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Megan N. Dethier, Jennifer Ruesink, Helen Berry, Amy G. Sprenger, Blain Reeves. Restricted ranges in physical factors may constitute subtle stressors for estuarine biota. *Marine Environmental Research*, 2010, 69 (4), pp.240. 10.1016/j.marenvres.2009.10.015 . hal-00564781

**HAL Id: hal-00564781**

**<https://hal.science/hal-00564781>**

Submitted on 10 Feb 2011

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## Accepted Manuscript

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PII: S0141-1136(09)00141-X

DOI: [10.1016/j.marenvres.2009.10.015](https://doi.org/10.1016/j.marenvres.2009.10.015)

Reference: MERE 3390

To appear in: *Marine Environmental Research*

Received Date: 26 August 2008

Revised Date: 4 September 2009

Accepted Date: 16 October 2009



Please cite this article as: Dethier, M.N., Ruesink, J., Berry, H., Sprenger, A.G., Reeves, B., Restricted ranges in physical factors may constitute subtle stressors for estuarine biota, *Marine Environmental Research* (2009), doi: [10.1016/j.marenvres.2009.10.015](https://doi.org/10.1016/j.marenvres.2009.10.015)

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M.N. Dethier et al.

Gradients on an estuarine shoreline

Restricted ranges in physical factors  
may constitute subtle stressors for estuarine biota

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Keywords: estuary, gradient, species richness, biomass, temperature stress, salinity variation

## ABSTRACT

Biotic trends along estuarine gradients can be affected by co-varying processes ranging from large-scale oceanographic to local-scale physico-chemical effects. As a baseline for future process studies, we investigated the distinct gradients in species richness and biomass in pebble-sand shorelines along the estuarine axis of Puget Sound, and the scales of variation of some of their physical correlates. Higher richness and biomass at beaches at the more marine end of the Sound are temporally consistent and seen in all trophic groups. Variables that correlate with biotic patterns include relatively subtle increases in beach surface and sediment temperatures and decreases in nearshore salinity near the head of the estuary, but not more localized parameters such as sediment grain size or porewater salinity. To understand whether these variables are true forcing functions of community structure, we are performing experimental work.

## 1. INTRODUCTION

Biodiversity in marine habitats is affected by oceanographic and biogeographic context, local physical gradients, propagule supply, and post-recruitment biotic interactions (Hawkins, 2004). In estuaries, physical gradients often covary with anthropogenic stressors such as pollutants, acting synergistically or antagonistically to impact biodiversity and, subsequently, ecosystem function (Raffaelli, 2006; Rakocinski et al., 2000). The key physical gradients that frequently correlate with estuarine biota are salinity (Giberto et al., 2004; Hirst, 2004; Rutger and Wing, 2006), sediment grain size and deposition rate (Anderson et al., 2004; Hernandez-Arana et al., 2003; Hewitt et al., 2005; Wieser, 1959) and oxygen content (e.g., Bishop et al. 2006). The physiological and ecological effects of particular physical factors, and in some cases their interactions, are known for some estuarine species; salinity has been particularly well studied (reviewed by Wolff 1983, Attrill 2002). The key parameter stressing or excluding species from parts of estuaries may not be absolute ranges (e.g. annual salinity range) but scales of local temporal variation; predictability or ‘return time’ from extreme events may have a greater ecological impact than seasonal changes, even if the latter are large, because seasonal acclimation is common (Hirst and Kilpatrick, 2007; McLeod and Wing, 2008).

Biotic diversity predictably declines from the outer towards the inner portions of estuaries (Attrill 2002, Dethier and Schoch 2005 and refs. therein, Rutger and Wing 2006) but because of the problem of co-variance of many estuarine gradients, determination of key forcing processes has been elusive. The diversity pattern holds in both pristine and anthropogenically impacted estuaries, suggesting that natural physical gradients may be critical. Primary productivity often positively affects diversity (e.g., Mittlebach et al. 2003), but is complex in estuaries. Consumers may use phytoplankton, macroalgae, or particulate carbon sources; these are affected to varying

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4 degrees by watershed-derived turbidity, nutrients, and detritus (Livingston et al., 1997; Ruesink  
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6 et al., In review.). As a result of these diverse inputs, trophic as well as species diversity may  
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8 vary along estuarine gradients. Inner estuaries may be dominated by deposit feeders or  
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10 suspension feeders that thrive on the abundant particulates from riverine sources (e.g., Giberto et  
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12 al. 2004; Currie and Small 2005); in such cases, biomass may be highest in inner estuaries,  
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14 showing the opposite pattern from biodiversity. Thus quantifying biomass patterns should  
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16 provide clues about the causes of biodiversity patterns. In other cases, shoreline development  
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18 such as extensive seawalls (bulkheads) in inner estuaries restricts allochthonous carbon input and  
19  
20 reduces density of deposit feeders and their predators (Seitz et al., 2006). Trophic diversity,  
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22 however, is usually greater near the mouths of estuaries (Currie and Small, 2005; Giberto et al.,  
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24 2004).

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31 Assessing factors controlling species diversity and biomass in estuaries thus must involve  
32  
33 an attempt to decouple large numbers of physical and food-web parameters. Research must occur  
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35 at a large enough spatial scale to encompass some of these gradients, as well as at multiple  
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37 trophic levels and a variety of life-history stages (Raffaelli, 2006). Analyzing the importance of  
38  
39 physico-chemical variability must be done at various spatial and temporal scales to determine  
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41 which parameters and what scales truly affect organismal assemblages. Are rare, annual, or daily  
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43 changes most critical? Most such studies have been done in estuaries with dramatic spatial and  
44  
45 temporal variation in physical parameters, e.g. striking differences in grain size, or along a  
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47 complete freshwater to marine salinity gradient (e.g., Hirst 2004). In a previous study (Dethier  
48  
49 and Schoch 2005) we assessed community structure patterns using a hierarchical sampling  
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51 design for 45 beaches in Puget Sound, Washington, a fjordal estuary with much more  
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53 constrained physical gradients. We controlled several key variables by working only at one tidal  
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4 height and only in pebble-sand beaches with no apparent pollution issues. Species richness  
5  
6 increased steadily towards the mouth of the estuary, correlated with shallow gradients in  
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8 nearshore wave energy, temperature, and salinity. However, we were unable to examine scales of  
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10 variation of potentially key physical parameters, or actual parameters on the beach itself. Here  
11  
12 we focus our studies on several sites spanning this gradient, testing 1) whether biomass of flora  
13  
14 and fauna follow the same gradient as species richness, which could indicate a key role of  
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16 trophic sources in controlling biotic parameters; 2) whether the general open-water physical  
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18 gradients described earlier are overlain by higher spatial and temporal variation in these  
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20 parameters on the shore, where the biota were studied, and 3) whether such variation correlates  
21  
22 with patterns of richness and biomass. These data will serve as a physical backdrop for process  
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24 studies on the roles of productivity, recruitment, and post-recruitment mortality in generating the  
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26 diversity gradient in this system.  
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## 32 33 2. STUDY SITES AND METHODS 34

