



*Padilla Bay*

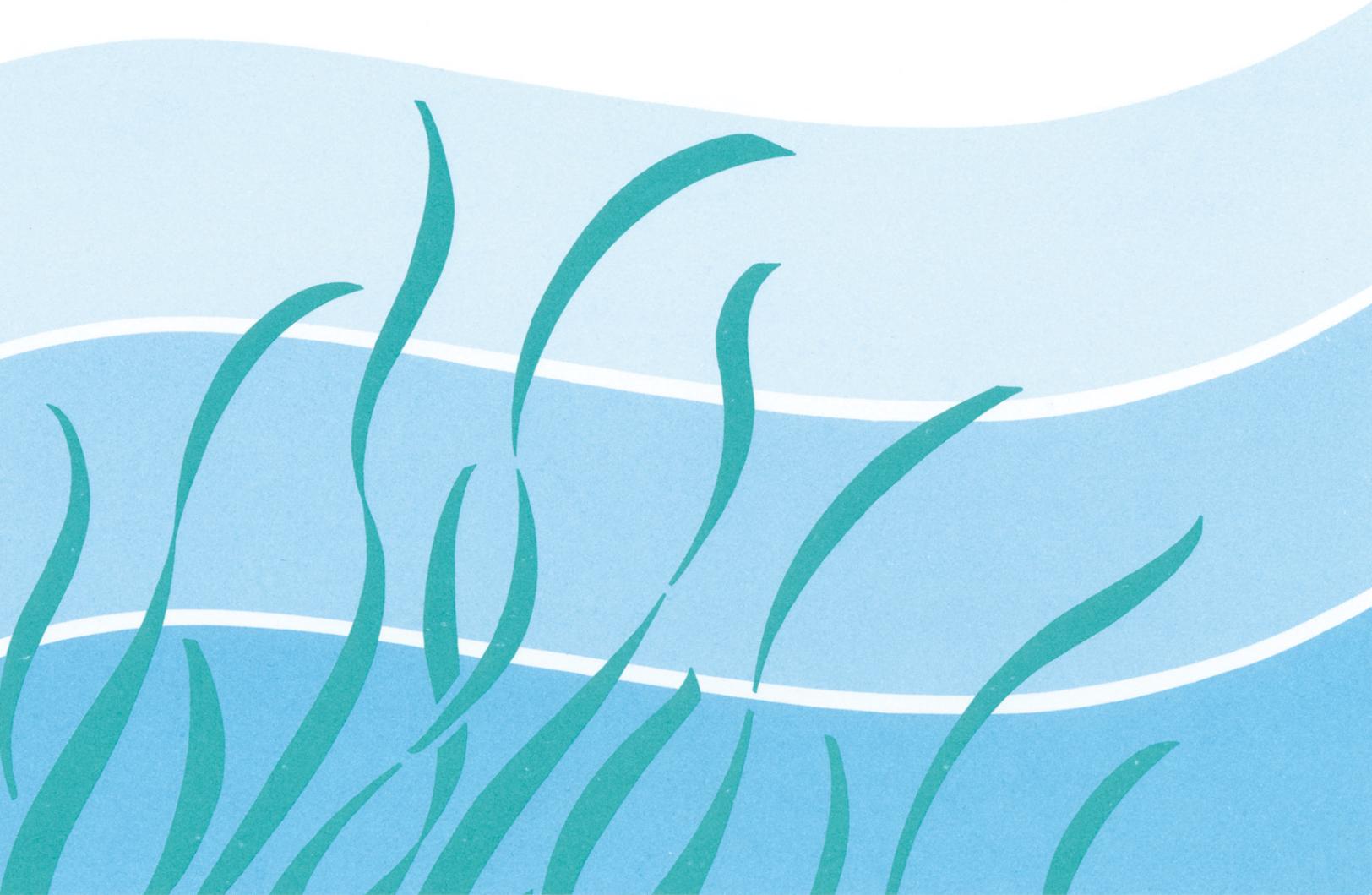
National Estuarine Research Reserve

Reprint Series No. 8  
Reprinted October 1990

**EFFECTS OF HABITAT CHARACTERISTICS ON MUSSEL  
GROWTH IN PADILLA BAY, WASHINGTON**

Mary H. Ruckelshaus

1988



The Padilla Bay National Estuarine Research Reserve is one of the reserves in the National Estuarine Research Reserve System. One of the purposes of the Reserve is to facilitate research and monitoring at Padilla Bay to provide information for the conservation and management of the nation's estuaries, in particular greater Puget Sound and other estuaries in the Pacific Northwest. The Padilla Bay National Estuarine Research Reserve assists the dissemination of this information from research and monitoring by publishing a Reprint Series and a Technical Report Series.

The **Reprint Series** includes research grant reports, out of print agency reports and student reports dealing with the Padilla Bay estuary. Reports are reprinted without revision or editing. Final reports for research grants and Masters Theses should be treated as unpublished data and should not be cited without permission of the author(s).

The **Technical Report Series** includes articles, reports of research projects, data reports, bibliographies and reviews dealing with the Padilla Bay estuary.

Communications concerning receipt or exchange of Technical Reports or Reprints or submission of manuscripts should be directed to the Research Coordinator at Padilla Bay National Estuarine Research Reserve. Communications concerning the content of reports and reprints should be directed to the author(s).

Padilla Bay National Estuarine Research Reserve  
10441 Bayview-Edison Road  
Mount Vernon WA 98273-9668  
(360)428-1558

Padilla Bay National Estuarine Research Reserve is managed by the Shorelands and Environmental Assistance Program, Washington State Department of Ecology, in cooperation with the Estuarine Reserves Division, National Oceanic and Atmospheric Administration (NOAA), U.S. Department of Commerce. The preparation of this document was financially aided through a grant to the Washington State Department of Ecology with funds obtained from NOAA/Office of Ocean and Coastal Resource Management, and appropriated for Section 306 or 315 of the Coastal Zone Management Act of 1972, as amended.



The Effects of Habitat Characteristics on Mussel Growth  
in Padilla Bay, Washington

by

MARY H. RUCKELSHAUS

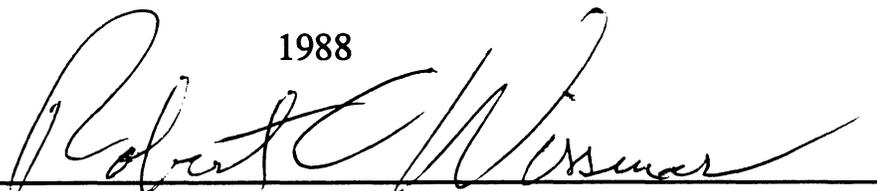
A thesis submitted in partial fulfillment  
of the requirements for the degree of

Master of Science

University of Washington

1988

Approved by



(Chairperson of Supervisory Committee)

Program Authorized  
to Offer Degree

Date

18 March 1988

**Bibliographic citation:** Ruckelshaus, Mary H. 1981. Effects of habitat characteristics on mussel growth in Padilla Bay, Washington. M.S. Thesis. Univ. Washington. 53 pp. Seattle, Washington. Padilla Bay National Estuarine Research Reserve Reprint Series No. 8, 1990.

In presenting this thesis in partial fulfillment of the requirements for a Master's degree at the University of Washington, I agree that the Library shall make its copies freely available for inspection. I further agree that extensive copying of this thesis is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Any other reproduction for any purposes or by any means shall not be allowed without my written permission.

Signature \_\_\_\_\_

Date \_\_\_\_\_

University of Washington

Abstract

THE EFFECTS OF HABITAT CHARACTERISTICS ON MUSSEL  
GROWTH IN PADILLA BAY, WA.

by Mary Ruckelshaus

Chairperson of the Supervisory Committee: Professor Robert C. Wissmar  
Fisheries Research Institute

Growth rates of estuarine suspension feeders represent a response to physical and biological characteristics of their habitat. In order to be able to use consumer growth rates as indicators of overall habitat quality, the effects of habitat characteristics; such as origins, quantity and quality of food, on growth must be better understood. This study addresses the question of how biological and physical habitat characteristics affect mussel growth in the Padilla Bay estuary in northern Puget Sound. Mussels (*Mytilus edulis*) were placed in cages in habitats dominated by different primary producers and physical characteristics. Growth rates of caged mussels were highest at the mouth of the estuary and lowest in a fresh water slough. However, concentrations of food sources (chlorophyll *a* and particulate organic carbon and nitrogen) showed an inverse relationship with growth rates. Physical stresses associated with the habitats appeared to depress growth rates despite high food concentrations. Decreases in growth rates showed a strong positive correlation with decreases in salinity, concentration of inorganic matter in the seston and submergence time. Additionally, natural abundances of stable

carbon isotopes suggested that different primary food sources for mussels in different habitats may have been partly responsible for variable growth rates. If food sources and physical conditions critical to consumer performance can be determined, prioritization of estuarine habitat management goals may be facilitated.

## TABLE OF CONTENTS

	<u>Page</u>
List of Figures.....	iii
List of Tables.....	iv
Introduction.....	1
Materials and Methods.....	4
Description of Study Sites.....	4
Experimental Design and Analytical Procedures.....	6
Results.....	11
Mussel Growth.....	11
Sources and Fates of Organic Carbon: $\delta^{13}\text{C}$ Data.....	11
Seston Characteristics: Particulate Matter and Phytoplankton.....	17
Physical and Chemical Characteristics.....	20
Discussion.....	22
Origins and Composition of Mussel Food Sources.....	22
Seston Quantity, Quality and Mussel Growth.....	28
Other Factors Influencing Mussel Growth.....	29
Conclusions and Further Questions.....	35
References.....	37
Appendix A: Data Tables.....	43

## LIST OF FIGURES

Number	Page
1. Map of Study Area.....	5
2. Cage Design.....	8
3. Monthly Mussel Growth Rates.....	12
4. Mussel Shell Length Increments.....	13
5. Standardized Mussel Growth Rates.....	14
6. $\delta^{13}\text{C}$ Data.....	16
7. Food Concentrations During a Tidal Cycle.....	18
8. Schematic of Carbon Cycling.....	25

## LIST OF TABLES

Number	Page
1. List of Sestonic Algal Species.....	21
2. Summary of Seston Characteristics.....	23
A1. Mussel Growth Rate Data.....	44
A2. $\delta^{13}\text{C}$ Data.....	45
A3. Coefficients of Variation for $\delta^{13}\text{C}$ Data.....	46
A4. Seston Characteristics Data.....	47
A5. Food Concentrations Over a Tidal Cycle.....	48
A6. Seston Quality Data.....	49
A7. Temperature and Salinity Data.....	50
A8. Clearance Rate Data.....	51
A9. Absorption Efficiency Data.....	52

## ACKNOWLEDGMENTS

The author wishes to express sincere appreciation to Professors Robert Wissmar and Charles Simenstad for their assistance in the field and laboratory, and in preparation of this manuscript. Professors James Anderson and John Baross also provided helpful comments. Thanks also to Terence Stevens, Sharon Riggs, Mark Olson and the staff at the Padilla Bay National Estuarine Research Reserve for logistical and moral support and to Mr. R.H. Race for his generosity in supplying the mussels. Finally, the author would like to thank Dr. A.O.D. Willows for permission to use the Friday Harbor Laboratories.

## INTRODUCTION

Growth rates of estuarine suspension feeders represent responses to physical and biological characteristics of their habitat. In order to be able to use consumer growth rates as indicators of overall habitat quality, the effects of habitat characteristics, such as origins, quantity and quality of food, on growth must be better understood. The major food for estuarine suspension feeders is suspended particulate organic matter (Griffiths 1980, Incze et al. 1980, Hummel 1985b, Lucas et al. 1987). There is evidence that the composition of suspended particulate matter (seston) changes with habitat in Pacific Northwest estuaries. Wissmar and Simenstad (1984) found differences in chlorophyll *a* concentrations, bacterial counts, primary production rates and natural stable carbon isotope composition ( $\delta^{13}\text{C}$ ) of surface and subsurface seston along a horizontal habitat gradient, through neritic, eelgrass, macroalgal and riverine habitats in Hood Canal, WA. Furthermore, estimates of food quantity in estuaries based on total carbon production values do not necessarily represent the ultimate availability of food to consumers. Although marine phytoplankton often account for the greatest percent of total net carbon production in an estuary, several studies using stable carbon isotope analyses suggest that estuarine suspension feeders and other consumers derive their carbon from a variety of endogenous autotrophic sources (e.g., seagrass detritus, macroalgae, epibenthic microalgae and epiphytes), as compared to their counterparts in marine-neritic communities which utilize primarily phytoplankton carbon (Fry and Parker 1979, McConnaughey and McRoy 1979, Fry 1984, Simenstad and Wissmar 1985). However, studies in other estuaries suggest that neritic phytoplankton can be the major sestonic food source throughout the estuary (Haines and Montague 1979, Incze et al 1982, Brinson and Matson 1983).

Several stable carbon isotope studies have attempted to identify origins of consumer foods (McConnaughey and McRoy 1979, Incze et al 1980, Simenstad and Wissmar 1985), but few have explored their relative importance to suspension feeders in different estuarine habitats. The goal of this study was to couple estimates of food origins and quantity with measurements of consumer growth as an indicator of food and habitat quality in a well-mixed estuary. In this paper I report on three aspects of this study: 1) spatial and temporal changes in stable carbon isotope composition of autotrophs and seston in habitats characterized by different primary producers; 2) the fates of major food resources by measuring the carbon isotopic composition of suspension feeders; and, 3) the relative importance of different food resources to consumers by measuring mussel growth in the different habitats.

Estuaries that receive appreciable riverine input may be amenable to stable carbon isotope analysis because terrestrial and marine carbon sources are isotopically distinct (Thayer et al. 1978, Stephenson and Lyon 1982, Incze et al. 1982, Simenstad and Wissmar 1985). Further, the study area we have chosen includes habitats dominated by estuarine autotrophs with isotopically distinct carbon isotope values (e.g., eelgrass and phytoplankton) (McConnaughey and McRoy 1979, Stephenson et al. 1986).

We surmised that determination of the sources and fates of sestonic food using stable carbon isotopes, in combination with measurements of consumer growth as a common performance indicator throughout the study habitats, would allow us to estimate the importance of consumer-autotroph linkages in different habitats. This approach assumed the effects of food quality on mussel growth could be detected despite differences in physical habitat characteristics.

Mussel growth rates can be used as an indicator of their physiological response to the natural environment (Bayne and Newell 1983). Food quantity and quality, temperature, salinity, concentration of inorganic material in the seston and aerial exposure have been

shown to alter growth rates of the mussel *Mytilus edulis* in both field and laboratory studies (Tenore and Dunstan 1973, Winter 1973 and 1976, Bayne 1976; Bayne and Widdows 1978, Widdows et al. 1979, and Kiorboe et al. 1981).

