EFFECTS OF SUBSTRATE MODIFICATION ON LITTORAL FLAT MEIOFAUNA: ASSEMBLAGE STRUCTURE CHANGES ASSOCIATED WITH ADDING GRAVEL

C.A. SIMENSTAD, J.R. CORDELL, AND L.A. WEITKAMP

WETLAND ECOSYSTEM TEAM

Technical Report to
Washington Department of Fisheries
Point Whitney Shellfish Laboratory
Brinnon, Washington
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ABSTRACT

Epibenthic meiofauna and small macrofauna in two littoral flat habitats (sandflat at Bywater Bay, northern Hood Canal, and mudflat at Oakland Bay, southern Puget Sound, Washington) were sampled biweekly between March 1 and May 31, 1989 to assess the effects of gravel additions to the natural flats’ substrates. Because of their acknowledged importance as fish prey, nine epibenthic invertebrate taxa were used as “indicators” of significant change in the ability of the littoral flat to sustain foraging by juvenile salmon and other marine fishes. The results were interpreted to vary as a function of the habitat sediment structure and the composition of the natural epibenthos assemblage. Species that are phytally associated, such as *Harpacticus uniremis*, *Tisbe* spp. and *Zaus* sp., are often enhanced by graveling, presumably due to the increased attachment material for macroalgae. Densities of certain gammarid amphipods (i.e., *Corophium* spp.) and cumaceans (*Cumella vulgaris*) also appear to be enhanced when mudflats are graved but appear to be depressed when gravel is applied to sandflats. Frequency of recruitment and other factors affecting epibenthic meiofauna, as well as subtle differences in the sampling efficiency of the epibenthic suction pump over the different substrates, cannot be precluded as potential causes of the observed results. However, differential site effects are likely due to contrasting initial sediment structure and the adaptability of the dominant epibenthos taxa to those substrates, factors that reflect sediment disturbance due to wave and current exposure. The somewhat contradictory results from graveling littoral flats in these two dissimilar habitats, and the differential effect on meiofauna important as prey of juvenile fishes, suggest that manipulating such littoral habitats must be considered with care and evaluated with scientific and statistical rigor.
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ACKNOWLEDGMENTS

We extend our appreciation to Mr. Doug Thompson, of the Washington Department of Fisheries, for facilitating our studies at Bywater Bay and Oakland Bay. We also thank the Taylor United Company for access to Oakland Bay and to their oyster culture grounds, and to Michael Kennedy, who spent many hours sorting and identifying epibenthic crustaceans.

KEY WORDS

estuarine, epibenthos, habitat modification, fish prey, aquaculture, impact
INTRODUCTION

Meiofauna are among the most sensitive organisms to variability in habitat structure (see Hicks and Coull 1983 and Fleeger and Decho 1987 for reviews). As a consequence, their assemblages are vulnerable to dynamic change as a result of both natural and anthropogenic disturbances. Habitat modification is often used to enhance the fishery of some estuarine organisms. The scale and persistence of such modifications vary considerably, from the simple supplementation of sediments to installation of semipermanent features such as dikes and drainage channels. However, often there has been little examination of the effects of these practices upon the original biotic communities and functions of these habitats.

One enhancement practice is that of applying coarse (e.g., gravel) substrates to littoral mud- or sandflats in Pacific Northwest estuaries. This is done to increase the survival and growth of hardshell clams that would otherwise suffer low growth and survival in the fine, unconsolidated sediments. However, the function of such “graveled” beaches and the effects of graveling on mudflat, sandflat, and other unconsolidated, fine-sediment substrate habitats have not been evaluated.

The Washington Department of Fisheries is responsible for both the advancement and regulation of such enhancement activities as well as for the protection of estuarine habitats important to fisheries species. In 1986, the Department initiated a comprehensive study to describe the different benthic communities that were associated with graveled beaches. As a result of this descriptive study, in 1989 the Department sought to conduct a more detailed study of the specific effects of beach graveling. The effects on epibenthic meiofauna and small macrofauna were specifically considered because they are important organisms to fishes that utilize littoral and shallow sublittoral habitats in Pacific Northwest estuaries (Simenstad et al. 1979, 1988; Thom et al. 1984). Investigators from the Wetland Ecosystems Team (WET) at Fisheries Research Institute (FRI) were contracted to conduct the latter study.

The criterion for evaluating graveling impacts was detectable differences in the occurrence and density of the epibenthic crustaceans (e.g., harpacticoid copepods, gammarid amphipods) that are prominent prey of juvenile salmon on graveled (treatment) beaches, as compared with non-enhanced (control) beaches. The research was divided into three phases: (I) statistical determination of optimum sampling size; (II) sampling; and (III) sample processing and data analysis. The first two phases were conducted in 1989 at two sites in Puget Sound—Bywater Bay on Hood Canal and Oakland Bay in southern Puget Sound (Fig. 1); the last phase was completed in 1990-1991.

MATERIALS AND METHODS

APPROACH

Because of the objective to statistically test the effect of the beach graveling “treatment” of littoral flats, the study was designed to incorporate the results of an initial pilot study. The pilot study was specifically designed to determine optimal statistical power that could be derived from
Figure 1. Location of study areas in Hood Canal (Bywater Bay) and southern Puget Sound (Oakland Bay), Washington, sampled in 1989 to evaluate the effects of habitat substrate modification on epibenthic meiofauna.
feasible sampling replication. This pilot sampling was conducted at the two study sites (Fig. 1) in June 1988 and the samples were processed prior to establishing the sampling design for the second, full-scale sampling program in 1989.

Pilot Study to Statistically Determine Sample Size (Replication)

The objective of the pilot study was to process 200 epibenthic pump samples (50 each from graved and natural intertidal habitats at each of the two proposed study sites) for the occurrence and abundance of juvenile salmon (Oncorhynchus spp.) prey species and to analyze the resulting data to determine the optimum (statistical and economical) sample size for subsequent sampling. Epibenthos samples were processed specifically for known fish prey taxa. The relationship between density estimates and the precision of the estimate (ratio of the standard error to the mean) was examined as a function of sample size (number of replicates). Use of the standard error of the mean as a measure of sampling precision is a well-accepted statistical technique (e.g., see Green 1979, Bros and Cowell 1987). On the basis of graphical representation of these functions for each selected prey taxa (Appendix A), we determined that, for most taxa, a sample size of n=25 for subsequent epibenthic crustacean sampling would provide acceptable precision to detect a 100% change in density within 95% confidence (Fig. 2).

