



Padilla Bay

National Estuarine Research Reserve

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**Trophic linkages from epibenthic crustaceans
in littoral flat habitats: Seasonal and regional
comparisons**

Charles A. Simenstad, Jeffrey R. Cordell, Kurt L. Fresh, and Mark Carr

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October 1995

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**TROPHIC LINKAGES FROM EPIBENTHIC CRUSTACEANS
IN LITTORAL FLAT HABITATS:
SEASONAL AND REGIONAL COMPARISONS**

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Abstract

Investigators at Fisheries Research Institute (FRI), University of Washington (UW), in collaboration with cooperative investigators from the State of Washington's Department of Fisheries, investigated the trophic importance of epibenthic crustaceans in littoral eelgrass (*Zostera marina*) habitats in the Padilla Bay National Estuarine Research Reserve (PBNERR), two other national estuarine research reserves (South Slough, Oregon, and Elkhorn Slough, California), and a number of other coastal estuaries within this zoogeographic province. The objectives of this study were to examine spatial and temporal variability in eelgrass epibenthic crustacean prey resources and predation upon them by epibenthic-feeding fishes at PBNERR, and zoogeographic variability among the other two NERR sites and other coastal estuaries. These investigations compared: (1) taxa composition and density of epibenthic crustaceans over a broad distribution of eelgrass habitat in PBNERR; (2) principal epibenthic crustacean prey of epibenthic-feeding fishes over spatial scales in PBNERR; (3) epibenthic crustacean assemblages and their importance as fish prey in eelgrass habitats of other NERR sites and selected coastal estuaries. Epibenthic crustaceans were sampled from the eelgrass habitat with an epibenthic pump and from eelgrass microhabitats (eelgrass sections) by sampling epiphytes from eelgrass blades. Fish were sampled from adjacent eelgrass habitats by beach seine. Despite that fact that the occurrence of prey organisms consumed by fish (juvenile chum and chinook salmon, shiner perch, Pacific herring, English sole, surf smelt) rearing in the eelgrass habitats shifted among the different locations in one estuary (PBNERR), and across large spatial scales (i.e., zoogeographic) we found that many of the same prey taxa were eaten regardless of the estuary. Spatial variability among the eelgrass habitats within Padilla Bay was reflected in the composition of epibenthic crustaceans. Higher consumption of harpacticoid copepods by fish caught in the interior of the eelgrass habitat (slough sites) corresponded with our results showing higher abundances of prey harpacticoids in these areas, and particularly those associated with eelgrass epiphytes. Our results from zoogeographic pump and eelgrass blade samples were marked by large differences in both species composition and abundances of single taxa across the area studied. A suite of harpacticoid copepods were uniquely associated with eelgrass blade surfaces or epiphytic microhabitats, including the genera *Porcellidium*, *Scutellidium*, *Zaus*, *Harpacticus*, *Dactylopusia*, *Diarthrodes*, *Mesochra*, and *Heterolaophonte*. While many eelgrass-associated harpacticoid taxa occur across the range of locations, often a given site was dominated by one or a few of these taxa, and the dominant taxa often differed among estuaries. Despite this variability, a few selected genera of harpacticoids (*Harpacticus uniremis* group, *Tisbe* spp., *Zaus* spp., *Dactylopusia* spp.) often comprised dominant portions of the diets of epibenthic-feeding fishes throughout the zoogeographic scope of our investigations. Thus, despite inherent spatial variability in epibenthic prey assemblages, predator-prey linkages to fishes often appear to be constrained to a few discrete harpacticoid copepod genera. A more thorough understanding of the habitat and microhabitat requirements of these unique "foundation" prey taxa in eelgrass habitats is warranted.

Introduction

In this report, we describe results of studies to evaluate spatial and temporal variability in the community structure and predator-prey linkages of epibenthic crustaceans occurring in littoral eelgrass (*Zostera marina*) habitats of the Padilla Bay National Estuarine Research Reserve (PBNERR) and other Pacific Northwest-northern California estuaries. Our objectives in these studies were to: (1) examine spatial variation in epibenthic crustacean assemblage structure and temporal and spatial variation in trophic linkages to fishes at PBNERR; and, (2) compare the habitat, microhabitat, and trophic associations found in the PBNERR with similar habitats in coastal estuaries of the same zoogeographic region, including two other NERR estuaries (South Slough, Oregon [SSNERR]; Elkhorn Slough, California [ESNERR]).

These investigations were prompted by earlier Padilla Bay NERR studies (Simenstad *et al.* 1988) that identified specific epibenthic crustaceans associated with eelgrass (*Zostera marina*) habitats which were important in the diets of fishes rearing in the estuary. The underlying goal of the subsequent studies described herein was to investigate whether these or other strong predator-prey linkages in eelgrass habitats persisted seasonally and spatially in Padilla Bay, and were representative of epibenthic crustacean-fish predator-prey associations across a diverse spectrum of estuaries from north-central California (ESNERR) to Puget Sound.

Importance of Epibenthic Crustaceans to Pacific Northwest Estuarine Food Webs

Epibenthic (or "hyperbenthic," *sensu* Hesthagen 1973 and Sibert 1981) or epiphytic crustaceans are prominent components of the bottom-associated meiofauna¹ and small macrofauna² characterizing estuaries throughout the world. These organisms inhabit the sediment-water column interface and include predominantly harpacticoid copepods, gammarid amphipods, tanaids, leptostracans, and cumaceans in the size spectrum between meiofauna and small macrofauna. As a group, epibenthic crustaceans (in particular harpacticoid copepods and gammarid amphipods) are known to constitute the primary food resources of many important estuarine and nearshore fishes in the Pacific Northwest (Simenstad *et al.* 1979). Except for several unique situations involving early estuarine residence of juvenile salmon (Simenstad *et al.* 1981; Simenstad and Wissmar 1984), the prey compositions of fish and other important epibenthic predators (e.g., crangonid shrimp) are seldom described at the prey species level of resolution. Even if prey taxa composition is known, the general lack of information on the distribution and ecology of these prey taxa does not normally allow us to predict reliably where the predator captured its prey. This lack of information severely limits our ability to relate fish production to specific nearshore habitats wherein prey production originates, and to identify the specific attributes of the habitat that promote strong trophic linkages. For example, recent evidence of extremely species/life history-specific predation by nearshore fish upon seagrass

¹ animals passing through a 0.5-mm sieve but retained on a ~0.063-mm sieve

² those passing through a 1.0-mm sieve and retained on a 0.5-mm sieve

(*Zostera* spp.) harpacticoids and gammarids suggests that these nearshore habitats may provide critical trophic pathways, in addition to refugia from predation, for many nearshore fishes unassociated with the eelgrass habitat (Simenstad and Wissmar 1984; Thom *et al.* 1984; Simenstad and Cordell, unpubl. data).

Prior Studies of Epibenthic Crustacean Assemblages and Predator-Prey Linkages in PBNERR

Information on habitat and microhabitat associations of epibenthic crustaceans in Pacific Northwest estuaries has been quite limited, although there is increasing evidence of persistent, discrete assemblage structures (Thom *et al.* 1984; Cordell and Simenstad 1988). Research funded in Padilla Bay during 1986-1987 involved a preliminary survey of epibenthic crustacean assemblages and their occurrence in fish diets during one sampling period among four estuarine habitats and three tidal stages (Simenstad *et al.* 1988). These four habitats were sampled across a littoral flat gradient: (1) saltmarsh; (2) mudflat; (3) the exotic eelgrass *Zostera japonica*; and, (4) native eelgrass, *Z. marina*. In early May 1986, the composition and standing stock of epibenthic crustacean assemblages were sampled over one tidal cycle. We used sampling techniques which determined those taxa which remained in surface sediments during tidal exposure (cores), those which were borne on the leading edge of the inundating tide (tidal inundation samplers), those found in the benthic boundary layer during tidal submergence (epibenthic suction), and the microhabitat distribution of organisms found by examining successive 10-cm sections of *Z. marina* blades colonized by epiphytes. During a previous tidal cycle, we sampled fishes in adjacent tidal channels and over the eelgrass and mudflats and samples of the most prominent taxa were retained and their stomach contents examined for overlap with the epibenthos.

Harpacticoid copepods completely dominated the crustacean meio- and small macrofauna, and subsequent, detailed analyses focused on these taxa. Sixty-two harpacticoid taxa were identified from the thirteen habitat sampling strata. The occurrence of harpacticoid copepod assemblages with habitat strata was analyzed using numerical classification (clustering) and nodal constancy techniques. The results of these analyses indicated that many assemblages could be identified uniquely with specific estuarine habitats, while other taxa and assemblages occurred or were transported throughout the littoral flat. Of particular importance was the overlap between the the distribution of littoral harpacticoids and those occurring in the fish diets. Based upon the Index of Relative Importance (Cailliet 1977), of the five species examined, harpacticoid copepods dominated the diets of four and were of almost equal importance as other prey items in the fifth fish species. Of the sixteen taxa identified from the stomach contents, three taxa comprised between 46.6% and 93.8% of the numerical composition, and between 68.2% and 97.3% of the gravimetric composition; the most prevalent taxa was *Harpacticus uniremis*, which dominated the diets of juvenile surf smelt (*Hypomesus pretiosus*), Pacific herring (*Clupea harengus pallasii*), Pacific sand lance (*Ammodytes hexapterus*) and chum salmon (*Oncorhynchus keta*), *Tisbe* sp., which dominated the diet of threespine stickleback (*Gasterosteus aculeatus*) and *Zaus* sp. which occurred in the diets of all the above.

When these apparently selective diet spectra are compared to the harpacticoid assemblage occurrence by habitat strata, it was apparent that two of the three selected harpacticoids originated from the eelgrass habitat. In fact, *Harpacticus uniremis* and *Zaus* sp. were found only in the *Zostera marina* epiphyte samples. *Tisbe* sp. was also prominent (between 50% and 70% occurrence of the assemblage taxa in the habitat strata clusters) in the eelgrass habitats but was also transported across the littoral flat all the way into the saltmarsh during the inundating tide. Thus, for two of the three prey taxa, there was strong evidence that these fish had derived a significant portion of their diet from feeding on epibenthic/epiphytic harpacticoids associated with *Zostera marina*. Other important prey taxa may have originated in eelgrass but their availability across the whole littoral flat indicated that they could have been produced by any habitat.

Given the seasonally pulsed occurrence of harpacticoid copepods, especially those which have univoltine (one generation) life histories, it was unclear whether the above data were representative of their importance to juvenile fishes in estuarine littoral flat habitats. Juvenile fishes, which pass through several morphological and ecological stanzas during their residence in estuarine "nursery" habitats, are characterized by a prey spectrum that shifts with their changing foraging capabilities and habitat affinities. There is also the possibility that these Padilla Bay data were not representative of estuarine habitats outside the Puget Sound region, such as the coastal estuaries of Washington, Oregon or northern California. With these questions in mind, we tested the generality of these results across a longer time scale in Padilla Bay (early spring through summer), across multiple habitats in Padilla Bay, and in comparable estuarine habitats on the outer coasts. To our knowledge, this is the first comprehensive (in zoogeographic terms) high resolution test of trophic linkages among estuarine fishes. It also represents the first comparison of predator-prey interactions among multiple NERR sites.

Hypotheses

Within the context of the basic question of the importance of eelgrass-associated crustaceans in the diets of estuarine fishes, we formulated the following null hypothesis:

- H₀: Epibenthic crustaceans, and especially the harpacticoid copepods *Harpacticus uniremis*, *Tisbe* sp. and *Zaus* sp., are not comprehensively important in the diets of estuarine littoral flat fishes in the Pacific Northwest.

The term "comprehensive" as used here refers to the winter-spring season when many species of juvenile fishes typically occupy shallow, estuarine habitats. This typically occurs between March and June; by late June and July many fish have either moved out of shallow water or their diets have changed to macroinvertebrates and fishes. We also posed two subhypotheses related to two disparate scales of spatial variability, at the level of epiphyte assemblages on the eelgrass blades and among eelgrass habitats across different estuaries in northern Pacific coast region.

- H₁: The dominant epibenthic prey of fishes are uniquely associated with particular eelgrass epiphytes;*
- H₂: There are no differences in epibenthos habitat and trophic linkages to fishes among comparable estuaries in the region.*

The study region included estuaries from northern Puget Sound (represented by PBNERR) to northern California, based on the basis of the general zoogeographic transition between a central and southern faunal at Cape Conception (Stephenson and Stephenson 1972).

Objectives

The following research objectives were designed to address these null hypotheses:

1. Describe the spatial variation in the species/life history stage assemblage structure of epibenthic crustaceans in discrete estuarine habitats and microhabitats in Padilla Bay by;
 - a. Sampling epibenthic crustacean assemblages in *Zostera marina* habitats during tidal submersion, when they are available as prey for fishes utilizing these habitats; and,
 - b. Sample the epibenthic crustacean assemblages at different locations, representing the potential scope of spatial variability in eelgrass habitat in the Bay;
2. Examine both the spatial and temporal variation in predation on discrete epibenthic crustacean assemblages by juvenile fishes in Padilla Bay; and,
3. Compare epibenthic crustacean assemblage structure, eelgrass habitat and epiphyte microhabitat distributions, and the relative importance of identifiable epibenthos assemblages as prey of eelgrass fishes in other, comparable estuaries by conducting synoptic survey of coastal estuaries encompassing two other NERR sites on the north Pacific coast--South Slough (Coos Bay, Oregon) and Elkhorn Slough (Monterey Bay, California).

Methods and Materials

Sampling Design

Sampling of epibenthos, eelgrass epiphytes and fishes in Padilla Bay was conducted approximately every three weeks between 14 March and 12 September 1989. Sampling for temporal variability occurred at an established site on Indian Slough along a transect representative of the littoral-shallow sublittoral gradient and habitat composition in Padilla Bay (Fig. 1). To evaluate temporal variability, fish were collected at this site on ten occasions between mid-March and mid-September 1989. To assess areal variability, fish were collected at five other locations (Fig. 1) on 24-25 May 1989.

The synoptic survey of epibenthic crustacean habitat and food web linkages in 13 locations along the West Coast of United States (4 in California, 4 in Oregon and 5 in Washington (Fig. 2) occurred between 25 May and 8 June 1989 employing techniques

similar to that performed in Padilla Bay in the previous NERR study (Simenstad *et al.* 1988). The sites included the three West Coast NERR sites, at Padilla Bay, WA, South Slough, OR, and Elkhorn Slough, CA.

Sampling Methodology

Epibenthos Sampling Methods

Two techniques were used to assess eelgrass epifauna: (1) epibenthic suctioning during tidal submergence; and, (2) sectioning eelgrass (*Z. marina*) blades with associated epiphyte growth. Sampling was repeated at each site during subsequent tidal submergence (flood tide) when approximately 1 m of water covered the habitat (except in the case of the high marsh, which was sampled at a shallower depth). Epibenthic crustaceans in the laminar or lower turbulent layer adjacent to the sediment surface were sampled with a battery-powered epibenthic suction pump (epibenthic pump equipped with 0.130-mm mesh screening over replacement water ports) which has been shown to effectively sample most epibenthic crustaceans in similar habitats (C. A. Simenstad and J. R. Cordell, unpubl.; Thom *et al.* 1986). Eelgrass blades were sequentially fractionated into 10-cm lengths and preserved *in toto* with epiphytes intact. In all cases, five replicate samples were collected and preserved in buffered 10% formalin. Epiphyte subsamples were retained and preserved for taxonomic analyses and measurement of biomass (dry weight).

Predator Sampling Methods

Epibenthic-feeding fishes were sampled along the habitat-gradient transect during the sampling period, i.e., within one day of the epibenthic crustacean sampling. Based upon previous information on fish species occurrence in Padilla Bay and adjacent region (Miller *et al.* 1980; R. Wissmar and C. Simenstad, UW School of Fisheries class field sampling; Simenstad *et al.*, in prep. a & b) and their typical diet composition (Simenstad *et al.* 1979; C. Simenstad and J. Cordell, unpubl. data), at least ten species of fishes were assumed to be available in sufficient abundance for diet analysis during the sampling period. During the synoptic survey, subsamples were retained from the fish catches which permitted sample sizes sufficient (e.g., 5-10) for quantitative stomach contents analyses; subsequently, species represented in all estuaries, if available, were selected for analysis, including: (1) English sole, *Pleuronichthys (Parophrys) vetulus*; (2) starry flounder, *Platichthys stellatus*; (3) staghorn sculpin, *Leptocottus armatus*; (4) shiner seaperch, *Cymatogaster aggregata*; and, (5) threespined stickleback, *Gasterosteus aculeatus*.

We employed standardized beach seine sampling (including those used for previous fish investigations in the region, e.g., Miller *et al.* 1980) to obtain quantitative (520 m²), replicated collections. Sampling effort was standardized or discretely estimated such that catches were converted to density and standing crop estimates on an areal or volumetric basis. All catches were sorted to species/life history stage, counted, and weighed, either in the field (usually in the case of large specimens which are released alive) or preserved in buffered 10% formalin for later

processing in the laboratory. Samples or subsamples (~5 of each species, size interval, life history stage) of the "target" predators were preserved in 70% isopropanol alcohol for later processing in the laboratory.

Laboratory Methodologies

Epibenthic Crustacean Sample Processing

All epibenthic crustacean samples were analyzed to provide the following basic data on assemblage composition and standing stock: (1) species/life history stage; (2) density of (1) by benthic or eelgrass area and epiphyte biomass (dry weight); and, (3) standing crop of (1) by area or volume, measured by damp wet weight.

Sample processing followed laboratory protocols comparable to those followed in the prior study at PBNERR (Simenstad *et al.* 1988). Epibenthic pump samples were sieved through a 0.125-mm sieve, and panned if necessary to separate the organisms from sediments. When present, epiphytes (diatoms and small macroalgae) will be separated from seagrass blades and macroalgae and sieved through the same nested screens. All samples were examined *in toto* or, if necessary because of high abundance, subsampled using a Hensen-Stempel pipette. Subsequently, organisms were sorted under an illuminated stereo microscope, identified, enumerated and weighted to species and life history stage (e.g., nauplii, copepodid, male, gravid female, etc.).

Predator Stomach Contents Analyses

For each species/life history/size interval of predator, stomach contents were analyzed to provide the following basic data on prey composition and occurrence:

- (1) taxa/life history stage;
- (2) frequency of occurrence (%) of (1) in sample;
- (3) abundance (number) per stomach;
- (4) biomass (damped wet weight) per stomach;
- (5) relative numerical and gravimetric composition (%) over sample;
- (6) relative (scaled) stomach fullness; and,
- (7) relative (scaled) state of contents digestion

To accomplish this, we systematically analyzed fish stomach contents according to standardized procedures which quantify the occurrence, numerical, and gravimetric composition of prey organisms. This methodology has been utilized extensively in quantitative descriptions of food habits of estuarine and coastal fishes throughout the Pacific Northwest (e.g., Simenstad *et al.* 1979a) and thus provides an extensive, comparable data base

We measured total or fork length, depending upon taxa, and wet weight (gr) of all fish. In processing individual stomach contents, all prey items were sorted to lowest phylogenetic level and life history stage possible under an illuminated dissecting microscope. Each category was enumerated and weighed. Stomach fullness was evaluated visually and coded from 1 (empty) to 7 (distended); similarly, digestion of stomach contents was evaluated visually and coded from 1 (all unidentifiable) to 6 (no

digestion evident). Taxonomic identifications vary according to the stage of contents digestion and the state of the taxonomic literature for the particular prey taxa.

Data Management, Manipulation, and Statistical Treatment

Epibenthic Crustacean and Predator Collection and Stomach Contents Data

All field collection and laboratory data were recorded on standardized (FRI estuarine-coastal marine fish/zooplankton formats) forms which utilize the format #100 series of the National Oceanographic Data Center (NODC). This format system has been utilized in almost all FRI sampling in Puget Sound and coastal estuaries since 1976, which provides for a widely comparable data base. The system also utilizes the NODC taxonomic code, a ten-digit code which enables encoding of all organisms to any phylogenetic level and life history stage.

Tabulation and basic statistical description of epibenthic crustacean, fish and macroinvertebrate catches, and predator stomach contents data was produced with FRI computer programs SUPERPLANKTON, CATCHSUM, and GUTBUGS/IRI, respectively, specifically developed for NODC-formatted data.

Definition of Prey Importance

Importance of prey taxa to the overall diet of fish predators was measured using the Index of Relative Importance (Pinkas *et al.* 1971; Cailliet 1977) as modified by substitution of prey biomass for prey volume. These data were standardized by calculating the proportion which each prey taxa constitutes of the total IRI (% Σ IRI).

Reference Collection

All species unique to our existing reference collection were catalogued and added to it. In addition, a representative reference collection of all species is available to be installed at the Padilla Bay National Estuarine Research Reserve Interpretive Center, and those collected from the other NERR sites are available for their collections.

Results

Fish Assemblage Composition and Diet

Padilla Bay Temporal Variability

A total of 22 fish species were captured between mid-March and mid-September 1989 (see Appendix I for latin binomial and common fish names, Appendix II for basic catch-per-unit-effort [CPUE] data). Species richness was lowest in March when only five species occurred, increased to a high of 16 in July and then declined to 7 by the time of the last collection in mid-September. Fish assemblages on each sampling date were a mixture of pelagic and demersal species. Most species caught were demersal whereas most individual fish were pelagic, reflecting the tendency of the pelagic fish to occur in schools. English sole was the only species that occurred on all sampling dates, while Pacific sand lance occurred on 9 of 10 sampling dates.

