Long-term and Seasonal Trends of Shoreline Biota in Puget Sound: Analyses of Data Collected through 2006

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Executive Summary

The SCALE monitoring program now has an excellent long-term database at a number of sites that defines the envelope for "normal" early-summer biological conditions in relatively undisturbed pebble-sand beaches. In the current project we focused on two issues: continued documentation of spatial and interannual patterns, and an exploration of variation among seasons.

Communities at the sites for which we have long-term data have remained predictably different through time (i.e. in multivariate analyses, the 'clouds' of points representing the biota at each site are distinct). Anomalies in the data continue to appear when individual beaches are impacted by sand. There is apparent stability through time at all of our regularly sampled beaches – i.e. our data suggest there have been neither gradual losses of biota because of anthropogenic effects, or gradual improvements following some past stressor. For sites sampled more than 3-4 times (those for which we can describe normal variation), if some event occurred that caused either rapid mortality or gradual loss of shoreline organisms, our data would detect this as a movement of the multivariate "point" outside of its normal cloud of points from previous years. Such long-term data (encompassing at least 3 years, although these years do not need to be contiguous) are thus invaluable for demarcating what is 'normal' interannual variation.

Univariate analyses of various parameters from these beaches and times do not show either the spatial or temporal patterns as clearly as the multivariate analyses. Graphs of species richness through time illustrate the overall spatial pattern of consistently higher richness at the northern sites relative to the southern sites, and suggest that richness is a moderately stable parameter. Analyses of the abundance and diversity of juvenile clams also show this north-south gradient, although not as clearly. The clam data suggest that recruitment or early survival of clams is fairly random among beaches and years. The data do, however, suggest a clear separation of South sound from the rest of the sound in terms of survival of recruited clams, a result analyzed in more detail in a parallel Sea Grant study (Dethier et al. in prep.). Juvenile clam abundances are also reasonably good predictors of the local abundance of adult clams. At this time, the parameters of species richness and clam abundance may be the best ones for communicating community stability and spatial patterns to non-technical groups. Ultimately, the information-rich multivariate analyses will be the most able to illustrate change due to external effects, as is visible in the data from the anomalous Point Wells beaches which presumably have suffered from pollution stressors in the past.

To begin to ascertain whether some of our apparent inter-annual differences are simply aliased seasonal differences, i.e. whether encountering different communities in different years could be caused by small shifts in the seasonal patterns, we sampled several sites at a higher frequency. This sampling protocol also filled a knowledge gap for these beaches about the degree of seasonal variation in abundance and diversity of the flora and fauna. Sampling of the biota at Edmonds and Case in February, April, June, and August showed that the communities remain fairly consistent through the year. Some taxa change seasonally in a predictable fashion, especially winter-appearing seaweeds, and mobile animals that require more stable (summertime) surface cobbles. Interestingly, the most common infaunal organisms were very similar in abundance among seasons. Overall, the results suggest that our monitoring program is at little risk for misinterpreting seasonal changes as interannual trends. The February and April samples fell outside the "cloud" of normal summertime samples for the biota of these beaches, showing that there is seasonal change. However, there is not an abrupt seasonal shift either just before or just after our standard mid-June sampling period that could be misinterpreted as an interannual change when it was just a seasonal change being 'caught' at different stages.

Variation noted in beach porewater conditions (salinity and temperature) among seasons and among beaches suggests that such data may be useful in understanding variation in biota among sites. We found that the south-sound beaches showed different patterns from the north-sound ones, e.g. in the degree of summer warming and the apparent influence of groundwater on beach porewater salinity. These patterns suggest that future effects of global warming on beach biota could either be direct, e.g. through increased stress or mortality from higher air temperatures on surface-dwelling organisms, or indirect, e.g. from changes in rainfall or snowpack making the north-sound physical conditions more like those in south-sound. More work needs to be done quantifying groundwater conditions, how they affect beach porewater, and how this in turns affects the biota.

Objectives

Ongoing monitoring of the shoreline biota of Puget Sound continues to provide data on the envelope of normal year-to-year variation in relatively undisturbed pebblesand beaches. In the current project we focused on two issues: continued documentation of spatial and interannual patterns, and an exploration of variation among seasons.

