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National Estuarine Research Reserve

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Assemblage Structure, Microhabitat Distribution, and Food Web Linkages of Epibenthic Crustaceans in Padilla Bay National Estuarine Research Reserve, Washington.

Charles A. Simenstad, Jeffrey R. Cordell, Robert C. Wissmar, Kurt L. Fresh, Steven L. Schroder, Mark Carr, Gene Sandborn, and Mary Burg

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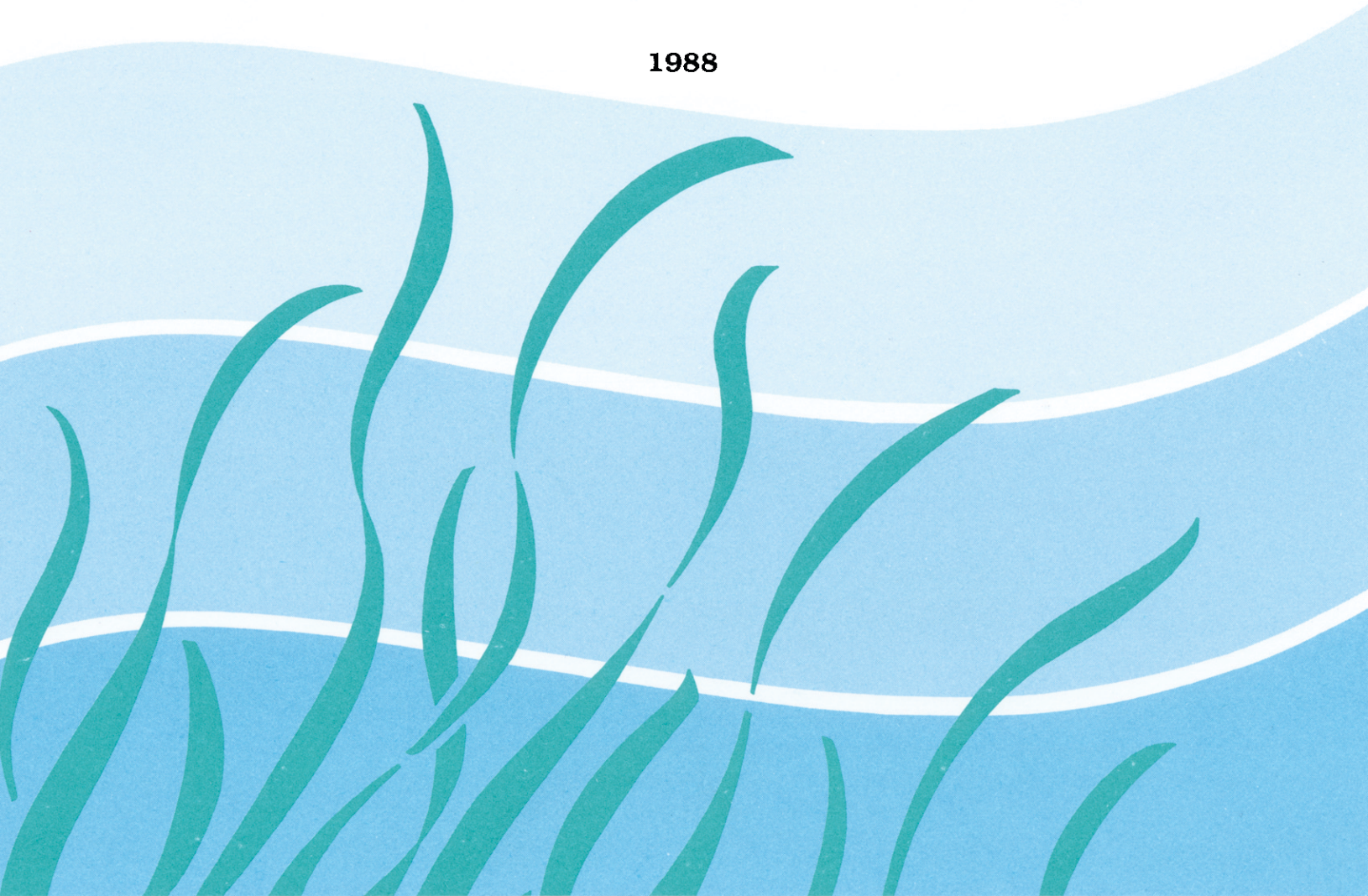

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ASSEMBLAGE STRUCTURE, MICROHABITAT DISTRIBUTION, AND FOOD WEB LINKAGES OF EPIBENTHIC CRUSTACEANS IN PADILLA BAY NATIONAL ESTUARINE RESEARCH RESERVE, WASHINGTON

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The assemblage structure and standing stock, relative abailability at different tidal stages and in different microhabitats, and importance as prey of fishes were determined for epibenthic crustaceans in four habitats across a littoral flat gradient in Padilla Bay National Estuarine Research Reserve in May 1986. Harpacticoid copepods generally dominated assemblages in surface sediments, the benthic boundary layer, the leading edge of the inundating tide and on Zostera marina eelgrass blades, but species compositions and standing stocks differed among the microhabitats. Four of five fish species prominent in the estuary at this time--surf smelt, juvenile chum salmon, adult Pacific sand lance, and adult threespine stickleback--had fed extensively upon epibenthic harpacticoids; only juvenile Pacific herring had fed on pelagic prey, which were burrowing shrimp larvae. Harpacticoid taxa in all the fishes' diets were predominantly (≈50%-94% total harpacticoid abundance) three taxa--Harpacticus uniremis, Zaus sp., and Tisbe spp. Numerical classification analyses indicated that the first two of these prey taxa were almost exclusive members of one assemblage unique to eelgrass blades, particularly associated with high epiphyte growth; Tisbe was dispersed broadly throughout the flat. These results provide evidence that the functional importance of eelgrass habitats in producing important prey resources for estuarine fishes extends beyond that habitat's resident fish community.

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ABSTRACT

In May 1986, the assemblage structure of epibenthic meiofauna and small macrofauna, their relative availability at different stages in the tidal cycle and in different microhabitats, and their trophic importance to fishes were examined in four habitats across a littoral flat gradient in Padilla Bay, Washington. Composition and standing stock of epibenthic crustaceans were described for three stages in the tidal cycle: (1) those in sediments during tidal exposure; (2) those carried by the leading edge of the inundating tide; and (3) those found in the benthic boundary layer during areal submergence. Microhabitat utilization of epibenthos living on the Bay's principal macrophyte, the eelgrass *Zostera marina*, was also examined among sections of eelgrass blades, which represented different degrees of epiphyte growth and blade morphology. Nematodes and harpacticoids numerically dominated surface sediments and the benthic boundary layer; harpacticoids predominated in the leading edge of the inundating tide and on *Z. marina* blades. Total epibenthos density and standing crop were an order of magnitude different in the three microhabitats, decreasing from 1 X 10^7 m^{-2} in the surface sediment to 1 X 10^6 m^{-2} during tidal inundation, and 1 X 10^5 to 1 X 10^4 m^{-2} in the benthic boundary layer. Harpacticoid densities on eelgrass blades with high epiphyte growth averaged twice as dense (113 100-cm^{-2}) as on plants with low epiphyte growth (54 100-cm^{-2}), excluding the basal segments adjacent to the substrate and rhizomes, where densities increased to almost 2000 100-cm^{-2} on the high epiphyte plant. Using numerical analysis techniques, we were able to discriminate eleven assemblages among six habitat clusters. Four assemblages were unique to specific habitats and/or microhabitats, while the others tended to be distributed ubiquitously across the littoral flat. Analyses of stomach contents of five fishes prominent in the estuary at this time—juvenile and adult surf smelt (*Hypomesus pretiosus*), juvenile Pacific herring (*Clupea harengus pallasi*), juvenile chum salmon (*Oncorhynchus keta*), adult Pacific sand lance (*Ammodytes hexapterus*), and adult threespine stickleback (*Gasterosteus aculeatus*)—indicated that epibenthic crustaceans, specifically harpacticoid copepods, dominated prey composition except in herring, which had fed on burrowing shrimp larvae. Furthermore, harpacticoid taxa in all the fishes' diets were predominantly (~50%-94% harpacticoid abundance) restricted to three taxa—*Harpacticus uniremis*, *Zaus* sp. and *Tisbe* sp. The first two of these harpacticoid taxa were prominent members of one assemblage unique to *Z. marina* blades, particularly the plant with high epiphyte growth; while *Tisbe* sp. was most abundant in the eelgrass habitats, it was one of the taxa dispersed broadly throughout the flat. These results provide evidence that the predominant prey of both resident and non-resident estuarine fishes in Padilla Bay are harpacticoid copepods, which originate in eelgrass beds, and therefore extend the functional importance of eelgrass habitats beyond the habitat's resident fish community.

TABLE OF CONTENTS

Page

LIST OF FIGURES v
LIST OF TABLES vi
PREFACE viii
INTRODUCTION 1
Definition, Composition, and Importance of Epibenthos 1
Research Questions 2
Objectives 2
MATERIALS AND METHODS 4
Description of Study Area and Sampling Sites 4
Epibenthos Sampling Transect 4
Fish Sampling Sites 7
Epibenthos Sampling 7
Sediment Cores 7
Tidal Inundation Samplers (TIS) 8
Epibenthos Suction Sampling 8
Eelgrass Blade Sampling 8
Fish Collections 8
Laboratory Processing 9
Epibenthic Crustaceans 9
Fish Stomach Contents 10
Data Management and Analyses 10
RESULTS 13
Habitat Composition of Epibenthos by Microhabitat 13
Littoral Flat Exposure 13
Tidal Inundation 13
Littoral Flat Submergence 13
Eelgrass Blade Segment Microhabitats 20
Epibenthos Density and Standing Crop 20
Epibenthic Harpacticoid Assemblage Structure 20
Fish Assemblage Composition and Diets 41
Overlap Among Fish Diet and Epibenthos 49
Prey Selection 49
DISCUSSION 53
REFERENCES 56

LIST OF FIGURES

Figure Page

1. Location of littoral flat transects along which epibenthic organisms and fish and were sampled in Padilla Bay, Washington, May 1986 5
2. Numerical composition of principal epibenthos taxa in surface sediments during tidal exposure..... 15
3. Numerical composition of principal epibenthos taxa in leading edge of inundating tide..... 17
4. Numerical composition of principal epibenthos taxa in benthic boundary layer during tidal submergence..... 19
5. Numerical composition of epibenthic organisms on eelgrass plants with low and high epiphyte growth. 23
6. Total epibenthos density and standing crop during tidal submergence, inundation and exposure; note log scale 24
7. Taxa richness and density of adult harpacticoid copepods on 10-cm segments of eelgrass plants with low and high epiphyte growth 40
8. Relationship between the taxa richness of adult harpacticoid copepods and the number of blades on 10-cm segments of eelgrass with low and high epiphyte growth..... 41
9. Nodal constancy plot of littoral flat habitat and adult harpacticoid copepod clusters discriminated by numerical classification of epibenthos density data..... 42

LIST OF TABLES

Table | Page

1. Habitat and environmental characteristics of sites sampled for epibenthos and fish in Padilla Bay National Estuarine Research Reserve, Washington, May 1986 6
2. Density and standing crop of principal epibenthos taxa in surface sediments during tidal exposure of four littoral flat habitats in Padilla Bay, Washington, May 1986 14
3. Density and standing crop of principal epibenthos taxa collected from tidal front during inundation of four littoral flat habitats in Padilla Bay, Washington, May 1986 16
4. Density and standing crop of principal epibenthos taxa in benthic boundary layer during tidal submergence of four littoral flat habitats in Padilla Bay, Washington, May 1986 18
5. Mean density and standing crop of principal epibenthos taxa collected on 10-cm segments of two *Z. marina* plants in Padilla Bay, Washington, May 1986 21
6. Densities of harpacticoid copepod taxa collected in surface sediment cores during tidal exposure of littoral flat habitats in Padilla Bay, Washington, May 1986 25
7. Densities of harpacticoid copepod taxa collected from tidal inundation samplers during tidal inundation of four littoral flat habitats in Padilla Bay, Washington, May 1986 28
8. Densities of harpacticoid copepod taxa collected in epibenthic layer during flood slack tide in four littoral flat habitats of Padilla Bay, Washington, May 1986 31
9. Densities of harpacticoid copepod taxa on 10-cm segments of *Z. marina* plant #1 in Padilla Bay, Washington, May 1986; numerical composition in parentheses 34
10. Densities of harpacticoid copepod taxa on 10-cm segments of *Z. marina* plant #2 in Padilla Bay, Washington, May 1986; numerical composition in parentheses 36
11. Adult harpacticoid assemblages discriminated by numerical classification using Bray-Curtis dissimilarity at 0.65 level 43
12. List of fish and macroinvertebrate species caught in the beach seine and purse seine in Padilla Bay, May 9, 1986 46
13. Fish analyzed for stomach contents in Padilla Bay, Washington, May 1986 47
14. Summary of the prey eaten by five species of fishes captured in Padilla Bay, Washington, May 1986 48

Table Page

15. Percent numerical and gravimetric composition of harpacticoid copepods identified as prey in the stomachs of fish predators collected from Padilla Bay, Washington, May 1986. 50

16. Comparison of the food habits of adult smelt from *Z. marina* habitat and adult and juvenile smelt from mudflat habitat in Padilla Bay, May 9, 1986; there were no empty stomachs 51

PREFACE

We sincerely appreciate the assistance and cooperation of Terry Stevens, Director, and the staff of the Padilla Bay National Estuarine Research Reserve in providing equipment, facilities and logistic support. The manuscript was greatly improved by the review of Ronald Thom and that of Marcus Duke, who provided the final editing and production.

This research describes the structure and ecology of littoral flat fauna, which are important prey resources for fishes utilizing Padilla Bay. These predator-prey relationships relate directly to concurrent research in the production and nutrient dynamics of seagrasses (Ronald Thom and Susan Williams, respectively), and indirectly to the research on the total distribution of seagrasses in the Bay (Thomas Mumford, Washington Department of Natural Resources, and Herbert Webber, Western Washington State University).

INTRODUCTION

Definition, Composition, and Importance of Epibenthos

Epibenthic (or "hyperbenthic", *sensu* Hesthagen 1973 and Sibert 1981) crustaceans are prominent components of the bottom-associated meiofauna and small macrofauna* inhabiting the sediment/water column interface in estuaries. The most common taxa found in the epibenthos include harpacticoid copepods, gammarid amphipods, tanaids, leptostracans, and cumaceans. Although their importance as prey of fishes and other secondary consumers is appreciated (Bregnballe 1961; McIntyre and Murison 1973; Alheit and Scheibel 1982; 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 and debated (McIntyre 1969; Coull 1970; Kuipers et al. 1981).

The spatial occurrence and distribution of epibenthic organisms in estuarine habitats reflect both environmental (e.g., hydrologic, biochemical) and biological (e.g., behavior, predation, competition) factors. Hicks and Coull (1983) have summarized distribution constraints for harpacticoid copepods as reflecting: (1) zonation patterns; (2) dispersion; and, (3) dispersal. Documentation of vertical and horizontal zonation typically indicates stratification of assemblages, as well as differences in faunal diversity and standing stock, by sediment or phytal habitats (Harris 1972; Heck and Wetstone 1977; Moore 1979; Coull et al. 1979). Microhabitat variations in the distribution of epibenthic assemblages have also been shown for characteristics such as sediment depth. In particular, heterogeneous distributions of meiofaunal crustaceans have been recently described for macrophytes (e.g., Bell 1979; Thistle et al. 1984) and other biogenic structures (e.g., Bell et al. 1978; Woodin 1978, 1981).