Epibenthos Sampling

The objective of the epibenthos sampling design was to typify the meiofauna assemblage structure and standing stock during the period encompassing the outmigration of epibenthic-feeding salmon in Puget Sound. The approach was to systematically sample epibenthic crustaceans in two littoral flat habitats biweekly between March and May during 1989. Effort was allocated to ensure sufficient within-site replication to test the treatment effects within the pair-wise comparison at each site. However, sampling sites were not intended to be replicates and no inference to the universal (i.e., Puget Sound being the sampling “universe”) effect of beach graveling is suggested.

Processing of Epibenthos Samples

Epibenthic organisms that would constitute prey resources of juvenile salmon were selected based on both taxa and size. Selected taxa were documented to be prominent, and perhaps preferred, prey of epibenthic feeding juvenile salmon (e.g., chum, pink and chinook “fry”). Documentation was from the scientific literature or our own unpublished database on juvenile salmon diets. Therefore, harpacticoid taxa such as Harpacticus uniremis and Tisbe spp., which have been described frequently in the literature as common prey, were chosen as primary indicator organisms for testing graveling effects. In addition, we included as indicator taxa other epibenthic crustaceans that we have documented as appearing, although less frequently, in the diets of juvenile salmon from Puget Sound (See Sample Processing). Because other epibenthic crustacean taxa >0.25 mm in length have appeared in the diets of other marine fishes, other harpacticoid copepods, gammarid amphipods and cumaceans falling into this size fraction were also counted. In addition, because many epibenthic crustacean taxa <0.25 mm may also be important prey of other marine fishes (e.g., recently metamorphosed flatfishes such as English sole, Pleuronectes (Parophrys)
Figure 2. Cumulative frequency of collections that would indicate a 100% change in density as a function of sample size (number of replicates) based upon the pilot study of collections in natural (control) and graveled (treatment) sites at Bywater Bay, Hood Canal, and Oakland Bay, southern Puget Sound, Washington; see Appendix A for taxa specific plots.
vetulus; K. Li, Washington Dept. Fisheries, unpubl.), semiquantitative descriptions of their assemblages were also considered important.

STUDY SITES

Two study sites were chosen as being representative of beach graveling of littoral flat habitats in several different regions of Puget Sound (Fig. 1). These sites were situated in different watersheds and exposed to different wave and current exposure, which resulted in two different sediment structures—a sandflat (Bywater Bay) and a mudflat (Oakland Bay).

Bywater Bay

Bywater Bay (47°52'38"N, 122°37'45"W) is a broad sandflat on the northwest shore of Hood Canal. It is representative of the moderately exposed beaches of Puget Sound that are situated at the base of a steep glacial till bluff. Sediments are composed of medium coarse sand (median grain size, 0.42-0.56 mm) eroding from these bluffs.

Oakland Bay

Oakland Bay (47°15'04"N; 123°02'03"W) is a low-gradient mudflat in a protected embayment at the end of Hammersley Inlet in southern Puget Sound. It is composed of fine mud sediments representative of many such "subestuaries" draining the lowlands surrounding southern and western Puget Sound.

SAMPLING AND STATISTICAL DESIGN

Sampling was deployed perpendicular to the tidal elevation gradient in order to minimize the effect of differential tidal inundation and exposure. Twenty-five replicate samples were distributed haphazardly along a sampling transect. The transect was established at approximately the 0.0-ft (MLLW) tidal elevation. This tidal elevation was selected because prior experience (e.g., Thom et al. 1984; Simenstad et al. 1988) had indicated maximal concentration of many epibenthic crustaceans in this general tidal zone. One transect each was located in a gravelled plot (treatment) and an adjacent (control) plot. The control plot was chosen as characteristic of the same beach gradient and substrate as the treatment plot prior to gravel addition. Although the gravel was added a year or more prior to sampling, the treatment plots were quite evident and visually and texturally different from the natural beach. The ends of each transect were permanently marked by stakes and buoys with floats.

The null hypothesis tested was as follows:

\[ H_0: \text{There are no significant differences in the densities of the selected juvenile salmon prey and other marine fish prey taxa between the gravelled (treatment) and the adjacent natural (control) transects}. \]

Thus, this design tested only for specific epibenthic taxa that might indicate the significance of littoral community changes as rearing habitats for economically-important fishes. The effects on other biota (e.g., benthic infauna) were not evaluated. The hypothesis was tested by one-way
analysis of variance (ANOVA, using a confidence interval range test at 95%) after evaluating for homoscedasticity and transforming the raw data by log_{10}+1.

EPIBENTHOS SAMPLING

Sampling was conducted according to established protocol using a battery-powered, 0.018-m\(^2\) epibenthic suction pump and 0.253-mm sieves. This sampling method has been used successfully in Puget Sound and coastal Pacific Northwest estuaries for sampling juvenile salmon prey (Simenstad et al. 1988, Thom et al. 1988). The twenty-five replicates were distributed haphazardly between the two ends of each transect, always progressing from the same end of the transect. This sampling was not considered destructive because only the meiofauna and a very small amount of surface sediment were removed during sampling. In addition, the 2-week intervals between sampling should have allowed the populations, which are highly mobile and turn over rapidly, to colonize the defaunated substrate. For each treatment and control transect, sampling occurred sequentially (e.g., samples taken initially along one transect and then, immediately following, along the second transect). The two sites (Oakland and Bywater bays) were sampled within 2 days of each other during the same period of the tidal month on a biweekly schedule from 26 March to 24 May 1989.

SAMPLE PROCESSING

All samples were sieved both in the field and in the laboratory through 0.253-mm mesh screens to retain a “juvenile salmon prey fraction” and the smaller “non-prey fraction” for separate analyses. The processing protocol included analysis of all epibenthos samples >0.253 mm specifically for the following prey taxa of the associated fishes:

