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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

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4 ABSTRACT
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6 Biotic trends along estuarine gradients can be affected by co-varying processes ranging
7 from large-scale oceanographic to local-scale physico-chemical effects. As a baseline for future
8 process studies, we investigated the distinct gradients in species richness and biomass in pebble-
9 sand shorelines along the estuarine axis of Puget Sound, and the scales of variation of some of
10 their physical correlates. Higher richness and biomass at beaches at the more marine end of the
11 Sound are temporally consistent and seen in all trophic groups. Variables that correlate with
12 biotic patterns include relatively subtle increases in beach surface and sediment temperatures and
13 decreases in nearshore salinity near the head of the estuary, but not more localized parameters
14 such as sediment grain size or porewater salinity. To understand whether these variables are true
15 forcing functions of community structure, we are performing experimental work.
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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
7
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
11
12 al. 2004; Currie and Small 2005); in such cases, biomass may be highest in inner estuaries,
13
14 showing the opposite pattern from biodiversity. Thus quantifying biomass patterns should
15
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
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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
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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
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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
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6 increased steadily towards the mouth of the estuary, correlated with shallow gradients in
7
8 nearshore wave energy, temperature, and salinity. However, we were unable to examine scales of
9
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
15
16 trophic sources in controlling biotic parameters; 2) whether the general open-water physical
17
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
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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

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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
41
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
45
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
14
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 m³ samples at each of the nine beaches. Samples were
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42 taken from a 50 m transect line laid parallel to the shore at mean lower low water (MLLW); this
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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 m² 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⁻² 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
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8 their biomasses converted to dried mass 0.3 m^{-3} . Use of 2 mm sieves was necessary because
9
10 smaller mesh sizes completely clog with this coarse pebble-sand sediment. All collected biota
11
12 were sorted to species in the laboratory, removed from shells if necessary, counted, and dried to
13
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
39
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 3. RESULTS

46 *3.1 Biotic Patterns*

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48 As in our previous, broader surveys of pebble-sand beaches throughout the Sound
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50 (Dethier and Schoch 2005), a clear pattern of higher species richness in the outer-Sound (more
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52 marine) beaches was seen in the samples collected for biomass measurements in both 2004 and
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54 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
9
10 previous study which used more replicate samples per beach (Dethier and Schoch 2005). The
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12 richness pattern is not driven by rare taxa; even though species found as only 1 or 2 individuals
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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
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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
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37 many beaches but are ephemeral and patchy; they showed no trends along the estuarine axis, and
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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
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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
24
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
50
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
13
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)
50
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
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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
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22 plots, sites appeared as strongly separated (Global R for Sites = 0.45, $p = 0.001$), with Brown
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24 beaches being especially different from the other two sites. Seasons were much less well
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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
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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,
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46 unlike in some estuaries where diversity and biomass show opposite patterns (Giberto et al.,
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48 2004). In addition, there is no evidence that trophic diversity is higher at the mouth of the
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50 estuary; all trophic levels sampled (e.g. we did not sample large vertebrate predators) are
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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
5
6 shoreline organisms are diverse. Targeted studies of growth rates of primary producers and
7
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
27
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
31
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
6
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
18
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
35
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
39
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
45
46 to take weeks (Dame, 1996), so that short-term variation may exceed physiological tolerances, or
47
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
5
6 diversity and biomass in the inner portions of Puget Sound, the most striking pattern here is the
7
8 large magnitude of the biotic gradients relative to the small magnitude of the physical ones.
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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
44
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
5
6 illustrated in Jackson et al. 2002); erosion of these leads to beaches that are a mix of many
7
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,
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14 meaning that the marine water table drains relatively rapidly at low tide compared with mud
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16 beaches (Dale and Miller, 2008). The level of the water table, in turn, has significant impacts on
17
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
25
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,
50
51 and post-recruitment survival, may be critical (Jackson et al., 2008; McLeod and Wing, 2008).
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54 These could provide the mechanisms underlying the processes that correlated with diversity; for
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56 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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37
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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.