The causal mechanisms that are hypothesized to structure epibenthic organisms over large scales (i.e., habitats) include both active (behavioral) and passive mechanisms (resuspension in liminar-turbulent layer). Bell and Sherman (1980), Sibert (1981), Fleeger et al. (1984), Palmer (1984), Palmer and Gust (1985), and Palmer and Malloy (1986) have all illustrated strong influences of the latter mechanism, while documentation of behavioral effects are less common. Explanations for heterogeneous distributions and assemblage structure over finer scales (i.e., microhabitats) include: (1) sediment disturbance (e.g., Sherman and Coull 1980) ; (2) predator avoidance (e.g., Reise 1978, 1979; Woodin 1978, 1981; Nelson 1979); and, (3) localized food

*Meiofauna are animals passing through a 0.5-mm sieve but retained on a ~0.063-mm sieve; macrofauna are those animals passing through a 1.0-mm sieves and retained on a 0.5-mm sieve.

enhancement (e.g., Ravenel and Thistle 1981; Thistle et al. 1984; Kern and Taghon 1986). See Findlay (1981) and Hicks and Coull (1983) for a review of this often conflicting literature.

In Puget Sound and coastal estuaries of the Pacific Northwest, we have a far more limited picture of epibenthic crustacean assemblages and have only recently begun to examine habitat and microhabitat associations (Simenstad et al. 1979a; Simenstad et al. 1980; Cordell and Simenstad 1981a&b; Sibert 1981; Simenstad 1984; Simenstad and Cordell 1985; Thom et al. 1986). Although many of the same functional relationships may structure epibenthos assemblages in the Pacific Northwest, some basic regional differences (such as the higher tidal range in this region) also suggest the potential for significant variation. Given the potentially unique associations among epibenthic organisms and their importance in food webs in this region, we conducted the study described herein to describe quantitatively the zonation of epibenthic assemblages and their standing stock along a horizontal and tidal elevation gradient that encompassed several discrete littoral flat habitats. Additional, subsidiary objectives were to investigate the potential mechanisms for observed heterogeneity in assemblage distributions across and within habitats and their contributions to the estuary's food web as prey of epibenthic-feeding fishes.

Research Questions

Four questions were addressed in this research:

1. How do assemblage structure, diversity and standing stock of epibenthic crustaceans differ among littoral flat habitats?
2. Are certain assemblages or taxa transported among littoral flat habitats?
3. Do the compositions and diversity of assemblages reflect microhabitat complexity?
4. Do discrete habitats and microhabitats produce epibenthic prey of juvenile fishes feeding in the estuary?

Objectives

In order to answer these questions, we conducted sampling and analyses were conducted with the following objectives.

1. Describe the species/life history stage assemblage structure of epibenthic crustaceans across the littoral flat with the tidal elevation range of approximately +4 m to -1 m (relative to MLLW*) by:

*MLLW = mean lower low water tidal datum

   a. stratifying sampling locations along a habitat gradient, where habitat is defined by differences in sediment structure and the composition of emergent or submergent plants; and
   b. stratifying sampling, where possible, within habitat by microhabitat, where microhabitat is defined as discrete segments of emergent or submergent plants.
2. Examine quantitative and qualitative differences in assemblage structure and standing stock during tidal processes of emergence, inundation and submergence as a measure of tidal transport of epibenthos across and among littoral flat habitats.
3. Relate assemblage structure to structural complexity of the microhabitat.
4. Examine assemblage, habitat and microhabitat origins of taxa that occur prominently as prey of fishes in the estuary.

MATERIALS AND METHODS

Description of Study Area and Sampling Sites

The assemblage structure of epibenthic organisms, their relative availability at different stages in the tidal cycle, and trophic importance to fishes feeding in the Bay were examined in four habitats across a littoral flat gradient in the Padilla Bay National Estuarine Research Reserve (PBNERR), in northern Puget Sound, Washington (Fig. 1). Padilla Bay is an estuarine embayment with no direct freshwater discharge other than drainage from agricultural lands via sloughs with tidegates. Freshwater enters Padilla Bay from Skagit Bay to the south via Swinomish Channel and from Samish Bay to the north. As a result of the discharge patterns from these sources and tidal energies, salinities generally range from 15 to 30 ppt (Cassidy and McKeen 1986). The Bay is shallow (generally <2 m deep) and sixty percent of the bay is a low gradient (approximately 0.3-m elevation change per mile) above MLLW (Washington Department of Ecology 1984). Numerous tidal channels 3-m to 5-m deep cut through the flats, including two major channels draining Indian Slough at the south end of the Bay and Joe Leary Slough in the northern third of the Bay. Water temperatures range from 7°C in the winter to over 20°C under solar warming of shallow water over the flats in summer.

All sampling was conducted during daylight hours between 9 and 12 May, 1986. During this sampling period, the weather was typically partially overcast, light to moderate winds from the south, light rain showers, and mid-day air temperatures of 18 to 20°C. Water temperatures in marine waters offshore averaged ~10°C; in tidal channels sampled for fish, the still saline (28.2‰ to 29.2‰) waters were slightly warmer, up to ~12°C; and during tidal inundation of the flats, temperatures increased from 18.0°C over the *Zostera marina* meadow to 26.0°C in the salt marsh (Table 1).

Epibenthos Sampling Transect

Epibenthos sampling sites were located along a transect utilized by a number of PBNERR researchers, and which extends in a southeast direction from a fringing salt marsh, across a mudflat, through *Zostera japonica*, and terminates in the middle of a *Z. marina* meadow (Fig. 1; Table 1). The tidal elevations of these habitats ranged from +7.2 ft. in the salt marsh to +0.5 ft. in the *Z. marina* meadow, relative to mean lower low water (MLLW).

The fringing salt marsh habitat site was located on the east shore (the "Sullivan-Minor" property) of the PBNERR. Sampling occurred at low elevations in and around salt pans associated

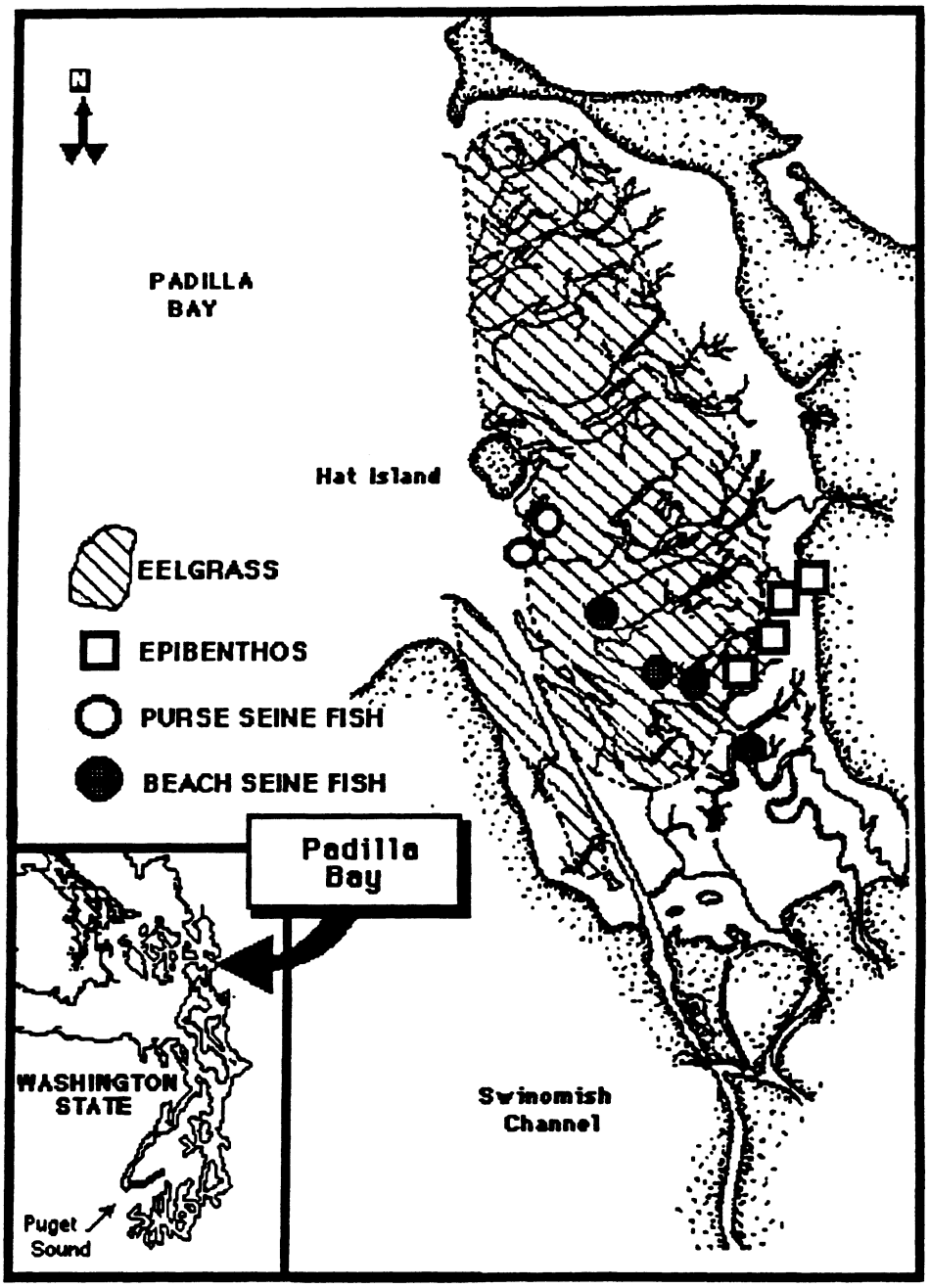

Figure 1. Location of littoral flat transects along which epibenthic organisms and fish and were sampled in Padilla Bay, Washington, May 1986.

Table 1 Habitat and environmental characteristics of sites sampled for epibenthos and fish in Padilla Bay National Estuarine Research Reserve, Washington, May 1986.

A. Epibenthos sampling, 10-11 May:

Site	Collections	No. of samples	Temperature (°C)	Habitat
SM1	cores	5		*Salicornia* salt marsh
	tidal inundation samplers	5		+7.2 ft. MLLW
	epibenthic suction	5	26.0	
MF1	cores	5		sand/mud flat
	tidal inundation samplers	5		+4.5 ft. MLLW
	epibenthic suction	5	23.0	
ZJ1	cores	5		*Zostera japonica* meadow
	tidal inundation samplers	5		+1.2 ft. MLLW
	epibenthic suction	5	20.5	
ZM1	cores	5		*Zostera marina* meadow
	tidal inundation samplers	5		+0.5 ft. MLLW
	epibenthic suction	5		
	eelgrass sections	1[a]	18.0	
ZM2	eelgrass sections	1[b]		

B. Fish sampling:

Site	# Sets	Temperature (°C)	Salinity (‰)	Habitat
Purse seine;				
A	1	9.8	---	Offshore
B	3	9.8	---	Offshore
Beach seine;				
E	1	12.2	28.2	Steep channel, mud, *Ulva*
D1	1	11.9	29.0	Sand, *Z. marina*
B1	2	11.9	28.2	Sand, *Z. marina*
C1	1	11.9	28.8	Sand, shallow, mixed eelgrass
D2	1	11.8	29.2	Sand/mud, mostly *Z. marina*

[a]nine blade segments from one plant; low epiphyte growth
[b]nine blade segments from one plant; high epiphyte growth

predominately with *Salicornia virginica* (90.6% cover, 100% frequency in quadrat plots) and, to a lesser extent, *Distichlis spicata* (7.4%, 80%) and *Atriplex patula* (9.4%, 67%) emergent plants (Granger and Burg 1986). Tidal water enters the sampling sites through a channel and breaks in the gravel berm that fronts the marsh; minor freshwater seepage enters the marsh from uplands.

The mudflat habitat was located approximately 100-m west of the salt marsh and was completely unvegetated but for thin diatom mats. The substrate was a combination of fine sand and mud, with small patches of bivalve shell and gravel.

Z. japonica, an exotic species of eelgrass believed to have been introduced with oyster seed from Japan in the 1930s (Harrison 1976), occupies a relatively narrow band between the mudflat and the more expansive *Z. marina* habitat. Substrate is a mixed coarse sand-gravel with bivalve shells. Sampling occurred approximately 750 to 800 m southwest of the saltmarsh.

The *Z. marina* habitat in Padilla Bay covers approximately 3,500 ha, and represents one of the largest contiguous eelgrass meadows in the Pacific Northwest (Thom 1988). The eelgrass habitat supports an overwintering population of black brant (*Branta bernicla*) and is a suspected spawning ground of Pacific herring (*Clupea harengus pallasi*), although there was no evidence of spawning within the boundaries of the PBNERR during four surveys in February-March 1987 (Penttila 1987). Epibenthos sampling occurred at the edge of a shallow tidal channel approximately 1.3 km southwest of the salt marsh. Substrate was coarse sand over a gravel matrix.

Fish Sampling Sites

Because of the limited water depths, fish sampling sites were located farther offshore than were epibenthic samples and along the Indian Slough tidal channel (Fig. 1). All fish sampling sites had heavy eelgrass cover.

Epibenthos Sampling

Sediment Cores

During tidal exposure of each habitat along the transect (ebb tide), five replicate samples were obtained with a ~3-cm I.D. core (~28 cm^2) inserted 10 cm into the sediments. Small scale heterogeneities of each habitat (e.g., rocks, pockets, ripple marks, etc.) were avoided during sampling to minimize variability. Upon removal from the sediments, the cores were fractioned into the surface (top 2 cm) and subsurface samples (remainder of core) and preserved separately in buffered 10% formalin.

Tidal Inundation Samplers (TIS)

During aerial exposure just prior to tidal inundation, replicated (n = 5) tidal inundation samplers were placed at each site along the transect. These samplers were composed of 300-cc plastic jars with ping-pong balls inside; they were buried in the sediment until the lip of each jar was at the level of the surface sediment. Designed to sample the tidal front as it floods across the littoral flat and into the salt marsh, they fill with the initial tidal front and seal as the buoyant ping-pong ball floats to the top of the jar and occludes the mouth. The traps were retrieved via a buoyed line attached to each trap, and the contents preserved immediately in buffered 10% formalin. The jar mouth's surface area, 11.34 cm^2, was assumed to sample a similar area of the tidal front, although they were observed to draw from a slightly larger surface area when filling.

Epibenthos Suction Sampling

The epibenthos was sampled 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 with approximately 0.3 m of water covering the marsh). The laminar or lower turbulent layer over 179 cm^2 of the sediment surface was 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). Five replicate samples were obtained from each habitat.

Eelgrass Blade Sampling

Eelgrass (*Z. marina*) plants covered by water in shallow tidal channels were sampled for indications of microhabitat stratification in epibenthos assemblages. Blades from one plant were fractioned into 10-cm lengths and preserved *in toto* with epiphytes intact. Two whole plants were sampled, one without and one with extensive epiphyte growth.

Fish Collections

Potential predators of epibenthic crustaceans in Padilla Bay were collected from approximately 2 h before the daytime low tide to approximately 2 h afterwards. Shallow, sublittoral habitats were sampled with a 37-m beach seine that was set 30 m from the waterline from the back of a small boat and hauled to shore by two 2-person teams. During submergence of the tidal flat and in deeper habitats, predators were collected with a 66-m by 6-m purse seine. The purse seine was set by making a round haul with the net on the bottom during most of the set.

At least one set was made at each of five sites with the beach seine and at each of two sites with the purse seine (Fig. 1). At each site, environmental data was recorded (temperature, salinity and qualitative description of the weather) and a general description of the habitat was made (vegetation, beach slope, sediment type) (Table 1).

Catches from most sets were sufficiently small so that they could be preserved in their entirety in labelled jars. In several instances, however, large quantities of seagrass (*Z. marina*) and macroalgae (*Ulva* sp.) in the seine made it impossible to quantitatively subsample and enumerate catches. Consequently, a representative sample of predators (i.e., encompassing the available species and size classes) was retained and the rest of the catch was released. All predators were preserved in the field in 10% buffered formaldehyde and then transferred to 90% ethanol within one week of capture.

Laboratory Processing

Epibenthic Crustaceans

Because of the complexity and abundance of epibenthic organisms, and thus the time required to process the samples, only three of the five replicate samples could be fully processed within the time and effort allocation of this study.