<table>
<thead>
<tr>
<th>Prey taxa</th>
<th>Fish predators</th>
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</thead>
<tbody>
<tr>
<td><strong>Harpacticoida</strong></td>
<td></td>
</tr>
<tr>
<td>Total other harpacticoid copepods</td>
<td>Juvenile English sole (<em>Pleuronectes Parophrys vetulus</em>), starry flounder (<em>Platichthys stellatus</em>)</td>
</tr>
<tr>
<td><strong>Amphipoda</strong></td>
<td></td>
</tr>
<tr>
<td><em>Corophium</em> spp., <em>Paracalliopiella prati</em>, <em>Anisogammarus pugettensis</em>,</td>
<td>Juvenile chinook salmon (<em>O tshawytscha</em>) and coho salmon (<em>O. kisutch</em>)</td>
</tr>
<tr>
<td>Total gammarid amphipods</td>
<td>Juvenile chinook salmon (<em>O tshawytscha</em>) and coho salmon (<em>O. kisutch</em>)</td>
</tr>
<tr>
<td><strong>Cumaceans</strong></td>
<td></td>
</tr>
<tr>
<td><em>Cumella vulgaris</em>, <em>Lamprops quadriplicata</em></td>
<td>Juvenile chinook salmon (<em>O tshawytscha</em>) and coho salmon (<em>O. kisutch</em>)</td>
</tr>
<tr>
<td>Total cumaceans</td>
<td>Juvenile chinook salmon (<em>O tshawytscha</em>) and coho salmon (<em>O. kisutch</em>)</td>
</tr>
</tbody>
</table>
Total number and wet weight for each taxa group, and basic life history stage within each group, were recorded. In addition to these groups, a subsample of 100 epibenthic crustaceans in the <0.253-mm (non-prey) fraction of the samples was scanned qualitatively for taxa composition in 10 of the 25 samples.

DATA ANALYSIS

For each sampling site, date, treatment (graveled, control), and replicate, the density and standing stock for each prey group was tabulated. Statistical summaries were tabulated over all replicates using the FRI program SUPERPLANKTON for DOS computers (C. Simenstad and C. Swanson, unpubl.). Numerical and gravimetric summary indices (e.g., diversity indices) were computed on all taxa differentiated to lowest taxonomic and life history level. Thus, because all samples were sorted under the same criteria, these indices can be compared among samples but should not be compared to similar datasets from other studies.

Analysis included (1) graphical plots of the density of each prey taxa group by site and treatment for each sampling date, and (2) statistical comparisons of the graveled and control epibenthos density. One-way analysis of variance tests (ANOVA; using a 95% confidence interval range test) were conducted using the STATGRAPHICS software package. Prior to analysis, the raw density data was $\log_{10}(x+1)$ transformed in order to meet the assumption of homogeneous error variance. A significance level of .05 was accepted as rejection of the null hypothesis ($H_0$), i.e., the densities of organisms along the treatment transect were significantly different from those along the control transect.

RESULTS AND DISCUSSION

DENSITY DISTRIBUTIONS OF EPIBENTHOS ALONG TRANSECT LINES

Distributions of epibenthic crustacean densities along the sampling transects were qualitatively examined as an indication of the homogeneity of the sampling plot. Plots of the density of each taxa by transect location indicated that the more abundant epibenthos taxa were relatively uniform along the sampling transects, while less abundant taxa had a more patchy distribution. Unidentified (e.g., non-prey taxa) Harpacticoida and Harpacticus spp. were particularly uniform along the Bywater Bay control transect, Tisbe spp. and Zaus sp. tended to be somewhat more variable, and gammarid amphipods and cumaceans were the most heterogeneously distributed (see example distribution for March 26 Bywater Bay control, Appendix B). The Bywater Bay gravel (treatment) transect illustrated somewhat more heterogeneity than the control transect, but seldom illustrated extreme variations for more than a few taxa at more than one consecutive site (e.g., March 26 Bywater Bay gravel, Appendix B). As Bywater Bay is moderately more exposed to wave and current action than Oakland Bay, the relatively homogeneity of the fauna distributions may represent the constant remixing of the surface sediments and comparatively more uniform sediment structure.
Epibenthos taxa in the Oakland Bay sampling transects tended to reflect the reverse order of Bywater Bay. There, the natural mudflat assemblage illustrated more heterogeneous density distributions than the graveled transect assemblage. On several sampling occasions, many of the taxa (usually all the harpacticoid copepods) appeared to respond similarly to features along the transect that enhanced or depressed their densities (i.e., March 26 Oakland Bay control, Appendix B). Conversely, the distribution of epibenthos over the graveled transect at Oakland Bay appeared to be much more homogeneous, and particularly so for general Harpacticoida (i.e., March 26 Oakland Bay gravel, Appendix B).

The response of meiofauna distributions to microtopography variation (Decho et al. 1985) imposed by the gravel at Bywater Bay may explain the somewhat higher heterogeneity in the treatment at that site. Conversely, the more heterogeneous density distributions found in the natural mudflat at Oakland Bay may be representative of microscale patterns in meiofauna distributions due to food resource patchiness (Decho and Fleeger 1987), biotic structure (Warwick et al. 1986) and interspecific interactions (Chandler and Fleeger 1987). Patchiness in food resources, such as diatom concentrations, as well as the meiofauna may be ephemeral, however, and may be more homogeneous during high tide periods (Decho and Fleeger 1988).

**DENSITIES OF EPIBENTHIC FISH PREY**

Differences between the densities of the indicator epibenthos taxa along the graveled treatment transects and the natural control transects were evident and prevalently significant at both sites. However, the directions of these differences, i.e., whether the treatment involved enhancement or depression of the respective taxa, were often quite diametric at the two sites.

**Bywater Bay**

Harpacticoids occurred in different densities at control and graveled transects (Table 1; Appendix C). Compared to the control transect, the densities of *Tisbe* spp. on the graveled transect were enhanced on all sampling occasions, and significantly so (p > 0.05) on four of the five. *Zaus* sp. was found to be significantly enhanced on all five occasions. In contrast, *Harpacticus* spp., *Dactylopodia* sp., and other harpacticoids were all depressed on all occasions, and significantly so for *Harpacticus* and other harpacticoids on three of the five sampling trips (April 10-May 9). As is evident from the time-series density plots (Appendix C), significant differences occurred when *Harpacticus* and the other harpacticoids were at density maxima, rather than originating from a decline in densities along the control transect.

Only one gammarid amphipod, *Paracalliopiella pratti*, consistently occurred at higher densities along the graveled transect and only significantly so on one occasion (Table 1). *Anisogammarus pugetensis* and total gammarid densities were enhanced only during the earliest sampling period (March 26), before their populations had started to increase dramatically at the graveled site (Appendix C).

---

1The following results and discussion of differences in epibenthos densities is not intended to represent change in the natural habitat due to graveling, nor response of the organisms to graveling, because the sampling design did not test pre- and post-treatment differences; thus, although the pair-wise comparison we conducted may suggest potential changes in the natural habitat since treatment, this cannot be verified.
Cumacean densities were universally depressed on the graveled transect compared to the natural control transect (Table 1; Appendix C). These differences were significant for *Cumella vulgaris* on four of the five sampling occasions, and for total cumaceans on all occasions; *Lamprops quadriplicata* were significantly depressed on only one of the five sampling occasions.

