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**EFFECTS OF SUBSTRATE MODIFICATION
ON LITTORAL FLAT EPIBENTHOS: ASSEMBLAGE
STRUCTURE CHANGES ASSOCIATED
WITH PREDATOR EXCLUSION NETS**

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ABSTRACT

We examined the effects on epibenthic crustacean assemblages of predator exclusion nets placed on gravel beach plots at two sites in Puget Sound, Washington, in April-June 1991. Densities of epibenthic harpacticoid copepods, gammarid amphipods, cumaceans and tanaids in plots covered with nets and adjacent, otherwise comparable plots without nets were compared as a test of the potential impacts on important prey resources of juvenile fishes that rear on beach habitats in Puget Sound. Consistent and often significant differences in epibenthic crustacean densities were found at both sites, but the direction of the (presumed) changes differed by site. Densities of selected, trophically important (fish prey) epibenthos taxa were generally depressed at the moderately exposed, pebble-fine sand beach at Bywater Bay, while densities of the same assemblage were generally enhanced at the protected, coarse-grained sediment beach at Oakland Bay. Randomized block ANOVA tests of differences in taxa-specific densities generally indicated, however, that within-plot effects were more consistently significant than treatment (net) effects, indicating that small-scale (e.g., >1 m) differences in beach substrates and other characteristics may be more influential on epibenthos assemblages. Quantitative sampling of substrates on control plots and beneath nets on treatment plots indicated that the Bywater Bay site had more fine sediments in both plots than Oakland Bay. Thus, initial sediment structure, irrespective of the induced change in substrates, may determine the extent and direction of epibenthos response to such beach substrate modifications.

CONTENTS

	Page
LIST OF FIGURES	iv
LIST OF TABLES	v
INTRODUCTION	1
MATERIALS AND METHODS	2
Approach.....	2
Processing of Epibenthos Samples	2
Sediment Sampling.....	2
Study Sites.....	3
Sampling and Statistical Design.....	3
Sediment Sampling	5
Epibenthos Sampling.....	5
Sediment Processing	5
Epibenthos Processing	5
Statistical Analyses	6
RESULTS.....	7
Sediment Structure.....	7
Assemblage Composition Of Epibenthos	8
Bywater Bay	8
Oakland Bay	8
Densities Of Epibenthic Fish Prey	8
Bywater Bay	9
Oakland Bay	9
DISCUSSION.....	10
SUMMARY AND RECOMMENDATIONS	12
LITERATURE CITED	14
Appendix A. Grain Size Results	41
Appendix B. Summaries (mean and standard deviations of organisms density) of epibenthos taxa.....	47

LIST OF FIGURES

Figure	Page
1. Location of Bywater Bay and Oakland Bay sites and predator exclusion net plots where impact of nets on epibenthos assemblages and sediment structure was investigated, April-June 1991	16
2. Comparison of mean grain size in sediments of natural gravel and predator exclusion net plots at Bywater Bay and Oakland Bay, Puget Sound, Washington, April-June 1991.....	17
3. Gravimetric composition of sediment grain size classes in natural gravel and predator exclusion net plots at (a) Bywater Bay and (b) Oakland Bay, Puget Sound, Washington, April-June 1991.....	18
4. Within-plot and total differences in total epibenthos density in natural and predator exclusion net plots at (a) Bywater Bay and (b) Oakland Bay, Puget Sound, Washington, April-June 1991.....	20
5. Within-plot and total differences in density of <i>Harpacticus uniremis</i> group adults in natural and predator exclusion net plots at (a) Bywater Bay and (b) Oakland Bay, Puget Sound, Washington, April-June 1991	22
6. Within-plot and total differences in density of <i>Harpacticus uniremis</i> group copepodites in natural and predator exclusion net plots at (a) Bywater Bay and (b) Oakland Bay, Puget Sound, Washington, April-June 1991	24
7. Within-plot and total differences in density of <i>Tisbe</i> spp. adults in natural and predator exclusion net plots at (a) Bywater Bay and (b) Oakland Bay, Puget Sound, Washington, April-June 1991	26
8. Within-plot and total differences in density of <i>Dactylopusia</i> spp. adults in natural and predator exclusion net plots at (a) Bywater Bay and (b) Oakland Bay, Puget Sound, Washington, April-June 1991	28
9. Within-plot and total differences in density of <i>Harpacticus spinulosus</i> adults in natural and predator exclusion net plots at Bywater Bay, Puget Sound, Washington, April-June 1991.....	30
10. Within-plot and total differences in density of <i>Cumella vulgaris</i> adults in natural and predator exclusion net plots at Bywater Bay, Puget Sound, Washington, April-June 1991	31

LIST OF TABLES

Table	Page
1. Epibenthos taxa composition for natural gravel and predator exclusion net substrate at both Bywater Bay and Oakland Bay, Puget Sound, Washington, April-June, 1991	33
2. Results of statistical analyses of differences in mean density of selected epibenthos taxa at Bywater Bay and Oakland Bay, Puget Sound, Washington, April-June 1991	37
3. Generalized responses of epibenthic crustaceans to the placement of predator exclusion nets on gravel beach substrates in Bywater Bay and Oakland Bay, Puget Sound, Washington, April-June 1991	40

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KEY WORDS

effects of habitat modification, estuarine epibenthos, fish prey, harpacticoid copepods, gammarid amphipods, cumaceans, tanaids, aquaculture

INTRODUCTION

Supplementing fine-sediment beach substrates with gravel has become an approach for enhancing hardshell clam habitat in areas that appear to be habitat-limited for clam culture (Thompson and Cooke 1991). An earlier study into the effects of this beach substrate modification on epibenthic crustaceans indicated that adding gravel to fine-sediment sediments produced different responses as a function of the habitat structure and the composition of the natural epibenthos assemblage (Simenstad et al. 1991a). Epibenthic harpacticoid copepod taxa that are phytally associated, such as *Harpacticus uniremis*, *Tisbe* spp. and *Zaus* spp., were often found to be enhanced by graveling, presumably owing to the increased attachment substrate for micro- and macroalgae. Graveling-associated changes in densities of gammarid amphipods such as *Corophium* spp. and cumaceans such as *Cumella vulgaris* varied by site, such that they were enhanced when gravel was added to a mudflat but depressed when a sandflat was graveled. These results were interpreted relative to the initial beach sediment structure and the adaptability of the dominant epibenthos taxa to those substrates.

An additional practice associated with clam culture on both natural gravel beaches and those that have been gravel-supplemented to enhance clam production is the placement of plastic netting over the beach after juvenile clams are introduced (“seeded”). The netting is considered to inhibit predators on the small clams, such as fish (e.g., starry flounder, *Platichthys stellatus*), crabs (e.g., *Cancer magister*) and diving birds (e.g., white-winged scoter, *Melanitta fusca*). This netting is secured directly to the gravel and forms an overlying artificial substrate. Over time, the netting traps sediments and becomes colonized by attached plants and animals, usually becoming incorporated into the beach profile within a few months, depending upon the degree of natural disturbance (e.g., wave and current energy), sediment transport, etc., at the site.

As with beach graveling, fisheries resource agency personnel are concerned that such modification of the natural beach character should be evaluated relative to potential impacts to economically important fish and wildlife that extensively utilize the beach habitat during critical periods of their life histories. In particular, a primary resource management concern is the potential effects of beach substrate modification on prey resources (e.g., epibenthic crustaceans) of juvenile fishes such as salmon and flatfishes that rear in beach habitats during their early life histories. Juvenile salmon, for instance, selectively prey upon specific taxa (and potentially life history stages such as ovigerous females) of harpacticoid copepods and gammarid amphipods that are common to certain classes of beach habitats (Simenstad et al. 1982; Simenstad and Wissmar 1984).

This report describes a study to assess the effects of predator exclusion nets on intertidal epibenthic crustaceans considered to be important as prey for juvenile fishes. In order to build on the previous studies of beach graveling influences on beach meiofauna and small macrofauna, this present study was conducted at the same sites as those utilized in Simenstad et al. (1991a). We do not address the temporal responses of the epibenthic crustacean assemblages after initiation of the beach modification, but rather examine beaches that have been modified with nets after time periods that we assume have resulted in “stable” beach conditions. Tests of the predator exclusion net effects were conducted as pair-wise comparisons with natural beach substrates. We

interpreted statistically significant changes in the densities of important epibenthic crustacean taxa as constituting an “effect” of the predator exclusion net “treatment.”

MATERIALS AND METHODS

APPROACH

The objective of the epibenthos sampling design was to examine differences in the epibenthos assemblage structure in the natural and the predator exclusion net treatments during the period encompassing the outmigration of epibenthic-feeding juvenile salmon in Puget Sound. In addition, sediment structure in the netted versus natural beach substrates was compared as a possible source of any observed differences in epibenthos.

Our approach was to systematically sample epibenthic crustaceans in two littoral habitats monthly between April and June 1991. Effort was allocated to ensure sufficient within-site replication to test for treatment effects within the pair-wise comparison at each site. However, sampling sites should not be interpreted as replicates and we intend no inference to the universal (i.e., Puget Sound being the sampling “universe”) effect of predator exclusion on intertidal epibenthos.

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 those that had been documented to be prominent, and perhaps preferred, prey of epibenthic-feeding juvenile Pacific salmon (e.g., chum [*Oncorhynchus keta*], pink [*O. gorbuscha*], and chinook [*O. tshawytscha*] “fry”). Documentation was from the scientific literature (e.g., Simenstad et al. 1982) or our own unpublished database on juvenile salmon diets. Therefore, harpacticoid copepod 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 the effects of predator exclusion nets on intertidal communities. We also included as indicator taxa other epibenthic crustaceans that we have documented as appearing, although less frequently, in the diets of juvenile salmon of Puget Sound (see Epibenthos Processing). Other harpacticoid copepods, gammarid amphipods, and cumaceans >0.25 mm in length that appear in the diets of other marine fishes were also counted. In addition, because some epibenthic crustacean taxa <0.25 mm (e.g., Ectinosomatidae) may also be important prey of other marine fishes (e.g., recently metamorphosed flatfishes such as English sole, *Pleuronectes (Parophrys) vetulus*), we counted such taxa as were readily recognizable.

Sediment Sampling

The effects of predator netting on sediment size was investigated concurrent to an investigation of its effects on epibenthic meiofauna and small macrofauna. The sediment investigations were conducted to determine: whether grain size structure of the sediments differs with or without

netting, and whether observed changes in the fauna and flora may be partly explained by changes in the sediments.

STUDY SITES

The same general study sites utilized in Simenstad et al.'s (1991a) study of beach graveling effects on epibenthos were adopted for predator exclusion net sampling (Fig. 1). These sites are situated on natural gravel beaches in different watersheds and subject to different wave and current exposure, which results in somewhat different sedimentary regimes—a mixed gravel-sand flat (Bywater Bay) and a mixed gravel beach (Oakland Bay).

Bywater Bay (47°52'38"N, 122°37'45"W), on the northwest shore of Hood Canal, has a relatively broad, moderate gradient. Predator exclusion nets were applied along a line of plots¹ centered at approximately the +4.0 ft MLLW tidal elevation.

Oakland Bay (47°15'04"N, 123°02'03"W) is a shallow, protected embayment at the end of Hammersley Inlet in southern Puget Sound. The study site was located on the outside (Inlet side) of a narrow gravel spit that forms the entrance to the bay. Intertidal dikes had been constructed to retain water and stabilize the area for oyster and clam production; this resulted in a sequence of low gradient, gravel "terraces." The predator exclusion nets were applied to plots entirely within one of these terraces. The terrace sampled had a uniform tidal elevation of approximately +3.5 ft MLLW; however, because the remnant dikes still retained tidal waters, or attenuated the rate of tidal exposure and inundation, this tidal elevation should not be considered representative of the frequency and duration of tidal flooding on these plots.

SAMPLING AND STATISTICAL DESIGN

The objective of the sampling and statistical design was to test the null hypothesis that

H₀: There are no significant differences in (1) the densities of selected juvenile salmon and other marine fish prey taxa and (2) sediment structure between the predator exclusion netted (treatment) and the adjacent natural (control) plots.

Thus, this design tested only for significant changes in *specific* epibenthic taxa that might indicate the significance of littoral community changes as rearing habitats for economically important fishes. We tested for differences in sediment structure to infer potential mechanisms (e.g., shifts in sediment structure) that might account for observed differences in fish prey taxa. As such, the effects of predator exclusion nets on other littoral biota (e.g., sessile epifauna, benthic infauna) were not evaluated and may not correspond to the results for epibenthos.

¹"Plot" refers to the individual plot, which is either netted or bare, while "unit" refers to the pair of plots, one of which is netted and one of which is bare.

All sampling occurred perpendicular to the tidal elevation gradient in order to minimize the effects of differential tidal exposure, which are documented to influence meiofauna assemblage composition and standing stock (Hicks and Coull 1983). The study area at each study site consisted of nine pairs (units) of experimental plots, arranged linearly along the beach. At Oakland Bay, all nine units were at approximately equal tidal elevations, while at Bywater Bay the study area sloped such that the southernmost unit was approximately 0.5 m above the northernmost unit. Each unit consisted of one plot that was covered by predator netting (treatment) and an adjacent plot that was not covered (control). The plots within each unit were directly adjacent to each other, while approximately 2 m separated the units. We numbered the nine units consecutively, with unit 1 as the southernmost unit at Bywater Bay and the southwesternmost unit at Oakland Bay.

The nine units were stratified by location into three areas (triplets) perpendicular to the beach gradient, such that area 1, 2, and 3 contained units 1-3, 4-6, and 7-9, respectively. This stratification was done to detect and control for differences in the units caused by their relative location on the beach, with respect to factors such as tidal currents and height; each triplet constituted the equivalent of a statistical "block." Thus, the position along the beach was considered as an independent source of variation that could be detected in a randomized block ANOVA (Zar 1984). For each stratum of three units, one was randomly selected to serve as the sample collection unit for both sediment and epibenthic pump samples. At Bywater Bay, the selected units were numbers 3, 6, and 8, while the selected units at Oakland Bay were numbers 2, 5, and 7. The selected units were sampled on all dates. Because the netting in unit 7 at Oakland Bay had been severely torn, unit 8 was used instead of unit 7 during the May and June sampling trips.

From each plot, we collected 3 replicated core samples for sediment grain-size and 15 epibenthic pump samples for epibenthos. The same experimental design was employed for both the epibenthos and sediment structure in order to test for differences in epibenthic composition and density, and sediment grain size structure in the presence and absence of predator netting. All samples were collected from at least 1 m inside the edge of the plot to minimize edge effects.

Sampling occurred monthly, with the two beaches sampled on consecutive days as follows:

Beach	Sampling dates		
Oakland Bay	3 April	7 May	5 June
Bywater Bay	2 April	6 May	4 June

This monthly sampling frequency encompassed the period when these littoral habitats are most likely to be used by juvenile salmon and other epibenthic-feeding (e.g., young-of-year flatfishes) fishes. It is not, however, intended to reflect population changes in the specific epibenthic taxa, which typically have generation times and turnover rates at higher frequencies (e.g., 2-week generation times; Hicks and Coull 1983).

SEDIMENT SAMPLING

For each unit, three haphazardly selected replicate sediment cores were collected by hand from each randomly selected plot type (three each from the netted and natural plots). The sediment cores were 2.2-cm dia (3.80 cm²) x 10-cm deep. Cores were frozen until processed.

EPIBENTHOS SAMPLING

Sampling was conducted using a battery-powered, 0.018-m² epibenthic suction pump and 253- μ m sieves (Simenstad et al. 1991b). The 15 samples were distributed haphazardly over the sampling plots uniquely on each sampling date (i.e., this should be considered a repeated-measures design). Sampling involved pumping over the enclosed area of substrate for 20 s while sieving the pump discharge through the 130- μ m sieve. Organisms and material (e.g., detritus) retained on the sieve were immediately conduring the May and June sampling trips, centrated and preserved with 5% seawater-buffered formalin. All sampling took place in the same plot sequence on a flooding tide.

SEDIMENT PROCESSING

In the laboratory, the sediment samples were analyzed using the method described by Folk (1965). Sediments were dry-sieved using the following screens (phi sizes given in parentheses): 2.0 mm (-1.0), 1.0 mm (0.0), 0.5 mm (1.0), 0.250 mm (2.0), 0.125 mm (3.0), and 0.063 mm (4.0). Total fines (material <63 m) were determined by pipette analysis, but were not separated into silts and clays.

EPIBENTHOS PROCESSING

In the laboratory, samples were screened simultaneously in 260- μ m and 120- μ m sieves; the >260- μ m fraction is considered the "juvenile fish prey fraction" and the smaller (120-260 μ m) fraction the "non-prey fraction." The juvenile fish prey fraction was sorted and the taxa identified under a dissecting microscope according to the categories listed in the table on the following page, which are based on the beach-graveling protocols (Simenstad et al. 1991a).

Other meiofauna and small macrofauna were identified to the lowest possible taxa. In addition to the taxonomic identification, certain key harpacticoid taxa were categorized by life history stage, including the *Harpacticus uniremis* group into copepodites, adults, and ovigerous females; and *Tisbe* spp., *Zaus* spp. and *Dactylopusia* spp. into adults, copepodites, and ovigerous females. All other harpacticoids were only classified into copepodites and adults.

In the case of exceedingly large numbers of organisms, the samples were subsampled using either a glass quartering dish, or the whole sample was thoroughly stirred with air bubbles and a smaller known volume stirred with a Hensen's Stempel pipette. The criteria for acceptance of a subsample was >100 of the most abundant taxa (Cordell et al. 1992). All small macrofauna (amphipods, cumaceans, tanaids) were enumerated and weighed; all harpacticoids were enumerated only.