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36 Puget Sound is a large, topographically complex fjordal estuary characterized by rivers  
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38 that enter at numerous locations along its length, and by sills and constricted passages that  
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40 promote mixing (Babson et al., 2006; Moore et al., 2008). Flow within the Sound is dominated  
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42 by tidal currents; the tidal range is large, reaching 4.6 m at the southern (inner) end of the  
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44 estuary. The Sound thus does not experience the large or unidirectional salinity gradients seen in  
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46 simple or shallow estuaries, although there is more seasonal stratification and greater variation in  
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48 temperature and salinity in the inner Sound than near the mouth (Moore et al., 2008). Greater  
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50 gradients are seen in Hood Canal, an isolated branch to the west, and in shallow finger inlets in  
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52 South Sound. All regions, especially near the mouths of the rivers nested within the Sound, show  
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4 seasonal patterns in salinity and temperature, driven largely by high precipitation in winter  
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6 and/or by snowmelt in late spring and summer.  
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9         Against this complex backdrop, we chose three of the sampling sites studied previously  
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11 by Dethier and Schoch (2005) that spanned most (83 km) of the overall estuarine gradient: one  
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13 site (Budd) in southern (inner) Puget Sound, one (Brown) in south-central, and one (Carkeek) in  
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15 north-central (Fig. 1). Detailed studies were carried out in 2004-5 at 3 beaches nested within  
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17 each of the sites; the ‘replicate’ beaches per site were within 3 km of each other along these  
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19 rather linear, open shorelines. We chose this subset of our previous sites to: a) span as much of  
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21 the Sound as possible, b) have 3 beaches that were reasonable “replicates” of each other in terms  
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23 of substratum, c) have no known history of pollution or unpredictable physical disturbances such  
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25 as waves of sand that bury the low shore, and d) be logistically accessible year-round. Use of  
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27 more sites would have been desirable in this complex system, but the labor-intensive nature of  
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29 our studies made this impossible.  
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36         To test whether there is a gradient in biomass of shoreline biota that parallels the gradient  
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38 in species richness, in June 2004 and June 2005 we quantified tissue biomass of all macroscopic  
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40 organisms in 5 randomly selected 0.3 m<sup>3</sup> samples at each of the nine beaches. Samples were  
41  
42 taken from a 50 m transect line laid parallel to the shore at mean lower low water (MLLW); this  
43  
44 level was determined from tidal predictions over numerous dates. For surface flora and fauna, we  
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46 picked off and bagged all algae, mobile invertebrates, and sessile invertebrates such as oysters  
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48 from a 0.1 m<sup>2</sup> quadrat. Percent cover of barnacles on cobbles was estimated and later converted  
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50 to dry biomass based on separately calculated regressions of dry tissue mass cm<sup>-2</sup> of live  
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52 barnacles. This biomass value is conservative because barnacles on the sides of cobbles were not  
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54 counted in percent cover estimates. Large infauna were quantified by digging up all sediment  
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4 below the quadrat down to 30 cm, and sieving on coarse (1 cm) mesh. Smaller infauna were  
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6 sampled with 10 cores (10 cm diam. x 15 cm deep) along the same transect, sieved to 2 mm, and  
7  
8 their biomasses converted to dried mass  $0.3 \text{ m}^{-3}$ . Use of 2 mm sieves was necessary because  
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10 smaller mesh sizes completely clog with this coarse pebble-sand sediment. All collected biota  
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12 were sorted to species in the laboratory, removed from shells if necessary, counted, and dried to  
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14 a constant weight. Species on these beaches and their trophic groups are listed in Dethier and  
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16 Schoch (2005). Differences in biomass values were tested with a 2-way nested ANOVA (Systat  
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18 9) with main effects of Year and Site, and between-subjects error of Beaches nested within Site.  
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24 We examined physical data from throughout the year because the macroscopic flora and  
25  
26 fauna we sampled each June constitute an integrated picture of the organisms that have managed  
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28 to survive over the previous months. Preliminary data suggested that temperature varies  
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30 substantially in both space and time on these beaches, so we used temperature dataloggers  
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32 (TidbiT, Onset Computer Corp.) to gather fine-scale data. At each of the nine beaches, TidbiTs  
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34 were attached to PVC pipes and installed in May 2004 in three habitats: on the surface of the  
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36 sediment at MLLW (to quantify temperature variation for surface flora and fauna); ca. 5-8 cm  
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38 beneath the sediment surface at MLLW (to quantify porewater temperatures experienced by  
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40 infauna); and above the sediment surface near extreme low water (to quantify nearshore water  
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42 temperatures). All TidbiTs logged temperatures every 40 min for up to 15 months. Data used in  
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44 analyses were maximum/day, average/day, and change in temperature/day for each TidbiT.  
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46 Weekly averages were calculated for some parameters. When TidbiTs were lost from some  
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48 habitats at some beaches, data were pooled among beaches per site.  
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56 There are no similar inexpensive loggers with long battery lives for recording variation  
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58 in the key parameter of salinity. Thus our salinity data are confined to periodic recordings using  
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4 a YSI Salinity Conductivity Temperature meter (model 30/10 ET). To measure seasonal changes  
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6 in the nearshore water, in 2004-5 we took readings every 1-2 months from a boat ca. 5 m  
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8 offshore. To measure interannual and local (within a beach) variation in porewater, in June of  
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10 2001, 2004, 2005, and 2006 we recorded porewater salinity in three randomly selected holes dug  
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12 at MLLW in each beach.  
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16 Finally, although our beaches were chosen from a set of sites with similar pebble-sand  
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18 surface sediments, we quantified grain sizes because of the importance of this parameter to  
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20 shoreline biota. We also were interested in the extent of seasonal variability in grain sizes, since  
21  
22 these sites experience considerable wintertime wave action. In April, July, and December 2005,  
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24 we collected five replicate samples of 120-150 ml (to ca. 6 cm depth) of sediment at each beach,  
25  
26 removing live organisms, shells, and pebbles larger than ~3 cm. Samples were placed in a drying  
27  
28 oven at ~60° C until completely dried, then hand-sieved through 2 mm and 1 mm sieves. We  
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30 weighed 60-100 g of the fine sand (<1 mm), placed it in a muffle furnace for 6 h at 500° C to  
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32 burn off organics, then cooled and reweighed it. The ashed dry sample was then sieved on a  
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34 standard sieve series for 6 min with a Ro-tap shaker, and each portion weighed. Grain size  
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36 fractions were analyzed as “species” in PRIMER multidimensional scaling plots to look for  
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38 variation in relative abundances of different size fractions at different beaches and dates.  
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### 45 46 3. RESULTS

