

Depth Distribution of Eelgrass in Greater Puget Sound

October 22, 2015



**PUGET SOUND ECOSYSTEM
MONITORING PROGRAM**



WASHINGTON STATE DEPARTMENT OF
Natural Resources
Peter Goldmark - Commissioner of Public Lands

The Submerged Vegetation Monitoring Program is a component of the Puget Sound Ecosystem Monitoring Program (PSEMP) (<http://sites.google.com/site/pugetsoundmonitoring/>).

Cover Photo: Eelgrass (*Zostera marina*) and kelp in Padilla Bay, WA, photo by Michael Hannam.

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The following document identifies the depth distribution of eelgrass (*Zostera marina*) in greater Puget Sound, as specified in the 2014 interim targets for the Puget Sound Partnership's Eelgrass Vital Sign.

Several people played a critical role in the video data collection and post-processing for the work summarized in this report including Kiri Kreamer, Dolores Sare, Andrew Ryan, Jessica Stowe, and Rose Whitson.

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Executive Summary

The Washington State Department of Natural Resources (DNR) manages 2.6 million acres of state-owned aquatic lands for the benefit of current and future citizens of Washington State. DNR's stewardship responsibilities include protection of native seagrasses such as eelgrass (*Zostera marina*) and surfgrass (*Phyllospadix spp.*), an important nearshore habitat in greater Puget Sound. DNR monitors the status and trends of native seagrass abundance and depth distribution throughout greater Puget Sound using underwater videography. Because of its sensitivity to reduced light availability and physical disturbance, the depth distribution of native seagrass may be a useful indicator of water quality degradation and anthropogenic disturbance. For this reason, the Puget Sound Partnership uses depth distribution, along with other measures, to evaluate the condition of native seagrass as one of their 21 Vital Signs. Here we examine the depth distribution of eelgrass, the predominant seagrass in the greater Puget Sound, during the period of 2004-2012, updating and expanding a previous study conducted in 2005.

Key Findings:

1. Eelgrass is found in PS between + 1.4 m to – 12.0 m (relative to MLLW). Approximately 62% of all the eelgrass in the greater Puget Sound is subtidal (deeper than -1 m relative to MLLW). This suggests that a large proportion of this resource is found on State-Owned Aquatic Land, underscoring the importance of continued stewardship activities by DNR.
2. The optimal depth range for *Zostera marina* appears to be between 0 and 2 m below MLLW in most of greater Puget Sound, based on frequency of occurrence by depth.
3. The depth distribution of eelgrass varies among regions and habitat types.
 - a) Near the San Juan Islands and the Strait of Juan de Fuca, eelgrass extends to deeper depths, but it does not reach as shallow as in other regions.
 - b) Eelgrass extends to deeper depths at fringe sites than at flats sites, but it extends shallower towards land at flats sites than at fringe sites.
4. Variability in depth limits among sites was greater than variability among regions and among years.
 - a) Owing to its glacial past, Puget Sound shoreline exhibits high geomorphic variability, which may be a considerable factor in eelgrass depth distribution. Other factors may include local differences in water quality, sediment resuspension, mixing, river plumes and/or shoreline modification.
 - b) The fine scale differences among sites highlight some of the challenges in managing and conserving eelgrass in greater Puget Sound. High site-to-site variability suggests the need for site-scale management. This does not preclude the need for basin-scale management, but basin-scale trends will be more difficult to detect amidst high site-scale variability.



1 Introduction

1.1 The SVMP Program

The Washington State Department of Natural Resources (DNR) stewards 2.6 million acres of state-owned aquatic land. As part of its stewardship responsibilities, DNR monitors native seagrasses such as eelgrass (*Zostera marina*) and surfgrass (*Phyllospadix spp.*) across the nearshore of greater Puget Sound. The monitoring data is used to characterize the status of native seagrass and is one of 21 vital signs used by the Puget Sound Partnership to track progress in the restoration and recovery of Puget Sound (PSP 2014). The Partnership defined the 2020 target for the Eelgrass Vital Sign to be a 20% increase in total areal extent. It also defined a series of interim targets for extent and depth distribution, which are available for download at <http://www.psp.wa.gov/downloads/interimtargets/Eelgrass%20Interim%20Targets%20-%20FINAL.pdf>

1.2 Data Access

The SVMP monitoring database and a User Manual are available through the DNR GIS data download web page. The data are also accessible through an online data viewer. The User Manual (NHP 2014) includes a more detailed description of project methods than are included in this report.

- Data Download: <https://fortress.wa.gov/dnr/adminsa/DataWeb/dmmatrix.html>
- User Manual: http://file.dnr.wa.gov/publications/aqr_nrsh_svmv_database_user_manual.pdf
- Data viewer: <http://www.dnr.wa.gov/programs-and-services/aquatics/aquatic-science/puget-sound-eelgrass-monitoring-data-viewer>

1.3 Background

Eelgrass (*Zostera marina*) is the dominant native seagrass in Puget Sound. It provides critical ecosystem services, offering spawning grounds for Pacific herring (*Clupea harengus pallasi*), outmigrating corridors for juvenile salmon (*Oncorhynchus spp.*) (Phillips, 1984; Simenstad, 1994), and important feeding and foraging habitats for waterbirds such as the black brant (*Branta bernicla*) (Wilson & Atkinson, 1995) and great blue heron (*Ardea herodias*) (Butler 1995). Additionally, eelgrass provides valued hunting grounds and ceremonial foods for Native Americans and First Nation People in the Pacific Northwest (Felger & Moser, 1973; Kuhnlein & Turner, 1991; Suttles, 1995; Wyllie-Echeverria & Ackerman, 2003). Eelgrass responds quickly to anthropogenic stressors such as physical disturbance, and reduction in water quality due to excessive input of nutrients and organic matter. This makes it an effective indicator of habitat condition (Dennison et al., 1993; Kenworthy, Wyllie-Echeverria, Coles, Pergent, & Pergent-Martini, 2006; Lee,

Short, & Burdick, 2004; R. J. Orth, Carruthers, Dennison, & Duarte, 2006; Short & Burdick, 1996).

Because of photosynthetic light requirements, seagrasses are sensitive to reductions in light availability. Worldwide, the deep extent of seagrass beds is well-predicted by water clarity (Duarte, 1991). The deep extent of eelgrass beds in a Danish fjord system has been closely linked to water clarity (Krause-Jensen, Pedersen, & Jensen, 2003), and eelgrass transplant survival in the Chesapeake Bay has been reduced by turbidity plumes (Moore, Wetzel, & Orth, 1997). As such, reductions in the deep edge of eelgrass beds may be a sensitive early indicator of water quality and nearshore disturbance.

Koch (2001) suggested wave energy, ice scour, and tidal exposure as primary limits to the shallow extents of seagrasses. Greater tidal amplitudes restrict the depth range within which seagrasses can survive. As a result of their highly reduced cuticles (Larkum, Orth, & Duarte, 2006), seagrasses tend to be acutely susceptible to desiccation, and so tend to be limited to depths that are rarely exposed by a low tide (Boese, Robbins, & Thursby, 2005). In water bodies such as the Puget Sound, which have large tidal ranges but are relatively protected from oceanic swell, desiccation is thought to be a common limit to the shallow extent of seagrass growth (Mumford, 2007).

1.4 Objectives

In this report, we update a previous analysis by Selleck, Berry, & Dowty (2005), on the depth distribution of *Zostera marina* in greater Puget Sound. We contrast different habitat types in 5 regions throughout the sound, and quantify variability in the shallow and deep extent of *Zostera marina* beds within and between sites. This report fulfills one of the 2014 interim targets for the Eelgrass Vital Sign (identification of the depth distribution of eelgrass in Puget Sound), and will be used as a baseline for testing interim targets for 2016 and 2018.



2 Methods

2.1 Data Sources

This investigation utilized a seagrass monitoring dataset from the Washington Department of Natural Resources' (DNR) Submerged Vegetation Monitoring Program (SVMP). This program monitors seagrass cover in the greater Puget Sound, including the Strait of Juan de Fuca and the San Juan Archipelago. The study area is divided into 5 regions based on bathymetry and oceanographic characteristics: Central Puget Sound (CPS), North Puget Sound (NPS), Saratoga Whidbey basin (SWH), Hood Canal (HDC), and San Juan Islands/Strait of Juan de Fuca (SJS) (Berry et al., 2003). Shoreline segments were classified into two habitat types named flats and fringe. Flats are characterized by broad shallow slopes, typically in embayments and river deltas. Fringe sites are characterized by steeper slopes.

Randomly selected sites are surveyed with shore-normal line transects, utilizing GPS-referenced underwater video and sonar. Sites consist of either a 1 km stretch of shoreline for fringe sites, or a portion of an embayment or delta for flats sites. On average, 12-15 transects are surveyed at each site, and 70 or more sites are surveyed each year. With the exception of 9 core sites that are monitored every year, 20% of sites in the sample are replaced annually. A technician analyzes the video producing a presence/absence measurement for each second of data. The compiled data include presence/absence data for native seagrass (*Z. marina* and *Phyllospadix spp.*), differentially corrected GPS coordinates, and a tide-corrected depth measurement relative to Mean Lower Low Water (MLLW). In this report we examined data for *Z. marina* only.

2.2 Depth Distribution of Eelgrass

We used soundwide survey data from 2004 to 2012. We focus on depth data collected from 2004 on because equipment upgrades yielded greater accuracy after 2003. For each sampled site, only the most recent year of data was selected for analysis. *Z. marina* observations were binned according to their depth relative to MLLW in 0.5 m bins. We also binned all video observations, regardless of eelgrass presence. The resulting data consisted of counts of seconds of video within each depth bin, for each site. These data were extrapolated to estimate the areal coverage of *Z. marina* in each depth bin throughout the SVMP study area (Appendix 1).

2.3 Conversion from Observation Scale to Area Scale

We converted observation-count histograms into areal estimates in order to construct regional and sound-wide histograms where site-level frequencies are properly weighted according to site area. Our method follows that of (Selleck et al., 2005). Conversion starts

on a per-site basis, and then site-level area bins are combined to regional and soundwide area bins.

2.3.1 Site-Scale Conversion

For each site, the number of eelgrass observations in each depth bin was divided by the total number of eelgrass observations at the site. This fraction was multiplied by the estimated eelgrass area at the site to estimate the area of eelgrass in each depth bin at the site. In other words, for each site, we estimated the area of *Z. marina* in each depth bin, using the formula:

$$a_{jk} = A_j \frac{c_{jk}}{\sum_{k=1}^n c_{jk}}$$

where a_{jk} is *Z. marina* area in each histogram bin (k) at site (j), c_{jk} is the count of observations per bin, and A_j is site area.

2.3.2 Regional Summary

Per-bin area estimates from sites were combined into regional and soundwide estimates using a weighting scheme that accounts for the fraction of potential habitat surveyed within each strata (Core, Flats, Wide Fringe, and Narrow Fringe). For each region and strata combination, we summed the sampled eelgrass area (a) in each depth bin (k):

$$a_k = \sum_{j=1}^n a_{jk}$$

These sampled eelgrass areas were extrapolated to estimate the total area in each depth bin within a stratum (s) and region (r). To do this, we multiplied the sampled eelgrass area by the inverse of the sampling fraction, a ratio that we call the expansion factor (E). In other words, the expansion factor is the ratio of the population size to the sample size, or in our case, the ratio of total area to sampled area in the region and stratum.

$$E_{sr} = \frac{P_{sr}}{p_{sr}}$$

Where P_{sr} is the sum of all SVMP site polygons areas within the region and stratum, and p_{sr} is the sum of the areas of sampled SVMP site polygons within the region and stratum.

Finally, we sum the extrapolated depth-bin (k) *Z. marina* areas within region (r), and habitat types (h):

$$A_{krh} = \sum_{s=1}^5 A_{krhs}$$

2.4 Proportional Occupancy by *Z. marina*

Areal coverage of eelgrass across a depth gradient is influenced both by the growth and survival of eelgrass across the depth gradient and the area of seafloor across the depth gradient. To better understand the effect of depth on eelgrass in the study area, we attempted to decouple these two components of eelgrass depth distribution. To do so, we

examined the ratio of *Z. marina* observations to total observations across depth bins to provide an estimate of the probability of *Z. marina* occurrence across depth.

For every depth bin (k) at each site (j) in each year (y), we divided the number of *Z. marina* observations (c) by the number of total observations (t):

$$P_{jky} = \frac{c_{jky}}{t_{jky}}$$

We assumed that transects covered the depth range at which *Z. marina* grew at a site, so if there were zero observations in a depth bin at a site, it was assigned a zero-value as though *Z. marina* was observed to be absent. We then averaged these proportions across sites, within regions (r), years, and habitat types (h):

$$P_{kyrh} = \frac{\sum_{j=1}^{N_{kyrh}} P_{jkyrh}}{N_{kyrh}}$$

Because SVMP sampling sometimes excludes shoreline segments within sites that are devoid of seagrass, such areas are not represented in the estimated probabilities.

2.5 Depth Limits

Also using soundwide survey data from SVMP surveys from 2004 to 2012, we calculated the 10th and 90th percentile depth at which eelgrass was observed along each transect surveyed within the scope of our study. Subsequently we refer to the 10th percentile depth as 'shallow extent', and the 90th percentile depth as 'deep extent'. The difference between the 90th and 10th percentile depth is subsequently referred to as 'depth range'. For this study, we used all years of data available between 2004 and 2012, not just the most recent year of data for each site.

We classified eelgrass as either intertidal or subtidal. The boundary between intertidal and subtidal lands can be defined in different ways. We use a delineation based on Cowardin et al. (1979), who defines the boundary between the intertidal and the subtidal as the extreme low water at spring tides (ELWS). We defined this boundary as -1 m (MLLW), which is a generalization of the variations in Extreme Low Tide depth in the Puget Sound region (<http://tidesandcurrents.noaa.gov/>). This value is slightly deeper than ELWS at Neah Bay and other locations near to oceanic influence and shallower than many stations within Puget Sound (Table A-4.1). Despite these limitations, it allows us to estimate the proportion of the population subjected to desiccation and other shallow water conditions.

2.6 Statistical Analyses

To understand differences in the shallow and deep extents of eelgrass and its depth range among SVMP regions and between habitat types, we employed linear mixed-effects models. We modeled the deep extent, shallow extent, and depth range as a function of SVMP region, habitat type, year, and two-way interactions among these predictors (fixed effects) while accounting for variation among sites and years nested within sites (random effects). We modeled the fixed effect of year as a continuous variable because we were interested in testing for a temporal trend in depth limits, but we modeled the random effect of year within site as a factor, to allow for non-linear year-to-year variation within each

site. Models were fit with maximum likelihood estimation using the lme4 package (Bates, Maechler, & Bolker, 2012) in R (R Core Team, 2013).

We examined the importance of variables in the full models using Likelihood Ratio Tests (LRT) to assess the decrease in model fit associated with excluding a given variable from the model using the afex package (Singmann, Bolker, & Westfall, 2015) in R. Non-significant interactions were dropped, and LRTs repeated to select the final model. Parametric bootstrap was used to compute confidence intervals for the predicted means for each modeled category using the boot package (Canty & Ripley, 2015) in R, and pairwise differences among Regional predictions were assessed using least-squares means and Tukey's Honestly Significant Difference (HSD) with the lsmeans package (Lenth & Herv, 2015) in R. We report marginal pseudo- R^2 (Nakagawa & Schielzeth, 2012) as a quantification of the variance explained by fixed effects in our models.