Prey Taxa	Fish Predators
<u>Harpacticoida</u> <i>Tisbe</i> spp., <i>Zaus</i> spp., <i>Harpacticus</i> spp., and <i>Dactylopusia</i> ² spp.	Juvenile chum salmon (<i>Oncorhynchus keta</i>) and pink salmon (<i>O. gorbuscha</i>), Pacific herring (<i>Clupea harengus pallasii</i>), surf smelt (<i>Hypomesus pretiosus</i>), Pacific sand lance (<i>Ammodytes hexapterus</i>), threespine stickleback (<i>Gasterosteus aculeatus</i>)
<i>Harpacticus spinulosus</i> , <i>Amphiascus</i> sp. A, Ectinosomatidae	Juvenile English sole (<i>Pleuronectes</i> [<i>Parophrys</i>] <i>vetulus</i>), starry flounder (<i>Platichthys stellatus</i>)
Other harpacticoid copepods	Juvenile English sole (<i>Pleuronectes</i> [<i>Parophrys</i>] <i>vetulus</i>), starry flounder (<i>Platichthys stellatus</i>)
<u>Amphipoda</u> <i>Corophium</i> spp., <i>Paracalliopiella pratti</i> , <i>Anisogammarus pugettensis</i>	Juvenile chinook salmon (<i>O. tshawytscha</i>) and coho salmon (<i>O. kisutch</i>)
Total gammarid amphipods	Juvenile chinook salmon (<i>O. tshawytscha</i>) and coho salmon (<i>O. kisutch</i>)
<u>Cumaceans</u> <i>Cumella vulgaris</i> , <i>Lamprops quadriplicata</i> , <i>Leucon</i> sp.	Juvenile chinook salmon (<i>O. tshawytscha</i>) and coho salmon (<i>O. kisutch</i>)
Total cumaceans	Juvenile chinook salmon (<i>O. tshawytscha</i>) and coho salmon (<i>O. kisutch</i>)
<u>Tanaids</u> <i>Tanais</i> sp.	Juvenile chinook salmon (<i>O. tshawytscha</i>) and coho salmon (<i>O. kisutch</i>) ?

STATISTICAL ANALYSES

Mean sediment grain sizes were analyzed using randomized block ANOVA. Because of heteroscedasticity, all data were transformed using $\ln(x + 1)$ before analysis. For the ANOVA analysis, the three units (representing the three strata) were treated as blocks and the plot type

²Formerly called *Dactylopodia*

(netted, natural) as treatment, with replicates within each plot. The analysis was conducted for each beach/date combination.

For each sampling site, date, treatment (net, control), and replicate, the density and standing stock for each epibenthos group (taxa x life history class) were tabulated and statistical summaries generated using the FRI computer 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 using the same criteria, these indices can be compared among samples but should not be compared to similar data sets from other studies.

Tests of significant differences in epibenthos density between treatment/control pairs were conducted similarly to the sediment structure using a randomized block ANOVA analysis, where the three units were treated as blocks and the plot type (net, natural gravel) as treatment, with replicates within each plot (Zar 1984). All tests were conducted on $\ln(x + 1)$ transformed data.

RESULTS

SEDIMENT STRUCTURE

On all dates at both beaches, the mean grain size in the natural plots (1.83-1.94 mm at Oakland Bay, 1.53-1.55 mm at Bywater Bay) exceeded the mean grain size in the netted plots (1.55-1.76 mm at Oakland Bay, 1.28-1.47 mm at Bywater Bay) (Fig. 2; Appendix 1). However, this difference was statistically significant ($P < 0.05$) only in June for both beaches. Samples collected in May from Oakland Bay also had significant treatment effects, but the interaction effects were also significant ($P < 0.05$), suggesting the treatment was not independent of the location within the study area.

The differences in mean grain sizes among the plot types were the result of changes in grain size-class contributions to the mean grain size (Fig. 3). In April, treated (net) and control (natural) sediments had similar mean grain sizes (1.55 mm [natural] vs. 1.47 mm [net] at Bywater Bay, 1.83 mm [natural] vs. 1.76 mm [net] at Oakland Bay), with differences between the treatment types evenly spread across all grain size classes. In May and June, the natural plots had mean grain sizes (1.52 [May] and 1.55 [June] for Bywater Bay, 1.94 [May] and 1.90 [June] for Oakland Bay) and grain size structures nearly identical to the April samples. However, for the netted plots in May and June, the contribution from the finer sediments increased. At Oakland Bay, size classes < 2.0 mm increased in May and June, while size classes < 1.0 mm increased at Bywater Bay. This trend occurred at both beaches despite the consistently larger mean grain sizes at Oakland Bay.

ASSEMBLAGE COMPOSITION OF EPIBENTHOS

Epibenthos assemblages at all of the Bywater Bay and Oakland Bay sites and plots were structurally similar to the gravel treatment assemblages documented at those sites in 1989 (Simenstad et al. 1991a). However, qualitative intersite and treatment differences were evident. On predator exclusion plots at both sites, the most obvious change in assemblage structure was that taxa usually associated with finer sediments increased coincident with the substrate changes in May and June.

Bywater Bay

Small to medium-sized (e.g., non-juvenile salmon prey taxa) harpacticoids (e.g., Ectinosomatidae, *Amphiascus* sp., *Robertsonia* sp. cf *knoxii*, Harpacticoida) tended to be more prominent in assemblages found in natural gravel substrates than in those in the predator exclusion net plots (Table 1a and b). Conversely, *Harpacticus uniremis* and its congeners in the taxa *H. uniremis* group, which are larger harpacticoids and documented prey of juvenile fishes using intertidal habitat, were proportionally more common in predator exclusion net plots. Gammarid amphipods also tended to represent a slightly greater proportion of the assemblages in the predator exclusion net plots than in the natural gravel plots. Only one taxa, the cumacean *Leucon* sp., occurred exclusively in one type of plot (in natural gravel plots). Increased numerical contributions by harpacticoid taxa such as Ectinosomatidae and Laophontidae may represent shifts in assemblage composition associated with the change in substrate (to increased fractions of fines in May and June) or increased attached filamentous algae in the predator exclusion net plots. There were no consistent differences in numerical or gravimetric diversity between the natural and treatment epibenthos assemblages over the 3-mo sampling period (Table 1a and b).

Oakland Bay

In contrast to the differences between control and treatment plots at Bywater Bay, the contribution of small, medium-sized, and large fish-prey taxa of harpacticoid copepods and cumaceans tended to be more prominent in predator exclusion net plots than in natural gravel plots at Oakland Bay (Table 1c and d). Conversely, tanaids and the medium-sized, sediment-dwelling harpacticoid *Nanopus palustris* were the more prominent taxa on the natural gravel plots. Coincident with increased fractions of fine particles, taxa diversity based on both density and standing stock was higher at the predator exclusion net plots in May and June compared with April, when the natural gravel assemblage was more diverse.

DENSITIES OF EPIBENTHIC FISH PREY

Differences in epibenthos densities between natural gravel and predator exclusion net plots varied between study sites and among taxa (Figs. 4-10; Table 2, Appendix B). In the following discussion, we present both descriptive and statistical evidence for differences in representative taxa; statistical tests, however, are limited to taxa that occur consistently (e.g., in more than one month) at sufficient densities to constitute valid comparisons.

Bywater Bay

In general, most taxa were more abundant on the natural gravel plots than on the predator exclusion net plots, and particularly so in April, suggesting that the predator exclusion nets depressed densities of many taxa. Total epibenthos densities on the natural plots were consistently higher but seldom significantly so given the variation in mean density in all plots in all months (Fig. 4a). This pattern was generally representative of adult *Dactylopusia* spp., *Harpacticus spinulosus* and *Cumella vulgaris*, as well as many of the other Harpacticoida taxa (e.g., *Amphiascus* sp., *Robertsonia* sp. cf. *knoxii*) (Figs. 8a, 9, 10; Appendix B). *Harpacticus uniremis* copepodite and adult abundances reflected the opposite pattern, showing consistently higher densities in the predator exclusion net plots (Figs. 5a, 6a). There was no consistent pattern in adult *Tisbe* spp. densities (Fig. 7a). Cumaceans (*Cumella vulgaris*) and tanaids (*Tanais* sp., *Leptochelia savignyi*) also tended to be more dense in gravel plots, but amphipods occurred sporadically on the plots and no general trend was evident (Appendix B).

Differences between the control (natural gravel) and treatment (predator exclusion net) plots were significant for *Harpacticus uniremis* copepodites and adults, as well as adult *Cumella vulgaris* in two to three of the months (Table 2). However, block (plot position) effects were also evident in most cases, indicating that the mean differences among the three pairs of treatment and control plots was confounded by the position of the plots. Except for *H. uniremis* copepodites (where only the treatment effect was significant), both treatment and block effects were significant for all three taxa in April and May. In June, differences between treatment and control plots were insignificant for *H. uniremis* copepodites, and only block effects were significant for adult *Cumella vulgaris*. Differences in *Tisbe* spp. densities were significant only for treatment effects in April. Although the densities of tanaids and amphipods were lower and more variable than the harpacticoids and cumaceans, significant treatment effects (depression) were detected for *Tanais* sp. in May, but block effects were evident in May and June. *Corophium* spp. amphipods were also significantly depressed by the treatment in May, but block effects were also significant in June and nearly so ($P < 0.1$) in April and May.

The prevalence of block effects and relative consistency of rank order epibenthos densities over the three plots indicate that the source of the differences was often specific to each plot. For instance, mean densities of many taxa in June decreased from Plot #1 to Plot #3.

Oakland Bay

The mean density of total epibenthos was not consistently different between treatment and control plots at Oakland Bay (Fig. 4b; Appendix B). Predator exclusion net plots contained on average ~5,300 m⁻² more organisms than on natural gravel plots in April, but little difference occurred between treatment and control plots in May or June. However, many of these differences were associated with the plot positions (block effects) and an enhanced effect of the treatment on mean epibenthos density was often detectable (Table 2).

Differences in mean densities of *Harpacticus uniremis* group copepodites and adults between the treatment and control plots were either marginal (April) or inconsistent (May, June) (Figs. 5b & 6b). However, mean densities of *Tisbe* spp. were consistently higher in treatment plots during all

months (Fig. 7b). In direct contrast to the situation at Bywater Bay, mean densities of *Dactylopusia* spp. at Oakland Bay were typically higher in predator exclusion net plots than in gravel plots (Fig. 8b).

The observed differences in *Harpacticus uniremis* group copepodites and adults (higher mean densities in treatment plots) were significant for treatment effects in April for copepodites and May for adults (Table 2). Block effects, however, were significant for copepodite densities in all three months and for adults in April. The increased densities of *Tisbe* spp. in treatments were also significant for the effects of the predator exclusion net in April and May, but block effects were also significant in all months (Table 2). Adult *Dactylopusia* spp. were significantly different (enhanced) by treatment effects in both April and May in the absence of any significant block effects in any month.

DISCUSSION

Analysis of the sediment structures with and without predator exclusion nets at both Bywater Bay and Oakland Bay indicates lower mean grain sizes in plots with netting. The change appears to occur from increased material <1-2 mm. This material is usually transported (longshore transport) along beaches by tidal currents and wave energy. We presume that the predator exclusion nets trap this material. One explanation for the evidence of increased sediment trapping in June is that, although wave energy is typically higher in early spring, any material trapped within the netted plots would still be subject to resuspension and export from the plot under sufficient wave turbulence and longshore transport. By June, however, net accretion may have occurred as the frequency and intensity of wave energy diminished. The remnant dikes at Oakland Bay may explain some of the observed differences in sediment structure between Oakland Bay and Bywater Bay. A somewhat higher proportion of fine sediments, as well as coarse sediments (>1.5 mm dia.), consistently occurred at Oakland Bay, suggesting that the dikes may be trapping fines but inhibiting longshore transport of the intermediate-sized sediments. These differences in sediment structure and the hydrologic processes that affect the structure, with Oakland Bay potentially representing an artifact, may also account for the observed differences in epibenthos responses to predator netting (i.e., fine sediments are more common at both treatment and control sites at Oakland Bay).

As was evident for the effect of beach graveling without nets at the same two study sites (Simenstad et al. 1991a), response of meio- and small macrofauna assemblages to substrate modification can be very site-specific (Table 3). Furthermore, variability in beach characteristics or other physical conditions along the same tidal elevation can often have a greater influence than the effect of the predator exclusion net. Predator exclusion nets at Bywater Bay generally depressed total epibenthos densities relative to the natural gravel substrate, with the notable exception (i.e., enhanced densities) of *Harpacticus uniremis* group copepodites and adults. This was the same general pattern that Simenstad et al. (1991a) found for graveled plots at Bywater Bay in 1989, in which they found densities of many epibenthos taxa were strongly (*Harpacticus spinulosus*, *H. arcticus*, other Harpacticoida, *Anisogammarus pugettensis*) or moderately (*H. uniremis*, *H.*

uniremis group, *Corophium* spp., *Lamprops quadriplicata*) depressed compared with few taxa that showed no response (*Dactylopusia* spp.) or were actually enhanced (*Tisbe* spp., *Zaus* spp. and *Paracalliopiella pratti*). However, different processes may well be operating in graveling as compared with the use of predator exclusion nets on natural gravel. For instance, while graveling may result in depression of the sand-dwelling taxa, the nets may actually be neutral or enhance these taxa because they result in more sediment trapping.

Predator exclusion nets at Oakland Bay, in contrast, often resulted in enhanced total epibenthos densities, especially in April. Similarly, densities of the same epibenthos taxa investigated on gravel plots at Oakland Bay in 1989 were broadly enhanced except for *Paracalliopiella pratti* and *Lamprops quadriplicata*, which showed no definitive responses in that study. Neither *P. pratti* nor *L. quadriplicata* were abundant enough at either site during the period of the predator exclusion net study to provide any comparison.

Differences in both natural and predator exclusion net-altered sediment structure may account for some of the observed differences in epibenthos assemblages and responses between the two sites. Substrate structure on gravel (control) plots at Bywater Bay had a higher (~10% by weight) proportion of mid-range (mean grain size, 0.35 mm, or “fine sand”) to finer (0.18-0.09 mm, “very fine sand” to “silt”) sediments than Oakland Bay, which had ~15% greater proportion of sediments of 4.5 mm mean grain size (“granules” to “pebbles”) (Fig. 2, Appendix A). Except for a slight decrease in the mid-range grain sizes at Oakland Bay between April and June, sediment structures at both sites remained relatively constant throughout the sampling period. Shifts in sediment structure associated with the predator exclusion nets reflected the same site-specific patterns although the plots in Oakland Bay appear to have accreted more fines than the net-covered plots at Bywater Bay (Fig. 2).

These differences in sediment structure are reflected in higher densities in the Bywater Bay gravel plots of taxa that are surface sediment dwellers or true epibenthic taxa associated with finer, more organic sediments, including Ectinosomatidae, *Harpacticus spinulosus*, Laophontidae, and *Amphiascus* spp. (Hicks and Coull 1983). True mud dwellers (e.g., including burrowers that may occur in the epibenthos or be sampled by the epibenthic pump when sediments are resuspended) such as *Nannopus palustris* are comparatively rare. However, taxa that are often particularly associated with algae (e.g., “phytal” taxa), such as *Tisbe* spp. and *Zaus* spp., were also abundant in the gravel plots. However, despite the apparent accretion of fines in the predator exclusion net plots at Bywater Bay, densities of even those epibenthos taxa associated with finer substrates were depressed; only *Harpacticus uniremis* group copepodite densities displayed enhancement that was not associated with plot effects (Table 2). This treatment effect often is not significant and is complicated by plot effects, and general depression of epibenthic organisms by the predator exclusion nets cannot be directly explained by these data. We suspect that biotic factors, such as increased predation, may be an important factor, which cannot be evaluated. It is possible, for example, that small predators such as small fishes (e.g., sculpins such as *Oligocottus* spp.), crabs, and crangonid shrimps that are known to feed extensively on meiofauna may be enhanced by the predator exclusion netting which they use for refuge. Under sufficient predator densities and foraging intensity, fishes and macroinvertebrates may control meiofauna populations and the predator exclusion net plots may be large enough to contain distinct (unit) populations of certain

harpacticoid copepods, gammarid amphipods, cumaceans, and tanaids. Testing of this hypothesis would require more experimental approaches than the descriptive, “natural experiment” strategy that we employed in this study.

The different beach characteristics at Oakland Bay may explain the differences in epibenthos assemblage responses to the predator exclusion nets (i.e., typical enhancement of most epibenthos taxa densities [Table 2]). Although the presence of the nets appeared to promote accretion of finer sediments at both sites, the natural and the netted substrates at Oakland Bay were obviously coarser (higher fractions of granules and pebbles) than at Bywater Bay. We cannot determine whether the difference is a consequence of different sediment sources (i.e., beach-transported sediments are not as fine) or physical turbulence (i.e., there is more turbulence, and less net settling of fine sediments) at Oakland Bay as compared with Bywater Bay, and the net effect is that applying predator exclusion nets at the two sites does not result in the same sediment structure. We suspect two factors may be responsible for epibenthos enhancement at Oakland Bay: (1) accretion of finer sediments in the predator exclusion net plots at Oakland Bay was not sufficient to inhibit most existing taxa, and (2) the net comprised a stabilizing influence on the substrate and provided additional substrate for colonization by microalgae (e.g., diatoms), which are used as food resources by many of the epibenthos taxa. We cannot explain why several taxa illustrated depressed densities (e.g., *Harpacticus uniremis* group copepodites, *Tanais* sp.), while other taxa of harpacticoids common to fine sand/mud sediments (e.g., *Tachidius triangularis*) were enhanced by predator exclusion nets. In the latter case, one potential explanation is that some taxa, such as the more epibenthic species, may be passively transported by longshore currents and accumulate in the netted plots with other fine particles. We also cannot explain why the nets in Oakland Bay would not provide additional refuge for meiofauna predators, as we suggest may have been the consequence at Bywater Bay.

Other fundamental differences between the Bywater and Oakland bays that might explain the observed differences in epibenthos responses to predator exclusion nets, such as ponding of tidal waters, interstitial water flow, detritus accumulation, benthic diatom and other epibenthos food resource production, benthic respiration and nutrients, cannot be evaluated because of the lack of data. Although some of these influences have been evaluated relative to placing gravel on fine-sediment beaches (Thom et al. in press), we have no basis for evaluating such factors relative to changes associated with predator exclusion nets. In part, our inability to readily explain the observed epibenthos responses may originate from both the lack of data on any other evident changes (other than sediment structure) as well as a general lack of conceptual theories on how disturbance of various magnitudes and frequencies affects soft-bottom benthic and epibenthic communities (Thistle 1981; Zajac and Whitlatch 1982).