Density was low in March, increased during the spring, and peaked in July. The numerically most abundant species in late winter and early spring were postlarval and juvenile surf smelt and Pacific sand lance. In late spring, threespine stickleback, shiner perch, and Pacific herring were the dominant species while shiner perch was most abundant throughout the summer.

Padilla Bay Spatial Variability

A total of eighteen species of fish were caught at the six sites sampled throughout Padilla Bay in May (Table 1). Species richness at sites varied from 8 to 13. Over 50% of all species caught were rare, i.e., occurring at only one or two sites. Pacific herring and English sole occurred at all six sites while shiner perch, threespine stickleback, surf smelt and chinook salmon occurred at five of the six sites. The numerically dominant species were three species of schooling fish--Pacific sand lance, surf smelt, and shiner perch--representing over 88% of the total number of all fish collected. The distribution of the most abundant fish was also patchy, perhaps reflecting their schooling nature. Typically, large catches of one species occurred at only one site as the most abundant fish at five of the six sites was not the same.

Zoogeographic Variability

Over all sites (including Padilla Bay), 59 different species were captured in late May and early June (Appendix II). The species richness of eelgrass habitats in the 13 estuaries ranged from 7 at the Coquille River estuary, OR to 27 in Tomales Bay, CA (Table 2). In general, estuaries in California had higher species richness (ave., 20.25) than did estuaries in Oregon (ave., 16.0) and Washington (ave., 17.3) (Table 2).

Total fish density (no. fish m⁻²) was greatest in Tomales Bay and least in Netarts Bay (Table 2). In addition, density was lower in Oregon estuaries than in estuaries of California and Washington. The four lowest fish densities occurred in the four Oregon estuaries. Mean density from the four Oregon estuaries was 0.41, compared to 1.16 and 0.95 at California and Washington sites, respectively.

Densities of most species were low (<10/haul). The three most abundant species in each estuary comprised between 58% and 97% of the total catch (Table 3). The fish communities were comprised of a mix of pelagic and demersal species with most of the species caught classified as demersal (22% pelagic vs. 78% demersal) while most individual fish caught were pelagic (70% pelagic vs. 30% demersal). The percentage of pelagic species caught at individual sites ranged from 11% to 46%. Most individual fish were juveniles as few adults of any species were found.

Of the 59 species collected, only shiner perch occurred in all estuaries (Appendix II). In addition, shiner perch was the most abundant species; shiner perch constituted over 50% of all fish caught. Shiner perch also ranked as either the first, second or third most abundant species in 10 of the 13 estuaries. Other frequently occurring species included Pacific staghorn sculpin which were found in 12 of 13 estuaries, English sole (12/13 sites), speckled sanddab (10/13 sites), surf smelt (9/13 sites), and threespine stickleback (8/13 sites). Snailfish was the only species that occurred in one estuary; all other species occurred in at least two.

The most pronounced geographical shift in species composition was an increase in the numbers of embiotocid species and density of embiotocids moving from north to south (Table 4). For example, dwarf perch, black perch and kelp perch were only found in California estuaries while white perch was most abundant in California estuaries and only found in Willapa Bay and Yaquina Bay outside of California.

Epibenthic Crustacean Assemblages

Padilla Bay Spatial Variability

Harpacticoid copepods dominated the epibenthic pump samples from the six *Z. marina* sites in Padilla Bay. They ranged from 58% of the total invertebrate abundance at the Hat Island channel site to 84 % of the total abundance at the Bay Channel site. The only other invertebrate group that consistently comprised more than five percent of the total abundance were cyclopoid copepods which ranged from one percent at the Bay Channel site to 16% at the Hat Island channel site (Appendix III). Abundances of epibenthic invertebrates differed considerably between the six sites. Particularly striking were high abundances of "other" harpacticoids and juvenile fish prey taxa (the harpacticoid genera *Harpacticus*, *Tisbe*, and *Zaus*, and the cumacean *Cumella vulgaris*) at Joe Leary Slough and the two Indian Slough sites, as compared with the densities of these taxa at the outer sites (Fig. 3).

Zoogeographic Variability

Epibenthic Pump

Harpacticoid copepods also dominated epibenthic pump samples from *Z. marina* in the eleven coastal estuaries that we sampled. They ranged from 64% of the total invertebrate abundance at Gray's Harbor to 99 % of the total abundance at Tomales Bay (Appendix IV). In some cases the harpacticoid fauna was dominated by one or two species, which were not consistent between estuaries: Padilla Bay was dominated by *Tisbe* spp. and *Zaus* spp., Netarts Bay by *Zaus* spp., the Coquille River estuary by *Microarthridion littorale* and *Cumella canadensis*, Tomales Bay by *Harpacticus obscurus* group and *Zaus* spp., San Francisco Bay by *Parathalestris californica*, and Elkhorn Slough by *Tisbe* spp. In Gray's Harbor, Willapa Bay, Yaquina Bay, South Slough NERR, and Humboldt Bay, harpacticoid density was more evenly distributed among a number of taxa (Fig. 4, Appendix IV). Abundances of prominent fish prey invertebrates varied greatly, often in orders of magnitude, between sampling locations (Fig. 4). Two trends in the latitudinal abundance of fish prey crustaceans appeared in our data: first, the cumacean *Cumella vulgaris* did not occur in any estuaries south of Humboldt Bay (Fig. 5); second, *Harpacticus* spp. in the *uniremis* group did not occur south of the Coquille River estuary, while those in the *obscurus* group persisted (Fig. 6).

Eelgrass Sections

Epibenthic crustaceans collected from eelgrass blades were also dominated by harpacticoid copepods, except at South Slough NERR, where Nematoda were the dominant taxon. Harpacticoids ranged from 21% of the total invertebrate abundance at South Slough to 98% of the total abundance at Humboldt Bay (Appendix V). Eelgrass

blade fauna was qualitatively much different than that from the epibenthic pumps in many cases, in that it was often dominated by specific epiphytic taxa that were not abundant in the pump samples: Gray's Harbor was dominated by *Dactylopusia* spp., Willapa Bay by *Heterolaophonte longisetigera* and *Diarthrodes* sp., Yaquina Bay by *H. longisetigera* and *Mesochra* sp., South Slough by *Robertsonia* cf. *knoxii*, *Mesochra* sp., and *Diarthrodes* sp., the Coquille River estuary by *Harpacticus arcticus*, Humboldt Bay by *Zaus* spp., and Elkhorn Slough by *Heterolaophonte variabilis* and *Dactylopusia* spp. (Appendix V). Four sampling sites had eelgrass blade faunas that were similar to those from epibenthic pump fauna from the same site: these were Padilla Bay, Netarts Bay, Tomales Bay, and San Francisco Bay. The latitudinal trend in *Harpacticus* spp. abundances was similar to that in the pump samples: *Harpacticus* spp. in the *uniremis* group did not occur south of Humboldt Bay, while those in the *obscurus* group were abundant throughout the sampling region (Appendix V).

Densities of the four harpacticoid taxa (i.e., *Harpacticus uniremis* group, *Zaus* spp., *Tisbe* sp., *Dactylopusia* spp.) that consistently appeared prominently in the diets of fish along the estuarine zoogeographic gradient displayed some latitudinal trends in the eelgrass section samples (Fig. 7). *Harpacticus uniremis* group species were distributed principally in the northern estuaries, primarily between Netarts Bay and Padilla Bay NERR. *Zaus* sp. densities increased from north to south, with the maximum in Humboldt Bay. Although the common juvenile fish prey harpacticoid *Tisbe* was abundant in pump samples, where it often comprised more than 25% of the total harpacticoid numbers (Fig. 5), in eelgrass blade samples, it never comprised more than 6% of the harpacticoid numbers, and was sometimes absent from these samples when it occurred in the pump samples (Appendix 3). Similarly, there was no evident trend in *Dactylopusia* spp. densities.

Epiphyte Composition and Standing Stock

Padilla Bay Temporal Variability

Z. marina epiphyte standing stock (g dry wt m⁻² eelgrass blade surface) increased progressively over the sampling period, from 0.35 g dry wt m⁻² in mid-March to 8.28 g dry wt m⁻² in mid-September (Fig. 8). Given a comparatively consistent dry weight (1.19±0.73 g dry wt) of the 10-cm eelgrass sections over that time, the relative epiphyte load (percentage of eelgrass dry wt) followed approximately the same trend, from 1.2±0.4% in mid-March to 48.5±31.5% in mid-September (Fig. 9).

Algae were the most prevalent epiphytes, including: unidentifiable diatoms and the filamentous diatoms, *Navicula*; the green algae *Enteromorpha* sp. and *Monostroma* sp.; and the red algae *Polysiphonia* sp. and *Antithamnion* sp. Animals were also included among the epiphytes, including encrusting bryozoans, hydrozoans and egg masses (primarily gastropod). Diatoms dominated the epiphyte assemblage standing stock, increasing throughout the period, except in early May, when *Navicula* (1.13 g dry wt m⁻²) exceeded the diatom (0.73 g dry wt m⁻²) standing stock (Figs. 10-12). The mean diatom standing stock was 0.18±0.27 g dry wt m⁻² over the entire period, with the maximum (6.67±3.89 g dry wt m⁻²) occurring in mid-September. Except for *Navicula*, other components of the epiphyte assemblage did not appear until late June and generally

averaged less than 1 g dry wt m⁻², although bryozoans contributed 1.58±2.81 g dry wt m⁻² in mid-July (Fig. 11). Diatoms constituted an additional 1.24% (mid-March) to 39.34% (mid-September) of the eelgrass biomass (average, 1 s.d.: 12.8±13.6%), while only a few of the other epiphyte components approached 5-10% (i.e., bryozoans, *Navicula*, *Enteromorpha*, *Polysiphonia*), and few exceeded 1% (i.e., *Monostroma*) (Figs.13-15).

Zoogeographic Variability

Epiphyte standing stock along the latitudinal estuarine gradient reached maxima at 7.6-8.4 g dry wt m⁻² at San Francisco Bay, South Slough NERR, and Yaquina Bay (Fig. 16). The other estuaries ranged between a minimum of 0.2 g dry wt m⁻² at Jamestown, 1.4-2.5 g dry wt m⁻² at six estuaries (Padilla NERR, Richmond Beach, Grays Harbor, Netarts Bay, Humbolt Bay, Tomales Bay), and intermediate levels (3.3-4.8 g dry wt m⁻²) at Willapa Bay (Tokeland), Coquille River and Elkhorn Slough. As the 10-cm eelgrass segment biomass was also comparable along this gradient (0.94±0.56 g dry wt m⁻²), the rank order of epiphyte percentage of eelgrass biomass followed the same patterns (Fig. 17).

Epiphyte composition varied among the estuaries but did not appear to explain differences in epiphyte standing stock (Fig. 18). In addition to the epiphyte constituents noted at Padilla Bay NERR, we also commonly found *Smithora*, *Membranipora*, and *Ceramium* among the epiphytes at some of the other estuaries. Diatoms completely dominated eelgrass epiphytes at five estuaries, constituting 86-100% of the epiphyte standing stock (San Francisco Bay, Coquille River, South Slough NERR, Jamestown and Padilla Bay) or comprised the predominant epiphyte component at four other estuaries (Tomales Bay, Willapa Bay, Grays Harbor and Richmond Beach). At the other estuaries, *Navicula* (i.e., Yaquina Bay), bryozoans (Humbolt Bay), *Smithora* (Netarts Bay), and *Monostroma* (Elkhorn Slough) were more prevalent.

The ratio of diatom to eelgrass biomass also varied by estuary, with six estuaries showing eelgrass with higher diatom epiphyte loads than Padilla NERR at the same time (Fig. 19). Diatom epiphyte loads at San Francisco Bay (ave. 65%) and South Slough NERR (72%) were higher than ever appeared at Padilla Bay NERR during the peak epiphyte (diatom) biomass in September.

Temporal and Spatial Variability in Fish Prey Selectivity

Zoogeographic Variation

Based on their relative abundance and distribution across many locations both within Padilla Bay and along the coast, we concentrated our assessment of latitudinal variation in fish diets on English sole, shiner perch, and chinook salmon. We focus here on estuaries other than Padilla Bay which is covered in greater detail in following sections. Shiner perch that were examined ranged in length from 86 to 108 mm and specimens tended to larger moving from north to south. Although shiner perch occurred in all but one estuary, a high proportion of the stomachs we examined were empty; at some sites, all the shiner perch specimens that we examined were empty. While there were differences in food items eaten by shiner perch in the different estuaries, several prey were consistently eaten in all estuaries. Harpacticoid copepods were eaten by shiner perch in all estuaries and were the major prey in 5 of 7 estuaries where there were sufficient samples. Many of the most

important harpactoidocid taxa were the same including *Tisbe* sp., *Harpacticus* spp, and *Zaus* spp. Other important prey of shiners included gammarid amphipods and cumaceans.

Juvenile English sole stomachs were analyzed from 9 estuaries; some English sole from all these estuaries had food in their stomachs. There was a considerable range in the size of English sole specimens that we examined, 49 mm to 98 mm, which makes a comparison of prey selection problematic. Some of the differences in diet that we observed could be due to a difference in fish size. As was the case with shiner perch, there was a geographic trend in size of specimens that we analyzed with, the fish becoming progressively smaller moving from south to north. Harpacticoids again figured prominently in the diets of English sole in most estuaries and included the same taxa in many of the estuaries, especially *Tisbe* sp., *Harpacticus* spp and Ectinosomidae. Polychaetes were also a major diet item in some estuaries as were cumaceans and gammarid amphipods. There was general tendency for harpacticoids to be more prevalent in diets with increasing latitude, perhaps reflecting the change in fish size.

Juvenile chinook salmon stomachs were analyzed from three Washington estuaries: Willapa Bay, Grays Harbor, and Padilla Bay. Chinook were comparably sized in the three estuaries. Chinook diets varied a great deal between estuaries. In Willapa Bay, the fish ate cumaceans, insects and amphipods while in Grays Harbor, fish ate almost entirely barnacle larvae. In Padilla Bay, insects and cumaceans dominated diets.

Temporal Variability

To analyze temporal variability in fish diets at the Upper Indian Slough sampling site in Padilla Bay (Indian Slough), we selected species that were caught in at least two months, that had at least four full stomachs in each month and had comparably sized specimens. Chinook salmon, chum salmon, English sole, and Pacific herring met these criteria (Table 5).

Chinook salmon stomachs were analyzed from May, June and July. The average monthly length of the specimens analyzed ranged from 67.2 to 75.6 mm FL while the average monthly weight ranged from 2.6 to 4.4 g. In all three months, insects were an important component of the diet (Figure 6). They were the major part of the diet in July, accounting 78% of the diet (Σ IRI). At least eight different taxa of insects were identified in July, including dipterans, homopterans, and brachycerans. In May, insects represented 49.7% of the Σ IRI, with cumaceans and fish the other main prey items; in June, insects were 25.9% of the Σ IRI. The most important dietary component in June was gammarid amphipods, primarily *Pontogenia* spp. and *Anisogammarus* spp.

English sole stomachs came from four sampling periods--March through June. While all the English sole analyzed were young of the year, there was an increase in size of the fish we analyzed from 49.2 mm SL in March to 68.6 mm SL in June. English sole ate only eight taxa, all of which were epifaunal or infaunal (Figure 7). The diet of English sole was primarily polychaetes in March and April (86.8% and 70.1% Σ IRI, respectively), tanaids (mostly *Leptocheilia*) and bivalves in May (a combined 67.6% Σ IRI), and largely harpacticoids and gammarids in June (a combined 65.6% Σ IRI). The dominant harpacticoids included several species of the genus *Harpacticus* and *Robertsonia* spp.

Chum salmon stomach samples were obtained in April, May, and June. The average fork length of specimens varied little, ranging from 53.4 mm to 55.0 mm. In April, the

chum salmon ate almost entirely crustaceans of the order Ploecyemata (Table 8). In both May and June, on the other hand, chum salmon consumed mostly harpacticoids and gammarid amphipods; 88.3% and 82.2% Σ IRI in May and June, respectively, was comprised of harpacticoids and gammarid amphipods. In May and June, the most important harpacticoid in diets was *Harpacticus uniremis* (48.5% and 47.7% Σ IRI, respectively).

The diets of Pacific herring were analyzed from May, June, and July, with the mean size of specimens ranging from 51.5 in May to 60.0 mm in July. The major food item of Pacific herring was copepods. In May, this included calanoids (34.9% Σ IRI), harpacticoids (35.5% Σ IRI), and cyclopoids (21.2% Σ IRI) (Table 9). However, in June and July, 99.5% and 91.9% of the prey IRI was comprised of harpacticoids, respectively (Table 9). Thirty-four taxa of harpacticoids were identified from the Pacific herring stomachs.

Spatial Variability

Spatial variability in diets within Padilla Bay were evaluated for five species--chinook salmon, chum salmon, Pacific herring, English sole and surf smelt (Table 10). These species met the following criteria: 1) collected at two or more sites; 2) at least 4 full stomachs; and 3) the size of the individuals of each fish within a species was comparable. Spatial variability in chinook salmon diets could be evaluated at two sites- the Upper Indian Slough site and a site in mid-Padilla Bay-Hat Island Channel (Table 11). The length and weight of chinook salmon examined ranged from 61-70 mm FL and 1.8-2.8 gr. Diets exhibited considerable variability at the two sites. At the Indian Slough station (the standard sampling site), chinook salmon ate primarily cumaceans and insects while at the mid-Padilla site, they ate primarily crab larvae and fish (Table 11).

Stomachs of Pacific herring also came from Hat Island Channel and Upper Indian Slough sites (Table 12). The herring that were examined ranged in length from 48-55 mm SL while their weight ranged from 0.3 to 2.5 g. The two major food items eaten at each site were harpacticoids and calanoids, although the importance of each varied between sites. At the Hat Island Channel site, calanoids accounted for 69.6% of the prey IRI while harpacticoids were 26.4%. In contrast, harpacticoids were 21.2% of the prey IRI at the Indian Slough site and calanoids were 35.3% of the Σ IRI (Table 12). Other important prey at the Indian Slough site were cyclopoid copepods primarily of the genus *Corycaeus*.

Chum salmon stomach samples came from three sites--two sites in Indian Slough and one in mid-Padilla Bay (Table 13). The chum salmon ranged in length from 47 to 57.5 mm FL and in weight from 0.9 to 1.4 g. Juvenile chum consumed harpacticoid and calanoid copepods (49% IRI) and fish larvae (27.4% IRI) at the mid-Padilla Bay site. In contrast, at the two sites sampled in Indian Slough, harpacticoids were the dominant prey eaten, accounting for 83.2% and 72.6% of Σ IRI (Table 13).

We examined English sole diets from two sites sampled in Indian Slough; the fish ranged in length from 58.5 mm SL to 72.9 mm SL and in weight from 1.5 to 3.23 g (Table 14). At the Lower Indian Slough site, the two primary prey taxa of the English sole were harpacticoids (64.7% Σ IRI) and tanaids (14.1% Σ IRI). At the Upper Indian Slough site, tanaids and bivalves accounted for a combined 67.6% of the Σ IRI (Table 14).

Stomach samples used to assess spatial variability in surf smelt diets came from the Upper Indian Slough site and from Hat Island Channel. At Hat Island Channel, 77.1% of ΣIRI was calanoids while in the Indian Slough site, less than 1.0% of ΣIRI was calanoid copepods (Table 15). At the Indian Slough site, over 90% ΣIRI was comprised of harpacticoids while harpacticoids were less than 12% ΣIRI at the other site. The most important harpacticoids included ectinosomids, *Tisbe* sp., and *Mesochra* spp.

Epibenthic Crustacean Associations with Epiphyte Variability

Correlations between epibenthic crustaceans and epiphytes were examined to explore potential mechanisms of microhabitat and trophic support of epibenthic crustacean, and particularly fish prey, production within the eelgrass habitat. Total harpacticoid density did not relate to epiphyte standing stock (Fig. 20). Maximum ratios of harpacticoid density/epiphyte standing stock, e.g., >4000 harpacticoids/g dry wt epiphytes, appeared in three of the California estuaries (Tomales Bay, Humboldt Bay, Elkhorn Slough NERR), but other estuaries with higher epiphyte standing stock (e.g., San Francisco Bay, South Slough NERR) had intermediate harpacticoid densities.

The association between total harpacticoid densities and diatom standing stock indicated that maximal densities occurred only at the lower extremes of diatom loading on eelgrass (Fig. 21). Densities of >2500 harpacticoids/g dry wt epiphytes occurred only below 0.2 g dry wt m⁻². While this relationship was not evident for *H. uniremis* group harpacticoids, it was a prevalent trend for the other three prominent fish prey (*Zaus* spp., *Tisbe* sp., *Dactylopodia* spp.) (Figs. 22-25).

Discussion

There were several notable patterns in the appearance of epibenthic crustaceans in the diets of the fish that we examined. First, across large spatial scales (i.e., zoogeographic), we found that many of the same prey were eaten regardless of the estuary the fish were found in. Another noteworthy pattern that we found was at the scale of microhabitat within the estuary. Fish diet shifted among the different locations where the fish were collected. For example, within the Indian Slough site, harpacticoids were a more important food item of juvenile chum salmon and Pacific herring than on the outer portions of the bay (e.g., mid-Padilla Bay) where more pelagic prey were eaten such as calanoid copepods. In addition, chinook salmon ate more insects at the Indian Slough site than in the mid portions of the bay. Insects are likely more available as prey in Indian Slough because of its proximity to the terrestrial habitats that produce these food items.

