japan including a comparison with other geographical regions. Mar. Biol. (Berl.) 80:315-321.

WINGERT, R. C., AND B. S. MILLER.
1979. Distributional analysis of nearshore and demersal fish species groups and nearshore fish habitat associations in Puget Sound. Fish. Res. Inst. Univ. Wash., FRI-UW-7901, 110 p.

ZARET, T. M., AND A. S. RAND.
1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52:3336-3342.