SUMMARY AND RECOMMENDATIONS

Addition of predator exclusion nets on gravel beach plots at two sites in Puget Sound, Washington, often resulted in significant but different responses from epibenthic crustacean assemblages. Densities of selected, trophically important (fish prey) epibenthos taxa were

generally depressed at the moderately exposed pebble/fine sand beach at Bywater Bay, while densities of the same assemblage were generally enhanced at the protected, coarse-grained sediment beach at Oakland Bay. However, any significant changes in epibenthos taxa densities were also associated with effects of the sampling plots, suggesting that small-scale influences of beach geomorphology or some other characteristic may predominate over changes due to the predator exclusion net treatment. This pattern generally follows that observed for the addition of gravel to fine-sediment intertidal areas at the same sites. Thus, both site and small-scale beach characteristics, in addition to beach modifications such as netting to exclude predators on juvenile hardshell clams, appear to determine the potential effects on epibenthos assemblages.

On the basis of these and earlier results (Simenstad et al. 1991a), we suggest that simple predictions about impacts of intertidal habitat modifications are not possible without considering site-specific factors. The extent and type of information required to develop such predictive understandings about intertidal epibenthos responses to habitat modifications will require the following:

- more basic studies of the ecology and population dynamics of key epibenthos taxa, such as *Harpacticus uniremis* and *Tisbe* spp. in order to determine taxa-specific responses;
- structured manipulation experiments in which substrate characteristics and other factors potentially controlling epibenthos responses are effectively controlled for (e.g., selected or manipulated) to separate the effects of natural changes and disturbances from those associated with habitat modifications; and,
- continued monitoring of a variety of intertidal modifications and the epibenthos assemblage structure relative to comparable unmodified habitats such that a spectrum of intertidal conditions and epibenthos assemblages can be compared.

Until such more “predictive” information is available, assessment of intertidal habitat modification impacts should be considered at the case- and site-specific level.

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FIGURES

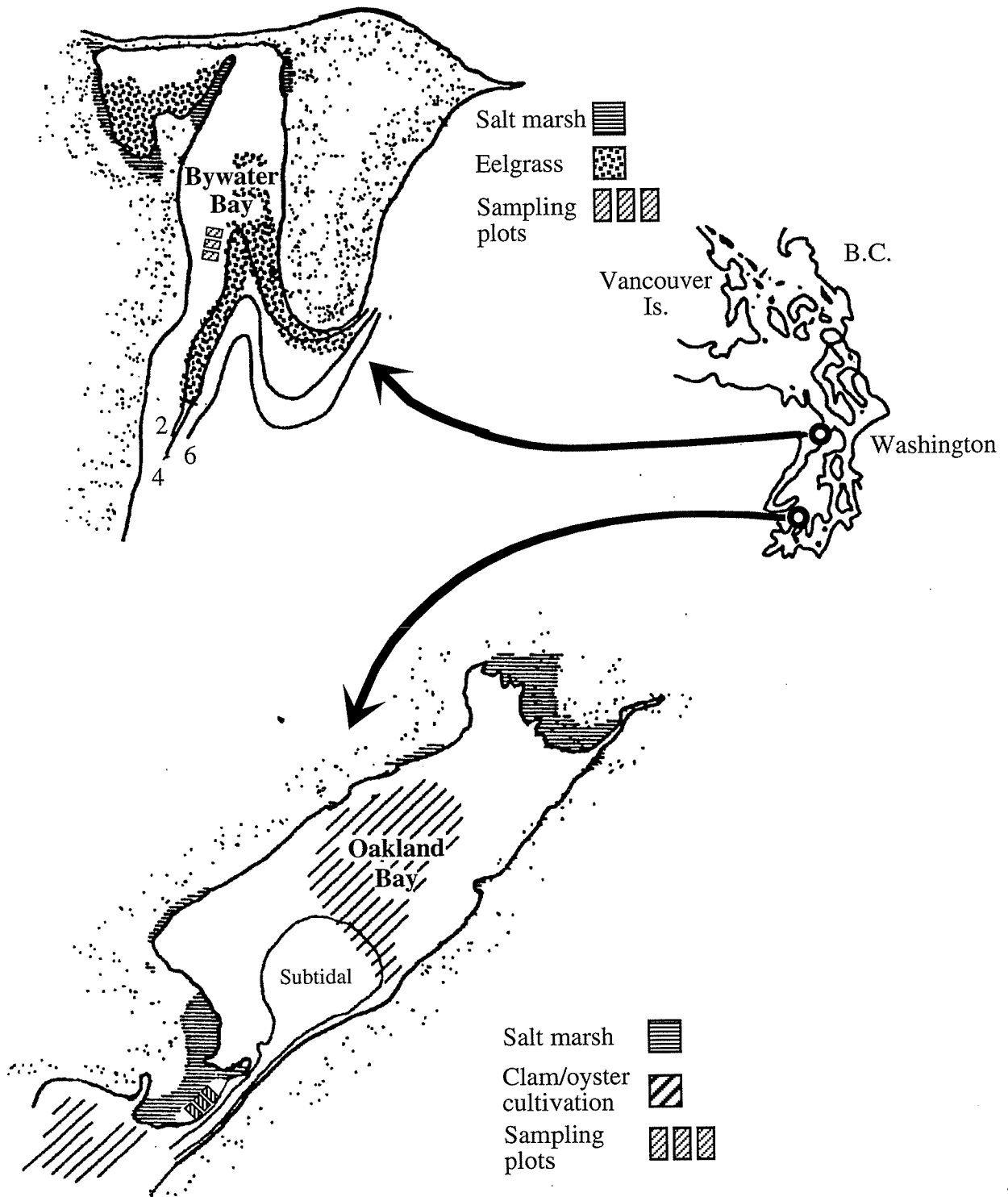


Figure 1. Location of Bywater Bay and Oakland Bay (Puget Sound, Washington) sites and predator exclusion net plots where impact of nets on epibenthos assemblages and sediment structure was investigated, April-June 1991. Contours are indicated in meters.

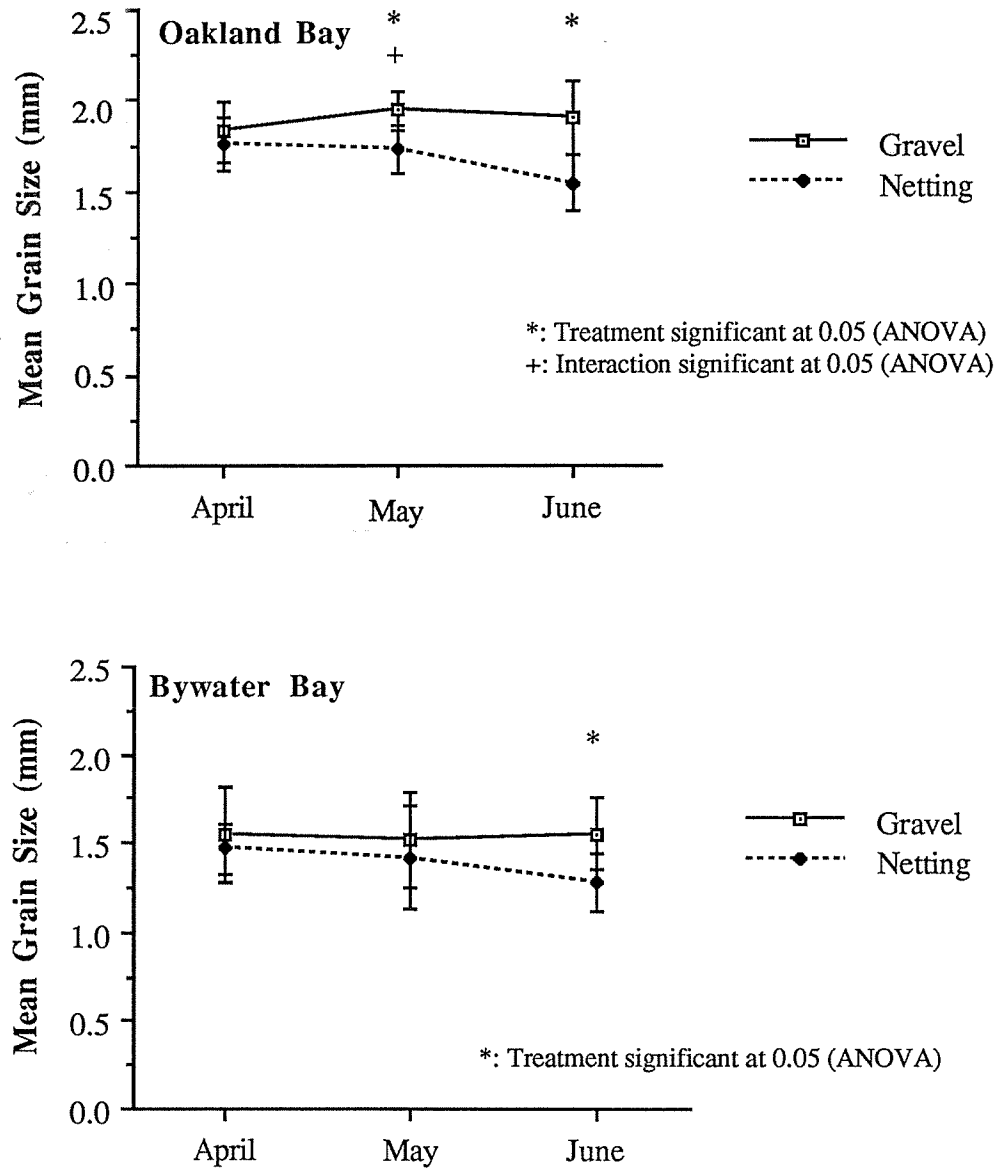


Figure 2. Comparison of mean grain size in sediments of natural gravel (control) and predator exclusion net (treatment) plots at Bywater Bay and Oakland Bay, Puget Sound, Washington, April-June 1991.

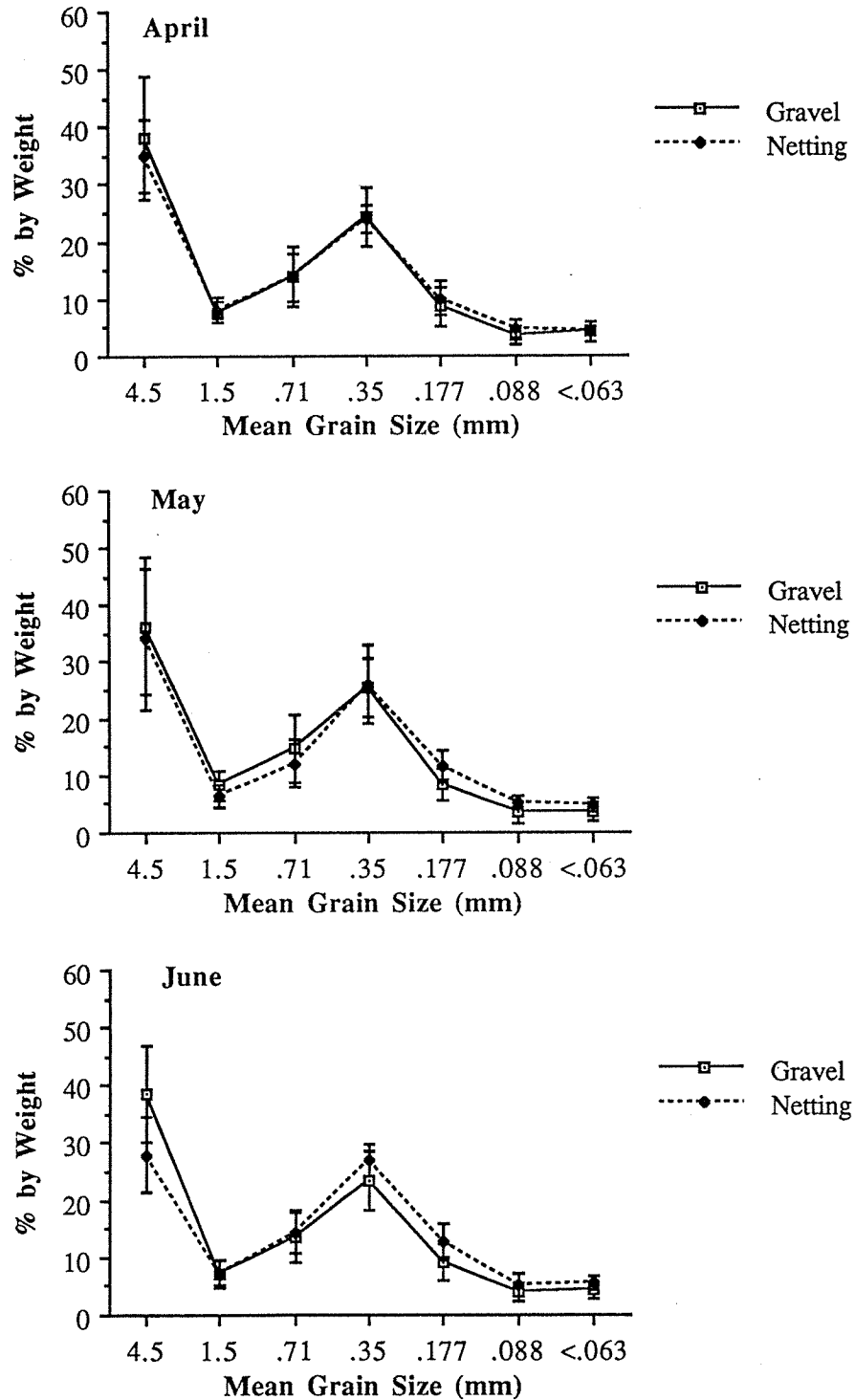


Figure 3. Gravimetric composition (%) of sediment grain size classes in natural gravel (control) and predator exclusion net (treatment) plots at (a) Bywater Bay and (b) Oakland Bay, Puget Sound, Washington, April-June 1991.

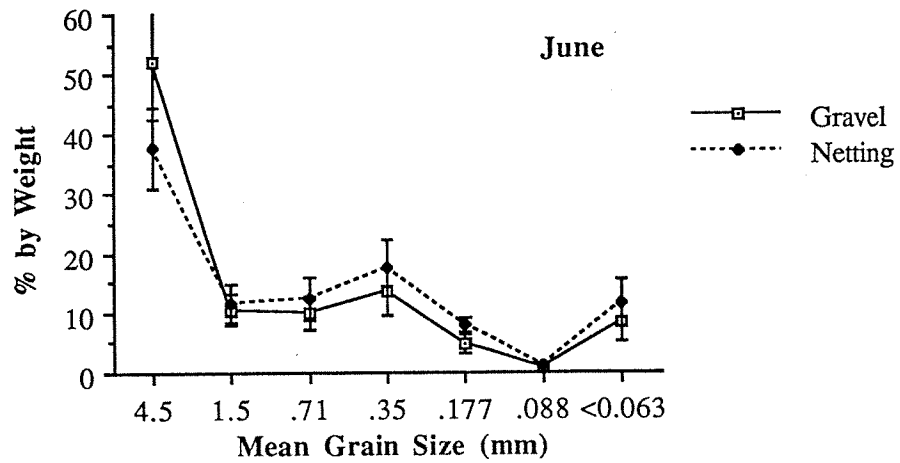
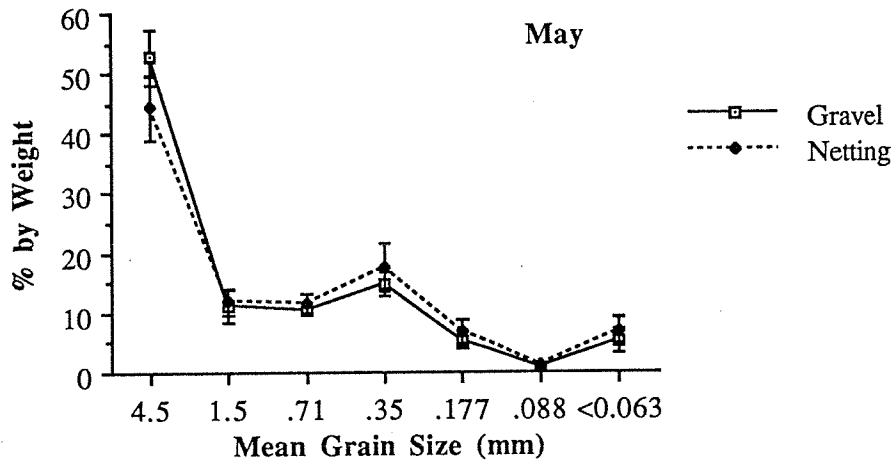
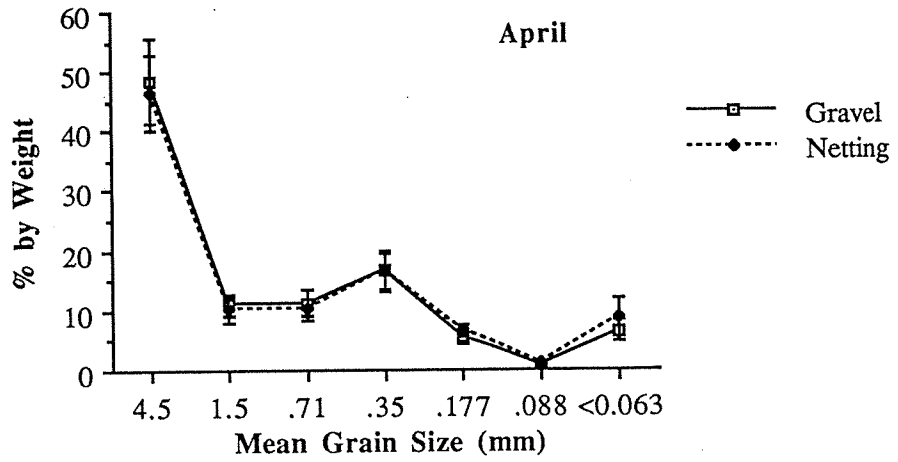


Figure 3—cont.

