PREDATION ON CAPITELLA SPP. BY SMALL-MOUTHED PLEURONECTIDS IN PUGET SOUND, WASHINGTON

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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
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 m³/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

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**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.

Fish 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 m² 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. Tsutsu 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 x 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.

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).

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Capitella spp./Total number of prey</th>
<th>Median size of Capitella spp.</th>
<th>Median size of polychaetes in benthos</th>
</tr>
</thead>
<tbody>
<tr>
<td>English</td>
<td>508/1,464*** 425/1,029*** 1,072/1,596*** 1,904/2,592***</td>
<td>16-90%</td>
<td>66-90%</td>
</tr>
<tr>
<td>Dover</td>
<td>329/861*** 114/416 ns 200/612** 218/461***</td>
<td>27-47%</td>
<td>27-47%</td>
</tr>
<tr>
<td>Rex</td>
<td>456/526*** 272/412*** 209/276*** 603/671***</td>
<td>35-73%</td>
<td>35-73%</td>
</tr>
</tbody>
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Percent numerical contribution by Capitella spp. to the total diet exceeded the proportion 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 0.62 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, 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

![Figure 4](image-url)
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 ob-
served 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 con-
tribution by Capitella spp. suggests that even
though this fish normally does not forage at
night, Capitella spp. could be captured quite suc-
cessfully 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 ad-
in, 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 ob-
served peak in feeding intensity at night is con-
tradictory 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 poly-
chaetes. The influence of Capitella spp. on noctur-
al 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 behav-
ioral differences of either the fishes or the poly-
chaetes. 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 contribu-
tion 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 ac-
cessible at night. Levinton (1971) found that the
bivalve Macoma tena foraged primarily at night
and suggested that this periodicity was used, in
part, to avoid diurnal predators (primarily winter
flounder, Pseudopleuronectes americanus). Al-
though this defense mechanism may succeed with
obligate diurnal predators, it would not be effect-
ive 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 domi-
nated by pioneering species, including oppor-
tunists such as Capitella spp. Because productiv-
ity of these early successional stages generally
exceeds that of later stages, Rhoads et al. (1978)
hypothesized that benthic assemblages domi-
nated by pioneering species represent an en-
hanced food resource for demersal fishes. The ob-
served importance of Capitella spp. as prey for the
three fishes considered in the present study sup-
ports this hypothesis. For example, all three fishes
selectively preyed upon Capitella spp.
throughout all or most of the diel cycle, and Eng-
lish 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 benefi-
cial 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., Mehrl 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, espe-
cially for rex sole. Given the influence of a bal-
anced diet on fish health, it is possible that pro-
longed 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.

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**LITERATURE CITED**

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