3 Results

3.1 Depth Distribution

Eelgrass was observed from 1.4 m above MLLW to 12.0 m below MLLW. Eelgrass depth distribution was asymmetrical, with eelgrass most abundant in shallow subtidal and intertidal water and a long 'tail' of more rare deep observations, although the shape of the depth distribution varied substantially among regions (Fig. 1). About 38% of eelgrass in the greater Puget Sound is shallower than 1 m below MLLW (Fig. 2). About half (51%) of the eelgrass present at river deltas and in gently sloping bays (flats) in the greater Puget Sound is intertidal, but at more steeply sloped fringing beaches (fringe), only about one-quarter (24%) is intertidal (Fig. 3). The median depth of eelgrass in greater Puget Sound is 1.4 m below MLLW. The greatest proportional occupancy of eelgrass was at a depth of about 1 m below MLLW (Fig. 4). Proportional occupancy profile shape also varied among regions.

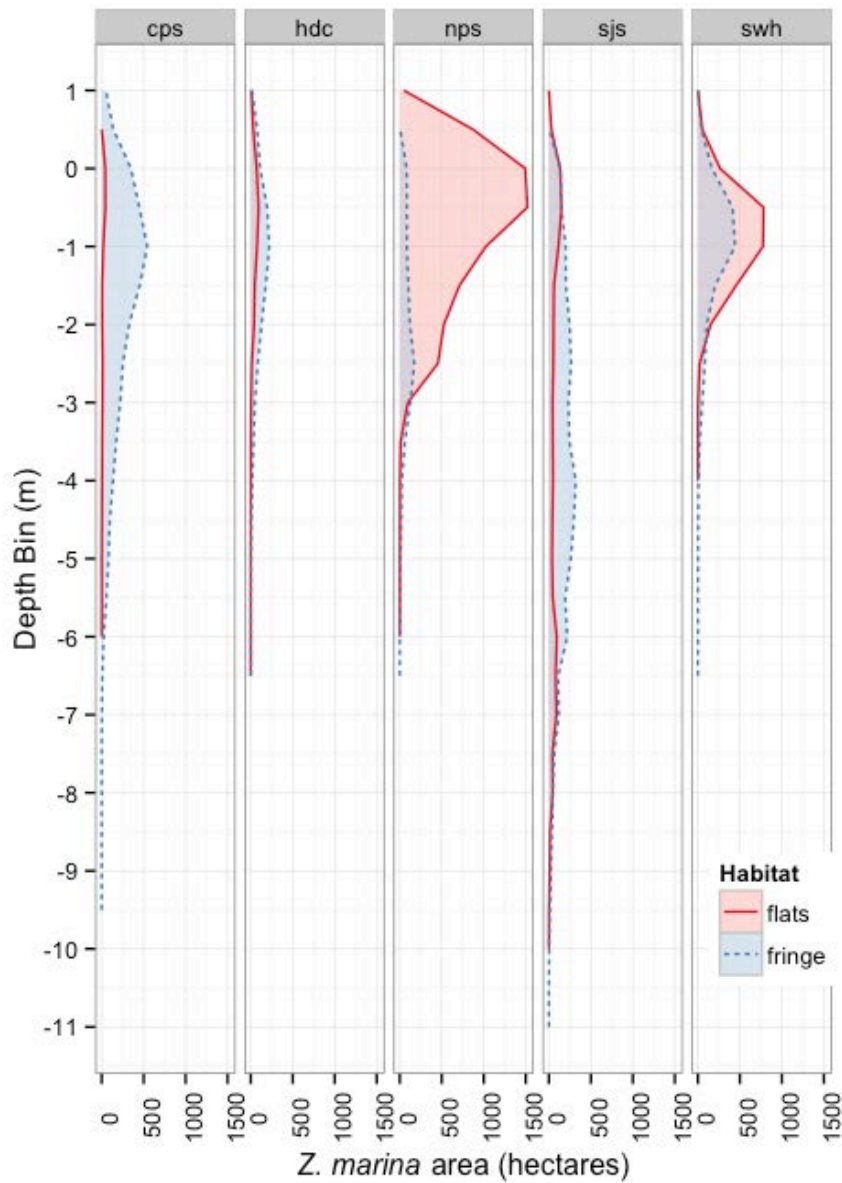


Fig 1. Distribution of estimated eelgrass area across a depth gradient in SVMP regions and habitat areas. Note that the most extreme shallow and deep observations are omitted from the figure because they round to zero-area within the precision of the analysis.

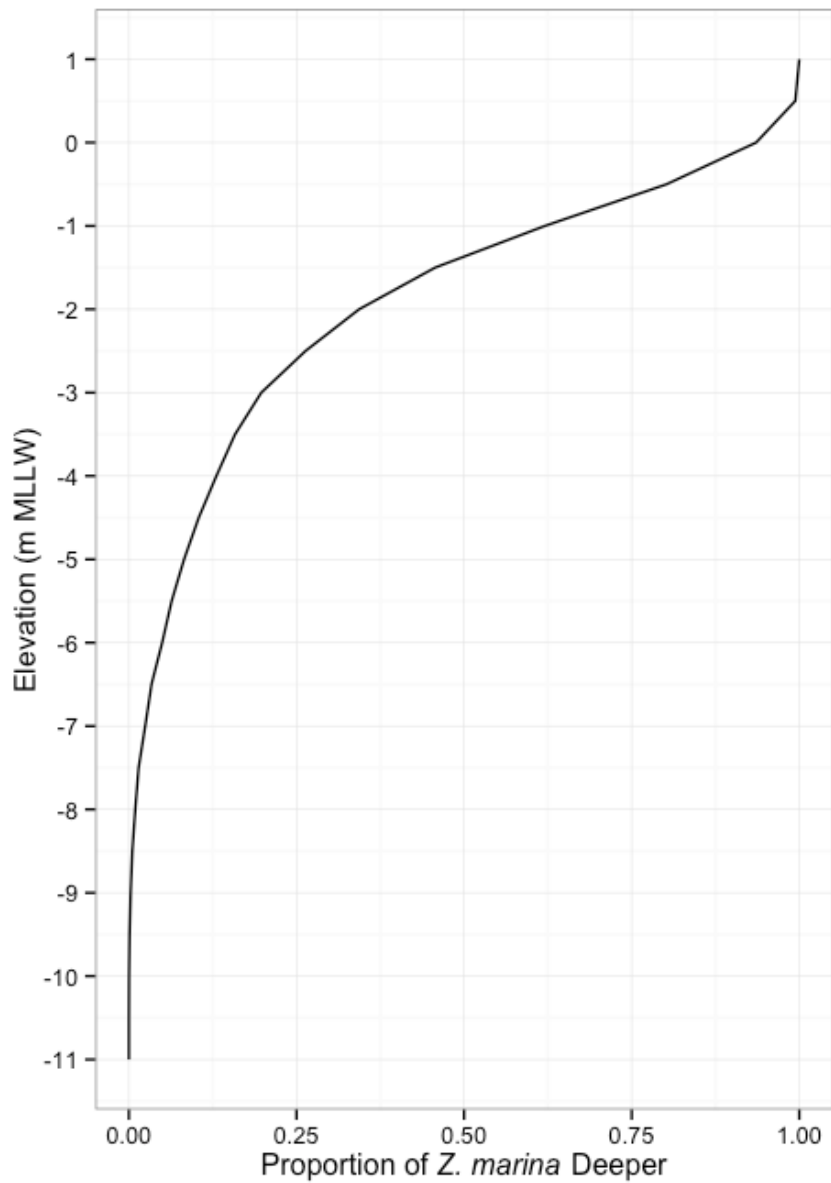


Fig 2. Cumulative density plot of eelgrass occurrence. Curve traces the proportion of eelgrass occurring deeper than the depth specified on the y-axis. Note that the most extreme shallow and deep observations are omitted from the figure because they round to zero-area within the precision of the analysis.

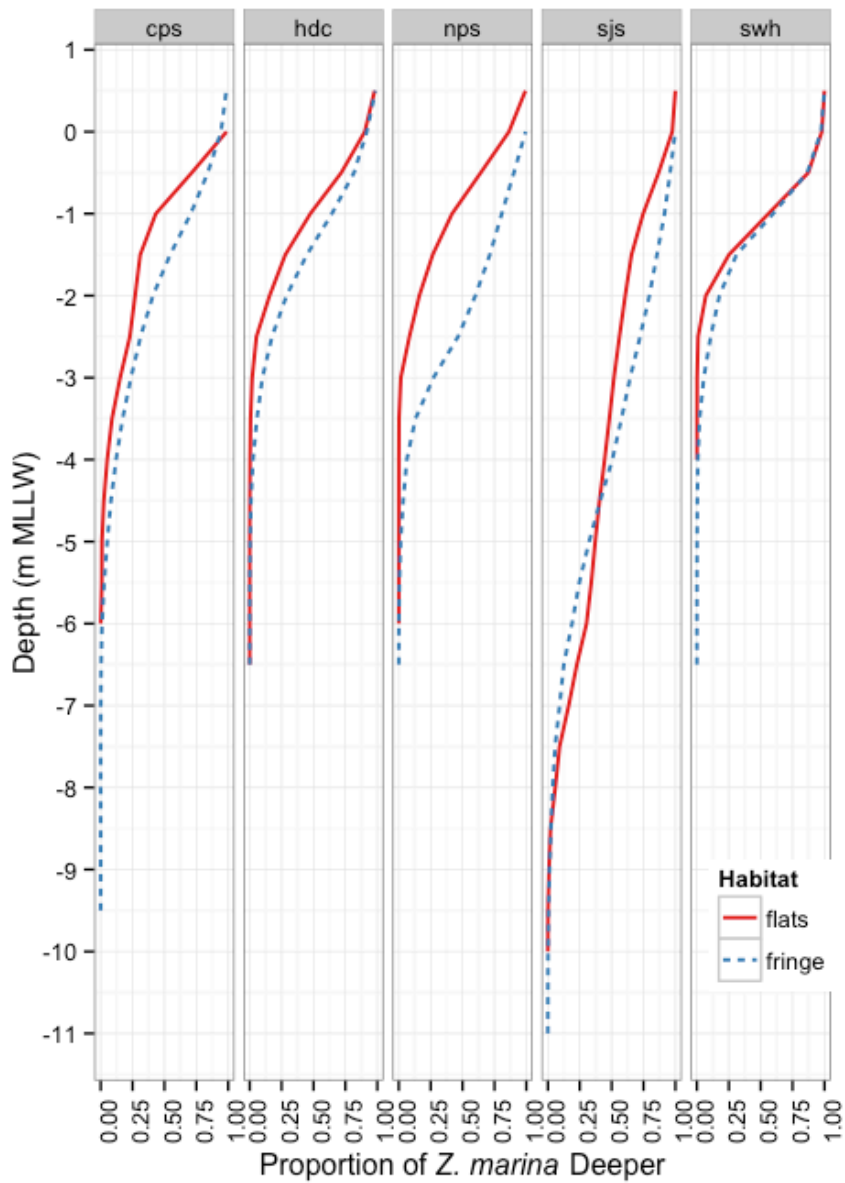


Fig 3. Cumulative density plot of eelgrass occurrence, by SVMP region and habitat type. Curve traces the proportion of eelgrass occurring deeper than the depth specified on the y-axis. Note that the most extreme shallow and deep observations are omitted from the figure because they round to zero-area within the precision of the analysis.

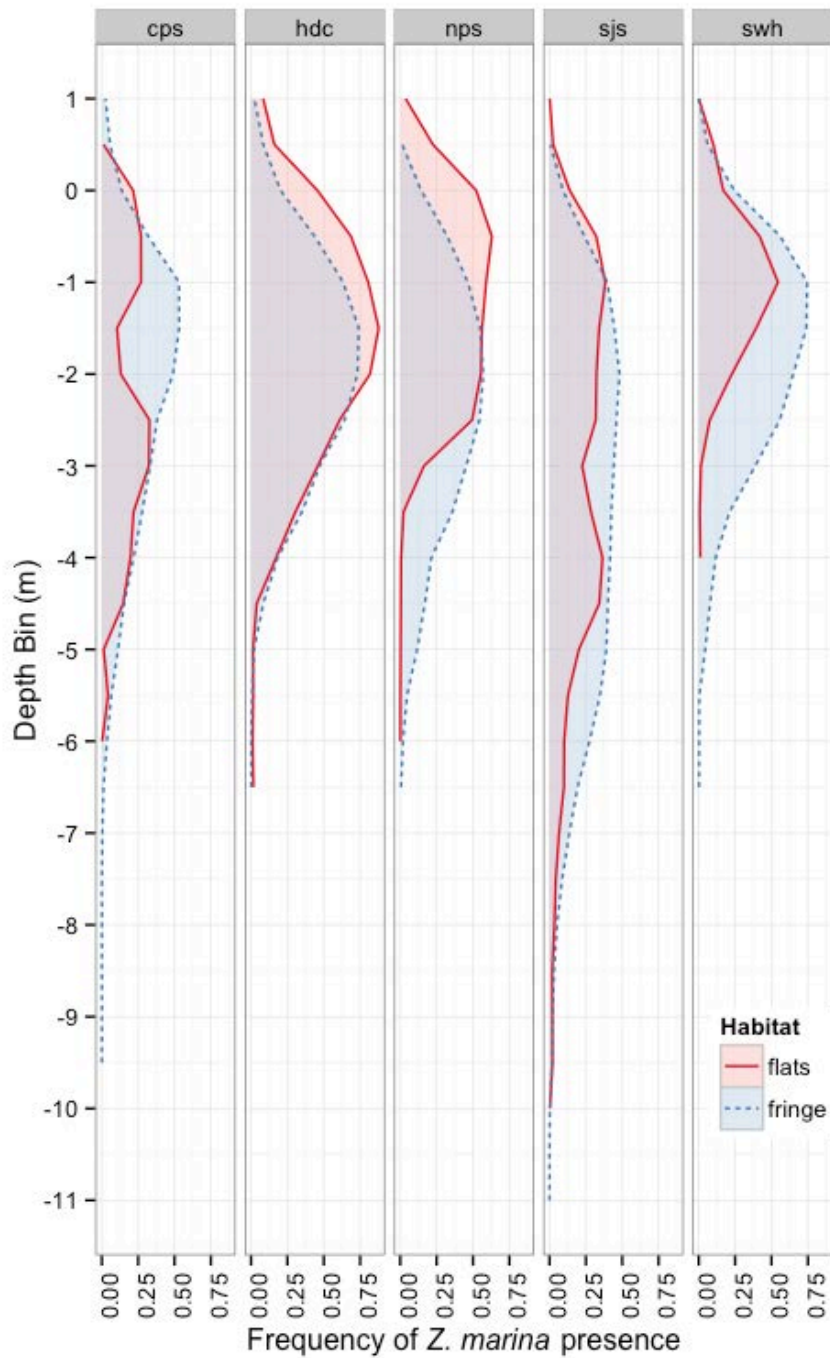


Fig 4. Proportional occupancy of eelgrass across depth gradients in flats and fringe habitats for different SVMP regions. Histograms show the proportion of observations for which eelgrass was present at a given depth within shoreline segments covered with SVMP sample polygons. Note that the most extreme shallow and deep observations are omitted from the figure because they round to zero-area within the precision of the analysis.

3.2 Shallow and Deep Limits

Best-fit models for the shallow extent, deep extent, and depth range of *Z. marina* included the fixed effects of habitat type and region. Best-fit models for shallow and deep extent of *Z. marina* additionally included an inter-annual trend. These fixed effects explained 35% of the variance in the deep extent, 23% of the variance in the shallow extent, and 11% of the variance in the depth range of *Z. marina*.