Our results thus suggest that microhabitat differences play a major role in fish diet. Although foraging over a large area such as Padilla Bay, the diets of the fish we evaluated appeared to reflect variability in prey availability of the habitat within which they were captured. The high consumption of harpacticoids in Indian Slough by chum salmon reflects its location within the eelgrass habitat while the consumption of the insects by the chinook reflects the proximity of this site to the insect producing habitats. Thus, capture location may be a stronger indicator of where the fish forage than has been previously believed. This also points out that when evaluating fish diets in a diverse landscape, location will have an important influence on results of diet analyses.

Similar to previous studies of fish feeding habitats in Padilla Bay (Simenstad *et al.* 1988), epibenthic crustaceans that are produced in eelgrass habitats were a significant part of the prey spectrum of several species that we analyzed (Table 16). In particular, chum salmon and surf smelt foraged extensively on harpacticoids, and prey species that were abundant in the eelgrass blades and epiphytes were important in the diets of both species.

Spatial variability among the eelgrass habitats within Padilla Bay was also suggested by data from the epibenthic pump samples. Higher consumption of harpacticoid copepods by fish caught in the interior of the eelgrass habitat (slough sites) concurs with our results showing higher abundances of prey harpacticoids in these areas. Factors that we did not test but that may be causing these different densities within Padilla Bay are temperature, exposure, epiphyte densities, or eelgrass density.

Our results from zoogeographic pump and eelgrass blade samples were marked by large differences in both species composition and abundances of single taxa across the area studied. Whereas there appears to be a suite of eelgrass-associated harpacticoid taxa, many of which occur across the range of locations, often a given site is dominated by one or a few of these taxa, and the dominant taxa often changes between estuaries. In some cases, there is a plausible explanation for this. For example, harpacticoid fauna from the pump samples at the Coquille River estuary was completely dominated by *Microarthridion littorale* and *Coullana canadensis*: these species are characteristic of low-salinity conditions and are clear indicators that this location was influenced by fresh water at the time of sampling. At the San Francisco Bay location, the invertebrate fauna was dominated by the harpacticoid copepod *Parathalestris californica*. This species, which is common throughout the sampling region (J. Cordell, unpubl.) was rare in samples from other estuaries. One possible explanation for this is that the water at this sampling site was very turbid. Because *P. californica* is one of the largest harpacticoids, it may be especially subject to predation by small fishes. The turbid conditions may have released this species from predation by visual predators.

There were also some notable differences between the pump and eelgrass blade invertebrate samples. The genus *Tisbe*, which is a common prey item for small fishes, was abundant in pump samples from many locations, but was never abundant in eelgrass blade samples. This fits in with earlier data from Padilla Bay, in which it was demonstrated that this genus was one of the members of an assemblage that does not have a strong affinity with eelgrass foliage, and is transported between intertidal flat habitats (Simenstad *et al.* 1988). It appears from our data that there is a suite of harpacticoid copepods that are characteristic of eelgrass blade surfaces or epiphytic microhabitats. This group consists of the genera *Porcellidium*, *Scutellidium*, *Zaus*, *Harpacticus*, *Dactylopusia*, *Diarthrodes*, *Mesochra*, and *Heterolaophonte*. These are genera that reached dominance only in the eelgrass blade samples, or that occurred only in these samples. Some of these harpacticoids (e.g. the first three genera mentioned above) are morphologically adapted to the planar surfaces of the leaf blades (Hicks 1977). At least one, the genus *Diarthrodes*, is known to tunnel through the blades and stipes of macroalgae (Fahrenbach 1962). Although some of the other genera in this assemblage have been shown to be associated specifically with eelgrass microhabitats (e.g., *Harpacticus*; Simenstad *et al.* 1988; Webb 1992), we do not as yet know what attributes of individual leaves or plants (proximity to blade union, epiphyte load, senescence, flowering state, etc.) support these taxa, either as

microhabitats or through their own trophic associations with food resources within the eelgrass microhabitats.

One of the largest issues still to be resolved is how the epibenthic crustaceans become available for foraging fish. There are a number of alternative theories about the mechanisms by which epibenthic crustaceans enter the benthic boundary layer of shallow-water habitats, whether it be due to passive (e.g., resuspension) or active (e.g., behavior) means (Sibert 1981; Hicks and Coull 1983; Marcotte 1983, 1984; Kern and Taghon 1986; Palmer 1986, and others). In all probability, both physical and biological factors can be involved depending upon the habitat structure, taxa and life history stage, water velocities, food availability, predators, etc. Combined with a potential flux of truly pelagic zooplankters from the water column (Sibert 1981), the epibenthos is obviously a taxa-rich, diverse assemblage of organisms in estuarine wetland habitats. Although their importance as prey of fishes and other secondary consumers has long been appreciated (Bregnballe 1961; McIntyre and Murison 1973; Alheit and Scheibel 1982; Tito de Morais and Bodiou 1984), their complex roles as critical transformers of detrital-microbial carbon to food resources available to higher consumers are still poorly understood (McIntyre 1969; Coull 1970; Kuipers *et al.* 1981). The fact that, compared to the diverse array of epibenthic and epiphytic crustaceans that are found in eelgrass habitats, only a relatively small component of these organisms actually contributes directly to the diets of fishes foraging in eelgrass. This implies that pathways of organic matter transfer from autotrophic and heterotrophic levels of the eelgrass food web to secondary consumers may be strongly structured.

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Table 1. Catch-per-unit-effort (CPUE) of fish caught by beach seine during sampling in the Padilla Bay National Estuarine Research Reserve, 24-25 May 4-25 1989.

Fish Species	Bay Channel	Hat Island Channel	Middle Channel	Joe Leary Slough	I
Pacific herring	7.5	8.0	1.0	21.0	
Chum salmon	1.0	35.0	0	0	
Chinook salmon	5.0	18.0	0	3.0	
Surf smelt	0	6.0	5.0	1.0	
Pacific cod	0.5	0	0	0	
Shiner perch	1.0	200.0	300.0	2.0	
Snake prickleback	0	0	1.0	0	
Saddleback gunnel	0	1.0	0	0	
Sand lance	1000.0	0	0	0	
Tubesnout	0	0	0	0	
Bay Pipefish	0.5	0	3.0	0	
Threespine stickleback	50.0	20.0	40.0	3.0	
Whitespotted greenling	0	13.0	3.0	3.0	
Staghorn sculpin	1.0	0	0	0	
Sharpnose sculpin	1.0	0	0	0	
Silver spotted sculpin	1.5	0	2.0	0	
Snailfish	0.5	0	0	0	
English sole	0.5	1.0	1.0	17.0	

Table 2. Numbers of species and average total fish density (no. fish m⁻²) collected by beach seine in eelgrass habitats of 13 estuaries in Washington, Oregon, and California, 25 May-8 June 1989. In Padilla Bay, samples were collected on two dates that have been combined; in all other estuaries, samples were collected on one day.

Estuary	Numbers of Species	Fish Density (no. fish m ⁻²)
Padilla Bay, WA	13	1.38
Richmond Beach, WA	19	0.94
Jamestown, WA	17	0.72
Grays Harbor, WA	17	1.18
Willapa Bay, WA	19	0.62
Netarts Bay, OR	21	0.30
Yaquina Bay, OR	20	0.38
Sought Slough, OR	16	0.47
Coquille River, OR	7	0.47
Humboldt Bay, CA	17	0.59
Tomales Bay, CA	27	1.91
San Francisco Bay, CA	18	0.63
Elkhorn Slough, CA	19	1.52
TOTAL	59	0.84

Table 3. Percentage of the overall catch comprised by the three most abundant species and the three most abundant species occurring in each estuary, 25 May -8 June 1989.

Estuary	% Comprised of the 3 Most Abundant Species	Most Abundant	Second Most Abundant	Third Most Abundant
Padilla Bay NERR, WA	58.9	Shiner perch	Surf smelt	Threespine stickleback
Richmond Beach, WA	70.7	Chum salmon	Shiner perch	Chinook salmon
Jamestown, WA	69.8	Tube-nose poacher	Tidepool sculpin	Shiner perch
Grays Harbor, WA	65.1	Threespine stickleback	Surf smelt	English sole
Willapa Bay, WA	88.2	Shiner perch	English sole	Threespine stickleback
Netarts Bay, OR	63.4	Pacific herring	Surf smelt	Staghorn sculpin
Yaquina Bay, OR	67.6	Shiner perch	English sole	Snake prickleback
South Slough NERR, OR	80.5	Shiner perch	Pacific herring	Pile perch
Coquille River, OR	92.3	Shiner perch	Staghorn sculpin	Coho salmon
Humboldt Bay, CA	58.3	Shiner perch	Surf smelt	White perch
Tomales Bay, CA	82.1	Shiner perch	English sole	Walleye perch
San Francisco Bay, CA	64.8	Staghorn sculpin	English sole	Striped perch
Elkhorn Slough NERR, CA	72.4	Shiner perch	White perch	Anchovy

Table 4. Number and density (no. fish m⁻²) of embiotocid species collected by beach seine from 13 estuaries in Washington, Oregon, and California, 25 May-8 June 1989. In Padilla Bay, sample were collected on two dates that have been combined; in all other estuaries, samples were collected on one day.

Estuary	Numbers of Embiotocid Species	Embiotocid Density
Padilla Bay, WA	2	0.70
Richmond Beach, WA	2	0.32
Jamestown, WA	1	0.07
Grays Harbor, WA	1	0.05
Willapa Bay, WA	4	0.87
Netarts Bay, OR	2	0.001
Yaquina Bay, OR	4	0.16
South Slough, OR	3	0.28
Coquille River, OR	1	0.38
Humboldt Bay, CA	3	0.26
Tomaes Bay, CA	6	1.54
San Francisco Bay, CA	6	0.19
Elkhorn Slough, CA	5	1.11

Table 5. Fish selected to evaluate temporal variability in food habits at the Padilla Bay National Estuarine Research Reserve, 1989. All fish came from catches made at the Upper Indian Slough sampling station. (SD= Standard Deviation)

<u>Species/Date</u>	<u>No. Full</u>	<u>No. Empty</u>	<u>Length (SD) mm</u>	<u>Weight (SD) g</u>
<u>Chinook salmon</u>				
5/25	5	0	67.2(0.8)	2.6(0.2)
6/18	5	0	67.2(3.2)	2.8(0.3)
7/18	5	0	75.6(3.7)	4.4(0.7)
<u>Chum salmon</u>				
4/24	5	0	53.4(1.7)	1.1(0.1)
5/25	5	0	54.8(2.7)	1.2(0.2)
6/19	5	0	55.0(2.4)	1.3(0.2)
<u>Pacific herring</u>				
5/25	4	0	51.5(0.3)	0.7(0.1)
6/19	5	0	52.8(3.6)	0.8(0.2)
7/18	5	0	60.0(0.4)	1.4(0.3)
<u>English sole</u>				
3/13	5	0	49.2(2.6)	1.2(0.3)
4/24	5	0	59.4(2.8)	1.9(0.3)
5/25	5	0	62.6(3.6)	1.9(0.4)
6/19	4	0	68.6(9.3)	2.8(1.1)

Table 6. Temporal changes in food habits (% Σ Index of Relative Importance, IRI) of chinook salmon at the Padilla Bay National Estuarine Research Reserve, 1989. All fish came from catches made at the Upper Indian Slough sampling station. Prey that were less than 0.1% of the prey IRI have not been included. (Blanks represent either prey with less than 0.1% prey IRI or the prey was not consumed)

Taxa	25 May 1989	19 June 1989	18 July 1989
Aranae	2.2		
Harpacticoida	1.3	1.9	
Valvifera		0.7	
Tanaidacea	0.6	0.7	1.9
Cumacea	30.1	4.8	2.4
Gammaridea	0.2	41.5	0.9
Brachyrncha		7.8	
Pleocyemata	0.5	7.8	
Insecta	49.7	25.9	78.0
Teleostei	15.0	7.8	15.2

Table 7. Temporal changes in food habits (% Σ Index of Relative Importance, IRI) of English sole at the Padilla Bay National Estuarine Research Reserve, 1989. All fish were collected at the Upper Indian Slough sampling station. Prey that were less than 0.1% of the prey IRI have not been included. (Blanks represent either prey with less than 0.1% prey IRI or the prey was not consumed)

Taxa	13 March 1989	24 April 1989	25 May 1989	19 June 1989
Oligochaeta			7.6	
Nematoda			0.6	
Bivalvia	11.0	1.8	26.4	4.3
Polychaeta	86.6	70.1	8.9	4.0
Harpacticoida		10.9	10.3	39.2
Tanaidacea	0.2	1.6	41.2	8.5
Cumacea	0.2		1.6	16.5
Gammaridea	1.8	15.7	3.0	26.4

Table 8. Temporal changes in food habits (% Σ Index of Relative Importance, IRI) of chum salmon at the Padilla Bay National Estuarine Research Reserve, 1989. All fish were collected at the Upper Indian Slough sampling station. Prey that were less than 0.1% of the prey IRI have not been included. (Blanks represent either prey with less than 0.1% prey IRI or the prey was not consumed)

Taxa	24 April 1989	25 May 1989	19 June 1989
Polychaeta		0.3	
Harpacticoida	0.4	72.6	77.6
Cumacea		0.6	0.5
Gammaridea		15.7	4.6
Pleocyemata	99.3		5.0
Insecta		2.6	
Teleostei		7.6	12.1

Table 9. Temporal changes in food habits (% Σ Index of Relative Importance, IRI) of Pacific herring at the Padilla Bay National Estuarine Research Reserve, 1989. All fish were collected at the Upper Indian Slough sampling station. Prey that were less than 0.1% of the prey IRI have not been included. (Blanks represent either prey with less than 0.1% prey IRI or the prey was not consumed)

Taxa	25 May 1989	19 June 1989	18 July 1989
Nematoda		0.1	
Polychaeta		0.1	
Acarina			0.2
Podocopa			0.1
Cladocera	1.9		
Calanoida	34.9	0.1	0.1
Harpacticoida	35.3	99.3	91.8
Cyclopoida	21.2	0.1	3.9
Balanomorpha	5.3	0.1	0.8
Caprelliidae			0.2
Cumacea			0.1
Gammaridea	1.4	0.1	
Euphausiacea			0.1
Decapoda	0.1	0.1	2.8

Table 10. Fish selected for analysis of spatial variability in food habits at the Padilla Bay National Estuarine Research Reserve, 1989.

Species/Location	No. Full	No. Empty	Length (SD) mm	Weight (SD) g
<u>Chinook salmon</u>				
Upper Indian Slough	5	0	67.2(0.8)	2.6(0.2)
Hat Island Channel	5	0	65.2(2.5)	2.1(0.3)
<u>Chum salmon</u>				
Upper Indian Slough	5	0	54.8(2.7)	1.2(0.2)
Lower Indian Slough	6	0	52.7(4.8)	1.1(0.3)
Hat Island Channel	5	0	55.2(1.8)	1.2(0.1)
<u>Pacific herring</u>				
Upper Indian Slough	4	0	51.5(0.3)	0.7(0.1)
Hat Island Channel	5	0	50.8(2.3)	0.6(0.3)
<u>English sole</u>				
Upper Indian Slough	5	0	62.6(3.6)	1.9(0.4)
Lower Indian Slough	5	0	68.8(3.6)	2.7(0.5)
<u>Surf smelt</u>				
Upper Indian Slough	5	0	79.0(4.7)	2.3(0.4)
Hat Island Channel	5	0	77.4(4.0)	2.1(0.3)

Table 11. Spatial variability in food habits (% Σ Index of Relative Importance, IRI) of chinook salmon at the Padilla Bay National Estuarine Research Reserve, May 1989. Prey that were less than 0.1% of the prey IRI have not been included. (Blanks represent either prey with less than 0.1% prey IRI or the prey was not consumed)

Prey Item	Hat Island Channel	Upper Indian Slough
Plants	10.7	
Arachnida		2.2
Harpacticoida		1.3
Cumacea	2.7	30.1
Tanaidacea	2.8	0.6
Gammaridea	1.4	0.2
Caprellidae	5.4	
Decapoda	50.0	0.8
Insecta	1.4	49.7
Teleostei	30.6	15.0

Table 12. Spatial variability in food habits (% Σ Index of Relative Importance, IRI) of Pacific herring at Padilla Bay National Estuarine Research Reserve, 1989. Prey that were less than 0.1% of the prey IRI have not been included. (Blanks represent either prey with less than 0.1% prey IRI or the prey was not consumed)

Prey Item	Hat Island Channel	Upper Indian Slough
Gastropoda	0.1	1.9
Cladocera	0.4	34.9
Calanoida	69.6	35.3
Harpacticoida	26.4	21.2
Cyclopoida	1.9	5.3
Balanomorpha	1.6	1.4
Gammaridea		1.4
Decapoda	0.1	0.1

Table 13. Spatial variability in food habits (% Σ Index of Relative Importance, IRI) of chum salmon at the Padilla Bay National Estuarine Research Reserve, May 1989. Prey that were less than 0.1% of the prey IRI have not been included. (Blanks represent either prey with less than 0.1% prey IRI or the prey was not consumed)

Prey Item	Hat Island Channel	Lower Indian Slough	Upper Indian Slough
Polychaeta		0.5	0.3
Araneae		0.1	
Cladocera	0.8		0.1
Calanoida	28.7	0.5	72.6
Harpacticoida	20.3	83.2	
Cyclopoida	3.2	0.3	0.1
Balanomorpha	0.3	0.1	
Tanaidacea		0.1	
Cumacea	1.0	0.3	
Hyperiidia	0.2		
Gammaridea	0.2	8.6	15.7
Caprellidea	0.6		0.2
Euphausiacea	0.1		
Pleocyemata	2.6	0.2	
Anomura	1.0	0.3	
Decapoda	3.2	0.1	0.1
Insecta	1.7	6.6	2.6
Larvacea	8.9		
Teleostei	27.4		7.6

Table 14. Spatial variability in food habits (% Σ Index of Relative Importance, IRI) of English sole at the Padilla Bay National Estuarine Research Reserve, May 1989. Prey that were less than 0.1% of the prey IRI have not been included. (Blanks represent either prey with less than 0.1% prey IRI or the prey was not consumed)

Taxa	Lower Indian Slough	Upper Indian Slough
Nematoda		0.6
Polychaeta	9.8	8.9
Oligochaeta		7.6
Bivalvia	6.5	26.4
Acarina	0.1	
Podocopa	0.4	
Calanoida		0.2
Harpacticoida	64.7	10.3
Cumacea	0.1	1.5
Tanaidacea	14.1	41.2
Gammaridea	4.5	3.0

Table 15. Spatial variability in food habits (% Σ Index of Relative Importance, IRI) of surf smelt at the Padilla Bay National Estuarine Research Reserve, May 1989. Prey that were less than 0.1% of the prey IRI have not been included. (Blanks represent either prey with less than 0.1% prey IRI or the prey was not consumed)

Taxa	Hat Island Channel	Upper Indian Slough
Polychaeta	0.1	0.1
Gastropoda	0.1	
Cladocera	1.3	
Calanoida	75.9	0.5
Harpacticoida	11.9	95.4
Cyclopoida	2.9	0.1
Balanomorpha	5.4	1.3
Epicaridea	0.1	
Gammaridea	0.1	
Caprellidea	1.5	2.5
Decapoda	0.4	0.1
Larvacea	0.5	
Teleostei	0.1	

Table 16. Relative importance (% Σ Index of Relative Importance, IRI) of harpacticoid copepod taxa in the diets of fish capture at the Padilla Bay National Estuarine Research Reserve, May 1989. All fish were obtained from the Upper Indian Slough sampling station.

Taxa	Chum salmon	Pacific herring	Chinook salmon	English sole	Surf smelt	Pacific sand lance
Harpacticoida	1.9	20.7		1.1	12.0	9.6
<i>Tegastes</i> sp.					0.1	
<i>Longepedia</i> sp.						0.1
Ectinosomidae		1.7			27.8	0.4
<i>Ectinosoma melaniceps</i>						0.1
<i>Microsetella</i> sp.					1.3	0.1
<i>Harpacticus</i> sp.		0.6				
<i>H. spinulosus</i>		0.7		2.4	0.1	1.0
<i>H. obscurus</i>	0.2					0.1
<i>H. arcticus</i>		0.2				14.0
<i>H. uniremis</i>	48.6		1.3	0.7		0.4
<i>Zaus</i> sp.	0.5	0.1			1.5	0.1
<i>Tisbe</i> sp.	2.4	8.1		0.1	17.3	0.4
Laophontidae	2.2					
<i>Paralaophonte</i> sp.		0.1				
<i>Paralaophonte perplexa</i>		0.1			0.6	
<i>P. pacifica</i>					0.1	
<i>Danielssenia</i> sp.		0.1				
<i>Heterolaophonte</i> sp.	0.1					0.1
<i>H. variabilis</i>					4.0	
<i>Tachidius triangularis</i>		0.2			1.3	0.1
<i>Ameira longipes</i>					0.1	
<i>Huntemania jadensis</i>		0.1				
<i>Amphiascus</i> sp.	8.2	0.1				0.4
<i>Stenhelia</i> sp.						
<i>Tymphlamphiascus pectinifer</i>				0.1		
<i>Robertsonia</i> sp.	0.4			0.1	0.6	
<i>Mesochra</i> sp.		1.8			16.9	0.1
<i>Dactylopodia</i> sp.		0.1				

Table . (cont'd)

Taxa	Chum salmon	Pacific herring	Chinook salmon	English sole	Surf smelt	Pacific sand lance
<i>Dactylopodia vulgaris</i>	0.1				0.3	1.0
<i>Paradactylopodia</i> sp.						0.1
<i>Parathalestris</i> sp.	0.1					
<i>P. californica</i>	4.6			0.9		
<i>Diathrodes</i> sp.		0.1			8.9	0.2

Appendices

Appendix I Latin binomial and common names of fishes captured in 1989 collections in northern California, Oregon and Washington estuaries.