(a)

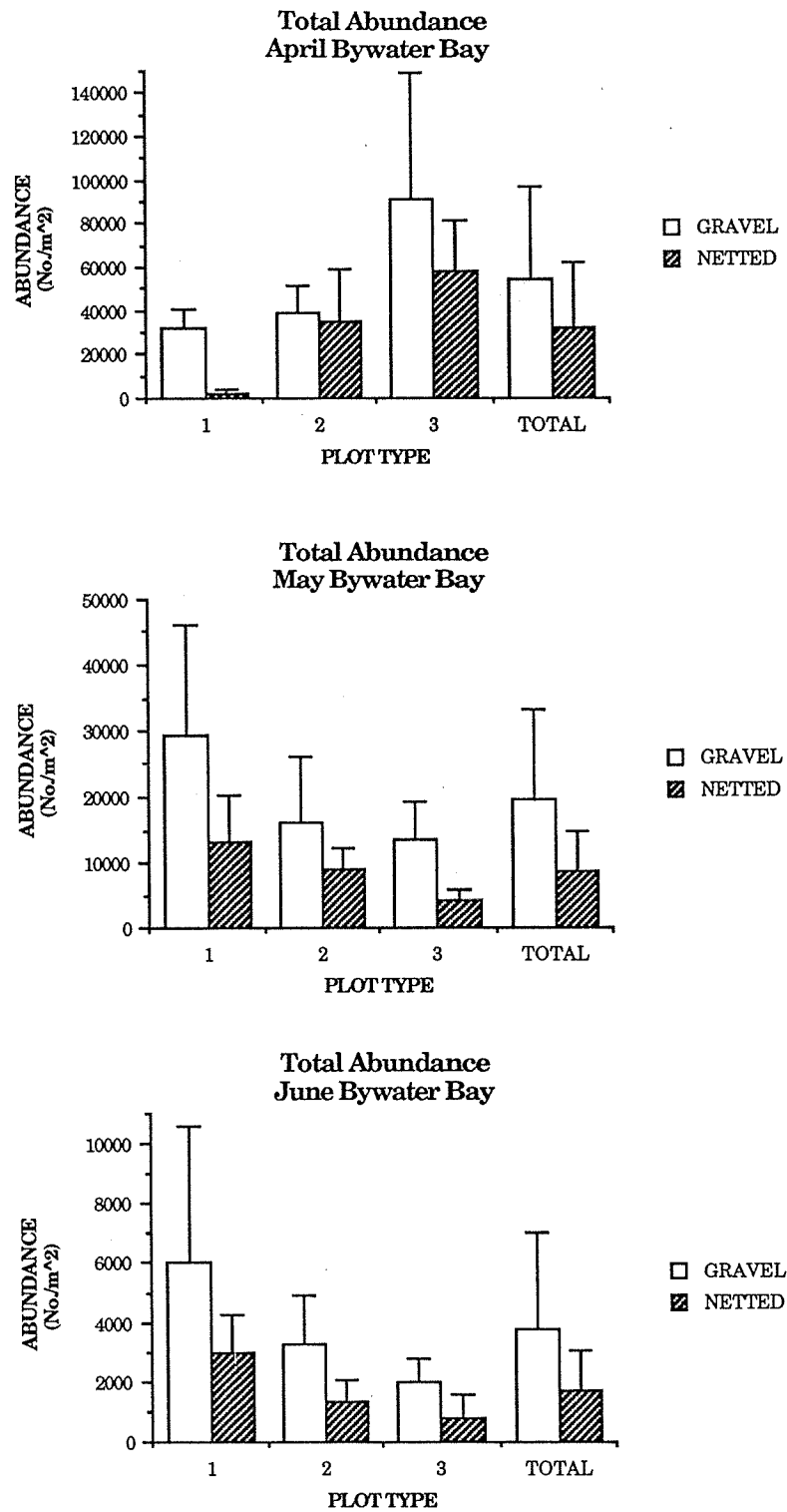


Figure 4. Within-plot and total differences in total epibenthos density in natural (gravel) and predator exclusion net (netted) plots at (a) Bywater Bay and (b) Oakland Bay, Puget Sound, Washington, April-June 1991.

(b)

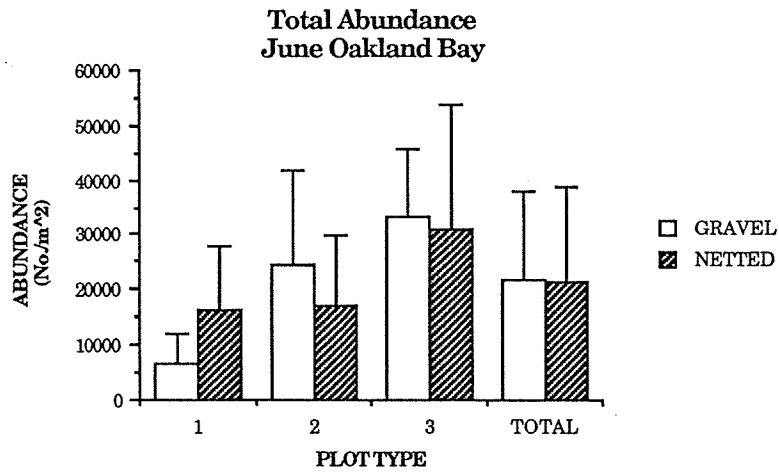
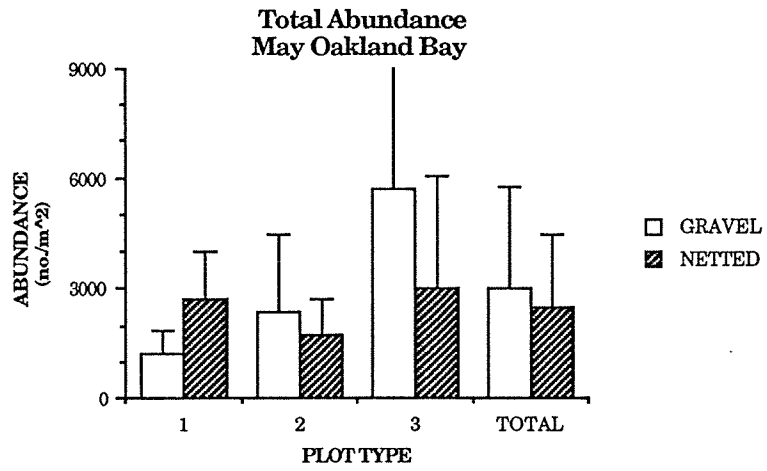
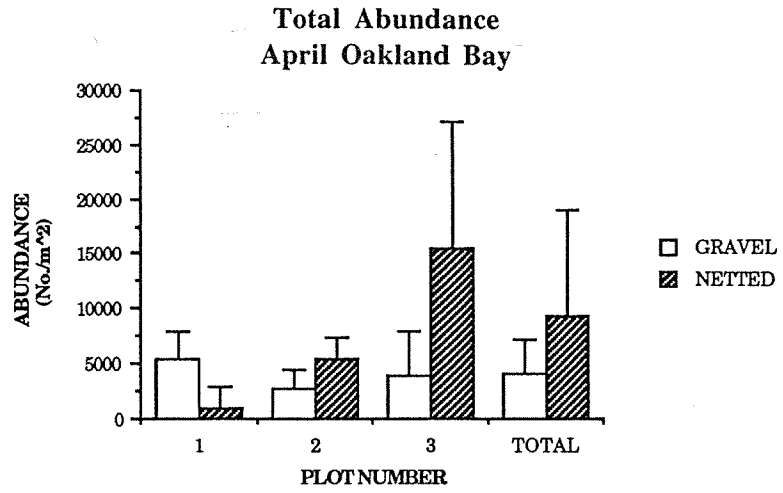


Figure 4—cont.

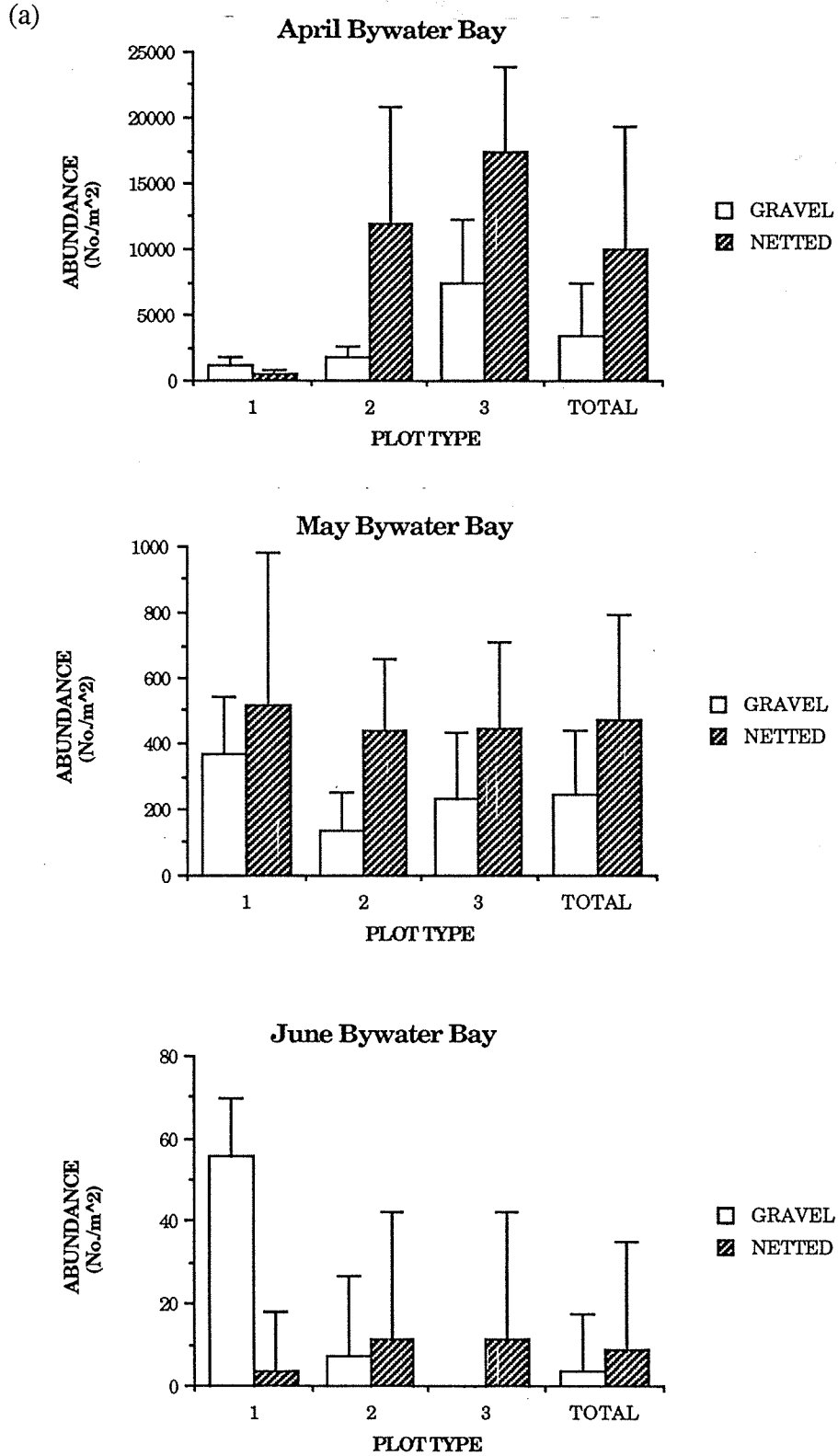


Figure 5. Within-plot and total differences in density of *Harpacticus uniremis* group adults in natural (gravel) and predator exclusion net (netted) plots at (a) Bywater Bay and (b) Oakland Bay, Puget Sound, Washington, April-June 1991.

(b)

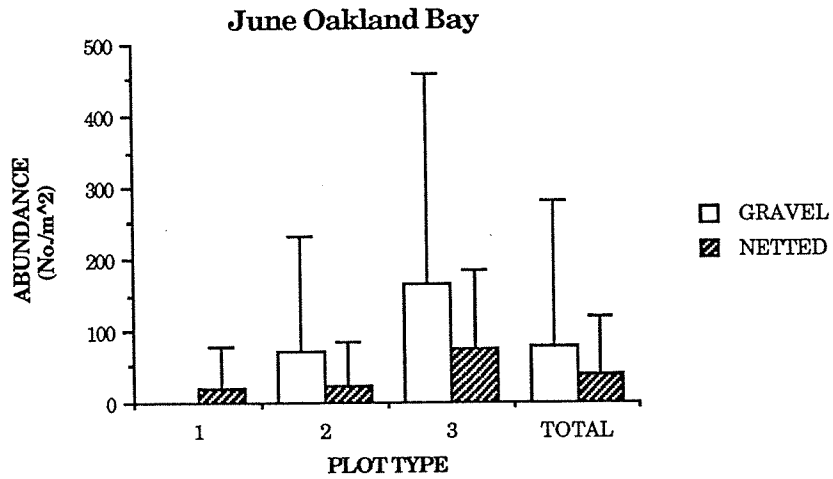
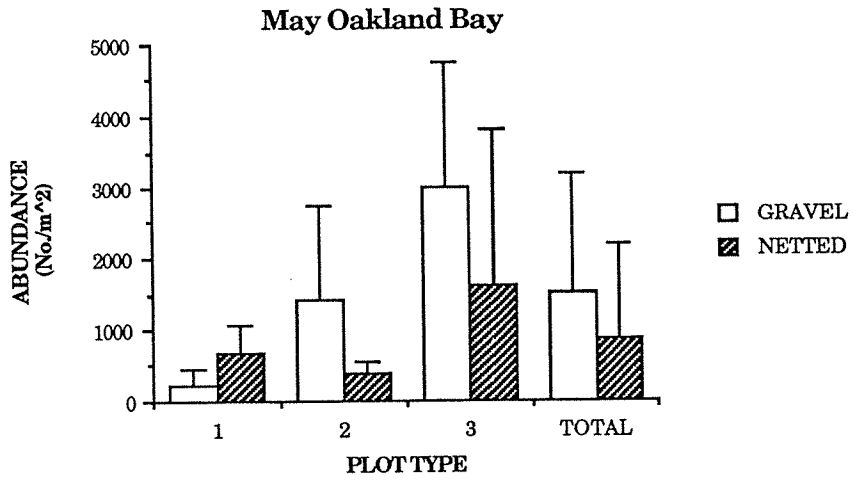
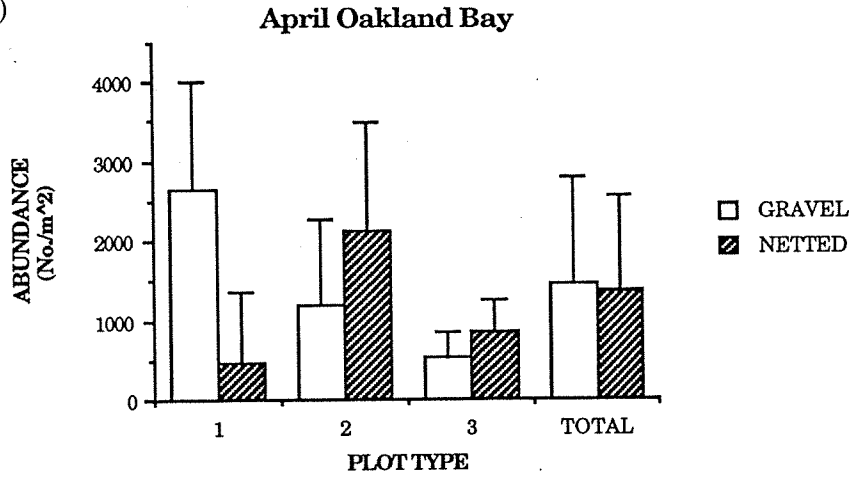


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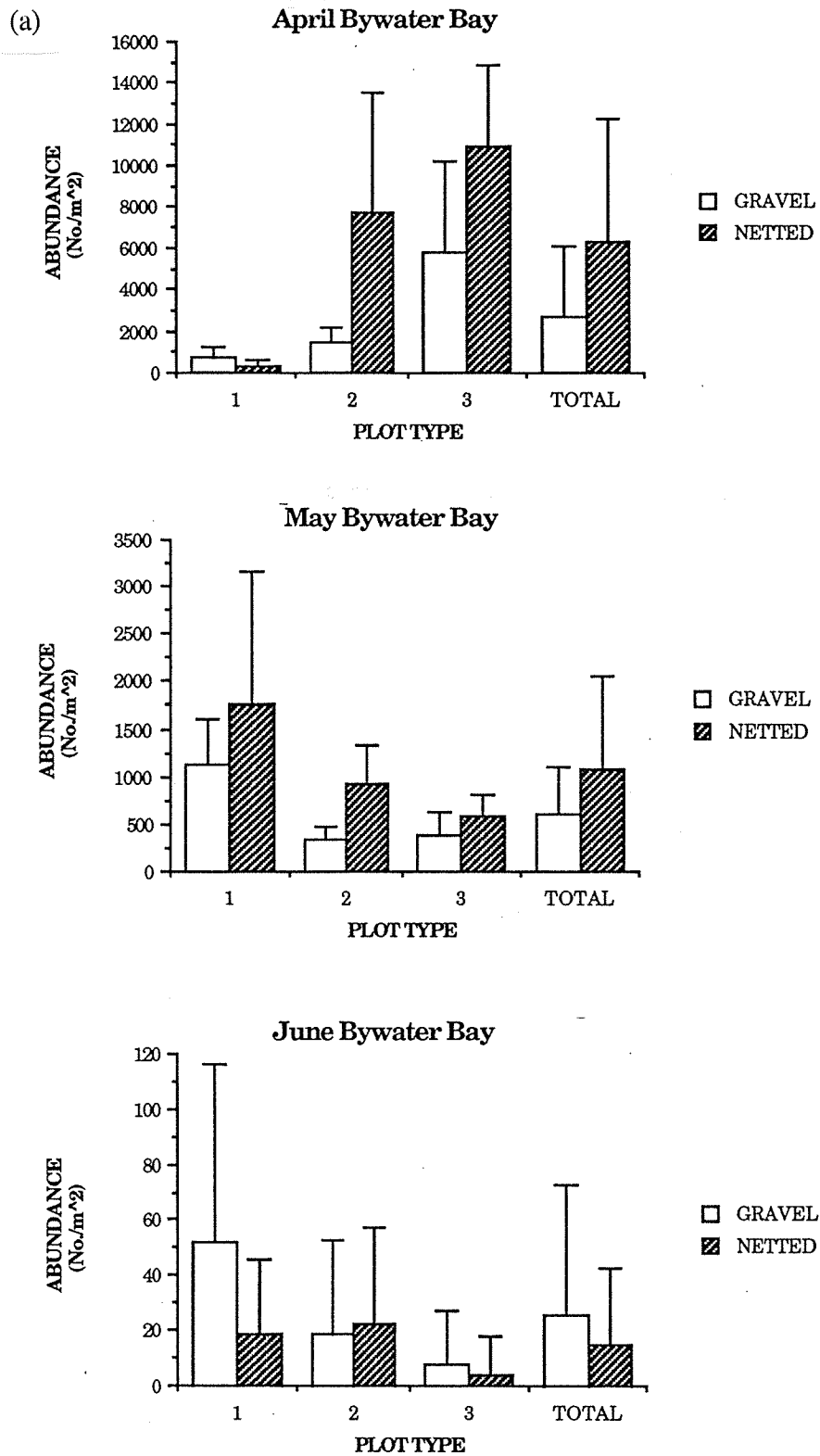


Figure 6. Within-plot and total differences in density of *Harpacticus uniremis* group copepodites in natural (gravel) and predator exclusion net (netted) plots at (a) Bywater Bay and (b) Oakland Bay, Puget Sound, Washington, April-June 1991.