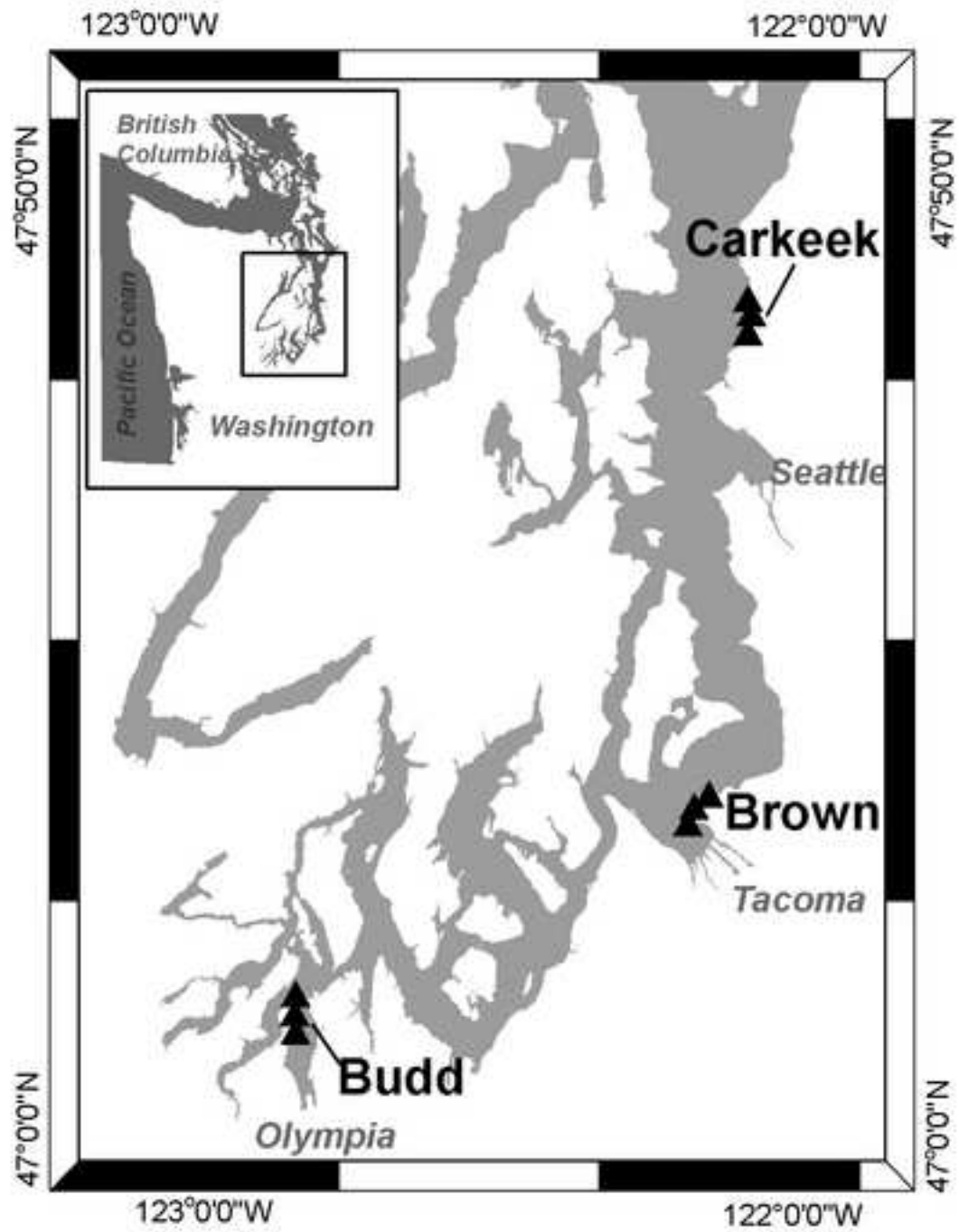


Figure 2.