Common Name	Scientific Name
Brown smoothhead	<i>Mustelus henlei</i>
American shad	<i>Alosa sapidissima</i>
Pacific herring	<i>Clupea harengus pallasii</i>
Northern anchovy	<i>Engraulis mordax</i>
Sockeye salmon	<i>Oncorhynchus nerka</i>
Chum salmon	<i>Oncorhynchus keta</i>
Coho salmon	<i>Oncorhynchus kisutch</i>
Chinook salmon	<i>Oncorhynchus tshawytscha</i>
Rainbow trout	<i>Oncorhynchus mykiss</i>
Surf smelt	<i>Hypomesus pretiosus</i>
Plainfin midshipman	<i>Porichthys notatus</i>
Pacific tomcod	<i>Microgadus proximus</i>
Topsmelt	<i>Atherinops affinis</i>
Jacksmelt	<i>Atherinopsis californiensis</i>
Tubesnout	<i>Aulorhynchus flavidus</i>
Threespine stickleback	<i>Gasterosteus aculeatus</i>
Bay pipefish	<i>Syngnathus leptorhynchus</i>
Kelp perch	<i>Brachyistius frenatus</i>
Shiner perch	<i>Cymatogaster aggregata</i>
Black perch	<i>Embiotica jacksoni</i>
Striped Perch	<i>Embiotoca lateralis</i>
Walleye surfperch	<i>Hyperprosopon argenteum</i>
Dwarf perch	<i>Micrometrus minimus</i>
White perch	<i>Phanerodon furcatus</i>
Pile perch	<i>Rhacochilus vacca</i>
Pacific sand lance	<i>Ammodytes hexapterus</i>

Appendix I. (cont.)

Common Name	Scientific Name
High cockscomb	<i>Anoplarchus purpurescens</i>
Snake prickleback	<i>Lumpenus sagitta</i>
Perpoint gunnel	<i>Apodichthys flavidus</i>
Saddleback gunnel	<i>Pholis ornata</i>
Bay goby	<i>Lepidogobius lepidus</i>
Tube-nose poacher	<i>Pallasina barbata</i>
Brown rockfish	<i>Sebastes auriculatus</i>
Copper rockfish	<i>Sebastes caurinus</i>
Widow rockfish	<i>Sebastes entomelas</i>
Bocaccio	<i>Sebastes paucispinis</i>
Grass rockfish	<i>Sebastes rastrelliger</i>
Olive rockfish	<i>Sebastes serranoides</i>
Kelp greenling	<i>Hexagrammus decagrammus</i>
Lingcod	<i>Ophiodon elongatus</i>
Scalyhead sculpin	<i>Areteus harringtoni</i>
Bonehead sculpin	<i>Areteus notospilotus</i>
Padded sculpin	<i>Areteus fenestralis</i>
Red Irish Lord	<i>Hemilepidotus hemilepidotus</i>
Brown Irish lord	<i>Hemilepidotus spinosus</i>
Pacific staghorn sculpin	<i>Leptocottus armatus</i>
Tidepool sculpin	<i>Oligocottus maculosus</i>
Fluffy sculpin	<i>Oligocottus snyderi</i>
Cabezon	<i>Scoorpaenichthys marmoratus</i>
Buffalo sculpin	<i>Enophrys bison</i>
Silverspotted sculpin	<i>Blepsias cirrhosus</i>
Snailfish	<i>Liparis spp.</i>

Appendix I. (cont.)

Common Name	Scientific Name
Speckled sanddab	<i>Citharichthys stigmaeus</i>
English sole	<i>Pleuronectes vetulus</i>
Rock sole	<i>Pleuronectes bilineatus</i>
C-O sole	<i>Pleuronichthys coeonus</i>
Curlfin sole	<i>Pleuronichthys decurrens</i>
Starry flounder	<i>Platichthys stellatus</i>
Sand sole	<i>Psettichthys melanostictus</i>

Appendix II. Beach seine catch-per-unit-effort (CPUE) of fish in estuarine liitoral eelgrass habitats at five locations in Washington, 24 May-8 June 1989; to convert CPUE values to density (no. fish m⁻²), divide CPUE values by 520.

Species	Willapa Bay	Grays Harbor	Jamestown	Richmond Beach	Padilla Bay NERR
Brown Smoothhead					
American shad		0.3			
Pacific herring	0.3				105.0
Northern anchovy	0.3				
Sockeye salmon				3.3	
Chum salmon			14.3	167.3	24.8
Coho salmon					
Chinook salmon	14.0	13.6		69.3	13.2
Rainbow trout	0.3	0.7		30.0	
Surf smelt		56.6		0.3	165.7
Plainfin midshipman					
Pacific tomcod					
Topsmelt					
Jacksmelt					
Tubesnout	0.7	0.3	16.0	3.3	
Threespine stickleback	34.0	107.3	0.3		121.2
Bay pipefish	2.7	2.3	2.3	0.7	
Kelp perch					
Shiner perch	452.0	24.0	35.6	111.3	145.0
Black perch					
Striped Perch				61.0	
Walleye surfperch	3.0				
Dwarf perch					
White perch	3.7				

Appendix II. (Washington cont'd).

Species	Willapa Bay	Grays Harbor	Jamestown	Richmond Beach	Padilla Bay NERR
Pile perch	1.0				1.4
Pacific sand lance			0.3	1.0	92.3
High cockscomb					
Snake prickleback	3.3				14.0
Penpoint gunnel					
Saddleback gunnel	27.0	19.0	11.0	0.3	13.2
Bay goby	0.3				
Tube-nose poacher			81.7		
Brown rockfish					
Copper rockfish					
Widow rockfish					
Bocacio					
Grass rockfish					
Olive rockfish					
Kelp greenling	2.0	1.3	5.0		2.0
Lingcod					
Scalyhead sculpin					
Bonehead sculpin					
Red Irish Lord					
Brown Irish lord					
Pacific staghorn sculpin	5.0	44.3	1.3	4.0	5.0
Tidepool sculpin			50.3		
Fluffy sculpin					
Cabezon	6.7	0.7	6.7		

Appendix II. (Washington cont'd).

Species	Willapa Bay	Grays Harbor	Jamestown	Richmond Beach	Padilla Bay NERR
Buffalo sculpin		0.7	1.0	0.3	
Silverspotted sculpin			33.3	0.3	
Padded sculpin				0.3	
Snailfish spp.			7.0		
Speckled sanddab	0.3	2.3			
English sole	55.0	44.7	20.0	31.7	17.0
C-O sole				1.3	
Curlfin sole					
Starry flounder	2.0	1.3			
Rock sole				2.0	
Sand sole				0.7	

Appendix II. Beach seine catch-per-unit-effort (CPUE) of fish in estuarine littoral eelgrass habitats at four locations in Oregon, 24 May-8 June 1989; to convert CPUE values to density (no. fish m⁻²), divide CPUE values by 520.

Species	Netarts Bay	Yaquina Bay	South Slough NERR	Coquille Bay
Brown Smoothhead				
American shad		0.7	6.0	
Pacific herring	53		55.7	
Northern anchovy		0.3	1.3	
Sockeye salmon				
Chum salmon	0.7			
Coho salmon			5.0	22.0
Chinook salmon				
Rainbow trout				
Surf smelt	37.7	9.3	3.0	2.5
Plainfin midshipman				
Pacific tomcod				
Topsmelt		14.3		
Jacksmelt	8.0			
Tubesnout	12.7	2.7		
Threespine stickleback	2.0		0.3	
Bay pipefish	0.3	1.3	13.3	4.5
Kelp perch				
Shiner perch	2.7	78.0	136.0	196.5
Black perch				
Striped Perch		1.0	1.0	
Walleye surfperch				
Dwarf perch				

Appendix II. (Oregon cont.)

Species	Netarts Bay	Yaquina Bay	South Slough	Coquille Bay
White perch	4.3	3.7		
Pile perch	0.3	1.0	6.3	
Pacific sand lance				
High cockscomb				
Snake prickleback	2.7			
Perpoint gunnel				
Saddleback gunnel	1.7	3.0	3.0	10.5
Bay goby				
Tube-nose poacher				
Brown rockfish				
Copper rockfish				
Widow rockfish		0.7		
Boccio				
Grass rockfish				
Olive rockfish				
Kelp greenling	7.0	8.0	0.7	
Lingcod	0.3		0.3	
Scalyhead sculpin				
Bonehead sculpin	0.3			
Red Irish Lord	0.3			
Brown Irish lord	1.0			
Pacific staghorn sculpin	3.7	9.0	9.0	7.5
Tidepool sculpin		0.3		

Appendix II. (Oregon cont.)

Species	Netarts Bay	Yaquina Bay	South Slough	Coquille Bay
Fluffy sculpin		0.3		
Cabezon	1.7	1.3		
Buffalo sculpin				
Silverspotted sculpin				
Padded sculpin				
Snailfish				
Speckled sanddab	1.0	8.3		
English sole	13.0	46.7	4.3	
C-O sole			0.3	
Curlfin sole				
Starry flounder		9.0		2.0
Rock sole				
Sand sole				

Appendix II. Beach seine catch-per-unit-effort (CPUE) of fish in estuarine littoral eelgrass habitats at four locations in California, 24 May-8 June 1989; to convert CPUE values to density (no. fish m²), divide CPUE values by 520.

Species	Elkhorn Slough NERR	San Francisco Bay	Tomaes Bay	Humboldt Bay
Brown smoothhead		0.5	0.3	1.3
American shad				20.3
Pacific herring	0.5		29.7	15.7
Northern anchovy	43.0		0.3	6.0
Sockeye salmon				
Chum salmon				
Coho salmon				
Chinook salmon				
Rainbow trout				
Surf smelt				63.0
Plainfin midshipman		0.5	7.3	
Pacific tomcod		0.5		
Topsmelt	35.0		4.0	
Jacksmelt	4.5		0.3	0.7
Tubesnout				5.7
Threespine stickleback		0.5		42.3
Bay pipefish		5.5	7.7	3.0
Kelp perch			5.0	
Shiner perch	284.5	27.0	730.0	74.7
Black perch	7.5	1.5		
Striped Perch				5.0
Walleye surfperch	5.5	9.0	39.3	
Dwarf perch	23.5	22.5	20.0	
White perch	170.5	20.5	2.7	47.0

Appendix II. (California cont.)

Species	Elkhorn Slough NERR	San Francisco Bay	Tomales Bay	Humboldt Bay
Pile perch		6.0	2.3	
Pacific sand lance				
High cockscomb				
Snake prickleback				
Perpoint gunnel			0.1	0.3
Saddleback gunnel	11.0			
Bay goby		0.5	4.3	
Tubenose poacher				
Brown rockfish			0.3	
Copper rockfish	0.5	2.5	1.7	
Widow rockfish	6.0		6.7	17.0
Bocacio	0.5			
Grass rockfish	3.0			
Olive rockfish	10.0			
Kelp greenling			0.7	1.7
Lingcod		0.5	0.3	0.3
Scalyhead sculpin			0.3	
Bonehead sculpin				
Red Irish Lord				
Brown Irish lord				
Pacific staghorn sculpin	37.0	109.5	11.0	
Tidepool sculpin			9.0	
Fluffy sculpin				
Cabezon	28.5	0.5	0.7	
Buffalo sculpin				

Appendix II. (California cont.)

Species	Elkhorn Slough NERR	San Francisco Bay	Tomales Bay	Humboldt Bay
Silverspotted sculpin				
Padded sculpin				
Snailfish				
Speckled sanddab	8.0	43.5	19.0	2.7
English sole	1.5	1.5	87.6	
C-O sole				
Curlfin sole			0.3	
Starry flounder				
Rock sole				
Sand sole				

Appendix III. Statistical summaries of epibenthic pump samples from *Zostera marina* habitats at eleven estuaries in Washington, Oregon, and California, June 1989.

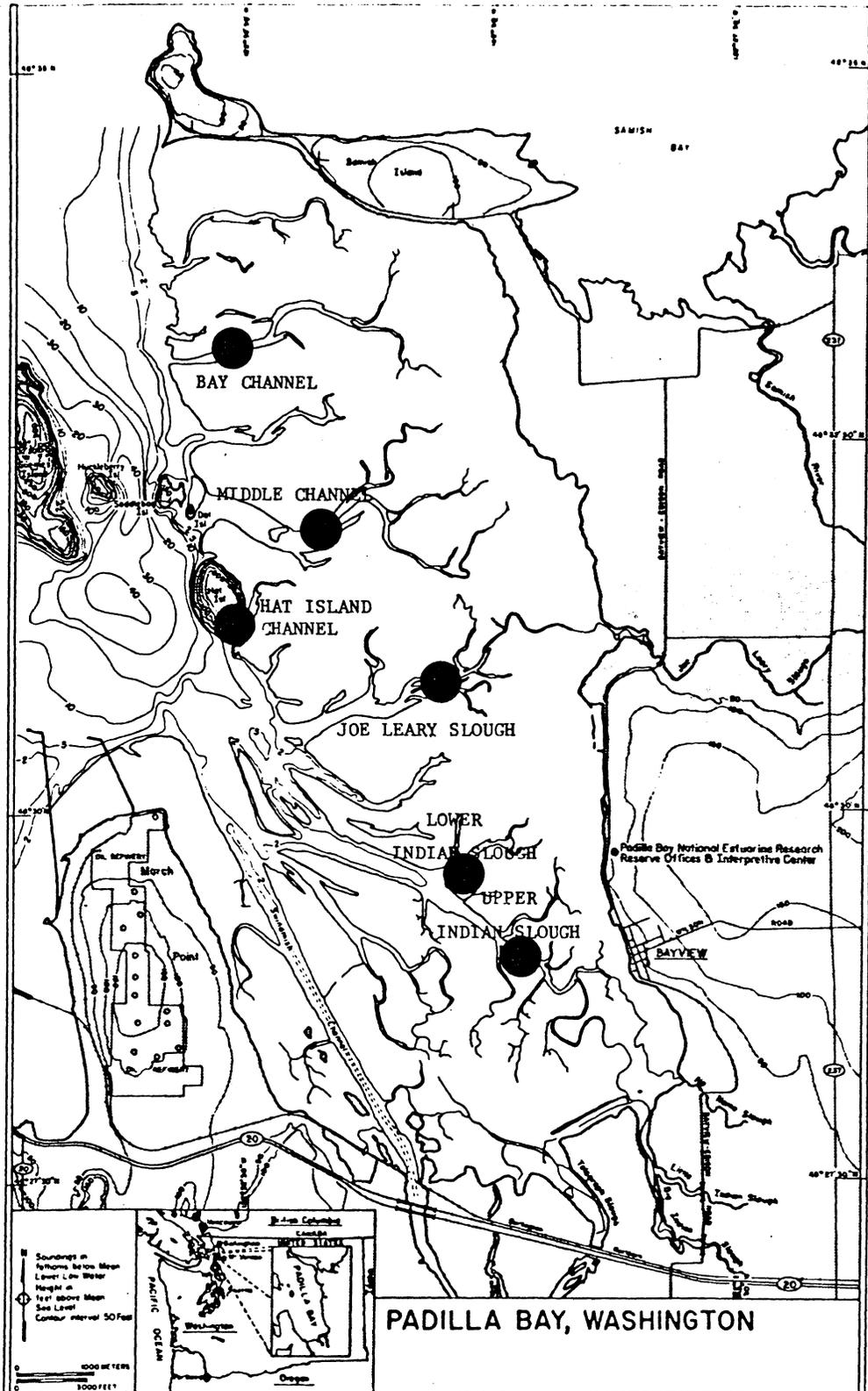
This appendix has not been included in this reprint. A copy of the full report, including this appendix, can be seen at the Padilla Bay National Estuarine Research Reserve Rod Mack Library

Appendix IV. Statistical summaries of eelgrass section epiphyte samples from *Zostera marina* habitats at eleven estuaries in Washington, Oregon, and California, June 1989.

This appendix has not been included in this reprint. A copy of the full report, including this appendix, can be seen at the Padilla Bay National Estuarine Research Reserve Rod Mack Library

Appendix V. Statistical summaries of epibenthic pump samples from *Zostera marina* habitats at six locations in the Padilla Bay National Estuarine Research Reserve, May 1989.

This appendix has not been included in this reprint. A copy of the full report, including this appendix, can be seen at the Padilla Bay National Estuarine Research Reserve Rod Mack Library