**Oakland Bay**

Epibenthos densities were enhanced on the graveled plot at Oakland Bay compared to transect on the natural mudflat control site in all but one of the 36 valid (where organisms occurred along at least one transect) statistical comparisons (Table 1); the one exception occurred when densities were equal for *Anisogammarus pugettensis*. Differences were strongly significant (e.g., p < .01) for *Tisbe* spp., *Harpacticus* spp., other harpacticoids, *Cumella vulgaris* and total cumaceans on at least three of the five sampling occasions, and moderately so on at least one of the two sampling occasions for *Corophium* spp. and total gammarids.2

**ASSEMBLAGE COMPOSITION OF EPIBENTHOS**

Numerical composition of the epibenthos assemblages at the two sites indicated both site differences and treatment effects coinciding with the natural disparity in sediment structure and the addition of surficial gravel (Appendix D, Tables 1-4). The total number of taxonomic categories (taxa richness) was consistently higher on the graveled plots than on the natural littoral flats (control) at both study sites except for the May 24 collections at Bywater Bay (Figs. 3 and 4). Numerical taxonomic diversity (Shannon-Weiner H') was generally higher in the natural sandflat than on the graveled plots at Bywater Bay (Figure 3) but was exclusively higher in the graveled plot than on the natural mudflat at Oakland Bay (Figure 4).

**Bywater Bay**

On the natural (control) sandflat at Bywater Bay, the dominant harpacticoid taxa were members of the family Ectinosomatidae (predominantly *Ectinosoma melaniceps* and *Harpacticus spinulosus*; combined, these taxa usually accounted for >20% of the fauna and as high as ~79% (May 8) (Appendix D Table 1). Other taxa that were periodically prevalent (e.g., >5% of scan samples) were unidentified harpacticoids (e.g., early stage copepodids), *Huntemannia jadensis*, *Paralaoephonte pacifica*, an unidentified species of *Amphiascoides* sp. A, and *Robertsonia* sp. cf. *knoxi*.

Where gravel had been added to the surface, the contribution of the ectinosomatids (including *Ectinosoma melaniceps*) to the epibenthos assemblage was somewhat less during several periods (early April-early May), coincident with an increase in the proportional representation by *Tisbe* spp. (Appendix D Table 2). *Tisbe* spp. along the control transect did not comprise a conspicuous portion of the assemblage until the last sampling date, in late May. Other prevalent taxa included the harpacticoids *Paralaoephonte pacifica*, *Amphiascus* sp. C-variants group, *Amphiascoides* sp. A, *Robertsonia* sp. cf. *knoxi*, and the gammarid amphipod *Paracalliopiella pratti*.

---

2Except for one common occurrence of *Anisogammarus pugettensis*, however, *Corophium* was the only gammarid taxa that could be tested.
Table 1. Statistical significance levels of one-way analyses of variance for differences in the densities of epibenthic crustaceans on natural (control) and treatment (gravel additions) littoral flats at Bywater Bay, Hood Canal, and Oakland Bay, Puget Sound, Washington, between March 26 and May 24, 1989; values in bold face type denote enhancement, and underlined indicates depression, of epibenthos densities at the graveled site relative to the control.

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<th>April 10-12</th>
<th>April 25-26</th>
<th>May 8-9</th>
<th>May 22-24</th>
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<td>Tisbe spp.</td>
<td>0.0164</td>
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<td>0.0000</td>
<td>0.0000</td>
<td>0.0825</td>
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<td>Zaus spp.</td>
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<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
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<td>0.1817</td>
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<tr>
<td>Lamprops quadriplicata</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>Total Cumaceans</td>
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<td>0.0000</td>
<td>0.0033</td>
<td>0.0010</td>
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</table>
BYWATER BAY EPIBENTHOS ASSEMBLAGE STRUCTURE

Figure 3. Taxa richness (number of taxonomic categories) and species diversity (Shannon-Weiner $H'$) of epibenthic organisms on natural (control) and graved (treatment) littoral flats at Bywater Bay, March 25-May 24, 1989.

OAKLAND BAY EPIBENTHOS ASSEMBLAGE STRUCTURE

Figure 4. Taxa richness (number of taxonomic categories) and species diversity (Shannon-Weiner $H'$) of epibenthic organisms on natural (control) and graved (treatment) littoral flats at Oakland Bay, March 25-May 22, 1989.
Oakland Bay

Halacarids (aquatic mites) and cyclopoid copepods (Cyclopoida-Cyclopinae) are a notably more prominent component of the epibenthos in the natural mudflat at Oakland Bay (Appendix D Table 3) than at Bywater Bay, although they may not have a strong affinity with the substrate. Other prominent taxa include the harpacticoids Ectinosomatidae, *Paralaophonte congenera, Laophonte inornata, Stenhelis sp. A, Amphiascoides subdebilis*, and the gammarid amphipod *Corophium* spp. Where gravel had been added, halacarids, cyclopoids, ectinosomatids, other harpacticoids mentioned above, and *Corophium* spp. continued to be prominent. However, taxa such as *Harpacticus* sp. uniremis group, *Amphiascus* sp. A-virians group, *Schizopera knabeni* and *Cumella vulgaris* appeared to be notably more common in the graveled treatment (Appendix D Table 4).

**EFFECTS OF GRAVELING ON LITTORAL FLAT EPIBENTHOS AND PREY RESOURCES OF JUVENILE FISHES**

The influence of adding gravel to natural littoral flats upon epibenthos assemblages is highly dependent upon both the taxa and substrate characteristics of the natural littoral flat (Table 2). The degree of gravel coverage and the age of the plot may also be important factors, but were not included in this study. At Bywater Bay, densities of certain sandflat epibenthos, such as *Cumella vulgaris*, members of *Harpacticus* spp. that are more common to sandy substrates (e.g., *H. spinulosus, H. arcticus*; Thom et al. 1984, Cordell and Simenstad 1988, Simenstad et al. 1988), and *Anisogammarus pugettensis* were depressed on the graveled plot compared to the natural (control) transect. However, the densities of other taxa such as *Tisbe* spp., *Zaus* spp., and *Paracalliopiella pratti* were enhanced. Graveling of the mudflat at Oakland Bay, however, appears to have resulted in enhancement of all the indicator epibenthos taxa prevalent at that site; in contrast, *Dactylopodia, Paracalliopiella pratti*, and *Lamprops quadriplicata* were rare or absent.