#### 47 48 *3.1 Biotic Patterns*

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50 As in our previous, broader surveys of pebble-sand beaches throughout the Sound  
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52 (Dethier and Schoch 2005), a clear pattern of higher species richness in the outer-Sound (more  
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54 marine) beaches was seen in the samples collected for biomass measurements in both 2004 and  
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56 2005 (Fig. 2A). Almost twice as many species are found on beaches in the outer than in the inner  
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4 Sound, and this pattern can be seen in virtually all trophic groups. No clear patterns are seen  
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6 within sites, i.e. between the South (S), Middle (M), and North (N) beaches in one region. In  
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8 these surveys, the richness at Brown is not higher than at Budd, but it distinctly was in our  
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10 previous study which used more replicate samples per beach (Dethier and Schoch 2005). The  
11  
12 richness pattern is not driven by rare taxa; even though species found as only 1 or 2 individuals  
13  
14 per transect made up over one third of the richness per beach, the proportion of rare taxa shows  
15  
16 no trend along the estuarine axis (unpubl. data). Some interannual variation was seen, e.g. at  
17  
18 Carkeek N where richness was much lower in 2004 than expected; the species 'missing' in that  
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20 year included various deposit feeders (some polychaetes and the clam *Macoma inquinata*) and  
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22 omnivores (such as crabs and isopods), but these were seen in 2005 as well as in the other  
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24 Carkeek beaches.  
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31 Biomass of organisms showed a parallel pattern of being greater in the outer beaches and  
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33 being quite consistent among years. Figure 2B shows this trend with two major biomass  
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35 components removed to illustrate that they do not drive the pattern. Ulvoid algae are abundant on  
36  
37 many beaches but are ephemeral and patchy; they showed no trends along the estuarine axis, and  
38  
39 removing their biomass (average 8.1 g dry in 2005) makes it possible to see patterns in the less  
40  
41 ephemeral primary producers (other macroalgae). Large edible clams were also removed from  
42  
43 the analysis, again because their biomass numbers swamped those of other suspension feeders  
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45 (average 14.6 g biomass, but ranging from 0 to 117 g per sample). In addition, because they are  
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47 sometimes harvested recreationally, differential digging at the sites could bias natural biomass  
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49 patterns. If clam data are included, the trend is even more obvious, because clams were much  
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51 more abundant in the outer beaches (all the samples with over 25 g clam tissue were at Carkeek).  
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58 Total biomass varied significantly among sites (2-way ANOVA on log-transformed data,  $F =$   
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4 24.28, 2 d.f.,  $p = 0.001$ , all pairwise comparisons significant) and was marginally higher in 2004  
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6 (F = 3.68, 1 d.f.,  $p = .10$ ). Beaches within sites were also variable (beaches nested in sites, F =  
7  
8 2.89, 6 d.f.,  $p = 0.014$ ). All individual trophic components except for deposit feeders likewise  
9  
10 showed significant site effects, with the trend always Budd < Brown < Carkeek. Figure 2C  
11  
12 shows the full biomass including ulvoids and large clams, with the data pooled into surface  
13  
14 organisms (flora and fauna) versus infauna. A trend of increasing mass towards the outer estuary  
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16 can be seen in both groups.  
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### 20 21 *3.2 Abiotic Conditions*