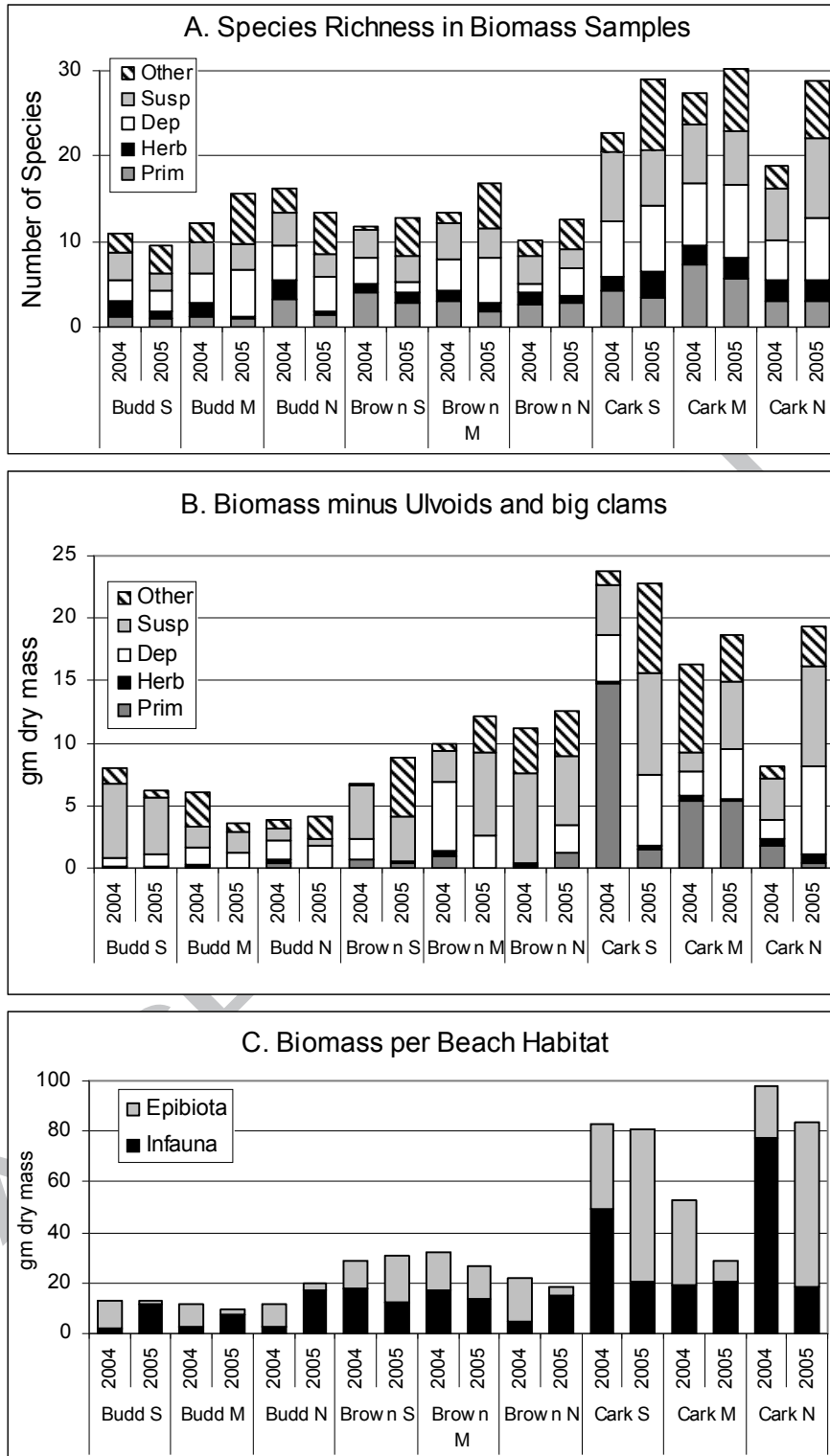


Figure 3.