In order to assess the effects of habitat characteristics on mussel growth rates, the following questions were posed: 1) What are the origins, quantities and qualities of mussel food resources in different Padilla Bay habitats?; 2) What are mussel growth rates in the different habitats?; and 3) What is the relationship between mussel growth rates and the biological and physical characteristics of the habitats?

## MATERIALS AND METHODS

### Description of Study Sites

Four intertidal sampling locations were located along a decreasing salinity gradient in Padilla Bay, northern Puget Sound: 1) a neritic site at the western extreme of the Bay (NR); 2) an extensive eelgrass bed near the mouth (EG); 3) a mudflat site in mid-estuary near a main tributary channel (MF); and, 4) a tidally-influenced slough at the head of the estuary (SL) (Fig. 1). Padilla Bay receives most of its freshwater input from the Skagit River, which enters Padilla Bay via the Swinomish Channel from the southwest (Fig. 1). Discharge from the Skagit River is highly seasonal, peaking during periods of spring snowmelt and winter rains (USGS 1985). Several small sloughs to the east of the Bay also contribute some fresh water. The sloughs entering Padilla Bay drain predominantly agricultural farm lands.

The bay is shallow (2-3 m average depth), and wind coupled with tidal mixing can create a homogeneous water column that is rarely stratified. It covers an area of approximately 81 km<sup>2</sup>. The benthic surface deposits consist of sand, silt and gravel. Tidal flats at lower elevations in the central and northern parts of the bay are characterized by dense beds of eelgrass (*Zostera marina* and *Z. japonica*) and patches of macroalgae (*Ulva* and *Enteromorpha* species) covering over 2500 hectares (Dr. Ron Thom, Fisheries Research Institute, University of Washington; personal communication). The average net primary production (NPP) of the eelgrass habitat is 361 gC m<sup>-2</sup> yr<sup>-1</sup>, of which *Zostera marina* accounts for 48% and epiphytic diatoms and macroalgae provide 49% (Ron Thom, per. comm.). Fringing salt marsh habitats characterized by *Carex lyngbyei*, *Salicornia virginica*, and *Distichlis spicata* occur along the sloughs and at higher tidal elevations.

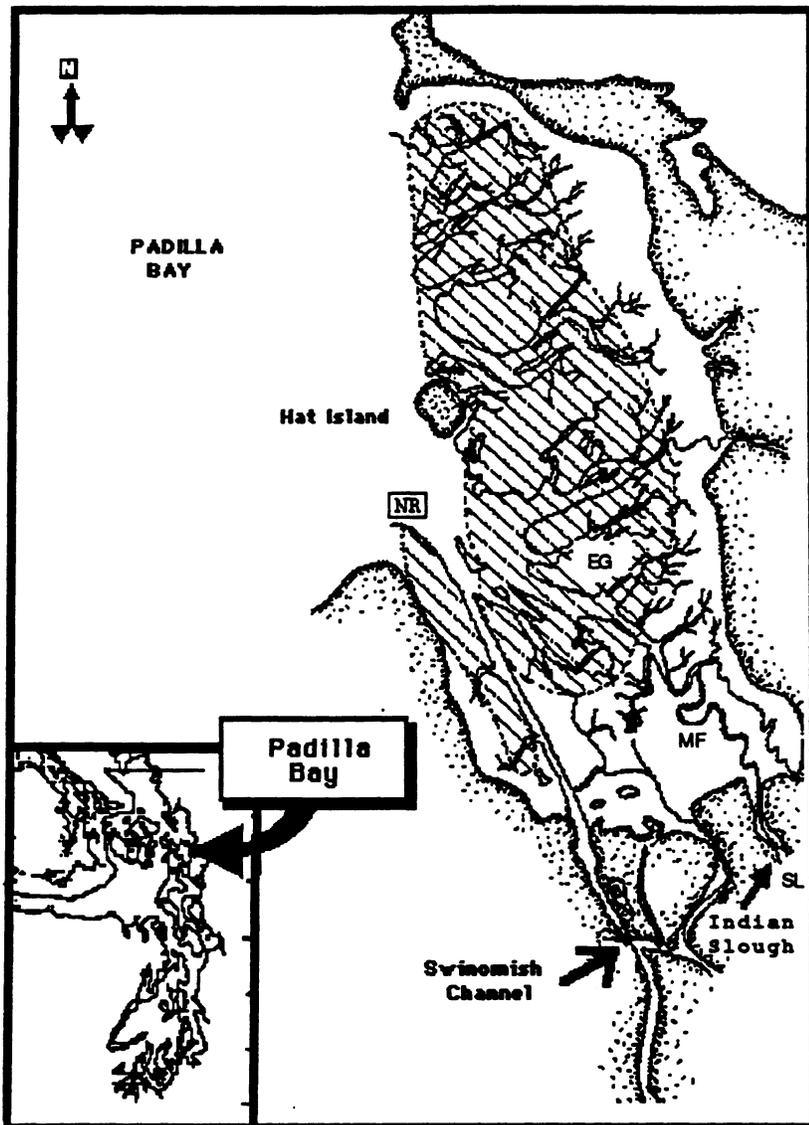


Figure 1. Map of neritic (NR), eelgrass (EG), mudflat (MF) and slough (SL) study habitats in Padilla Bay, WA.

### Experimental Design and Analytical Procedures

Suspended particulate matter (SPM = seston) was collected (April-August 1987 only) as filtrate from nutrient water samples at each site. The inorganic fraction of the seston was determined by obtaining the ash weight after burning at 450 °C for four hours. The organic fraction of the SPM was determined by obtaining the ash-free dry weight (AFDW) (Strickland and Parsons 1972). Particulate organic carbon (POC) and nitrogen (PON) components of the seston were determined by a Perkin-Elmer CHN analyzer. POC:PON ratios are expressed as C:N.

The principal sources of autotrophic carbon in Padilla Bay include: terrestrial/fresh water runoff, vascular marsh plants, estuarine and marine macrophytes, phytoplankton, and epiphytic and epibenthic microalgae (Ron Thom, pers. comm.). Acid-washed forceps were used to collect macrophytes. Macrophyte samples were systematically subsampled over the whole blade and pooled to compose an integrated sample. Epiphytes were scraped off the eelgrass blades and epibenthic microalgae were separated from the surface of sediment cores. Phytoplankton were sampled by passing water through a 64-73 µm prefilter and retained on a pre-combusted glass-fiber filter (Simenstad and Wissmar 1985). Chlorophyll *a* (chl *a*) measurements were made according to Strickland and Parsons (1972). Qualitative observations of phytoplankton species composition were made by Dr. Dennis Kunkel (University of Washington) from water samples taken in June 1987. Water-column and near-bottom algae (<63 µm) were sampled during high tides (except at the slough site, where the low tide water column was also sampled.) Common habitat associations of the species were determined from local surveys (Whiting and McIntire 1985, Amspoker and McIntire 1986) and from personal communication with Dr. Ron Thom.

Stable carbon isotope analyses were conducted by Coastal Marine Laboratories, Inc.  $\delta^{13}\text{C}$  is calculated as a parts per thousand difference from the standard PDB reference:

$$\delta^{13}\text{C} = \frac{(^{13}\text{C}/^{12}\text{C} \text{ sample}) - (^{13}\text{C}/^{12}\text{C} \text{ standard})}{(^{13}\text{C}/^{12}\text{C} \text{ standard})} \times 1000$$

$\delta^{13}\text{C}$  values are expressed in ‰ and, in this paper, they are presented as enriched (heavier, with more  $^{13}\text{C}$ , less negative values) or deplete (lighter, with less  $^{13}\text{C}$ , more negative values) (Fry and Sherr 1984). Machine error on the data reported did not exceed  $\pm 0.3$  ‰. All biotic samples were immediately filtered and acid-washed (5% HCl) to remove carbonates on pre-combusted 1.0  $\mu\text{m}$  glass-fiber filters (Strickland and Parsons 1972, Simenstad and Wissmar 1985). Filters were wrapped in pre-combusted aluminum foil and placed in scintillation vials with dessiccant until processed.

The bay or blue mussel, *Mytilus edulis*, was used as a representative consumer organism because of its adaptability to a variety of environmental conditions, particularly estuarine (Bayne 1976). *Mytilus* (1-3 cm) were collected from one location in northern Puget Sound to ensure similar environmental histories and genetic composition, which are known to influence growth rates (Dickie et al. 1984). The mussels were placed in cages at each of the four study sites. Cages were attached to a channel marker at the neritic site and at two different heights (approximately 5 and 20 cm) above the substratum at the remaining three sites (Fig. 2). The bi-level cage design was used to compare the effects of near-bottom and water column habitat conditions on mussel growth rates (Frechette and Bourget 1985). Habitat characteristics the mussels experienced were assumed constant within each cage. Twenty to sixty *Mytilus* individuals were placed at each site in April 1986, July 1986, and December 1986 in order to monitor growth rates during different seasons. Mussel growth rates were determined by measuring shell lengths (to the nearest 0.2 mm) of at least five mussels from each cage (Incze et al 1980, Frechette and Bourget 1985). Statistical comparisons of growth rates in top and bottom cages were made with two-sample t-tests (Zar 1984).

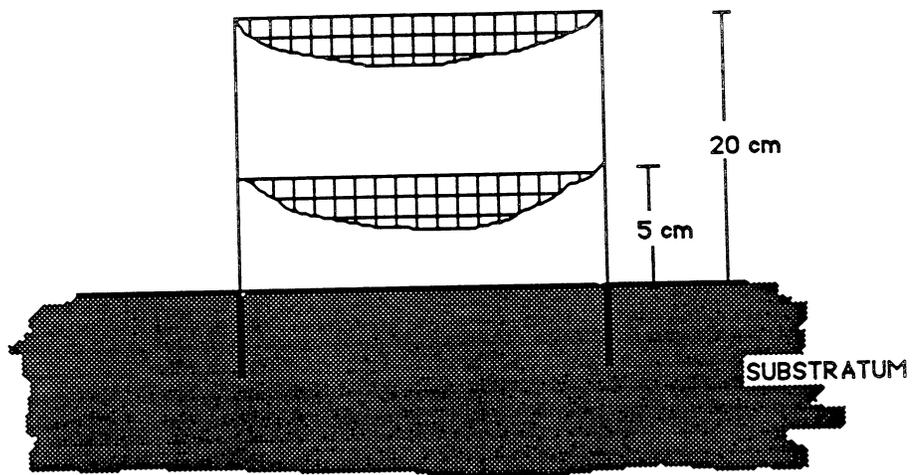


Figure 2. Schematic of cage design used at the eelgrass, mudflat and slough study sites in Padilla Bay, WA.

The mussel mantle, a metabolically stable tissue (Bayne 1976), was dissected from the mussels for use in  $\delta^{13}\text{C}$  analyses.

*Mytilus* is a generalist suspension-feeder (Foster-Smith 1975, Bayne 1976, Vahl 1980), therefore, its carbon isotope signature should reflect whatever carbon source is most readily available, rather than a selected food. It has been well documented in laboratory and field studies that consumer carbon isotope values are close to those of their food sources, typically enriched by 1 to 2 ‰ (Fry and Sherr 1984). Since consumer  $\delta^{13}\text{C}$  values reflect the signatures of their combined food sources over time, estimation of a consumer's primary carbon food sources is possible (DeNiro and Epstein 1978). The degree of precision in estimates of carbon sources depends on their relative  $\delta^{13}\text{C}$  values, compared to the number of food sources included in the consumer's diet.

A problem cited in the use of  $\delta^{13}\text{C}$  isotope analyses is intraspecific and intraorganismal variability. For instance, individuals within a species can have variable  $\delta^{13}\text{C}$  values due to different amounts of storage products with variant  $\delta^{13}\text{C}$  values (Fry and Sherr 1984). Mussel mantle tissue, therefore, is expected to show little variability in  $\delta^{13}\text{C}$  due to its metabolic stability (McConnaughey and McRoy 1979).

Decomposition of plant carbon and/or metabolic breakdown of carbon in a food web can also result in changes in  $\delta^{13}\text{C}$ ; however, most studies have indicated that such fractionations are minimal (Haines and Montague 1979, Gearing et al. 1984). Accordingly, by selectively sampling tissues with low metabolic variability and integrating whole plants, we assume that stable isotopic composition of carbon remains relatively constant in our samples.

Sampling of primary producers, water, seston, mussels, and physical parameters occurred approximately bi-monthly during low tides from April 1986 through August 1987 at each of the sites. A separate set of measurements designed to detect changes in particulate organic carbon and nitrogen (POC and PON) during a tidal cycle were

conducted in August 1986 at the SL and EG habitats, in which POC and PON were sampled at first exposure of the cages to water on the flood tide, at slack tide, and at peak ebb tide.

Temperature and salinity were obtained using a salinometer. The exposure/inundation time and elevation of the sites were determined by surveying of the cage locations and in reference to local tidal charts; NR and EG cage elevations were -1.3 feet below mean low low water level (MLLW), the MF cage was located at +3.2 feet; and, the SL cage was at +4.2 feet above MLLW (Terence Stevens, Padilla Bay National Estuarine Research Reserve, Bayview, WA). Given the diurnal tides through the period of the study, estimated cage submergence times from the above elevations were: 22-24 hours day<sup>-1</sup> at the NR and EG sites; 19-22 hrs day<sup>-1</sup> at the MF, and 18-20 hrs day<sup>-1</sup> at the SL site.

Table and Figure numbers cited in the text that are preceded by the letter "A" are located in Appendix A.

## RESULTS

### Mussel Growth

Average mussel growth rates ( $\text{mm month}^{-1}$ ) in top vs. bottom cages from all habitats were not significantly different among seasons ( $t = -0.06$ ,  $df = 270$ ;  $p = .96$ ). However, growth rates in top and bottom cages within habitats were significantly different. Mussel growth rates in the top cage were significantly greater at the eelgrass site ( $t = 2.09$ ,  $df = 85$ ;  $p = .04$ ), yet significantly lower at the MF and SL habitats ( $t = -2.03$ ,  $df = 97$ ;  $p = .05$  and  $t = -3.14$ ,  $df = 84$ ;  $p = .002$ , respectively).

Mussels from the NR and EG sites had the highest average monthly growth rates (2.5 and  $2.6 \text{ mm month}^{-1}$ , respectively), and the SL site mussels grew at the slowest average rate ( $0.76 \text{ mm month}^{-1}$ ) (Fig. 3, Table A1). The highest growth rates occurred from July-August 1986 in the NR, EG, and MF habitats; and from August-December 1986 in the SL habitat. Between June and August 1987 shell growth was greatly reduced in all habitats (Fig. 4). Ultimate mussel shell lengths attained were consistently greater at the NR and EG sites and decreased towards the SL site.