Sediment cores were divided into two increments: 0-1 cm in depth, and >1 cm in depth. All samples were preserved in 5% formalin and transferred to 45% isopropyl alcohol preservative with a biological stain (rose bengal) after sieving and other separation. *Z. marina* blades were measured for later calculation of blade area. Sediment cores, TIP, and epibenthic pump samples were sieved through nested 0.125-, 0.250-, and 0.500-mm screens; if necessary, organisms were separated from fine sediments by panning. When present, epiphytes (diatoms and small macroalgae) were separated from seagrass blades and macroalgae and were sieved through the same nested screens.

All 0.500-mm size fractions (macroepibenthos) were examined *in toto*. The 0.250-mm size fractions were subsampled, if necessary, using a Hensen-Stempel pipette; the 0.125-mm size fraction was retained for further reference (they contained principally early, unidentifiable stages of crustaceans and larvae of other organisms).

Under an illuminated stereo microscope, epibenthic organisms were sorted, identified, enumerated and weighed by species and life history stage (e.g., nauplii, copepodid, male, gravid female, etc.).

Fish Stomach Contents

Stomach contents of predators were systematically analyzed using standardized procedures which quantify the occurrence, numeric composition, and gravimetric composition of prey (Terry 1977). Predators selected for stomach analysis were first measured for fork length (FL) and weighed (nearest 0.01 g). Stomachs were removed from the esophagus just prior to the pylorus, the contents removed as a bolus, blotted on tissue paper and weighed to the nearest 0.01 g. Qualitative measures of stomach fullness (1 = empty to 7 = distended) and digestion (1 = complete to 6 = no digestion) were also made.

Small samples of prey organisms were processed in their entirety while larger samples were split to a more manageable size of up to several hundred organisms using a Folsom plankton splitter. Prey organisms were sorted to convenient taxonomic groups, typically order, although harpacticoids and gammarid amphipods were identified to species when possible. Each prey category was enumerated and weighed to the nearest 0.01 g. Precision in identifying food items depended on the life history stage of the prey and the stage of digestion. Thus, food habits data often encompassed several taxonomic levels for perhaps the same or homologous species.

Data Management and Analyses

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, thus providing 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. All data was entered by an experienced data entry operator and was automatically verified at the time of entry.

Tabulation and basic statistical descriptions of epibenthic crustacean sample composition and predator stomach contents data were produced with FRI computer programs (SUPERPLANKTON and GUTBUGS/IRI, respectively, which run on the UW's Cyber 180-855 mainframe computer; Swanson and Simenstad 1984) specifically developed for NODC-formatted data. These tabulations standardized all data to standing stock on a unit area (m^2) basis. Summarized data were analyzed further on either the Cyber mainframe or on a microcomputer using commercial statistical software.

A modification of the Index of Relative Importance (IRI; Pinkas et al. 1971) was utilized to help describe food habits. An IRI value for each prey item was computed, where IRI = (%

frequency occurrence [% numerical composition + % gravimetric composition]) and was standardized to % ΣIRI.

Comparisons were made between epibenthic assemblage compositions and between predator diets and the available prey using several indices. To assess the overall similarity between diets and the available prey in each of the habitats that were sampled and to compare the similarity in diets between predator species, the percent similarity index (PSI) was used (Chesson 1983):

$$PSI = \text{minimum } (p_i, r_i),$$

where p_i is the percentage of prey i in the predator x, and r_i is the percentage of prey i obtained from epibenthic samples. A value of 100% indicates complete overlap between what the fish has eaten and what is found in the environment. The smaller size classes (e.g., nauplii) of organisms that were found in the epibenthos but not in fish stomachs were not included in these analyses. Prey organism abundances were used to calculate PSI indices.

To assess the degree of selection for specific epibenthic organisms (those that were most important in fish diets) the Standard Forage Ratio (SFR) was used (Manly et al. 1972, Chesson 1983) where:

$$SFR = \frac{(p_i/r_i)}{(\Sigma p_i/r_i)} .$$

Values range between 0 and 1, with preference indicated when SFR >1/m (where m is the number of available prey species) and avoidance indicated for values <1/m. All values were calculated using organism abundances.

Assemblage structure was examined quantitatively through agglomerative hierarchical classification (clustering) of density data using the Bray-Curtis dissimilarity measure (Bray and Curtis 1957; Boesch 1973) and group average sorting. Collections (samples from habitats and microhabitats) constituted the entities, and species densities were utilized as the attributes. Similarities among sampling sites were determined using transformed ($\ln[X_{ij} + 1]$) data, and taxa assemblages were clustered using standardized (X_{ij}/X_{ik}) data. The coincidence among site (including discrete habitat/microhabitat samples) and taxa clusters was illustrated in two-way constancy plots (Williams and Lambert 1961; Lambert and Williams 1962; Noy-Meir 1971; Boesch 1973; Beals 1984), where constancy (i.e., the relative degree of site group and taxa cluster coincidence) is expressed as $C_{ij} = a_{ij}/[n_i n_j]$ and a_{ij} is the number of occurrences of taxa i in site

cluster j and n_i, and n_j are the numbers of entities in the respective clusters. A Bray-Curtis dissimilarity level of 0.65 was used as the threshold of cluster similarity because of its common occurrence in the literature.

In reporting and discussing the results, we chose to emphasize those epibenthic crustaceans known or suspected to be of primary importance as prey of estuarine fishes (i.e., harpacticoid copepods and gammarid amphipods) for the basis of these analyses.

RESULTS

Habitat Composition of Epibenthos by Microhabitat

Littoral Flat Exposure

During tidal exposure, invertebrate taxa found in the surface sediments were numerically dominated by nematodes, harpacticoid copepods, turbellarians and oligochaetes (Table 2, Fig. 2). The least taxa categories (17, including life history stages) occurred in the *Salicornia* marsh and the maxima in the two *Z. japonica* and *Z. marina* habitats (57 and 51, respectively); the mudflat was intermediate (32) (Table 2). The proportion of harpacticoid copepods increased from the marsh to the outer eelgrass (*Z. marina*) habitat, while nematodes and polychaetes fluctuated among the four habitats. Certain taxa, such as turbellarians and oligochaetes, tended to be most prominent in the marsh; other taxa, such as gammarid amphipods (*Corophium ascherusicum, C. insidiosum, Allorchestes* sp.), cumaceans (*Cumella vulgaris*), tanaids (*Leptochelia dubia, Tanais* sp.), and ostracods occurred predominantly in the mudflat and *Z. japonica* habitats. Numerical diversity was lowest (Shannon-Weiner H'= 2.15) in the marsh and highest (4.92) in the *Z. japonica* habitat; gravimetrically, diversity was also lowest (1.11) in the marsh but was highest (4.27) in the *Z. marina* habitat (Table 2). Much of the differences among numerical and gravimetric diversity in the four habitats reflected the relative contribution of polychaete and oligochaete annelids and gammarid amphipods, which are generally larger in individual biomass than the rest of the epibenthos.

Tidal Inundation

The invertebrate fauna associated with the leading edge of the inundating tide was dominated by harpacticoid copepods across all four habitats, from ~95% in the *Z. marina* habitat to ~50% in the *Salicornia* marsh (Table 3; Fig. 3). Other prominent taxa were insects (Collembola, Nematocera) in the mudflat habitat and turbellarians in the saltmarsh. Similar to the surface sediment samples, taxa richness was lowest (38) in the marsh habitat and highest (58) in the *Z. japonica* habitat (Table 3). Gravimetric diversity, however, increased from 3.15 in the *Z. marina* habitat to 4.19 in the mudflat habitat (Table 3).

Littoral Flat Submergence

During tidal submergence of the littoral flat, harpacticoid copepods were also numerically prominent and increased across the littoral flat gradient from 14% in the *Salicornia* marsh to 86% in the *Z. marina* habitat (Table 4; Fig. 4); other dominant taxa were nematodes and turbellarians (marsh), ostracods (mudflat), calanoids (copepodids, *Acartia longiremis*) and undifferentiated

Table 2. Density (no. m^{-2}) and standing crop (in parentheses; mg m^{-2}) of principal epibenthos taxa in surface sediments during tidal exposure of four littoral flat habitats in Padilla Bay, Washington, May 1986.

Taxa	Habitats			
	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Turbellaria	1,433,333 (12,000)	400,000 (2,667)	3,333 (333)	
Kinorhyncha		390,000 (8,000)		
Nematoda	6,486,670 (12,667)	2,633,333 (3,000)	3,263,333 (8,000)	1,833,333 (4,000)
Annelida				
Polychaeta	946,667 (36,667)	1,533,333 (38,666)	136,667 (13,999)	613,333 (51,333)
Oligochaeta	993,333 (414,667)	106,667 (6,667)	66,667 (2,667)	166,667 (27,333)
Bivalvia				40,000 (18,000)
Araneae		13,333 (1,333)		13,333 (667)
Ostracoda		196,667 (3,000)	110,000 (3,666)	6,667 (667)
Copepoda				
Harpacticoida	1,373,332 (19,322)	2,056,667 (36,000)	1,580,000 (27,329)	2,720,000 (62,000)
Poecilostomatoida				6,667 (667)
Tanaidacea	(1,333)	230,000	23,333 (25,666)	86,667 (4,000)
Cumacea			140,000 (4,000)	6,667 (1,333)
Amphipoda				
Gammaridea		106,667 (48,000)	170,000 (43,999)	13,333 (1,333)

Table 2. Density (no. m^{-2}) and standing crop (in parentheses; mg m^{-2}) of principal epibenthos taxa in surface sediments during tidal exposure of four littoral flat habitats in Padilla Bay, Washington, May 1986 - cont'd.

Taxa	Habitats			
	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Caprellidea				6,667 (667)
Insecta	26,667 (1,335)	70,000 (3,000)	56,667 (4,000)	
Total density (mean)	11,300,002	7,736,667	5,540,000	5,800,000
(s.d.)	9,153,619	6,826,697	3,026,558	5,028,471
Total standing crop (mean)	498,000	139,000	110,000	188,000
(s.d.)	389,528	112,654	19,468	26,907
Total number of taxa categories	17	32	57	51
Shannon-Weiner Diversity Index, H';	2.15	3.38	4.92	3.52
numerical biomass	1.11	3.97	2.28	4.27

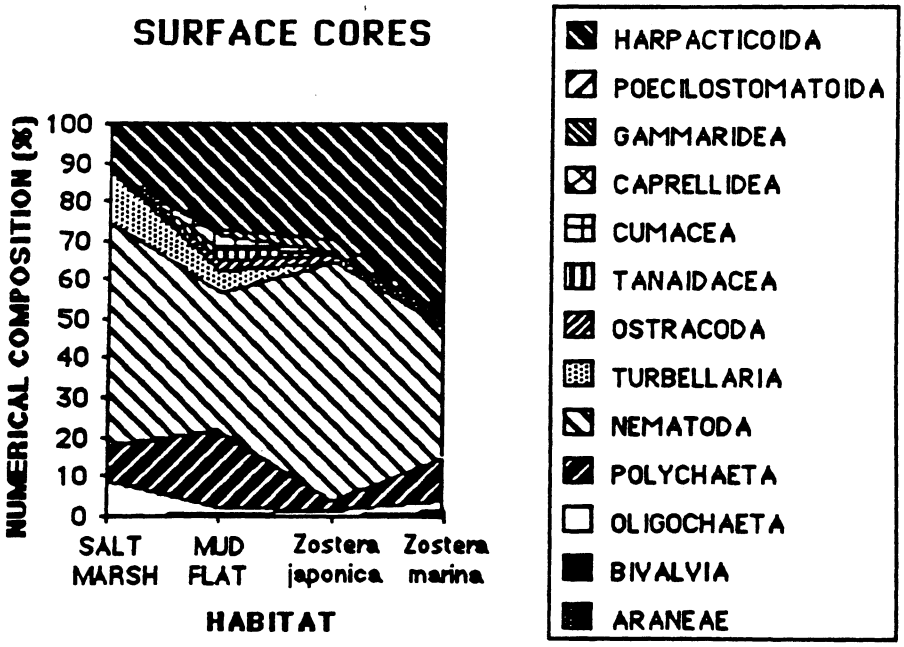

Figure 2. Numerical composition (% total density) of principal epibenthos taxa in surface sediments during tidal exposure.

Table 3. Density (no. m^{-2}) and standing crop (in parentheses; mg m^{-2}) of principal epibenthos taxa collected from tidal front during inundation of four littoral flat habitats in Padilla Bay, Washington, May 1986.

Taxa	Habitats			
	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Turbellaria	233,333 (10,444)			
Nemertea	1,111 (14,556)			
Nematoda	38,889 (222)	10,000 (222)	45,556 (667)	7,778 (222)
Annelida				
Polychaeta	1,111 (111)	2,222 (111)		
Oligochaeta	35,556 (8,889)			
Araneae	2,222 (4,778)			
Ostracoda	7,778 (333)	11,111 (222)	42,222 (778)	
Copepoda				
Calanoida		50,000 (1,100)	246,667 (7,444)	2,222 (111)
Harpacticoida	1,373,332 (19,322)	2,056,667 (36,000)	1,580,000 (27,329)	2,720,000 (62,000)
Poecilastomatoida	2,222 (222)	8,889 (333)	40,000 (1,334)	8,889 (556)
Balanomorpha		1,111 (111)	5,556 (556)	
Cumacea	1,111 (111)	21,111 (2,555)	72,222 (13,000)	2,222 (333)
Amphipoda				
Gammaridea		17,778 (778)	26,667 (4,889)	3,333 (778)
Caprellidea		1,111 (111)	2,222 (222)	4,444 (333)

Table 3. Density (no. m^{-2}) and standing crop (in parentheses; mg m^{-2}) of principal epibenthos taxa collected from tidal front during inundation of four littoral flat habitats in Padilla Bay, Washington, May 1986 - cont'd.

Taxa	Habitats			
	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Decapoda		1,111 (111)	1,111 (111)	
Insecta	6,667 (6,222)	9,111 (11,333)	7,778 (1,000)	
Total density (mean)	644,444	517,778	2,085,555	825,556
(s.d.)	380,122	578,603	1,695,034	520,303
Total standing crop (mean)	54,000	27,000	42,444	12,000
(s.d.)	45,732	19,877	23,892	4,910
Total number of taxa categories	38	49	58	48
Shannon-Weiner Diversity Index, H';	3.31	4.19	3.49	3.15
numerical biomass	3.22	3.38	4.53	5.22

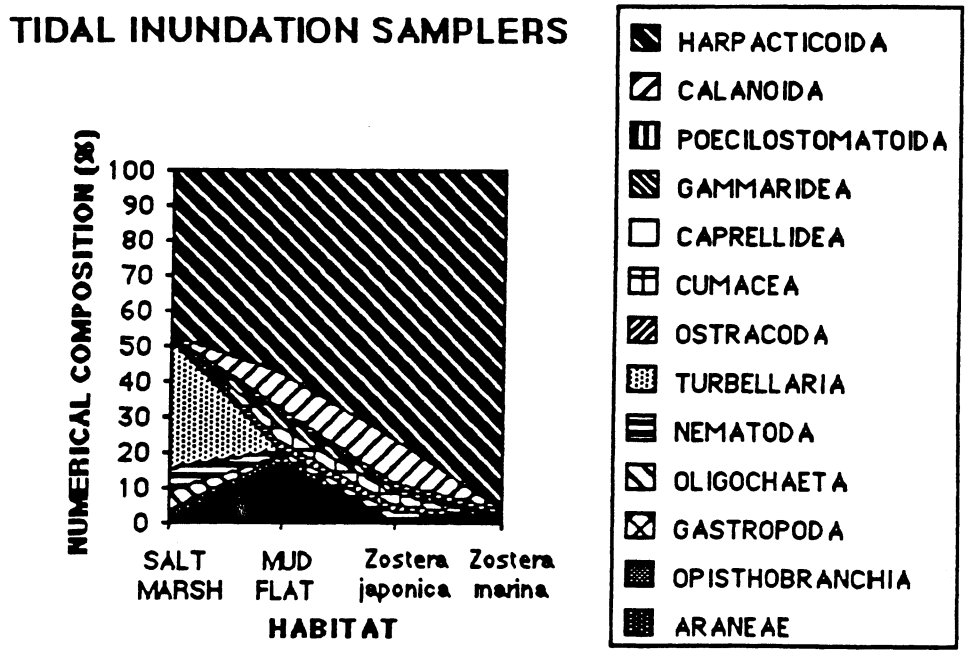

Figure 3. Numerical composition (% total density) of principal epibenthos taxa in leading edge of inundating tide.