Eelgrass depth distribution was shifted deeper and covered a wider range at fringe sites compared to flats sites. At fringe sites, eelgrass's shallow extent was 0.46 m (± 0.21 m) deeper (Fig. 6), its deep extent was 1.16 m (± 0.24 m) deeper (Fig. 5), and it spanned a depth range 0.69 m (± 0.18 m) greater compared to flats sites (Fig. 7). We also detected a positive inter-annual trend in both the deep limit (1.9 cm / year ± 0.8 cm) and the shallow limit (1.9 cm / year ± 0.7 cm) of eelgrass.

The depth distribution of *Z. marina* was generally shifted deeper in the SJS region relative to other regions in the study area. On average, eelgrass in the SJS region extended more than two meters deeper than in the HDC, CPS, or SWH regions, and 1.7 m deeper than in the NPS region (Table 1). Likewise, the shallow extent of eelgrass in the SJS region tended to be more than 1 m deeper than in any other SVMP region (Table 2). Eelgrass beds tended to span a broader depth range in SJS than in either SWH or CPS, but differences among other regions were less apparent (Table 3).

Variability in depth limits among sites was greater than year-to-year or transect-to-transect variability within a site. Mixed models estimated the average among-site variability (standard deviation) in the population from which our samples were drawn to be about 1 m for shallow extent, deep extent, and depth range (Table 4). This was almost an order of magnitude larger than the variability estimated among years within sites.

Table 1. Least Squares Means for differences in eelgrass deep extent among regions. P-values are adjusted for all pairwise region comparisons using Tukey's HSD.

Regions Compared	Diff. in Deep Extent (m)	SE (m)	df	t	p
cps - hdc	0.0	0.33	148.80	0.08	1.000
cps - nps	0.3	0.33	148.80	1.04	0.836
cps - sjs	2.1	0.26	150.68	8.01	0.000
cps - swh	-0.4	0.31	149.95	-1.39	0.634
hdc - nps	0.3	0.37	147.99	0.85	0.914
hdc - sjs	2.0	0.31	148.98	6.54	0.000
hdc - swh	-0.5	0.36	148.54	-1.29	0.699
nps - sjs	1.7	0.30	148.94	5.68	0.000
nps - swh	-0.8	0.35	148.55	-2.20	0.185
sjs - swh	-2.5	0.29	150.16	-8.53	0.000

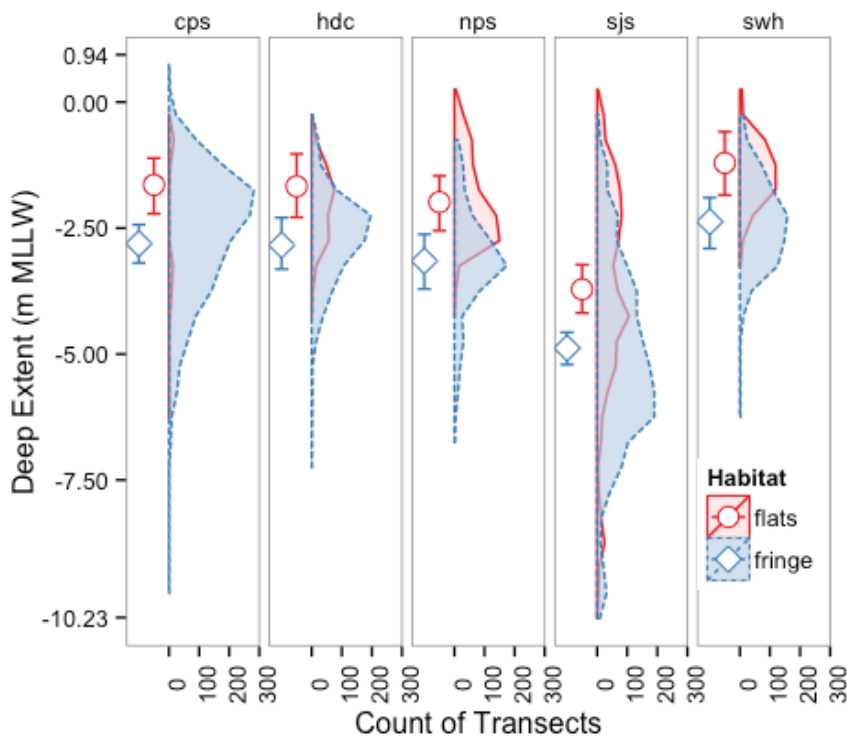


Fig 5. Distribution and predicted mean of deep extent of eelgrass at flats and fringe habitats in SVMP monitoring sub-regions. Histograms depict the number of monitoring transects at which eelgrass extended to the depth specified on the y-axis. Points depict the mean deep extent and 95% confidence intervals predicted by parametric bootstraps of the best linear mixed effect model of deep extent.

Table 2. Least Squares Means for differences in eelgrass shallow extent among regions. P-values are adjusted for all pairwise region comparisons using Tukey's HSD.

Regions Compared	Diff. in Shallow Extent (m)	SE (m)	df	t	p
cps - hdc	-0.1	0.29	148.89	-0.43	0.993
cps - nps	0.2	0.29	148.94	0.86	0.912
cps - sjs	1.4	0.23	150.65	6.25	0.000
cps - swh	-0.2	0.28	149.92	-0.70	0.957
hdc - nps	0.4	0.33	148.18	1.15	0.780
hdc - sjs	1.6	0.28	149.03	5.63	0.000
hdc - swh	-0.1	0.32	148.61	-0.21	1.000
nps - sjs	1.2	0.27	149.07	4.38	0.000
nps - swh	-0.4	0.31	148.68	-1.42	0.618
sjs - swh	-1.6	0.26	150.08	-6.25	0.000

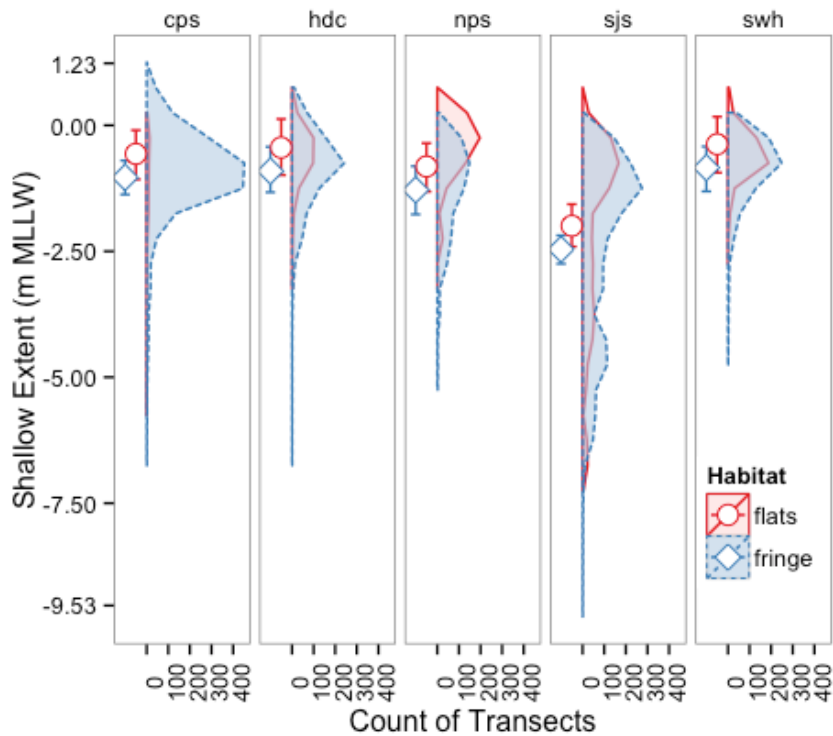


Fig 6. Distribution and predicted mean of shallow extent of eelgrass at flats and fringe habitats in SVMP monitoring sub-regions. Histograms depict the number of monitoring transects at which the shallow extent of eelgrass extended to the depth specified on the y-axis. Points depict the mean shallow extent and 95% confidence intervals predicted by parametric bootstraps of the best linear mixed effect model of shallow extent.

Table 3. Least Squares Means for differences in eelgrass depth range among regions. P-values are adjusted for all pairwise region comparisons using Tukey's HSD.

Regions Compared	Diff. in Depth Range (m)	SE (m)	df	t	p
cps - hdc	-0.1	0.25	148.30	-0.60	0.974
cps - nps	-0.1	0.25	148.36	-0.38	0.995
cps - sjs	-0.6	0.19	150.85	-3.33	0.010
cps - swh	0.2	0.23	149.83	1.06	0.828
hdc - nps	0.1	0.28	147.25	0.20	1.000
hdc - sjs	-0.5	0.23	148.17	-2.12	0.216
hdc - swh	0.4	0.27	148.04	1.47	0.581
nps - sjs	-0.6	0.23	148.24	-2.42	0.117
nps - swh	0.3	0.27	148.04	1.29	0.697
sjs - swh	0.9	0.22	149.60	4.06	0.001

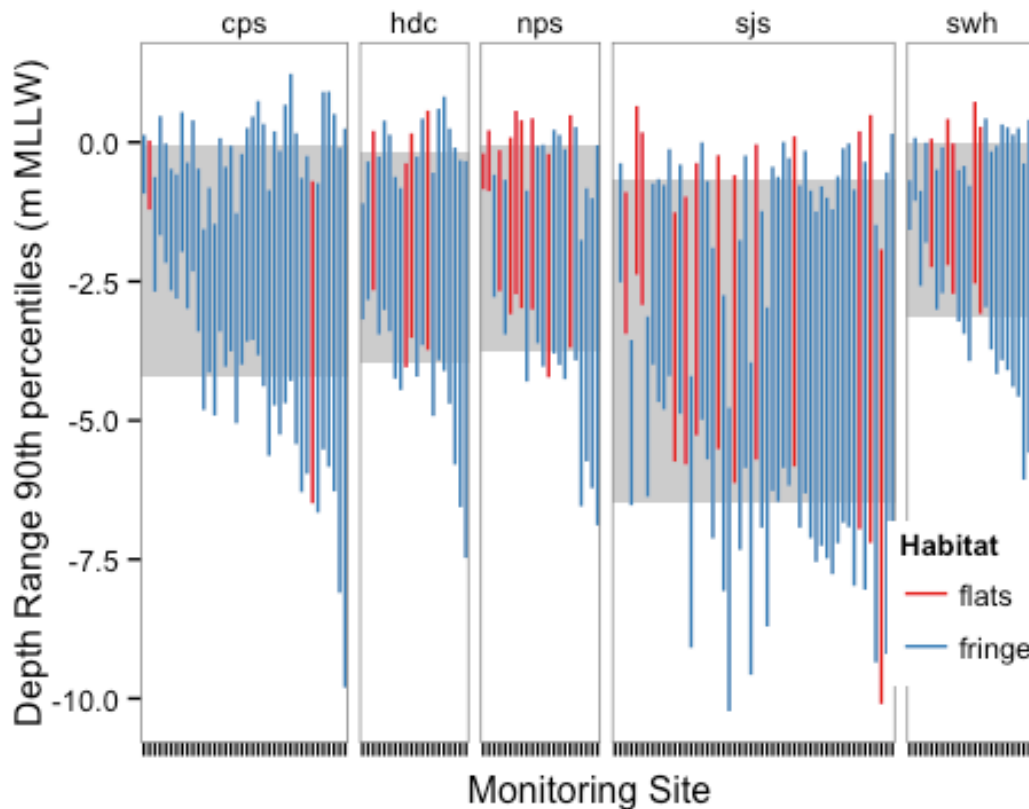


Fig 7. Depth range of eelgrass in monitoring transects at each site in SVMP subregions and habitat types. For each site, a line extends from the shallowest transect shallow extent observed to the deepest transect deep extent observed over the course of the study, where transect shallow extent and transect deep extent presented in the figure are the 10th to the 90th percentile of eelgrass depth in each transect. Grey rectangles cover the median of these extents for each region. Sites ordered by increasing depth extent within region.

Table 4. Variability of the population from which samples were drawn, as estimated by mixed model analysis. The Standard Deviations (SD) represent the average difference expected between two sites sampled from the population in the same region and habitat type

	SD Year within Site (m)	SD Among Sites (m)	SD Among Transects (m)
Shallow Extent	0.12	1.04	0.74
Deep Extent	0.17	1.17	0.86
Depth Range	0.10	0.88	0.85



4 Discussion

By examining a multi-year seagrass monitoring dataset, we have identified spatial and habitat-related patterns in seagrass depth distribution in the greater Puget Sound. The median depth of eelgrass in the Puget Sound is approximately -1.4 m relative to MLLW. More than half of the eelgrass present at river deltas and in gently sloping bays (flats) in the greater Puget Sound is intertidal. At more steeply sloped fringing beaches (fringe), less eelgrass is intertidal. Eelgrass is found at greater depths in the San Juan Islands and Strait of Juan de Fuca than elsewhere in the greater Puget Sound. It extends to deeper depths at fringe sites than at flats sites, but it extends shallower towards land at flats sites than at fringe sites. Variability in depth limits among sites was greater than year-to-year or transect-to-transect variability within a site.

Based on the frequency of *Z. marina* occurrence by depth in SVMP sampling polygons, it appears that the optimal habitat for eelgrass is between 0 and 2 m below MLLW in most of the greater Puget Sound. This range appears to extend deeper in the SJS region than elsewhere. The frequency of eelgrass presence by depth within sample polygons is not a perfect estimate of the probability of eelgrass occurrence at that depth. Because SVMP sample polygons intentionally exclude areas known to be devoid of eelgrass, the estimates provided by frequency of presence are likely to be biased toward greater proportions. Nevertheless, the relative frequencies across depths provide some information about habitat suitability.

The San Juan/Straits region was distinct among the regions in this study site. Eelgrass in this region tended to extend to deeper depths, but not reach as shallow as in other regions, and no region exceeded the range of depths over which eelgrass grows in the San Juan Straits Region (SJS). Selleck et al. (2005) also reported deeper eelgrass maximum depths in SJS than in other regions. Compared to other SVMP regions, SJS experiences reduced tidal amplitude which is predicted to increase the depth range suitable for eelgrass (Koch, 2001).

SJS appears to be the most variable region as well, exhibiting greater variability in shallow and deep extents than any other region, and complex depth distribution profile shapes. Similar patterns of increased deep extents in more oceanic environments (Greve & Krause-Jensen, 2005) and increased variability in eelgrass cover in locations with greater hydrodynamic exposure (Frederiksen, Krause-Jensen, Holmer, & Laursen, 2004) have been found in Danish fjords. Substrate availability and local geomorphology may play an important role in shaping this variability in the SJS region.

Compared to flats sites, eelgrass in fringe sites was shifted downslope, and occupied a larger depth range. This finding generally agrees with Selleck et al. (2005), who describe similar patterns, albeit non-significant ones, attributable to habitat type. Fringe sites may

present fewer water quality challenges than flats. Where flats sites occur at river deltas, they are likely subject to periodic pulses of turbidity that can reduce seagrass growth through light limitation (K. A. Moore et al., 1997). Where flats sites occur in bays, water circulation may be reduced, which may reduce water quality. For example, modeled predictions of surface chlorophyll are higher in the distal portions of southern Puget Sound inlets compared to more proximal locations (Ahmed et al., 2014). The same model also predicts higher chlorophyll concentrations in the embayments west of Bainbridge Island and in Quartermaster Harbor. The processes leading to reduced water clarity are complex, and the resultant patterns variable, but more directed study of water quality influence on eelgrass in different habitat types is warranted.