A concern with any low-frequency (e.g., annual) ecological monitoring program is the confounding of long-term changes or trends with short-term, higher-frequency events such as regular seasonal changes (Alden et al. 1997). For instance, if sampling occurs regularly at a time near a major seasonal recruitment event, changing the sampling date slightly might 'hit' just before vs. just after this event, giving the appearance of a significant change from one year to the next when in fact it was just the time of sampling. This phenomenon of misinterpretation of a recorded signal due to under-sampling is known as 'aliasing'. To begin to ascertain whether some of our apparent inter-annual differences are simply aliased seasonal differences, we sampled several sites at a higher frequency (4 times per year rather than once per year) and analyzed the relative differences. This sampling protocol also filled a knowledge gap for these beaches about the degree of seasonal variation in abundance and diversity of the flora and fauna.

Methods

Basic sampling and analytical methods have been described in previous reports (Dethier and Schoch 2000). For our continuing documentation of interannual trends, in

this project we sampled different sets of beaches in 2005 and 2006. In 2005 in our regular June sampling period, we sampled the 3 sites being studied intensively in a parallel Sea Grant-funded project (Budd, Brown, and Carkeek) plus 3 'matched' sites that were spatially close to the intensive sites (Case, Normandy, and West respectively). In addition, we sampled beaches at Possession, to add to the continuous dataset from that diverse site. Four of these sites (Budd, Brown, Carkeek, and Possession) were also sampled in June 2006. In 2006 we focused most of our sampling on quantifying seasonal change at two sites (3 beaches each): Edmonds and Case (beaches 15-17). Each of these sites had been sampled in previous years. We chose Edmonds as representing a northern, high-diversity site, and Case as a southern, lower-diversity site. For each of these 6 beaches we sampled the biota using our standard SCALE methods (quantifying epibiota and infauna) in February, April, June, and August. The only variation from our normal methods is that we staked the ends of the transects to ensure that we returned to the same tidal height each time, and on each date we shifted our sampling locations along the transect so that we were not resampling areas disturbed on the previous date.

Results

Spatial and Interannual Patterns

Figure 1 illustrates a multidimensional scaling (MDS) analysis of the biota at the four sites where we have the longest-term data. The sites show consistent separation across all years (i.e. the 'clouds' of points representing the biota at each site are distinct); the communities on these beaches have remained predictably different through time.



Figure 1. MDS graph of the surface and infaunal biota at 4 sites (3 beaches each). Each point represents the biota at one beach; points closer together indicate more similar biota in terms of species and abundances.

Figure 2 shows the same data for Budd Inlet by itself, to more clearly illustrate a general pattern of the points tending to 'wander' from 1998-2002 at the upper left down to 2004-6 at the bottom. This suggests that the communities have changed somewhat at each beach over time, but that most beaches have changed in a similar manner. Analyses of the species driving these changes (with the SIMPER subroutine in Primer) suggest that the differences are not caused by dramatic appearances or disappearances, but by abundances of common species changing somewhat with time. A number of algal species were seen mostly in the earlier period (*Punctaria, Gracilaria, Scytosiphon, Porphyra*), others later (*Caulacanthus*). Hermit crabs and *Crepidula* spp. were more abundant in the later years. No one species ever contributed more than 6% of the difference between years, illustrating the absence of large, single-species driven changes. It is perhaps significant that in 1999-2002, our sampling at Budd was done in May, whereas for 2004-6 it was always done in June. The 1998 sampling was also in June, and the points for this year are highly variable. It will be very interesting to continue to monitor Budd to see if these subtle changes continue. Species richness (see Figure 7) has not shown unidirectional increases or decreases over these years.



Figure 2. MDS graph of the surface and infaunal biota at Budd Inlet (3 beaches shown separately).

Figure 3 illustrates 2-3 years' worth of data for the three sites used for the Sea Grant study and their 'matched' sites. Substantial year-to-year continuity in biota within a site is again visible, as well as distinct separation among sites, with the southern sites to the left and the northern sites to the right. Note, however, that the 'matched' sites are not very matched in terms of the biota – Budd and Case are especially different, Brown and Normandy slightly less so, and West and Carkeek are most similar. This illustrates, as noted in earlier reports, how hard it is to find "replicate" sites or even replicate beaches within a site.





Figure 3 also shows two points that are distinct outliers from the rest of the data for that site (Normandy pink 2004 and 2005 points at the top center of the figure). These data represent the communities at Normandy South, which were very different from Normandy Mid and North in both years. One major biological difference was that in 2004, Normandy South had no juvenile clams, while Mid and North had quite a few. Normandy South had an enormous amount of sand in both years when this parameter was quantified, especially in 2005 (Figure 4). In contrast, Normandy Mid seemed to have a sand mass that shifted away between 2004 and 2005. Limited substrate data from 1999 (from photographs) suggest that at that time, Normandy North had the largest quantity of sand (an average of 75%, versus 25% at Mid and 15% at South). These data suggest that the 3 beaches at this site are characterized by substrate instability, with high alongshore or across-shore sand movement.