Due to the different cage elevations, growth rates were standardized to submergence regimes at the NR and EG sites. Re-calculated growth rates in the MF and SL habitats increased slightly (Table A1), but the general trend of decreasing growth rates from the mouth to the head of the estuary did not change. For example, the magnitude of differences between standardized growth rates in the three main Bay habitats did not change appreciably in May 1986, yet was dampened in December 1986 (Fig. 5).

### Sources and Fates of Organic Carbon: $\delta^{13}\text{C}$ Data

Within all habitats, mussel  $\delta^{13}\text{C}$  values were more enriched than the POC values (mean difference =  $2.1 \text{ ‰}$ ) but deplete relative to epibenthic algae and macrophyte

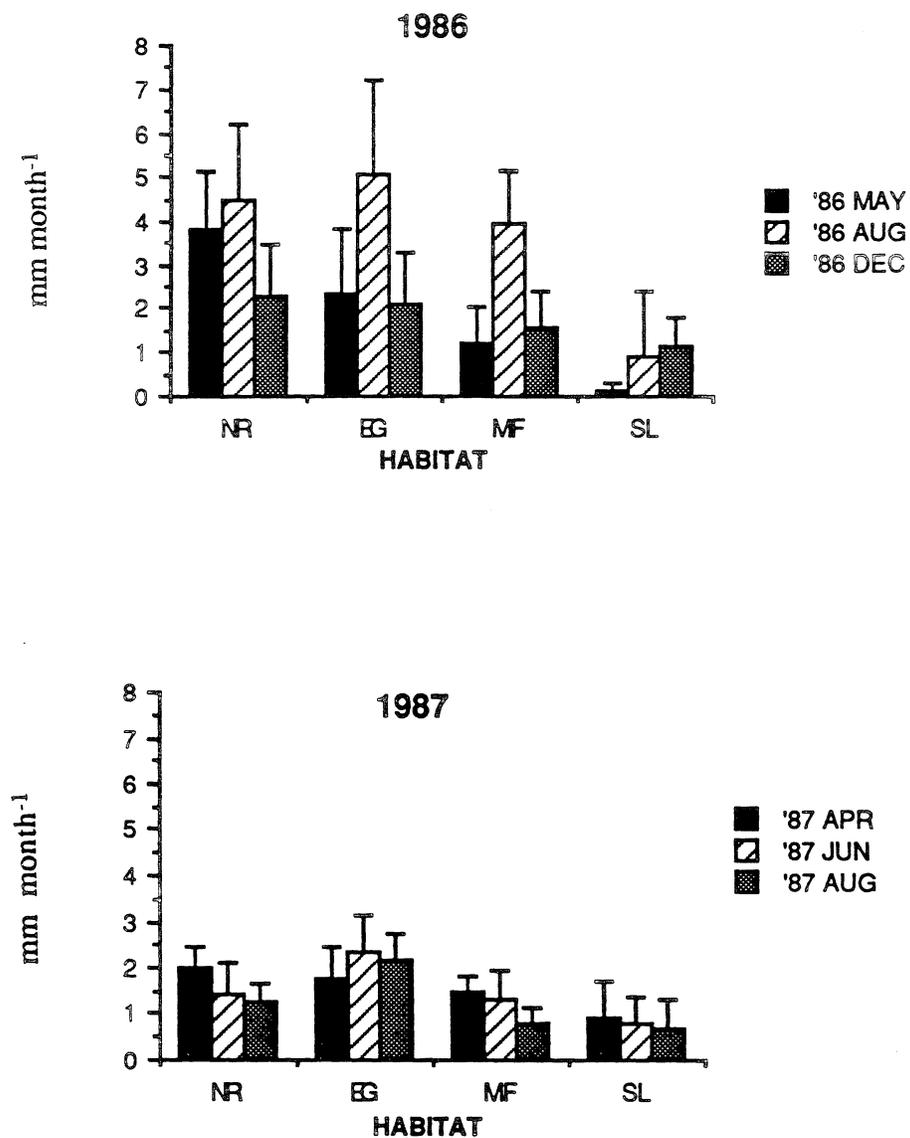


Figure 3. Monthly mussel growth rates at the neritic (NR), eelgrass (EG), mudflat (MF) and slough (SL) study habitats in Padilla Bay, WA. in 1986 and 1987; growth rates are based on shell length increases of at least five mussels per site per date; and error bars represent one standard deviation.

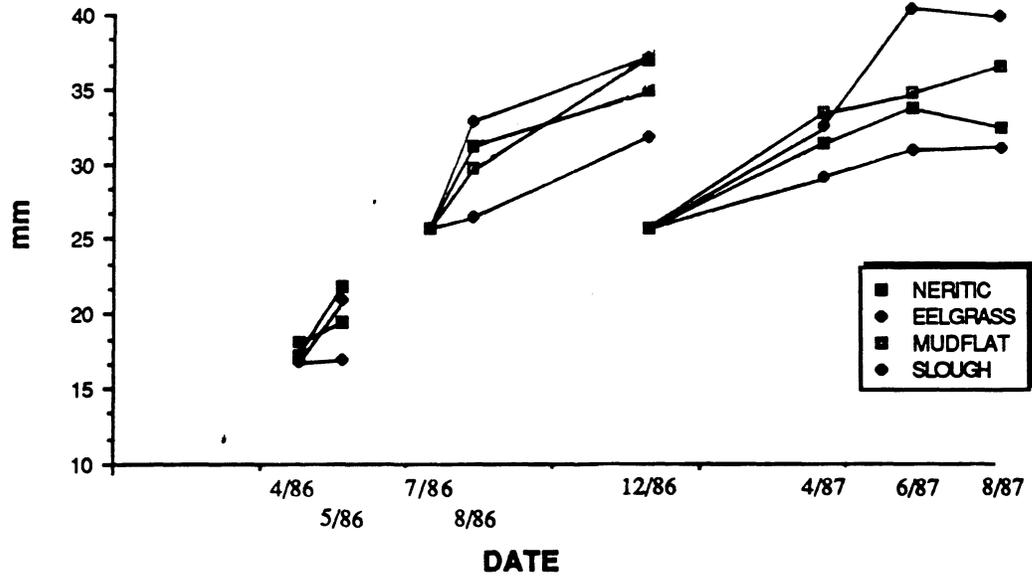


Figure 4. Incremental mussel shell lengths (mm) at the neritic, eelgrass, mudflat and slough study habitats in Padilla Bay, WA. in 1986 and 1987. Shell length of three groups of mussels were measured; from April to May 1986, July to December 1986 and from December 1986 to August 1987.

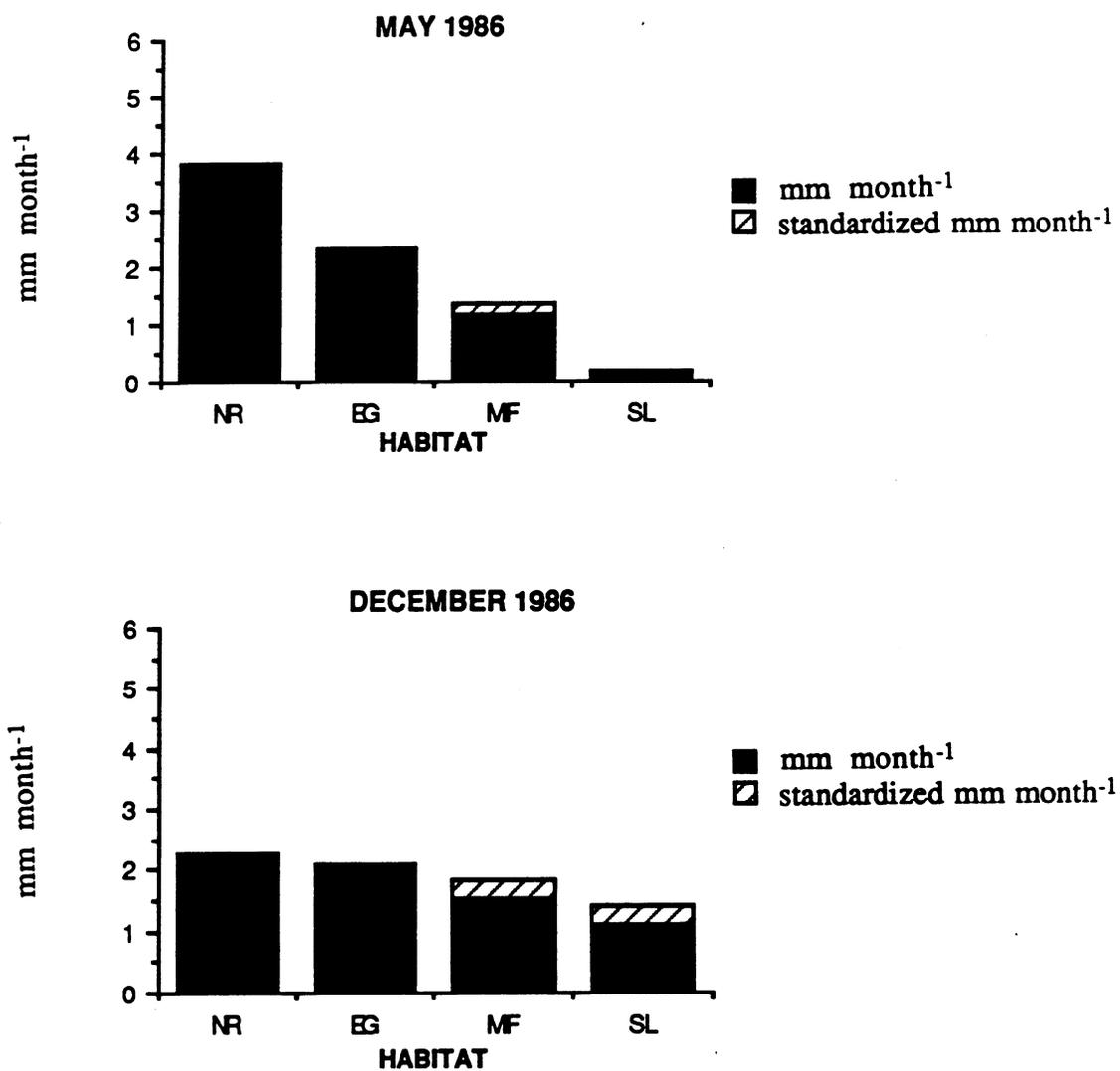


Figure 5. Mussel growth rates standardized to the submergence regime at the neritic (NR) and eelgrass (EG) habitats in Padilla Bay, WA. in May and December 1986. MF = mudflat and SL = slough.

values (Fig. 6, Table A2).  $\delta^{13}\text{C}$  values presented in Table A2 are averages of 2-5 individual samples. The coefficients of variation associated with the  $\delta^{13}\text{C}$  data ranged from 0 to -0.15 (Table A3). The most highly variable values occurred in the eelgrass and mudflat habitats.  $\delta^{13}\text{C}$  values of native bivalve suspension feeders (*Tapes japonica*, *Mytilus edulis*) near the mudflat and eelgrass sites were within the ranges of caged mussel values (-16.5 to -19.2 ‰). The differences between POC and mussel  $\delta^{13}\text{C}$  values were greater in the spring and winter than in summer. Mussels were most  $^{13}\text{C}$ -enriched in the winter in all habitats except the SL.

The carbon isotope data reveal some separation of autotrophic carbon sources within the four habitats. Overlap between the eelgrass and mudflat  $\delta^{13}\text{C}$  values was generally high; the slough autotrophs, however, were distinctly more  $^{13}\text{C}$ -deplete. (Fig. 6). In general, autotrophs in the slough and neritic habitats (-19.2 to -28.5 ‰) were more  $^{13}\text{C}$ -deplete than those in the eelgrass and mudflat habitats (-8.1 to -17.1 ‰). The neritic site autotrophic carbon was primarily from marine phytoplankton, as interpreted from POC  $\delta^{13}\text{C}$  values ranging from -19.2 to -22.5 ‰.

In the eelgrass habitat, *Zostera* showed the greatest enrichment (-8.1 to -9.7 ‰). Epiphytes and other macroalgal species were less enriched (-12.3 to -13.4 ‰) than *Zostera*, but more than the epibenthic algae (-16 to -18.1 ‰). POC  $\delta^{13}\text{C}$  values in the EG habitat were more  $^{13}\text{C}$ -deplete than the autotrophic carbon sources (-18.0 to -21.5 ‰), but were still enriched relative to POC from the NR habitat.

Carbon isotope values of macroalgal and epibenthic algae in the mudflat habitat (-10.4 to -17.1 ‰) were similar to autotrophs in the EG habitat, excluding *Zostera*. Average mudflat POC values ( $-20.0 \pm 1.1$  ‰) were similar to POC values in the neritic habitat.

Autotrophic carbon isotope values in the slough habitat were highly deplete, represented by the abundant sedge, *Carex lyngbyei* (-20.2 to -28.5 ‰), and epibenthic algae (-17.9 to -21.7 ‰). POC (-23.5 to -26.2 ‰) values were also deplete.