Table 4. Density (no. m^{-2}) and standing crop (in parentheses; mg m^{-2}) of principal epibenthos taxa collected in benthic boundary layer during tidal submergence of four littoral flat habitats in Padilla Bay, Washington, May 1986.

Taxa	Habitats			
	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Turbellaria	13,083 (117)		21 (2)	
Nematoda	30,250 (54)	250 (6)		188 (4)
Annelida				
Polychaeta	1,771 (83)	125 (8)	125 (6)	125 (6)
Oligochaeta	729 (85)			
Opisthobranchia	208 (21)			
Araneae	229 (23)	42 (4)		63 (4)
Ostracoda	583 (29)	1,729 (17)	21 (2)	146 (4)
Copepoda-nauplii	1,083 (10)	583 (6)	333 (6)	438 (6)
Calanoida	83 (8)	208 (8)	188 (6)	271 (6)
Harpacticoida	8,271 (259)	1,021 (54)	1,271 (50)	13,083 (192)
Poecilostomadoida	229	42 (23)	250 (4)	(12)
Balanomorpha	646 (52)	83 (4)	188 (6)	229 (6)
Cumacea		42 (4)	42 (2)	229 (14)
Amphipoda				
Gammaridea		21 (2)	112 (17)	104 (33)
Caprellidea	21 (2)			

Table 4. Density (no. m^{-2}) and standing crop (in parentheses; mg m^{-2}) of principal epibenthos taxa collected in benthic boundary layer during tidal submergence of four littoral flat habitats in Padilla Bay, Washington, May 1986 - cont'd.

Taxa	Habitats			
	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Decapoda-larvae		21 (2)	21 (2)	
Total density (mean)	58,688	4,333	2,458	15,292
(s.d.)	54,918	1,445	806	9,871
Total standing crop (mean)	815	129	108	300
(s.d.)	716	22	10	132
Total number of taxa categories	36	35	27	53
Shannon-Weiner Diversity Index, H';	2.61	3.57	3.81	3.93
numerical biomass	4.60	4.87	4.52	5.10

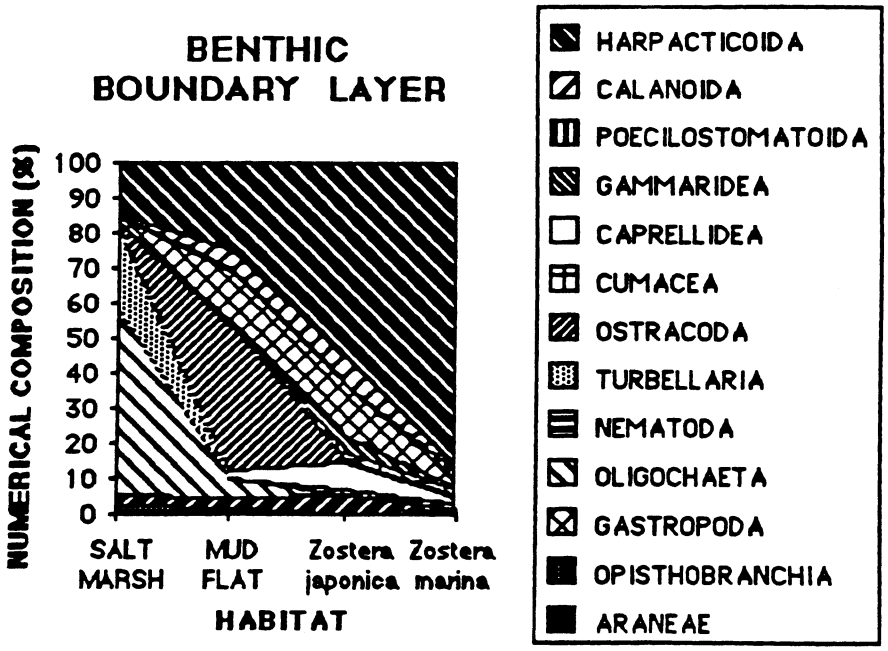

Figure 4. Numerical composition (% total density) of principal epibenthos taxa in benthic boundary layer during tidal submergence.

copepod nauplii (mudflat and *Z. japonica*), and barnacle larvae (*Z. japonica*). During tidal submergence, the epibenthos was least taxa rich in the *Z. japonica* habitat (27), and most taxa rich (53) in the adjacent *Z marina* habitat. Again, numerical diversity was lowest (2.61) in the marsh habitat, but was approximately the same (3.57-3.93) across the other habitats; gravimetric diversity was also equally high (4.52-5.10) across all habitats.

Eelgrass Blade Segment Microhabitats

Averaged over the whole eelgrass plants, harpacticoids dominated epibenthos density numerically (64%) on the low epiphyte plant and were secondary (39%) to nematodes (54%) on the high epiphyte plant (Table 5; Fig. 5). Nematodes were also abundant on both plants, especially at the base of the plant, near the sediment surface and the rhizomes; gastropods (largely *Lacuna* sp.), gammarid amphipods (principally *Pontogeneia* sp., cf *rostrata*), and turbellarians were also common (but still <10% of total density) in several segments. On both plants, gammarid amphipods comprised the greatest portion (62%-63%) of the mean standing crop (Table 5). Taxa richness and numerical and gravimetric diversity were higher on the high epiphyte plant than on the low epiphyte plant.

Epibenthos Density and Standing Crop

Densities of epibenthic organisms in the surface sediment cores ($x = 5.6$ to 11.3×10^6 m^{-2}) were higher than in the leading edge of the inundating tide (0.5 to 2.1×10^6 m^{-2}) and the benthic boundary layer during tidal submergence (2.5 to 58.7×10^3 m^{-2}) (Tables 2-4). Densities in the surface sediments declined across the habitat gradient from the salt marsh to the *Z. marina* habitat, while the epibenthos captured on the front of the inundating tide increased slightly in the *Z. japonica* habitat (Fig. 6a). Densities in the benthic boundary layer were lower in the mudflat and *Z. japonica* habitats than in the other habitats at either end of the gradient. Corresponding patterns in epibenthos standing crop (Tables 3-5; Fig. 6b) were generally similar.

Epibenthic Harpacticoid Assemblage Structure

Given the prominence of harpacticoids in the epibenthos across all habitats, and microhabitats in the case of the *Z. marina* blade segments, the structure of these assemblages was examined in more detail. Sixty-two taxa were identified (Tables 6-10), although some were identified only to the family level (uncommon taxa or those presenting particular taxonomic problems). All samples increased in taxa richness from the saltmarsh to the *Z. marina* habitat. As measured by PSI, overlap in numerical composition of harpacticoids was always greatest (PSI = 27.5 to 73.2) between

Table 5. Mean density (no. 100-cm^{-2} of blade surface) and standing crop (in parentheses: mg 100-cm^{-2}) of principal epibenthos taxa collected on 10-cm segments of two (with low and high epiphyte load) *Z. marina* plants in Padilla Bay, Washington, May 1986.

	Plants	
	#1	#2
Taxa	Low epiphyte	High epiphyte
Foraminiferida	617 (6)	
Hydroida		21 (6)
Turbellaria	645 (15)	624 (23)
Nemertea		139 (500)
Nematoda	5448 (49)	79847 (401)
Annelida		
Polychaeta	802 (821)	2178 (579)
Oligochaeta	370 (111)	417 (500)
Gastropoda	33 (10)	170 (175)
Araneae	1158 (5)	38 (4)
Ostracoda	1077 (46)	3782 (91)
Copepoda		
Calanoida	62 (6)	216 (14)
Harpacticoida	22453 (580)	57464 (1073)
Poecilostomatoida	213 (15)	274 (22)

Table 5. Mean density (no. 100-cm^{-2} of blade surface) and standing crop (in parentheses; mg 100-cm^{-2}) of principal epibenthos taxa collected on 10-cm segments of two (with low and high epiphyte load) *Z. marina* plants in Padilla Bay, Washington, May 1986.

	Plants	
	#1	#2
Taxa	Low epiphyte	High epiphyte
Cumacea	62 (6)	285 (15)
Tanaidacea		715 (391)
Isopoda	62 (6)	
Amphipoda		
Gammaridea	1927 (2913)	1300 (6158)
Caprellidea		7 (<1)
Unidentified egg case	152 (9)	
Density		
(mean)	34,957	147,478
(s.d.)	47,056	337,344
Standing crop		
(mean)	4,616	9,951
(s.d.)	9,010	26,275
Number taxa categories		
(mean)	14.8	29.9
(range)	3 - 53	16 - 57
Shannon-Weiner Diversity Index, H';		
Numerical (mean)	2.56	3.42
(range)	1.46 - 4.41	2.72 - 4.69
Biomass (mean)	2.16	3.22
(range)	1.12 - 3.40	2.10 - 4.15

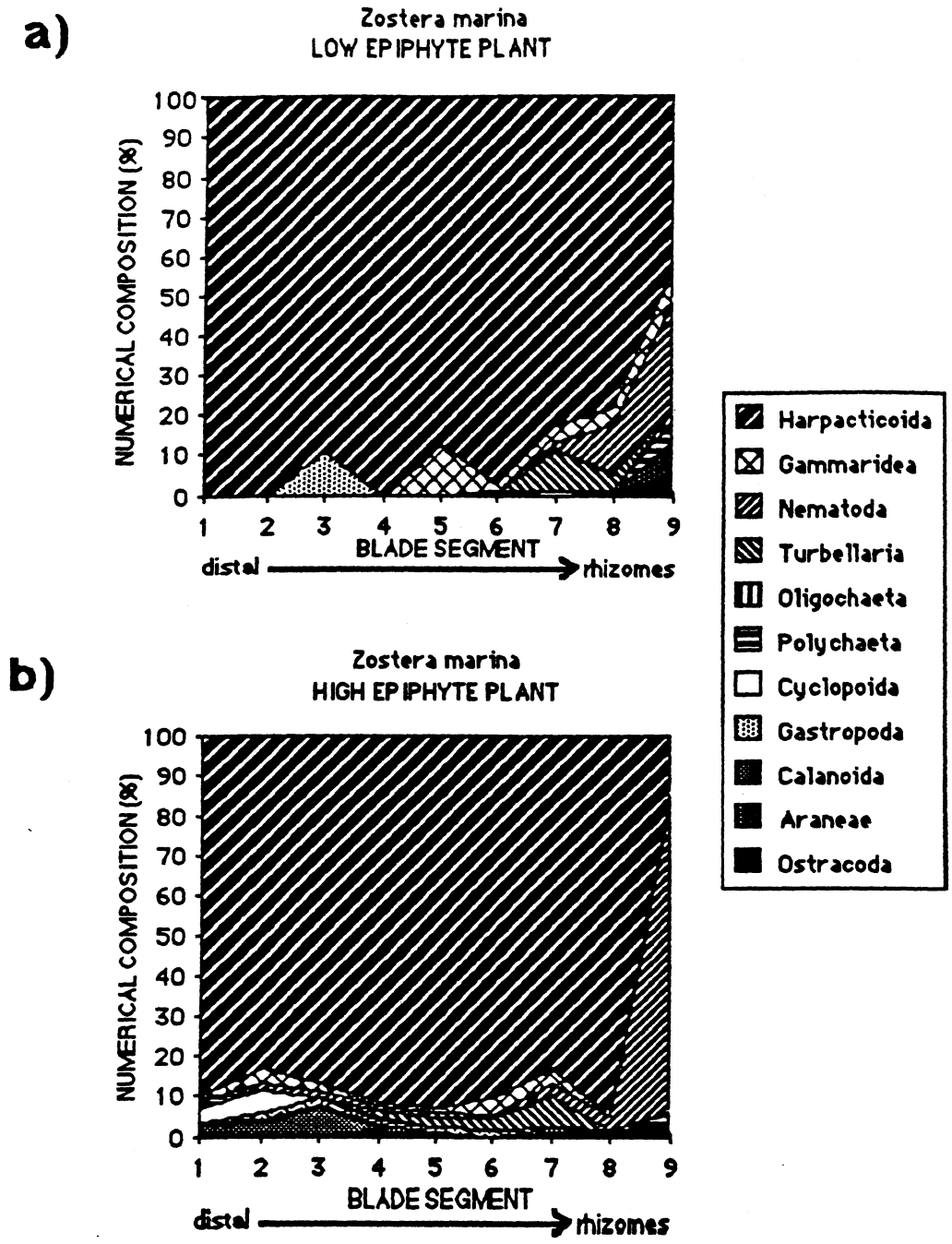

Figure 5. Numerical composition (% mean density on blade surface) of epibenthic organisms on eelgrass (*Zostera marina*) plants with low (a) and high (b) epiphyte growth.

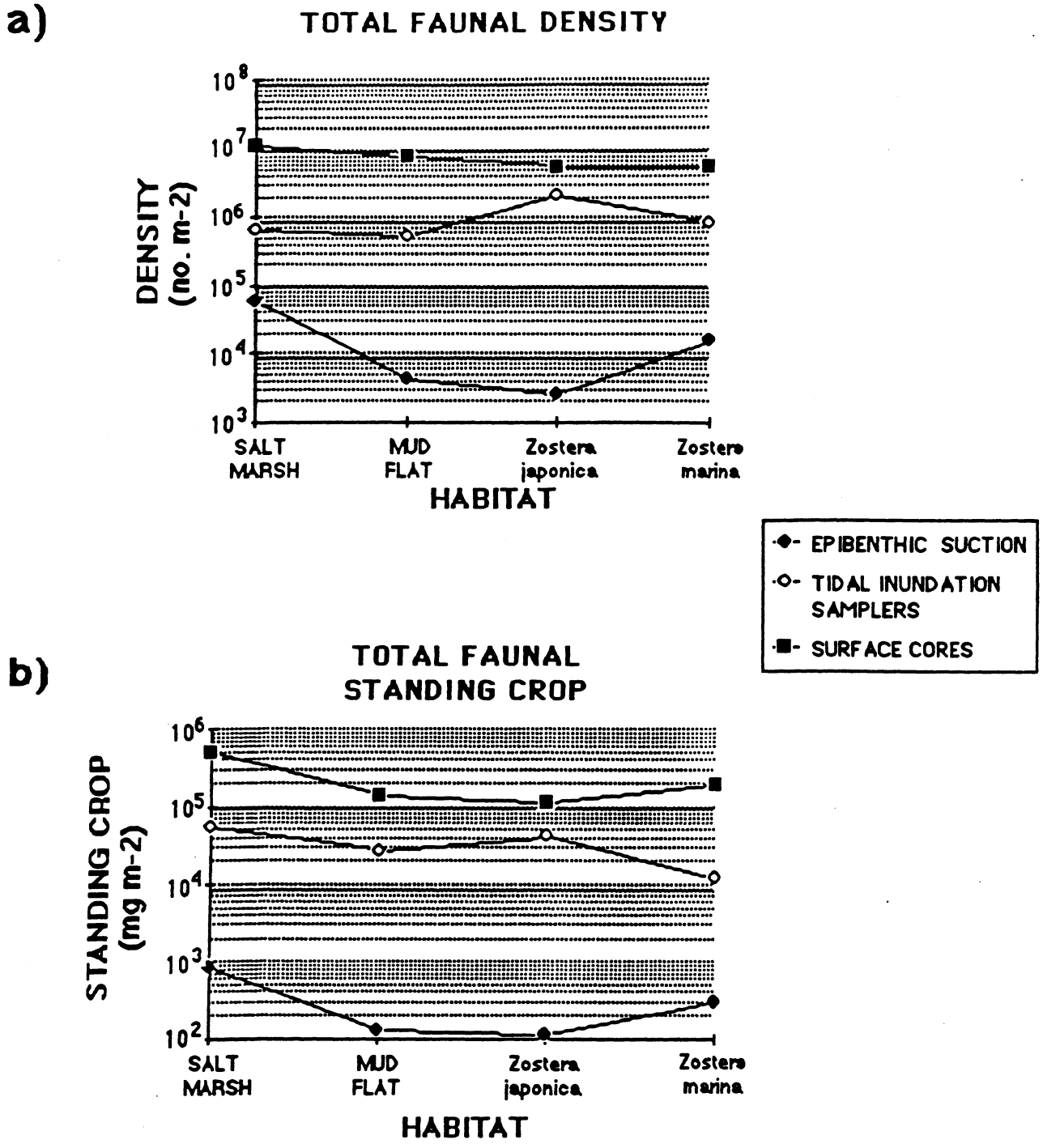

Figure 6. Total epibenthos density (a; organisms m^{-2}) and standing crop (b; mg m^{-2}) during tidal submergence (epibenthic suction), inundation (tidal inundation samplers) and exposure (surface cores); note log scale.