Factors constraining the shallow extent of seagrass beds are not as well-studied as those controlling the deep extent, but desiccation (Boese et al., 2005) and wave-related disturbance (Infantes, Terrados, Orfila, Canellas, & Alvarez-Ellacuria, 2009) may be important in greater Puget Sound. Shallower extents of eelgrass have been linked to gentler slopes and reduced wave-exposure in the Puget Sound (Hannam, 2013), both of which may be expected at flats sites. Wave-energy might also account for the deeper shallow extents found in the SJS region, as this region has greater exposure to oceanic swell.

Our mixed model analysis detected a minor upslope migration of seagrass beds across the study area. Both shallow and deep extents exhibited the same trend, and no change in depth range was detected. The scale of the trend (2 cm / year), compared to the expected error from the depth and locational measurement systems does not lend great confidence in this result. That said, the trend was detected despite the measurement uncertainty in the data. Other targeted monitoring efforts may be better suited to detect or confirm fine-scale vertical migration of seagrass beds in greater Puget Sound.

Our results suggest that the depth distribution of Puget Sound eelgrass is not driven solely by regional-scale patterns, nor is it overwhelmed by year-to-year variability. Site-to-site variability exceeded region-to-region differences for any pair not including the SJS region and far outweighed year-to-year variability within sites. Owing to its glacial past, Puget Sound shoreline exhibits high geomorphic variability (Finlayson, 2006) which may be a considerable factor in eelgrass depth distribution (Hannam, 2013). Other factors may include local differences in water quality, sediment resuspension, the presence of river plumes and/or shoreline modification. Furthermore, many parts of the Puget Sound are well-mixed by large daily tides, which may reduce broader-scale gradients in water quality.

The relatively fine-scale variability observed in the SVMP depth data highlights some of the challenges of managing and conserving eelgrass in the greater Puget Sound. High site-to-site variability suggests the need for site-scale management, but does not preclude the need for basin-scale management. Basin-scale trends will be more difficult to detect amidst high site-scale variability. This difficulty is aggravated by a rotational sampling scheme that incorporates site-to-site variability into year-to-year change detection efforts. The substantial proportion of Puget Sound eelgrass that occupies subtidal habitat suggests that a sizeable proportion of this resource is found on State-Owned Aquatic Land, underscoring the importance of continued stewardship activities.



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6 Appendix 1: Histogram calculations

6.1 Data Loading and Preparation

We'll start by loading and prepping data. A table containing sites, sampled years, and average area is loaded and filtered to remove sites which have not been sampled.

```
Site.Area = read.csv('../Data/SVMP_Site_Area.csv', skip=5)
names(Site.Area) = c('site', 'yrs.Sampled', 'mean.area')
Site.Area = subset(Site.Area, yrs.Sampled>0)
summary(Site.Area)
```

```
##   site   yrs.Sampled   mean.area
## core001: 1   Min.   :1.000   Min.   : 0.000
## core002: 1 1st Qu.: 3.000 1st Qu.:  0.480
## core003: 1 Median : 5.000 Median :  2.943
## core004: 1 Mean   : 4.769 Mean   : 46.877
## core005: 1 3rd Qu.: 5.000 3rd Qu.:  8.507
## core006: 1 Max.   :14.000 Max.   :3257.086
## (Other):232
```

We then load a table containing the area of each SVMP site, to be used for extrapolation later.

```
Site.Polygon = read.csv('../Data/SitePolygon.txt')
```

Then we load a table that, among other things, contains the habitat type and region for each site,

```
Site.Info = read.csv('../Data/SVMP_Site_Info.csv')
summary(Site.Info)
```

```
##   site_code   region   focus_area   hab_type   samp_frame
## core001: 1   cps:876   :513       flats : 81   elwha : 6
## core002: 1   hdc:300   cps :876   fringe: 2714 flats : 81
## core003: 1   nps:222   hdc :300   fringe :2544
## core004: 1   sjs:948   nps :222   orphan : 161
## core005: 1   sps:165   sj-cyp:600 outfall2013 : 3
## core006: 1   swh:284   swh :284
## (Other):2789
```

```

## strat2004      strat2001      strat2000      strat_focus
## frn:2083      : 14          : 13          frn :1296
## frw: 455      core :6       core:6        : 518
## frn_orphan :141 fl2001 : 76     fl2000 : 77     fro : 375
## flr : 73      frn : 2083    frhi :2371    frw : 271
## frw_orphan : 20 frn_orphan :141 frhi_orphan:161 fra : 125
## : 14         frw : 455     frlo : 166    fra_orphan: 57
## (Other): 9   rw_orphan :20 frlo_orphan: 1 (Other) : 153

```

and next, a table with results from each year's survey at each site. We will later use this table to exclude sites that were not part of the soundwide random sample, so after loading, we filter out those sites (a total of 342).

```

Site.Results = read.csv('../Data/SVMP_Site_Results.csv')
Site.Results.1 = Site.Results[,c('site_code','Year','soundwide')]
Site.Results.1 = subset(Site.Results.1, soundwide=='svmp_sw')
Site.Results.2 = subset(Site.Results, soundwide=='0')
#342 out of 1429 sites are not part of 'soundwide random', so are excluded:
dim(Site.Results);dim(Site.Results.1);dim(Site.Results.2)

## [1] 1429  28
## [1] 1087  3
## [1] 342  28
rm(Site.Results.2)

```

We load the histogram data from our python scripts, filter out years before 2003, and take a quick look at these raw data.

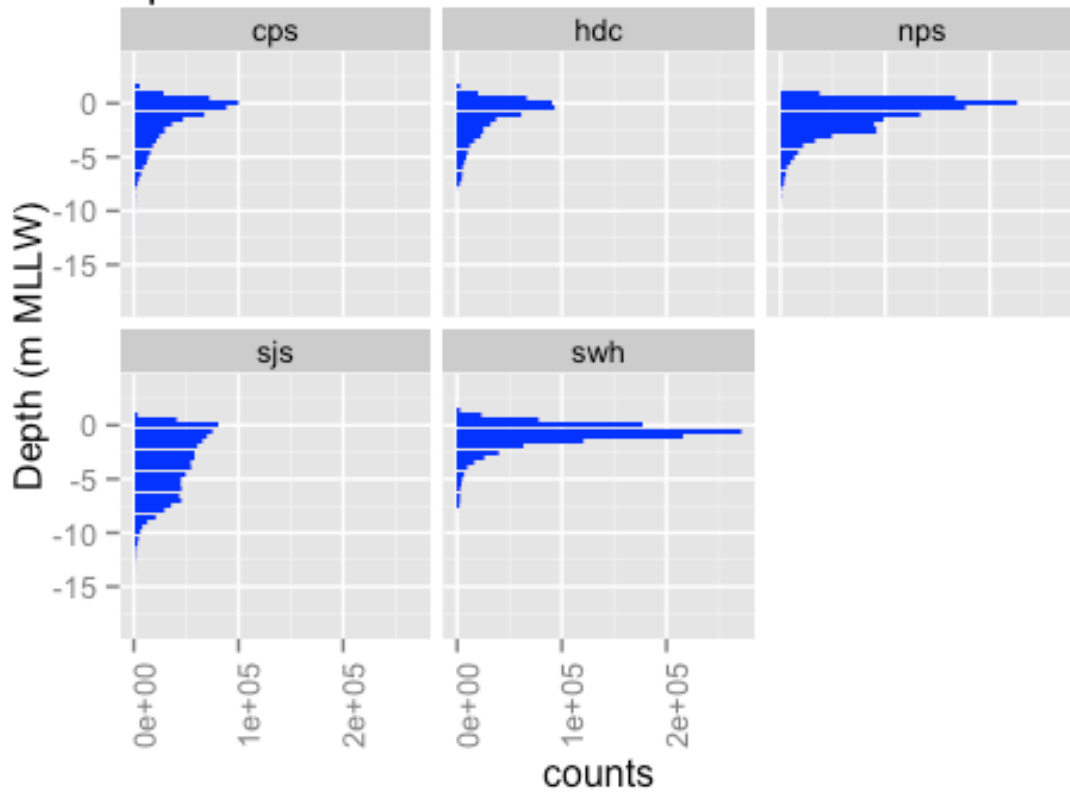
```

Bathy.Histo = read.csv('../Data/Bathy_Histo.csv')
Bathy.Histo = subset(Bathy.Histo, year>2002)
Zm.Histo = read.csv('../Data/Zm_histo.csv')
Zm.Histo = subset(Zm.Histo, year>2002)
Zj.Histo = read.csv('../Data/Zj_Histo.csv')
Zj.Histo = subset(Zj.Histo, year>2002)

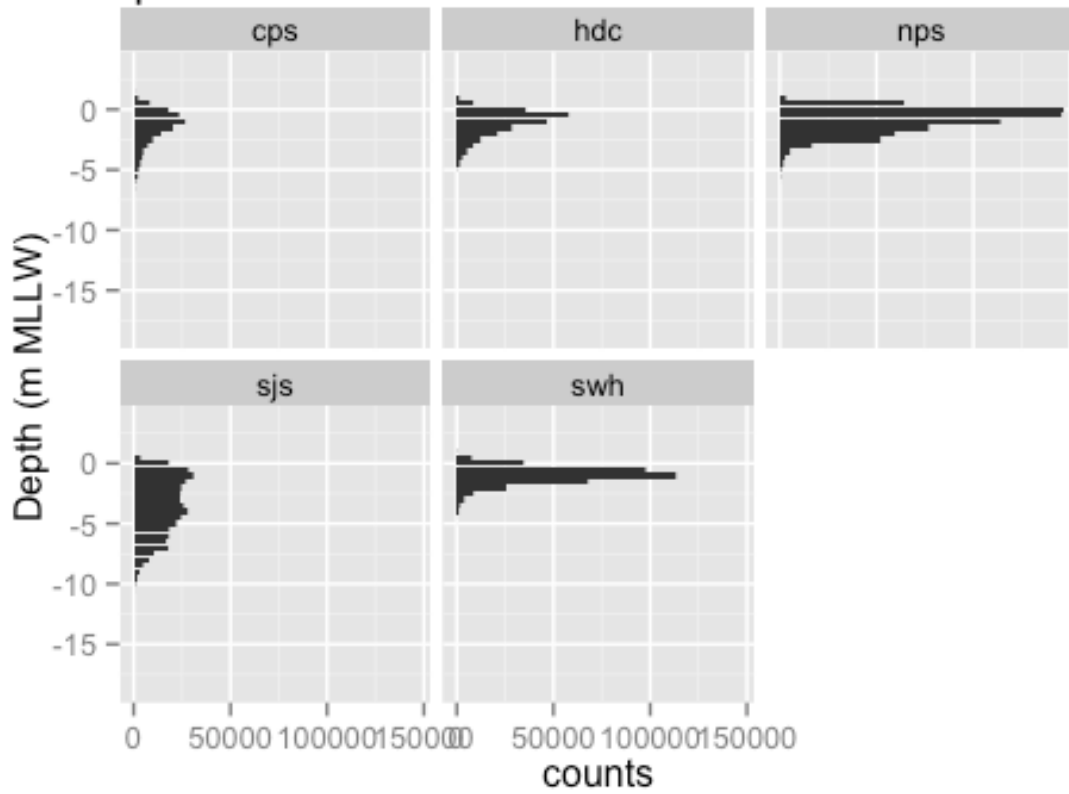
Bathy.Histo.MSL = read.csv('../Data/MSL Version/Bathy_Histo_MSL.csv')
Bathy.Histo.MSL = subset(Bathy.Histo.MSL, year>2002)
Zm.Histo.MSL = read.csv('../Data/MSL Version/Zm_histo_MSL.csv')
Zm.Histo.MSL = subset(Zm.Histo.MSL, year>2002)
Zj.Histo.MSL = read.csv('../Data/MSL Version/Zj_Histo_MSL.csv')
Zj.Histo.MSL = subset(Zj.Histo.MSL, year>2002)

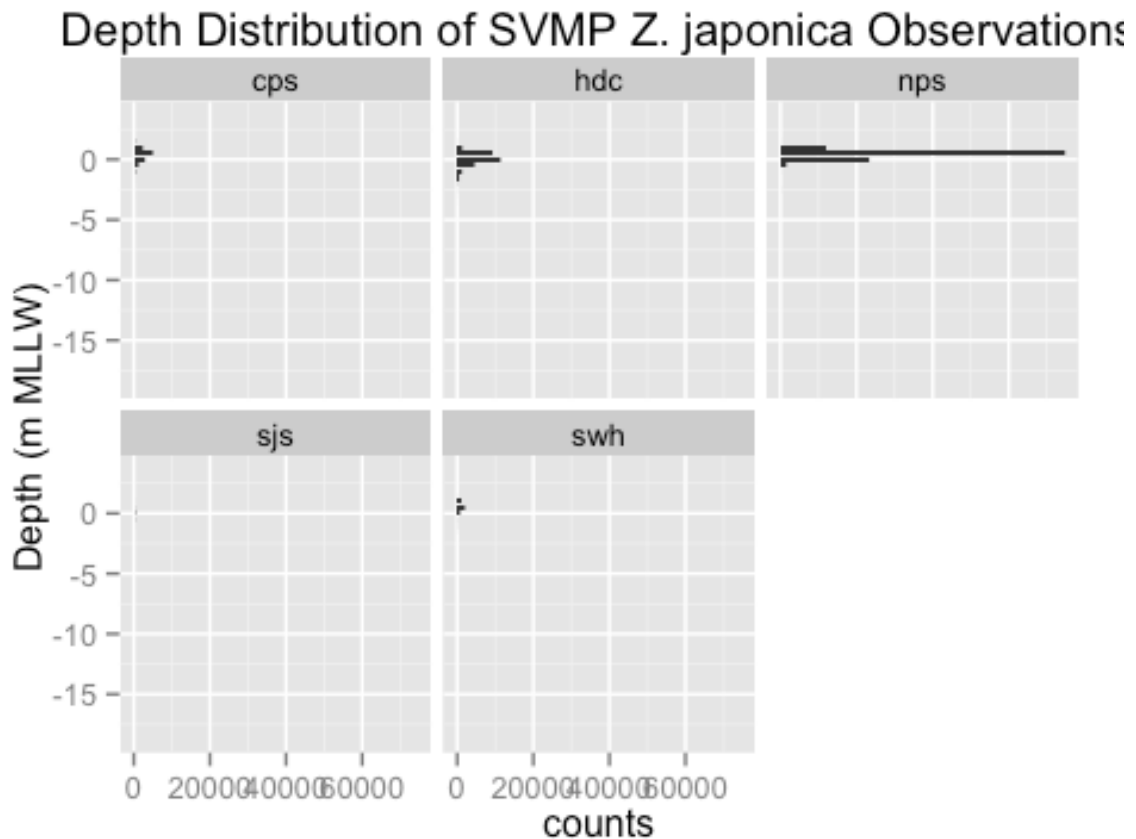
```


Depth Distribution of all SVMP video Observations



Depth Distribution of SVMP *Z. marina* Observations





Finally, we combine the *Z. marina* histogram data with the all depth histogram data, to allow for computation of probability of presence later. To this table we add the habitat type and mean site area, and remove sites that are not part of the soundwide sample.

```
#Join zm observations with depth observations:
Zm.Bathy.Histo = merge(Zm.Histo,Bathy.Histo, by = c('site','year','right_bin'))
#Join with site area estimates for weighting by area
Zm.Bathy.Histo1 = merge(Zm.Bathy.Histo,Site.Area, by = 'site') #This drops 80k observations
dim(Zm.Bathy.Histo1)
## [1] 83700 11
names(Zm.Bathy.Histo1)[5] = 'Zm.Count'
names(Zm.Bathy.Histo1)[8] = 'Total.Count'

#Remove focus sites:
Zm.Bathy.Histo2 = merge(Zm.Bathy.Histo1, Site.Results.1, by.x = c('site','year'),
by.y = c('site_code','Year'))
#Add habitat type:
Zm.Bathy.Histo2 = merge(Zm.Bathy.Histo2, Site.Info[,c(1,4,6)], by.x='site', by.y = 'site_code')
```

```
#Zm.Bathy.Histo2$Proportion = with(Zm.Bathy.Histo2, Zm.Count/(Total.Count+.000001)
)
Zm.Bathy.Histo2$Proportion = with(Zm.Bathy.Histo2, ifelse(Total.Count==0,0,Zm.Count
/(Total.Count)))
```

6.2 Conversion from Observation Scale to Area Scale

Next we converted these observation count histograms into areal estimates in order to construct regional and sound-wide histograms where site-level frequencies are properly weighted according to site area. Conversion starts on a per-site basis, and then site-level area bins are combined to regional and soundwide area bins

6.2.1 Site-Scale Conversion

For each site, the number of eelgrass observations in each depth bin was divided by the total number of eelgrass observations at the site. This fraction was multiplied by the estimated eelgrass area at the site to estimate the area of eelgrass in each depth bin at the site.