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23 The background physical conditions for all beaches are set by those of the nearshore  
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25 waters, which cover our sampled intertidal level (MLLW) ca. 90% of the time. Daily average  
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27 temperatures of the nearshore waters over 15 months show predictable seasonal patterns but also  
28  
29 distinct regional differences (Fig. 3A); Carkeek and Brown temperatures are virtually  
30  
31 indistinguishable, but water adjacent to the 3 southernmost sites (Budd) gets distinctly warmer  
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33 (by  $\sim 2^{\circ}\text{C}$ ) each summer than water adjacent to the central and northern sites. This difference  
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35 disappears mid-winter as all temperatures reach their minima. These data are very similar to mid-  
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37 channel water temperatures (Moore et al. 2008), except for reaching slightly higher summer  
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39 values.  
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45 Beach surface temperatures (Fig. 3B) reflect localized effects overlaid on the regional  
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47 water temperature conditions. Daily averages show predictable seasonal patterns, peaking in July  
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49 and August when higher air temperatures and midday low tides warm the beach surface above  
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51 the temperature of the nearshore waters. Average minima occur in February when ambient air is  
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53 coldest and low tides fall in the middle of the night. There is a consistent pattern for the inner-  
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55 sound sites (Budd) to experience warmer daily average beach temperatures than the Brown or  
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4 Carkeek sites by about 2° C each summer, and to be about 2° higher than the nearshore water  
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6 temperatures at those times (Fig. 3A).  
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9       Temperatures in the sediment (Fig. 3C) are affected by a complex mix of air and sun  
10 warming the beach surface, nearshore water rising and falling through the water table with the  
11 tide, and groundwater percolating down from the land. Sediment temperatures are consistently  
12 cooler than the beach surface but show almost identical patterns, both seasonally and in terms of  
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14 the higher temperatures seen at the Budd beaches.  
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21       Potentially stressful temperature variation experienced on fine spatial and temporal scales  
22 is better illustrated in Figure 4, which shows the average daily maxima during the summer at  
23 each site (daily summer minima are equal to the nearshore water temperature, when the tide  
24 covers the beach). The higher temperatures at Budd for all 3 habitats are clearly visible, as is the  
25 contrast among habitats. Maximum temperatures at Budd beaches rise an average of approx. 3°  
26 over ambient (nearshore) temperatures each day in the sediment and 6° on the surface, and  
27 slightly smaller rises occur at Brown and Carkeek (Fig. 4). A two-way ANOVA on these data  
28 from all the functioning Tidbits (pooled per site) showed both a Site effect ( $F = 98.72$ , 2 d.f.,  $p <$   
29  $0.001$ ; Budd > Brown = Carkeek) and a Habitat effect ( $F = 1157$ , 2 df,  $p < 0.001$ ; nearshore <  
30 sediment < surface) but no interaction ( $p = 0.47$ ).  
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45       No fine-scale (daily) salinity data are available to compare with the temperature data.  
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47 Nearshore salinities measured adjacent to each beach every 1-2 months from June 2004 to Sept.  
48 2006 were highly variable among sites and times (data not shown); all showed maxima of 30-32  
49 psu, usually in late summer, and minima at irregular times, during periods of high rain (autumn)  
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51 or snow melt (spring). Recorded minima were lower at Budd (23, 20, and 22 near the three  
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53 beaches) than at Carkeek (28, 29, and 28). Brown was intermediate (24, 24) except at Brown S,  
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4 which experienced some very low values (e.g. 9, 19) because of its proximity to the mouth of the  
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6 Puyallup River.  
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9 Salinity of the beach porewater during low tide measurements in June of each year  
10 showed substantial variability among the 3 holes per beach, the 3 beaches per site, and the 3  
11 regions, as expected with such a ‘snapshot’ view. Figure 5 shows these data averaged over June  
12 observations from 2001, 2004, 2005, and 2006, and compared to the nearshore values adjacent to  
13 each beach. There was both a Site effect ( $F = 5.661$ , 2 df,  $p = 0.005$ ; Brown < Budd = Carkeek)  
14 and a Habitat effect ( $F = 15.744$ , 1 df,  $p < 0.001$ ; Nearshore > Porewater) and no interaction.  
15 Porewater salinity showed no correlation with nearshore salinity measured at the same time ( $r^2 =$   
16  $0.07$ ,  $N=40$ ); porewater values ranged from 7 psu lower to 12 psu higher. Interestingly, over the  
17 four years of June measurements, four beaches always had porewater salinities that were less  
18 than the nearshore water, presumably affected by seeping groundwater. One beach, Brown S,  
19 always had higher porewater salinity, presumably because of the pulses of riverine influence on  
20 the nearshore water. The other four beaches varied from date to date.  
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38 The differing physical regimes experienced by the nearshore waters vs. the beach are  
39 illustrated by different correlations between temperature and salinity. In the nearshore waters,  
40 there is a weak negative correlation among sites between temperature and salinity (June data;  $r^2$   
41  $= 0.24$ ,  $p = .016$ ); the outer-estuarine sites, influenced by oceanic water coming in through the  
42 Strait of Juan de Fuca (Fig. 1), are cooler and more saline than the inner sites. In the beach  
43 porewater from June, however, there is a positive correlation – cooler temperatures are  
44 associated with lower salinities ( $r^2 = 0.34$ ,  $p < 0.001$ ). This pattern may be driven by rain or  
45 snowmelt in the watershed delivering cooler and less saline groundwater to the beach.  
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4 Grain sizes varied somewhat among sites and dates in these pebble-sand beaches. Figure  
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6 6A contrasts the overall ratio of coarse (>1 mm) sand and pebbles to finer (<1 mm) sediments  
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8 over all beaches and dates; in general, the winter samples were characterized by fewer pebbles  
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10 and more sand, as sand moved onto the low shore in winter storms. There was no overall trend  
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12 along the estuarine axis in coarse sediments, however; rather, each beach had a characteristic and  
13  
14 persistent mix, with two of the Brown beaches being the most coarse. Figure 6B shows the  
15  
16 relative abundances of just the finer grain sizes (summer data). All beaches were dominated by  
17  
18 coarse to fine sands (Phi 1-3), with low proportions of fines and organics, and no gradient along  
19  
20 the estuarine axis. When all the grain size fractions and dates were analyzed in Primer MDS  
21  
22 plots, sites appeared as strongly separated (Global R for Sites = 0.45,  $p = 0.001$ ), with Brown  
23  
24 beaches being especially different from the other two sites. Seasons were much less well  
25  
26 separated than sites (Global R for Dates = 0.07,  $p = 0.002$ ), with December significantly different  
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28 from April and July.  
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#### 35 36 4. DISCUSSION 37