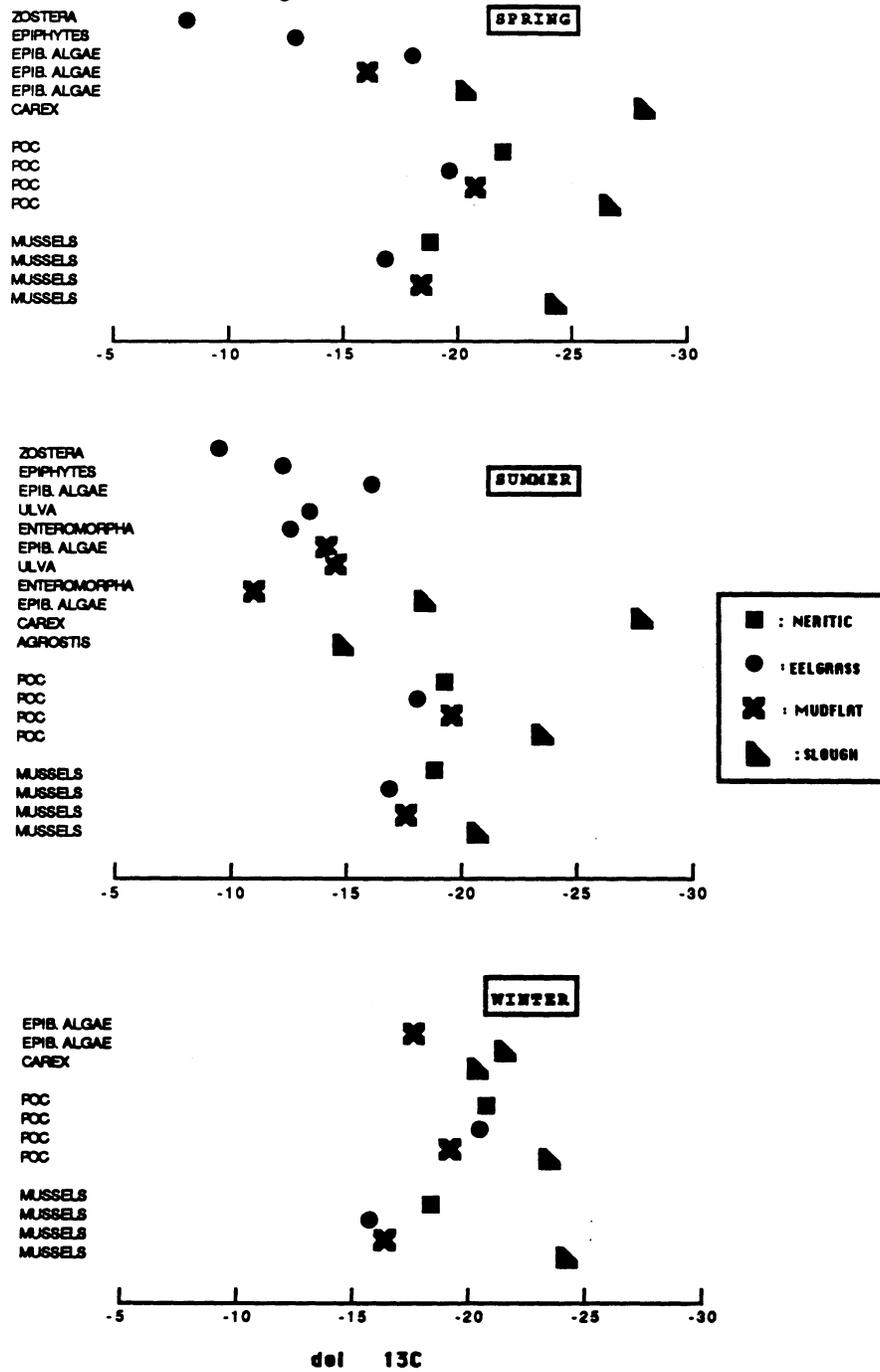


Figure 6. Stable carbon isotope ( $\delta^{13}\text{C}$ ) values of autotrophs, POC and consumers in neritic, eelgrass, mudflat and slough habitats in Padilla Bay, WA. in spring, summer and winter 1986 - 1987.

Only one autotroph sampled in the slough, the bunch grass, Agrostis, was comparatively enriched (-14.8 ‰).

During the winter, autotrophic carbon sources and POC were more  $^{13}\text{C}$ -deplete in all habitats, except at the SL site, where Carex and POC were enriched relative to the other seasons.

#### Seston Characteristics: Particulate Matter and Phytoplankton

The average concentrations of suspended particulate matter (SPM) and particulate inorganic matter (PIM) in the seston were highest at the mudflat and slough habitats (SPM=33.6 and 28.4  $\text{mg l}^{-1}$ , respectively; PIM=28.6 and 24.1  $\text{mg l}^{-1}$ , respectively) and decreased towards the neritic (NR) habitat (SPM=10.5  $\text{mg l}^{-1}$ ; PIM=8.5  $\text{mg l}^{-1}$ ). SPM and PIM concentrations were greater in summer than spring at all habitats except the SL (Table A4).

Food quantities also generally increased landward. The average concentrations of POC (430-1600  $\mu\text{g l}^{-1}$ ), PON (60-170  $\mu\text{g l}^{-1}$ ) and chl a (1.8-3.7  $\mu\text{g l}^{-1}$ ) generally increased from the NR towards the SL habitat, respectively (Table A4). At the neritic and eelgrass sites, highest concentrations of POC, PON and chl a occurred in summer months. Mudflat and slough chl a concentrations peaked in spring and summer, respectively, and POC and PON concentrations were highest in the winter.

During a single summer tidal cycle, POC and PON concentrations within the EG site did not vary by more than 0.1  $\text{mg l}^{-1}$  POC and 0.02  $\text{mg l}^{-1}$  PON during the tidal stages sampled (flood, slack, and ebb) (Fig. 7, Table A5). At the slough site, however, tidal stage concentrations varied by up to 2  $\text{mg l}^{-1}$  POC and 0.36  $\text{mg l}^{-1}$  PON. POC and PON concentrations were highest at flood and slack in the slough, and decreased by 67 and 72%, respectively, at low tide. C:N ratios were comparable in magnitude at both

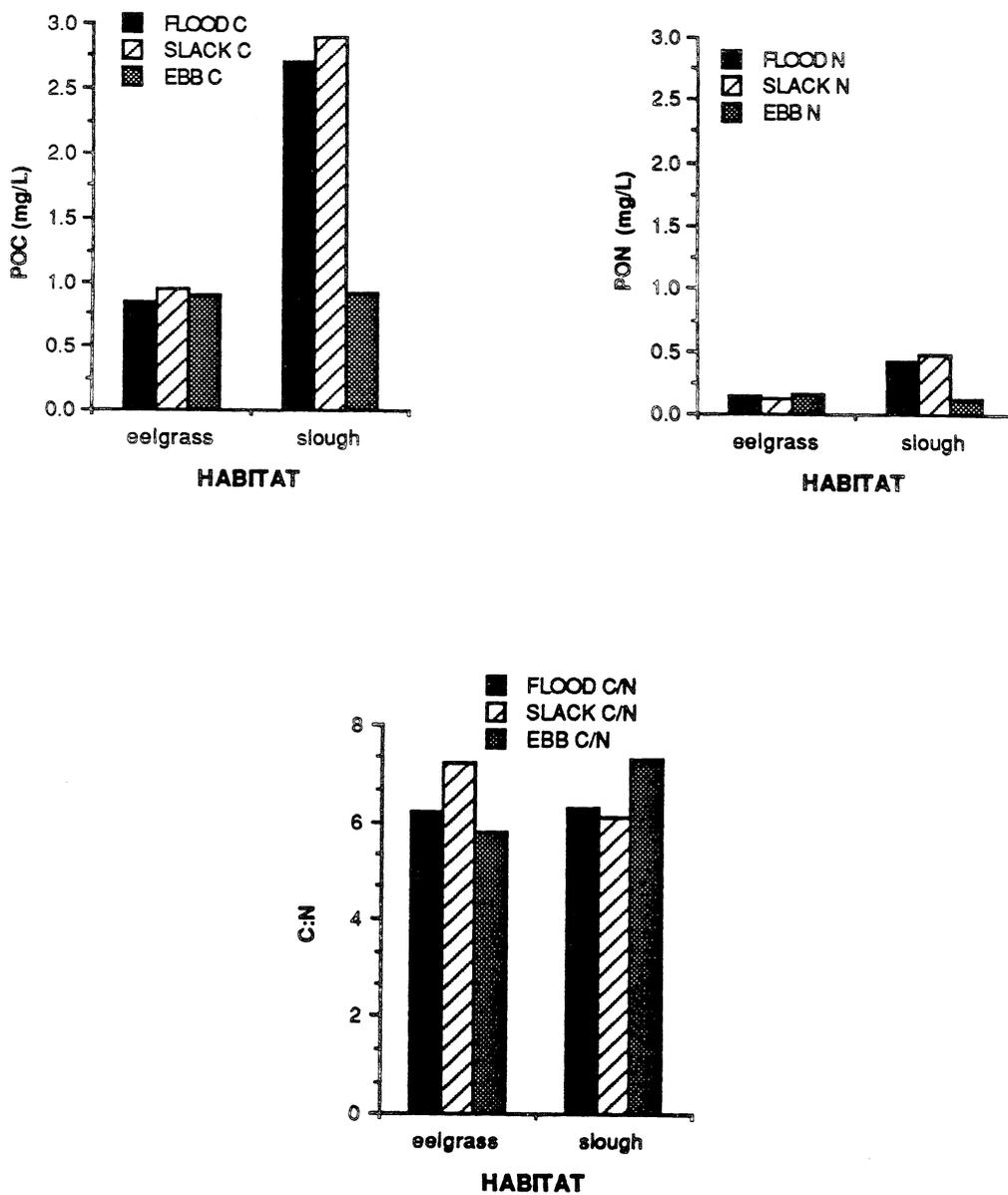


Figure 7. Sestonic POC, PON and C:N concentrations during the flood, slack and ebb stages of a tidal cycle at the eelgrass and slough habitats in Padilla Bay, WA. in August 1986.

habitats, although they were greatest during slack tide at the EG site (7.2) and during ebb tide at the SL site (7.3).

Seston quality indicators (the percentage of organic matter, chl  $a$  and POC in the SPM) in the three habitats in the main part of the bay (NR, EG, MF) generally decreased between the NR site and the MF habitat, but were highly variable at the slough habitat (Table A6). The average percent chl  $a$ :SPM (16%) was lower in the slough than in the eelgrass and neritic habitats. Two other seston quality indicators, POC:chl  $a$  (799) and C:N (13) were also highest in the slough, indicating low food quality of the seston. On the other hand, average percent organic matter (AFDW = 21%) and POC (5%) in the seston at the SL site were comparable to the levels at NR and EG sites.

Bay-wide, seston quality was higher during the spring and summer than the winter. In all habitats, the proportions of organic matter, chl  $a$ , and POC in the seston were greatest in the spring, and the POC:chl  $a$  ratios were lowest in the summer. POC:chl  $a$  ratios in all habitats were more than two times greater in December than in any other month. C:N values in the summer months were closest to those of phytoplankton (6-7) (Redfield ratio) in the three main bay habitats. In early spring, the C:N ratios were up to three times greater.

The proportion of planktonic algal species decreased, and benthic species increased from the NR (60%) to the MF and SL (20%) habitats (Table 1). The number of planktonic species in the SL habitat was slightly greater than in the MF site. As would be expected, the near-bottom samples had a greater proportion of benthic species in all habitats. Differences in species composition between planktonic and near-bottom samples were the least at the MF site, and greatest at the EG site.

### Physical and Chemical Characteristics

Temperatures ranged from 6 °C at all sites in December to 22.7 °C at the slough (SL) site in August 1986 (Table A7). The greatest range in temperatures occurred at the slough site (6-22.7 °C), and the least variable habitat was the neritic (NR) site (6-15.5 °C). The slough habitat had the lowest mean salinity and the greatest range in salinity (3.2-26.2 ppt). The highest salinities occurred at the NR and eelgrass (EG) sites. Salinities were lowest in winter and early spring, during peaks in freshwater runoff into the Bay.

Table 1. List of sestonic algal species (<63  $\mu\text{m}$ ) and their habitat associations from neritic, eelgrass, mudflat and slough habitats in Padilla Bay, WA. in August 1987. "p" refers to planktonic samples, "e" refers to epibenthic samples. The most abundant species in each habitat are denoted by a bold "x". (FW) refers to freshwater algal species. Species noted with an "L" were found in low tide samples only.

SPECIES	NERITIC	EELGRASS		MUDFLAT		SLOUGH	
		p	e	p	e	p	e
<b>PLANKTONIC</b>							
<i>Asterionella japonica</i>	x						
<i>Chaetocerus radicans</i>	x					x (L)	
<i>C. seriacanthus</i>						x (L)	x
<i>C. sp.</i>	x	x		x			
<i>Gyrodinium sp.</i>	x						
<i>Nitzschia closterium</i>	x	x			x	x	
<i>N. seriata</i>		x					
<i>N. sp.</i>							x
<i>Peridinium sp.</i>	x						
<i>Rhizosolenia sp.</i>	x						
<i>Scenedesmus sp. (FW)</i>						x (L)	
<i>Skeletonema costatum</i>	x	x	x	x	x		x
<i>Tetraselmis sp. (FW)</i>						x	
<i>Thalassionema nitzschioides</i>	x	x	x				
<i>Thalassiosira condensata</i>	x						
<i>T. decipiens</i>	x						
<i>T. gravida</i>	x	x					
<b>BOTH</b>							
<i>Coscinodiscus radiatus</i>	x	x		x			
<i>C. sp.</i>	x			x		x	x (L)
<b>BENTHIC</b>							
<i>Achnanthes sp.</i>		x	x		x		x
<i>Arthrospira sp.</i>						x (L)	
<i>Biddulphia sarita</i>	x	x	x				
<i>B. sp.</i>							x
<i>Cocconeis sp.</i>	x	x	x	x	x	x	x
<i>Fragillaria striatata</i>							x
<i>F. sp.</i>		x	x	x	x		x
<i>Licmophora sp.</i>	x	x	x	x	x		
<i>Melosira moniliformis</i>	x		x			x	x
<i>M. sp.</i>				x		x	x
<i>Navicula distans</i>		x	x	x	x	x	x
<i>N. seriata</i>		x	x	x	x	x	x
<i>N. sp.</i>	x	x	x	x	x	x	x
<i>Pleurosigma fasciola</i>	x	x	x		x	x	
<i>P. formosum</i>			x		x	x	x
<i>P. sp.</i>		x				x	x
<i>Tropidoneis antarctica</i>			x		x	x	

## DISCUSSION

The goal of this study was to determine the relationship between mussel growth rates and habitat characteristics. Mussel  $\delta^{13}\text{C}$  composition and growth rates in Padilla Bay were poorly correlated to the isotopic composition and quantities of primary producers in their habitats. In the following section we discuss data regarding the composition, quantity and quality of mussel foods in different habitats, and suggest possible explanations for observed growth rates.

### Origins and Composition of Mussel Food Sources

The isotopic composition of carbon in the mussels reflected the temporal and spatial variability in the isotopic composition of the seston. This supports our assumption that mussels derive their food from suspended particulate organic matter; i.e., sestonic carbon. However, the origins and composition of carbon sources in the POC varied across habitats and in different seasons.

The stable carbon isotope analyses, C:N ratios and phytoplankton identifications facilitated the identification and assessment of sestonic food sources most available to the mussels in different estuarine habitats (Table 2). In general, carbon depleted in  $^{13}\text{C}$  suggested terrestrial and marsh or neritic sources of carbon to the seston in the form of detrital and planktonic matter. On the other hand,  $^{13}\text{C}$ -enriched values probably represented autochthonous sources, primarily epibenthic and epiphytic algae, eelgrass, and macroalgae (Fry and Sherr 1984, Simenstad and Wissmar 1985).