Figure 4. Percent cover of sand at the surface of the quadrats (average value from 10 quadrats per beach) at the Normandy beaches in two years.

The anomalous nature of the substrate at the Normandy beaches can be seen when compared to all the other beaches sampled in 2005 (Figure 5). Overall, there is a very clear pattern of more sand in the southern beaches and more cobble to the north, but Normandy South (and to a lesser extent North) have far more sand (and less cobble) than expected from their location. Previous reports (e.g. Dethier 2005) have detailed the correlation between quantity of surface sand and biota, so it is not unexpected that the biota at Normandy South is different than that at its 'replicate' beaches (Fig. 3).



Figure 5. Percent covers of surface sand and cobble in the years and beaches where both these parameters were measured. All beaches are shown from south (left) to north (right) (e.g. Normandy South is the left-most of the 3 Normandy bars). Normandy, West, and Edmonds were not sampled in 2006.

Although none of our data suggest that there have been substantial changes through time in the biota of the beaches studied, one other analysis leads us to believe that we would be able to detect a perturbation (or recovery) in our data if one existed. A reanalysis of our broadest geographic sampling to date, in 1999, illustrates the anomalous nature of the biota in several beaches, including at Point Wells (Figure 6). These beaches (blue triangles labeled 'North') fall outside the 'cloud' of points from adjacent beaches (Edmonds, Carkeek, and West are closest), even though in general, biota are very similar in geographically close sites. We expect that similarly, any beach that suffered a perturbation such as an oil spill or a change in substrate type would move well outside a cloud of points from nearby beaches and *times*; this predictability of biota in the absence of external change is the basic tenet of the SCALE system. Examination of the species that drove this 'movement' would then allow us to assess the nature of the change, e.g. a loss of pollution-sensitive amphipods, an increase in deposit feeders, etc.



Figure 6. MDS plot of the 1999 SCALE data from sites in central and northern Puget Sound. Site names in the key are shown from south to north.

Univariate analyses of various parameters from these beaches and times do not show either the spatial or temporal patterns as clearly as the multivariate graphs. Figure 7 illustrates trends in species richness per site. The overall spatial pattern of consistently higher richness at the northern sites relative to the southern sites is clearly visible. Most sites appear to have relatively stable species richness through time, although a longer data series will show patterns more clearly. The variability at Possession is interesting, especially the seemingly regular pattern of alternating high and low richness in adjacent years. The very high richness at Possession in 2005 is indicative of the sampling error that year when we sampled lower on the shore than usual, where richness is expected to be higher. Species richness was surprisingly low at Normandy in 1999, presumably related to sand inundation. On that date, Normandy Mid had higher richness (40 taxa) than either South or North (32 and 33 taxa, respectively).



Figure 7. Species richness (average among the 3 beaches per site) at 8 sites over 3-8 years. Site names in the key are shown from North to South.

Two parameters that closely follow species richness in terms of north-sound patterns are the abundance and diversity of juvenile clams (<1.5 cm) in the cores. Figures 8-10 show the data for juvenile clams over time; the numbers and richness are greater in the northern sites than in the southern sites, and are moderately consistent within a site over time. Possession had fewer juvenile clam individuals than expected given its northernmost position, but did have many species of clams. Budd and Case had extremely few juvenile clams at any time. Numbers fluctuated most widely at the northern sites, especially at Carkeek where there was a large recruitment of clams in 2000 and at West in 2005 (in each case of a variety of species, varying among beaches).



Figure 8. Total number of juvenile clams per core at 8 sites over time.

Interestingly, Brown had more species than expected both from its north-south location and for its total clam abundance, although the number of species dropped steadily from 2001 onwards (Figure 9). Normandy also had more species than expected given its low numbers and its relatively southern location. The richness data suggest a clear separation of South sound from the rest of the sound in terms of survival of recruited clams, a result analyzed in more detail in the Sea Grant study. The richness pattern at Brown (the Central site closest to South sound) suggests that a "set" of diverse

juvenile clams settled and survived sometime just prior to the 2001 sampling, but that the South sound stressors (probably high temperature and low salinity) have caused a gradual reduction since then.