Table 6. Densities (no. m^{-2}) of harpacticoid copepod taxa collected in surface (to 1 cm) sediment cores during tidal exposure of littoral flat habitats in Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses.

Taxa	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
HARPACTICOIDA		**30000.0** (2.7)	**16666.7** (2.2)	**13333.3** (0.9)
Family Longipediidae *Longipedia* sp.				**20000.0** (1.4)
Family Ectinosomatidae		**440000.0** (40.0)	**33333.4** (4.3)	**106666.7** (7.5)
Family Harpacticidae *Harpacticus* sp.	**13333.3** (1.8)			
Family Tisbidae *Tisbe* spp.				**60000.0** (4.2)
Robertsonia sp. cf *knoxi*		**13333.3** (1.2)	**10000.0** (1.3)	**233333.3** (16.5)
Family Tachidiidae *Tachidius triangularis*			**3333.3** (0.4)	
Danielssenia typica				**26666.7** (1.9)
Family Laophontidae		**26666.7** (2.4)	**20000.0** (2.6)	**26666.7** (1.9)
Heterolaophonte discophora			**333.3** (0.4)	
Heterolaophonte hamondi	**13333.3** (1.8)			
Heterolaophonte variabilis			**6666.7** (0.9)	**20000.0** (1.4)
Family Ameiridae	**6666.7** (0.9)	**30000.0** (2.7)	**3333.3** (0.4)	

Table 6. Densities (no. m^{-2}) of harpacticoid copepod taxa collected in surface (to 1 cm) sediment cores during tidal exposure of littoral flat habitats in Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses - cont'd.

Taxa	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Family Cletodidae				
Enhydrosoma sp.			**3333.3** (0.4)	
Nannopus palustris	**33333.3** (4.5)	**13333.3** (1.2)		
Rhizothrix sp.			**16666.7** (2.2)	
Family Diosaccidae		**13333.3** (1.2)		
Amonardia perturbata				**6666.7** (0.5)
Amphiascopsis cinctus				**20000.0** (1.4)
Amphiascus undosus				**13333.3** (0.9)
Amphiascus sp.A-*varians* gp.			**23333.3** (3.0)	**6666.7** (0.5)
Stenhelia cf *inopinata*			**130000.0** (16.9)	
Stenhelia peniculata			**206666.7** (26.8)	**113333.4** (8.0)
Stenhelia sp.A		**80000.0** (7.3)		
Tymphlamphiascus pectinifer				**40000.0** (2.8)
Amphiascoides cf *subdebilis*	**6666.7** (0.9)	**453333.4** (41.2)	**90000.0** (11.7)	**93333.4** (6.6)
Amphiascoides sp.A			**6666.7** (0.9)	**40000.0** (2.8)
Family Canthocamptidae			**3333.3** (0.4)	**73333.4** (5.2)

Table 6. Densities (no. m^{-2}) of harpacticoid copepod taxa collected in surface (to 1 cm) sediment cores during tidal exposure of littoral flat habitats in Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses - cont'd.

Taxa	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Mesochra sp.	**673333.3** (90.2)		**53333.3** (6.9)	**6666.7** (0.5)
Mesochra sp.A		**26666.7** (3.5)		
Family Thalestridae				
Paradactylopodia serrata				**66666.7** (4.7)
Diarthrodes sp.			**10000.0** (1.3)	**353333.3** (25.0)
Family Parastenheliidae				
Parastenhelia hornelli			**106666.7** (13.9)	
Total adult harp. density	**746666.6**	**1100000.0**	**770000.0**	**1413333.5**
Total harpacticoid density	1373333.2	2056666.7	1570000.0	2720000.2
Total species richness	6	9	20	21

PSI overlap (%)

+---------3.0---------+ +----------27.5---------+
+---------22.2--------+
+----------------8.2---------------+
+-----------------------1.4----------------------+
+-----------------20.0------------

Table 7. Densities (no. m^{-2}) of harpacticoid copepod taxa collected from tidal inundation samplers during tidal inundation of four littoral flat habitats in Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses.

Taxa	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Family Tegastidae				
Tegastes sp.				**1111.1** (0.4)
Family Longipediidae				
Longipedia sp.			**1111.1** (0.4)	**5555.6** (2.3)
Family Ectinosomatidae		**1111.1** (13.0)	**16666.7** (6.6)	**12222.2** (5.2)
Ectinosoma melaniceps				**7777.8** (3.3)
Family Harpacticidae				
Harpacticus sp.			**1111.1** (0.4)	**4444.4** (1.9)
Harpacticus sp.- *obscurus* group			**2222.2** (0.9)	**11111.1** (4.7)
Harpacticus pacificus	**1111.1** (0.5)	**3333.3** (3.9)	**4444.4** (1.8)	
Zaus spp.		**1111.1** (1.3)		
Family Tisbidae				
Tisbe spp.	**7777.8** (3.4)	**14444.4** (16.9)	**124444.4** (49.3)	**86666.7** (36.6)
Bulbamphiascus sp.		**1111.1** (1.3)		
Robertsonia sp. cf *knoxi*			**5555.6** (2.2)	**2222.2** (0.9)
Family Tachidiidae				
Microarthridion littorale				**1111.1** (0.4)

Table 7. Densities (no. m^{-2}) of harpacticoid copepod taxa collected from tidal inundation samplers during tidal inundation of four littoral flat habitats in Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses - cont'd..

Taxa	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Tachidius triangularis	**1111.1** (0.5)	**2222.2** (2.6)		
Danielssenia typica		**1111.1** (1.3)	**13333.3** (5.3)	**5555.6** (2.3)
Family Laophontidae				
Heterolaophonte hamondi	**36666.7** (16.2)			
Heterolaophonte variabilis	**1111.1** (0.5)		**2222.2** (0.9)	
Family Ameiridae				
Nitocra spinipes armata	**14444.4** (6.4)			
Ameira sp.			(3.3)	**1111.1** (0.4)
Family Cletodidae				
Enhydrosoma sp.		(0.4)		**1111.1**
Huntemannia jadensis	**1111.1** (0.5)			
Family Diosaccidae		**1111.1** (1.3)		
Amonardia perturbata	**1111.1** (0.5)			
Diosaccus spinatus			**7777.8** (3.1)	
Amphiascopsis cinctus			**1111.1** (0.4)	**1111.1** (0.4)

Table 7. Densities (no. m^{-2}) of harpacticoid copepod taxa collected from tidal inundation samplers during tidal inundation of four littoral flat habitats in Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses - cont'd..

Taxa	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Amphiascus sp.A-*varians* gp.	**1111.1** (0.5)		**2222.2** (0.9)	
Schizopera sp.	**1111.1** (0.5)			
Stenhelia peniculata		**36666.7** (42.9)	**53333.3** (21.2)	**62222.2** (26.3)
Amphiascoides cf *subdebilis*		**1111.1** (0.4)		
Family Canthocamptidae				
Mesochra sp.	**160000.0** (70.6)	**1111.1** (1.3)	**13333.3** (5.3)	**6666.7** (2.8)
Orthopsyllus illgi				**2222.2** (0.9)
Family Thalestridae				
Dactylopodia sp.				**1111.1** (0.4)
Dactylopodia vulgaris			**1111.1** (0.4)	**2222.2** (0.9)
Paradactylopodia serrata		**1111.1** (1.3)		**3333.3** (1.4)
Diarthrodes sp.		**1111.1** (1.3)	**4444.4** (1.8)	**17777.8** (7.5)
Family Parastenheliidae				
Parastenhelia horneili		**10000.0** (11.7)		
Total adult harp. density	**226666.7**	**85555.3**	**252221.8**	**236666.4**
Total harpacticoid density	302222.1	297777.4	1,593332.7	796666.3
Total species richness	11	13	17	20

PSI overlap (%)

+----------5.7----------+ +----------73.2----------+

+----------50.3----------+

+----------10.2----------+

+----------6.2----------+

+----------53.6----------+

Table 8. Densities (no. m^{-2}) of harpacticoid copepod taxa collected in epibenthic (boundary) layer during flood slack tide in four littoral flat habitats of Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses.

Taxa	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Family Tegastidae				
Tegastes sp.				**20.8** (0.3)
Family Ectinosomatidae				**104.1** (1.4)
Ectinosoma melaniceps				**333.3** (4.5)
Family Harpacticidae				
Harpacticus arcticus				**62.5** (0.8)
Harpacticus sp.- *obscurus* group	**208.3** (2.9)			**41.7** (0.6)
Family Tisbidae				
Tisbe spp.	**20.8** (0.3)	**208.4** (25.6)	**83.3** (13.3)	**1708.3** (23.0)
Family Tachidiidae				
Tachidius triangularis		**83.3** (10.3)	**20.8** (3.3)	
Danielssenia typica			**41.6** (6.7)	**104.1** (1.4)
Family Laophontidae			**20.8** (3.3)	**41.7** (0.6)
Paralaophonte sp.		**41.7** (5.1)		
Laophonte inornata	**41.7** (0.6)	**20.8** (2.6)		
Heterolaophonte capillata		**20.8** (2.6)		

Table 8. Densities (no. m^{-2}) of harpacticoid copepod taxa collected in epibenthic (boundary) layer during flood slack tide in four littoral flat habitats of Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses - cont'd.

Taxa	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Heterolaophonte hamondi	**250.0** (3.5)			
Heterolaophonte variabilis				**83.3** (1.1)
Family Ameiridae				
Ameira sp.			**20.8** (3.3)	**41.6** (0.6)
Ameira parvuloides		**20.8** (2.6)		
Family Cletodidae				
Nannopus palustris	**812.5** (11.4)			
Family Diosaccidae				
Amonardia normani				**20.8** (0.3)
Amphiascopsis cinctus				**20.8** (0.3)
Amphiascus sp.A-*varians* gp.		**62.5** (7.7)	**20.8** (3.3)	
Stenhelia peniculata	**20.8** (2.9)	**166.7** (20.5)	**20.8** (3.3)	**333.3** (4.5)
Tymphlamphiascus pectinifer				**20.8** (0.3)
Amphiascoides cf *subdebilis*	**645.8** (9.1)		**145.9** (23.4)	**83.3** (1.1)
Family Canthocamptidae				
Mesochra sp.	**4520.8** (63.5)	**62.5** (7.7)	**62.5** (10.0)	**812.5** (10.9)

Table 8. Densities (no. m^{-2}) of harpacticoid copepod taxa collected in epibenthic (boundary) layer during flood slack tide in four littoral flat habitats of Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses - cont'd.

Taxa	Salt marsh	Mudflat	*Zostera japonica*	*Zostera marina*
Orthopsyllus illgi				**20.8** (0.3)
Family Thalestridae				
Dactylopodia sp.				**41.7** (0.6)
Paradactylopodia serrata				**62.5** (0.8)
Diarthrodes sp.	**229.2** (3.2)	**145.8** (17.9)	**187.5** (30.0)	**3479.2** (46.8)
Total adult harp. density	**7124.9**	**812.5**	**624.8**	**7437.1**
Total harpacticoid density	8270.7	1020.8	1270.7	13082.8
Total species richness	9	10	10	20

PSI overlap (%)

+----------14.7----------+ +----------60.3----------+

+----------48.8----------+

+----------25.5----------+

+----------19.0----------+

+----------53.1----------+

Table 9. Densities (no. 100 cm^{-2} of total blade surface) of harpacticoid copepod taxa on 10-cm segments of *Z. marina* plant #1 (with low epiphyte load) in Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses.

	(distal end)				Segments				(rhizomes)
Taxa	1	2	3	4	5	6	7	8	9
Number of *Zostera* blades:	1	2	2	2	3	3	4	2	2
Family Porcellidiidae									
Porcellidium sp.						**10.3** (31.5)	**27.5** (30.6)	**5.0** (2.8)	
Family Ectinosomatidae								**40.0** (22.2)	
Halectinosoma sp.									**33.3** (7.1)
Family Harpacticidae									
Harpacticus uniremis									**11.1** (2.4)
Zaus spp.	**168.8** (100)	**263.6** (100)	**20.6** (100)	**100.0** (100)	**47.9** (95.8)	**13.8** (42.2)	**35.0** (38.8)	**7.5** (4.2)	
Family Tisbidae									
Tisbe spp.					**2.1** (4.2)			**7.5** (4.2)	**11.1** (2.4)
Scutellidium arthuri						**8.6** (26.3)		**2.5** (1.4)	
Family Tachidiidae									
Danielssenia typica									**27.8** (6.0)
Family Laophontidae									**5.6** (1.2)
Paralaophonte pacifica									**44.5** (9.5)
Normanella confluens									**5.6** (1.2)
Family Ameiridae									
Ameira longipes							**2.5** (2.8)	**5.0** (2.8)	**33.3** (7.1)
Family Cletodidae									
Enhydrosoma sp.									**5.6** (1.2)
Family Diosaccidae									**11.1** (2.4)

Table 9. Densities (no. 100 cm^{-2} of total blade surface) of harpacticoid copepod taxa on 10-cm segments of *Z. marina* plant #1 (with low epiphyte load) in Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses - cont'd.

	(distal end)			Segments					(rhizomes)
Taxa	1	2	3	4	5	6	7	8	9
Number of *Zostera* blades:	1	2	2	2	3	3	4	2	2
Amonardia perturbata								**2.5** (1.4)	**11.1** (2.4)
Amphiascus undosus								**15.0** (8.3)	**50.0** (10.7)
Stenhelia peniculata									**111.1** (23.7)
Stenhelia sp.A									**11.1** (2.4)
Typhlamphiascus pectinifer									**16.7** (3.6)
Family Canthocamptidae									**16.7** (3.6)
Mesochra pygmaea							**17.5** (19.4)	**80.0** (44.3)	**33.3** (7.1)
Family Thalestridae								**5.0** (2.8)	
Dactylopodia glacialis							**2.5** (2.8)		
Diarthrodes sp.							**5.0** (5.6)	**10.0** (5.6)	**27.8** (6.0)
Total adult harp. den.	**168.8**	**263.6**	**20.6**	**100.0**	**50.0**	**32.7**	**90.0**	**180.0**	**466.8**
Total harpacticoid den.	168.8	281.8	23.5	107.1	62.5	167.2	247.5	370.0	600.0
Total harp. spp. richness	1	1	1	1	2	3	7	11	19

Table 10. Densities (no. 100 cm^{-2} of total blade surface) of harpacticoid copepod taxa on 10-cm segments of *Z. marina* plant #2 (with high epiphyte load) in Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses.