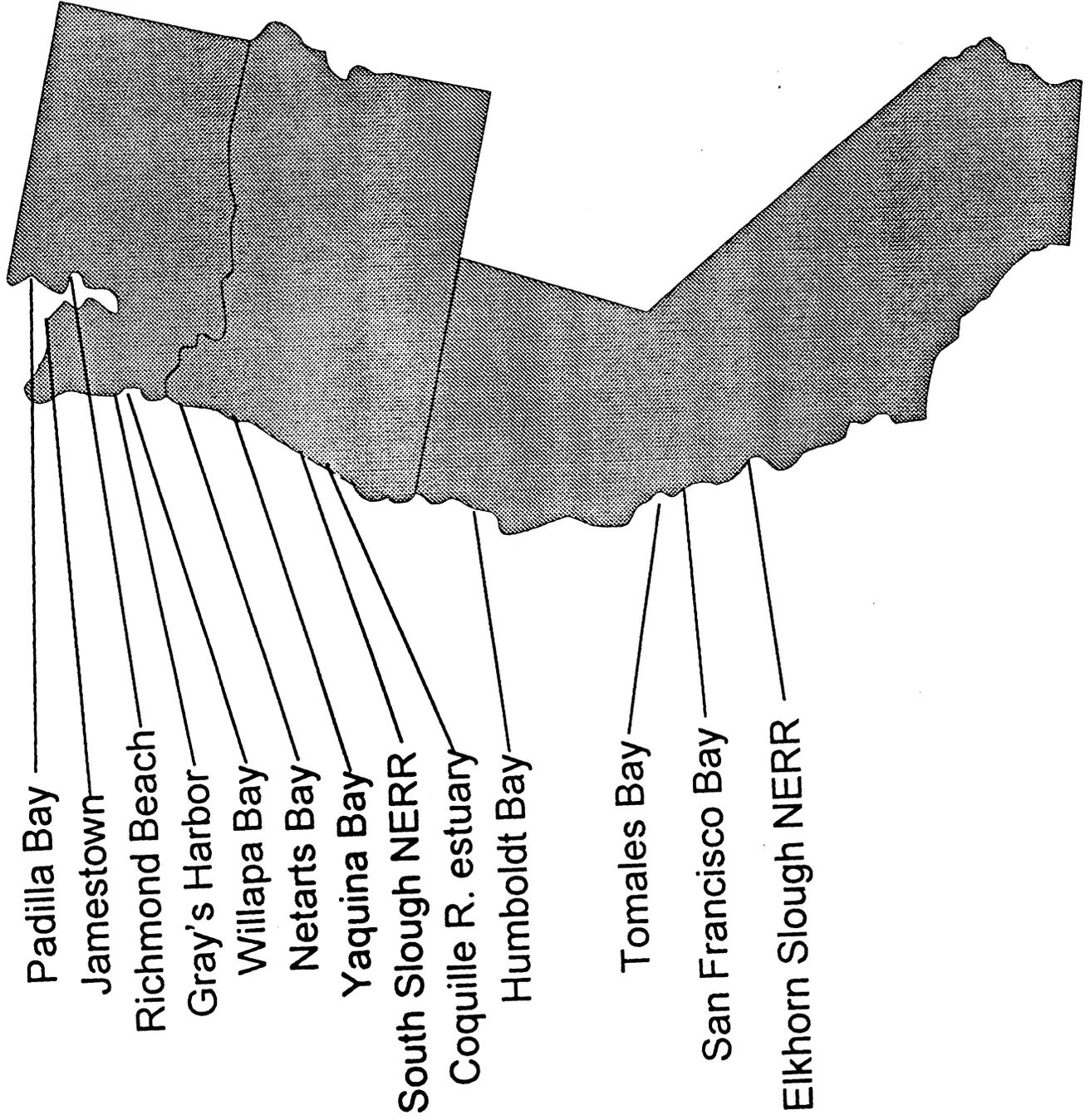
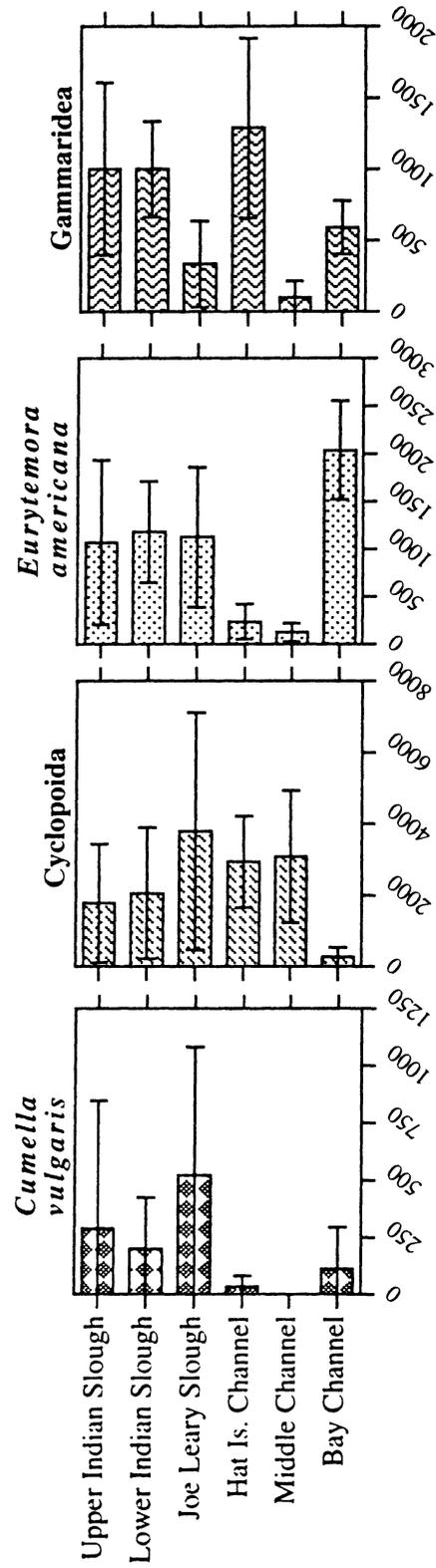
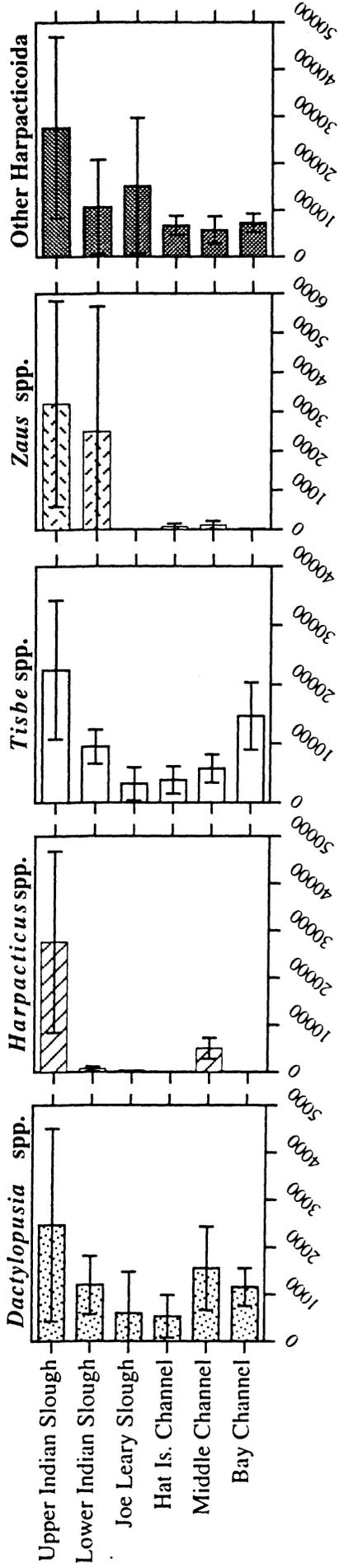
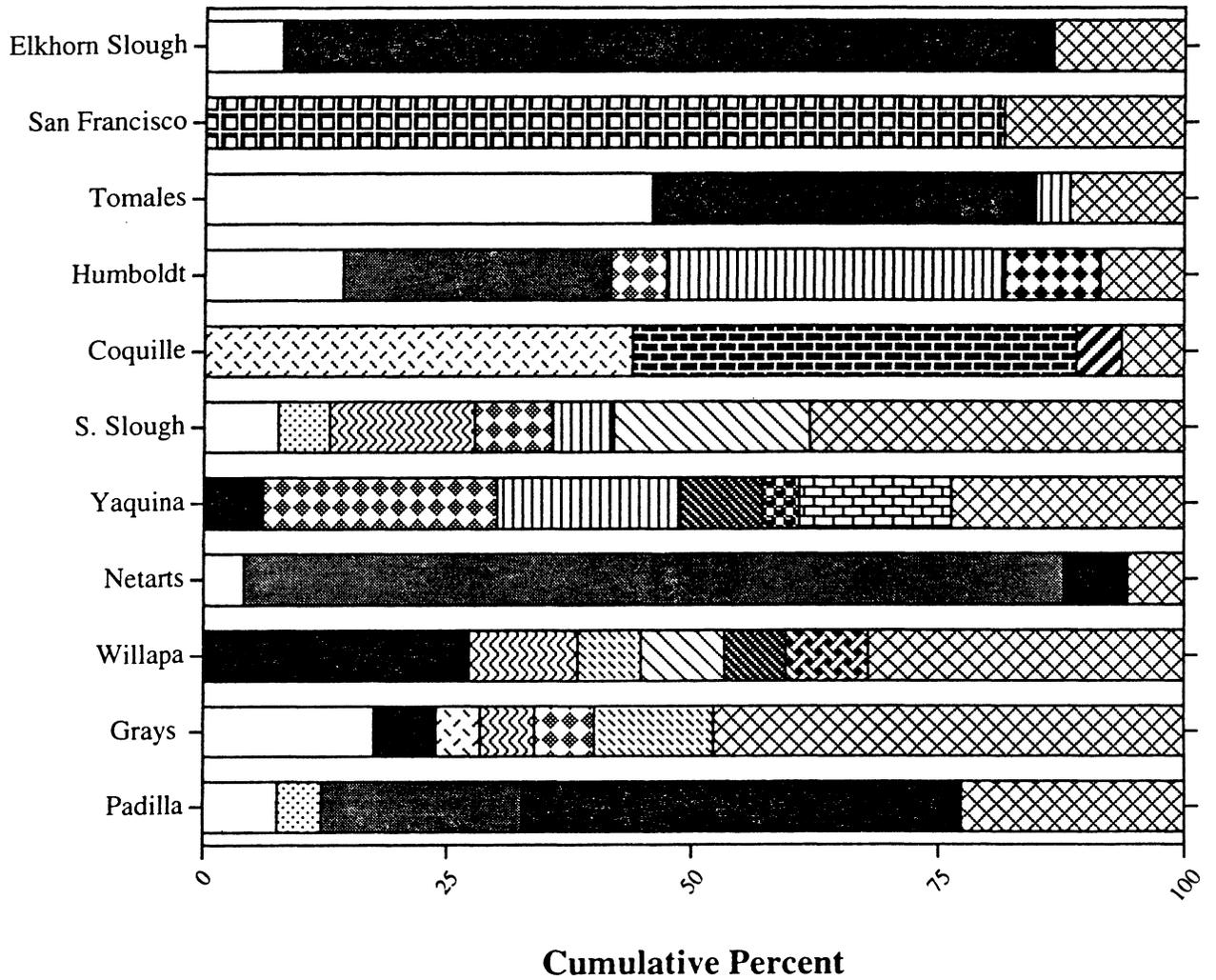
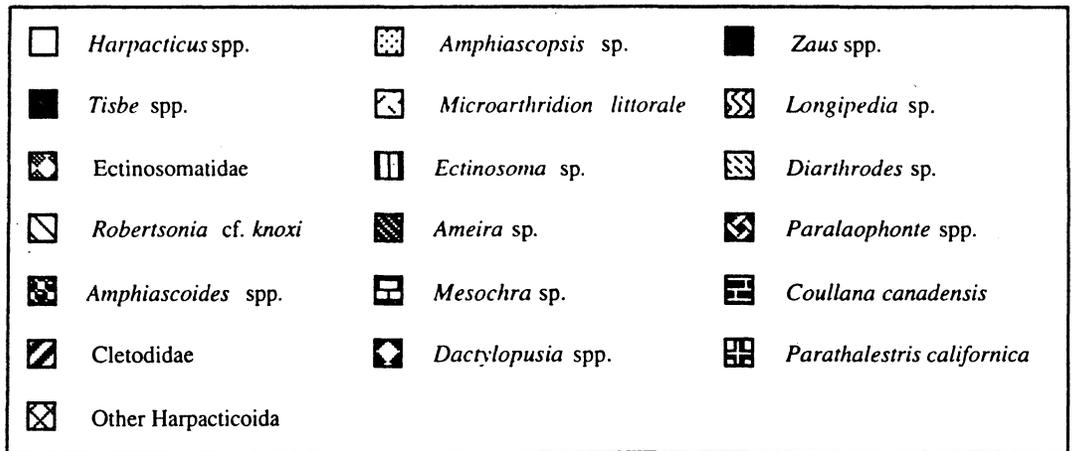
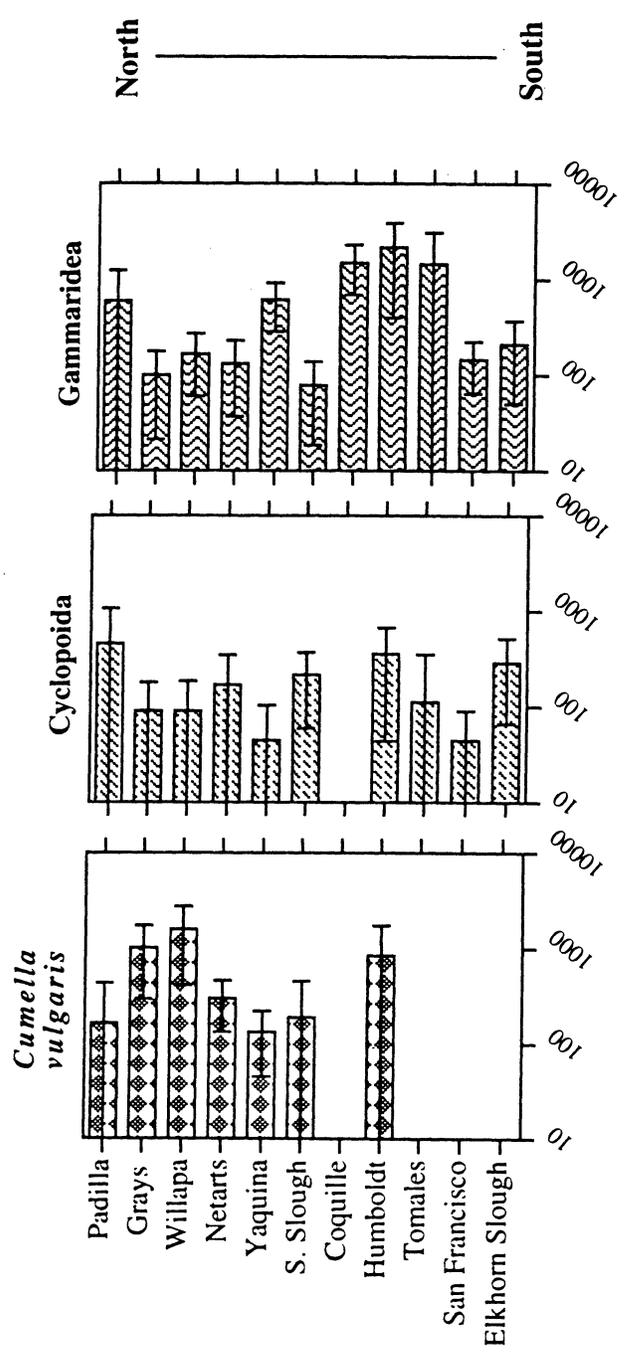
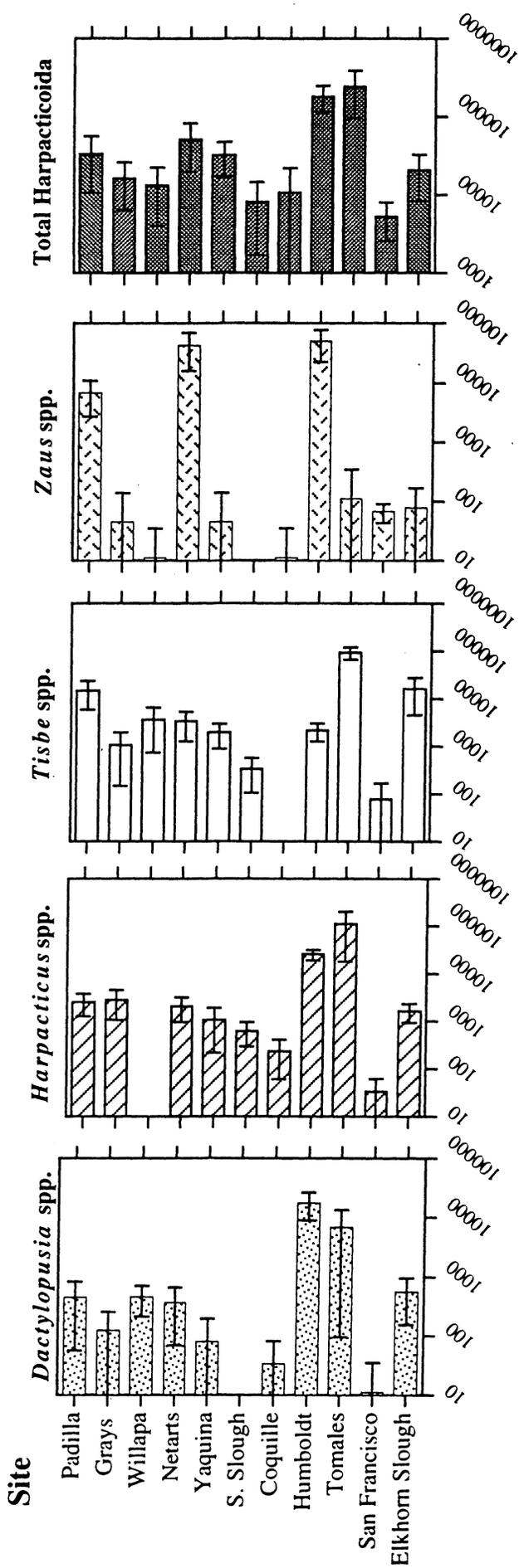