38 Our results for pebble-sand beaches in the Puget Sound estuary show that there are  
39  
40 distinct and persistent trends in biomass that parallel the previously described (Dethier and  
41  
42 Schoch 2005) trend in species richness from the inner (more enclosed) end to the outer (more  
43  
44 marine) end. The gradients in both parameters are towards much higher values at the marine end,  
45  
46 unlike in some estuaries where diversity and biomass show opposite patterns (Giberto et al.,  
47  
48 2004). In addition, there is no evidence that trophic diversity is higher at the mouth of the  
49  
50 estuary; all trophic levels sampled (e.g. we did not sample large vertebrate predators) are  
51  
52 represented along the whole gradient, but with more species in each level at the marine end (Fig.  
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54 2A). This implies that whatever broad process(es) cause low biodiversity in the inner portions of  
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4 the Sound do not disrupt trophic function in this habitat type, i.e. that the food sources for these  
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6 shoreline organisms are diverse. Targeted studies of growth rates of primary producers and  
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8 suspension feeders at our sites show that they vary among species, suggesting that biomass  
9  
10 patterns are not driven by consistently faster growth in the outer Sound (Ruesink et al. in  
11  
12 review). The biomass gradient is also spatially large and is consistent in both epi- and infauna,  
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14 suggesting that forcing mechanisms operate on a large scale (Edgar and Barrett, 2002) and affect  
15  
16 both the surface and the sediment. The relative lack of interannual variability in biota also  
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18 implies that the key processes are likely to be chronic, such as annual high summer temperatures,  
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20 rather than temporally unpredictable (such as occasional defaunation events in some estuaries).  
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26 Dethier and Schoch (2005) described correlations of this trend in richness with physical  
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28 characteristics of regional climate (air temperature and precipitation) and open water (mid-Sound  
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30 sea surface temperature and salinity), but abiotic factors measured on local beaches were limited  
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32 to surface sediment characteristics, estimates of wave power, and ‘snapshot’ summertime  
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34 porewater temperatures and salinities. We found that physico-chemical conditions on the beach,  
35  
36 i.e. those experienced by the shoreline flora and fauna, show variation at all temporal and spatial  
37  
38 scales measured. Factors that vary on a site (or smaller) scale, such as local riverine influence  
39  
40 and porewater salinity, are only poorly related to the large-scale patterns. Sediment grain sizes  
41  
42 also show no patterns along the estuarine axis, but rather beach-specific characteristics that vary  
43  
44 somewhat with season, and probably depend on local wave conditions and alongshore drift.  
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46 Temperature and salinity encountered by the organisms on the beaches do covary with the biotic  
47  
48 gradient, and are affected by variation from several sources. The backdrop is the nearshore water  
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50 conditions, which affect all the sites and are slightly more variable in the inner Sound. Added to  
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52 this is variation caused by ambient air conditions warming the beach surface; again, this leads to  
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4 higher extremes in the inner Sound, primarily because low tides fall approximately 1 h later at  
5 those sites than at our outer ones, i.e. into the warmer part of the day during spring and summer  
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7 daytime low tides. Temperatures may also reach colder extremes in the winter in the inner Sound  
8  
9 when low tides are at night, but this signal was harder to detect. Epibiota on the beach surface  
10  
11 encounter these more variable conditions. Finally, greater warming of the upland surface and  
12  
13 greater rainfall in the inner Sound (Dethier and Schoch 2005) can affect groundwater conditions  
14  
15 that impact the beach during low tide, when the marine water table is low. These fluctuations in  
16  
17 groundwater properties, compounded by variation on the beach surface that propagates into the  
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19 sediment, will especially impact infauna.  
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26 Does the physical variation in Puget Sound beaches provide a mildly stressful  
27  
28 background condition, or is it actually important to the composition of the biota? Work in other  
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30 estuaries (references in Introduction) has often drawn conclusions about the key roles of salinity  
31  
32 and sediment type based largely on correlative evidence, either simple linear correlations or  
33  
34 complex multivariate analyses. It is harder to determine, however, whether low or variable  
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36 salinity (for example) actually *causes* low diversity in upper estuaries, and if so via what  
37  
38 mechanism. Recent evidence (including field observations and lab experiments) suggest that the  
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40 range of a factor, especially salinity, and the time span over which that range occurs, is more  
41  
42 important to organisms than the absolute minima (Attrill, 2002; Hirst and Kilpatrick, 2007;  
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44 McLeod and Wing, 2008). Acclimation to seasonal changes in salinity and temperature is likely  
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46 to take weeks (Dame, 1996), so that short-term variation may exceed physiological tolerances, or  
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48 at least negatively affect growth or reproduction (Beukema et al., 2009). To affect an integrative  
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50 pattern such as richness, however, a parameter must consistently cause mortality at some life  
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52 stage of multiple species; studying such effects at the community level is challenging.  
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4 If physical stresses are a significant cause, rather than just a correlate, of the lower  
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6 diversity and biomass in the inner portions of Puget Sound, the most striking pattern here is the  
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8 large magnitude of the biotic gradients relative to the small magnitude of the physical ones.  
9  
10 While grain size correlates with diversity in other estuaries (e.g., Mannino and Montagna 1997),  
11  
12 we largely controlled for this factor by only working in one beach type (pebble-sand) rather than  
13  
14 the broad range (silt to sand or pebbles) studied elsewhere. Similarly, nearshore salinity appeared  
15  
16 to affect the biota even though the range at our sites was only on the order of 22-32 psu, a far  
17  
18 more subtle gradient than the 5-28 or even 0-40 psu differences noted as important to infauna in  
19  
20 other estuaries (Rutger and Wing 2006; Rakocinski et al. 2000, respectively). However,  
21  
22 mechanisms behind the roles of salinity or temperature stressors in Puget Sound may well  
23  
24 involve extreme events not captured by our sampling; and with predictions that extreme weather  
25  
26 events may become more common in the future (Cardoso et al., 2008), such mechanisms will  
27  
28 become increasingly important. As in most estuaries (Dame, 1996), combinations of temperature  
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30 and salinity extremes may affect organisms more than just the sum of their individual stress  
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32 effects.  
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41 Many previous studies along estuarine gradients have investigated subtidal rather than  
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43 intertidal biota, and thus factors such as moisture retention and temperature variation in the  
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45 sediment have not been considered. These issues have received attention in the growing  
46  
47 geomorphological literature about the shoreline water table, especially on sandy beaches  
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49 (Jackson et al., 2002; Li et al., 2006), but have seldom been related directly to their impacts on  
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51 beach biota. Several recent studies have shown that local groundwater characteristics, especially  
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53 low-salinity seeps, can significantly affect flora and fauna (Dale and Miller, 2008; Rumrill and  
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55 Sowers, 2008; Zipperle and Reise, 2005) and thus behavior of predators such as birds (Rosa et  
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4 al., 2007). The shorelines of Puget Sound are mostly backed by bluffs of glacial deposits (as  
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6 illustrated in Jackson et al. 2002); erosion of these leads to beaches that are a mix of many  
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8 sediment types. The beaches studied here and that are characteristic of most of the estuary's open  
9  
10 shorelines are exposed to waves that remove the fine sediments (Fig. 6B), leaving relatively  
11  
12 coarse substrates at all tidal elevations. Hydraulic conductivity of such coarse beaches is high,  
13  
14 meaning that the marine water table drains relatively rapidly at low tide compared with mud  
15  
16 beaches (Dale and Miller, 2008). The level of the water table, in turn, has significant impacts on  
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18 factors important to infauna such as temperature and moisture content (Dale and Miller, 2008;  
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20 Jackson et al., 2008; Li et al., 2006). In our study, elevation was constant among beaches but the  
21  
22 moisture content clearly varied, as evidenced by the rate of filling of holes dug for porewater  
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24 measurements (one of the Brown beaches was usually dry when sampled, for example); this  
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26 variation could be due to hydraulic conductivity of the beach and/or to the amount of  
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28 groundwater percolating down from the land. Most of the beaches studied are bulkheaded, as are  
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30 approximately half of the open shorelines of central and southern Puget Sound, but this did not  
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32 seem to affect the passage of groundwater (as suggested by Plant and Griggs 1992).  
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41 Potentially important factors that were not included in our analyses of the drivers of  
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43 diversity patterns are levels of anthropogenic disturbance (e.g., bulkheading of the shore; see  
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45 Seitz et al. 2006) and biotic factors such as nutrient sources, dispersal, recruitment, competition,  
46  
47 and predation. Food sources can affect growth rates and therefore biomass, although connections  
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49 to diversity are less direct. Physical variables affecting dispersal to and recruitment at each site,  
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51 and post-recruitment survival, may be critical (Jackson et al., 2008; McLeod and Wing, 2008).  
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55 These could provide the mechanisms underlying the processes that correlated with diversity; for  
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57 example, sand cover may not directly drive diversity trends, but sand burial could affect post-  
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4 recruitment survival. Disentangling these diverse physical and biological processes, which co-  
5 vary, is a challenge and is the focus of ongoing experimental work.  
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## 10 11 5. CONCLUSIONS