	(distal end)			Segments					(rhizomes)
Taxa	1	2	3	4	5	6	7	8	9
Number of *Zostera* blades:	2	3	6	9	17	11	9	2	2
Family Porcellidiidae									
Porcellidium sp.					**1.3** (4.7)	**3.2** (11.0)			
Family Longipediidae									
Longipedia sp.	**2.9** (2.7)	**3.7** (6.2)					**2.2** (9.2)		**25.0** (1.3)
Family Ectinosomatidae		**1.9** (3.2)	**1.4** (3.0)	**0.8** (3.4)	**1.3** (4.7)	**1.6** (5.5)		**11.1** (5.6)	**212.5** (11.3)
Halectinosoma sp.	**17.6** (16.1)	**9.3** (15.6)							
Family Harpacticidae									
Harpacticus sp.	**20.6** (18.9)	**5.6** (9.4)	**9.5** (20.4)	**2.3** (9.8)	**2.0** (7.3)	**3.2** (11.0)		**97.2** (49.4)	**37.5** (2.0)
Harpacticus sp.-*obscurus* grp.						**0.8** (2.8)		**2.8** (1.4)	
Harpacticus spinulosus	**2.9** (2.6)				**0.7** (2.6)				**12.5** (0.7)
Harpacticus uniremis	**14.7** (13.5)	**7.4** (12.4)	**1.4** (3.0)	**1.5** (6.4)	**0.7** (2.6)	**37.5** (2.0)			
Zaus spp.	**14.7** (13.5)	**13.0** (21.8)	**21.6** (46.5)	**13.6** (57.9)	**11.33** (41.2)	**6.5** (22.4)	**2.2** (9.2)	**5.6** (2.8)	
Family Tisbidae									
Tisbe spp.	**11.8** (10.8)	**9.3** (15.6)	**8.1** (17.4)	**4.5** (19.1)	**4.0** (14.6)	**6.5** (22.4)	**6.5** (27.0)	**13.9** (7.0)	**37.5** (2.0)
Scutellidium sp.[a]						**0.8** (2.8)	**2.2** (9.2)		
Scutellidium arthuri				**0.8** (3.4)		**1.6** (5.5)			
Family Tachidiidae									
Microarthridion littorale									**25.0** (1.3)
Danielssenia typica								**2.8** (1.4)	**12.5** (1.3)

Table 10. Densities (no. 100 cm^{-2} of total blade surface) of harpacticoid copepod taxa on 10-cm segments of *Z. marina* plant #2 (with high epiphyte load) in Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses - cont'd.

	(distal end)				Segments				(rhizomes)
Taxa	1	2	3	4	5	6	7	8	9
Number of *Zostera* blades:	1	2	2	2	3	3	4	2	2
Family Laophontidae									
Paralaophonte pacifica									**212.5** (11.3)
Heterolaophonte longisetigera									**12.5** (0.7)
Family Ameiridae									
Ameira sp.								**2.8** (1.4)	**25.0** (1.3)
Family Cletodidae									
Acrenhydrosoma perplexum									**12.5** (0.7)
Family Diosaccidae									
Amonardia perturbata					**0.7** (2.6)				**12.5** (0.7)
Amphiascus undosus						**0.8** (2.8)		**5.6** (2.8)	**87.5** (4.6)
Amphiascus sp.B-*minutus* grp.						**0.8** (2.8)			
Stenhelia peniculata		**1.9** (3.2)							**50.0** (2.6)
Stenhelia sp.A									**12.5** (0.7)
Typhlamphiascus pectinifer									**12.5** (0.7)
Amphiascoides sp.A	**3.3** (3.0)	**1.9** (3.2)	**1.5** (3.2)		**2.0** (7.3)	**0.8** (2.8)	**2.2** (9.2)	**22.2** (11.3)	**337.5** (17.9)
Bulbamphiascus sp.									**550.0** (29.1)
Robertsonia sp. cf *knoxi*									**112.5** (6.0)
Family Canthocamptidae									
Mesochra sp.								**13.9** (7.0)	

Table 10. Densities (no. 100 cm^{-2} of total blade surface) of harpacticoid copepod taxa on 10-cm segments of *Z. marina* plant #2 (with high epiphyte load) in Padilla Bay, Washington, May 1986; numerical composition (%) in parentheses - cont'd.

	(distal end)			Segments					(rhizomes)
Taxa	1	2	3	4	5	6	7	8	9
Number of *Zostera* blades:	1	2	2	2	3	3	4	2	2
Mesochra pygmaea		**1.9** (3.2)			**2.7** (9.9)		**6.5** (27.0)	**8.3** (4.2)	
Orthopsyllus illgi									**25.0** (1.3)
Family Thalestridae *Paradactylopodia serrata*					**0.7** (2.6)			**2.8** (1.4)	**12.5** (0.7)
Diarthrodes sp.	**20.6** (18.9)	**3.7** (6.2)	**3.0** (6.5)			**2.4** (8.2)	**2.2** (9.2)	**8.3** (4.2)	**12.5** (0.7)
Total adult harp. den.	**109.1**	**59.6**	**46.5**	**23.5**	**27.4**	**29.0**	**24.0**	**197.3**	**1887.5**
Total harpacticoid den.	150.0	81.5	60.8	99.2	150.7	145.2	176.1	1858.3	2450.0
Total harp. spp. richness	9	11	7	6	11	12	7	13	23

[a]predominantly copepodids

the *Z. marina* and *Z. japonica* habitats. The lowest taxa overlap was between the saltmarsh and mudflat habitats.

Among the *Z. marina* segments, taxa richness of harpacticoids increased gradually from one at the distal end to 19 at the rhizomes of the low epiphyte plant. Taxa richness was consistently higher (6-12 taxa), however, along the length of the high epiphyte blade until increasing to 23 taxa at the rhizomes (Fig. 7a). However, these differences were not reflected in the densities of adult harpacticoids, which, except for the second 10-cm segment, were quite similar until increasing at the rhizomes (Fig. 7b); harpacticoids were five times denser on the last segment of the high epiphyte plant than on the same segment of the low epiphyte plant, which was due primarily to the unique presence of several diosaccid taxa (*Bulbamphiascus* sp., *Amphiascoides* sp. A, *Robertsonia* sp. cf *knoxi*; Table 10). The trends in taxa richness did not appear to be related to the number of blades within each segment (Fig. 8), and the segment densities were similarly unrelated.

Numerical classification of the habitat X taxa density matrix discriminated 10 habitat and 11 taxa clusters at the 0.65 Bray-Curtis dissimilarity level (Fig. 9; Table 11). Further inspection of the habitat cluster dendogram suggested that six clusters at the 0.75 dissimilarity level formed more logical associations. This analysis indicated that certain harpacticoid assemblages were discretely associated with littoral flat habitat clusters, while other assemblages were distributed ubiquitously across the littoral flat. For instance, taxa assemblage D characterized by *Heterolaophonte hamondi* was almost uniquely associated with the saltmarsh habitat, specifically in the leading edge of the inundating tide. Assemblage F, composed of the rare taxon *Laophonte inornata*, was also unique to the benthic boundary layer in the three higher habitats. The best representative of an azygous assemblage is cluster J, composed predominately of large epibenthic forms that characterized both eelgrasses, but predominately the *Z. marina* habitats; only two of these taxa (*Zaus* sp. and *Bulbamphiascus* sp.) did not originate exclusively from the *Z. marina* blade segments. The lack of these taxa in tidal inundation and benthic boundary layer samples suggests that they have developed morphological or behavioral mechanisms that counteract forces that would advect them from their normal microhabitat.

Conversely, assemblage C, represented by *Mesochra* sp., was present throughout the flats in all microhabitats; assemblages H (characterized by ectinosomatids) and I (*Diarthrodes* sp., *Robertsonia* sp. cf *knoxi*, *Danielsennia typica*) were similarly distributed. The taxa in these assemblages appeared to either occupy all habitats or to actively or passively move from the habitats of origin.

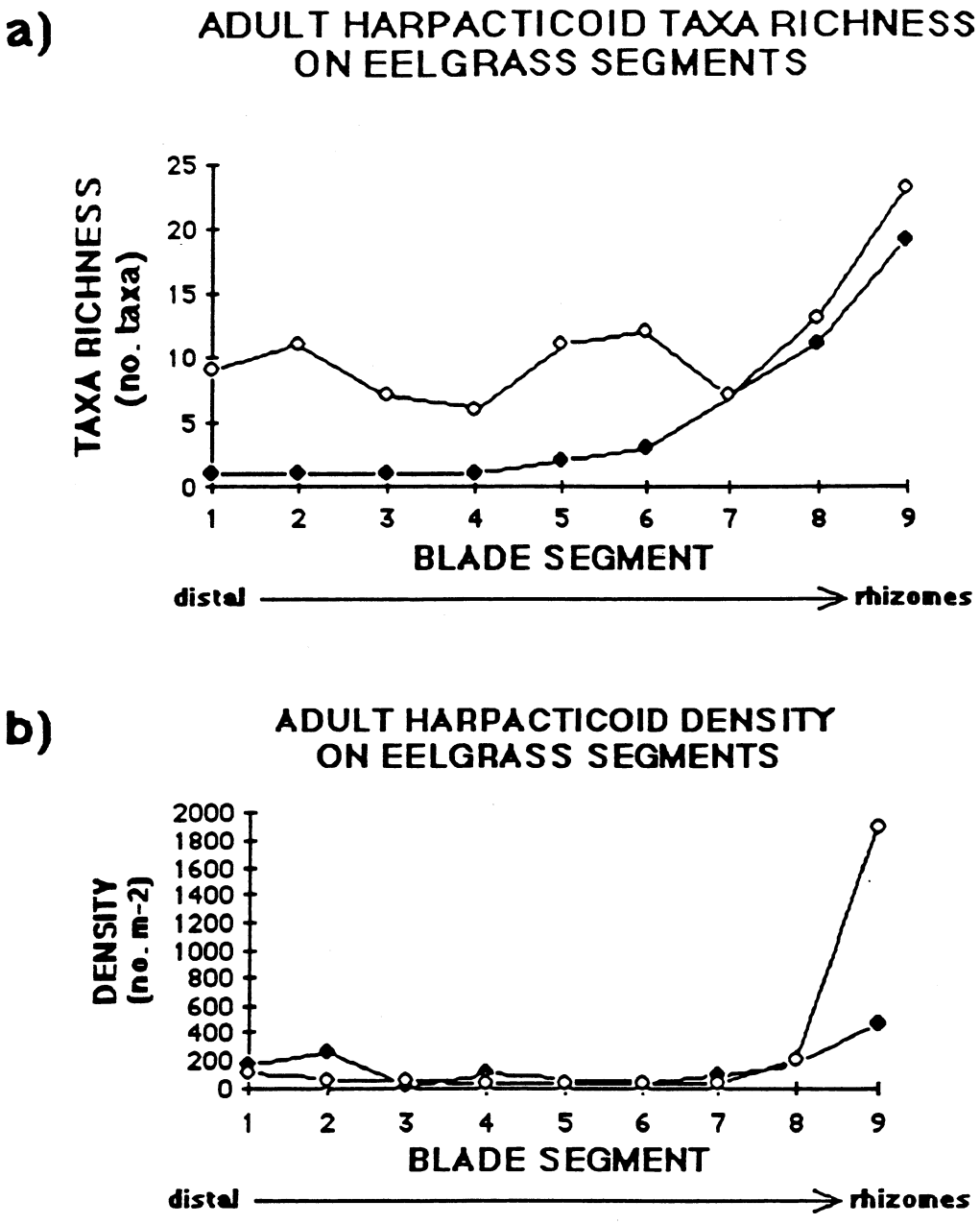

Figure 7. Taxa richness (a; no. taxa 100-cm^{-2}) and density (b; no. organisms 100-cm^{-2}) of adult harpacticoid copepods on 10-cm segments of eelgrass (*Zostera marina*) plants with low and high epiphyte growth.

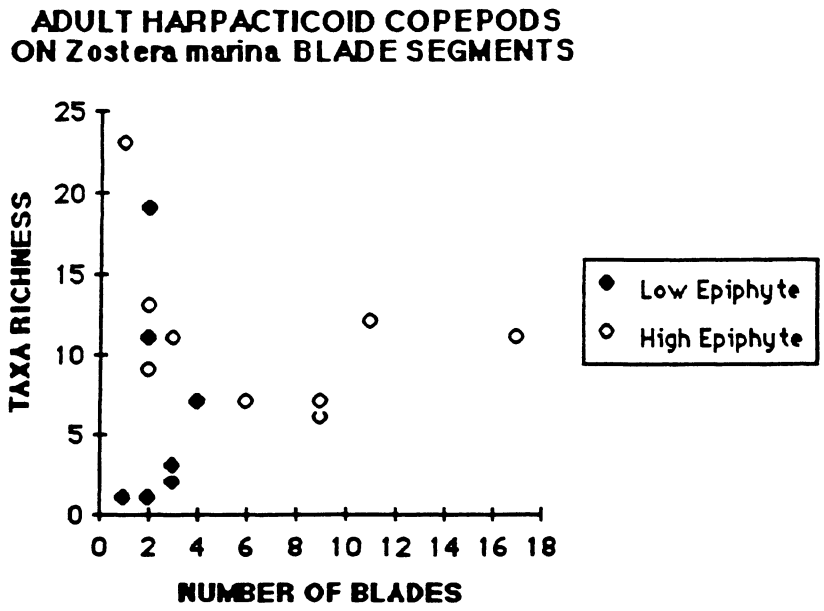

Figure 8. Relationship between the taxa richness of adult harpacticoid copepods and the number of blades on 10-cm segments of eelgrass (*Zostera marina*) with low and high epiphyte growth.

The microhabitat distribution of harpacticoids on the *Z. marina* blade segments was also taxa-specific (Tables 9-10). For example, *Zaus* sp. was distributed along the length of both low and high epiphyte blades except in the basal segment at the rhizomes. Other taxa, such as *Danielssenia typica*, *Tymphamphiascus pectinifer*, and *Stenhelia* sp. A, are concentrated along the basal segments regardless of the extent of epiphyte growth, perhaps more in association with the rhizomes and sediments. As reflected in their dorsally-ventrally flattened shape, certain taxa, i.e., *Porcellidium* sp. and *S. arthuri*, generally reside in the spaces between blades within or adjacent to the sheath. But the occurrence of many taxa appears to be directly related to the extent of epiphyte growth, as illustrated by the occurrence of the ectinosomatids, *Harpacticus uniremis*, *Tisbe* spp., and *Diarthrodes* sp. to the distal end of the blades in the plant with high epiphyte growth.

Fish Assemblage Composition and Diets

Ten species of fish and two macroinvertebrates were captured during purse and beach seine sampling (Table 12). With the exception of adult surf smelt and threespine stickleback, these fishes were predominately juveniles. Only two fish, one juvenile chum salmon and one Pacific sand lance, were caught in purse seine hauls. The magnitude of beach seine catches ranged from several dozen fish to in excess of 1,000 fish (mostly surf smelt and sand lance). Surf smelt,

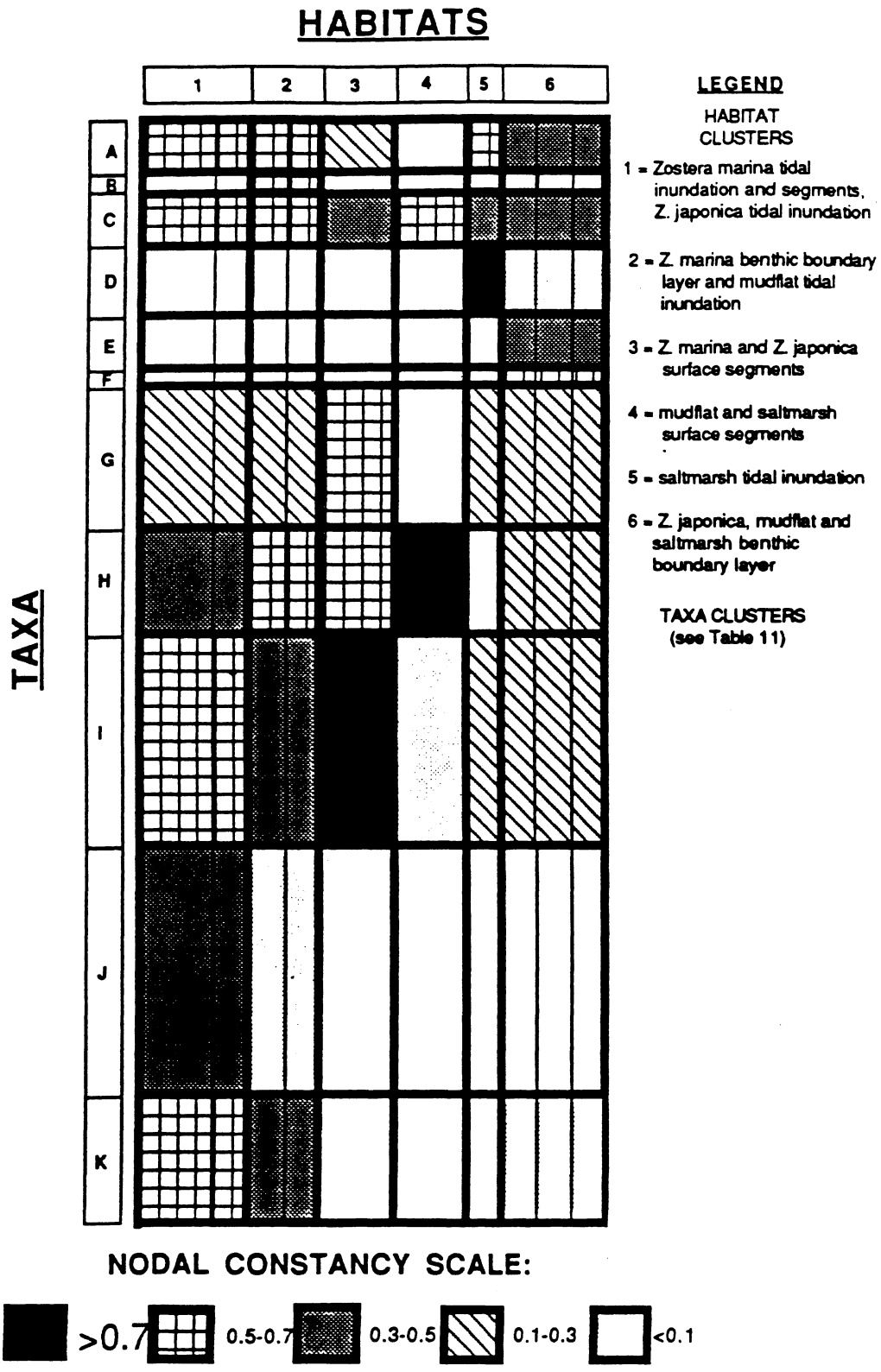

Figure 9. Nodal constancy plot of littoral flat habitat and adult harpacticoid copepod clusters discriminated by numerical classification (see text) of epibenthos density data.