Figure 9. Average species richness of juvenile clams at 8 sites over time. One s.d. is shown for each average.

Figure 10 shows the Shannon-Weaver diversity measure, which takes into account both the number of species and the evenness of distribution of abundances among those species; a higher value of H indicates that individuals are more evenly spread among more species. For this measure the north-south pattern is less clear except for the abrupt discontinuity between all the central and northern locations and the south-sound locations. No consistent differences exist through time among the more northern beaches. These Figures suggest that diversity and abundance of juvenile clams may be a useful proxy for spatial and temporal patterns in the overall biota.



Figure 10. Shannon-Weaver Diversity (H') of clams at 8 sites over time.

The potential utility of counts of juvenile clams can be seen in two other analyses, comparing these counts with data for adult clams (which are recreationally harvested, in many cases). There is a strong positive correlation between numbers of juvenile and adult clams per beach (Fig. 11); while this may not seem surprising, it does indicate that there is no major site-specific mortality that occurs between juvenile and adult stages. Thus counting juvenile clams (which are easier to dig, because they live close to the sediment surface) can serve as a proxy for adult clams. Similarly, in the limited locations for which we have biomass data, there is also a positive correlation between juvenile clam number and adult clam biomass (Fig. 12).



Figure 11. Correlation between numbers of juvenile and numbers of adult clams per core; data from 7 sites and 6 years, pooled.



Figure 12. Correlation between numbers of juvenile clams and the biomass of adults at a beach; data from Budd, Brown, and Carkeek (9 beaches) in 2005.

Multivariate statistics cannot be run on the juvenile clam dataset for all sites and years because it is very zero-rich, but Figure 13 shows an analysis of three sites with relatively large and consistent clam numbers. There is a rather vague clustering by sites, i.e. there is some similarity within a site among years. When data are recoded by year (not shown), all the colors are interspersed, i.e. there is no within-year consistency in recruitment across sites (such as a large set of *Tresus* at all sites in a given year). This suggests a fair degree of randomness in recruitment or early survival of clams among

beaches and years. However, this figure does not include the sites (e.g. all the southsound sites) where juvenile clam numbers were consistently very low.



Figure 13. MDS plot of juvenile clams (only) over 4 years at 3 sites.

Seasonal Patterns: Aliasing

Sampling of the biota at Edmonds and Case in February, April, June, and August showed that the communities remain fairly consistent through the year, although some taxa change seasonally in a predictable fashion. Figure 14 illustrates that beach biota at the Edmonds and Case sites remain distinct from each other across all the sampling dates (Case points on the left, Edmonds on the right), as expected for these sites at the far ends of the Puget Sound north-south gradient. Case sites are far more variable within and among seasons than Edmonds. Figure 14 also illustrates that in general, winter and spring samples from a given beach are quite similar, and summer and fall (really late summer: August) are quite similar, but summer and winter are distinct. Species that were consistently more abundant in the February and April samples were diatoms, hippolytid shrimp, the small snail *Alia*, and the ephemeral algae *Scytosiphon* and *Petalonia*. Species more abundant in June and August were ulvoids, amphipods, juvenile sand dollars, barnacles, and *Lacuna*.



Figure 14. MDS plot illustrating community change among years and seasons; data from 2004 and 2005 are from June only; data from 2006 include Winter (Feb), Spring (April), Summer (June), and Fall (August). In this graph, all the Case sites are in the left cluster, all the Edmonds sites in the right cluster.

Figure 15 shows some of the seasonal patterns more clearly, with the points relabeled to show individual beaches. Case 17, for example, had similar biota to the other Case beaches in the summer and fall, but its winter and spring biota (lower left corner) were different both from the other seasons and from the other beaches. This beach is sandier than the other Case beaches and always had fewer of some taxa (surface fauna

such as *Alia*, crabs, and amphipods) and more of others (e.g. sand dollars, the anemone *Edwardsia*). The seasonal differences at Case 17 were driven by some taxa that were more abundant in the winter and spring (sabellids, adult sand dollars, *Littorina*) and some that were more abundant in the summer (barnacles, amphipods, ulvoids, *Hemigrapsus*, *Pagurus*). The relatively sparse surface cobbles at this beach are probably more stable in the late spring and summer, allowing more surface flora and fauna to develop then. Interestingly, the most common infaunal organisms (the polychaetes *Notomastus* and *Hemipodus*) were very similar in abundance among seasons.



Figure 15. The same data as shown in Figure 14, but with the points recoded to illustrate the individual beaches.