In other words, For each site, we estimated the area of *Z. marina* in each depth bin, using the formula:

$$a_{jk} = A_j \frac{c_{jk}}{\sum_{k=1}^n c_{jk}}$$

where a_{jk} is *Z. marina* area in each histogram bin (k) at site (j), c_{jk} is the count of observations per bin, and A_j is site area.

First we summed the eelgrass observations at the site for each year ($\sum_{k=1}^n c_{jk}$):

```
Zm.Bathy.Histo2$Zm.Sum.of.Site = with(Zm.Bathy.Histo2,
ave(Zm.Count,site,year,
FUN='sum'))
```

Then we divided the bin count (c_{jk}) by that site total, adding a tiny value to avoid div/0 errors:

```
Zm.Bathy.Histo2$Zm.Bin.Frac = with(Zm.Bathy.Histo2, Zm.Count/(Zm.Sum.of.Site+.00
00001))
```

And finally multiplied that by the site area (A_j):

```
Zm.Bathy.Histo2$Zm.Bin.Area = with(Zm.Bathy.Histo2, Zm.Bin.Frac*mean.area)
```

6.2.2 Regional Summary

Per-bin area estimates from sites were combined into regional and soundwide estimates using a weighting scheme that accounts for the fraction of potential habitat surveyed within each strata (Core, Persistent Flats, Flats, Wide Fringe, and Narrow Fringe). For each region and strata combination, we summed the eelgrass area in each depth bin:

$$a_k = \sum_{j=1}^n a_{jk}$$

```
# Sum the area of Zm in each bin for each region and hab type/Stratum and year (sum_j a_0jk)
```

```
Rgn.Hab.Yr.Bins = ddply(Zm.Bathy.Histo2,
  .(year, hab_type, strat2004, region.x, right_bin),
  summarise,
  Rgn.hab.bin.area = sum(Zm.Bin.Area))
```

These sampled eelgrass areas were extrapolated to estimate the total area in each depth bin within a stratum (s) and region (r). To do this, we multiplied the sampled eelgrass area by the inverse of the sampling fraction, a ratio that we call the expansion factor (E_h). The sampling fraction is the ratio of the sample size to the population size, or in our case, the ratio of sampled area to total area in the region and stratum.

$$E_{sr} = \frac{P_{sr}}{p_{sr}}$$

where P_{sr} is the sum of the areas of SVMP site polygons within the region and stratum, and p_{sr} is the sum of the areas of sampled SVMP site polygons region and stratum.

```
#Calculate the expansion factor:
```

```
# Make list of sampled site names
```

```
Site.List = unique(Zm.Bathy.Histo2$site)
```

```
#Combine fringe and orphans for area calculation
```

```
Site.Polygon$STRATUM2004[Site.Polygon$STRATUM2004=='frn_orphan']='frn'
```

```
Site.Polygon$STRATUM2004[Site.Polygon$STRATUM2004=='frw_orphan']='frw'
```

```
#Select sampled sites from the area table
```

```
Sampled.Sites.Polygons = subset(Site.Polygon, SITE_CODE%in%Site.List)
```

```
#Sum site polygon areas by region and stratum
```

```
Population.Area = ddply(Site.Polygon, .(STRATUM2004, REGION), summarise,
```

```
  Area = sum(Shape_Area))
```

```
Sampled.Area = ddply(Sampled.Sites.Polygons, .(STRATUM2004, REGION), summarise
```

```
,
```

```
  Area = sum(Shape_Area))
```

```
#Combine the sum tables (needed because the population table has a SPS region that was never sampled)
```

```
Region.Areas = merge(Population.Area, Sampled.Area, by = c('STRATUM2004','REGION'))
```

```
#Calculate the expansion factor
```

```
Region.Areas$Expansion.Factor = with(Region.Areas, Area.x/Area.y)
```

```
### multiply by expansion factor:
```

```
#first combine tables
```

```
Rgn.Hab.Yr.Bins1 = merge(Rgn.Hab.Yr.Bins, Region.Areas,
```

```
  by.x=c('strat2004','region.x'),
```

```
  by.y=c('STRATUM2004','REGION'))
```

#Now multiply:

```
Rgn.Hab.Yr.Bins1$Extrap.Bin.Area = with(Rgn.Hab.Yr.Bins1,  
  Rgn.hab.bin.area*Expansion.Factor)
```

Finally, we sum the extrapolated depth-bin (k) *Z. marina* areas within region (r), year (y), and habitat types (h), and plot histograms.

$$A_{krhy} = \sum_{s=1}^5 A_{krhys}$$

#summarize by Region and habitat type:

```
Rgn.Hab.Histos = ddply(Rgn.Hab.Yr.Bins1, .(year,hab_type,region.x,right_bin),summaris  
e,
```

```
  Zm.Area = sum(Extrap.Bin.Area))
```

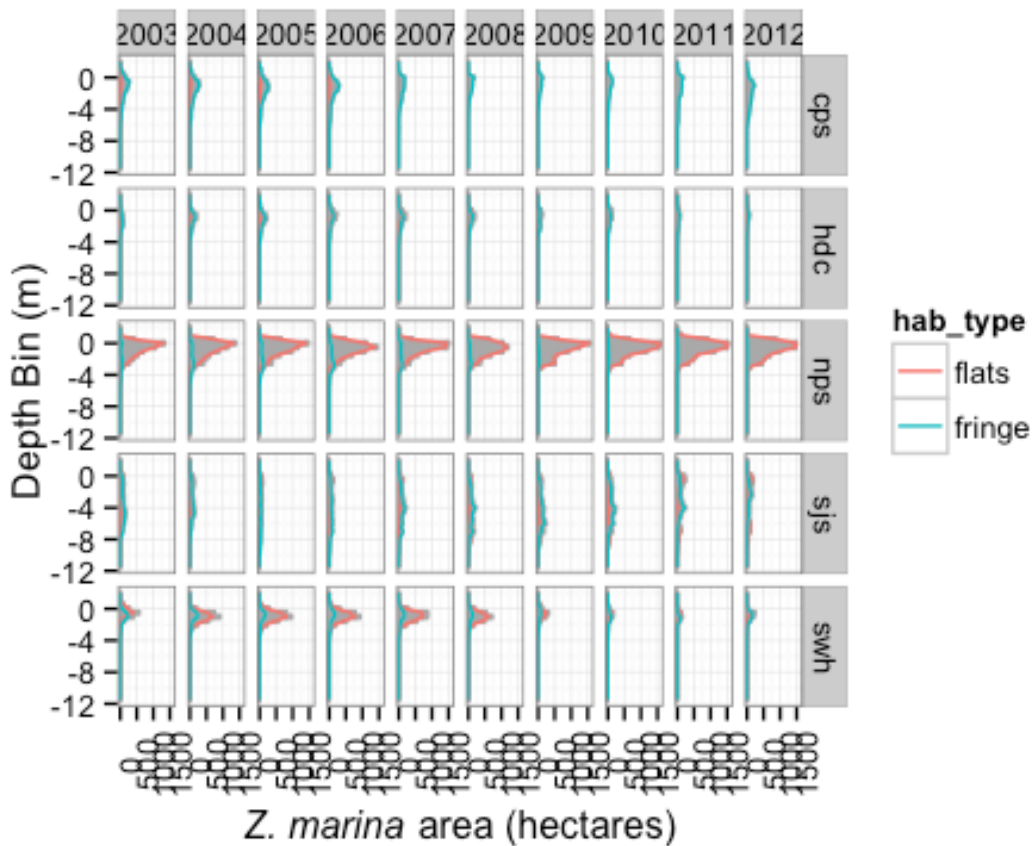
#Trim histogram to depth limits

```
max.depth = min(subset(Zm.Bathy.Histo2, Zm.Count>0)$right_bin)
```

```
min.depth = max(subset(Zm.Bathy.Histo2, Zm.Count>0)$right_bin)
```

```
Rgn.Hab.Histos = subset(Rgn.Hab.Histos,  
  right_bin>max.depth &  
  right_bin<min.depth)
```

```
ggplot(Rgn.Hab.Histos, aes(x = right_bin, y = Zm.Area))+  
  geom_bar(stat='identity', colour = 'dark grey', fill = 'dark grey')+  
  geom_path(aes(colour = hab_type))+  
  facet_grid(region.x~year)+theme_bw()+  
  coord_flip()+xlab('Depth Bin (m)')+  
  ylab(expression(paste(italic("Z. marina"),' area (hectares)')))+  
  theme(axis.text.x=element_text(angle=90))
```



The process is repeated using only data for the latest year that each site was sampled.

#Repeat, combining the latest year of data for each site:

#get latest year for each site:

```
Latest.Year = ddply(Zm.Bathy.Histo2, .(site), summarise,
                    year = max(year))
```

```
Recent.Zm.Bathy.Histo2 = merge(Zm.Bathy.Histo2, Latest.Year, by = c('site','year'))
```

Sum the area of Zm in each bin for each region and hab type/Stratum and year (sum_j a_0jk)

```
Rgn.Hab.Bins = ddply(Recent.Zm.Bathy.Histo2,
                    .(hab_type, strat2004, region.x, right_bin),
                    summarise,
                    Rgn.hab.bin.area = sum(Zm.Bin.Area))
```

#multiply by expansion factor:

#first combine tables

```
Rgn.Hab.Bins1 = merge(Rgn.Hab.Bins, Region.Areas,
                    by.x=c('strat2004','region.x'),
                    by.y=c('STRATUM2004','REGION'))
```

#Now multiply:

```
Rgn.Hab.Bins1$Extrap.Bin.Area = with(Rgn.Hab.Bins1,
```

```
Rgn.hab.bin.area*Expansion.Factor)
```

```
#summarize by Region and habitat type:
```

```
Rgn.Hab.Histos = ddply(Rgn.Hab.Bins1, .(hab_type,region.x,right_bin),summarise,  
  Zm.Area = sum(Extrap.Bin.Area))
```

```
#Trim histogram to depth limits
```

```
max.depth = min(subset(Zm.Bathy.Histo2, Zm.Count>0)$right_bin)
```

```
min.depth = max(subset(Zm.Bathy.Histo2, Zm.Count>0)$right_bin)
```

```
Rgn.Hab.Histos = subset(Rgn.Hab.Histos,
```

```
  right_bin>max.depth &
```

```
  right_bin<min.depth)
```

```
ggplot(subset(Rgn.Hab.Histos, Zm.Area!=0)
```

```
  , aes(x = right_bin, y = Zm.Area))+
```

```
  geom_ribbon(aes(fill = hab_type, ymax = Zm.Area, ymin=0), alpha=.5)+
```

```
  geom_line(aes(colour = hab_type, linetype=hab_type))+
```

```
  #geom_bar(stat='identity', colour = 'dark blue', fill = 'dark blue')+
```

```
  facet_grid(~region.x)+#hab_type)#, margin=TRUE)+
```

```
  theme_bw()+
```

```
  scale_colour_brewer(name = 'Habitat', palette=6, type = 'qual')+
```

```
  scale_fill_brewer(name="Habitat",palette=4, type = 'qual')+
```

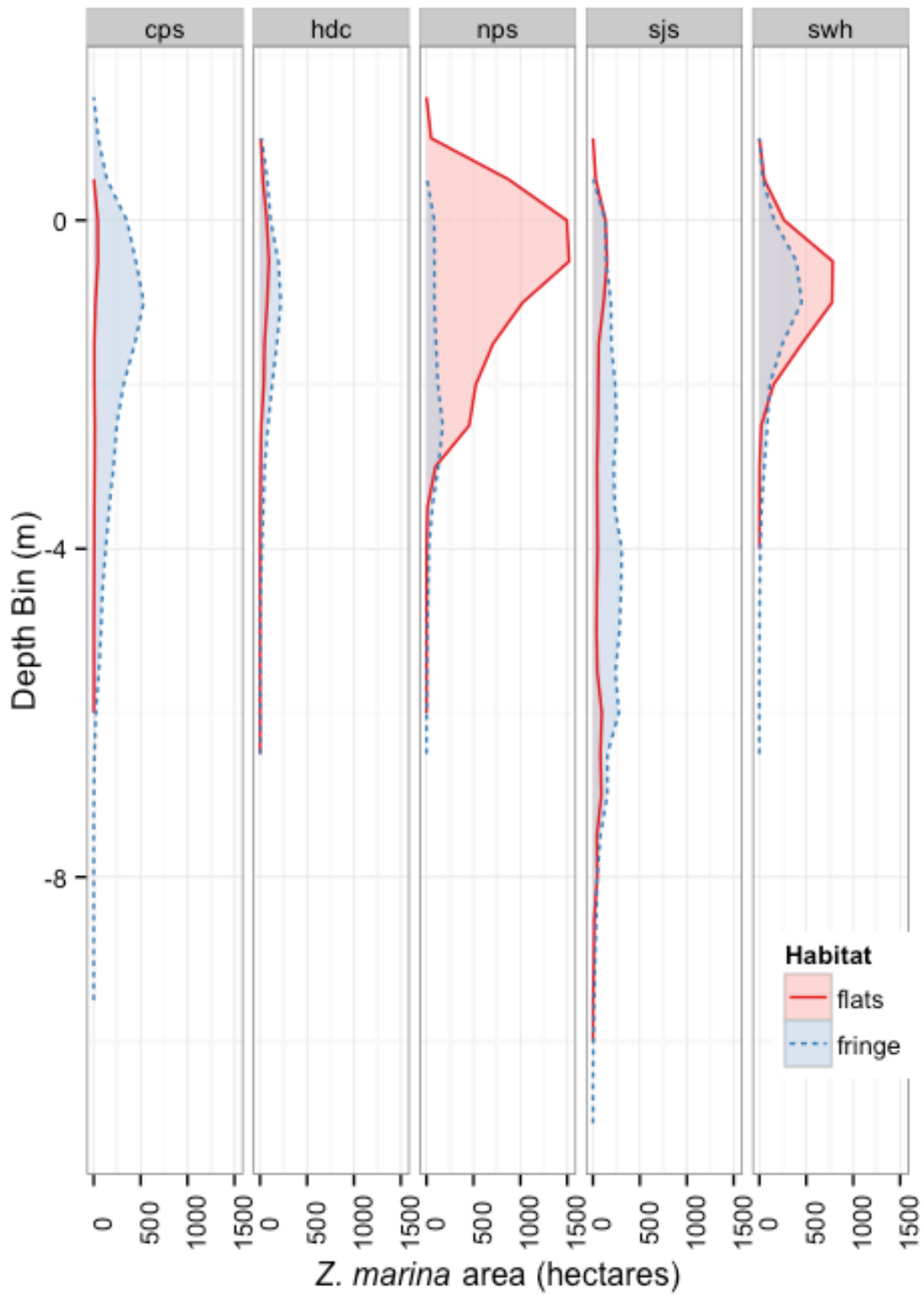
```
  scale_linetype(name="Habitat")+
```

```
  coord_flip()+xlab('Depth Bin (m)')+
```

```
  ylab(expression(paste(italic('Z. marina'),' area (hectares)')))+
```

```
  theme(axis.text.x=element_text(angle=90),
```

```
    legend.position = c(.92,.15))
```