Table 11. Adult harpacticoid assemblages (clusters) discriminated by numerical classification using Bray-Curtis dissimilarity at 0.65 level; relationships among these clusters and the habitat clusters resulting from the inverted matrix is illustrated in nodal constancy plot, Fig. 9.

Cluster	Adult Harpacticoid Taxa
A	*Harpacticus pacificus* *Diosaccus spinatus* *Tisbe* spp.
B	*Amonardia normani*
C	*Nannopus palustris* *Mesochra* sp. *Harpacticus arcticus*
D	*Nitocra spinipes armata* *Huntemannia jadensis* *Schizopera* sp. *Heterolaophonte hamondi*
E	*Paralaophonte* sp. *Heterolaophonte capillata* *Ameira parvuloides*
F	*Laophonte inornata*
G	*Heterolaophonte discophora* *Rhizothrix* sp. *Stenhelia cf inopinata* *Parastenhelia hornelli* *Enhydrosoma* sp. *Amphiascus* sp. A *-varians* group *Stenhelia peniculata* *Tachidius triangularis*
H	*Stenhelia* sp. *A* *Diosaccidae* *Ameira* sp. *Ectinosomatidae* *Amphiascoides* cf *subdebilis* Laophontidae unidentified

Table 11. Adult harpacticoid assemblages (clusters) discriminated by numerical classification using Bray-Curtis dissimilarity at 0.65 level; relationships among these clusters and the habitat clusters resulting from the inverted matrix is illustrated in nodal constancy plot, Fig. 9 - cont'd.

Cluster	Adult Harpacticoid Taxa
I	*Paradactylopodia serrata*
	Diarthrodes sp.
	Amphiascopsis cinctus
	Tymphlamphiascus pectinifer
	Canthocamptidae unidentified
	Robertsonia sp. cf *knoxi*
	Heterolaophonte variabilis
	Danielssenia typica
	Longipedia sp.
	Amphiascus undosus
	Amphiascoides sp. *A*
	Amonardia perturbata
J	*Dactylopodia glacialis*
	Porcellidium sp.
	Halectinosoma sp.
	Harpacticus spinulosus
	Harpacticus uniremis
	Scutellidium arthuri
	Paralaophonte pacifica
	Heterolaophonte longisetigera
	Normanella confluens
	Acrenhydrosoma perplexum
	Amphiascus sp. B *-minutus* group
	Mesochra pygmaea
	Zaus sp.
	Bulbamphiascus sp.
K	*Tegastes* sp.
	Dactylopodia sp.
	Ectinosoma melaniceps
	Harpacticus sp. - cf *obscurus*
	Dactylopodia vulgaris
	Orthopsyllus illgi
	Microarthridion littorale

Pacific herring, Pacific sand lance, chum salmon, and threespine stickleback were selected for stomach analyses because they are economically important or because they were the most abundant in catches.

Mean indices of stomach fullness were generally high, ranging from an average of 4.0 for herring to 5.4 for sand lance (Table 13). None of the stomachs analyzed were empty and the digestion index was quite high, indicating that the fish had been recently feeding.

Fish diets included a variety of epibenthic, benthic and pelagic food items (Table 14). As a group, epibenthic organisms (primarily harpacticoid copepods and gammarid amphipods) were the most important food items eaten. They were found in the stomach of every fish analyzed and were the dominant prey (> 93% IRI) of chum salmon, Pacific sand lance, surf smelt and threespine stickleback. Non-epibenthic food items, primarily pelagic larvae of the decapod crustacean *Upogebia pugettensis*, were an important dietary component for only Pacific herring.

Epibenthic harpacticoid copepods were the single most important food item eaten by predators in Padilla Bay (Table 14). They were found in the stomachs of 95% of the fish that were analyzed and were the dominant prey (>50% IRI) in all predator species but herring. Twelve harpacticoid taxa were positively identified, of which the genera *Harpacticus*, *Zaus*, and *Tisbe* were the most important (Table 15). Overall (i.e., including all prey items), the numeric contribution of *Harpacticus* ranged from 48.0% in smelt to 2.1% in threespine stickleback, while the gravimetric contribution ranged from 72.0% in sand lance to 1.1% in stickleback. Among just the harpacticoids consumed, the genus *Harpacticus* comprised 2.5% (in stickleback) to 83.0% (herring) of the abundance, and 8.0% (stickleback) to 92.0% (herring) of the biomass of harpacticoids (Table 16). All of the *Harpacticus* that could be positively identified from stomachs were *H. uniremis*.

Zaus and *Tisbe* were also found in the stomachs of 98.0% of these five fishes (Table 15). They were the most important harpacticoid taxa in threespine stickleback stomachs, comprising 91.3% and 89.3% of the harpacticoids counted and weighed, respectively. In surf smelt, chum salmon, herring, and sand lance, they were much less important dietary components than *Harpacticus*. In these four predators, *Zaus* comprised between 11.4% (surf smelt) and 2.9% (herring) of the total abundance, and between 4.8% (chum salmon) and 1.0% (herring) of the total weight of harpacticoids in the stomach samples. *Tisbe*, on the other hand, were most important in chum salmon (10.2% and 13.6% by number and weight, respectively), and least important to herring (3.5% and 1.0%).

Sufficient numbers of fish were caught to compare the food habits of adult (length x = 138 mm) and juvenile (x = 70 mm) smelt from the mudflat habitat. Harpacticoid copepods dominated

Table 12. List of fish and macroinvertebrate species caught in the beach seine and purse seine in Padilla Bay, May 9, 1986.

Scientific Name	Life history stages[a]	Common name
Fish:		
Family Clupeidae		
Clupea harengus pallasi	J	Pacific herring
Family Salmonidae		
Oncorhynchus keta	J	Chum salmon
Family Osmeridae		
Hypomesus pretiosus	J,A	Surf Smelt
Family Gasterosteidae		
Gasterosteus aculeatus	J,A	Threespine stickleback
Family Syngnathidae		
Syngnathus leptorhynchus	J	Bay pipefish
Family Ammodytidae		
Ammodytes hexapterus	J	Pacific sand lance
Family Pleuronectidae		
Lepidopsetta bilineata	J	Rock sole
Pleuronectes (Platichthys stellatus)	J	Starry flounder
Pleuronectes (Parophrys) vetulus	J	English sole
Psettichthys melanostictus	J	Sand sole
Macroinvertebrates:		
Decapoda;		
Pleocyemata-Caridea		
Family Crangonidae		
Crangon spp.	J	Sand shrimp
Brachyura		
Family Cancridae		
Cancer magister	A	Dungeness crab

[a]J = juvenile, A = adult

Table 13. Fish analyzed for stomach contents in Padilla Bay, Washington, May 1986.

Species	Sample size n[a]	Length (mm)	Weight (gr)	Contents digestion[b]	Stomach fullness[c]	Fullness (%)[d]
Surf Smelt	26	124.3+27.9	12.6+6.2	4.2	4.7	1.35
Pacific herring	5	108.0+ 2.9	7.5+0.4	4.0	4.4	1.30
Pacific sand lance	5	99.6+10.0	2.4+0.6	5.4	5.0	4.40
Chum salmon	5	33.6+ 3.4	0.2+0.1	5.4	4.8	2.10
Threespine stickleback	7	73.0+ 2.6	4.0+0.3	4.3	4.7	2.00

[a]No stomachs were empty.
[b]Index of state of contents digestion factor was scaled from 0 (completely digested) to 6 (none digested).
[c]Index of stomach fullness was scaled from 0 (empty) to 7 (distended).
[d]Stomach contents weight as percent of total fish weight.

the diet of both juveniles and adults (Table 16). The numerical and gravimetric contribution of harpacticoids was 87.9% and 71.8%, respectively, in juvenile smelt and 93.3% and 56.0%, respectively, for the adults. The genus *Harpacticus* was the dominant harpacticoid for both life history stages, although it appeared to be a more important component of the diet in adults than in juveniles; 79.7% and 49.2% of all prey items counted and weighed, respectively, in adult smelt were *Harpacticus* sp., while *Harpacticus* comprised 36.0% and 42.1%, respectively, in juveniles. In comparison, juvenile smelt had eaten more *Tisbe* and *Zaus* and had more unidentifiable harpacticoids than adult smelt, while adult smelt utilized polychaetes to a greater extent than juveniles.

Enough specimens were also obtained to compare the prey eaten by adult smelt obtained from eelgrass (*Z. marina*) to that of adult smelt caught in the mud/algae habitats (Table 16). Smelt from both habitats ate primarily harpacticoids. For smelt from the mud/algae habitat, the numeric and gravimetric contribution of harpacticoids was 93.3% and 56.0%, respectively, while for smelt from the eelgrass habitat, harpacticoids contributed 85.3% and 38.2%, respectively. There were two striking differences in the food eaten by smelt from the two habitats. First, there was a greater gravimetric contribution of polychaetes to the prey spectra of smelt from the eelgrass habitat (42.0% versus 17.9%). Second, the genus *Harpacticus* was considerably more important as food for smelt from the mud/algae area while other harpacticoid genera (including unidentified harpacticoids) contributed more to smelt from the eelgrass habitat.

Table 14. Summary of the prey eaten by five species of fishes captured in Padilla Bay, Washington, May 1986.

Prey item	Frequency of occurrence	Numerical composition	Gravimetric composition	% ΣIRI
A. Surf smelt				
Nematoda	7.7	0.2	-	-
Polychaeta	26.9	3.7	27.4	**5.2**
Calanoida	19.2	0.4	0.1	-
Harpacticoida	96.2	88.6	47.5	**86.3**
Poecilostomatioda	23.1	0.1	0.1	-
Balanomorpha	42.3	0.1	-	-
Cumacea	80.8	1.0	1.6	**1.4**
Gammaridea	92.3	3.8	21.5	**6.5**
B. Pacific herring				
Gastropoda	20.0	-	-	-
Cladocera	20.0	-	-	-
Calanoida	60.0	0.6	0.3	**0.2**
Harpacticoida	100.0	44.6	29.1	**37.0**
Poecilostomatioda	40.0	0.2	-	-
Balanomorpha	60.0	0.2	0.1	**0.1**
Cumacea	20.0	-	-	-
Gammaridea	100.0	1.7	2.7	**1.1**
Decapoda	100.0	52.7	67.7	**61.6**
C. Pacific Sand Lance				
Cladocera	40.0	-	-	-
Calanoida	80.0	3.7	2.6	**3.5**
Harpacticoida	100.0	80.0	91.0	**92.6**
Poecilostomatioda	80.0	0.5	0.3	**0.2**
Caligoida	20.0	-	0.2	-
Balanomorpha	100.0	2.0	0.1	**1.1**
Cumacea	60.0	0.2	0.5	**0.2**
Gammaridea	100.0	0.7	3.4	**1.2**
Decapoda	80.0	1.6	3.0	**1.1**
D. Chum salmon				
Calanoida	80.0	6.3	4.1	**4.4**
Harpacticoida	100.0	85.9	71.0	**83.2**
Balanomorpha	20.0	0.2	0.7	**0.1**
Gammaridea	80.0	3.9	19.3	**9.8**
Euphausiacea	40.0	0.5	1.4	**0.5**
Decapoda	60.0	3.1	3.5	**2.1**

Table 14. Summary of the prey eaten by five species of fishes captured in Padilla Bay, Washington, May 1986 - cont'd.

Prey item	Frequency of occurrence	Numerical composition	Gravimetric composition	% ΣIRI
E. Threespine stickleback				
Polychaeta	14.3	0.1	1.8	**0.1**
Calanoida	57.1	0.8	0.1	**0.3**
Harpacticoida	100.0	84.6	14.8	**50.7**
Poecilostomatioda	28.6	1.0	0.1	**0.2**
Balanomorpha	28.6	0.1	0.1	**0.1**
Gammaridea	100.0	13.0	82.3	**48.6**
Caprellidea	28.6	0.1	0.8	**0.1**

Overlap Among Fish Diet and Epibenthos

Diet overlap was highest between sand lance, chum salmon and surf smelt (PSI >63%). This similarity in prey composition was due mainly to the reliance of all three species on *Harpacticus* primarily and *Zaus* and *Tisbe* secondarily; non-harpacticoid prey were also scarce in the diets of these three species. The lowest overlap values (PSI <35%) were between stickleback and the other four species. These low overlaps occurred because stickleback preyed extensively on *Zaus* and *Tisbe* but much less so on *Harpacticus*. Stickleback also preyed heavily on gammarids, which were a less important food item to the other species. Intermediate overlap values (PSI = 43% to 52%) occurred between herring, sand lance, surf smelt and chum salmon. The similarity in diets was due mainly to harpacticoids, while the main difference was in the consumption of pelagic prey by herring and not by the other three species.

Prey Selection

There was not a great deal of overlap between the food items eaten by any of the predators and the harpacticoid prey community associated with any macro- or microhabitat. The highest overlap value measured was 49.3% and occurred between threespine stickleback and the *Z. japonica* tidal inundation samples. Only 7 out of a possible 112 overlap comparisons were greater than 30%. The smallest PSI values (<11.5%) were found in those comparisons involving the core samples, adult smelt from the mud/algae habitat and herring. The lack of overlap occurred because the dominant harpacticoids eaten by the predators were not well represented in the samples from the environment.

Table 15. Percent numerical (a) and gravimetric (b) composition of harpacticoid copepods identified as prey in the stomachs of fish predators collected from Padilla Bay, Washington, May 1986.