Figure 16 illustrates longer-term data from all the sites sampled in 2006, with the relatively few non-summer samples shown in a different color. It is easy to see that while there is much variation between beaches and years in the summer (wide scatter of green points), as expected from these geographically separate sites, the winter and spring samples stand out as different. Again, the fall (red: August) samples are most similar to all the summer (green: June) samples.



Figure 16. MDS of all sites sampled in 2006, with data stretching back to 1999 in some sites. South-sound sites are generally on the left, north-central sites on the right.

Figure 17 illustrates the univariate parameter of species richness across the seasons at the 6 beaches sampled seasonally. As shown previously, Case beaches are much less species-rich than Edmonds beaches. The sites differed somewhat in their seasonal patterns. Richness at Case was consistently lowest in August, perhaps due to the very high summertime air and water temperatures stressing the organisms there. It was highest in either April or June. At Edmonds, richness was consistently lowest in February; it may be that at these more wave-exposed beaches, the disturbance caused by winter storms decreases diversity. Diversity was highest in June. For all sites, this high June diversity may represent a period when some new organisms have recruited (following winter disturbances and spring reproduction) but few have yet been killed off by summer physical stresses. This result suggests that June represents a good sampling period for regular SCALE monitoring.



Figure 17. Species richness at each beach during each of the four sampling periods in 2006.

Figures 18A-E illustrate seasonal variation in a variety of physical parameters at the 6 beaches. Amount of surface cobble (Fig. 18A) was fairly stable across the seasons; note, however, that there is much more cobble at Edmonds (some of the most-cobbly sites of all the monitoring locations) and that the three beaches at Case vary amongst themselves (with Case 17, as mentioned above, being the most sandy and least rocky). Note that the variation within a site among dates may simply be a sampling artifact, since these were not fixed quadrats.



Figure 18A. Percent cover of surface cobble at 4 sampling dates.

Open-water salinity (measured nearshore, from the boat) was fairly consistent both among sites and seasons but showed some interesting variation (Fig. 18B). Salinity at the Case sites was always lowest in February, presumably driven by fall and winter rains. At Edmonds, however, salinity was lowest in April, perhaps driven more by snowmelt from the Cascades. Edmonds North, closest to the large freshwater influx from the Whidbey Basin, had the lowest springtime salinities. Salinities were highest at all beaches in August.



Figure 18B. Nearshore salinity measured at 4 sampling dates.

Porewater salinity on the beach, however, was much more variable both among beaches and among dates (Figure 18C). As expected, lowest values were always in February and highest were in August. The low wintertime values (down to 22 psu, as opposed to a nearshore low of 26) probably reflect direct percolation of rainwater down from the land. Case 17 had consistently lower beach salinities than the other Case sites, perhaps reflecting a greater influence of terrestrial runoff; Case 16 and 15 are both on islands (Stretch and Reach) with little watershed area to affect groundwater conditions. These low salinities (along with the high sand content) could contribute to the anomalous nature of the biota of the Case 17 transect.



Figure 18C. Porewater salinity measured in holes dug on the beach at 4 sampling dates.

Nearshore and porewater temperatures showed similar variation in land vs. sea effects. Open water temperatures (Figs. 18D) show a predictable seasonal pattern, with low winter temperatures (quite consistent between south and central Sound) and higher summer temperatures. The south-sound beaches had much higher summer temperatures than at Edmonds, however, with a winter-summer range of about 11° C versus 6°. Case 15, which is the most 'enclosed' of the Case beaches (i.e. nearest the head of the bay) had the highest summer temperatures.



Figure 18D. Nearshore temperature measured at 4 sampling dates.

Temperatures in the beach porewater (Fig. 18E) showed some subtle differences among regions. Case porewater temperatures very closely tracked the open-water temperatures through the year. Edmonds porewater, however, was cooler than the ocean (and than Case) in the winter, and warmer than the ocean in the summer. These differences may again reflect the greater influence of the adjacent landmasses at Edmonds; the land and thus the groundwater heat up in the summer, especially in this urban setting, and this warmed water then percolates down through beach sediments. Our more detailed Tidbit data from Budd, Brown, and Carkeek similarly indicate a tendency for beach porewater to be warmer in the summer and cooler in the winter than the nearshore water.



Figure 18E. Porewater temperature measured in holes dug on the beach at 4 sampling dates.