7 Appendix 2: Mixed-Effects Model Results

Predictors	Dependent Variables					
	Deep Extent		Shallow Extent		Depth Range	
	B (CI)	p	B (CI)	p	B (CI)	p
Fixed Parts						
Intercept (CPS,Flats)	-1.64 (-2.23 - -1.06)	<.001	-0.57 (-1.08 - -0.05)	.032	1.08 (0.64 - 1.52)	<.001
Annual Trend	0.02 (0.00 - 0.03)	.020	0.02 (0.01 - 0.03)	.005		
HDC	-0.03 (-0.67 - 0.62)	<.001	0.13 (-0.44 - 0.70)	<.001	0.15 (-0.34 - 0.63)	<.001
NPS	-0.34 (-0.99 - 0.30)	<.001	-0.25 (-0.82 - 0.32)	<.001	0.09 (-0.39 - 0.58)	<.001
SJS	-2.07 (-2.58 - -1.56)	<.001	-1.43 (-1.87 - -0.98)	<.001	0.65 (0.27 - 1.03)	<.001
SWH	0.44 (-0.18 - 1.05)	<.001	0.19 (-0.35 - 0.73)	<.001	-0.25 (-0.71 - 0.21)	<.001
Fringe	-1.17 (-1.64 - -0.69)	<.001	-0.47 (-0.88 - -0.05)	.029	0.70 (0.35 - 1.06)	<.001
Random Parts						
N _{Year.fac:site_code}	579		579		579	
N _{site_code}	156		156		156	
ICC _{Year.fac:site_code}	0.013		0.009		0.007	
ICC _{site_code}	0.644		0.658		0.510	
Observations	7350		7350		7350	

Table A-1. Summaries of best-fit mixed effects models of *Z. marina* deep extent, shallow extent, and depth range showing coefficient estimates (B), 95% confidence intervals (CI) and approximate p-values from Wald chi-squared test (p). Modeled intercepts estimate the average depth extent or range in the flats habitat of the CPS region in 2008. Annual trend estimates the change in the specified depth extent in meters per year, and region and habitat type coefficients estimate the average difference in meters between that region or habitat type and the intercept. Random effects summary includes the number of groups in each random effect as well as the Intra-class Correlation Coefficient and estimate of how correlated observations are within a group.

8 Appendix 3: Mixed-Modeling Methods

8.1 Model Fitting

To understand differences in the shallow and deep extents of eelgrass and its depth range among SVMP regions and between habitat types, we employed linear mixed-effects models. We modeled the deep extent, shallow extent, and depth range as a function of SVMP region, habitat type, year, and two-way interactions among these predictors (fixed effects) while accounting for variation among sites and years nested within sites (random effects). We modeled the fixed effect of year as a continuous variable because we were interested in testing for a temporal trend in depth limits, but we modeled the random effect of year within site as a factor, to allow for non-linear year-to-year variation within each site. Models were fit with maximum likelihood estimation using the lme4 package (Bates, Maechler, & Bolker, 2012) in R (R Core Team, 2013).

```
library(lme4)

#Shallow Extent -----

Shallow.lmer4 = lmer(Shallow.Extent ~ Year.cen * REGION + Year.cen * hab_type +
  REGION * hab_type + (1|site_code/Year.fac),
  data = mydata)

summary(Shallow.lmer4, correlation=FALSE)

## Linear mixed model fit by REML ['lmerMod']
## Formula:
## Shallow.Extent ~ Year.cen * REGION + Year.cen * hab_type + REGION *
##   hab_type + (1 | site_code/Year.fac)
##   Data: mydata
##
## REML criterion at convergence: 17207.5
##
## Scaled residuals:
##   Mi      1Q      Median      3Q      Max
## -8.5167  -0.3478   0.0791   0.4860   5.6393
```

```

## Random effects:
##
Groups              Name          Variance   Std.Dev.
## Year.fac:site_code (Intercept)  0.01422   0.1193
## site_code         (Intercept)  1.09026   1.0442
## Residual                    0.54383   0.7374
## Number of obs: 7350, groups: Year.fac:site_code, 579; site_code, 156
##
## Fixed effects:
##              Estimate   Std. Error   t value
## (Intercept) -0.944731    0.750116    -1.259
## Year.cen     0.019542    0.020582     0.950
## REGIONhdc   0.367792     0.916144     0.402
## REGIONnps   0.396933     0.829263     0.479
## REGIONsjs  -1.097138     0.805789    -1.362
## REGIONswh   0.409358     0.884692     0.463
## hab_typefringe -0.060175    0.770961    -0.078
## Year.cen:REGIONhdc -0.012962    0.024084    -0.538
## Year.cen:REGIONnps  0.002475    0.023161     0.107
## Year.cen:REGIONsjs  0.022678    0.020170     1.124
## Year.cen:REGIONswh  0.020717    0.022299     0.929
## Year.cen:hab_typefringe -0.016929    0.015300    -1.107
## REGIONhdc:hab_typefringe -0.249303    0.969569    -0.257
## REGIONnps:hab_typefringe -0.876007    0.896820    -0.977
## REGIONsjs:hab_typefringe -0.356539    0.842709    -0.423
## REGIONswh:hab_typefringe -0.191049    0.934160    -0.204

```

8.2 Variable Selection

We examined the importance of variables in the full models using Likelihood Ratio Tests (LRT) to assess the decrease in model fit associated with excluding a given variable from the model using the afex package (Singmann, Bolker, & Westfall, 2015) in R. Non-significant interactions were dropped, and LRTs repeated to select the final model.

```

library(afex)
library(pbkrtest)
library(MuMIn)

```

```

mixed(Shallow.lmer4, data = mydata, method = 'LRT')
## Fitting 7 (g)lmer() models:
## [.....]

##   Effect          df    Chisq      p.value
## 1 Year.cen         1     0.89       .35
## 2 REGION           4    15.42      .004
## 3 hab_type         1     0.01       .94
## 4 Year.cen:REGION  4     3.80      .43
## 5 Year.cen:hab_type 1     1.22      .27
## 6 REGION:hab_type  4     1.69      .79

# Drop interactions, Final Shallow Model:
Shallow.lmer4.1 = update(Shallow.lmer4, ~.-Year.cen:REGION-Year.cen:hab_type-
REGION:hab_type)

mixed(formula(Shallow.lmer4.1), data = mydata, method = 'LRT')
## Fitting 4 (g)lmer() models:
## [....]

##   Effect          df    Chisq      p.value
## 1 Year.cen         1     7.96      .005
## 2 REGION           4    57.75     <.0001
## 3 hab_type         1     4.91      .03

summary(Shallow.lmer4.1, correlation=FALSE)
## Linear mixed model fit by REML ['lmerMod']
## Formula:
## Shallow.Extent ~ Year.cen + REGION + hab_type + (1 | site_code/Year.fac)
##   Data: mydata
##
## REML criterion at convergence: 17187.7
##
## Scaled residuals:
##   Min       1Q       Median       3Q      Max
## -8.5149 -0.3463  0.0827  0.4862  5.6371
##
## Random effects:
##   Groups             Name             Variance  Std.Dev.
##   Year.fac:site_code (Intercept)  0.01427   0.1195
##   site_code          (Intercept)  1.07275   1.0357
##   Residual                               0.54386   0.7375
##
## Number of obs: 7350, groups: Year.fac:site_code, 579; site_code, 156
##
##

```

```

Fixed effects:
##              Estimate   Std. Error   t value
## (Intercept)  -0.567343   0.264017  -2.149
## Year.cen     0.018708   0.006616   2.828
## REGIONhdc    0.125558   0.290912   0.432
## REGIONnps   -0.249314   0.290639  -0.858
## REGIONsjs   -1.427032   0.228160  -6.255
## REGIONswh    0.192453   0.275465   0.699
## hab_typefringe -0.466374   0.212991  -2.190

```

Two other approaches to model selection are via AICc, and model comparison by parametric bootstrap. Both yield similar conclusions to the likelihood ratio test:

```

dredge(update(Shallow.lmer4, na.action='na.fail', REML=FALSE))
## Global model call: lmer(formula = Shallow.Extent ~ Year.cen * REGION + Year.cen *
##   hab_type + REGION * hab_type + (1 | site_code/Year.fac),
##   data = mydata, REML = FALSE, na.action = "na.fail")
## ---
## Model selection table
##   (Int)   hab_typ   REG   Yer.cen   hab_typ:REG   hab_typ:Yer.cen
## 24 -0.5613   +       +   0.030390           +
## 8  -0.5674   +       +   0.018700
## 7  -1.0090           +   0.018790
## 40 -0.5722   +       +   0.003168
## 56 -0.5649   +       +   0.020220           +
## 4  -0.5588   +       +
## 39 -1.0050           +   0.002677
## 32 -0.9127   +       +   0.029800           +   +
## 16 -0.9488   +       +   0.018330           +
## 3  -1.0040           +
## 48 -0.9983   +       +   0.002584           +
## 64 -0.9458   +       +   0.019230           +   +
## 12 -1.0070   +       +           +
## 5  -1.3980           0.017390
## 22 -1.1550   +           0.028520           +
## 6  -1.1530   +           0.017350
## 1
## 2  -1.1500   +
##

```


	REG:Yer.cen	df	logLik	AICc	delta	weight
## 24		11	-8584.345	17190.7	0.00	0.392
## 8		10	-8585.476	17191.0	0.26	0.345
## 7		9	-8587.931	17193.9	3.16	0.081
## 40	+	14	-8583.155	17194.4	3.64	0.064
## 56	+	15	-8582.505	7195.1	4.35	0.045
## 4		9	-8589.456	17196.9	6.21	0.018
## 39	+	13	-8585.513	17197.1	6.35	0.016
## 32		15	-8583.561	17197.2	6.46	0.016
## 16		14	-8584.643	17197.3	6.62	0.014
## 3		8	-8591.943	17199.9	9.18	0.004
## 48	+	18	-8582.272	17200.6	9.91	0.003
## 64	+	19	-8581.663	17201.4	10.70	0.002
## 12		13	-8588.455	17203.0	12.23	0.001
## 5		5	-8615.170	17240.3	49.62	0.000
## 22		7	-8613.316	17240.6	49.92	0.000
## 6		6	-8614.349	17240.7	49.98	0.000
## 1		4	-8618.566	17245.1	54.41	0.000
## 2		5	-8617.730	17245.5	54.74	0.000

##

Models ranked by AICc(x)

Random terms (all models):

'1 | site_code/Year.fac'

#PBmodcomp(Shallow.lmer4, Shallow.lmer4.1)

Parametric bootstrap test; time: 433.62 sec; samples: 1000 extremes: 650;

*# large : Shallow.Extent ~ Year.cen * REGION + Year.cen * hab_type + REGION **

hab_type + (1 | site_code/Year.fac)

small : Shallow.Extent ~ Year.cen + REGION + hab_type + (1 | site_code/Year.fac)

#	stat	df	p.value
# LRT	7.3705	9	0.5986
# PBtest	7.3705		0.6503

#PBmodcomp(Shallow.lmer4.1, update(Shallow.lmer4.1, .~-hab_type))

Parametric bootstrap test; time: 345.23 sec; samples: 1000 extremes: 36;

large : Shallow.Extent ~ Year.cen + REGION + hab_type + (1 | site_code/Year.fac)

small : Shallow.Extent ~ Year.cen + REGION + (1 | site_code/Year.fac)

#	stat	df	p.value
# LRT	4.8739	1	0.02727 *
# PBtest	4.8739		0.03696 *

8.3 Model Inference

Parametric bootstrap was used to compute confidence intervals of the predicted means for each modeled category using the boot package (Canty & Ripley, 2015) in R:

```
library(boot)

# Make lmer prediction function for bootstrapping
predFun <- function(fit) {
  predict(fit, newDat, re.form=NA)
}

#create data for predictions
newDat = data.frame(REGION = rep(c('cps', 'hdc', 'nps', 'swh', 'sjs'), 2),
  hab_type = c(rep('flats', 5), rep('fringe', 5)),
  Year.cen = rep(0, 10),
  x = c(rep(500, 5), rep(450, 5)))

bbS <- bootMer(Shallow.lmer4.1, nsim=999, FUN=predFun, seed=101)
Shallow.CI = newDat
Shallow.CI$Estimate = NA
Shallow.CI$Upper = NA
Shallow.CI$Lower = NA
ci.type = c('basic', 'perc')

for(i in 1:10){
  Shallow.CI$Estimate[i] <- boot.ci(bbS, type=ci.type, index=i)$t0
  Shallow.CI$Upper[i] <- boot.ci(bbS, type=ci.type, index=i)$basic[,4]
  Shallow.CI$Lower[i] <- boot.ci(bbS, type=ci.type, index=i)$basic[,5]
}

print(Shallow.CI)
```

##	REGION	hab_type	Year.cen	x	Estimate	Upper	Lower
## 1	cps	flats	0	500	-0.5673434	-1.0735873	-0.09750524
## 2	hdc	flats	0	500	-0.4417852	-0.9889047	0.12485317
## 3	nps	flats	0	500	-0.8166575	-1.3168701	-0.35510432
## 4	swh	flats	0	500	-0.3748905	-0.9397354	0.16930598
## 5	sjs	flats	0	500	-1.9943750	-2.4068161	-1.56602166
## 6	cps	fringe	0	450	-1.0337171	-1.3729712	-0.69926365
## 7	hdc	fringe	0	450	-0.9081589	-1.3293919	-0.42728977
## 8	nps	fringe	0	450	-1.2830312	-1.7677466	-0.81222697
## 9	swh	fringe	0	450	-0.8412642	-1.3111446	-0.42117472
## 10	sjs	fringe	0	450	-2.4607488	-2.7481125	-2.18479531

Pairwise differences among Regional predictions were assessed using least-squares means and Tukey's Honestly Significant Difference (HSD) with the lsmeans package (Lenth & Herv, 2015) in R.

```
library(lsmeans)

Shallow.Mean = lsmeans(Shallow.lmer4.1, pairwise~REGION, adjust="Tukey")
Shallow.Mean

## $lsmeans
## REGION    lsmean      SE        df      lower.CL    upper.CL
## cps      -0.8005302  0.1951206  149.81    -1.186074    -0.4149863
## hdc      -0.6749721  0.2422883  148.05    -1.153762    -0.1961822
## nps      -1.0498444  0.2240173  148.68    -1.492513    -0.6071755
## sjs      -2.2275619  0.1550067  149.92    -2.533842    -1.9212821
## swh      -0.6080773  0.2225476  148.94    -1.047836    -0.1683188
##
## Results are averaged over the levels of: hab_type
## Confidence level used: 0.95
##
## $contrasts
## contrast    estimate      SE        df      t.ratio    p.value
## cps - hdc   -0.12555814  0.2909145  148.89    -0.432     0.9927
## cps - nps    0.24931417  0.2906419  148.94     0.858     0.9117
## cps - sjs    1.42703169  0.2281646  150.65     6.254    <.0001
## cps - swh   -0.19245288  0.2754679  149.92    -0.699     0.9565
## hdc - nps    0.37487231  0.3260957  148.18     1.150     0.7798
## hdc - sjs    1.55258983  0.2757696  149.03     5.630    <.0001
## hdc - swh   -0.06689473  0.3167686  148.61    -0.211     0.9996
## nps - sjs    1.17771752  0.2685795  149.07     4.385     0.0002
## nps - swh   -0.44176705  0.3118402  148.68    -1.417     0.6180
## sjs - swh   -1.61948457  0.2590764  150.08    -6.251    <.0001
##
## Results are averaged over the levels of: hab_type
## P value adjustment: tukey method for comparing a family of 5 estimates
#lsmeans(Shallow.lmer4.1, pairwise~hab_type, adjust="Tukey")
```