Neritic phytoplankton were an important component to the seston in all Padilla Bay habitats. Sestonic POC at the neritic site was predominantly composed of marine phytoplankton, as evidenced by the dominance of planktonic algal species in the seston,

Table 2. Summary of seston characteristics in Padilla Bay, WA. 1986-1987.  $\delta^{13}\text{C}$  = POC  $\delta^{13}\text{C}$  values; C:N = particulate organic carbon : particulate organic nitrogen; habitat associations of algal species were determined from the literature.

HABITAT	$\delta^{13}\text{C}$	C:N	ALGAL HABITAT ASSOCIATIONS (%)	
			Planktonic	Benthic
NERITIC	-19 to -23	7 to 11	60	40
EELGRASS	-18 to -22	6 to 14	35	65
MUDFLAT	-19 to -21	6 to 14	20	80
SLOUGH	-24 to -26	6 to 29	20	80

as well as the relatively  $^{13}\text{C}$ -deplete POC values and the C:N ratios characteristic of marine phytoplankton (Table 2) (Russell-Hunter 1970, Velimirov 1987).

In all seasons, mussels at the eelgrass site were more  $^{13}\text{C}$ -enriched than the mussels at the neritic site. C:N ratios of sestonic POC at this site were slightly greater and more  $^{13}\text{C}$ -enriched than the NR site; indicating additional sources of particulates in the seston besides phytoplankton, such as *Zostera*, micro- and macroalgae, and epiphytes (Kirby-Smith 1976, Fry and Sherr 1984). Eelgrass and epiphytic and benthic algal carbon can enter the POC pool through resuspension of detritus from senesced or grazed leaf particles (McConnaughey and McRoy 1979) or via leached DOC from the leaves, which can subsequently become POC through flocculation (Sholkovitz 1976, Morris et al 1978) or bacterial transformation processes (Paerl 1978) (Fig. 8).

The  $\delta^{13}\text{C}$  of *Zostera* did not appear to change appreciably through decomposition processes. The difference in  $\delta^{13}\text{C}$  of dead vs. live *Zostera* was only 0.2 ‰; so, its incorporation into the seston via resuspension of detrital material would enrich the POC  $\delta^{13}\text{C}$  value. Epibenthic algae also tended to be more  $^{13}\text{C}$ -enriched than the POC samples from the same habitat; thus, their resuspension could also have contributed to the enrichment of seston composed partly of marine-derived phytoplankton. The relatively higher percentage of sestonic benthic microalgal species substantiates the prominence of resuspended epibenthic particulates in the EG habitat seston.

The significance of *Zostera* and benthic algal contributions to the seston carbon in the EG habitat is difficult to determine because of their varying degrees of  $^{13}\text{C}$ -enrichment relative to marine phytoplankton. Using a mixing equation to estimate the contribution of eelgrass carbon to an Alaskan food web (McConnaughey and McRoy 1979), we estimated the percentage of *Zostera* carbon in the POC at the EG site to range from 2% in December to 36% in August 1986. Other relatively  $^{13}\text{C}$ -enriched sources such as

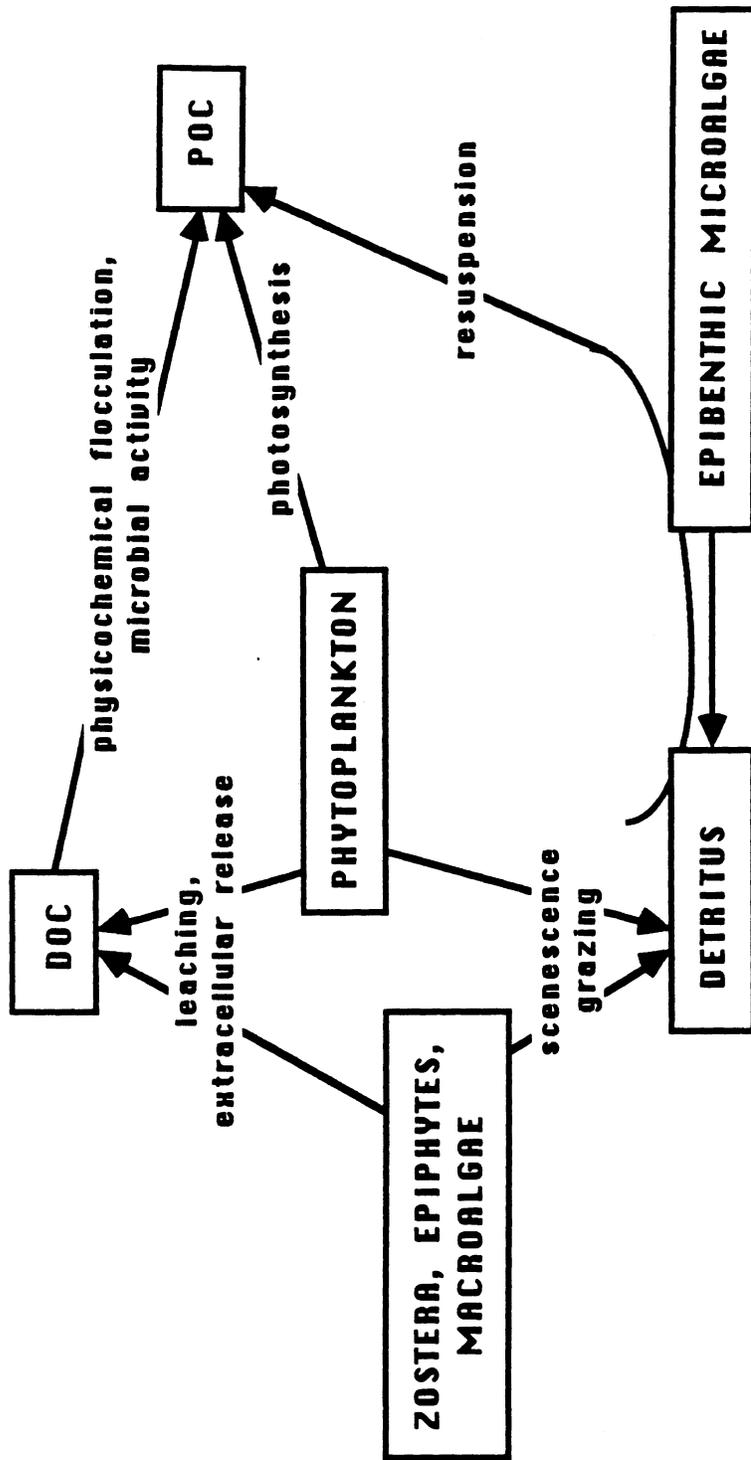


Figure 8. Schematic of possible pathways of carbon cycling in an eelgrass bed; DOC = dissolved organic carbon, POC = particulate organic carbon.

epibenthic algae and epiphytes were not included in the mixing model; thus our estimates based on *Zostera* as the only  $^{13}\text{C}$ -enriched carbon source are probably high.

Similarly, we estimated the contribution of *Zostera* carbon to mussel diets to range from 19 % in June 1987 to 39% in December 1986. The discrepancy in estimates of contributions of *Zostera* carbon to sestonic POC and mussel tissue could be due to: 1) a lag time in assimilation of consumed carbon into mantle tissue; 2) utilization of non-sestonic carbon sources by the mussels; and/or 3) a high lipid content in the mussel mantle, which is relatively  $^{13}\text{C}$ -enriched. Studies in other estuarine and nearshore habitats estimate contributions of seagrass carbon in food webs to range from low (Thayer et al. 1978, Fry 1984, Stephenson et al 1986) to substantial (McConnaughey and McRoy 1979). However, most studies including bivalve suspension feeders as indicator consumers indicate a low contribution of seagrass carbon relative to phytoplankton, similar to what we found in *Mytilus* diets in Padilla Bay.

The mudflat seston is also likely composed of a mixture of phytoplankton and resuspended benthic algal particles. Sestonic carbon sources in this habitat appear to be affected by wind and tidal mixing, because of the site's physical location (Fig. 1) and a scarcity of macrophytic cover at the site to dampen turbulence. The  $\delta^{13}\text{C}$  and C:N data suggest that POC carbon sources are predominantly from the neritic habitat (Table 2), reflecting the site's proximity to the main channel. POC  $\delta^{13}\text{C}$  values closely resembled those from the NR site, especially in the spring and summer. In winter and early spring, the difference between mudflat POC and neritic POC is the greatest, which suggests increased resuspension of more enriched epibenthic algae or macroalgal detritus at the MF site and/or increased contribution of terrestrial carbon due to storms and freshwater runoff at the NR site. In addition, the proportion of benthic microalgal and planktonic phytoplankton species is almost the same in both the water column and near-bottom samples from the MF site. This indicates that the MF habitat receives a well-mixed water

mass, with both resuspended autochthonous epibenthic and benthic particles and phytoplankton contributing to the seston pool utilized by suspension feeders. Seasonal variability of MF mussel  $\delta^{13}\text{C}$  is less than any other mussels, further indicating the constancy of seston composition.

Tidal and seasonal fluctuations in fresh-and saltwater inputs provide a varied pool of carbon sources in the slough habitat. The SL mussels appear to utilize primarily  $^{13}\text{C}$ -deplete carbon sources; i.e., terrestrially-derived seston and marine phytoplankton. Within-habitat sources such as resuspended epibenthic algae and marsh macrophyte detritus likely contribute a lesser proportion of carbon to the seston. Although  $^{13}\text{C}$ -deplete, *Carex* carbon is highly refractory and therefore probably not an important dietary carbon source (Kirby-Smith 1976). Additional  $^{13}\text{C}$ -enriched sources from the adjacent mudflat and eelgrass habitats may also mix with the slough seston; the exact mixing model is difficult to predict.

As expected, C:N values in the slough were the highest of any of the habitats and the  $\delta^{13}\text{C}$  values were consistently  $^{13}\text{C}$ -deplete due to the proximity to terrestrial carbon and nitrogen sources (Head 1976, Farfan and Alvarez-Borrego 1983, Table 2). The C:N ratios were the highest and the  $\delta^{13}\text{C}$  most deplete from April-June 1986, when freshwater inputs into the slough were the greatest. Some of the phytoplankton species from the SL habitat were uniquely freshwater forms (*Scenedesmus* and *Tetraselmis* spp.), which supports the C:N and  $\delta^{13}\text{C}$  data indicating terrestrial carbon inputs. Also, the greatest proportion of planktonic phytoplankton species in the SL occurred in a sample at low tide, when freshwater flows predominated.

Seasonal and spatial changes in  $\delta^{13}\text{C}$  values of the mussels most likely reflect differences in food sources rather than metabolic changes within the organisms (Haines and Montague 1979, Simenstad and Wissmar 1985). The greater magnitude of differences in the  $\delta^{13}\text{C}$  of potential sestonic foods suggests that they could influence the

degree of enrichment more significantly than metabolically-induced variations on the order of 20/100.

#### Seston Quantity, Quality and Mussel Growth

In addition to changing composition, the seston quantity and quality was expected to influence mussel growth rates. Both the total seston available and the proportion of food in the seston were expected to affect the seasonal growth patterns in *Mytilus edulis* (Bayne and Worrall 1980). But, neither food quantity nor quality trends in the habitats offer completely satisfactory explanations for the mussel growth patterns observed.

Estimates of food quantity were poorly correlated with mussel growth, even after the apparent effects of cage elevations were accounted for in standardized growth rates. Average concentrations of POC, PON, and chl *a* in all seasons declined as growth rates increased along the habitat gradient from the slough to the neritic site. However, seasonal variability in the concentrations of POC, PON, and chl *a* may be related to seasonal deviations from mean growth rates. For example, increases in the concentration of POC, PON, and chl *a* at the EG site relative to other sites in August 1986 and 1987 corresponded with higher growth rates in eelgrass mussels during those months. Also, a drop in POC and PON concentrations in all habitats in August 1987 relative to August 1986 may partially explain the lower growth rates observed Bay-wide in August 1987. The observation that food quantity indicators do not usually correspond with growth suggests that measures of food concentration are not necessarily a reflection of the proportion of water column food that is utilizable or especially energy-rich, or that the temporal function between food assimilated and shell growth response cannot be resolved within our sampling scheme.

Food quality indicators were somewhat more positively related to growth rate trends across habitats. Growth rates increased coincident with increased proportions of

organic matter, chl  $a$  and POC in the seston in the three main Bay habitats. The food quality indicators in the slough habitat, however, did not show a consistent relationship with growth rates. The percentages of organic matter and POC in the seston were comparable to those at the NR habitat, yet mussel growth rates were consistently lowest in the SL habitat. The percentage of chl  $a$  in the seston at the slough site was the lowest of any of the habitats, suggesting that suspended microalgae may constitute a major growth-limiting resource in this habitat.

As discussed earlier, seston composition in the slough was highly variable. Sestonic POC was probably composed of more refractory materials (e.g., salt marsh macrophyte and terrestrial detritus) that are considered nutritionally poorer food sources for organisms than are components of marine POC (Williams 1981, Fontugne and Jouanneau 1987). Food C:N ratios greater than 17 are generally considered to be nutritionally inadequate for benthic estuarine invertebrates (Russell-Hunter 1970, but see Kirby-Smith 1976). Only the SL habitat had C:N values greater than 17; in April, May and June 1986 the C:N values were 17, 29, and 20, respectively. Thus, even though organic and POC components to the seston were typically high in the SL habitat, they may not have been in a nutritionally adequate form. Phytoplankton, on the other hand, are considered to be highly nutritional (Russell-Hunter 1970). Growth rates throughout Padilla Bay were positively correlated with percent chl  $a$ :SPM ( $R=0.60$ ). Thus, the chl  $a$ :SPM ratio may be a better reflection of the food quality in the slough habitat.

#### Other Factors Influencing Mussel Growth

Habitat characteristics inferred from periodic and spatially patchy sampling in a highly variable environment such as Padilla Bay must be interpreted with caution. However, the observation that seston quantity and quality indicators did not generally reflect mussel

growth indicates that there may be other factors besides food quality and quantity that were important in determining growth rates.

1) **Additional Foods.** Other potential food sources were not measured. Bacteria can be important in nutrient recycling and as food sources in estuarine habitats (Hollibaugh et al. 1980, Prieur 1981, Azam et al. 1983, Pomeroy 1984). Data on bacterial biomass and production rates are lacking for Padilla Bay, but local studies indicate that Pacific Northwest estuaries support bacterial populations with significant biomass (Wissmar and Simenstad 1984). However, even if biomass is high, the nutritional value of ingested bacteria to bivalves in estuarine environments has been questioned. *Mytilus* has been shown to most efficiently retain particles in a larger size range (5-25  $\mu\text{m}$ ) than the bacteria (Lucas et al. 1987, Wright et al. 1982). Although bacteria can aggregate to form particles that fall within the mussel's filtering size range (Parsons and Seki 1970, Azam and Hodson 1977, Pomeroy 1984), the high concentrations of particulate food greater than 5  $\mu\text{m}$  throughout the bay suggest that *Mytilus* is not food limited. Therefore, we suspect that bacteria are probably not of primary importance in the mussels' energy intake.