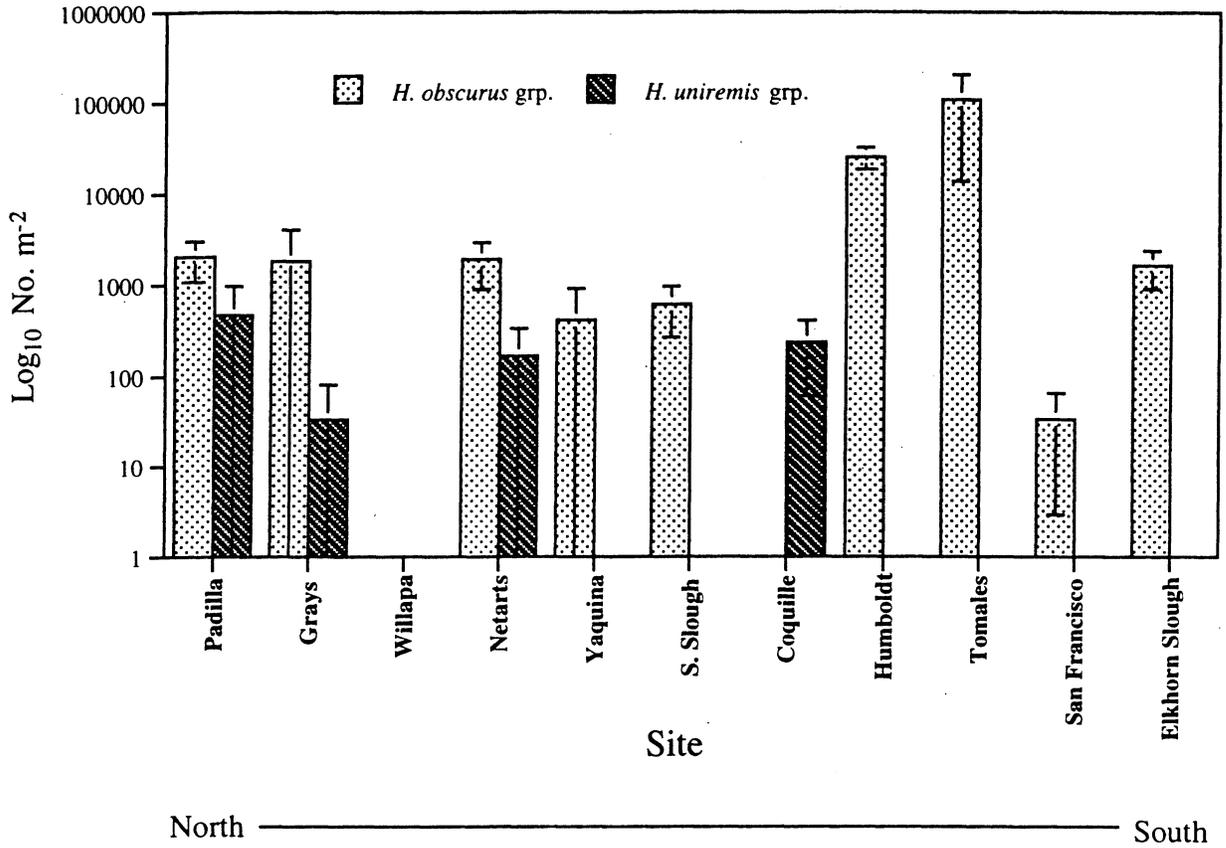
FIG 2

Site

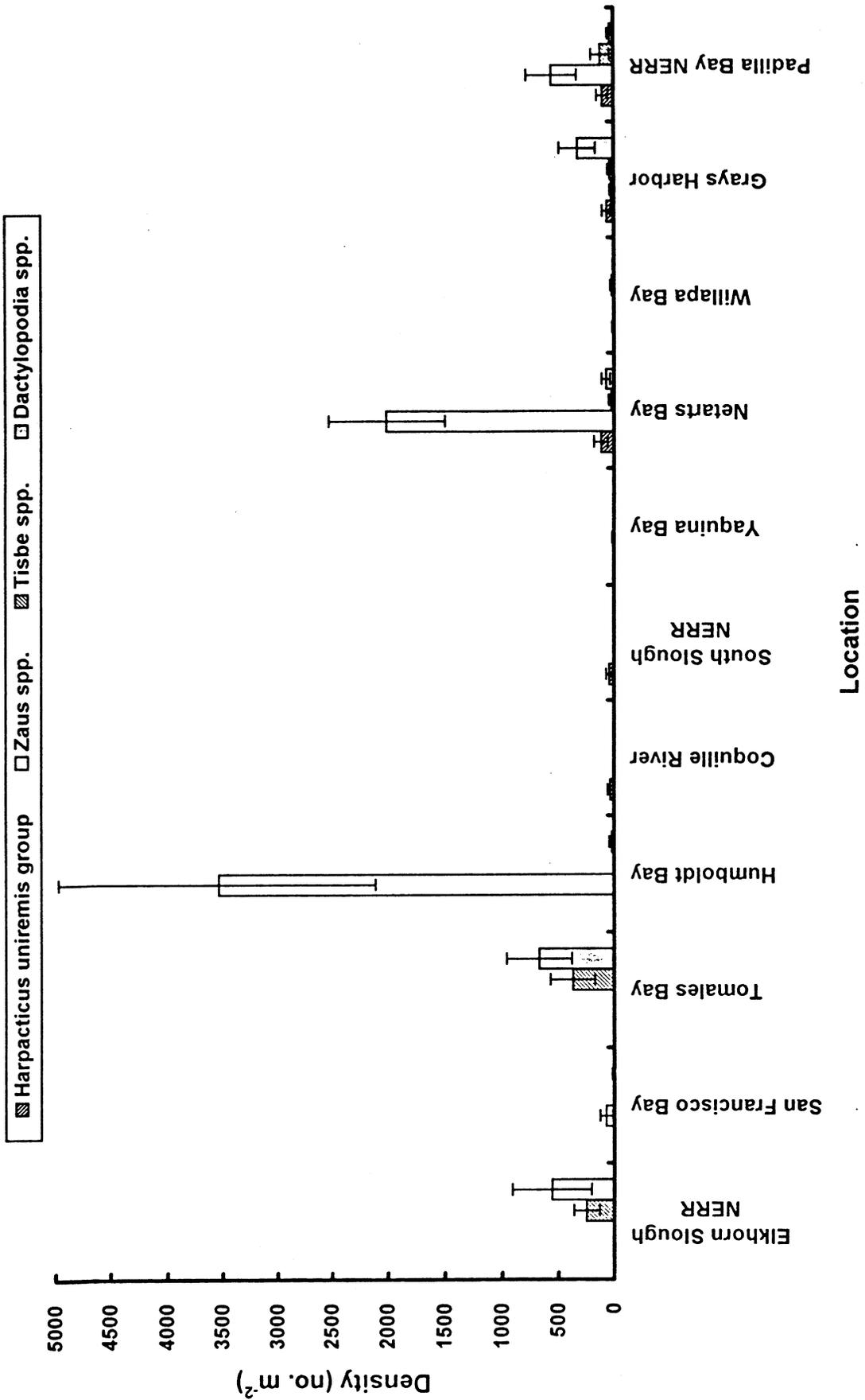




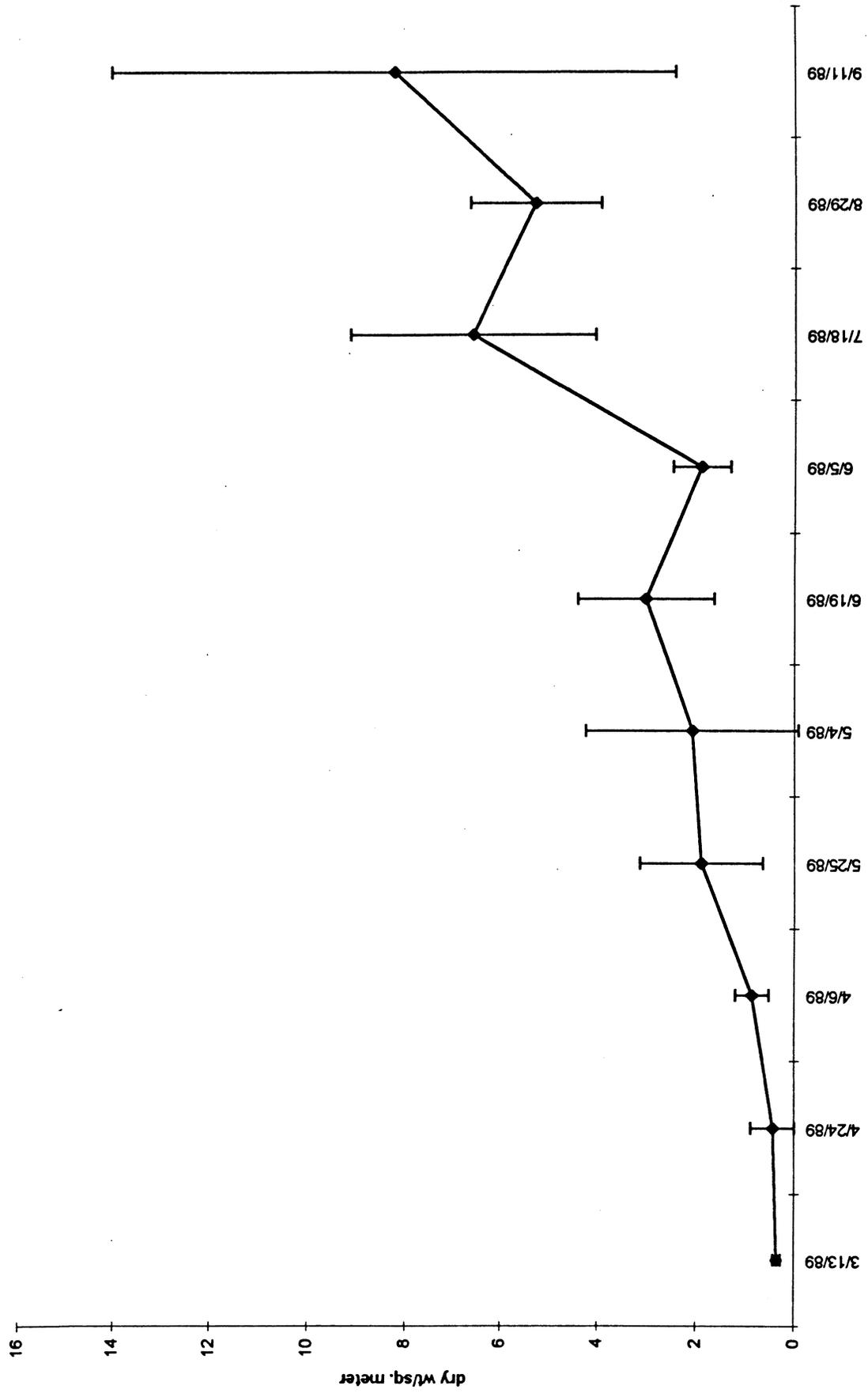




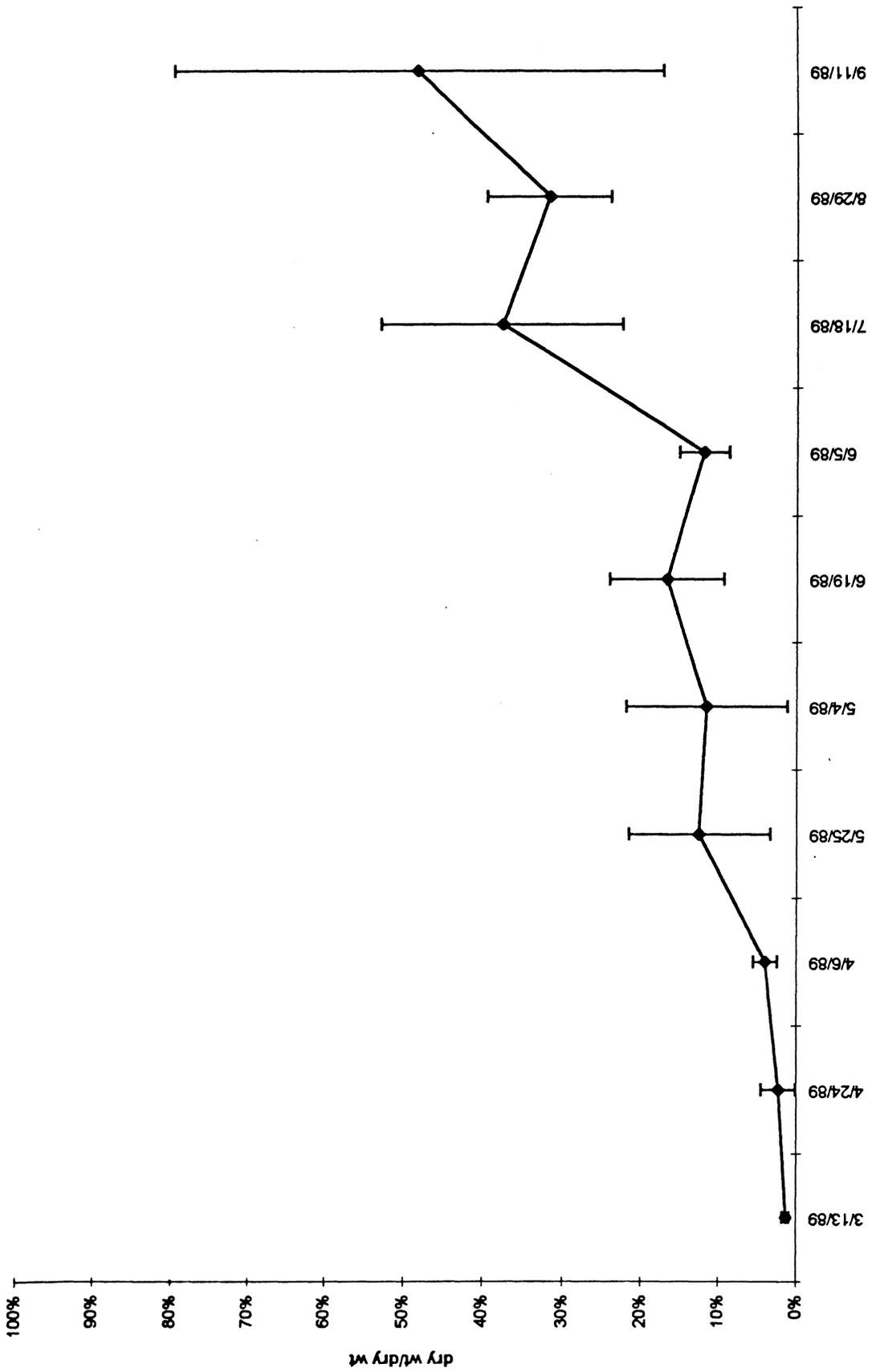
Zoogeographic Variability of Harpacticoid Prey Taxa Density



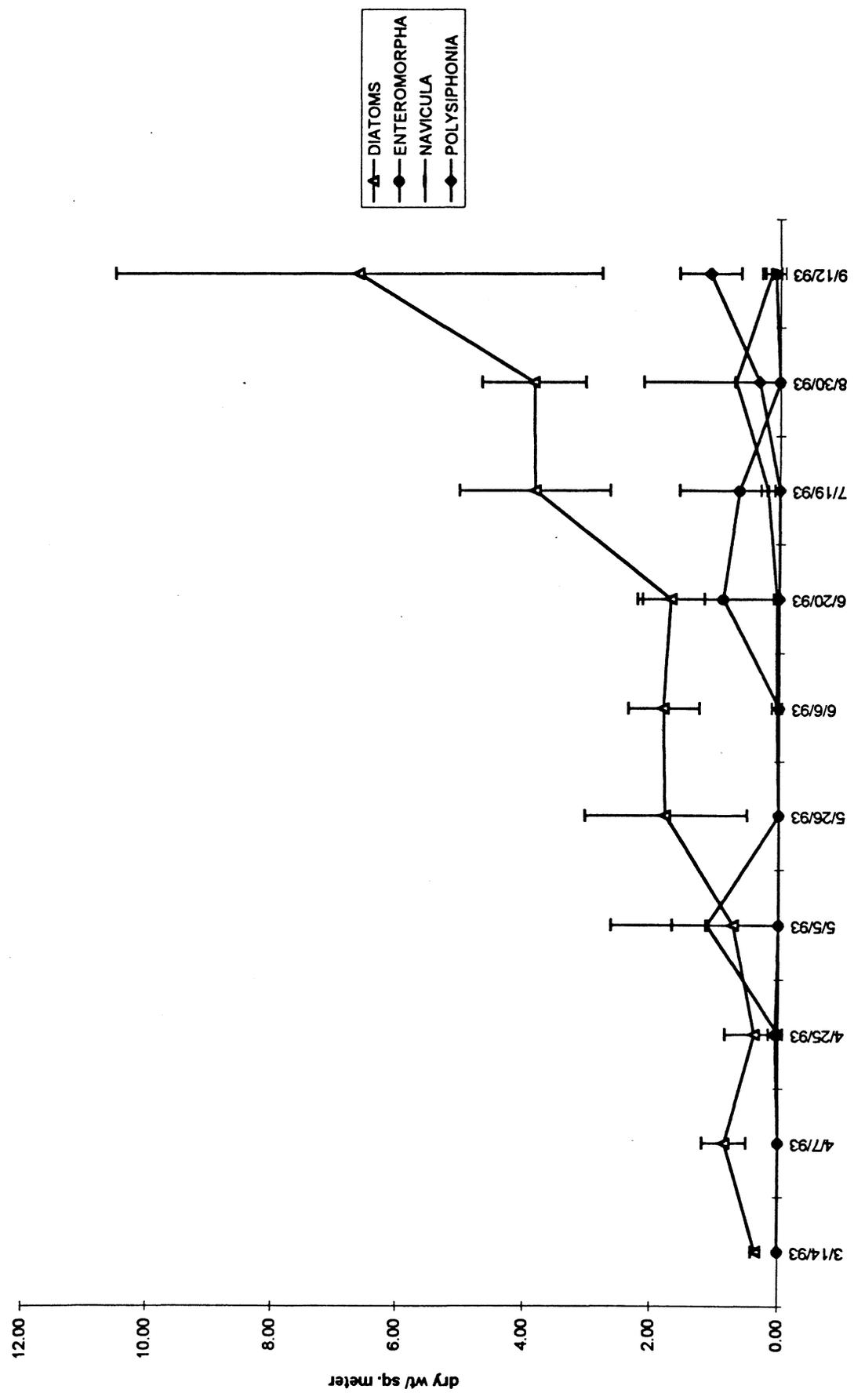
Total dry wt of all Epiphytes
per square meter of eel grass



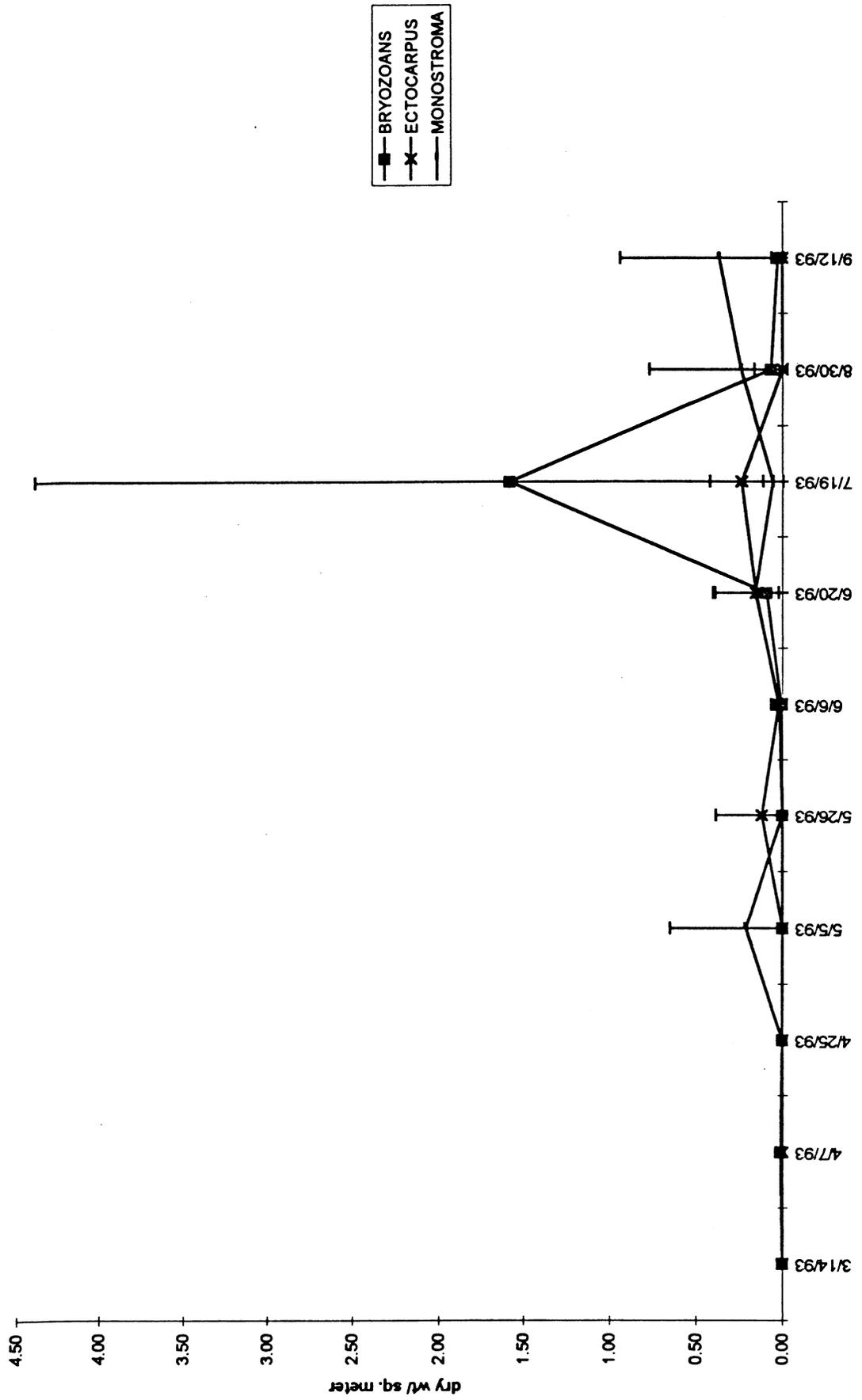
Total percent dry wt of all epiphytes
per dry wt of eel grass



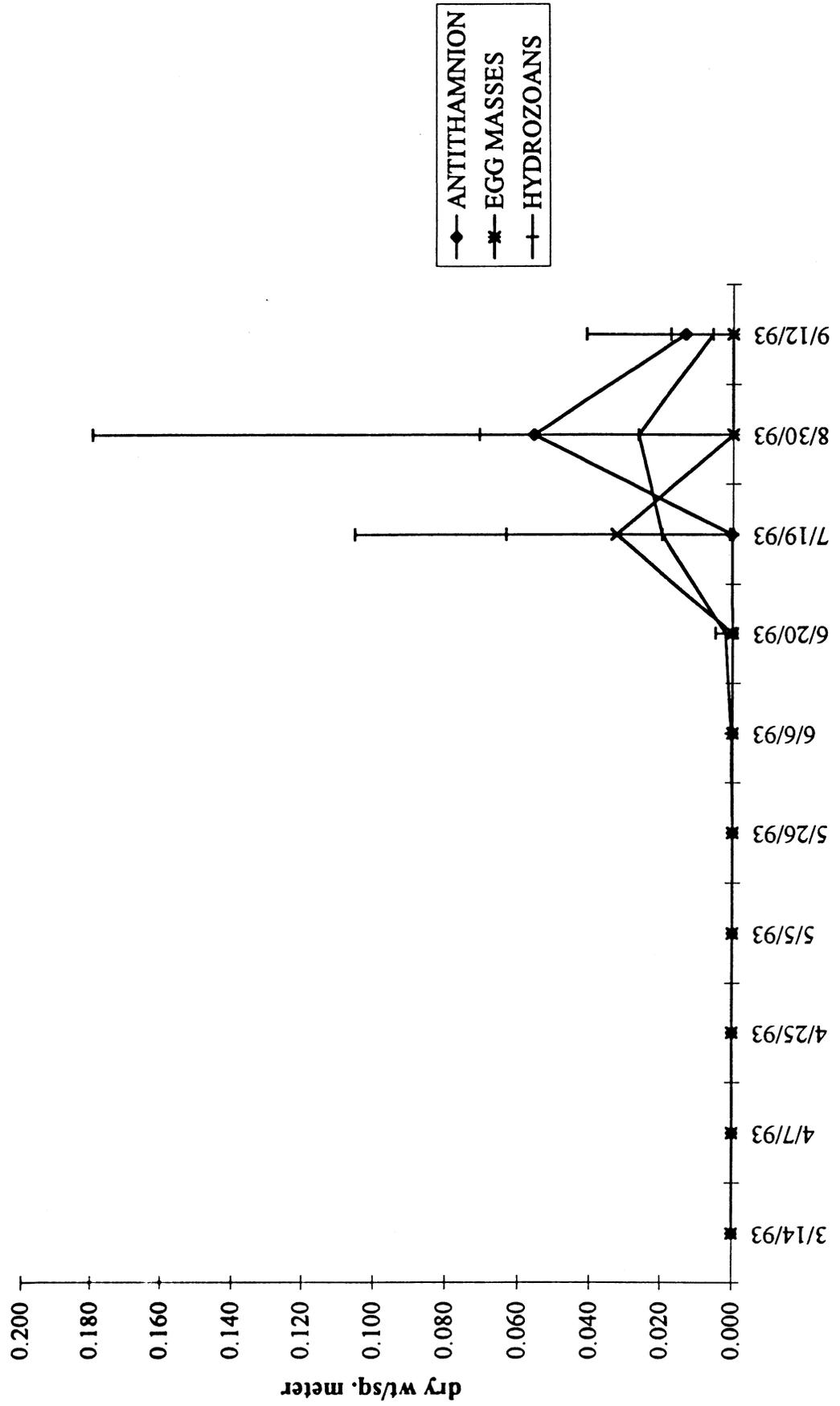
Dry wt of Epiphytes per sq. meter eel grass



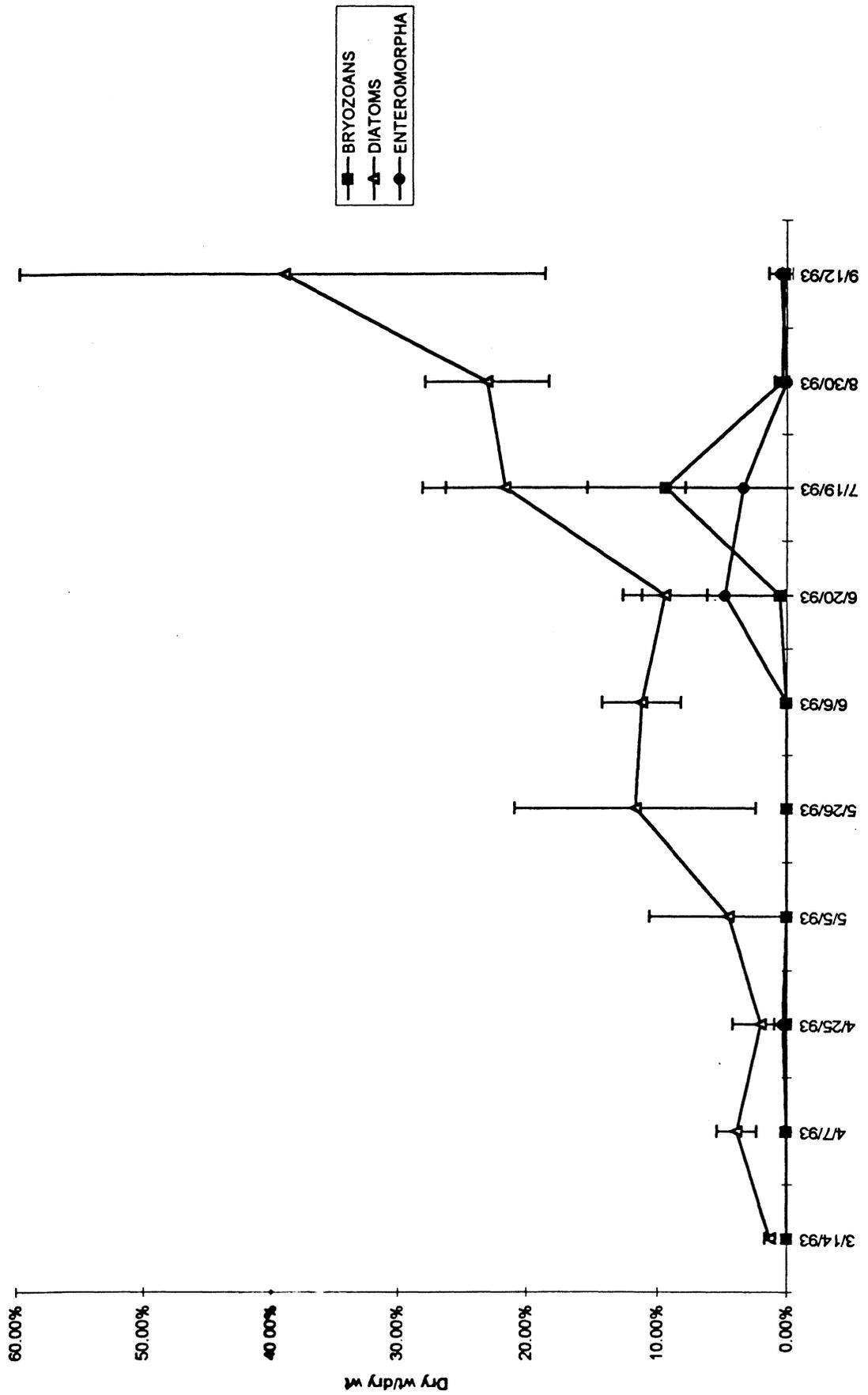
Dry wt of Epiphytes per sq. meter eel grass