These results can be interpreted, at least in part, by the adaptations and ecology of the different epibenthos taxa. *Tisbe* spp. and *Zaus* sp. are both relatively epiphytal, e.g., they live directly on or have an affinity for plant (e.g., macroalgae, eelgrass) microhabitats. Both tend to be broadly dispersed and rapid colonizers in littoral flat habitats (Simenstad et al. 1988). The gravel plots at both sites, but especially at Bywater Bay, were heavily colonized by algae, most commonly *Ulva lactuca*, which were attached to the gravel. Any direct sampling of an algae-dominated patch would likely have resulted in high concentrations of these organisms.

It appears that total replacement of the sandflat substrate with gravel actually removed a critical habitat element for taxa such as *Harpacticus spinulosus*, some ectinosomatids, and *Cumella vulgaris*, all of which inhabit fine surface sediments, resulting in lower densities despite sand and finer substrates in the interstitial spaces among the gravel. Thus, the gravel was a true inhibitor rather than a neutral factor for these taxa. However, we cannot entirely preclude several alternative explanations unassociated with the change in sediment structure. Competition between the enhanced epibenthos taxa and the “fine-sediment taxa” might also produce an apparent inhibition of the latter. Similarly, although our sampling methods were designed to avoid biases imposed by differential sampling of the control and treatment substrates, the sampling pump may have actually
Table 2. Summary of effects of addition of gravel to littoral flat habitats at Bywater Bay, Hood Canal, and Oakland Bay, southern Puget Sound, Washington, March 25-May 24, 1989 as inferred from difference between natural and graveled treatments; ++ = strongly enhanced densities, + = moderately increased densities, * = no detectable effect; - = moderate decrease in densities, and — = strongly decreased densities.

<table>
<thead>
<tr>
<th>Prey</th>
<th>Differences</th>
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<tr>
<td></td>
<td>Bywater Bay</td>
</tr>
<tr>
<td>Harpacticoid Copepods</td>
<td></td>
</tr>
<tr>
<td><em>Tisbe</em> spp.</td>
<td>++</td>
</tr>
<tr>
<td><em>Zaus</em> sp.</td>
<td>++</td>
</tr>
<tr>
<td><em>Harpacticus</em> spp.</td>
<td></td>
</tr>
<tr>
<td><em>(H. uniremis</em> and <em>sp. uniremis</em> group)</td>
<td>-</td>
</tr>
<tr>
<td><em>(H. spinulosus, H. arcticus)</em></td>
<td>—</td>
</tr>
<tr>
<td><em>Dactylopodia</em> sp.</td>
<td>*</td>
</tr>
<tr>
<td>Other Harpacticoida</td>
<td>—</td>
</tr>
<tr>
<td>Gammarid Amphipods</td>
<td></td>
</tr>
<tr>
<td><em>Corophium</em> spp.</td>
<td>—?</td>
</tr>
<tr>
<td><em>(C. salmonis, C. spinicorne)</em></td>
<td></td>
</tr>
<tr>
<td><em>Paracalliopiella pratti</em></td>
<td>+</td>
</tr>
<tr>
<td><em>Anisogammarus</em> pugettensis</td>
<td>—</td>
</tr>
<tr>
<td>Total Gammaridea</td>
<td>-</td>
</tr>
<tr>
<td>Cumaceans</td>
<td></td>
</tr>
<tr>
<td><em>Cumella vulgaris</em></td>
<td>—</td>
</tr>
<tr>
<td><em>Lamprops quadrillicata</em></td>
<td>—</td>
</tr>
<tr>
<td>Total Cumacea</td>
<td>—</td>
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</table>

extracted proportionally more of these taxa from the natural surface sediments than in the graveled treatment. This may have occurred periodically if more sediment was in suspension in the benthic boundary layer during sampling on windy days, when the beach area was exposed to more wave energy; more sediment in suspension at the control plot could have induced more clogging of the sampler (port) screens and caused more infaunal organisms to be extracted from the sediment. The results at Oakland Bay illustrated a more dramatic change in sediment structure, from mud and silt to gravel. In this case, the extensive increase in usable interstitial space and habitat complexity appears to enhance most common epibenthic taxa. In addition to most of the indicator taxa, other harpacticoid species were also relatively more abundant on graveled substrates.

In the case of both habitats, these often starkly significant differences would probably decrease with the age of the habitat. Over time, natural sediment transport and settling on the gravel plots should result in an increase of fine sediments (i.e., sand at Bywater Bay and mud/silt at Oakland Bay) in the gravel matrix. The increased diversity in sediment composition and patchiness would probably result in an increase in the densities of the depressed taxa, perhaps without a concomitant
decline in the enhanced taxa until the gravel is covered. Continued clam harvesting on these sites, however, may continue to maintain a highly mixed substrate over time.

Comparisons between the graveling treatment effects and the preferred prey taxa indicate that prey resources for many fish species would be enhanced by the surface addition of gravel. Although fish collections and fish prey analyses were not included as elements of this study, several lines of evidence can provide an indication of the more trophically important components of the epibenthos in both the natural and gravelled littoral flat habitats. Available literature on other littoral habitats (e.g., Hood Canal, Simenstad and Wissmar, 1984; and Simenstad and colleagues, unpubl.; Padilla Bay, Simenstad et al. 1988; central Puget Sound, Thom et al. 1984) has identified distinct epibenthic harpacticoid taxa important to juvenile salmon and certain baitfish such as juvenile Pacific herring, surf smelt, Pacific sand lance, and threespine stickleback. The ubiquitous appearance of Harpacticus uniremis, Tisbe spp., Zaus spp., and Dactylopodia sp. in the diets of these fish suggests that littoral flats, especially those with submergent macrophytes (e.g., Zostera marina, Z. japonica, and macroalgae), are important habitats from the standpoint of both foraging habitats for the fish and for the production of prey resources that are exported into adjacent habitats.

Recent information has highlighted several other epibenthic harpacticoid taxa that may also be important as requisite prey of juvenile flat fish (Pleuronectidae). Weitkamp (1991) included the diet composition of juvenile starry flounder and English sole at Bywater Bay in her analysis of disturbance effects upon littoral flat meiofauna. In addition to Tisbe spp. and Harpacticus uniremis, she identified several other harpacticoid taxa as appearing conspicuously in these fishes diets, including Harpacticus spinulosus, Huntemannia jadensis, Ectinosomatidae, and Robertsonia spp. (Appendix E Figures 1-4). These, and other taxa such as Microarthridion littorale (K. Li, Washington Dept. Fisheries, unpubl.), may constitute strongly selected prey at sequential, short-term stanzas in the early estuarine growth of recently metamorphosed fishes such as juvenile flatfish.