Bivalves can also derive nutrition from dissolved organic carbon (Pequignat 1973, Stewart 1979), which most likely occurs in significant concentrations in Padilla Bay, given the extensive eelgrass and macroalgal production (Sieburth and Jensen 1970, Wissmar and Simenstad 1984). A pulse of DOC likely occurred in fall and winter due to leaching from senescent macrophytes, phytoplankton, or epiphytic and epibenthic algae (Widdows et al. 1979). The observation that mussel  $\delta^{13}\text{C}$  values were the most enriched during winter months and POC  $\delta^{13}\text{C}$  were not suggests that the major food sources for mussels were not sestonic during that time.

Additional food sources such as DOC or detritus from senescent autotrophs could explain the ability of mussels to grow during winter months when phytoplankton biomass was low. Furthermore, the biologically-labile fraction of seston is characterized by

relatively rapid and seasonally changing decomposition rates. Such fractions may be important food sources (Banoub and Williams 1973, Van Es and Meyer-Reil 1982), yet could have escaped detection during our sampling periods.

**2) Physiological Food Availability.** Mussel physiology changes seasonally in response to ambient physical characteristics, food availability, and the energy demands of gametogenesis (Bayne 1976). Mussel growth represents an integration of mussel physiology and environmental stresses in addition to their food intake. For example, low temperatures and low food quality in winter are known to cause a decrease in mussel clearance rates and absorption efficiencies (Bayne and Newell 1983). Therefore, despite high concentrations of POC and PON in the mudflat and slough habitats in the winter, the "physiologically useful ration" would have been low, and energy intake and growth would have been reduced (Bayne and Widdows 1978, Gabbott 1983). Gametogenesis in *Mytilus edulis* occurs primarily during the winter (Gabbott 1980, Zandee et al. 1980) when energy intake is low, leaving very little, if any, energy left over for growth. Energetically-costly gonad maturation in the spring may have contributed to the relatively low growth rates observed throughout the Bay at that time, despite high food quantity and quality.

Direct effects of physical processes on mussel physiology can, in some habitats, override the effects of biological processes in determining growth rates (Bayne and Worrall 1980, McIntire and Amspoker 1986). Growth rates of *Mytilus edulis* in the upper reaches of the Damariscotta River estuary, in which the temperature and salinity were similar to Padilla Bay values, were comparable to those measured in Padilla Bay (Incze et al. 1980). Temperature and salinity extremes at the slough and mudflat habitats likely contributed directly to depressed growth rates. *Mytilus edulis* is able to acclimate physiologically to temperatures between 5 and 20 °C (Bayne 1976, Widdows 1978).

Outside of this range, filtration rate and absorption efficiency decline rapidly, altering the mussel's energetic allocations. Summer water temperatures exceeding 20 °C were recorded at both the MF and SL habitats (21 and 22.7 °C, respectively).

*Mytilus* is an osmoconformer, and, although known for its adaptability to a wide range of habitats, salinities below 15 ppt are considered stressful due to increased costs associated with amino acid production and ammonia excretion (Livingstone et al 1979, Tedengren and Kautsky 1986) and reduction of food intake and gas exchange capabilities due to shell closure in low salinity areas (Davenport 1979, Stickle and Sabourin 1982). Essink and Bos (1985) found a decrease in *Mytilus edulis* growth rates along a habitat gradient of decreasing salinity, similar to our results.

Inorganic matter in the seston in concentrations greater than 55-200 mg l<sup>-1</sup> can overload the filtering apparatus of *Mytilus*, reducing the efficiency of its food intake and/or reducing by dilution the food available (Widdows et al. 1979, Foster-Smith 1975). In a pilot experiment conducted in August 1986 with mussels acclimated to the SL and EG habitats, we found that mussel clearance rates were negatively correlated with concentrations of particulate inorganic matter in the two habitats (Table A8). The concentration of total seston particulates during the study ranged from 12-20 x10<sup>3</sup> parts ml<sup>-1</sup> in the EG site and 33-45 x 10<sup>3</sup> parts ml<sup>-1</sup> at the SL site. EG mussels removed 32 % of the total particulates from EG water, yet the SL mussels only cleared 17.5 % of the particulate matter from their water (clearance rates: EG=1.6 l hr<sup>-1</sup>; SL=0.72 l hr<sup>-1</sup>).

Lower absorption efficiencies in mussels from habitats such as the slough, with high concentrations of PIM, may also explain depressed growth rates. In a set of laboratory pilot experiments conducted in May-June 1987, absorption efficiencies of Padilla Bay mussels were negatively related to the concentration of PIM in natural seawater (Table A9). Mussel growth rates and concentration of PIM in this study and others have been

shown to be negatively related (Widdows et al 1979, Bayne 1984, Essink and Bos 1985).

Cage elevations likely have a direct impact on mussel performance, evidenced by slight increases in standardized growth rates in MF and SL mussels. Griffiths (1981) and Newell (1976) detected no compensation for periods of tidal exposure in filtration rate and absorption efficiency of mussels. If intertidal mussels cannot increase their energy intake at higher tidal elevations (via increased feeding or absorption efficiency), energy intake is directly related to submergence time. In addition to a decreased energy input, intertidal mussels undergo anaerobiosis during exposure to air at low tides, resulting in the build up of an energetically costly oxygen deficit that must be paid back upon re-immersion (Bayne 1976). Reduced energy inputs due to decreased submergence time in conjunction with physiological costs associated with temperature and desiccation stresses mean less energy left over for growth and reproduction at higher cage elevations (Suchanek 1978 and 1985, Hummel 1985a, Incze et al 1980, Seed 1969, Jordan and Valiela 1982, Jorgensen 1976). Intertidal mussels may, therefore, suppress metabolic expenditures during exposure and, to a certain extent, limit energy input into growth and reproduction to conserve limited resources (Coleman and Trueman 1971, Griffiths 1981, Bayne and Newell 1983). For example, the SL mussels were exposed to the air for an estimated 4-6 hours day<sup>-1</sup>, and in the spring and summer when low tides occurred during the day, stress due to desiccation was probably high. Likewise, in winter, night time low tides likely exposed the mussels to temperatures below their acclimation range (<5 °C). Faced with such physical stresses and the reduced feeding time discussed above, the SL mussels likely had less energy left over for growth than those in the other habitats.

**3) Physical Food Availability.** In addition to direct effects of the environment on mussel physiology discussed above, physical processes can indirectly affect the

mechanisms of energy supply to the mussels. Small scale temporal and spatial differences in food availability are easily missed when sampling occurs bi-monthly and at specific sites. The between- and within-habitat variability in POC and PON concentrations measured during a single tidal cycle at the EG and SL habitats is just one example (Fig. 5). Hummel (1985a) detected not only variability in the concentration of POC, but also changes in chl *a* concentration and the proportion of chl *a* in the POC over the course of a tidal cycle in the Dutch Wadden Sea.

The significant differences in mussel growth rates in the top and bottom cages also reflected the response of the mussels to habitat quality differences on a small spatial scale. For example, changes in the degree of physical stability in the water column due to variable wind and tidal mixing and freshwater runoff affect phytoplankton growth and distribution patterns on a scale that could create microenvironments with significantly different food sources (Sinclair et al. 1981, Hummel 1985a, Frechette and Bourget 1987). The chl *a* content of surface intertidal sediments has been measured at 2-4 times that of the water column (Pamatmat 1977, Rhoads et al. 1975). As dense epibenthic algal (diatom) mats were characteristic of the MF and SL habitats, especially in the spring and summer, resuspended epibenthic algae (and detritus) could increase the near-bottom concentration and quality of food at the MF and SL habitats. Kiorboe et al. (1981) found that mussel growth at the bottom of the benthic boundary layer was greater due to resuspension of organic matter. The higher growth rates in bottom cage mussels at the MF and SL sites may have been due to a similar phenomenon.

On the contrary, dense growth patterns of *Zostera* are known to stabilize sediments and dampen laminar turbulence, allowing the retention of POC throughout the plant canopy (Rasmussen 1973, Wildish and Kristmanson 1984, Hummel 1985a, Muschenheim 1987), thus decreasing the chances for resuspension of additional food sources for the mussels in the bottom cage. Our measurements of POC and PON

concentrations in the EG habitat showed only slight differences between tidal stages, further supporting the idea that *Zostera* blades dampen flow-induced resuspension.

### Conclusions and Further Questions

Sestonic food sources of Padilla Bay mussels were comprised of organic carbon from terrestrial, salt marsh, estuarine and neritic habitats, the relative contributions from which varied seasonally. The heterogeneous nature of food availability in estuarine habitats has been discussed, but spatial and temporal changes in composition of suspended food resources need to be further explored. The use of multiple stable isotopes (e.g.  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  in addition to  $\delta^{13}\text{C}$ ) can facilitate further separation of the origins of sestonic foods (Stephenson et al. 1986, Peterson et al. 1986).

In addition to its composition, dynamic physical processes also determine the distribution of food in estuarine habitats. The relative rates of allochthonous carbon inputs and production and resuspension of autochthonous carbon are influenced by a wide range of climatological and hydrodynamic factors, including wind-induced and tidal mixing, freshwater runoff, nutrient levels, light, temperature, and flow rates. For instance, integrated measurements of water flow at each site would give a better estimate of the rates of food delivery over time.

These results support the need for a better understanding of the mechanisms behind the differences in food availability to estuarine consumers such as are represented in Padilla Bay. Both "physical" and "physiological" food availability to bivalves and other suspension feeders need to be further explored if consumer growth is to be used as an indicator of food availability and quality. It is evident that food that was detectable by our measuring techniques was not necessarily utilized by the mussels. For example, as I have suggested, the biologically-labile fraction of sestonic carbon is likely an important food source that was not measured. Development of a sampling plan to estimate the rates

of change of DOC concentrations is suggested in order to more adequately assess its importance as a food source. In general, we need to couple more definitive estimates of food composition with variation in mussel physiological states.

Finally, in order to be able to use mussel growth rates as indicators of estuarine habitat quality, a greater understanding of the relative magnitudes of the effects of habitat characteristics on growth is needed.

## References

- Amspoker, M.C. and C.D. McIntire. 1986. Effects of sedimentary processes and salinity on the diatom flora of the Columbia River estuary. *Bot. Mar.* 29:391-399.
- Azam, F., T. Fenchel, J.G. Field, J.S. Gray, L.-A. Meyer-Reil, and F. Thingstad. 1983. The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* 10:257-263.
- Azam, F. and R.E. Hodson. 1977. Size distribution and activity of marine heterotrophs. *Limnol. and Oceanogr.* 22:492-501.
- Banoub, M.W. and P.J. LeB. Williams. 1973. Seasonal changes in the organic forms of carbon, nitrogen, and phosphorous in sea water at E1 in the English Channel during 1968. *J. mar. biol. Ass. U.K.* 53:695-703.
- Bayne, B.L. (ed.). 1976. *Marine Mussels: Their Ecology and Physiology*. Cambridge University Press, London.
- Bayne, B.L. and R.C. Newell. 1983. Physiological energetics of marine molluscs. *The Mollusca*, Vol. 4. Physiology Part 1. Acad. Press, New York.
- Bayne, B.L. and C.M. Worrall. 1980. Growth and production of mussels, *Mytilus edulis* from two populations. *Mar. Ecol. Prog. Ser.* 3:317-328.
- Bayne, B.L. and J. Widdows. 1978. The physiological ecology of two populations of *Mytilus edulis* L. *Oecologia* 37:137-162.
- Brinson, M.M. and E.A. Matson. 1983. Carbon isotope distribution in the Pamlico River estuary, North Carolina, and its tributaries. *Estuaries*. 6: 306.
- Coleman, N. and E.R. Trueman. 1971. The effect of aerial exposure on the activity of the mussels *Mytilus edulis* L. and *Modiolous modiolous* L. *J. exp. mar. biol. ecol.* 7:295-304.
- Conover, R.J. 1966. Assimilation of organic matter by zooplankton. *Limnol. Oceanogr.* 11:338-354.
- Davenport, J. 1979. The isolation response of mussels (*Mytilus edulis* L.) exposed to falling sea-water concentrations. *J. Mar. Biol. Assoc. U.K.* 59:123-132.
- DeNiro, M.J. and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta.* 42:495-506.
- Dickie, L.M., P.R. Boudreau, and K.R. Freeman. 1984. Influences of stock and site on growth and mortality in the blue mussel (*Mytilus edulis*). *Can. J. Fish. Aquat. Sci.* 41:134-140.
- Essink, K. and A.H. Bos. 1985. Growth of three bivalve molluscs transplanted along the axis of the Ems estuary. *Neth. J. Sea Res.* 19(1):45-51.