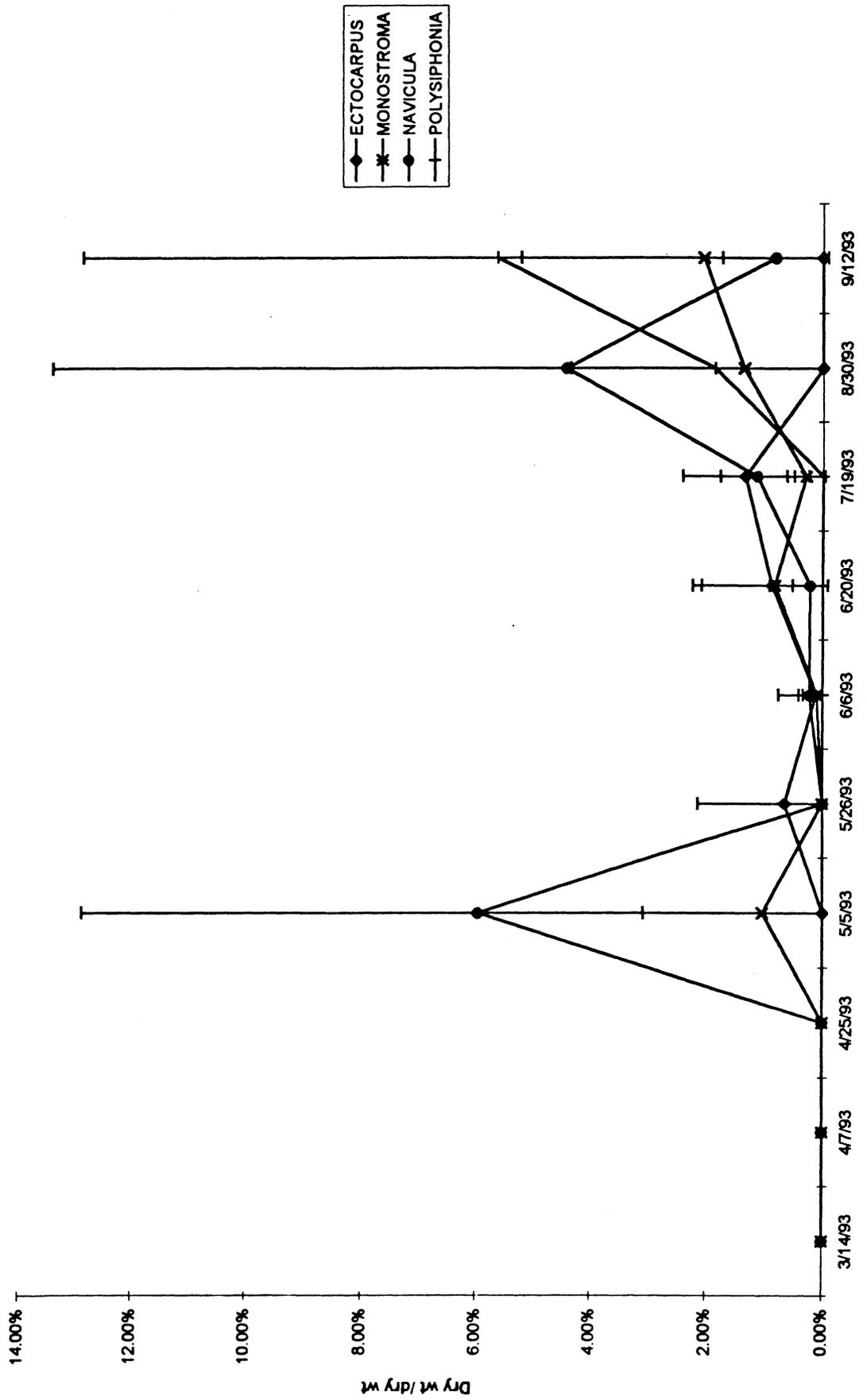
Dry wt of epiphytes per sq. meter of eel grass



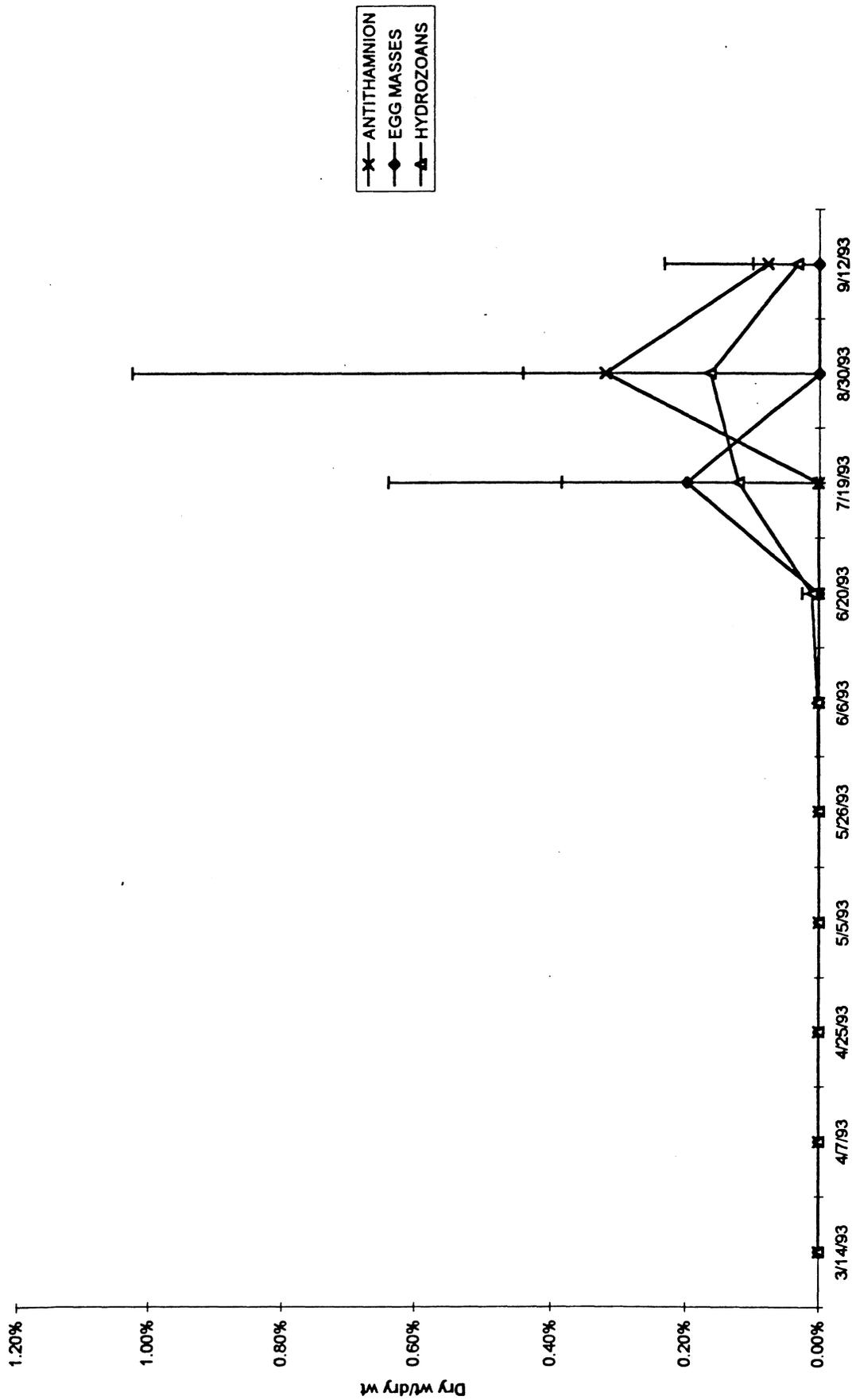
Percentage dry wt of epiphytes per dry wt of eel grass



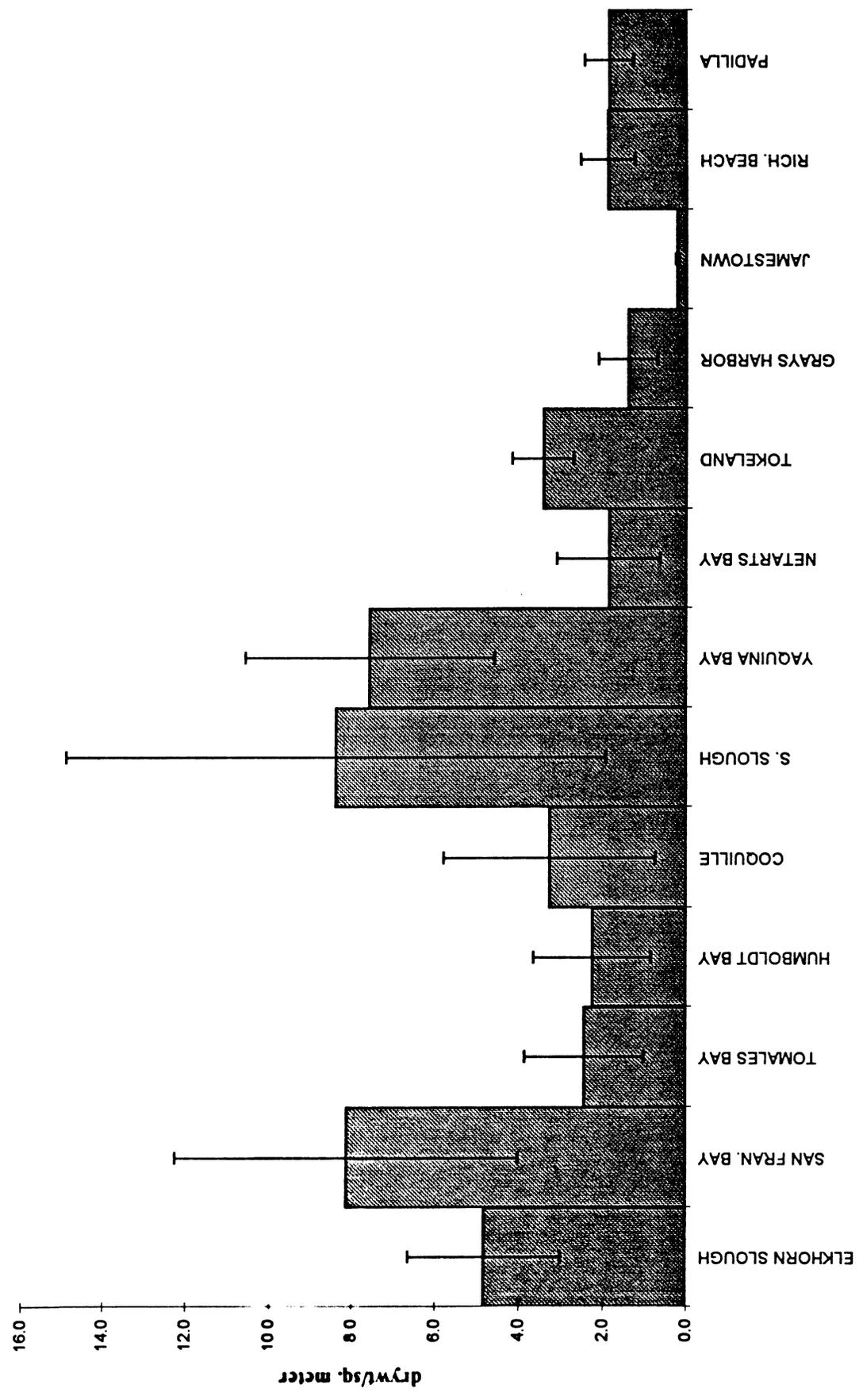
Percentage dry wt of epiphytes per dry wt of eel grass



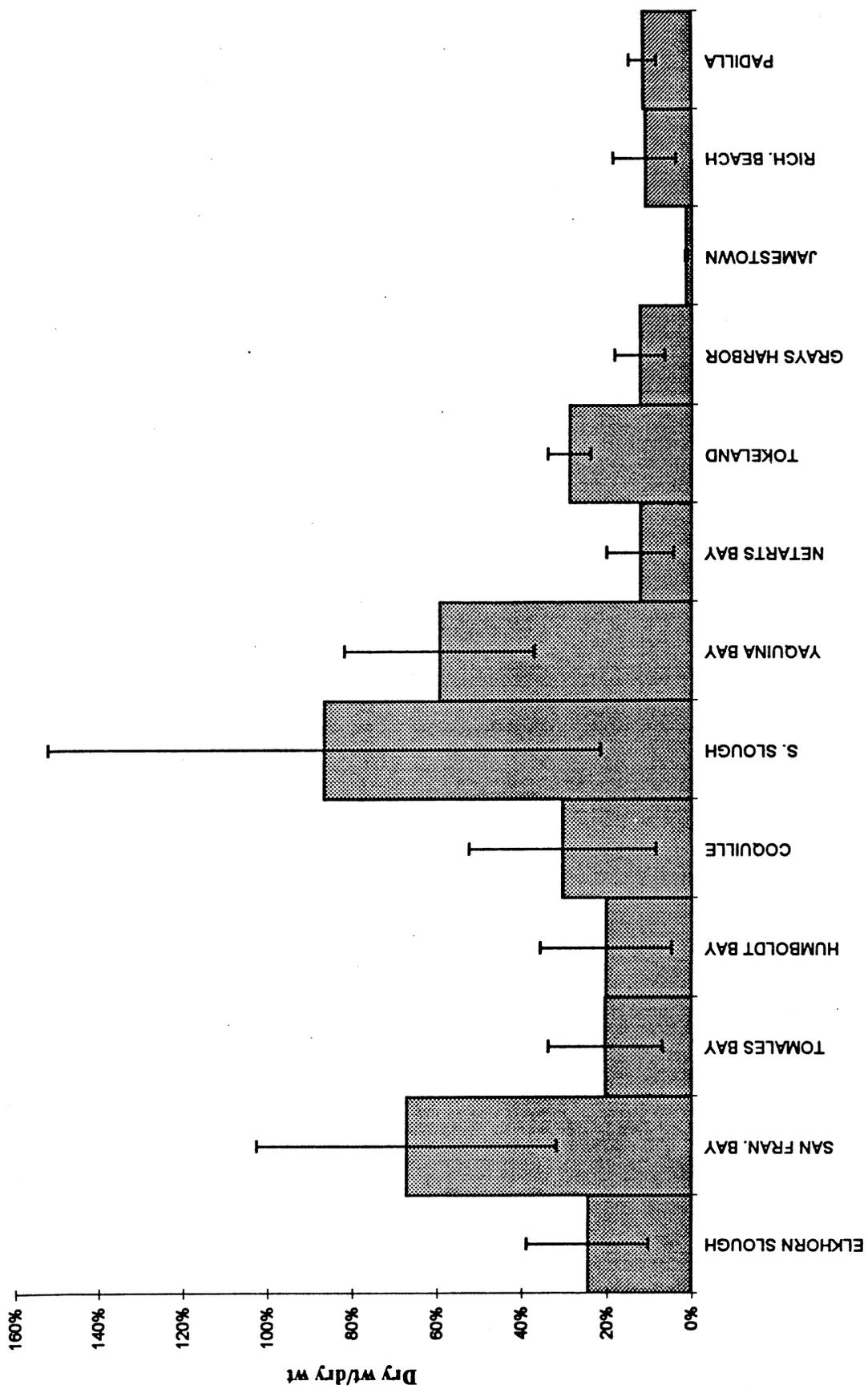
Percentage dry wt epiphytes per dry wt of eel grass