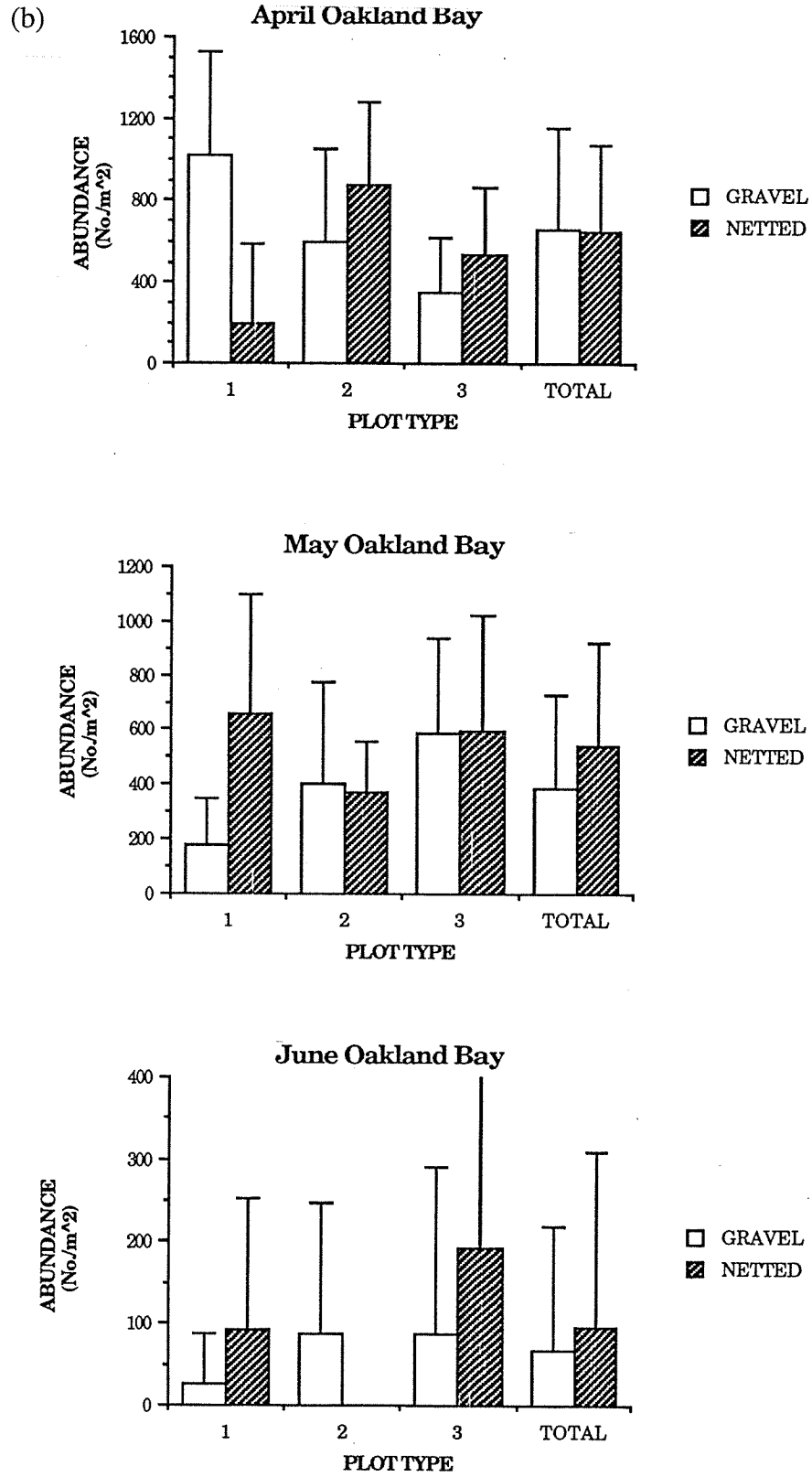


Figure 6—cont.

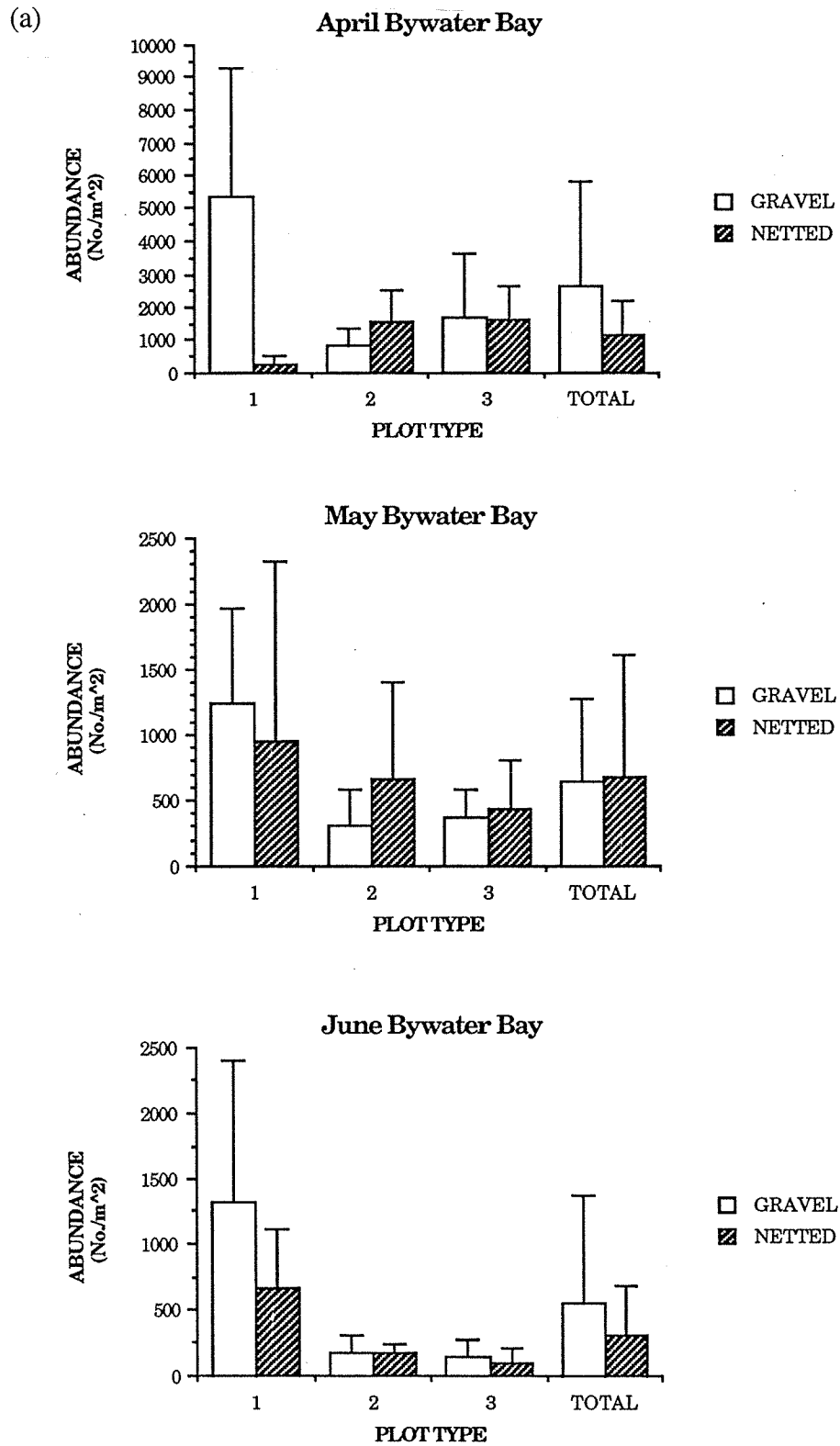


Figure 7. Within-plot and total differences in density of *Tisbe* spp. adults in natural (gravel) and predator exclusion net (netted) plots at (a) Bywater Bay and (b) Oakland Bay, Puget Sound, Washington, April-June 1991.

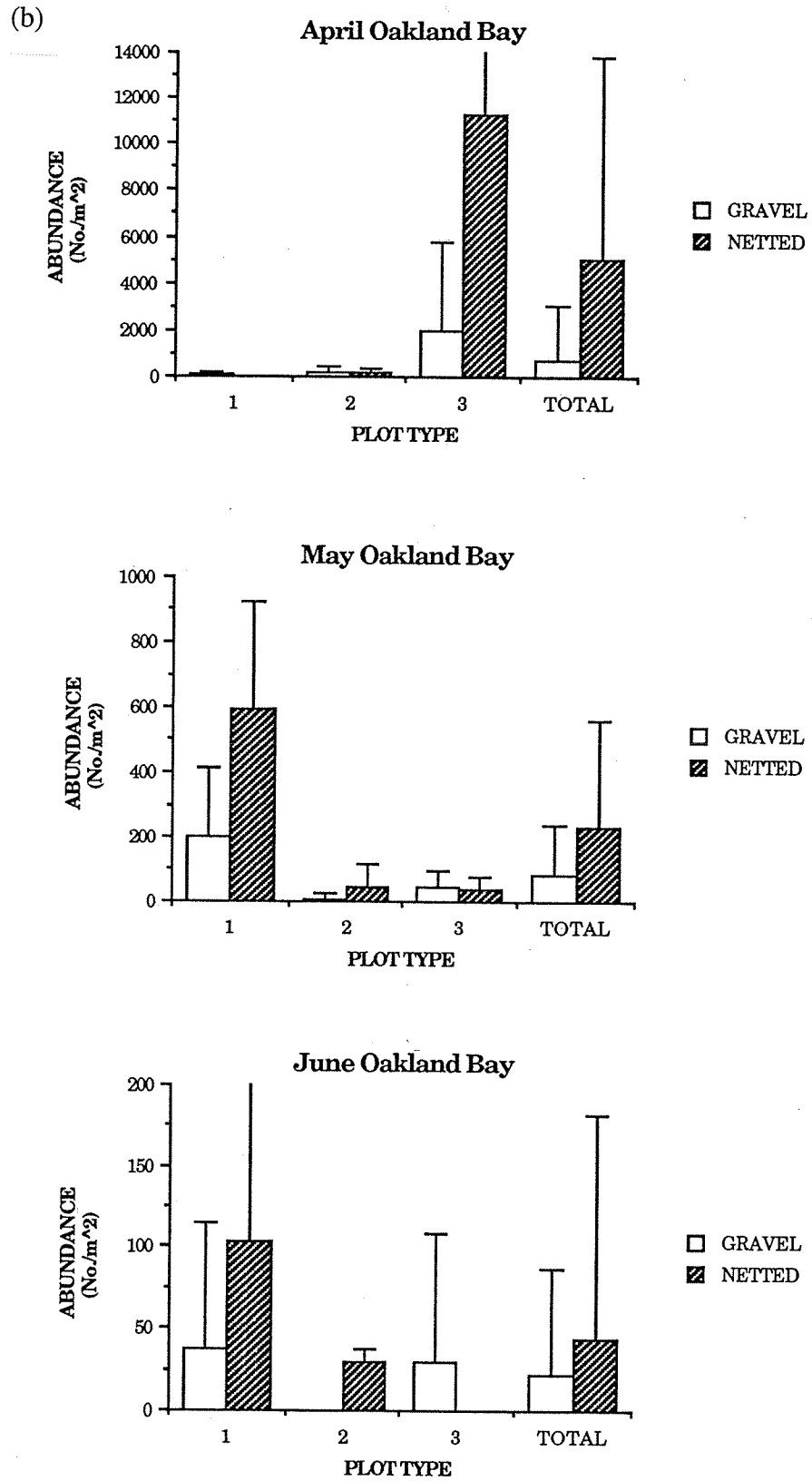


Figure 7—cont.

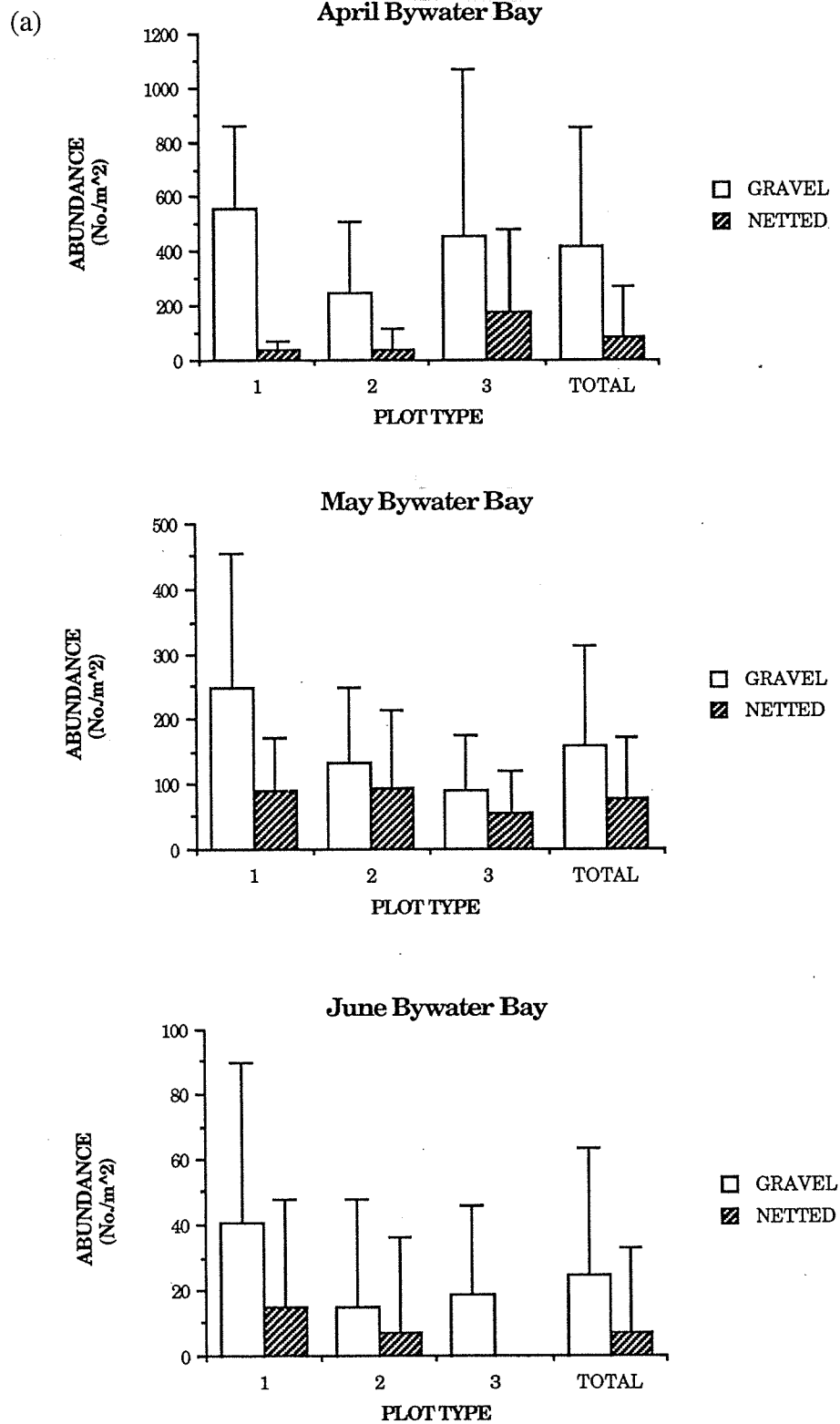


Figure 8. Within-plot and total differences in density of *Dactylopusia* sp. adults in natural (gravel) and predator exclusion net (netted) plots at (a) Bywater Bay and (b) Oakland Bay, Puget Sound, Washington, April-June 1991.