Harpacticoid copepod taxa	Surf smelt	Pacific herring	Pacific sand lance	Chum salmon	Threespine stickleback
a. Numerical					
Porcellidium sp.	-				
Longepedia sp.	0.1	0.4	0.2		
Ectinosomatidae	1.0	0.7	5.5	0.8	
Harpacticus sp.	3.9	0.9	2.0	1.1	
Harpacticus uniremis	50.1	82.1	50.6	25.9	2.5
Zaus spp.	11.4	2.9	8.9	10.5	18.8
Tisbe spp.	10.2	3.5	6.8	10.2	72.5
Scutellidium sp.	0.8		0.6	1.0	
Tachidius sp.	-			15.5	
Laophontidae	0.1			0.4	
Huntemannia jadensis	0.1				
Mesochra sp.	1.8		0.3		
Diathrodes sp.	0.3		0.9	0.9	
Parathalestris sp.	5.7	3.9	1.8	0.5	
Idomene sp.	0.1				
Unidentified	14.3	5.6	22.4	30.9	6.4
b. Gravimetric					
Porecellidium sp.	-				
Longipedia sp.	0.1	0.1	0.1		
Ectinosomatidae	0.2	0.1	1.3	1.0	
Harpacticus sp.	1.6	0.1	1.4	1.0	
Harpacticus uniremis	67.7	91.9	77.9	49.8	8.0
Zaus spp.	2.6	1.0	4.5	4.8	16.1
Tisbe spp.	3.0	1.0	3.7	13.6	73.2
Scutellidium sp.	1.2		0.3	2.0	
Tachidius sp.				2.8	
Laophontidae	0.1			1.0	
Huntemannia jadensis	3.4				
Mesochra sp.	0.2		0.1		
Diathrodes sp.	0.1		0.1	1.0	
Parathalestris sp.	7.2	4.1	3.2	1.0	
Idomene sp.	0.2				
Unidentified	5.6	1.7	7.3	22.4	2.7

Table 16. Comparison of the food habits of adult smelt (n=7; x = 136.6 mm FL) from *Z. marina* habitat and adult (n = 7; x = 138.6 mm FL) and juvenile (n = 5; x = 70.0 mm FL) smelt from mudflat habitat in Padilla Bay, May 9, 1986; there were no empty stomachs.

	Numeric Composition			Gravimetric Composition		
	Adult-*Z. marina*	Adult-mudflat	Juvenile-mudflat	Adult-*Z. marina*	Adult-mudflat	Juvenile-mudflat
No. of stomachs	14	7	5			
No. empty	0	0	0			
Mean length						
Prey Item						
Polychaetes	7.4	0.3	0.3	42.0	17.9	0.1
Calanoids	0.2	0.6	0.9	0.1	0.2	0.4
Harpacticoids						
Harpacticus sp.	24.3	79.7	36.0	17.2	49.2	42.1
Zaus spp.	17.6	1.9	8.2	4.5	0.4	4.2
Tisbe spp.	14.1	0.7	17.1	5.1	0.2	11.2
Other harp.	29.3	11.0	26.6	11.4	6.2	14.3
Balanomorpha	0.3	-	-	0.1	-	-
Cumaceans	0.6	1.5	0.1	1.2	2.2	0.1
Gammarids	1.2	4.2	10.5	15.6	23.2	27.2
Decapods	3.7	-		1.3	-	
Other	1.3	0.1	0.3	1.5	0.5	0.4

SFRs were computed for the three most important harpacticoids (*Harpacticus uniremis*, *Zaus*, and *Tisbe*) eaten by the fish. SFRs for *Harpacticus uniremis* were 1.00 (indicating strong preference) in the non-eelgrass habitats sampled because, although they were the dominant component of predator diets, they were only found associated with the two *Z. marina* plants. With the exception of threespine stickleback, SFRs were also high in comparisons involving the two eelgrass plants.

In the case of *Zaus*, SFRs were all high (>0.50) for the samples from the surface sediment, inundating tidal front, and epibenthic boundary layer, indicating preferential foraging on *Zaus* in all these microhabitats. Again, many of the SFRs were 1.00 because *Zaus* was consumed by the predators but was not present in these habitats. The forage ratios for the eelgrass with low epiphyte growth were all less than 1.0, principally because *Zaus* was one of the most abundant members of the harpacticoid assemblage on the eelgrass plant with low epiphyte growth; on the plant with the high epiphyte load, SFRs were close to 1.0.

The SFRs computed for *Tisbe* indicated that there were differences in preference that were a function of predator species, microhabitat and macrohabitat. Stickleback had a strong preference for *Tisbe* regardless of the habitat. As a group, the highest SFR values were observed for the saltmarsh habitat and for the core samples in all macrohabitats. On the other hand, the lowest SFR values (in many cases just slightly greater or less then 1.0) were computed for benthic boundary layer samples from the *Z. marina* habitat. The forage ratios for the eelgrass plants were all slightly greater than 1.0, with the exception of adult smelt from the mud/algae macrohabitat and herring, which were both less than 1.0. In the tidal inundation samples, SFR values indicated preference for *Tisbe* in the marsh and *Z. marina* habitats and avoidance of *Tisbe* in the mudflat and *Z. japonica* habitats.

DISCUSSION

Habitat and microhabitat associations among harpacticoid copepod assemblages are generally non-random and have been attributed to a number of biotic and physical factors, including: (1) morphology and behavior, e.g., shape usually reflects whether the taxa burrows or actively swims; (2) substrate characteristics, e.g., grain size and presence of micro- and macroalgae; (3) tidal velocities and wave exposure; (4) physiology, i.e. salinity, oxygen, desiccation tolerance; (5) food resources, i.e., detritus, and algae sources and accumulations; and (6) competition and predation, e.g., density and distribution of congeners and other "similar" taxa and fishes and macroinvertebrates. Although many of these characteristics are relatively stable, having been formed by evolutionary processes, not much is known about the behavioral plasticity of these organisms over short-term (e.g., tidal cycles) scales.

Most descriptions of habitat distribution have focused on horizontal zonation over littoral and shallow sublittoral habitats. For instance, Moore (1979) defined three groups over a sandflat on the Isle of Man as potentially reflecting zonation controlled by interstitial space at the lower elevations and salinity and desiccation tolerances at the upper elevations. In examining harpacticoid distribution across a depth gradient in a salt marsh, Coull et al. (1979) found certain taxa in a South Carolina *Salicornia alterniflora* marsh to be distributed across all elevations from the creek bottom to the high marsh vegetation and others to be confined to certain elevations/habitats. Restricted distributions of several of the genera coincided with the Padilla Bay assemblages, e.g., *Nitocra* and *Schizopera* restricted to the salt marsh, *Nannopus* in the mudflat, and *Halectinosoma* in the low elevations of the transects. In a long-term (1-year) analysis of harpacticoid distributions in a *Spartina* marsh in Louisiana, Fleeger (1980) attributed similar distributions to possible microhabitat specializations, biotic (e.g., *Spartina* root mass) and physical (e.g., microtopography) heterogeneity, sediment depth characteristics, seasonal partitioning of resources, and predation by fish, shrimp and crabs. While, as far as we know, no one has examined the distribution of harpacticoid assemblages over a tidal cycle in relation to their availability to predation by epibenthic-feeding fishes, the flux of harpacticoids into the benthic boundary layer and dispersion across littoral flat habitats may indicate their susceptibility to such predation.

Harpacticoid copepods have been noted to be conspicuous in the diets of benthic- and epibenthic-feeding fishes (see review by Hicks and Coull 1983), and may be particularly important as the initial food resource of recently-metamorphosed flatfishes and other post-larval and early juvenile benthic fishes (Bregnballe 1961; Alheit and Scheibel 1982; Morais and Bodiou 1984). Recent information on the importance of harpacticoid copepods in the diets of estuarine fishes indicates that this taxa alone may form the principal source of meiofauna biomass transferred to

higher trophic levels (Gee 1987). There is also ample evidence for foraging selectivity upon the suite of available harpacticoid taxa. Bodiou and Villers (1978/1979) indicated that 80% of the harpacticoids consumed by the goby *Deltentosteus quadrimaculatus* belonged to but two taxa, *Halectinosoma canaliculatum* and *Longipedia scotti*. Similarly, Morais and Bodiou (1984) indicated that the harpacticoid preyed upon by three species of juvenile flatfish was also *L. scotti*. Hicks (1984) also found that *Parastenhelia megarostrum* constituted 95% to 100% of the diet of juveniles of two species of flatfish.

In the northeast Pacific, there is growing evidence of intensive foraging upon the epibenthic harpacticoid *Harpacticus uniremis* by juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) (Bakshtansky 1965; Sibert et al. 1977; Sibert 1979; Healey 1979; Simenstad and Wissmar 1984; Cordell 1986; C. Simenstad and J. Cordell, unpubl.); *Tisbe* spp. have also been shown to be a prominent prey in a few reports (Bakshtansky 1965; Cordell 1986). However, the salience of harpacticoids in the diets of the non-salmonids examined from Padilla Bay was unexpected. Even as juveniles, surf smelt, herring, and sand lance have been shown to be fundamentally planktonic feeders (Hart 1973; Simenstad et al. 1979b); only threespine stickleback have been reported to feed extensively on epibenthic or benthic prey (*ibid*).

Among the harpacticoids consumed by these fishes (Table 15), the most conspicuous taxa—*H. uniremis*, *Tisbe* and *Zaus*—constitute the largest, epibenthic forms compared to the other taxa, which are typically epiphytal (e.g., *Porcellidium*), smaller or burrowing (e.g., *Huntemannia*) forms. Therefore, in respect to size and availability in the water column, these taxa may be the most susceptible to fish predation. In fact, *Harpacticus* (*uniremis*?), *Tisbe* and *Zaus* were reported in samples taken 30 cm over a mudflat in the Nanaimo River estuary, at densities from 2% to 9% (*Harpacticus*) and 83%-333% (*Zaus*) of the densities 5 cm from the bottom (Sibert 1981). In Padilla Bay, however, we found *H. uniremis* to be exclusively associated with *Z. marina* epiphytes and *Zaus* sp. only on *Z. marina* segments (with no correlation to epiphyte growth) and in the mudflat tidal inundation samplers, while *Tisbe* was found in every habitat and in all microhabitats but the *Z. japonica* and higher elevation surface sediments. Thus, although there may have been minor tidal transport of *H. uniremis* and *Zaus*, it appeared that they were available only to fish foraging directly in the *Z. marina* eelgrass habitat. It is impossible to determine whether the fish were actually foraging on the eelgrass blades and within the epiphytes or whether these harpacticoids were available to the fish outside the epiphyte microhabitat. We did not sample subtidal *Z. marina* habitats nor did we sample the benthic boundary layer or water column over eelgrass when the flat was completely inundated by the tide. *Harpacticus* and *Tisbe*, however, are capable of colonizing substrates ~1 m from the bottom (Hauspie and Polk 1973), and we have observed them

aggregating in the water column immediately adjacent to eelgrass and epiphytes in mesocosms (Simenstad and Cordell, unpubl.). It is important to remember, however, that *H. uniremis* was not found in any other habitat outside the *Z. marina* epiphytes, suggesting their behavioral association with the epiphytes is tenacious.

As indicated by the tidal inundation samples, *Tisbe* was the only harpacticoid prey taxa to be distributed ubiquitously across the littoral flat at Padilla Bay. Coincidentally, it was prevalent only in the diet of threespine stickleback, indicating that they, more than any of the other five fish, could also have fed more over other habitats across the flat and into the salt marsh. Our tidal inundation sampler may not have assessed effectively as tidal transport across the littoral flat, and other harpacticoid prey may be available outside the *Z. marina* habitat. Transport could lag behind initial tidal inundation or occur under higher wave conditions, when benthic boundary layer velocities and turbulence may be higher. In some cases, as in the salt marsh, the tidal inundation samplers may have been placed outside of the principal path of transport, e.g., in the more quiescent reaches of the marsh.

Despite these caveats, the data imply the importance of *Z. marina* habitats as sources of selected prey resources of estuarine fishes, in particular those which occupy estuaries during their early life histories. In addition to their function as refugia from predation and a source of detrital matter to the estuarine food web, eelgrass beds also appear to produce and export considerable abundances of meiofaunal prey for fishes feeding within and without the habitat. On the basis of an average *Z. marina* shoot density of 500 m^{-2} for the +0.1-m tidal elevation in Padilla Bay (Thom 1988), estimates of the total densities of the three dominant harpacticoid prey taxa (*H. uniremis*, *Tisbe* sp., and *Zaus* sp.) on the eelgrass blades would be between 10.1 X 10^7 m^{-2} (low epiphyte) and 16.1 X 10^7 m^{-2} (high epiphyte)—many orders of magnitude higher than estimated for any of the other habitats/microhabitats. Regardless of the habitats occupied by fishes, an extensive component of their prey resources may have originated from this one source. Thus, management of wetland habitats for maintenance of functions such as food web support must consider such potential food web contributions and habitat interdependencies.

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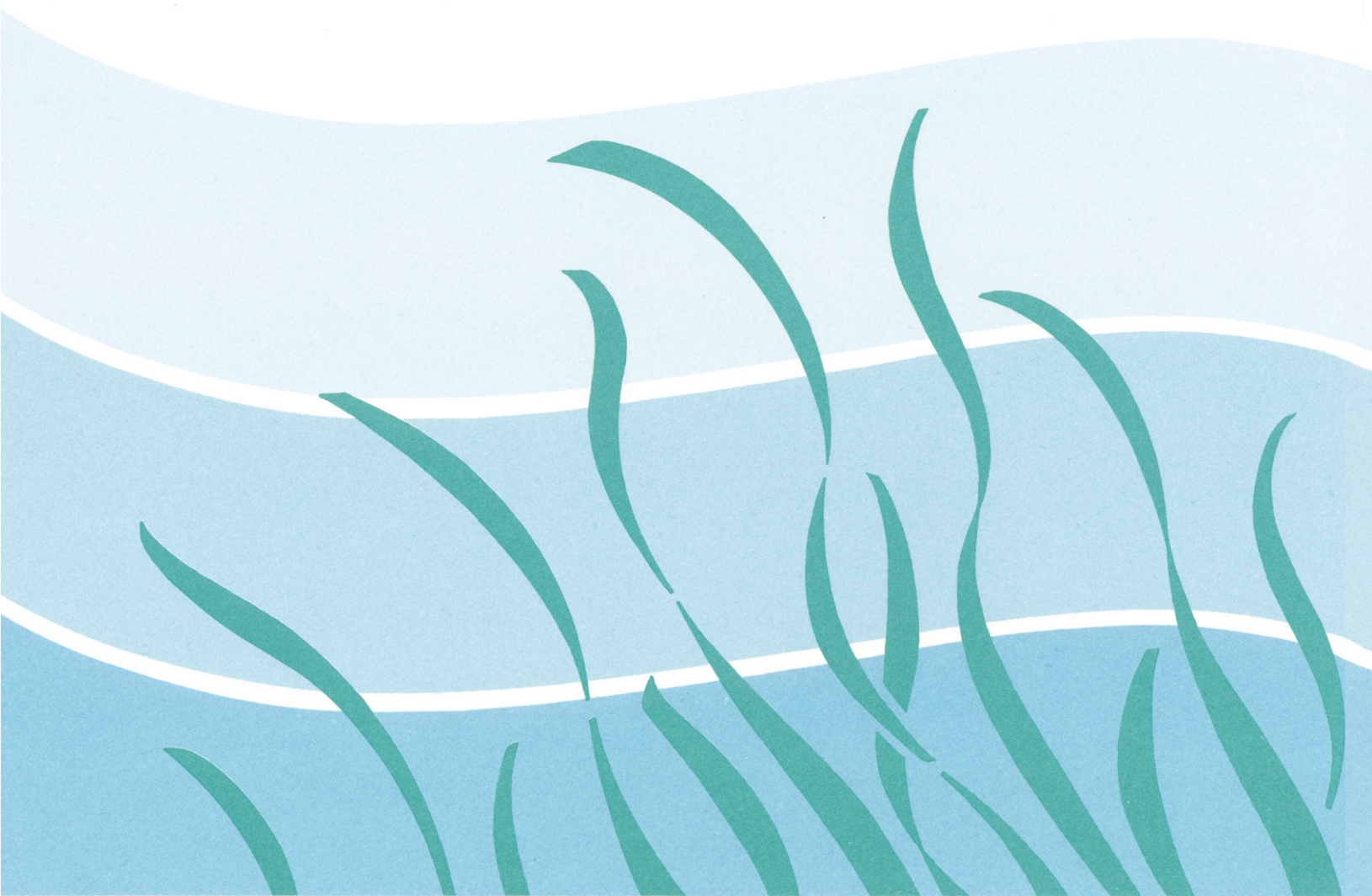
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