All these presumptions are contingent upon the concept that prey resources can potentially limit juvenile fish production (vis a vis growth and growth-associated survival) under sufficient fish densities; that is, there is a carrying capacity of a habitat for the production of fish.

SUMMARY AND RECOMMENDATIONS

The approach was to systematically sample epibenthic crustaceans in two littoral flat habitats biweekly between March 1 and May 31, 1989. A list of nine epibenthic invertebrate taxa were used as “indicators” of significant change in the ability of the littoral flat to sustain foraging by juvenile salmon and other marine fishes. The results were interpreted to vary as a function of the habitat sediment structure and the composition of the natural epibenthos assemblage.

1. Artificially supplementing habitat structure, e.g., by adding gravel over finer-sediment substrate, does not necessarily constitute a de facto enhancement or depression of associated meiofauna. Different components of the epibenthos respond to changes in habitat structure differently, and the epibenthos of different littoral flat habitats are unique.
2. Analysis of impacts on littoral and shallow sublittoral habitats relative to foraging of juvenile salmon and other fishes cannot be conducted at coarse taxa resolution without ambiguity. Both the fish prey selectivity and the discrete epibenthos taxa sensitivity to microhabitat differences require that evaluations of habitat changes such as graveling be assessed at the genus or species (group) level.

3. Prey assessment based upon juvenile salmon may be contrary to the habitat's function as foraging habitat for other fish (and wildlife) species. Artificial enhancement of foraging habitat for juvenile salmon, which could be proposed via graveling and other habitat modifications, could simultaneously be deleterious to other juvenile fishes, especially flatfishes.

4. Assessment of habitat impacts such as graveling on littoral flats depends completely upon the question being asked, the resource priorities, and the commitment to statistical rigor. It is apparent from this study that a reduced allocation of effort expended on the level of taxonomic identification and sample size (replication) could have produced results contrary or ambiguous to those described here. For example, while several species of harpacticoids (e.g., *Harpacticus spinulosus* and *H. arcticus*) within one of the indicator taxa (*Harpacticus* spp.) appeared to suffer depressed population densities on the gravelled sandflat at Bywater Bay, other congeners (species in the *H. uniremis* group) were enhanced. Similarly, reduction in sample size below the n=25 determined to be sufficient to detect a 100% change in the mean density of organisms at 95% confidence would have diffused the results of testing the less dramatic differences.


APPENDICES
APPENDIX A

CUMULATIVE SAMPLE REPLICATION-STATISTICAL POWER PLOTS FOR EPIBENTHIC TAXA EVALUATED FROM PILOT STUDY SAMPLING AT BYWATER BAY AND OAKLAND BAY, PUGET SOUND, WASHINGTON
Oakland Bay Mud (Control) Corophium sp.
Oakland Bay Gravel (Treatment) Corophium sp.
Bywater Bay Mud (Control) Harpacticus uniremis

Sample size

Number / m²

Standard Error

S.E. Mean
S.E. Min
S.E. Max
Dect. Diff.
Density
Bywater Bay Gravel (Treatment) Harpacticus uniremis

![Graph showing sample size vs. number of units and standard error]

- S.E. Mean
- S.E. Min
- S.E. Max
- Dect. Diff.
- Density
Bywater Bay Mud (Control) Tisbe spp.
Bywater Bay Gravel (Treatment) Tisbe spp.

![Graph showing the relationship between sample size and standard error for Bywater Bay Gravel treatment, with number of individuals per m² indicated. The graph illustrates the standard error, mean, maximum, and minimum values at various sample sizes.]
Bywater Bay Mud (Control) Zaus sp.

Sample size

Number / m²

Standard Error

- S.E. Mean
- S.E. Min
- S.E. Max
- Dect. Diff.
- Density

0 20 30 40 50 60 70 80 90 100 110 120

0 40 80 120 160 200 240 280 320
Bywater Bay Mud (Control) Cumella vulgaris

- S.E. Mean
- S.E. Min
- S.E. Max
- Dect. Diff.
- Density

Sample size

Number / m$^2$

Standard Error

[Graph showing the number of specimens per sample size with standard error lines for various conditions.]
Bywater Bay Gravel (Treatment) Cumella vulgaris

Number / m^2

Sample size

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Legend:
- S.E. Mean
- S.E. Min
- S.E. Max
- S.E. Mean
- Dect. Diff.
- Density
Bywater Bay Mud (Control) Total Epibenthos

Sample size

Number / m\(^2\)

- S.E. Mean
- S.E. Min
- S.E. Max
- Dect. Diff.
- Density

Standard Error

0 50 100 150 200 250 300 350 400

0 100 200 300 400 500 600 700 800
Bywater Bay Gravel (Treatment) Total Epibenthos

Sample size

Number / m$^2$

- S.E. Mean
- S.E. Min
- S.E. Max
- Dect. Diff.
- Density

Standard Error

0 5 1 1 2 2 3 3 4 4 5 5

Density
Oakland Bay Mud (Control) Harpacticus uniremis

Number / m²

- S.E. Mean
- S.E. Min
- S.E. Max
- Dect. Diff.
- Density

Sample size

Standard Error
Oakland Bay Gravel (Treatment) Harpacticus uniremis

![Graph showing data for Oakland Bay Gravel Treatment with Harpacticus uniremis. The graph plots sample size on the x-axis and standard error, mean, and max on the y-axis. The data points are represented with different lines for S.E. Mean, S.E. Min, S.E. Max, and Density.]}
Oakland Bay Mud (Control) Tisbe spp.
Oakland Bay Gravel (Treatment) Tisbe spp.