(b)

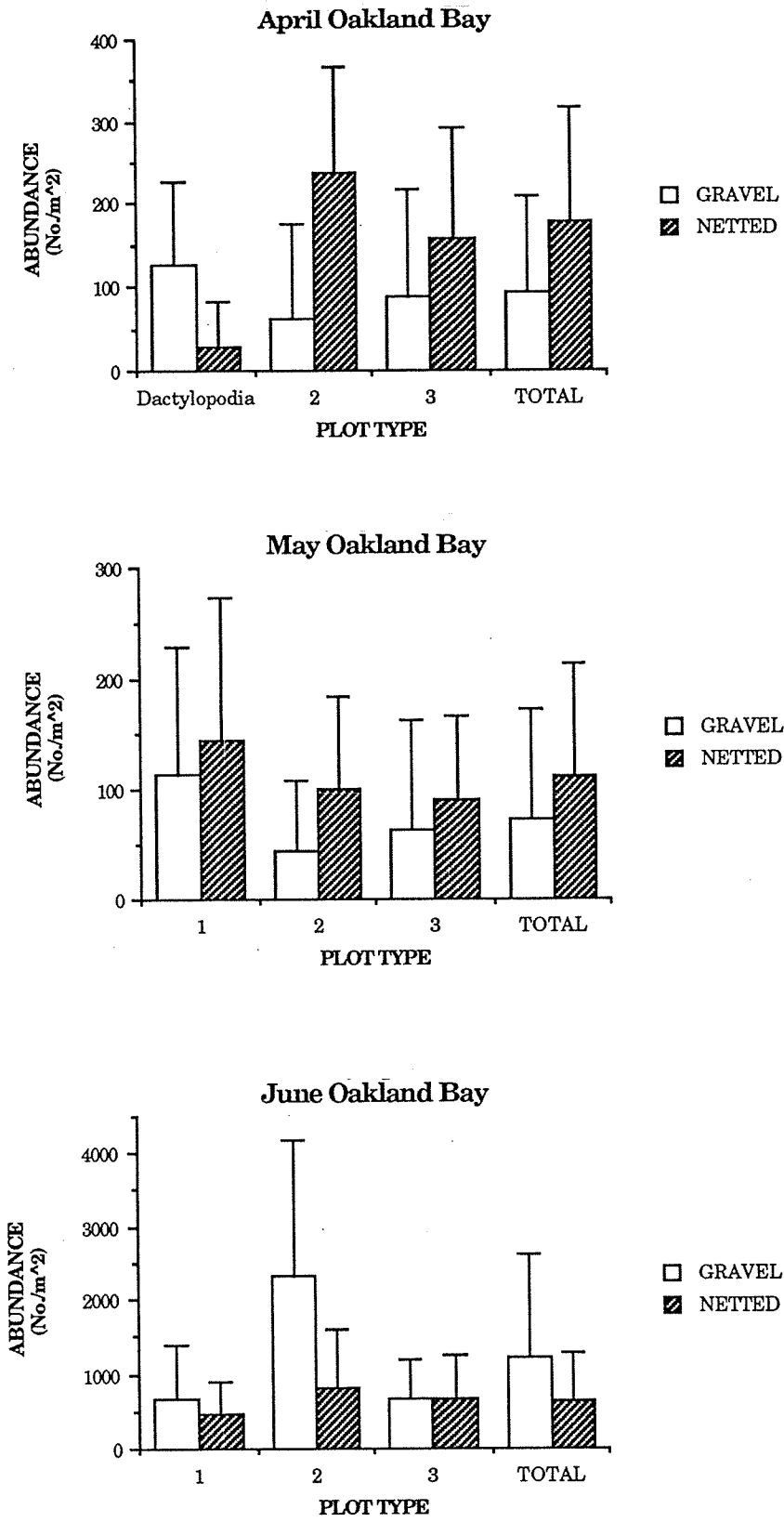


Figure 8—cont.

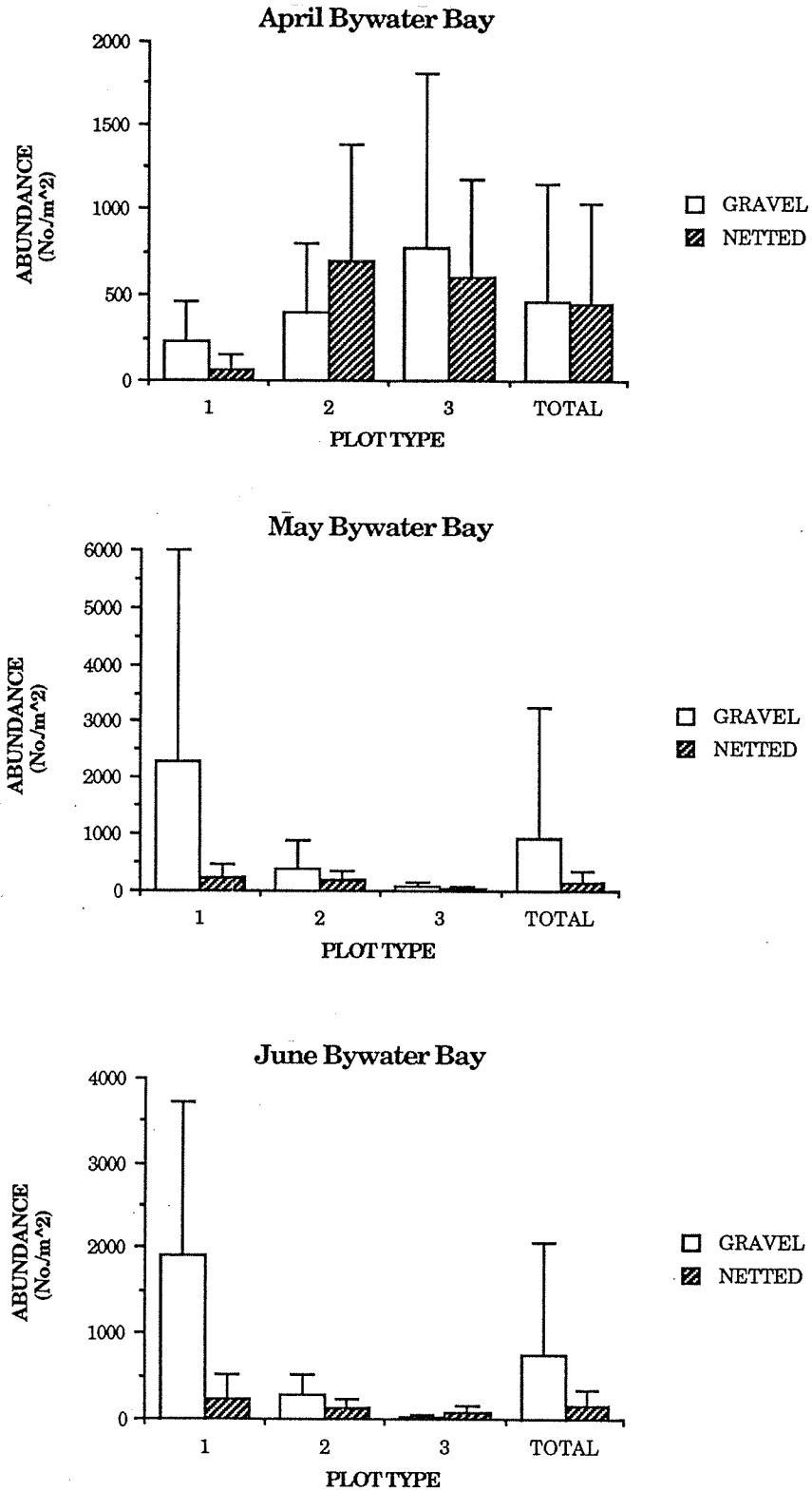


Figure 9. Within-plot and total differences in density of *Harpacticus spinulosus* adults in natural (gravel) and predator exclusion net (netted) plots at Bywater Bay, Puget Sound, Washington, April-June 1991.

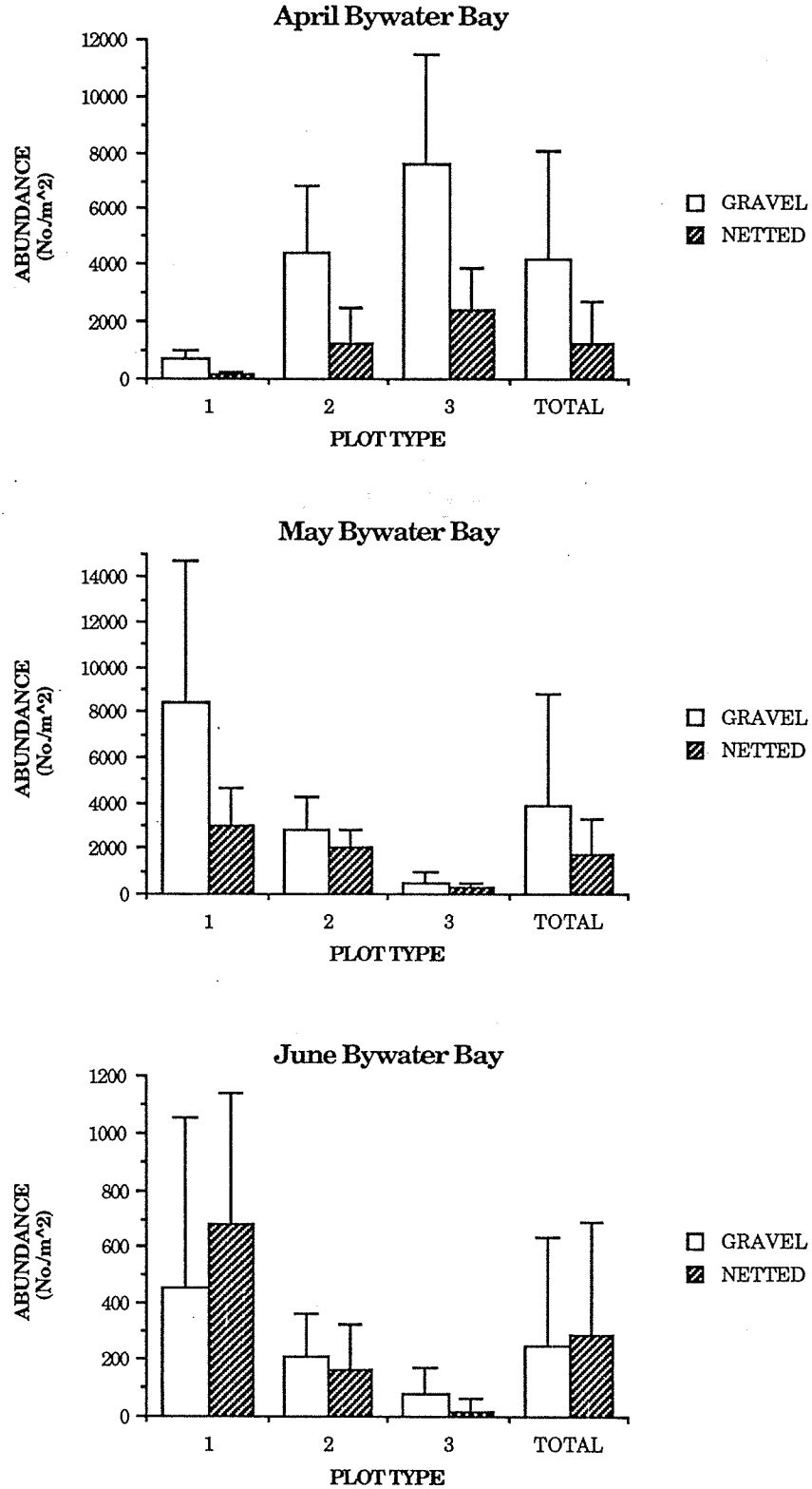


Figure 10. Within-plot and total differences in density of *Cumella vulgaris* adults in natural (gravel) and predator exclusion net (netted) plots at Bywater Bay, Puget Sound, Washington, April-June 1991.

TABLES

Table 1a. Epibenthos taxa composition (% total density, standing stock) for natural gravel (control) substrate at Bywater Bay, Puget Sound, Washington, April-June, 1991.

Taxa	Life history stages*	April		May		June	
		Density	Standing stock	Density	Standing stock	Density	Standing stock
Harpacticoida	A	17.30	6.83	20.12	8.30	21.02	11.94
Ectinosomatidae	A	14.90	3.94	9.77	3.24	7.08	6.73
<i>Harpacticus uniremis</i>	8,L	4.97	7.49	3.15	6.28	0.69	2.55
<i>Harpacticus spinulosus</i>	A,L	0.87	1.61	4.69	2.83	19.66	17.77
<i>Harpacticus</i> sp.- <i>uniremis</i> group	7	6.31	3.68	1.24	1.54	0.10	0.51
<i>Zaus</i> spp.	A,L	12.03	6.48	0.65	0.99	0.20	0.85
<i>Tisbe</i> spp.	A,L	4.85	3.47	3.27	2.78	14.62	10.92
<i>Tachidius triangularis</i>	A			0.15	0.24	0.16	0.17
Laophontidae	A			1.70	1.21	9.57	7.53
<i>Nanopus palustris</i>	A					0.49	0.85
<i>Amphiascopsis cinctus</i>	A	1.43	2.87	0.95	0.96	0.20	1.02
<i>Amphiascus</i> sp.	A	16.16	7.24	21.64	8.88	10.76	8.21
<i>Robertsonia</i> sp. cf. <i>knoxi</i>	A	11.82	4.79	8.86	3.70	7.24	6.90
<i>Dactylopusia</i> spp.	A,L	0.78	1.10	0.80	1.46	0.65	2.72
Cumacea	7,A	0.01	0.05				
<i>Leucon</i> sp.	7			0.01	0.05		
<i>Cumella vulgaris</i>	A	7.80	43.10	19.56	32.46	6.55	17.32
Tanaidacea							
<i>Tanais</i> sp.	A,7	0.06	0.60	0.53	1.10	0.46	1.87
<i>Leptocheilia savignyi</i>	A	0.04	0.58	0.10	0.04		
Gammaridea	7,A	0.28	0.77			0.48	1.81
<i>Paracalliopiella pratti</i>	7	0.36	4.22	0.15	2.23		
<i>Corophium</i> spp.	7			0.04	0.21	0.07	0.34
Gammaridae	7			1.89	8.07		
<i>Anisogammarus pugettensis</i>	7	0.01	1.12	0.80	13.41		
<i>Eogammarus confervicolus</i>	7	0.01	0.05	0.16	0.68		
Density (no. m ⁻²)							
Mean		54,058.84		19,601.65		3,769.96	
Standard deviation		42,946.79		13,587.37		3,221.85	
Standing stock (wet g m ⁻²)							
Mean			1.310		0.437		0.055
Standard deviation			1.034		0.420		0.052
Total Number of Taxa Categories		19		21		18	
Diversity Indices:							
Shannon-Weiner H'-abundance		3.24		3.15		3.09	
-biomass		3.07		3.33		3.46	
Brillouin's-abundance		3.24		3.15		3.09	

A = adults and juveniles, L = ovigerous females, 7 = juveniles, 8 = adults

Table 1b. Epibenthos taxa composition (% total density, standing stock) for predator exclusion net (treatment) substrate at Bywater Bay, Puget Sound, Washington, April-June, 1991.

Taxa	Life history stages*	April		May		June	
		Density	Standing stock	Density	Standing stock	Density	Standing stock
Harpacticoida	A	14.23	3.12	15.75	4.88	19.74	11.06
Ectinosomatidae	A	6.39	1.17	11.06	3.46	9.08	8.54
<i>Harpacticus uniremis</i>	8,L	19.95	17.22	12.29	20.00	0.86	2.76
<i>Harpacticus spinulosus</i>	A,L	1.43	0.82	1.81	2.03	8.43	9.05
<i>Harpacticus</i> sp.- <i>uniremis</i> group	7	31.40	9.80	5.28	3.11	0.50	1.26
<i>Zaus</i> spp.	A,L	11.71	3.19	0.72	0.89	0.50	1.76
<i>Tisbe</i> spp.	A,L	3.59	1.34	7.72	3.26	18.23	11.56
<i>Tachidius triangularis</i>	A	0.11	0.09	0.08	0.05	0.07	0.25
Laophontidae	A			3.91	1.89	15.78	11.06
<i>Amphiascopsis cinctus</i>	A	2.06	0.84	1.48	1.08	0.22	0.75
<i>Amphiascus</i> sp.	A	2.19	0.93	10.23	3.67	3.31	5.28
<i>Robertsonia</i> sp. cf. <i>knoxi</i>	A	0.91	0.62	2.79	1.51	3.24	5.03
<i>Dactylopusia</i> spp.	A,L	0.27	0.35	0.89	1.45	0.43	1.01
Cumacea	7,A						
<i>Cumella vulgaris</i>	A	3.94	12.21	20.01	22.67	16.71	26.13
Tanaidacea							
<i>Tanais</i> sp.	7	0.02	1.70	0.17	0.47	0.29	0.75
<i>Leptocheilia savignyi</i>	A,8	0.11	2.01				
Gammaridea	7,A	0.40	0.57			0.72	2.26
<i>Paracalliopiella pratti</i>	7	0.90	5.86	0.39	3.04		
<i>Corophium</i> spp.	7			0.04	0.14		
Gammaridae	7			5.27	13.15		
<i>Anisogammarus pugettensis</i>	7,8	0.23	37.49	0.13	13.25		
<i>Eogammarus confervicolus</i>	7	0.16	0.68				
Density (no. m ⁻²)							
Mean		31,730.86		8,861.73		1,713.58	
Standard deviation		29,911.17		5,859.49		1,319.90	
Standing stock (wet g m ⁻²)							
Mean			1.393		0.244		0.029
Standard deviation			2.231		0.245		0.027
Total Number of Taxa Categories		19		19		17	
Diversity Indices:							
Shannon-Weiner H'-abundance		2.92		3.38		3.08	
-biomass		2.94		3.33		3.36	
Brillouin's-abundance		2.92		3.38		3.08	

A = adults and juveniles, L = ovigerous females, 7 = juveniles, 8 = adults

Table 1c. Epibenthos taxa composition (% total density, standing stock) for natural gravel (control) substrate at Oakland Bay, Puget Sound, Washington, April-June, 1991.