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14 Variation in physical parameters on estuarine shorelines in Puget Sound is quite low  
15 compared to many other estuaries, but particular parameters nonetheless correlate with strong  
16 gradients in species richness and biomass. Temperatures, salinities, and grain sizes on studied  
17 beaches vary among seasons, beaches, and regions; parameters that most closely match the  
18 estuarine-marine biotic gradients in the Sound are the temperatures on the beach itself, and the  
19 open-water salinity that bathes the beaches at high tide. The relatively minor changes in daily  
20 and annual values of these physical parameters raise the question of whether they are directly,  
21 indirectly, or not at all responsible for the biotic patterns seen.  
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## 36 6. ACKNOWLEDGEMENTS

37  
38 This project could never have been accomplished without field assistance from many  
39 people, including Aaron Galloway and numerous DNR and UW volunteers. Carl Schoch  
40 generously gave input at many levels. Space and use of facilities at the Friday Harbor  
41 Laboratories were provided by the Director. This research was funded in part by a grant from the  
42 Washington Sea Grant Program, University of Washington, pursuant to National Oceanic and  
43 Atmospheric Administration Award No. R/ES-57. The views expressed herein are those of the  
44 authors and do not necessarily reflect the views of NOAA or any of its sub-agencies. Matching  
45 funds were generously provided by the Washington Dept. of Natural Resources.  
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## FIGURE CAPTIONS

Fig. 1. Map of the 3 study sites (Budd, Brown, and Carkeek) in Puget Sound.

Fig. 2. Data from biomass samples taken at the 9 beaches in 2004 and 2005; each site has 3 beaches nested within it: South (S), Middle (M), and North (N). **A.** Species richness in these samples, divided by trophic categories. Other = carnivores and scavengers, Susp = suspension feeders, Dep = deposit feeders, Herb = herbivores, and Prim = primary producers (algae). **B.** Biomass (average per beach) divided by trophic categories, with two disproportionately large taxa removed (see text). **C.** Biomass including all taxa, categorized by surface vs. infaunal taxa.

Fig. 3. Temperatures from 3 sets of TidbiT dataloggers at each beach. Points are weekly averages of the average value per TidbiT per day. Sediment TidbiTs (panel C) were removed earlier than the other sets.

Fig. 4. Temperature extremes reached at each of the 3 sites during May-August (2004 and 2005). Each bar is the mean (1 s.e.) temperature from N = 311-598 daily-maximum points per site (beaches within sites pooled: not all loggers were functioning on all dates).

Fig. 5. Salinities in nearshore waters and porewater averaged over 4 June sampling dates. Bars are means and one s.d. For each date and beach, the salinity from the 3 holes per beach were pooled, then the averages of these pooled values taken over 4 years.

Fig. 6. Sediment grain sizes at all 9 beaches. **A.** Ratio by mass of coarse (>1 mm) to fine (<1 mm) sediments during 3 seasons. Bars are one s.d. The error bar for Brown M in April was cut off to clarify the rest of the plot (s.d. = 1.2). **B.** Proportion of fine (<1 mm) sediments in each size class in July 2006.