- S.E. Mean
- S.E. Min
- S.E. Max
- Dect. Diff.
- Density

Number / m²

Standard Error

Sample size
Oakland Bay Gravel (Treatment) Total Harpacticoids

![Graph showing the relationship between sample size and number of harpacticoids, with lines indicating standard error and density.](image-url)
Oakland Bay Mud (Control) Total Harpacticoids

Sample size

Number / m²

---

S.E. Mean
S.E. Min
S.E. Max
Dect. Diff.
Density
Oakland Bay Mud (Control) Cumella vulgaris

Number / m²

Sample size

- S.E. Mean
- S.E. Min
- S.E. Max
- Dect. Diff.
- Density
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Oakland Bay Gravel (Treatment) Cumella vulgaris
Oakland Bay Mud (Control) Total Epibenthos

Number / m$^{-2}$

Sample size

Standard error

Mean S.E.
Min S.E.
Max S.E.
Density
Dect. diff.
Oakland Bay Gravel (Treatment) Total Epibenthos

Sample size
APPENDIX B

REPRESENTATIVE EXTREMES IN THE HOMOGENEITY OF DENSITY ($\log_{10}+1$) DISTRIBUTIONS OF EPIBENTHOS TAXA ALONG TWENTY-FIVE SAMPLE (REPLICATE) TRANSECT AT BYWATER BAY, HOOD CANAL, AND OAKLAND BAY, PUGET SOUND, WASHINGTON, MARCH 26, 1989
MARCH 26 BYWATER BAY CONTROL

REPLICATE NUMBER (transect location)
MARCH 26 OAKLAND BAY GRAVEL

EPIBENTHOS DENSITY (log10+1)

REPLICATE NUMBER (transect location)
APPENDIX C

STATISTICAL DIFFERENCES AND TEMPORAL TRENDS IN THE DENSITIES (TRANSFORMED BY LOG10+1) OF EPIBENTHIC MEIOFAUNA AND SMALL MACROFAUNA IN NATURAL (CONTROL) AND TREATMENT (GRAVEL ADDITIONS) LITTORAL FLATS AT BYWATER BAY, HOOD CANAL, AND OAKLAND BAY, PUGET SOUND, WASHINGTON, BETWEEN MARCH 26 AND MAY 24, 1989
Effects of Beach Graveling on Littoral Flat Epibenthos

*Tisbe furcata*  Bywater Bay

![Graph showing the effects of beach graveling on *Tisbe furcata* in Bywater Bay. The graph displays the density of *Tisbe furcata* over different dates, with control and treatment groups compared. The data points and error bars indicate fluctuations in density throughout the study period.](image-url)
Effects of Beach Graveling on Littoral Flat Epibenthos

Tisbe furcata  Oakland Bay

Control  Treatment

DATE

26 Mar 10 Apr 25 Apr 9 May 22 May
Effects of Beach Graveling on Littoral Flat Epibenthos

*Zaus aurellii* Bywater Bay

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<tr>
<td>12 Apr</td>
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<tr>
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<td></td>
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<tr>
<td>24 May</td>
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(DENSITY (NO. m$^{-2}$))
Effects of Beach Graveling on Littoral Flat Epibenthos

Zaus aurelii Oakland Bay

DATE

26 Mar 25 Apr 10 Apr 9 May 22 May

DENSIITY (No. m²)

0.000
0.000
0.3223

Control
Treatment
Effects of Beach Graveling on Littoral Flat Epibenthos

*Harpacticus spp.* Bywater Bay

**Graph:**

- **Y-axis:** DENSITY (No. m^-2)
- **X-axis:** DATE (26 Mar, 12 Apr, 26 Apr, 8 May, 24 May)
- **Legend:**
  - ■ Control
  - ○○ Treatment

**Data Points:**
- 26 Mar: 0
- 12 Apr: 0
- 26 Apr: Increase
- 8 May: Peak
- 24 May: Decline
Effects of Beach Graveling on Littoral Flat Epibenthos

*Harpacticus spp.* Oakland Bay

<table>
<thead>
<tr>
<th>DATE</th>
<th>26 Mar</th>
<th>10 Apr</th>
<th>25 Apr</th>
<th>9 May</th>
<th>22 May</th>
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<tr>
<td>DENSITY (No. m(^{-2}))</td>
<td>0.0000</td>
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<td>0.2610</td>
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</tr>
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- **Control**
- **Treatment**
Effects of Beach Graveling on Littoral Flat Epibenthos

*Dactylopodia sp.* Bywater Bay

**DENSITY** (No. m$^{-2}$)

<table>
<thead>
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<tr>
<td>26 Mar</td>
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<tr>
<td>26 Apr</td>
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<td>0.2395</td>
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<tr>
<td>8 May</td>
<td>0.0000</td>
<td>0.0000</td>
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<tr>
<td>24 May</td>
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<td>0.0000</td>
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</tbody>
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Effects of Beach Graveling on Littoral Flat Epibenthos

*Dactylopodia sp.*  
Oakland Bay

### DENSITY (No. m⁻²)

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<td>25 Apr</td>
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<td>9 May</td>
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<tr>
<td>22 May</td>
<td>.0000</td>
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</tbody>
</table>

- **Control**
- **Treatment**
Effects of Beach Graveling on Littoral Flat Epibenthos
Other Harpacticoida  Bywater Bay

DENSITY (No. m⁻²)

DATE
26 Mar 12 Apr 26 Apr 8 May 24 May

Control
Treatment
Effects of Beach Graveling on Littoral Flat Epibenthos
Other Harpacticoida  Oakland Bay

DATE

DENSITY (No. m$^{-2}$)

- Control
- Treatment

26 Mar  10 Apr  25 Apr  9 May  22 May
Effects of Beach Graveling on Littoral Flat Epibenthos

*Corophium spp.*  Bywater Bay

![Graph showing density (No. m\(^{-2}\)) over dates: 26 Mar, 12 Apr, 26 Apr, 8 May, 24 May. The graph indicates a significant increase in density around 8 May. Control and Treatment lines are shown.](image_url)
Effects of Beach Graveling on Littoral Flat Epibenthos

*Corophium spp.* Oakland Bay

![Graph showing changes in density over time with dates from Mar 26 to May 22.](image-url)

- Control
- Treatment

<table>
<thead>
<tr>
<th>DATE</th>
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<td>10 Apr</td>
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<td>25 Apr</td>
<td>0.5883</td>
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<tr>
<td>9 May</td>
<td>0.0000</td>
</tr>
<tr>
<td>22 May</td>
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Effects of Beach Graveling on Littoral Flat Epibenthos

*Paracalliopiella pratti*  Bywater Bay

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<tr>
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Control: [Graph Line]

Treatment: [Graph Line]
Effects of Beach Graveling on Littoral Flat Epibenthos

*Paracalliopiella pratti*  Oakland Bay

**DATE**

- 26 Mar
- 10 Apr
- 25 Apr
- 9 May
- 22 May

**DENSITY (No. m⁻²)**

- Control
- Treatment
Effects of Beach Graveling on Littoral Flat Epibenthos

*Anisogammarus pugettensis*  Bywater Bay

![Graph showing the effect of beach graveling on the density of *Anisogammarus pugettensis* over time.](image)
Effects of Beach Graveling on Littoral Flat Epibenthos