Taxa	Life history stages*	April		May		June	
		Density	Standing stock	Density	Standing stock	Density	Standing stock
Harpacticoida	A	17.35	3.14	8.92	5.64	24.92	11.44
Ectinosomatidae	A	1.09	0.60			2.55	3.16
<i>Harpacticus uniremis</i>	8,L	16.60	6.78	12.66	13.08	0.32	1.03
<i>Harpacticus spinulosus</i>	A	0.06	0.07	0.04	0.13	0.05	0.23
<i>Harpacticus</i> sp.- <i>uniremis</i> group	7	36.40	5.34	49.67	20.26	0.36	1.25
<i>Zaus</i> spp.	A			0.04	0.13		
<i>Tisbe</i> spp.	A,L	18.87	3.67	2.78	2.69	0.10	0.39
<i>Tachidius triangularis</i>	A			2.78	2.69	0.71	1.56
Laophontidae	A					20.71	9.47
<i>Nanopus palustris</i>	A			11.54	4.10	32.38	15.90
<i>Amphiascus</i> sp.	A	0.84	0.50	0.04	0.13	0.05	0.14
<i>Stenhelia</i> sp.	A			0.37	0.13		
<i>Robertsonia</i> sp. cf. <i>knoxi</i>	A					0.10	0.39
<i>Dactylopusia</i> spp.	A,L	2.33	1.07	2.45	2.95	5.67	6.97
Cumacea	7,A						
<i>Lamprops quadriplicata</i>	A	0.03	0.05				
<i>Leucon</i> sp.	7			0.66	2.56	2.18	5.13
<i>Cumella vulgaris</i>	A	0.25	0.83			0.07	0.19
Tanaidacea							
<i>Tanais</i> sp.	A	3.42	58.88	9.09	24.74	5.44	14.25
<i>Leptochelia savignyi</i>	A			0.04	19.23		
Gammaridea	7,8,A	1.52	8.51	0.79	2.56	1.17	6.63
Corophiidae	8A	0.12	5.47	0.04	0.13		
<i>Corophium</i> spp.	7	0.99	4.27	0.66	1.28	3.21	21.89
<i>Eogammarus confervicolus</i>	7	0.12	0.37				
<hr/>							
Density (no. m ⁻²)							
Mean		3,971.60		3,042.93		21,505.76	
Standard deviation		3,122.13		2,709.57		16,613.33	
Standing stock (wet g m ⁻²)							
Mean			0.365		0.086		0.416
Standard deviation			0.439		0.135		0.461
<hr/>							
Total Number of Taxa Categories		15		17		17	
Diversity Indices:							
Shannon-Weiner H ¹ -abundance		2.49		2.36		2.59	
-biomass		2.28		2.95		3.24	
Brillouin's-abundance		2.49		2.36		2.59	

A = adults and juveniles, L = ovigerous females, 7 = juveniles, 8 = adults

Table 1d. Epibenthos taxa composition (% total density, standing stock) for predator exclusion net (treatment) substrate at Oakland Bay, Puget Sound, Washington, April-June, 1991.

Taxa	Life history stages*	April		May		June	
		Density	Standing stock	Density	Standing stock	Density	Standing stock
Harpacticoida	A	15.19	3.34	15.97	8.47	31.35	13.28
Ectinosomatidae	A	3.43	1.31	0.76	0.72	11.38	5.65
<i>Harpacticus uniremis</i>	8,L	6.97	6.07	21.77	27.57	0.44	1.52
<i>Harpacticus spinulosus</i>	A	0.04	0.08	0.10	0.36	0.38	0.88
<i>Harpacticus</i> sp.- <i>uniremis</i> group	7	14.63	4.53	35.25	15.32	0.18	0.72
<i>Zaus</i> spp.	A			0.15	0.54		
<i>Tisbe</i> spp.	A,L	54.46	20.43	9.31	5.41	0.21	0.46
<i>Tachidius triangularis</i>	A			0.41	0.54	2.80	2.70
Laophontidae	A					21.83	9.18
<i>Nannopus palustris</i>	A			1.73	1.98	8.05	4.65
<i>Amphiascus</i> sp.	A	0.86	0.92			0.11	0.35
<i>Stenhelia</i> sp.	A			2.03	0.72		
<i>Robertsonia</i> sp. cf. <i>knoxi</i>	A			0.05	0.18	0.18	0.37
<i>Dactylopusia</i> spp.	A,L	1.90	1.49	4.53	6.31	3.04	4.35
Cumacea							
<i>Lamprops quadriplicata</i>	A	0.03	0.04				
<i>Leucon</i> sp.	A			1.63	10.27	7.56	13.82
<i>Cumella vulgaris</i>	A	0.04	0.29	0.15	0.36	0.12	0.46
Tanaidacea							
<i>Tanais</i> sp.	A	1.13	37.11	4.83	15.32	4.49	11.43
<i>Leptocheilia savignyi</i>	A			0.05	0.18		
Gammaridea	7,A	0.73	14.86	1.02	3.60	2.83	20.39
Corophiidae	7					0.05	0.09
<i>Corophium</i> spp.	7	0.47	5.05	0.25	2.16	5.02	9.70
Gammaridae	7						
<i>Eogammarus confervicolus</i>	7	0.13	4.46				
<hr/>							
Density (no. m ⁻²)							
Mean		9,296.84		2,482.32		21,427.16	
Standard deviation		9,620.13		1,998.63		17,405.00	
Standing stock (wet g m ⁻²)							
Mean			0.355		0.057		0.463
Standard deviation			0.293		0.051		0.437
<hr/>							
Total Number of Taxa Categories		15		18		18	
Diversity Indices:							
Shannon-Weiner H'-abundance		2.08		2.70		2.94	
-biomass		2.71		3.14		3.37	
Brillouin's-abundance		2.08		2.70		2.94	

A = adults and juveniles, L = ovigerous females, 7 = juveniles, 8 = adults

Table 2—cont.

BYWATER BAY

OAKLAND BAY

Tisbe spp.

Cumella vulgaris

Tisbe spp.

Dactylopodia spp.

April

	d.f.	S.S.	M.S.	F	P
Total	87	708.071			
Treatment	1	17.883	17.883	12.710	< 0.05
Block	2	572.000	286.000	0.204	0.816
Error	84	118.188	1.407		

	d.f.	S.S.	M.S.	F	P
Total	87	288.014			
Treatment	1	60.732	60.732	57.088	< 0.05
Block	2	137.906	68.953	64.817	< 0.05
Error	84	89.376	1.064		

	d.f.	S.S.	M.S.	F	P
Total	76	392.234			
Treatment	1	27.271	27.271	11.099	< 0.05
Block	2	185.602	92.801	37.771	< 0.05
Error	73	179.361	2.457		

	d.f.	S.S.	M.S.	F	P
Total	76	321.726			
Treatment	1	35.474	35.474	9.248	< 0.05
Block	2	6.224	3.112	0.811	0.448
Error	73	280.028	3.836		

May

	d.f.	S.S.	M.S.	F	P
Total	87	77.483			
Treatment	1	0.073	0.073	0.101	0.751
Block	2	17.182	8.591	11.980	0.270
Error	84	60.228	0.717		

	d.f.	S.S.	M.S.	F	P
Total	87	142.077			
Treatment	1	4.385	4.385	8.155	< 0.05
Block	2	92.500	46.250	85.998	< 0.05
Error	84	45.192	0.538		

	d.f.	S.S.	M.S.	F	P
Total	86	617.964			
Treatment	1	30.078	30.078	7.697	< 0.05
Block	2	263.522	131.761	33.716	< 0.05
Error	83	324.364	3.908		

	d.f.	S.S.	M.S.	F	P
Total	86	480.639			
Treatment	1	50.666	50.666	10.007	< 0.05
Block	2	9.744	4.872	0.962	0.386
Error	83	420.229	5.063		

June

	d.f.	S.S.	M.S.	F	P
Total	87	380.840			
Treatment	1	0.120	0.120	0.038	0.846
Block	2	115.784	57.892	18.354	0.350
Error	84	264.936	3.154		

	d.f.	S.S.	M.S.	F	P
Total	87	541.544			
Treatment	1	9.666	9.666	3.029	0.085
Block	2	263.834	131.917	41.341	< 0.05
Error	84	268.044	3.191		

	d.f.	S.S.	M.S.	F	P
Total	87	268.659			
Treatment	1	0.017	0.017	0.006	0.940
Block	2	23.866	11.933	4.095	< 0.05
Error	84	244.776	2.914		

	d.f.	S.S.	M.S.	F	P
Total	87	446.569			
Treatment	1	11.243	11.243	2.289	0.134
Block	2	22.718	11.359	2.312	0.105
Error	84	412.608	4.912		

Table 2—cont.

BYWATER BAY

Tanais sp.Corophium spp.April

	d.f.	S.S.	M.S.	F	p
Total	76	312.132			
Treatment	1	0.275	0.275	0.066	0.798
Block	2	6.498	3.249	0.777	0.464
Error	73	305.359	4.183		

	d.f.	S.S.	M.S.	F	p
Total	76	363.429			
Treatment	1	0.153	0.153	0.031	0.860
Block	2	25.284	12.642	2.578	0.083
Error	73	357.992	4.904		

May

	d.f.	S.S.	M.S.	F	p
Total	86	492.591			
Treatment	1	32.697	32.697	6.665	< 0.05
Block	2	52.696	26.348	5.371	< 0.05
Error	83	407.198	4.906		

	d.f.	S.S.	M.S.	F	p
Total	86	189.641			
Treatment	1	8.467	8.467	4.100	< 0.05
Block	2	10.028	5.014	2.431	0.094
Error	83	171.146	2.062		

June

	d.f.	S.S.	M.S.	F	p
Total	87	482.043			
Treatment	1	1.717	1.717	0.457	0.501
Block	2	164.738	82.369	21.923	< 0.05
Error	84	315.588	3.757		

	d.f.	S.S.	M.S.	F	p
Total	87	407.489			
Treatment	1	8.257	8.257	1.996	0.161
Block	2	51.724	25.862	6.252	< 0.05
Error	84	347.508	4.137		

Table 3. Generalized responses of epibenthic crustaceans to the placement of predator exclusion nets on gravel beach substrates in Bywater Bay and Oakland Bay, Puget Sound, Washington, April-June 1991.

Taxa Category	Site			
	Bywater Bay		Oakland Bay	
	Treatment	Block	Treatment	Block
<u>Harpacticoid copepods</u>				
<i>Harpacticus uniremis</i> group				
copepodites	++	++	-	--
adults	++	++	+	+
<i>Harpacticus spinulosus</i> adults	-	-	+	-
<i>Tisbe</i> spp. adults	-	0	+	+
<i>Dactylopusia</i> spp. adults	-	-	++	0
<u>Cumaceans</u>				
<i>Cumella vulgaris</i>	--	--	0	-
<u>Tanaids</u>				
<i>Tanais</i> sp.	-	--	+	-
<u>Amphipods</u>				
<i>Corophium</i> spp.	-	-	-	-
Total epibenthos	-	-	+	-

++ = significant enhancement
 -- = significant depression
 + = moderate, variable enhancement
 - = moderate, variable depression
 0 = no detectable effect
 - = not determined

APPENDICES

APPENDIX A. GRAIN SIZE RESULTS

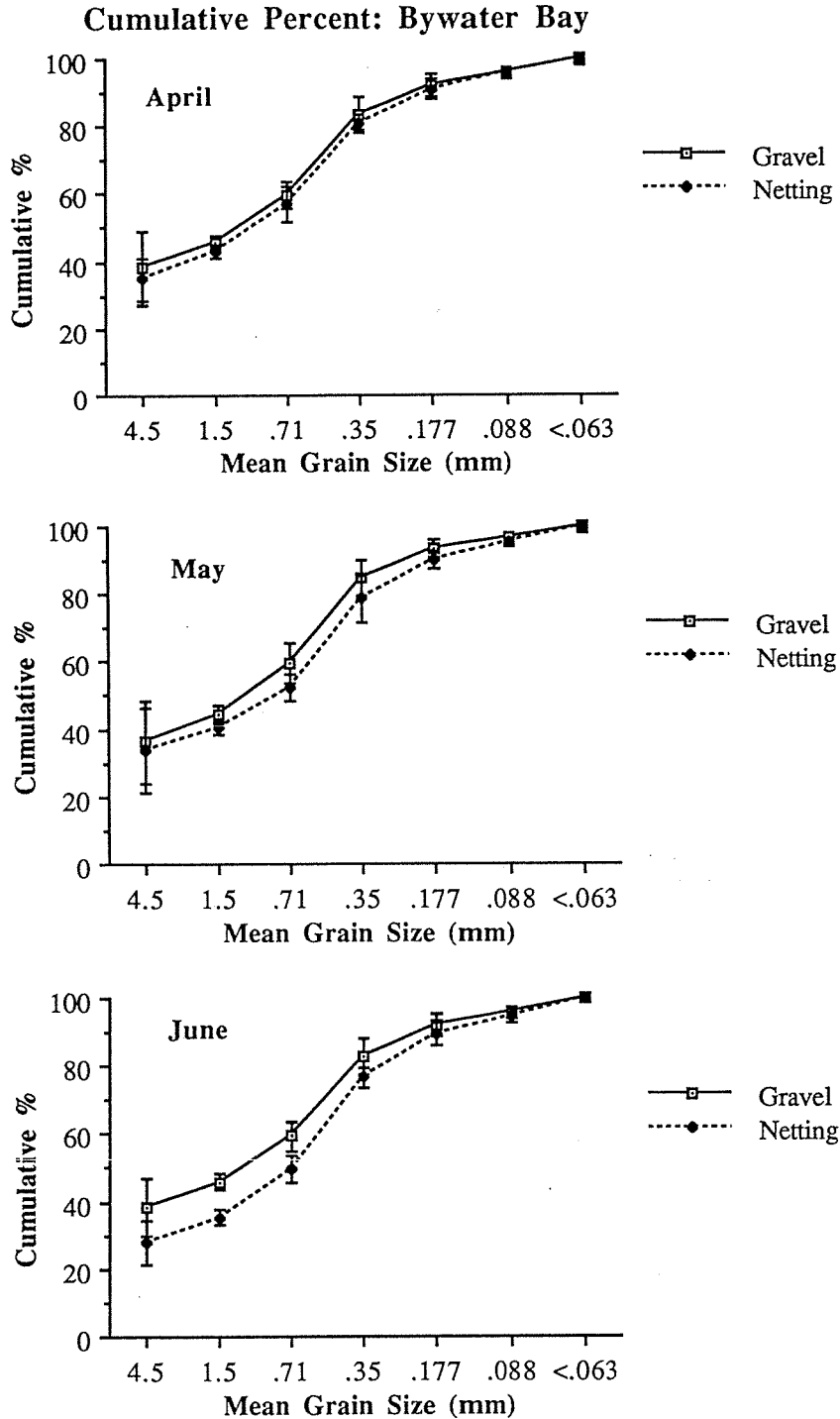
APPENDIX B. SUMMARIES (MEAN AND STANDARD DEVIATIONS OF ORGANISMS DENSITY) OF EPIBENTHOS TAXA

Appendix A1. Table of sediment grain size class composition (% , gravimetric) in natural gravel (control) and predator exclusion net (treatment) intertidal plots at Bywater Bay and Oakland Bay, Puget Sound, Washington.

BYWATER BAY								
GRAVEL (CONTROL)					NET (TREATMENT)			
APRIL	Part. size	%	Cum %	S.D.	Part. size	%	Cum %	S.D.
	2.0 mm	38.07	38.07	10.78	2.0 mm	35.03	35.03	6.28
	1.0 mm	7.74	45.82	1.94	1.0 mm	7.95	42.98	2.23
	0.5 mm	13.80	59.61	4.20	0.5 mm	13.80	56.79	5.19
	0.25 mm	24.05	83.67	5.17	0.25 mm	23.90	80.69	2.45
	0.125 mm	8.63	92.30	3.26	0.125 mm	10.08	90.77	2.97
	0.063 mm	3.49	95.80	1.65	0.063 mm	4.91	95.68	1.64
	<0.063 m	4.20	100.00	1.89	<0.063 m	4.32	100.00	0.66
		Mean	Stdev.			Mean	Stdev.	
	Mean grain size:	1.548	0.263		Mean grain size:	1.466	0.138	
MAY	Part. size	%	Cum %	S.D.	Part. size	%	Cum %	S.D.
	2.0 mm	36.31	36.31	12.23	2.0 mm	34.03	34.03	12.47
	1.0 mm	8.24	44.55	2.66	1.0 mm	6.43	40.45	1.96
	0.5 mm	14.84	59.39	5.98	0.5 mm	12.07	52.53	4.06
	0.25 mm	25.39	84.78	5.18	0.25 mm	26.03	78.56	7.10
	0.125 mm	8.30	93.09	2.69	0.125 mm	11.39	89.95	2.84
	0.063 mm	3.35	96.44	1.82	0.063 mm	5.23	95.17	1.09
	<0.063 m	3.56	100.00	1.74	<0.063 m	4.83	100.00	1.12
		Mean	S.dev			Mean	S.dev	
	Mean grain size:	1.517	0.274		Mean grain size:	1.418	0.291	
JUNE	Part. size	%	Cum %	S.D.	Part. size	%	Cum %	S.D.
	2.0 mm	38.52	38.52	8.47	2.0 mm	28.02	28.02	6.64
	1.0 mm	7.33	45.86	2.41	1.0 mm	7.27	35.29	2.31
	0.5 mm	13.44	59.29	4.34	0.5 mm	14.45	49.74	3.83
	0.25 mm	23.52	82.82	5.09	0.25 mm	26.97	76.71	2.92
	0.125 mm	9.18	92.00	3.32	0.125 mm	12.69	89.40	3.05
	0.063 mm	3.85	95.85	1.69	0.063 mm	5.21	94.61	1.99
	<0.063 m	4.15	100.00	1.48	<0.063 m	5.39	100.00	1.21
		Mean	S.dev			Mean	S.dev	
	Mean grain size:	1.551	0.200		Mean grain size:	1.279	0.162	