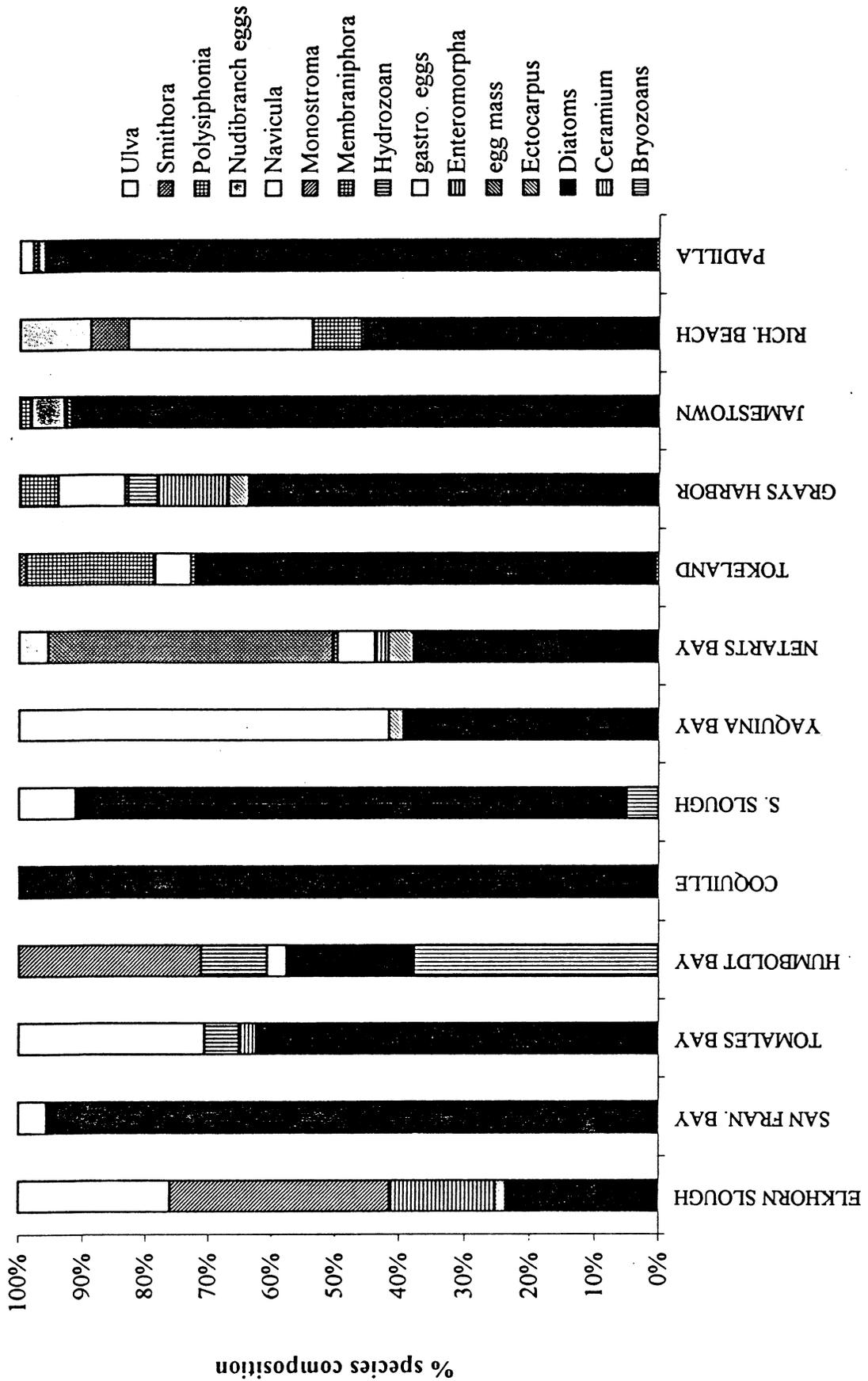
Average Drywt/sq. meter for all species



Average percent dry wt/dry wt of eelgrass for all species



Percent species composition for all estuaries



Dry wt of epiphyte per dry wt of eel grass

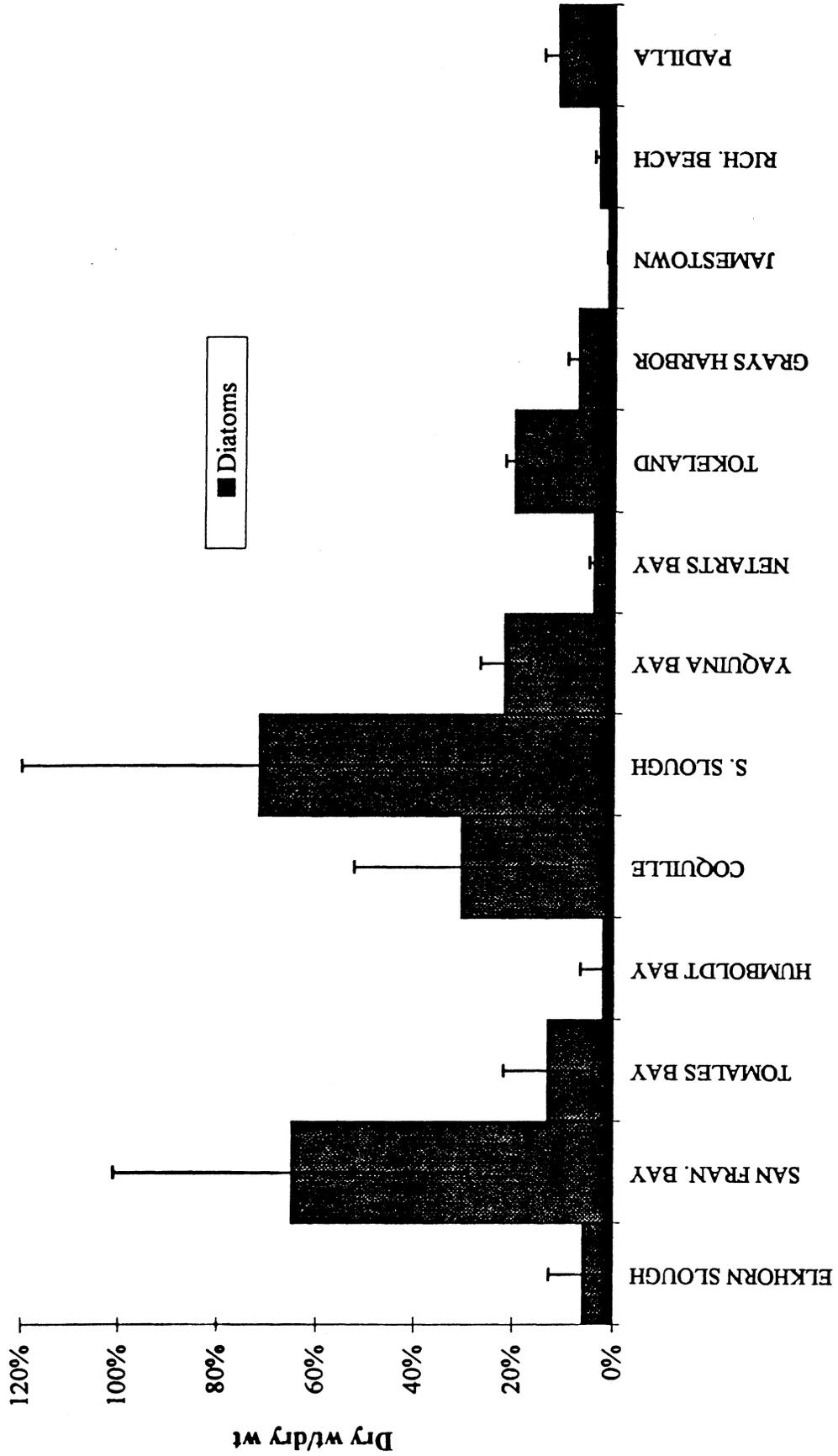
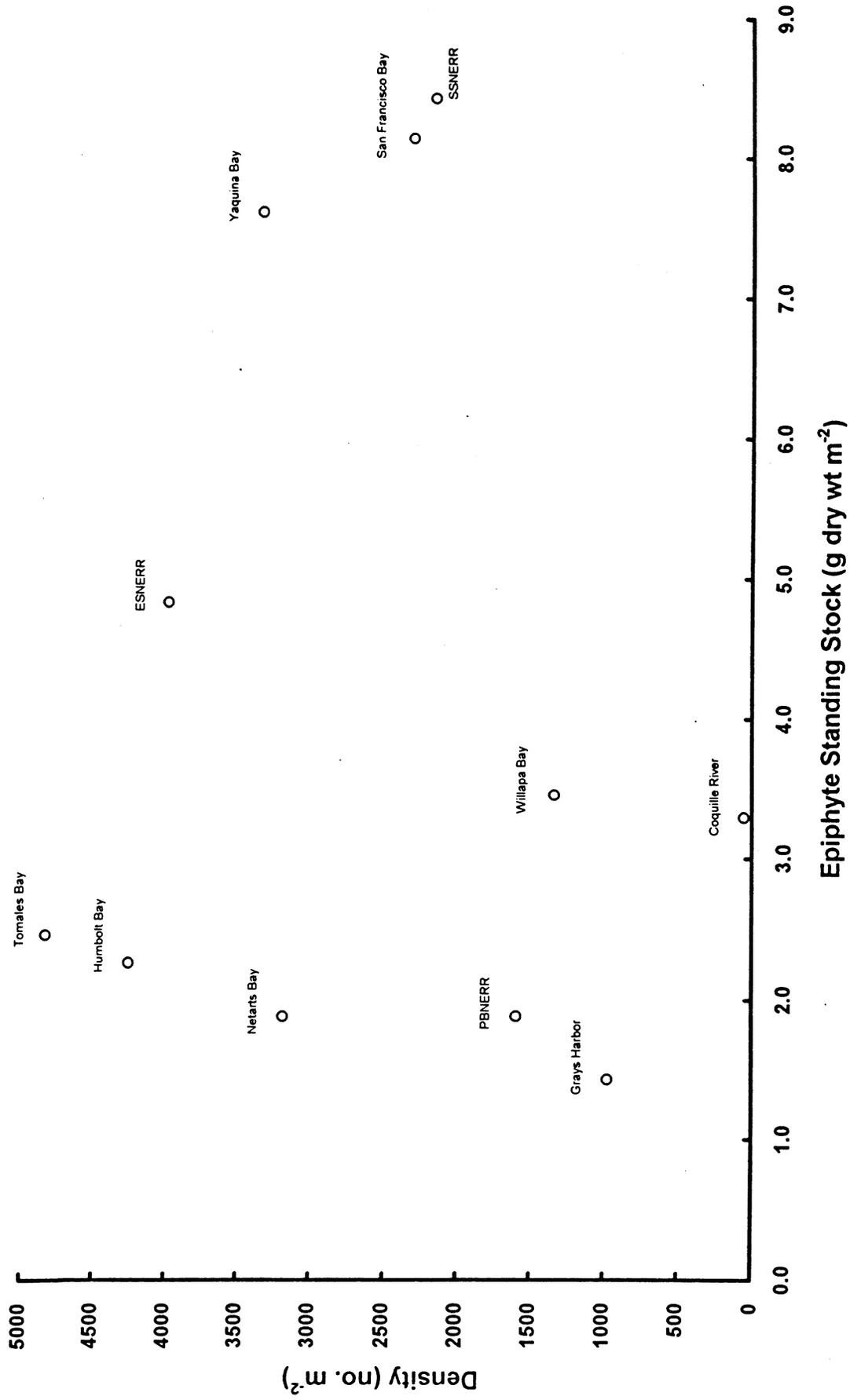
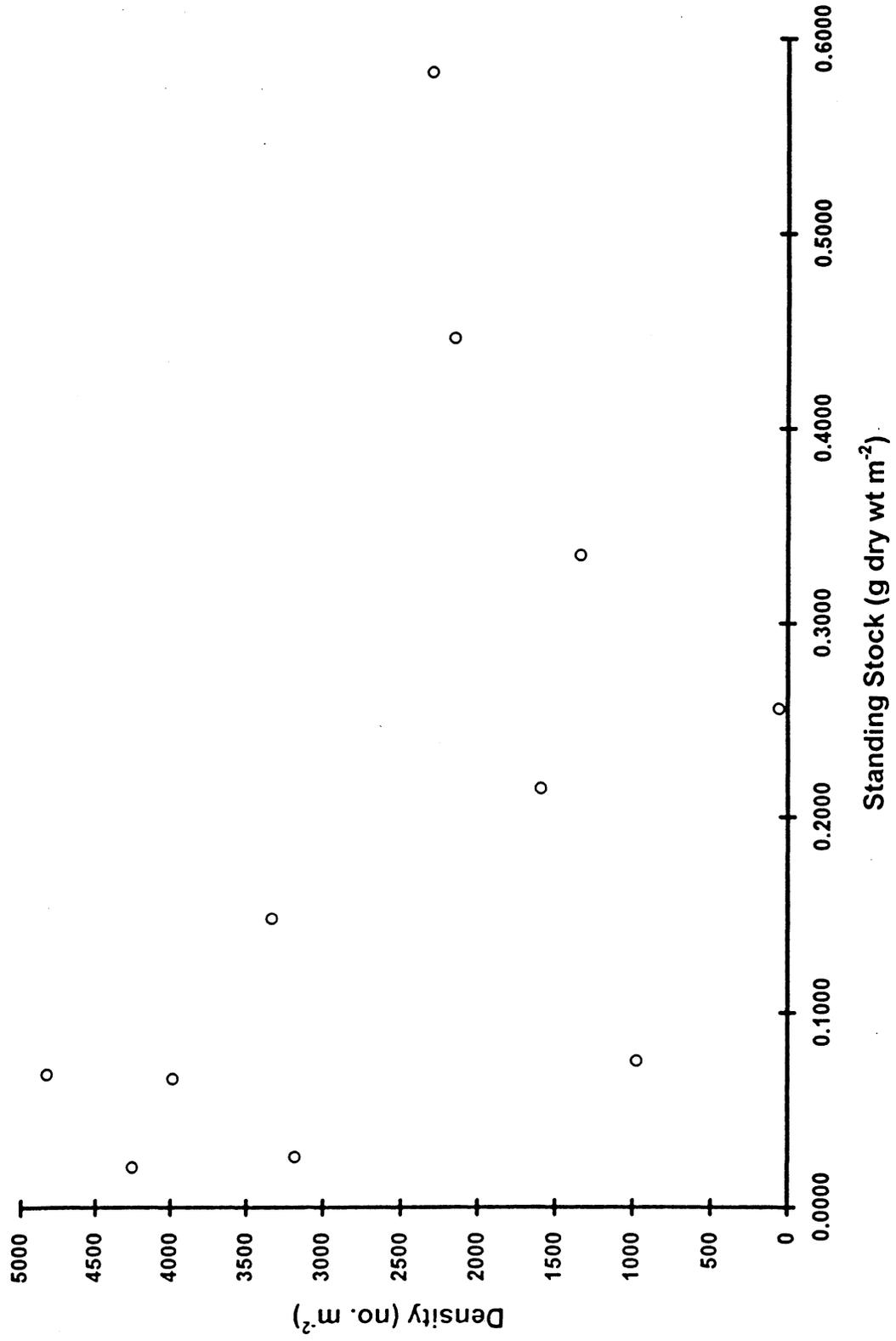


FIG 19

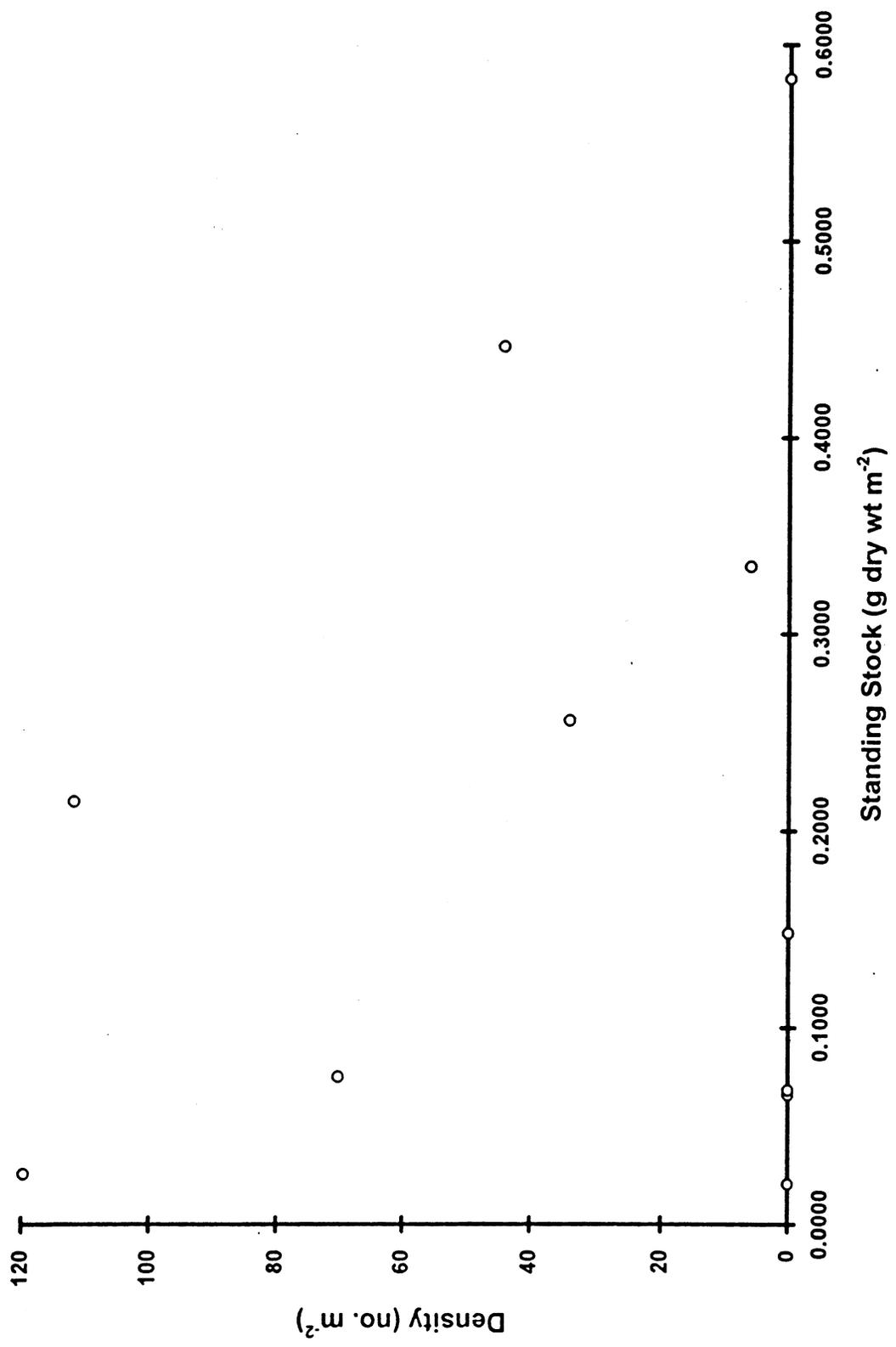
TOTAL HARPACTICOID DENSITY vs.
EPIPHYTE STANDING STOCK



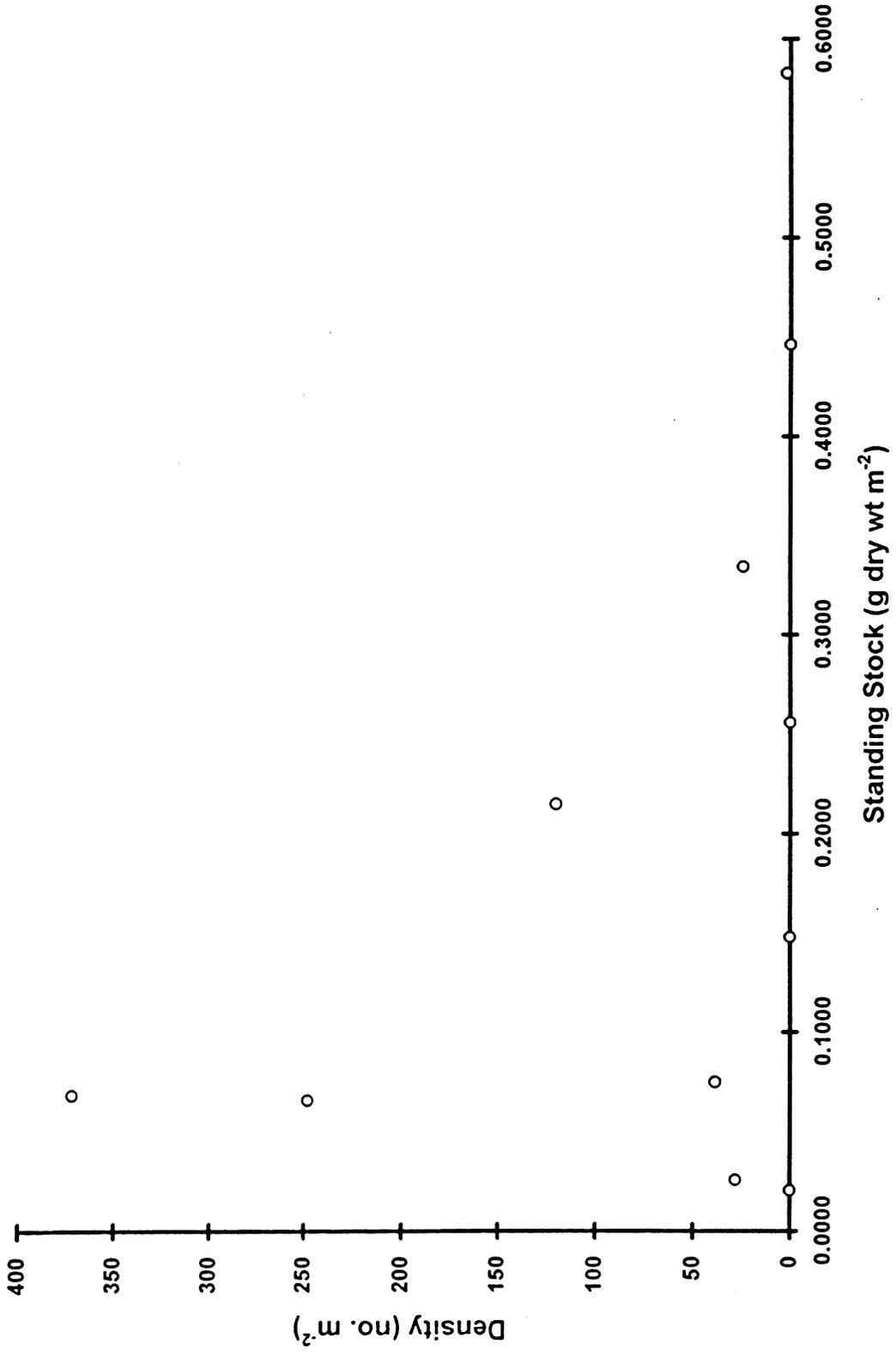
Total Harpacticoids vs. Diatom Standing Stock



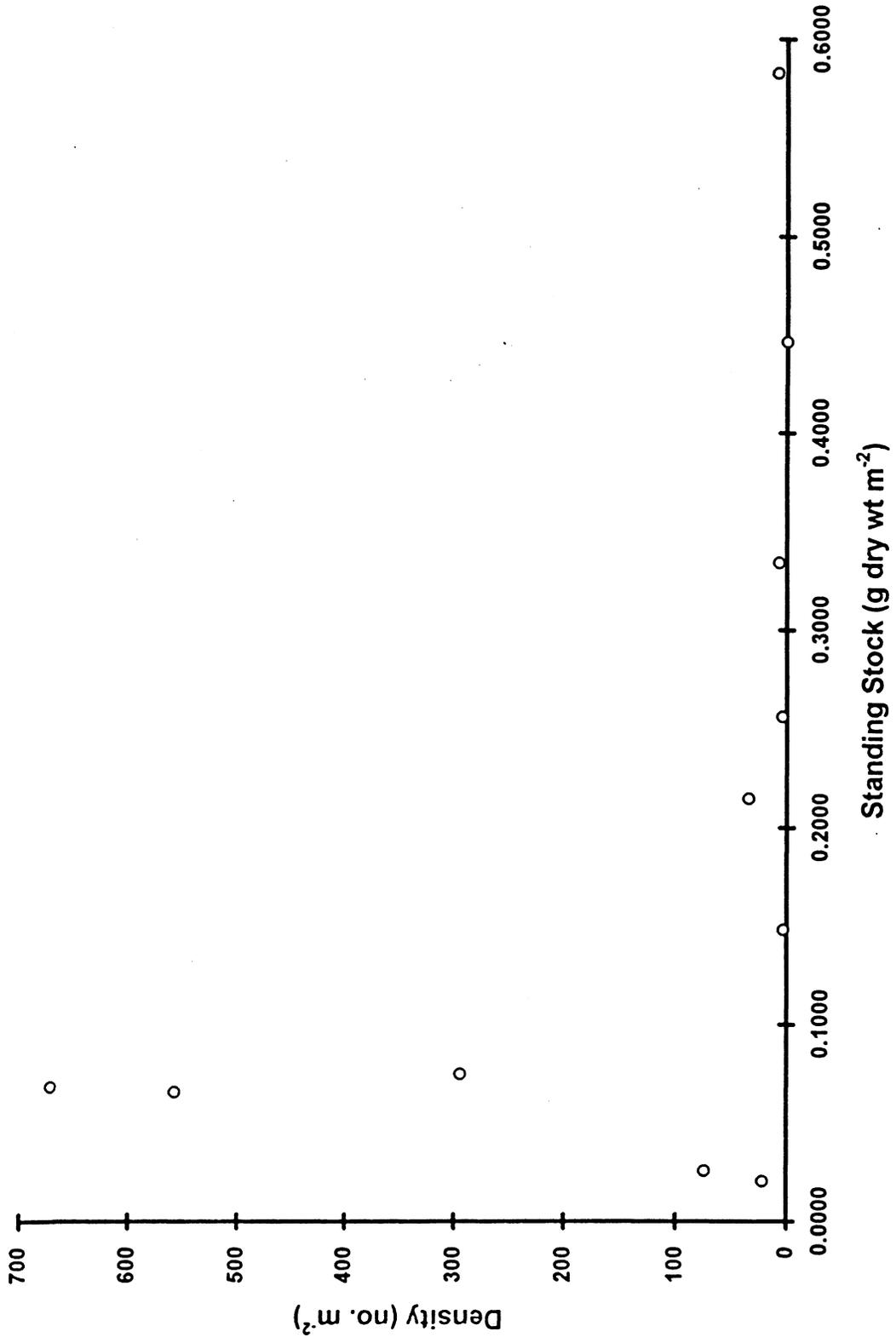
Harpacticus uniremis group vs. Diatom Standing Stock



Tisbe sp. vs. Diatom Standing Stock



Dactylopodia spp. vs. Diatom Standing Stock



Bibliographic citation: Simenstad, Charles A., Jeffrey R. Cordell, Kurt L. Fresh, and Mark Carr. 1995. Trophic linkages from epibenthic crustaceans in littoral flat habitats: Seasonal and regional comparisons. Washington State Department of Ecology Publication No. 01-06-029, Padilla Bay National Estuarine Research Reserve Reprint Series No. 35.

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