We report marginal pseudo-R2 (Nakagawa & Schielzeth, 2012) as a quantification of the variance explained by fixed effects in our models.

```
library(MuMIn)

r.squaredGLMM(Shallow.lmer4.1)

##      R2m      R2c
## 0.2272085 0.7422918
```

The same process was used to examine deep extent and depth range, shown below without annotation.

```
##### Deep Extent #####

Deep.lmer4 = lmer(Deep.Extent ~ Year.cen * REGION + Year.cen * hab_type +
  REGION * hab_type + (1|site_code/Year.fac),
  data = mydata)

#dredge(update(Deep.lmer4, na.action='na.fail', REML=FALSE))

mixed(Deep.lmer4, data = mydata, method = 'LRT')
## Formula (the first argument) converted to formula.
## REML argument to lmer() set to FALSE for method = 'PB' or 'LRT'
## Fitting 7 (g)lmer() models:
## [.....]
##      Effect      df    Chisq    p.value
## 1  Year.cen      1     0.06     .81
## 2  REGION        4    16.44 **    .002
## 3  hab_type      1     0.32     .57
## 4  Year.cen:REGION  4     3.02     .55
## 5  Year.cen:hab_type  1     0.52     .47
## 6  REGION:hab_type  4     2.51     .64
#### Drop Interactions ####

Deep.lmer4.1 = update(Deep.lmer4, .~-Year.cen:hab_type-
  Year.cen:REGION-REGION:hab_type)

mixed(Deep.lmer4.1, data = mydata, method = 'LRT')
## Formula (the first argument) converted to formula.
## REML argument to lmer() set to FALSE for method = 'PB' or 'LRT'
## Fitting 4 (g)lmer() models:
## [....]
##      Effect      df    Chisq    p.value
## 1  Year.cen      1     5.39     * .02
## 2  REGION        4    86.13     *** <.0001
## 3  hab_type      1    22.54     *** <.0001
```

```

summary(Deep.lmer4.1, correlation=FALSE)
## Linear mixed model fit by REML ['lmerMod']
## Formula:
## Deep.Extent ~ Year.cen + REGION + hab_type + (1 | site_code/Year.fac)
## Data: mydata
##
## REML criterion at convergence: 19427
##
## Scaled residuals:
##      Min          1Q          Median          3Q          Max
## -5.8205   -0.4965   -0.0194    0.4751    5.5705
##
## Random effects:
## Groups              Name          Variance  Std.Dev.
## Year.fac:site_code  (Intercept)  0.02736   0.1654
## site_code           (Intercept)  1.37575   1.1729
## Residual                        0.73437   0.8570
## Number of obs: 7350, groups: Year.fac:site_code, 579; site_code, 156
##
## Fixed effects:
##              Estimate      Std. Error    t value
## (Intercept)  -1.642671    0.299469   -5.485
## Year.cen      0.018697    0.008055    2.321
## REGIONhdc    -0.027965    0.329967   -0.085
## REGIONnps   -0.343117    0.329635   -1.041
## REGIONsjs   -2.072239    0.258859   -8.005
## REGIONswh    0.435014    0.312516    1.392
## hab_typefringe -1.166626    0.241566   -4.829
r.squaredGLMM(Deep.lmer4.1)
##      R2m      R2c
##      0.3537078  0.7779553
##mixed(Deep.lmer4.1, data = data, method = 'PB')
lsmeans(Deep.lmer4.1, pairwise~REGION, adjust="Tukey")
## $lsmeans
## REGION  lsmean      SE          df      lower.CL      upper.CL
## cps     -2.225984  0.2213389  149.76  -2.663335  -1.788634
## hdc     -2.253949  0.2747886  147.91  -2.796967  -1.710930
## nps     -2.569101  0.2540427  148.46  -3.071108  -2.067094
## sjs     -4.298224  0.1758612  149.95  -4.645710  -3.950737
## swh     -1.790970  0.2524481  148.90  -2.289814  -1.292127
##
## Results are averaged over the levels of: hab_type
## Confidence level used: 0.95

```

```
##
## $contrasts
## contrast      estimate      SE      df      t.ratio    p.value
## cps - hdc      0.02796465  0.3299696  148.80    0.085     1.0000
## cps - nps      0.34311678  0.3296390  148.80    1.041     0.8359
## cps - sjs      2.07223946  0.2588650  150.68    8.005     <.0001
## cps - swh     -0.43501370  0.3125200  149.95   -1.392     0.6338
## hdc - nps      0.31515213  0.3698170  147.99    0.852     0.9136
## hdc - sjs      2.04427481  0.3128169  148.98    6.535     <.0001
## hdc - swh     -0.46297835  0.3593010  148.54   -1.289     0.6987
## nps - sjs      1.72912268  0.3046299  148.94    5.676     <.0001
## nps - swh     -0.77813048  0.3536860  148.55   -2.200     0.1854
## sjs - swh     -2.50725315  0.2939493  150.16   -8.530     <.0001
##
## Results are averaged over the levels of: hab_type
## P value adjustment: Tukey method for comparing a family of 5 estimates
```

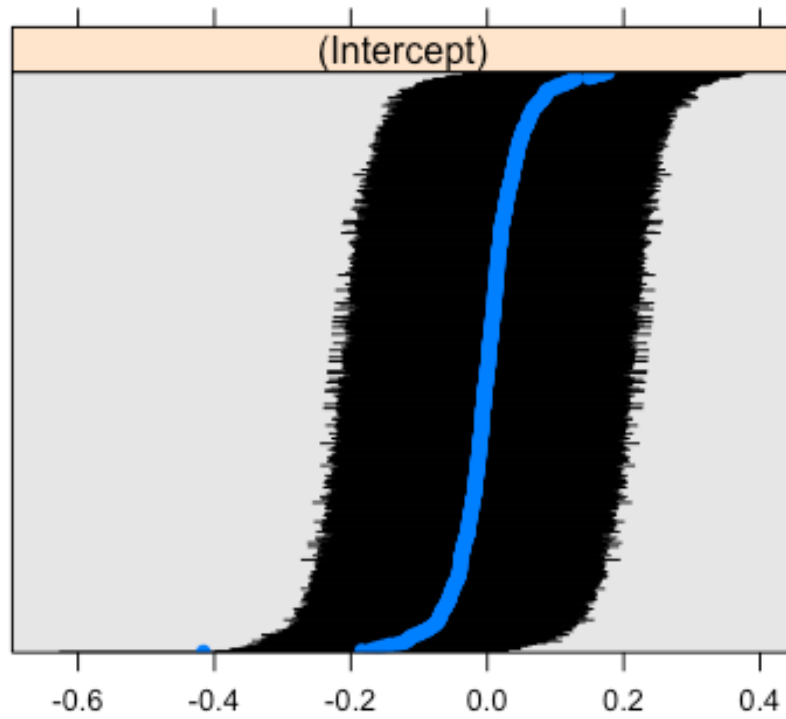
8.4 *Random Effects Exploration*

Site-level random effects quantify the difference between observed values at the site, and the values predicted by year, habitat type, and region. As such, they are a useful tool for identifying sites that are particularly abnormal, as well as understanding the overall patterns of variability among sites.

They can quickly be plotted like this:

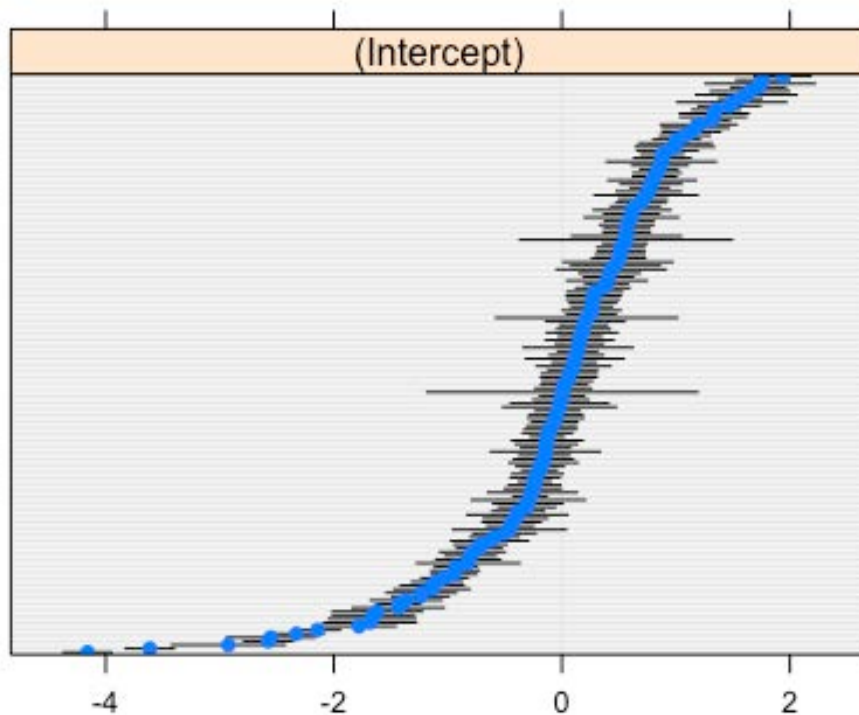
```
library(lattice)
##
## Attaching package: 'lattice'
##
## The following object is masked from 'package:boot':
##
##   melanoma
dotplot(ranef(Shallow.lmer4.1, condVar=TRUE))
## $`Year.fac:site_code`
```

Year.fac:site_code



```
##  
## $site_code
```

site_code



Below demonstrates a more-involved approach that examines the value of sub-regions for the SVM. This could help to understand if the Straits of Juan de Fuca should be modeled differently than the San Juan archipelago.

```
library(ggplot2)
meta = ddply(mydata, .(site_code), summarise,
  east    = mean(POINT_X),
  north   = mean(POINT_Y),
  sub_region = unique(SUBREGION_)[1])

fit = Shallow.lmer4.1
fit = Deep.lmer4.1
fit = Range.lmer4.2

fits = list(Deep.lmer4.1, Shallow.lmer4.1, Range.lmer4.2)
plots = vector('list', 3)

for(i in 1:3){
  fit  = fits[[i]]
  rand = ranef(fit, condVar=TRUE)
```



```

Var    = attr(rand, which='postVar')
toplot.a = data.frame(site_code = rownames(rand$site_code),
                      int      = unname(rand$site_code),
                      SE       = sqrt(c(attr(rand$site_code,'postVar'))),
                      Response = names(fit@frame[1]))
plots[[i]] = toplot.a
}

toplot = rbind(plots[[1]],plots[[2]],plots[[3]])

#toplot = data.frame('rand' = ranef(Shallow.lmer4.1)$site_code, 'site_code'=rownames(ranef(Shallow.lmer4.1)$site_code))
#toplot1 = merge(toplot, SVMP_Metadata, by='site_code', drop=TRUE)
#toplot1 = merge(toplot1, meta, by='site_code')

# ggplot(toplot1,
#   aes(y = int, colour = sub_region, ymin = int-SE, ymax=int+SE,
#       x = reorder(site_code,int)))+
#   geom_pointrange()+
#   theme(axis.text.x=element_text(angle=90),
#         legend.position = 'top')+
#   xlab("Site")+ylab("Random Effect Offset (m MLLW)")+
#   #facet_wrap(~region, scales='free_x')
#   facet_grid(Response~region, scales = 'free', space='free')

myplot = (vector('list',3))
for(i in 1:3){
  toplot1 <- merge(plots[[i]], SVMP_Metadata, by='site_code', drop=TRUE)
  toplot1 <- merge(toplot1, meta, by='site_code')
  myplot[[i]]<-ggplot(toplot1,
    aes(y = int,colour = sub_region,ymin = int-SE, ymax=int+SE,
        x = reorder(site_code,int)))+
    geom_pointrange()+
    theme(axis.text.x=element_text(angle=90),
          legend.position = 'top')+
    xlab("Site")+ylab("Random Effect Offset (m MLLW)")+
    #facet_wrap(~region, scales='free_x')
    facet_grid(.~region, scales = 'free', space='free')+
    theme_bw()
}
## [[1]]

```

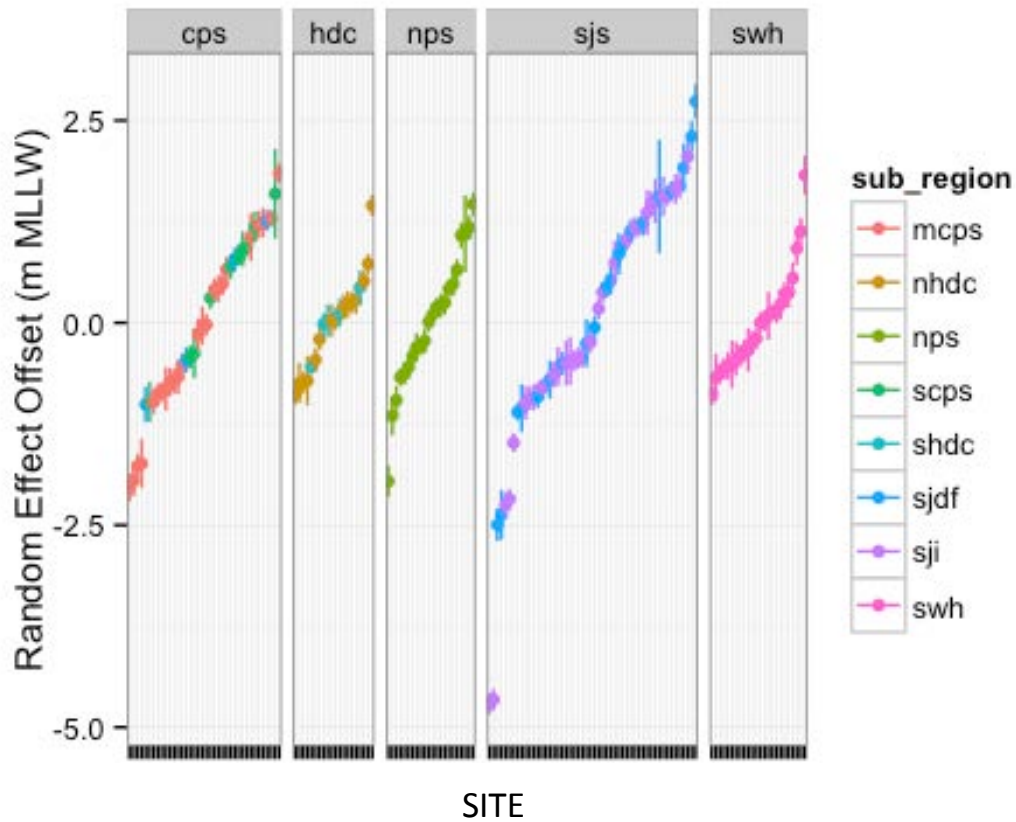


Fig A-3.1 Site-to-site variability in deep extent as function of region and sub-region, as estimated by linear mixed effects models. Error-bars and random-effects estimates are conditional on the fixed-effects estimates, that is, they do not account for uncertainty in the estimation of the fixed effects.