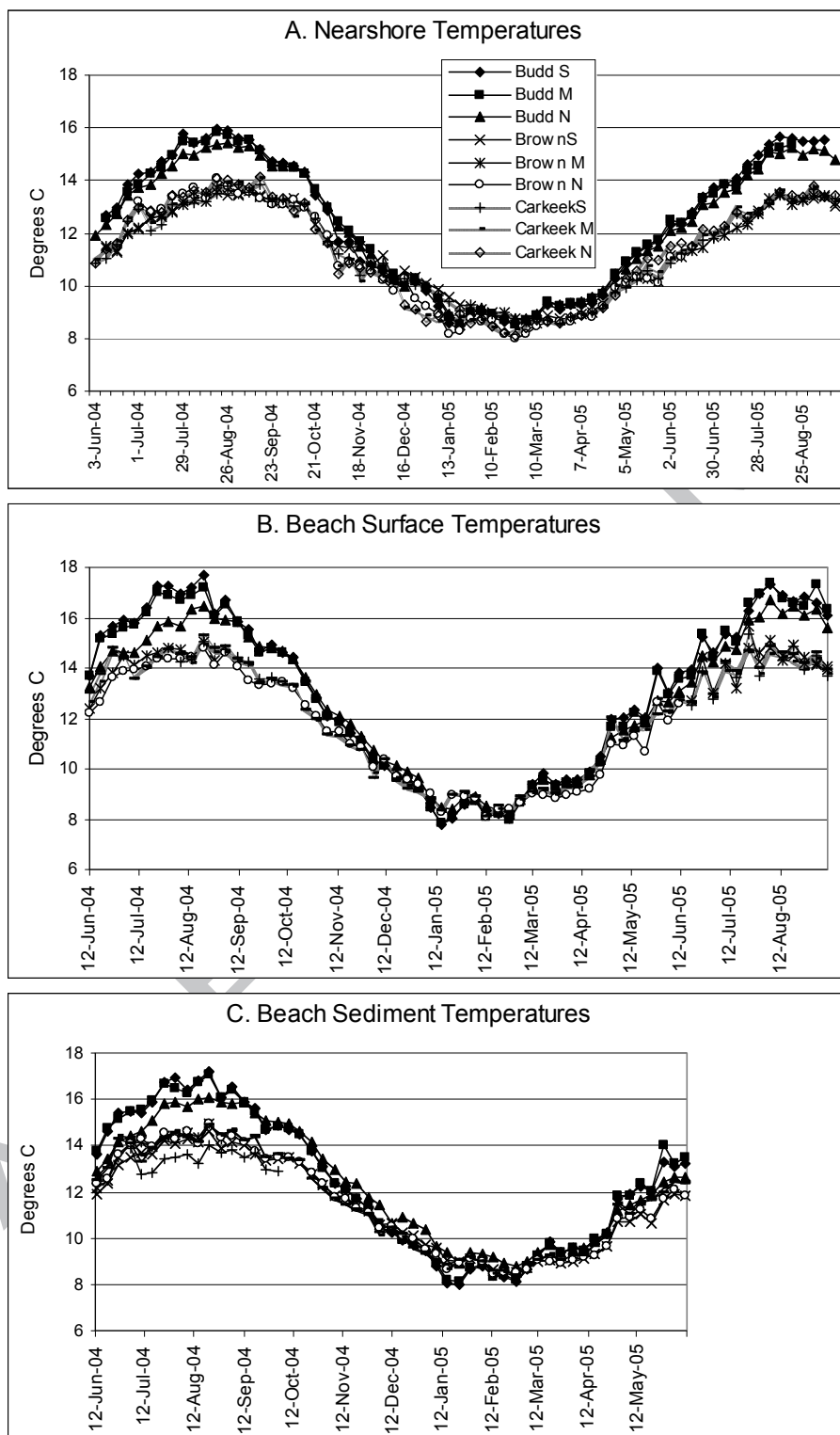


Figure 4.

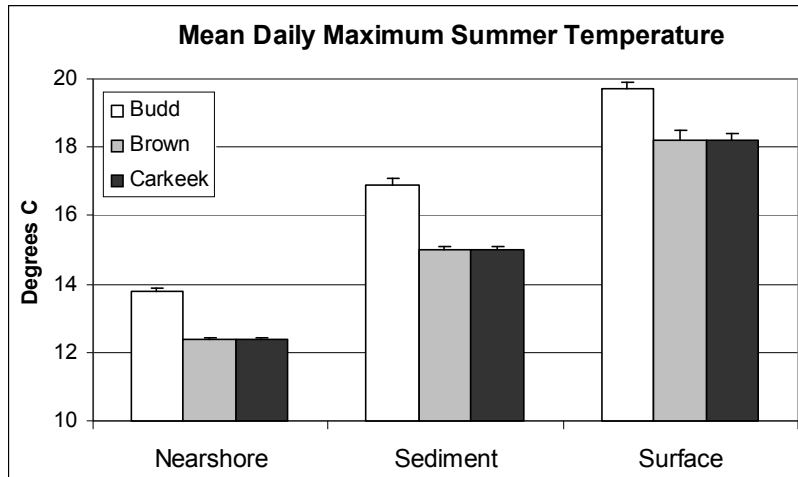


Figure 5.

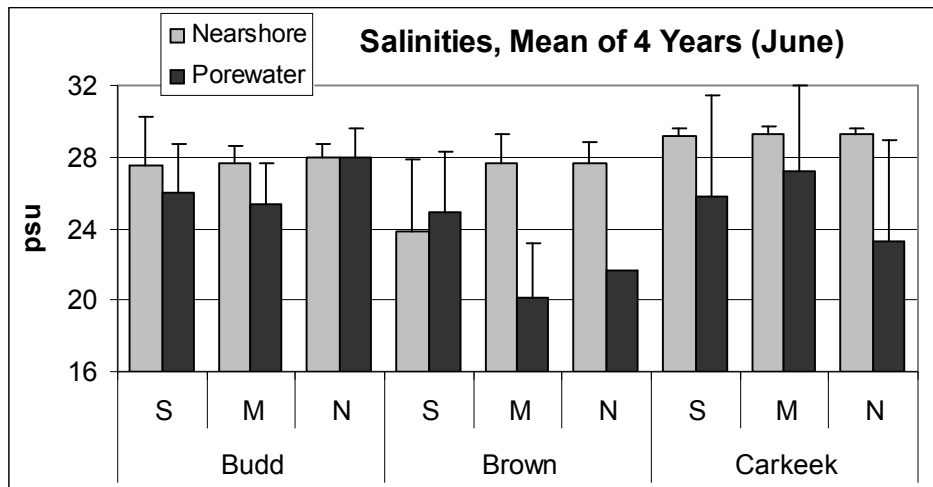


Figure 6.