- Farfan, B.C. and S. Alvarez-Borrego. 1983. Variability and fluxes of nitrogen and organic carbon at the mouth of a coastal lagoon. *Est. Coast. Shelf Sci.* 17:599-612.
- Fontugne, M.R. and J-M. Jouanneau. 1987. Modulation of the particulate organic carbon flux to the ocean by a macrotidal estuary: evidence from measurements of carbon isotopes in organic matter from the Gironde system. *Est. coast. shelf sci.* 24:377-387.
- Foster-Smith, R.L. 1975. The effect of concentration of suspension on the filtration rates and pseudofecal production for *Mytilus edulis* L., *Cerastoderma edule* L. and *Venerupis pullastra* (Montagu). *J. exp. mar. biol. ecol.* 17:1-22.
- Frechette, M. and E. Bourget. 1987. Significance of small-scale spatio-temporal heterogeneity in phytoplankton abundance for energy flow in *Mytilus edulis*. *Mar. Biol.* 94:231-240.
- Frechette, M. and E. Bourget. 1985. Food-limited growth of *Mytilus edulis* L. in relation to the benthic boundary layer. *Can. J. Fish. Aquat. Sci.* 42:1166-1170.
- Fry, B. 1984.  $^{13}\text{C}/^{12}\text{C}$  ratios and the trophic importance of algae in Florida *Syringodium filiforme* seagrass meadows. *Mar. Biol.* 79:11-19.
- Fry, B. and P.L. Parker. 1979. Animal diet in Texas seagrass meadows:  $^{13}\text{C}$  evidence for the importance of benthic plants. *Estuar. coast. mar. sci.* 8:499-509.
- Fry, B and E.B. Sherr. 1984.  $^{13}\text{C}$  measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contrib. Mar. Sci.* 27:13-47.
- Gabbott, P.A. 1983. Developmental and seasonal metabolic activities in marine molluscs. In: Hochachka, P.W. (ed). *The Mollusca*. Vol. 2. *Environmental Biochemistry and Physiology*. Academic Press, N.Y. pp 165-217.
- Gearing, J.N., P.J. Gearing, D.T. Rudnick, A.G. Requejo, and M.J. Hutchins. 1984. Isotopic variability of organic carbon in a phytoplankton-based, temperate estuary. *Geochim. Cosmochim. Acta.* 48:1089-1098.
- Griffiths, R.J. 1981. Aerial exposure and energy input in the bivalve *Choromytilus meridionalis* (Kr.) (Bivalvia). *J. exp. mar. biol. ecol.* 52:219-229.
- Griffiths, R.J. 1980. Natural food availability and assimilation in the bivalve *Choromytilus meridionalis*. *Mar. Ecol. Prog. Ser.* 3:151-156.
- Haines, E.B. and C.L. Montague. 1979. Food sources of estuarine invertebrates analyzed using  $^{13}\text{C}/^{12}\text{C}$  ratios. *Ecology.* 60(1):48-56.
- Head, P.C. 1976. Organic processes in estuaries. In: Burton, J.D. and P.S. Liss (eds). *Estuarine Chemistry*. Acad. Press, N.Y. pp. 54-85.
- Hollibaugh, J.T., J.A. Fuhrman, and F. Azam. 1980. Radioactively labeling of natural assemblages of bacterioplankton for use in trophic studies. *Limnol. Oceanogr.* 25:172-181.

- Hummel, H. 1985a. An energy budget for a *Macoma balthica* (Mollusca) population living on a tidal flat in the Dutch Wadden Sea. *Neth. J. Sea Res.* 19(1):84-92.
- Hummel, H. 1985b. Food intake of *Macoma balthica* (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. *Neth. J. Sea Res.* 19(1):52-76.
- Incze, L.S., L.M. Mayer, E.B. Sherr and S.A. Macko. 1982. Carbon inputs to bivalve mollusks: a comparison of two estuaries. *Can. J. Fish. Aquat. Sci.* 39:1348-1352.
- Incze, L.S., R.A. Lutz, and L. Watling. 1980. Relationships between effects of environmental temperature and seston on growth and mortality of *Mytilus edulis* in a temperature northern estuary. *Mar. Biol.* 57:147-156.
- Jordan, T.E. and I. Valiela. 1982. A nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its significance in nitrogen flow in a New England salt marsh. *Limnol. Oceanogr.* 27:75-90.
- Jorgensen, C.B. 1975. On gill function in the mussel *Mytilus edulis* L. *Ophelia* 13:187-232.
- Jorgensen, C.B. 1976. Growth efficiencies and factors controlling size in some Mytilid bivalves, especially *Mytilus edulis* L., a review and interpretation. *Ophelia* 15:175-192.
- Kiorboe, T., F. Mohlenberg, and O. Nohr. 1981. Effect of suspended bottom material on growth and energetics in *Mytilus edulis*. *Mar. Biol.* 61:283-288.
- Kirby-Smith, W.W. 1976. The detritus problem and the feeding and digestion of an estuarine organism. In: Wiley, M. (ed.) *Estuarine Processes. Volume I.* Academic Press, London.
- Livingstone, D.R., J. Widdows and P. Fieth. 1979. Aspects of nitrogen metabolism of the common mussel, *Mytilus edulis*: adaptations to abrupt and fluctuating changes in salinity. *Mar. Biol.* 53:41-55.
- Lucas, M.I., R.C. Newell, S.E. Shumway, L.J. Seiderer and R. Bally. 1987. Particle clearance and yield in relation to bacterioplankton and suspended particulate availability in estuarine and open coast populations of the mussel *Mytilus edulis*. *Mar. Ecol. Prog. Ser.* 36:215-224.
- McConnaughey, T. and C.P. McRoy. 1979. <sup>13</sup>C label identifies eelgrass (*Zostera marina*) carbon in an Alaskan estuarine food web. *Mar. Biol.* 53:263-269.
- McIntire, C.D. and M.C. Amspoker. 1986. Effects of sediment properties on benthic primary production in the Columbia River estuary. *Aquat. Bot* 24:249-267.
- Morris, A.W., R.F.C. Mantoura, A.J. Bale and R.J.M. Howland. 1978. Very low salinity regions of estuaries: important sites for chemical and biological reactions. *Nature.* 274:678-680.

- Muschenheim, D. K. 1987. The dynamics of near-bed seston flux and suspension-feeding benthos. *J. Mar. Res.* 45:473-496.
- Newell, R.C. 1976. Adaptations to intertidal life. In Newell, R.C. (ed.) *Adaptation to Environment: Essays on the Physiology of Marine Animals*. Butterworths, London.
- Paerl, H. 1978. Microbial organic carbon recovery in aquatic ecosystems. *Limnol. and Oceanogr.* 23:927-935.
- Pamatmat, M.M. 1977. Benthic community metabolism: a review and assessment of present status and outlook. In: Coull, B.C. (ed.) *Ecology of Marine Benthos*. Volume 6. University of South Carolina Press, Columbia, S.C. pp. 89-111.
- Parsons, T.R. and H. Seki. 1970. Importance and general implications of organic matter in aquatic environments. In Hood, D.W. (ed.) *Symposium on Organic Matter in Natural Waters*. University of Alaska, Alaska. pp. 1-27.
- Pequignat, E. 1973. A kinetic and autoradiographic study of the direct assimilation of amino acids and glucose by organs of the mussel *Mytilus edulis*. *Mar. Biol.* 19:227-244.
- Peterson, B.J., Howarth, R.W. and R.H. Garritt. 1986. Sulfur and carbon isotopes as tracers of salt-marsh organic matter flow. *Ecology.* 67:865-874.
- Pomeroy, L.R. 1984. Significance of microorganisms in carbon and energy flow in marine ecosystems. In: Klug, M.J. and C.A. Reddy (eds.) *Current Perspectives in Microbial Ecology*. American Soc. for Microbiology. Washington, D.C.
- Prieur, D. 1981. Experimental studies of trophic relationships between marine bacteria and bivalve molluscs. *Kieler Meeresforsch. Sonderh.* 5:376-383.
- Rasmussen, E. 1973. Systematics and ecology of the Isefjord marine fauna (Denmark) with a survey of the eelgrass (*Zostera*) vegetation and its communities. *Ophelia* 11:1-507.
- Rhoads, D.C., K. Tenore and M. Browne. 1975. The role of resuspended bottom mud in nutrient cycles of shallow embayments. In: Cronin, L.E. (ed.) *Estuarine*. Vol. I. Academic Press, New York.
- Russell-Hunter, W.D. 1970. *Aquatic productivity: an introduction to some basic aspects of biological oceanography and limnology*. Collier-Macmillan, London. 306 pp.
- Seed, R. 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores II: growth and mortality. *Oecologia* 3:317-350.
- Sholkovitz, E.R. 1976. Flocculation of dissolved organic and inorganic matter during mixing of river water and seawater. *Geochim. Cosmochim. Acta.* 40:831-845.
- Sieburth, J. McN. and A. Jensen. 1970. Production and transformation of extracellular organic matter from littoral marine algae: a resume. In: Hood, D.W. (ed.) *Symposium on Organic Matter in Natural Waters*. University of Alaska, Alaska.

- Simenstad, C.A. and R.C. Wissmar. 1985.  $\delta^{13}\text{C}$  evidence of the origins and fates of organic carbon in estuarine and nearshore food webs. *Mar. Ecol. Prog. Ser.* 22:141-152.
- Sinclair, M., S. Rao and R. Couture. 1981. Phytoplankton temporal distribution in estuaries. *Oceanol. Acta.* 4:239-246.
- Stephenson, R.L. and G.L. Lyon. 1982. Carbon-13 depletion in an estuarine bivalve: detection of marine and terrestrial food sources. *Oecologia (Berl).* 55:110-113.
- Stephenson, R.L., F.C. Tan, and K.H. Mann. 1986. Use of stable carbon isotope ratios to compare plant material and potential consumers in a seagrass bed and a kelp bed in Nova Scotia, Canada. *Mar. Ecol. Prog. Ser.* 30:1-7.
- Stewart, M.G. 1979. Absorption of dissolved organic nutrients by marine invertebrates. *Oceanogr. Mar. Biol. Ann. Rev.* 17:168-192.
- Stickle, W.B. and T.D. Sabourin. 1979. Effects of salinity on the respiration and heart rate of the common mussel, *Mytilus edulis* L. and the black chiton, *Katherina tunicata* (Wood). *J. exp. mar. biol. ecol.* 41:257-268.
- Strickland, J.D.H. and T.R. Parsons. 1972. A Practical Handbook of Seawater Analysis. Bull 167. Fish. Res. Bd. Can., Ottawa.
- Suchanek, T.H. 1985. Mussels and their role in structuring rocky shore communities. In: Moore and Seed, (eds). *The Ecology of Rocky Coasts*. Hodder and Stoughton Press.
- Suchanek, T. H. 1978. The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. *J. exp. mar. biol. ecol.* 31:105-120.
- Tedengren, M. and Kautsky, N. 1986. Comparative study of the physiology and its probable effect on size in blue mussels (*Mytilus edulis* L.) from the North Sea and the northern Baltic proper. *Ophelia* 25:147-156.
- Tenore, K.R. and W.M. Dunstan. 1973. Comparison of feeding and biodeposition of three bivalves at different food levels. *Mar. Biol.* 21:190-195.
- Thayer, G.W., P.L. Parker, M.W. LaCroix and B. Fry. 1978. The stable carbon isotope ratio of some components of an eelgrass, (*Zostera marina*), bed. *Oecologia.* 35:1-12.
- United States Geological Survey Water-Data Report WA- 85 - 1. 1985. Water Resources Data Washington. Water Year 1985.
- Vahl, O. 1980. Seasonal variations in seston and in the growth rate of the Iceland scallop, *Chlamys islandica* (O.F. Muller) from Balsfjord 70 N. *J. exp. mar. biol. ecol.* 48:195-20.
- Van Es, F. B. and L. A. Meyer-Reil. 1982. Biomass and metabolic activity of heterotrophic marine bacteria. In: K. C. Marshall (ed.) *Advances in Microbial Activity*. Vol. 6. pp. 111-170.

- Velimirov, B. 1987. Organic matter derived from a seagrass meadow: origin, properties and quality of particles. *Mar. Ecol.* 8:143-173.
- Whiting, M.C. and C.D. McIntire. 1985. An investigation of distributional patterns in the diatom flora of Netarts Bay, Oregon, by correspondence analysis. *J. Phycol.* 21:655-661.
- Widdows, J. 1978. Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. *J. mar. biol. Ass. U.K.* 58:109-124.
- Widdows, J., P. Fieth, and C.M. Worrall. 1979. Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. *Mar. Biol.* 50:195-207.
- Williams, P.J. Le B. 1981. Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. *Kieler Meersforsch. Sonderh.* 5:1-28.
- Wildish, D.J. and D.D. Kristmanson. 1984. Importance to mussels of the benthic boundary layer. *Can. J. Fish. Aquat. Sci.* 41:1618-1625.
- Winter, J.E. 1976. Feeding experiments with *Mytilus edulis* L. at a small laboratory scale. The influence of suspended silt in addition to algal suspensions on growth. In Personne, G. and E. Jaspers (eds.) *Proc. 10th Europ. Mar. Biol. Symp. Vol. 2.* Universa Press, Wetteren.
- Winter, J.E. 1973. The filtration rate of *Mytilus edulis* and its dependence on algal concentration, measured by a continuous automatic recording apparatus. *Mar. Biol.* 22:317-328.
- Wissmar, R.C. and C.A. Simenstad. 1984. Surface foam chemistry and productivity in the Duckabush River estuary, Puget Sound, Washington. In: V.S. Kennedy (ed.) *The Estuary as a Filter.* New York, Academic Press.
- Wright, R.T., R.B. Coffin, C.P. Ersing, and D. Pearson. 1982. Field and laboratory measurements of bivalve filtration of natural marine bacterioplankton. *Limnol. and Oceanogr.* 27(1):91-98.
- Zandee, D.I., J.H. Kluytmans, W. Zurburg, and H. Pieters. 1980. Seasonal variations in biochemical composition of *Mytilus edulis* with reference to energy metabolism and gametogenesis. *Neth. J. Sea Res* 14:1-29.
- Zar, J.H. 1984. *Biostatistical Analysis.* Prentice Hall, New York.

## APPENDIX A: DATA TABLES

Table A1. Mussel growth rate ( $\text{mm month}^{-1}$ ) and standardized growth rate ( $\text{mm month}^{-1}$ ) data from May 1986 through August 1987 in Padilla Bay, WA. NR = neritic; EG = eelgrass; MF = mudflat and SL = slough study habitats. Errors presented are  $\pm$  one standard deviation.

Habitat	$\text{mm month}^{-1}$	standardized $\text{mm mon}^{-1}$	Date
NR	$3.8 \pm 1.3$	3.8	5/86
EG	$2.3 \pm 1.5$	2.3	5/86
MF	$1.2 \pm .85$	1.4	5/86
SL	$.12 \pm .15$	0.16	5/86
NR	$4.5 \pm 1.7$	4.5	8/86
EG	$5.1 \pm 2.2$	5.1	8/86
MF	$3.9 \pm 1.2$	4.7	8/86
SL	$.91 \pm 1.5$	1.1	8/86
NR	$2.3 \pm 1.2$	2.3	12/86
EG	$2.1 \pm 1.2$	2.1	12/86
MF	$1.6 \pm .85$	1.9	12/86
SL	$1.1 \pm .70$	1.4	12/86
NR	$2.0 \pm .45$	2.0	4/87
EG	$1.8 \pm .66$	1.8	4/87
MF	$1.5 \pm .34$	1.8	4/87
SL	$.90 \pm .82$	1.2	4/87
NR	$1.5 \pm .64$	1.5	6/87
EG	$2.3 \pm .84$	2.3	6/87
MF	$1.3 \pm .63$	1.5	6/87
SL	$.82 \pm .53$	1.0	6/87
NR	$1.3 \pm .39$	1.3	8/87
EG	$2.2 \pm .58$	2.2	8/87
MF	$.78 \pm .39$	0.91	8/87
SL	$.71 \pm .60$	0.88	8/87

Table A2.  $\delta^{13}\text{C}$  data from Padilla Bay study habitats (neritic, eelgrass, mudflat and slough). Values expressed are in (0/00).