Discussion

Spatial and Interannual Patterns: The Search for Indicators Continues

The SCALE monitoring program now has an excellent long-term database at a number of sites that defines the envelope for "normal" biological conditions for earlysummer periods. The search for "trends", or indicators thereof, remains elusive because the biota appear to be relatively stable at our sampled beaches -i.e. there does not appear to be either gradual loss of biota because of anthropogenic effects, or gradual improvement following some past stressor. We clearly see interannual variation; and for sites sampled more than 3-4 times, if some event occurred that caused either rapid mortality or gradual loss of shoreline organisms, our data would detect this as a movement of the multivariate "point" outside of its normal "cloud" of points from previous years. An extensive literature on pollution gradients and other anthropogenic impacts shows that multivariate plots of biotic communities are very effective at "detecting" and illustrating these effects (Clarke and Warwick 2001). The only simplerto-communicate (non-multivariate) 'indicators' that might show such a change in our data are 1) species richness, and 2) abundance or diversity of juvenile clams. Both of these parameters also show year to year variation, and neither is likely to be as sensitive as the multivariate analyses since they so greatly condense or restrict community-level information. It is possible that a significant change in the community could occur that would affect neither clam recruitment nor overall richness (e.g. some species might disappear but new ones appear, leaving the overall richness per beach the same). At this time, however, these parameters appear to be the best ones for communicating relative community stability to non-technical groups.

Seasonality vs. Interannual Patterns

Our results from the seasonal sampling effort at 2 sets of beaches suggest that our monitoring program is at little risk for misinterpreting seasonal changes as interannual trends. Our February and April samples fell outside the "cloud" of normal summertime samples for the biota of these beaches, showing that there is seasonal change in abundances of many species. A few species appeared exclusively only in the winter or only in the summer. However, the relatively small changes in richness (Fig. 17) between April, June, and August (and the small shifts in biotic communities between June and August, Figure 15), suggest that our normal June sampling is unlikely to encounter significantly different communities in different years caused by small shifts in the seasonal patterns– i.e. there is not an abrupt seasonal shift either just before or just after the mid-June sampling that could be misinterpreted as an interannual change when it was just a seasonal change being 'caught' at different stages.

We also found interesting seasonal variation in nearshore and beach temperatures and salinities, with the south-sound beaches showing different patterns from the northsound ones, e.g. in the degree of summer warming or the apparent impacts of groundwater on beach porewater salinity. These patterns suggest that possible future effects of global warming on beach biota could either be direct, e.g. increased stress or mortality from higher air temperatures on surface-dwelling organisms, or indirect, e.g. changes in rainfall or snowpack making the north-sound physical conditions more like those in south-sound. More work needs to be done quantifying groundwater conditions, how they affect beach porewater, and how this in turns affects the biota.

Seasonal changes in benthic infauna (either intertidal or subtidal) have been documented in a number of other systems. In the North Sea, subtidal benthic communities are very seasonal; MDS plots show communities varying highly through the year but returning to roughly the same condition each spring (Reiss and Kroncke 2005) (we will be able to test for such a cyclical seasonal pattern in our data once the 2007 SCALE samples are analyzed). The changes in the North Sea seem to be driven in part by predictable springtime recruitment events, but also by an annual increase in food settling to the bottom after spring phytoplankton blooms. Sites differed in their extent of seasonality, but these differences could be due to variation in recruitment, in food supply, or in predation on recruits. Drivers of seasonal patterns in other systems include summertime stressors such as high temperatures or low-oxygen events; for instance, in Japan, an estuarine intertidal sandflat suffers mass mortalities in autumn, apparently due to algal decay at the end of the summer (Magni et al. 2006). Noren and Lindegarth (2005) found that some seasonal changes were consistent among sites on the Swedish coast and were caused by mortality or emigration associated with cold winter temperatures, whereas others were inconsistent, for instance varying with levels of local reproduction.

Such interactions between locations and seasons may make it difficult to identify regular seasonal patterns and their causes. This highlights a problem with any sampling regime that attempts to define seasonal patterns; predictable seasonal changes may be obscured by even shorter-term variability (Noren and Lindegarth 2005). To study the issue of seasonality thoroughly, it is necessary to sample extensively *within* seasons (Alden et al. 1997). If within-season variability is low, then samples taken at relatively consistent times within a season should not run much risk of confounding seasonal biotic changes with interannual changes. Although we did not sample within seasons in our study, the generally low degree of variation among samples taken around our usual June period (especially between June and August) suggests that we run little risk of misinterpreting seasonal trends as annual trends.

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