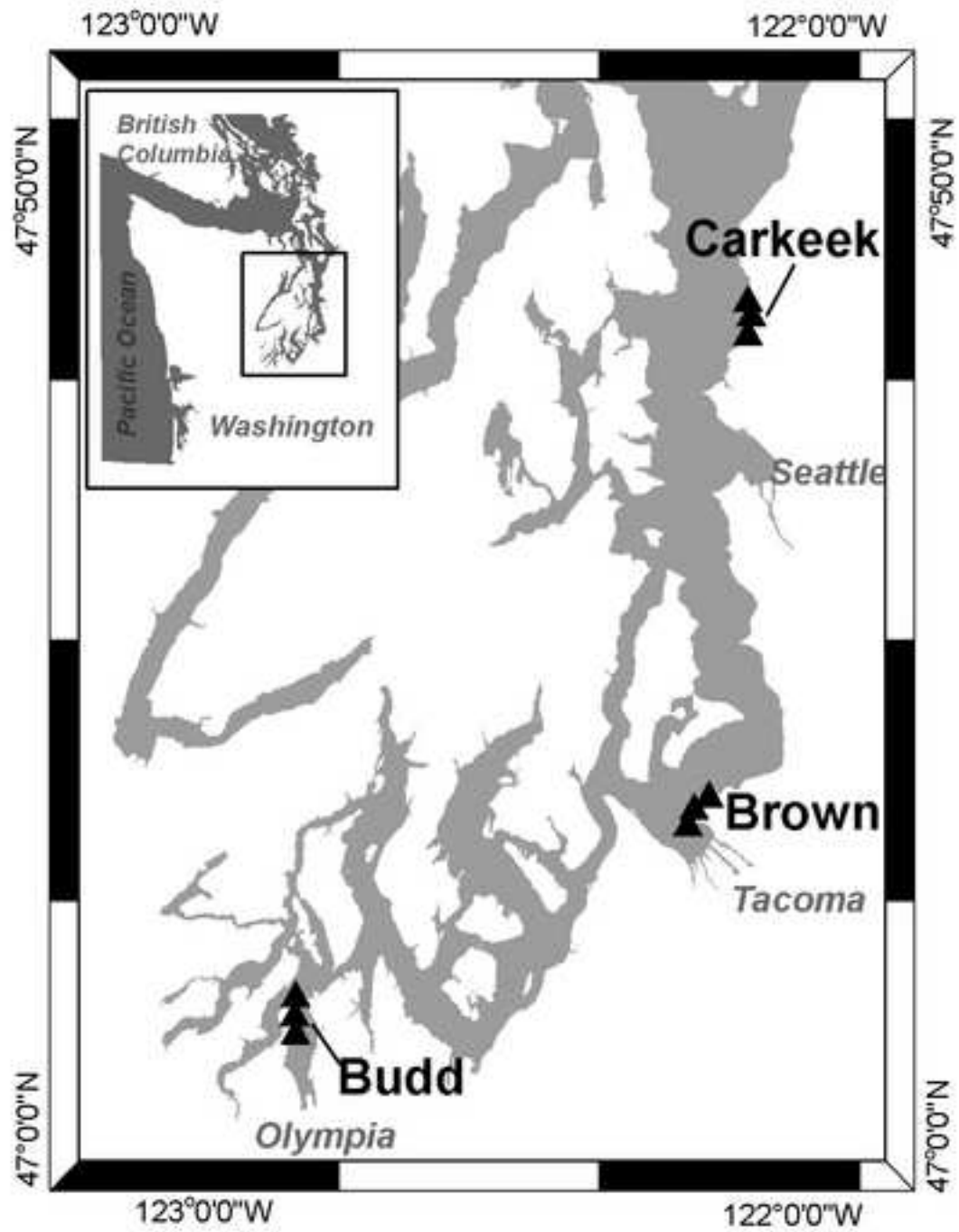


Figure 2.

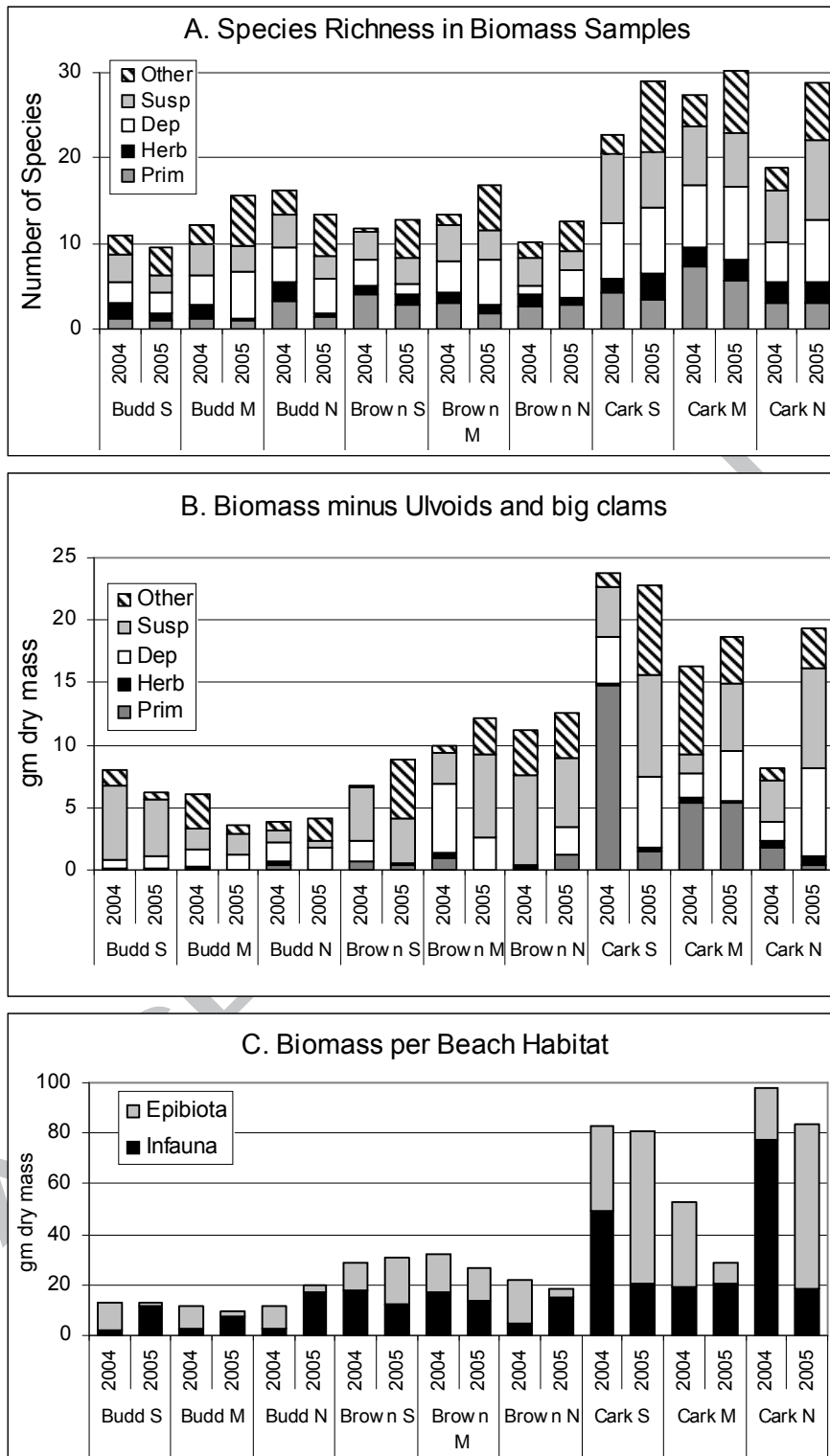


Figure 3.