	HABITAT	5/86	8/86	12/86	4/87	6/87	8/87
POC	NR	-21.8	-19.5	-21.6	-23.2	-19.4	-18.7
POC	EG	-19.7	-17.4	-21.5	-19.6	-18.7	-17.8
POC	MF	-21.0	-20.4	-19.5	-21.3	-18.7	-18.9
POC	SL	-26.9	-21.7	-23.5	-25.4	-25.7	-24.3
ZOSTERA	EG	-8.1	-9.7	ND	ND	-8.6	-8.7
EPIPHYTE	EG	-10.4	-13.2	ND	-15.2	-12.2	-11.4
EPI ALGAE	EG	-19.6	-15.6	ND	-16.5	-16.7	-15.7
ULVA	EG	ND	-11.7	ND	ND	-14.2	ND
ENTEROMOR.	EG	ND	-12.7	ND	ND	ND	ND
EPI ALGAE	MF	-19.0	-13.8	-17.1	-15.2	ND	ND
ULVA	MF	ND	ND	ND	ND	ND	-14.2
ENTEROMOR.	MF	ND	-10.4	ND	ND	ND	ND
EPI ALGAE	SL	-21.6	-18.5	-21.7	-20.0	-19.6	-17.9
CAREX	SL	-28.5	-27.6	-20.2	ND	-27.9	ND
MUSSELS	NR	-18.5	-17.6	-17.6	-19.7	-19.9	ND
MUSSELS	EG	-16.6	-16.6	-16.0	-18.0	-18.2	-17.8
MUSSELS	MF	-18.0	-17.4	-16.2	-17.9	-18.4	-17.6
MUSSELS	SL	-24.7	-19.6	-24.0	-24.1	-22.0	-21.5
MUSSELS	INITIAL	-21.8	-19.3	ND	-18.5	ND	ND
MUSSELS	MF PILING	ND	ND	ND	ND	-19.1	-16.8
TAPES	EG	-16.8					

Table A3. Coefficients of variation for  $\delta^{13}\text{C}$  data included in Table A2.

	HABITAT	5/86	8/86	12/86	4/87	6/87	8/87
POC	NR	-0.03	-0.03	-0.01	-0.04	ND	0
POC	EG	-0.04	-0.10	-0.13	-0.004	-0.01	-0.004
POC	MF	-0.03	-0.03	-0.02	-0.02	-0.01	-0.01
POC	SL	-0.002	-0.02	-0.02	-0.02	-0.01	-0.003
ZOSTERA	EG	ND	-0.04	ND	ND	-0.01	ND
EPIPHYTE	EG	ND	-0.06	ND	-0.14	-0.03	ND
EPI ALGAE	EG	ND	-0.02	ND	ND	-0.01	-0.004
ULVA	EG	ND	-0.13	ND	ND	-0.05	ND
ENTERO	EG	ND	-0.02	ND	ND	ND	ND
EPI ALGAE	MF	ND	-0.01	-0.15	-0.11	ND	ND
ULVA	MF	ND	ND	ND	ND	ND	-0.05
ENTERO	MF	ND	0	ND	ND	ND	ND
EPI ALGAE	SL	ND	-0.01	0	-0.01	-0.02	-0.02
CAREX	SL	-0.01	-0.01	ND	ND	-0.06	ND
MUSSELS	NR	-0.03	-0.01	-0.01	-0.004	-0.02	ND
MUSSELS	EG	-0.06	-0.03	-0.01	0	-0.01	-0.008
MUSSELS	MF	-0.02	-0.01	-0.01	-0.02	0	-0.008
MUSSELS	SL	-0.09	-0.03	-0.02	-0.03	-0.003	-0.06
MUSSELS	MF piling	ND	ND	ND	ND	-0.01	-0.02
TAPES	EG	-0.02	ND	ND	ND	ND	ND

Table A4. Seasonal seston characteristics in neritic (NR), eelgrass (EG), mudflat (MF) and slough (SL) habitats in Padilla Bay, WA. in 1986 and 1987. PIM = particulate inorganic matter ( $\text{mg l}^{-1}$ ); SPM = suspended particulate matter ( $\text{mg l}^{-1}$ ); CHL  $a$  = chlorophyll  $a$  ( $\mu\text{g l}^{-1}$ ); POC = particulate organic carbon ( $\mu\text{g l}^{-1}$ ); and PON = particulate organic nitrogen ( $\mu\text{g l}^{-1}$ ).

PARAMETER	SPRING	SUMMER	WINTER
<b>PIM</b>			
NR	3.5	11.0 $\pm$ 3.0	ND
EG	4.3	15.3 $\pm$ 9.4	ND
MF	23.0	31.4 $\pm$ 1.0	ND
SL	28.9	19.2 $\pm$ 5.0	ND
<b>SPM</b>			
NR	5.0	13.2 $\pm$ 2.8	ND
EG	5.5	17.9 $\pm$ 10	ND
MF	28.8	35.9 $\pm$ 2.5	ND
SL	38.1	23.5 $\pm$ 5.0	ND
<b>CHL <math>a</math></b>			
NR	2.1 $\pm$ .82	2.1 $\pm$ .50	.21
EG	1.2 $\pm$ .54	3.8 $\pm$ .52	.20
MF	4.0 $\pm$ 1.1	3.7 $\pm$ 1.4	2.3
SL	2.0 $\pm$ .08	5.2 $\pm$ 2.5	.88
<b>POC</b>			
NR	310 $\pm$ 140	560 $\pm$ 170	250
EG	380 $\pm$ 270	740 $\pm$ 110	60
MF	1000 $\pm$ 260	970 $\pm$ 230	3330
SL	1900 $\pm$ 990	1400 $\pm$ 620	1900
<b>PON</b>			
NR	30 $\pm$ 10	89 $\pm$ 38	40
EG	39 $\pm$ 31	116 $\pm$ 21	80
MF	115 $\pm$ 34	154 $\pm$ 49	380
SL	139	171 $\pm$ 122	220

Table A5. Particulate organic carbon, nitrogen and POC : PON values during flood, slack and ebb stages of a tidal cycle in the eelgrass and slough habitats in Padilla Bay, WA. in August 1986. Errors are  $\pm 1$  standard deviation.

HABITAT	C (mg l <sup>-1</sup> )	N (mg l <sup>-1</sup> )	C:N
EELGRASS			
FLOOD	0.84 $\pm$ .01	0.14 $\pm$ .001	6.2 $\pm$ .06
SLACK	0.95 $\pm$ .15	0.13 $\pm$ .02	7.2 $\pm$ .02
EBB	0.90 $\pm$ .12	0.16 $\pm$ .01	5.8 $\pm$ .23
SLOUGH			
FLOOD	2.7 $\pm$ .41	0.42 $\pm$ .08	6.3 $\pm$ .26
SLACK	2.9	0.48	6.1
EBB	0.92 $\pm$ .17	0.13 $\pm$ .03	7.3 $\pm$ .35

Table A6. Seston quality indicators in neritic (NR), eelgrass (EG), mudflat (MF) and slough (SL) habitats in Padilla Bay, WA. in 1986 and 1987. AFDW = percent organic matter in the seston; CHL  $a$  : SPM = percent chlorophyll  $a$  in the seston; POC : SPM = percentage of particulate organic carbon in the seston; C : N = ratio of particulate organic carbon to particulate organic nitrogen; and POC : CHL  $a$  = ratio of particulate organic carbon to chlorophyll  $a$ . Errors presented are  $\pm$  one standard deviation.

PARAMETER	SPRING	SUMMER	WINTER
AFDW			
NR	30	17 $\pm$ 4	ND
EG	23	16 $\pm$ 4	ND
MF	20	13 $\pm$ 2	ND
SL	24	19 $\pm$ 4	ND
CHL $a$ : SPM			
NR	.41	.16 $\pm$ .05	ND
EG	.21	.21 $\pm$ .19	ND
MF	.14	.10 $\pm$ .05	ND
SL	.05	.22 $\pm$ .18	ND
POC : SPM			
NR	8.9	5.0 $\pm$ 1.0	ND
EG	9.5	4.5 $\pm$ 2.0	ND
MF	3.6	2.8 $\pm$ 0.2	ND
SL	7.9	4.1 $\pm$ 1.0	ND
C : N			
NR	10.4 $\pm$ 0.4	6.7 $\pm$ 1.0	6.6
EG	11.4 $\pm$ 3.0	6.5 $\pm$ 0.8	7.8
MF	9.2 $\pm$ 4.0	6.5 $\pm$ 0.8	8.8
SL	18.6 $\pm$ 9.0	10.2 $\pm$ 0.6	8.8
POC : CHL $a$			
NR	187 $\pm$ 26	269 $\pm$ 67	1183
EG	509 $\pm$ 246	199 $\pm$ 45	3064
MF	220 $\pm$ 7	285 $\pm$ 102	1452
SL	1054 $\pm$ 573	328 $\pm$ 189	2174

Table A7. Low-tide temperature and salinity data from neritic (NR), eelgrass (EG), mudflat (MF) and slough (SL) habitats in Padilla Bay, WA. in 1986 and 1987.

HABITAT	DATE	TEMPERATURE (°C)	SALINITY (0/00)
NR	4/11/86	7.0	23.0
NR	5/9/86	6.0	25.0
NR	6/21/86	11.0	25.5
NR	8/20/86	15.5	27.5
NR	12/2/86	6.0	15.2
NR	4/17/87	10.0	19.0
NR	6/9/87	13.8	15.0
NR	8/9/87	17.6	16.0
EG	4/11/86	8.0	22.5
EG	5/9/86	12.0	21.0
EG	6/21/86	15.0	22.5
EG	8/20/86	16.3	28.0
EG	12/2/86	6.0	15.4
EG	4/17/87	11.0	18.0
EG	6/9/87	14.5	17.0
EG	8/9/87	20.2	17.2
MF	4/11/86	9.0	19.0
MF	5/9/86	12.0	21.0
MF	6/21/86	15.1	22.0
MF	8/20/86	21.0	27.7
MF	12/2/86	6.0	13.8
MF	4/17/87	13.0	17.0
MF	6/9/87	15.0	17.0
MF	8/9/87	20.5	18.0
SL	4/11/86	7.0	4.7
SL	5/9/86	11.0	2.0
SL	6/21/86	20.0	3.7
SL	8/20/86	22.7	26.2
SL	12/2/86	6.0	3.5
SL	4/17/87	11.6	3.2
SL	6/9/87	18.0	5.0
SL	8/9/87	21.0	9.0

Table A8. Clearance rate of mussels from the eelgrass and slough habitats in Padilla Bay, WA., August 1986.

HABITAT	(PARTICLES ml <sup>-1</sup> ) x 10 <sup>3</sup> (± s.d.)		% REMOVAL	CLEAR.RATE (L hour <sup>-1</sup> )
	INFLOW	OUTFLOW		
EELGRASS	12.8 (4.1)	7.8 (.07)	32.2	1.8
SLOUGH	39.0 (5.8)	25.8 (4.5)	17.5	1.1

Table A9. Absorption efficiency (AE)\* and concentrations of particulate inorganic matter (PIM) using eelgrass (EG) and slough (SL) mussels from Padilla Bay, WA. [ADD] and [ACTUAL] = added and actual concentrations of PIM in experimental waters, respectively. EXP. NO. refers to experiment numbers.

EXP. NO.	[ADD]	[ACTUAL]	HABITAT	AE
1	20	6.9	SL	7.51
1	20	6.9	EG	15.89
1	20	6.9	SL	14.79
1	20	6.9	EG	-8.52
1	20	6.9	SL	9.79
2	200	4.2	EG	28.71
2	200	4.2	SL	13.84
2	200	4.2	SL	13.08
2	200	4.2	EG	17.71
2	200	4.2	SL	6.98
3	2	3.4	SL	88.33
3	2	3.4	SL	93.21
3	2	3.4	EG	85.50
3	2	3.4	EG	90.79
3	2	3.4	EG	92.28
3	2	3.4	SL	94.10
3	2	3.4	EG	90.94
3	2	3.4	SL	96.75
4	200	4.6	SL	-12.98
4	200	4.6	EG	-16.87
4	200	4.6	SL	.28
4	200	4.6	EG	-3.04
4	200	4.6	EG	-13.86
4	200	4.6	EG	-3.69
4	200	4.6	SL	1.98
4	200	4.6	SL	-3.44
5	400	7.5	SL	-13.78
5	400	7.5	EG	-38.28
5	400	7.5	SL	-9.78
5	400	7.5	SL	-13.18
5	400	7.5	SL	-17.70
6	200	4.6	EG	.53
6	200	4.6	SL	-6.92
6	200	4.6	SL	-4.89
6	200	4.6	EG	-9.01
6	200	4.6	SL	-6.06
6	200	4.6	EG	-8.95
6	200	4.6	SL	-16.53
6	200	4.6	EG	-21.04
7	400	7.0	SL	1.93
7	400	7.0	EG	-76.78
7	400	7.0	SL	-43.02
8	2	4.2	EG	30.62
8	2	4.2	SL	9.42
8	2	4.2	EG	20.58
8	2	4.2	SL	13.07
8	2	4.2	EG	21.96
8	2	4.2	EG	20.01

Table A9, cont'd. Absorption efficiency (AE)\* and concentrations of particulate inorganic matter (PIM) using eelgrass (EG) and slough (SL) mussels from Padilla Bay, WA. [ADD] and [ACTUAL] = added and actual concentrations of PIM in experimental waters, respectively. EXP. NO. refers to experiment numbers.

9	2	3.4	EG	8.73
9	2	3.4	SL	-9.50
9	2	3.4	EG	.28
9	2	3.4	EG	.36
9	2	3.4	EG	-9.90
9	2	3.4	SL	2.86
10	200	5.4	EG	-26.68
10	200	5.4	EG	-17.78
10	200	5.4	SL	-22.54
10	200	5.4	EG	-36.46
10	200	5.4	SL	-14.48
10	200	5.4	SL	-20.63
10	200	5.4	SL	-12.76
10	200	5.4	EG	-30.15
11	400	7.9	SL	-54.87
11	400	7.9	EG	-54.46
11	400	7.9	EG	-30.41
11	400	7.9	EG	-86.00
11	400	7.9	SL	-74.09
11	400	7.9	SL	-73.36
11	400	7.9	EG	-39.72

$$*: AE = \frac{F - E}{(1-E)F} \times 100$$

F = proportion of organics in seston  
E = proportion of organics in feces

after Conover (1966)