*Anisogammarus pugettensis* Oakland Bay

---

![Graph showing the effects of beach graveling on littoral flat epibenthos. The x-axis represents date (26 Mar, 10 Apr, 25 Apr, 9 May, 22 May) and the y-axis represents density (No. m$^{-2}$). The graph compares control and treatment groups.]
Effects of Beach Graveling on Littoral Flat Epibenthic Total Gammarids, Bywater Bay

DATE

26 Mar 26 Apr 12 Apr 8 May 24 May

DENSITY (No./m²)

60 50 40 30 20 10 0

0.0000 0.0003 0.0180 0.5956

Control
Treatment
Effects of Beach Graveling on Littoral Flat Epibenthos
Total Gammarids  Oakland Bay

DENSITY (No. m\(^{-2}\))

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<th>Treatment</th>
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DATE

- CONTROL
- TREATMENT
Effects of Beach Graveling on Littoral Flat Epibenthos

*Cumella vulgaris*  Bywater Bay

---

**DENSITY (No. m⁻²)**

- **Control**
- **Treatment**

---

**DATE**

- 26 Mar
- 12 Apr
- 26 Apr
- 8 May
- 24 May

---

- .1006
- .0000
- .0000
- .0000
- .0003
Effects of Beach Graveling on Littoral Flat Epibenthos

*Cumella vulgaris*

Oakland Bay

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<th>Treatment</th>
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<tr>
<td>22 May</td>
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DENSITY (No. m⁻²)

400x592
Effects of Beach Graveling on Littoral Flat Epibenthos

*Lamprops quadriplactal* Bywater Bay

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<td>1.551</td>
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DENSITY (No. m$^{-2}$)
Effects of Beach Graveling on Littoral Flat Epibenthos

*Lamprops quadriplicata*  Oakland Bay

![Graph showing density over time for control and treatment groups.](image)

- **DENSITY (No. m$^{-2}$)**
- **DATE**
  - 26 Mar
  - 10 Apr
  - 25 Apr
  - 9 May
  - 22 May

---

Control

Treatment
Effects of Beach Graveling on Littoral Flat Epibenthos
Total Cumaceans Bywater Bay

Control
Treatment

DATE
26 Mar 12 Apr 26 Apr 8 May 24 May

DENSI TY (No./m²)
Effects of Beach Graveling on Littoral Flat Epibenthos
Total Cumaceans  Oakland Bay

DENSITY (No. m$^{-2}$)

- Control
- Treatment

DATE
26 Mar 10 Apr 25 Apr 9 May 22 May
APPENDIX D

PERCENT NUMERICAL COMPOSITION OF EPIBENTHIC TAXA >253 μM ON NATURAL (CONTROL) AND GRAVELED (TREATMENT) LITTORAL FLATS AT BYWATER BAY, HOOD CANAL, AND OAKLAND BAY, SOUTHERN PUGET SOUND, WASHINGTON, MARCH 25-MAY 24, 1989

<table>
<thead>
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<th>April 12</th>
<th>April 26</th>
<th>May 8</th>
<th>May 24</th>
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<td>Halacaridae</td>
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<tr>
<td><strong>HARPACTICOIDEA</strong></td>
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<tr>
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<td>6.95</td>
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<td>Longipediidae</td>
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<td><em>Ectinosoma melaniceps</em></td>
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<td><em>Harpacticus uniremis</em></td>
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<tr>
<td><em>Harpacticus</em> sp.-uniremis group</td>
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<td><em>Harpacticus spinulosus</em></td>
<td>3.17</td>
<td>32.26</td>
<td>36.64</td>
<td>58.97</td>
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<td><em>Tisbe</em> spp.</td>
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<td>-</td>
<td>18.33</td>
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<td><strong>Tachidiidae</strong></td>
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<td><em>Microarthridion littorale</em></td>
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<td><em>Tachidius triangularis</em></td>
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<td><em>Daniellsenia</em> sp.</td>
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<td><strong>Laophontidae</strong></td>
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<td><em>Paralaophonte congenera</em></td>
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Table 2—cont.

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<th>April 26</th>
<th>May 8</th>
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<td><em>Amphiascus sp.-minutus group</em></td>
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<td><em>Amphiascus sp. B-minutus group</em></td>
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<td><em>Amphiascus sp.</em></td>
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<tr>
<td><em>Robertgurneya</em> sp. A</td>
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<td>4.97</td>
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<td><em>Amphiascoides subdebilis</em></td>
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<tr>
<td><em>Bulbhamphiascus</em> sp.</td>
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</tr>
<tr>
<td><em>Bulbhamphiascus cf. inermis</em></td>
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<td><em>Corophium insidiosum</em></td>
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<td>-</td>
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<td>TOTAL NUMBER OF TAXA CATEGORIES</td>
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<td>NUMERICAL TAXA/LIFE HISTORY DIVERSITY (Shannon-Weiner H')</td>
<td>4.31</td>
<td>3.76</td>
<td>4.22</td>
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APPENDIX E

JUVENILE FLATFISH DIETS FROM BYWATER BAY
(FROM WEITKAMP 1991)
Figure 1. Index of Relative Importance (IRI) diagram of the diet of juvenile starry flounder (Platichthys stellatus) captured at Bywater Bay on 27 April 1990. (From Weitkamp 1991.)

**FISH DIMENSIONS**

- **Harpacticus spinulosus**
  - Length (mm): 14.9
  - Weight (g): 0.033
  - Mean: 1.71
  - S.D.: 0.033

- **Harpacticus arcticus**
  - Length (mm): 1.71
  - Weight (g): 0.012
  - Mean: 0.12
Figure 2. Index of Relative Importance (IRI) diagram of the diet of juvenile starry flounder (*Platichthys stellatus*) captured at Bywater Bay on 25 May 1990 (From Weitkamp 1991.)
Bywater Bay 25 May 90 English Sole

FISH DIMENSIONS

Weight (g) 1.486 0.550
Length (mm) 54.8 36.2
Mean 56.2

Figure 3. Index of Relative Importance (IRI) diagram of the diet of juvenile English sole (Pleuronectes fimbriatus) captured at Bywater Bay on 25 May 1990. (From Weitkamp 1991.)
Bywater Bay 19 June 1990 English sole

<table>
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<th>FISH DIMENSIONS</th>
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<th>2.33</th>
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<td>Weight (g)</td>
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<td>Length (mm)</td>
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Figure 4: Index of Relative Importance (IRI) diagram of the diet of juvenile English sole (Pleuronectes Parophrys vetulus) captured at Bywater Bay on 19 June 1990. (From Weitkamp 1991.)