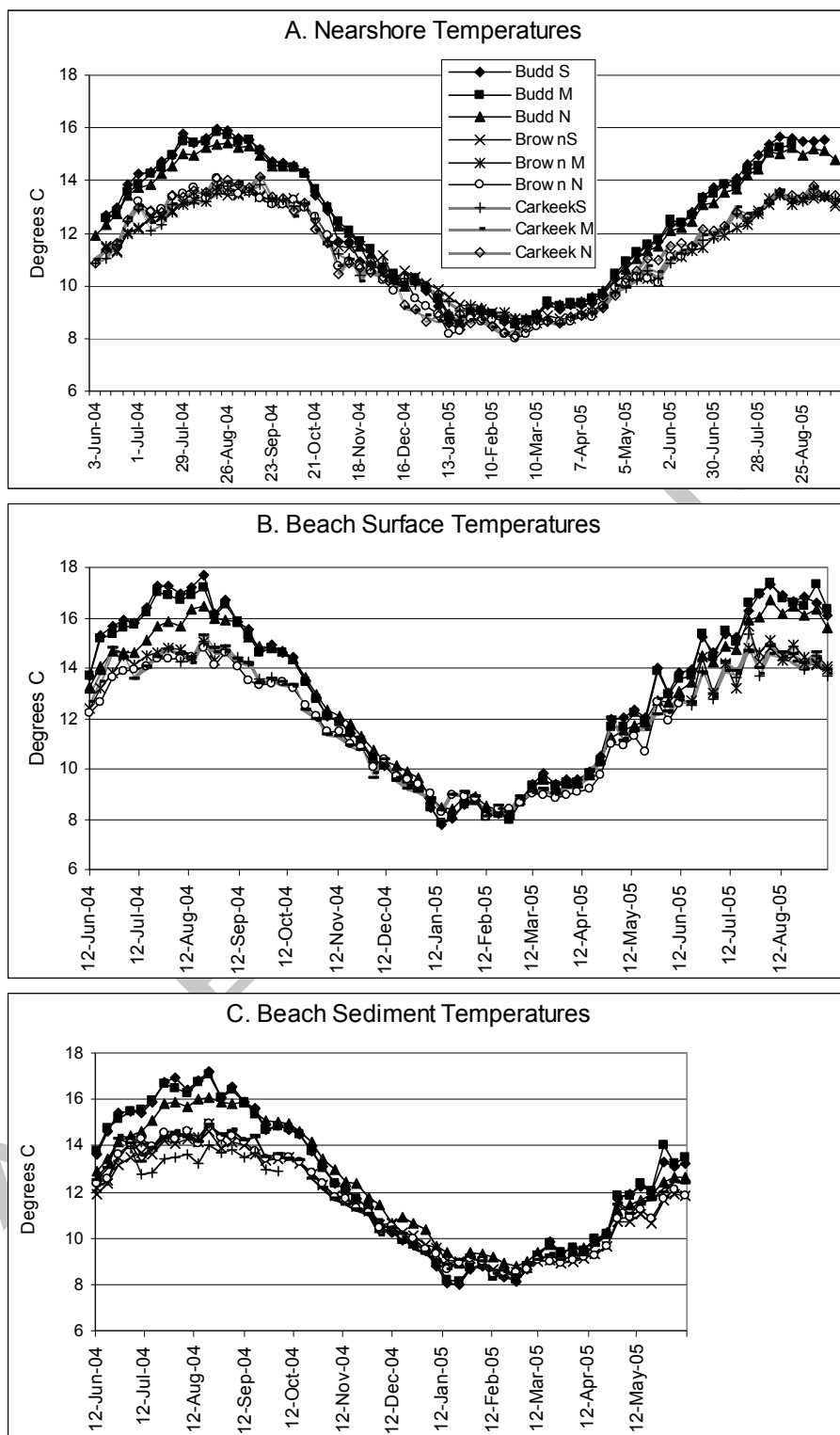


Figure 4.

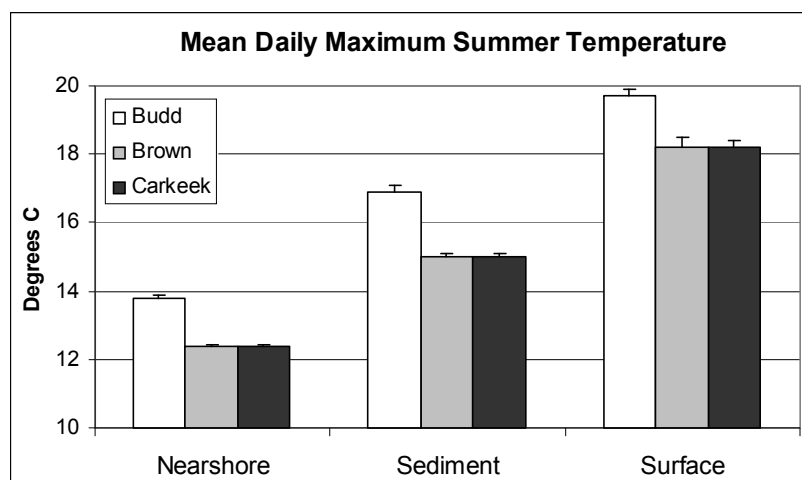


Figure 5.

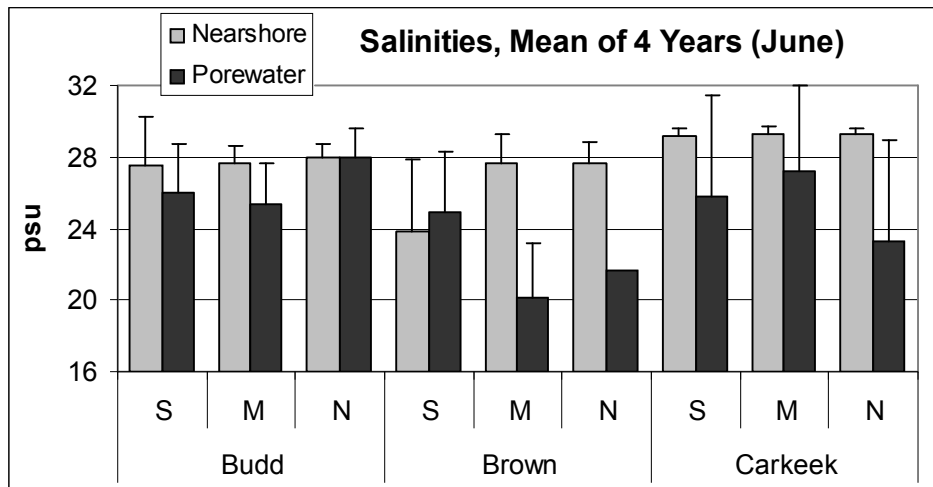


Figure 6.