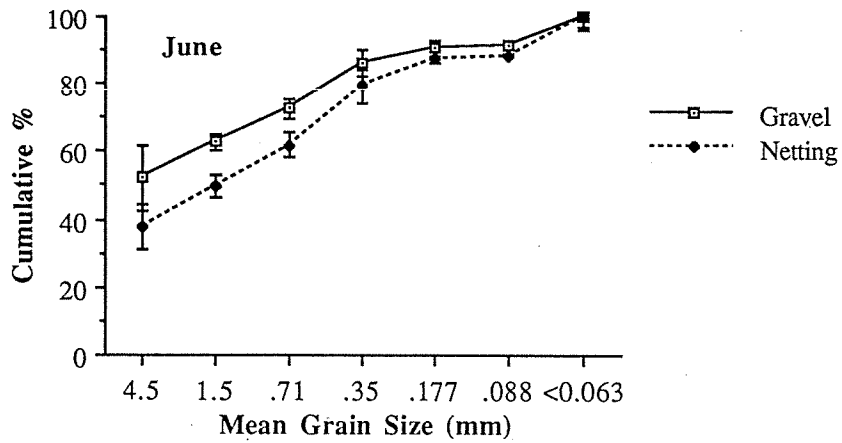
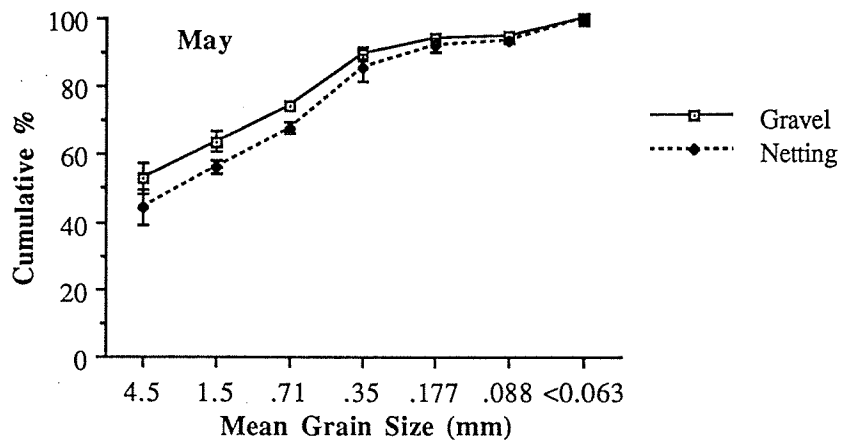
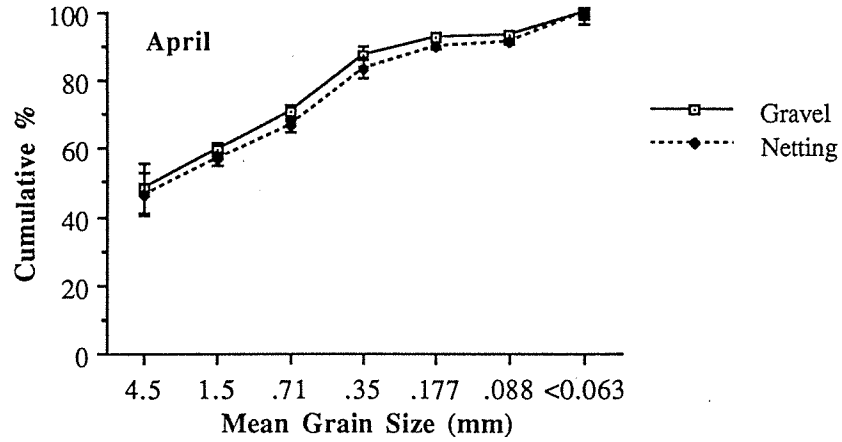
OAKLAND BAY

		GRAVEL (CONTROL)				NET (TREATMENT)			
APRIL	Part. size	%	Cum %	S.D.	Part. size	%	Cum %	S.D.	
	2.0 mm	48.41	48.41	7.23	2.0 mm	46.58	46.58	6.28	
	1.0 mm	10.97	59.37	1.93	1.0 mm	10.30	56.89	2.23	
	0.5 mm	11.25	70.62	2.30	0.5 mm	10.23	67.11	1.89	
	0.25 mm	16.51	87.13	3.22	0.25 mm	16.51	83.62	2.98	
	0.125 mm	5.51	92.64	1.18	0.125 mm	6.64	90.25	0.99	
	0.063 mm	0.91	93.55	0.32	0.063 mm	1.02	91.28	0.26	
	<0.063 m	6.45	100.00	1.94	<0.063 m	8.72	100.00	3.14	
		Mean	S.dev			Mean	S.dev		
	Mean grain size:	1.828	0.165		Mean grain size:	1.761	0.147		
MAY	Part. size	%	Cum %	S.D.	Part. size	%	Cum %	S.D.	
	2.0 mm	52.77	52.77	4.60	2.0 mm	44.36	44.36	5.32	
	1.0 mm	11.14	63.91	2.93	1.0 mm	11.86	56.21	2.22	
	0.5 mm	10.49	74.39	1.08	0.5 mm	11.60	67.81	1.70	
	0.25 mm	14.74	89.14	1.96	0.25 mm	17.60	85.41	3.98	
	0.125 mm	4.89	94.03	0.98	0.125 mm	6.64	92.05	1.96	
	0.063 mm	0.81	94.84	0.39	0.063 mm	1.14	93.20	0.45	
	<0.063 m	5.16	100.00	1.93	<0.063 m	6.80	100.00	2.16	
		Mean	S.dev			Mean	S.dev		
	Mean grain size:	1.942	0.106		Mean grain size:	1.733	0.132		
JUNE	Part. size	%	Cum %	S.D.	Part. size	%	Cum %	S.D.	
	2.0 mm	52.08	52.08	9.43	2.0 mm	37.77	37.77	6.84	
	1.0 mm	10.53	62.61	2.64	1.0 mm	11.71	49.48	3.15	
	0.5 mm	10.05	72.66	2.77	0.5 mm	12.28	61.76	3.61	
	0.25 mm	13.53	86.18	3.92	0.25 mm	17.54	79.30	4.78	
	0.125 mm	4.78	90.97	1.49	0.125 mm	7.85	87.15	1.13	
	0.063 mm	0.68	91.65	0.16	0.063 mm	1.25	88.40	0.21	
	<0.063 m	8.35	100.00	3.21	<0.063 m	11.60	100.00	4.05	
		Mean	S. dev.			Mean	Stdev.		
	Mean grain size:	1.903	0.205		Mean grain size:	1.546	0.150		



Appendix A2. Figures of cumulative composition (% , gravimetric) of sediment grain size classes in natural gravel (control) and predator exclusion net (treatment) intertidal plots at Bywater Bay and Oakland Bay, Puget Sound, Washington.

Cumulative Percent: Oakland Bay



Appendix A3. Statistical analysis (ANOVA) tables for tests of differences in sediment mean grain size in natural gravel (control) and predator exclusion net (treatment) intertidal plots at Bywater Bay and Oakland Bay, Puget Sound, Washington.

OAKLAND BAY**3 AP 91**

<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F</u>	<u>Prob.</u>
Total	17	0.0516			
Treatment	1	0.0025	0.0025	0.67	0.430
Block	2	0.0023	0.0012	0.30	0.743
Interaction	2	0.0010	0.0005	0.14	0.873
Error	12	0.0457	0.0038		

7 MY 91

<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F</u>	<u>Prob.</u>
Total	17	0.0535			
Treatment	1	0.0245	0.0245	18.74	0.001
Block	2	0.0026	0.0013	0.98	0.404
Interaction	2	0.0107	0.0054	4.11	0.044
Error	12	0.0157	0.0013		

5 JN 91

<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F</u>	<u>Prob.</u>
Total	17	0.1439			
Treatment	1	0.0766	0.0766	14.02	0.003
Block	2	0.0008	0.0004	0.07	0.931
Interaction	2	0.0010	0.0005	0.09	0.912
Error	12	0.0655	0.0055		

BYWATER BAY**2 AP 91**

<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F</u>	<u>Prob.</u>
Total	17	0.1129			
Treatment	1	0.0039	0.0039	0.67	0.427
Block	2	0.0133	0.0066	1.16	0.348
Interactio	2	0.0269	0.0135	2.35	0.138
Error	12	0.0688	0.0057		

6 MY 91

<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F</u>	<u>Prob.</u>
Total	17	0.2193			
Treatment	1	0.0076	0.0076	0.54	0.478
Block	2	0.0021	0.0011	0.07	0.929
Interactio	2	0.0405	0.0202	1.44	0.276
Error	12	0.1692	0.0141		

4 JN 91

<u>Source</u>	<u>d.f.</u>	<u>S.S.</u>	<u>M.S.</u>	<u>F</u>	<u>Prob.</u>
Total	17	0.1526			
Treatment	1	0.0567	0.0567	9.83	0.009
Block	2	0.0057	0.0029	0.49	0.622
Interactio	2	0.0211	0.0105	1.82	0.203
Error	12	0.0692	0.0058		

Statistically significant probabilities ($p < 0.05$) are in bold typeface.

Appendix B. Summaries (mean and standard deviations of organisms density) of epibenthos taxa.

BYWATER BAY

TAXA	MEAN DENSITY (no. m-2)					
	APRIL		MAY		JUNE	
	GRAVEL	NETTED	GRAVEL	NETTED	GRAVEL	NETTED
Total Abundance	54,058.84	31,730.86	19,601.65	8,861.73	3,769.96	1,713.58
Harpacticoida	33,568.40	8,225.51	12,586.60	4,017.20	2,197.23	914.31
Ectinosomatidae	8,056.00	2,026.30	1,916.00	979.80	267.10	155.60
<i>Harp. uniremis</i>	2,687.20	6,330.00	617.30	1,088.90	25.90	14.80
<i>H. spinulosus</i>	468.30	452.70	920.20	160.10	741.20	144.40
H. un. gr. copep.	3,413.60	9,962.60	244.00	467.90	3.70	8.60
<i>Zaus</i>	6,505.00	3,716.90	127.60	64.20	7.40	8.60
<i>Tisbe</i>	2,623.50	1,139.90	641.20	684.00	551.00	312.30
<i>Dactylopodia</i>	421.40	85.60	156.80	79.00	24.70	7.20
<i>Leucon</i>	0.00	0.00	2.50	0.00	0.00	0.00
<i>Cumella</i>	4,214.80	1,251.40	3,834.20	1,772.80	246.90	286.40
<i>Tanais</i>	34.60	4.90	103.70	14.80	17.30	4.90
<i>Leptochelia</i>	23.90	34.20	1.60	0.00	0.00	0.00
<i>Paracalliopiella</i>	193.40	286.00	29.20	34.60	0.00	0.00
<i>Anisogammarus</i>	4.90	72.80	156.40	11.10	0.00	0.00
Gammaridea	153.10	128.00	370.80	466.70	18.10	12.30
<i>Corphium</i>	0.00	0.00	7.40	3.70	2.50	0.00
<i>Eogammarus</i>	6.60	49.40	0.00	0.00	0.00	0.00
Included as "Harpacticoida", above, are:						
Harpactoida	9,349.80	4,515.60	3,944.40	1,395.50	792.60	338.30
Laophontidae	0.00	0.00	333.30	346.90	360.90	270.40
<i>Nannopus</i>	0.00	0.00	0.00	0.00	18.50	32.10
<i>Amphiascopsis</i>	773.30	655.10	186.80	130.90	7.40	3.70
<i>Amphiascus</i>	8,734.60	695.10	4,242.40	906.60	405.80	56.80
<i>Robertsonia</i>	6,387.20	289.70	1,736.20	246.90	272.80	55.60
<i>Tach. triang.</i>	0.00	34.60	29.60	7.40	6.20	1.20

Appendix B—cont.

BYWATER BAY

TAXA	STANDARD DEVIATION					
	APRIL		MAY		JUNE	
	GRAVEL	NETTED	GRAVEL	NETTED	GRAVEL	NETTED
Total Abundance	42,946.70	29,911.17	13,587.37	5,859.49	3,221.85	1,319.90
Harpacticoida	28,355.97	9,887.02	7,500.51	2,499.09	1,300.08	647.6
Ectinosomatidae	6,949.50	3,264.50	1,955.50	972.90	309.90	176.70
<i>Harp. uniremis</i>	3,389.80	5,989.40	483.90	968.10	46.80	27.50
<i>H. spinulosus</i>	680.20	582.10	2,327.80	175.80	1,328.90	188.20
<i>H. un. gr. copep.</i>	4,015.70	9,429.70	191.90	326.60	14.00	26.40
<i>Zaus</i>	5,398.20	3,849.80	196.10	152.60	22.50	20.40
<i>Tisbe</i>	3,175.20	1,035.30	626.10	929.60	827.80	365.70
<i>Dactylopodia</i>	432.40	186.80	156.30	90.60	38.50	25.40
<i>Leucon</i>	0.00	0.00	16.60	0.00	0.00	0.00
<i>Cumella</i>	3,834.90	1,435.70	4,997.40	1,538.00	387.50	399.40
<i>Tanais</i>	215.60	33.10	234.60	34.30	33.10	26.00
<i>Leptochelia</i>	93.80	83.90	11.00	0.00	0.00	0.00
<i>Paracalliopiella</i>	680.80	371.30	60.50	59.60	0.00	0.00
<i>Anisogammarus</i>	23.20	250.80	543.80	55.00	0.00	0.00
Gammaridea	285.90	224.80	577.60	431.40	41.30	26.20
<i>Corphium</i>	0.00	0.00	34.70	18.30	11.60	0.00
<i>Eogammarus</i>	25.30	236.40	0.00	0.00	0.00	0.00
Included as "Harpacticoida", above, are:						
Harpacticoida	10,282.10	5,289.00	2,570.90	767.00	603.50	256.50
Laophontidae	0.00	0.00	331.90	250.20	216.50	244.90
<i>Nannopus</i>	0.00	0.00	0.00	0.00	58.00	132.20
<i>Amphiascopsis</i>	1,545.20	824.10	744.80	216.50	19.10	14.00
<i>Amphiascus</i>	6,039.40	904.10	3,188.90	720.90	354.10	98.00
<i>Robertsonia</i>	9,544.50	424.60	2,132.00	475.20	346.30	114.20
<i>Tach. triang.</i>	0.00	177.00	90.70	49.70	41.40	8.30

Appendix B—cont.

OAKLAND BAY

TAXA	MEAN DENSITY (no. m ⁻²)					
	APRIL		MAY		JUNE	
	GRAVEL	NETTED	GRAVEL	NETTED	GRAVEL	NETTED
Total Abundance	3,971.60	9,296.84	3,042.93	2,482.32	21,505.76	21,427.16
Harpacticoida	804.35	1,446.84	643.72	510.28	17,524.71	16,393.76
Ectinosomatidae	43.20	318.60	0.00	18.90	549.40	2,438.50
<i>Harp. uniremis</i>	659.30	647.60	385.10	540.40	67.90	95.10
<i>H. spinulosus</i>	2.50	3.30	1.30	2.50	11.10	81.50
H. un. gr. copep.	1,445.70	1,360.00	1,511.40	875.00	77.80	38.30
<i>Zaus</i>	0.00	0.00	1.30	3.80	0.00	0.00
<i>Tisbe</i>	749.40	5,063.20	84.60	231.10	22.20	44.40
<i>Dactylopodia</i>	92.60	177.00	74.50	112.40	1,220.20	652.30
<i>Leucon</i>	0.00	0.00	20.20	40.40	468.70	1,618.90
<i>Lamprops</i>	1.20	1.60	0.00	0.00	0.00	0.00
<i>Cumella</i>	9.90	3.30	0.00	3.80	14.40	24.70
<i>Tanais</i>	135.80	105.10	276.50	119.90	1,170.40	961.70
Gammaridea	60.50	67.50	24.00	25.30	252.70	605.30
<i>Paracalliopiella</i>	0.00	1.60	0.00	0.00	0.00	0.00
<i>Corophium</i>	39.50	44.10	0.00	0.00	689.70	1,074.90
<i>Eogammarus</i>	4.90	12.00	0.00	0.00	0.00	0.00
<i>Corophium</i>	0.00	0.00	20.20	6.30	0.00	0.00
<i>Leptocheilia</i>	0.00	0.00	1.30	1.30	0.00	0.00
Included as "Harpacticoida", above, are:						
Harpactoida	688.90	1,412.30	271.50	396.50	5,359.30	6,716.50
<i>Nannopus</i>	0.00	0.00	351.00	42.90	6,963.00	1,725.50
<i>Tach. triang.</i>	0.00	0.00	6.30	10.10	152.30	599.60
Laophontidae	0.00	0.00	0.00	0.00	4,454.70	4,677.40
<i>Amphiascus</i>	33.30	79.50	1.30	0.00	9.90	23.50
<i>Robertsonia</i>	0.00	0.00	0.00	1.30	22.20	39.50
<i>Stenhelia</i>	0.00	0.00	11.40	50.50	0.00	0.00

Appendix B—cont.

OAKLAND BAY

TAXA	STANDARD DEVIATION					
	APRIL		MAY		JUNE	
	GRAVEL	NETTED	GRAVEL	NETTED	GRAVEL	NETTED
Total Abundance	3,122.13	9,620.13	2,709.57	1,998.63	16,613.33	17,405.00
Harpacticoida	793.21	1,452.65	855.71	515.93	14,841.02	14,139.38
Ectinosomatidae	82.00	429.30	0.00	93.50	972.10	3,932.90
<i>Harp. uniremis</i>	495.20	430.70	345.30	380.80	152.10	213.40
<i>H. spinulosus</i>	11.60	13.30	8.40	11.70	46.80	237.40
H. un. gr. copep.	1,336.50	1,185.70	1,676.50	1,333.80	201.80	81.90
<i>Zaus</i>	0.00	0.00	8.40	14.20	0.00	0.00
<i>Tisbe</i>	2,340.30	8,722.10	151.80	327.90	64.20	136.90
<i>Dactylopodia</i>	115.40	140.00	97.30	99.90	1,402.30	623.10
<i>Leucon</i>	0.00	0.00	38.10	48.50	436.00	1,370.40
<i>Lamprops</i>	8.30	9.50	0.00	0.00	0.00	0.00
<i>Cumella</i>	24.50	13.30	0.00	18.60	51.00	69.60
<i>Tanais</i>	137.40	90.20	279.60	150.10	1,300.00	1,326.10
Gammaridea	125.80	93.50	55.40	54.20	413.10	885.10
<i>Paracalliopiella</i>	0.00	9.50	0.00	0.00	0.00	0.00
<i>Corophium</i>	69.70	69.40	0.00	0.00	1,031.90	1,413.40
<i>Eogammarus</i>	26.00	58.20	0.00	0.00	0.00	0.00
<i>Corophium</i>	0.00	0.00	48.10	21.50	0.00	0.00
<i>Leptocheilia</i>	0.00	0.00	8.40	8.40	0.00	0.00
Included as "Harpacticoida", above, are:						
Harpactoida	671.70	1,106.10	209.30	355.10	6,695.70	8,813.20
<i>Nannopus</i>	0.00	0.00	712.30	95.00	8,264.70	1,793.40
<i>Tach. triang.</i>	0.00	0.00	29.90	42.00	249.60	988.70
Laophontidae	0.00	0.00	0.00	0.00	3,718.30	3,352.30
<i>Amphiascus</i>	59.70	135.20	8.40	0.00	38.00	104.90
<i>Robertsonia</i>	0.00	0.00	0.00	8.40	64.20	136.40
<i>Stenhelis</i>	0.00	0.00	75.40	244.90	0.00	0.00