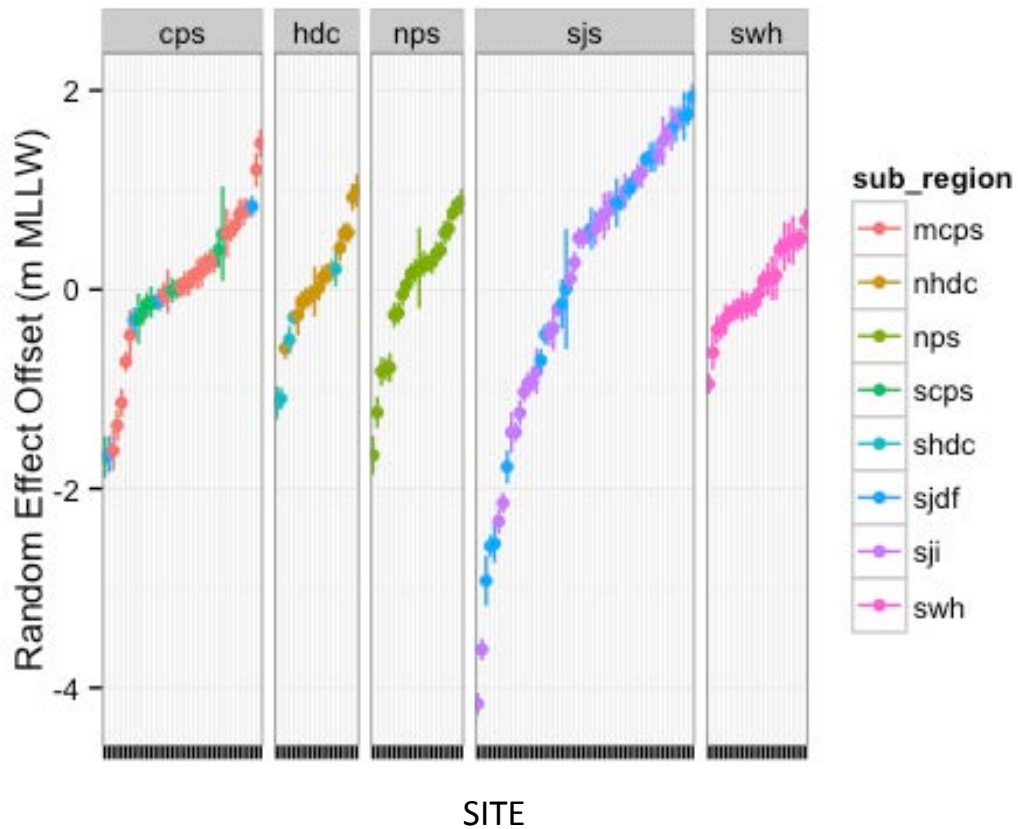


Fig A-3.2 Site-to-site variability in shallow extent as function of region and sub-region, as estimated by linear mixed effects models. Error-bars and random-effects estimates are conditional on the fixed-effects estimates, that is, they do not account for uncertainty in the estimation of the fixed effects.

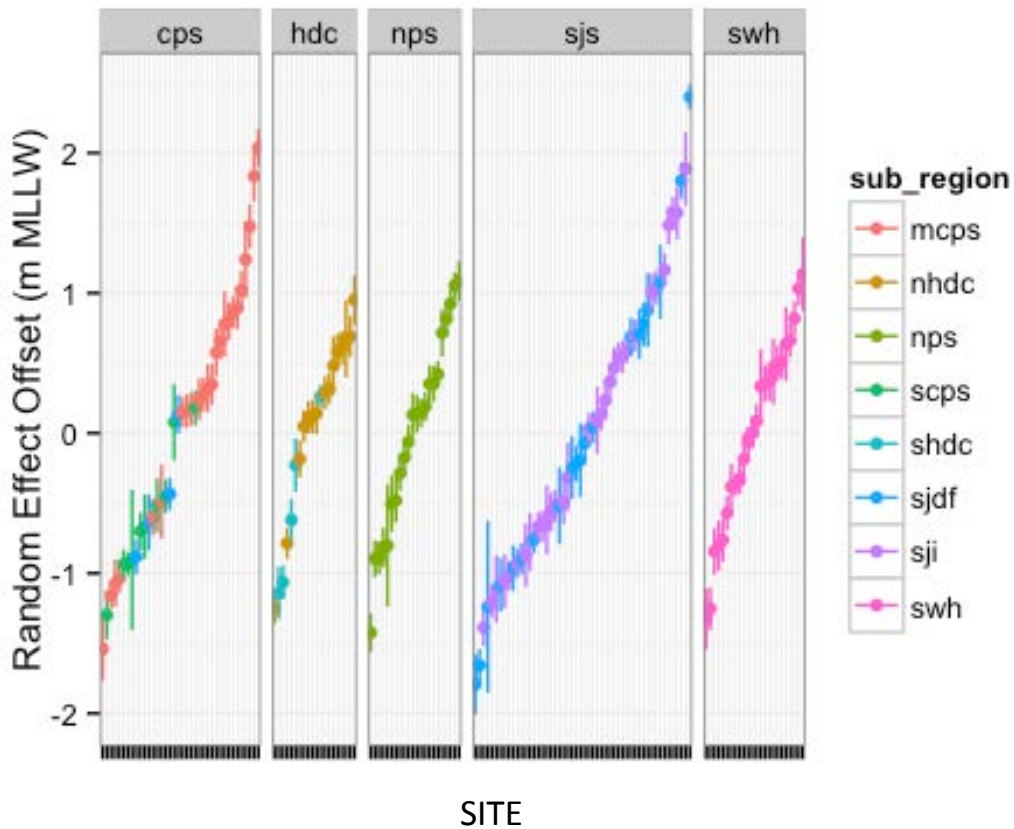


Fig A-3.3 Site-to-site variability in depth range as function of region and sub-region, as estimated by linear mixed effects models. Error-bars and random-effects estimates are conditional on the fixed-effects estimates, that is, they do not account for uncertainty in the estimation of the fixed effects.

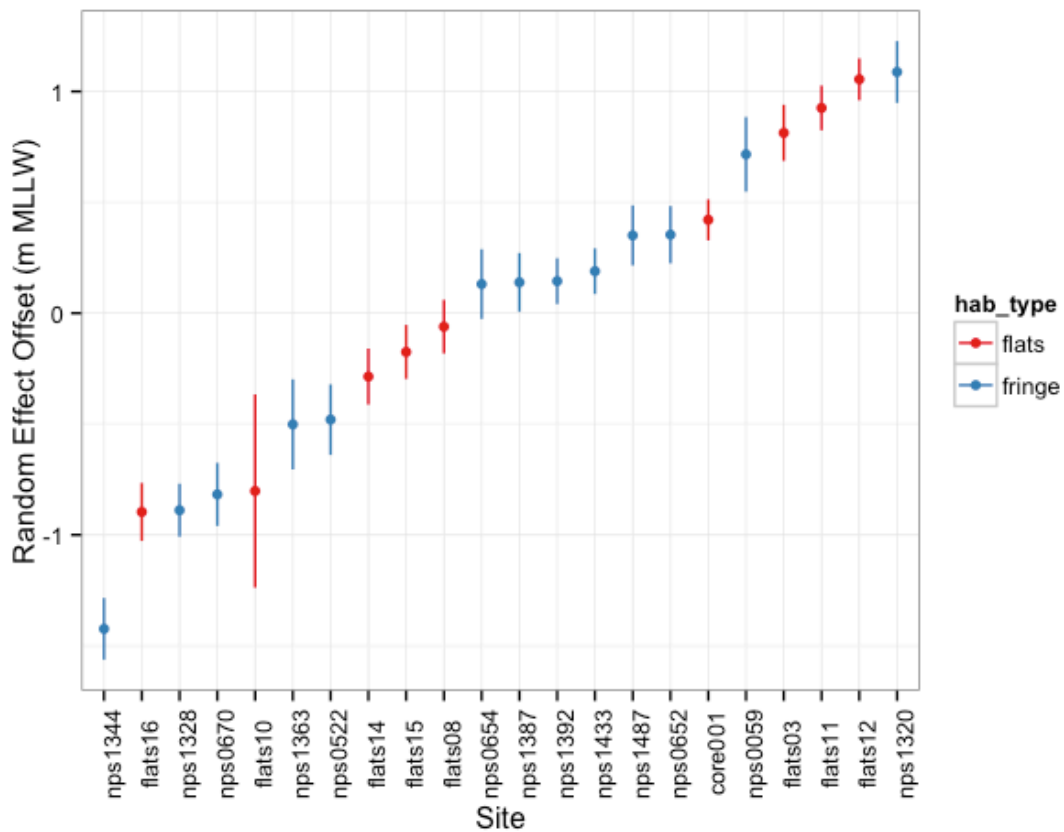


Fig A-3.4 Site-to-site variability in depth range in the NPS region as function of habitat type, as estimated by linear mixed effects models. Error-bars and random-effects estimates are conditional on the fixed-effects estimates, that is, they do not account for uncertainty in the estimation of the fixed effects.

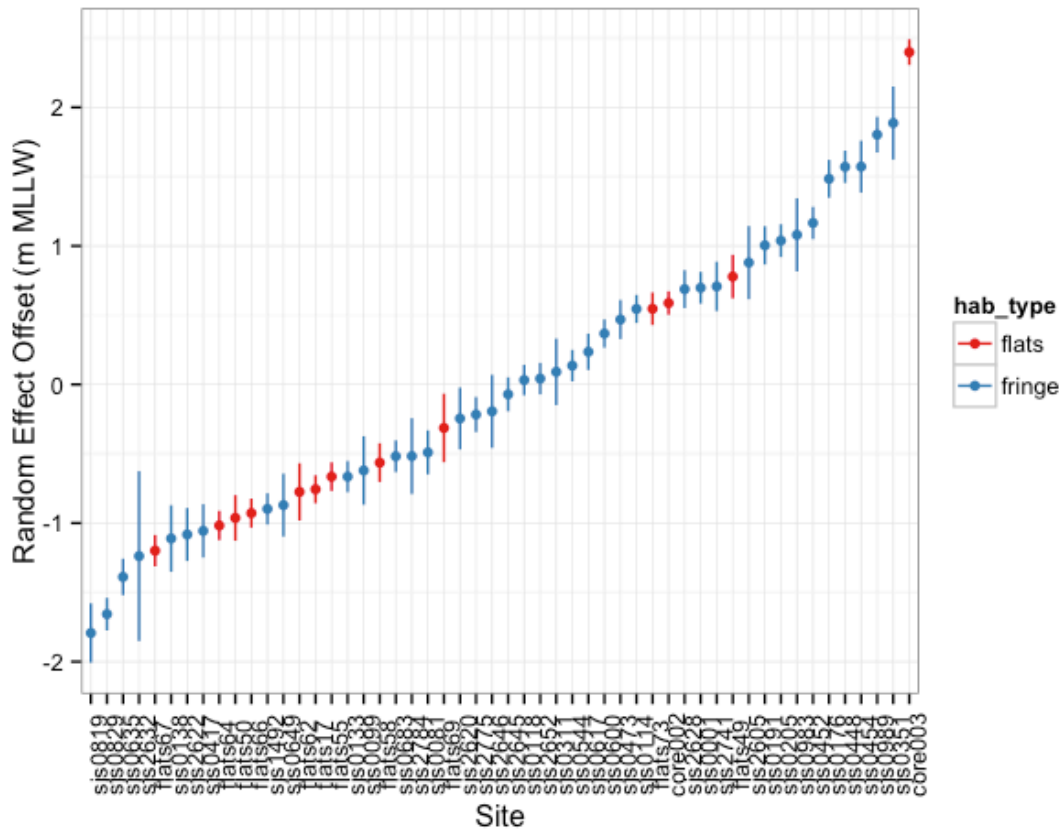


Fig A-3.5 Site-to-site variability in depth range in the SJS region as function of habitat type, as estimated by linear mixed effects models. Error-bars and random-effects estimates are conditional on the fixed-effects estimates, that is, they do not account for uncertainty in the estimation of the fixed effects.

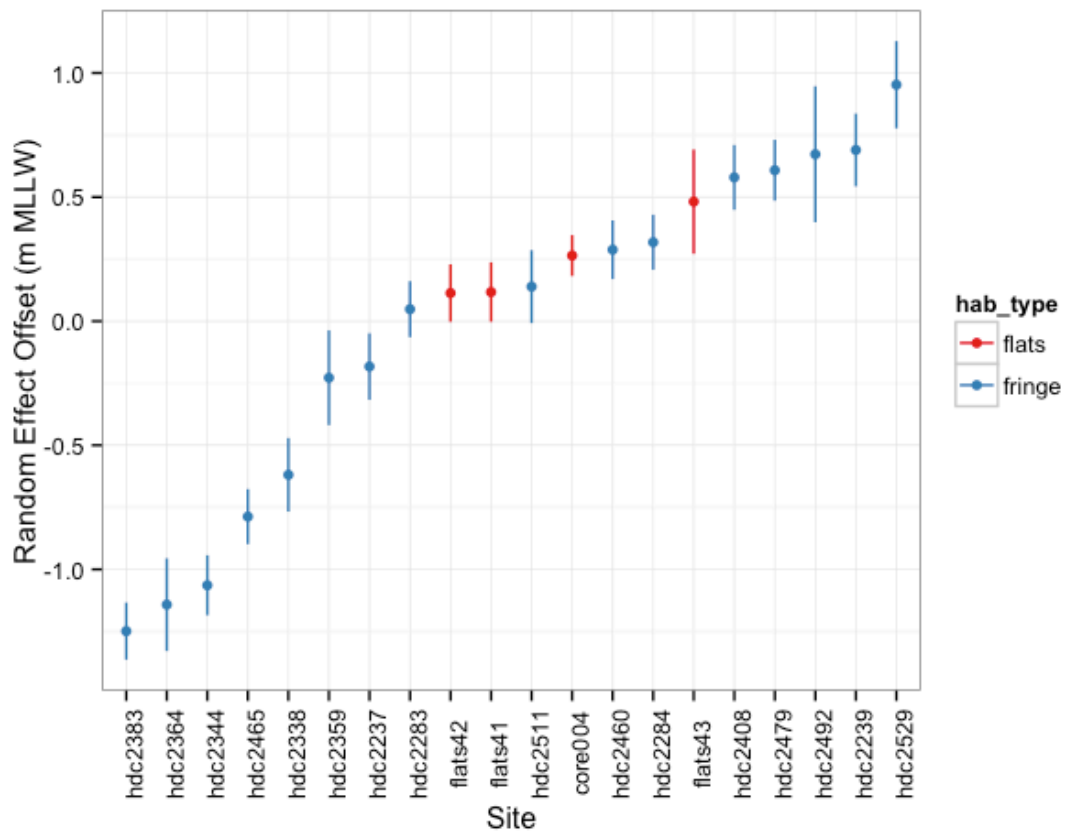


Fig A-3.6 Site-to-site variability in depth range in the HDC region as function of habitat type, as estimated by linear mixed effects models. Error-bars and random-effects estimates are conditional on the fixed-effects estimates, that is, they do not account for uncertainty in the estimation of the fixed effects.

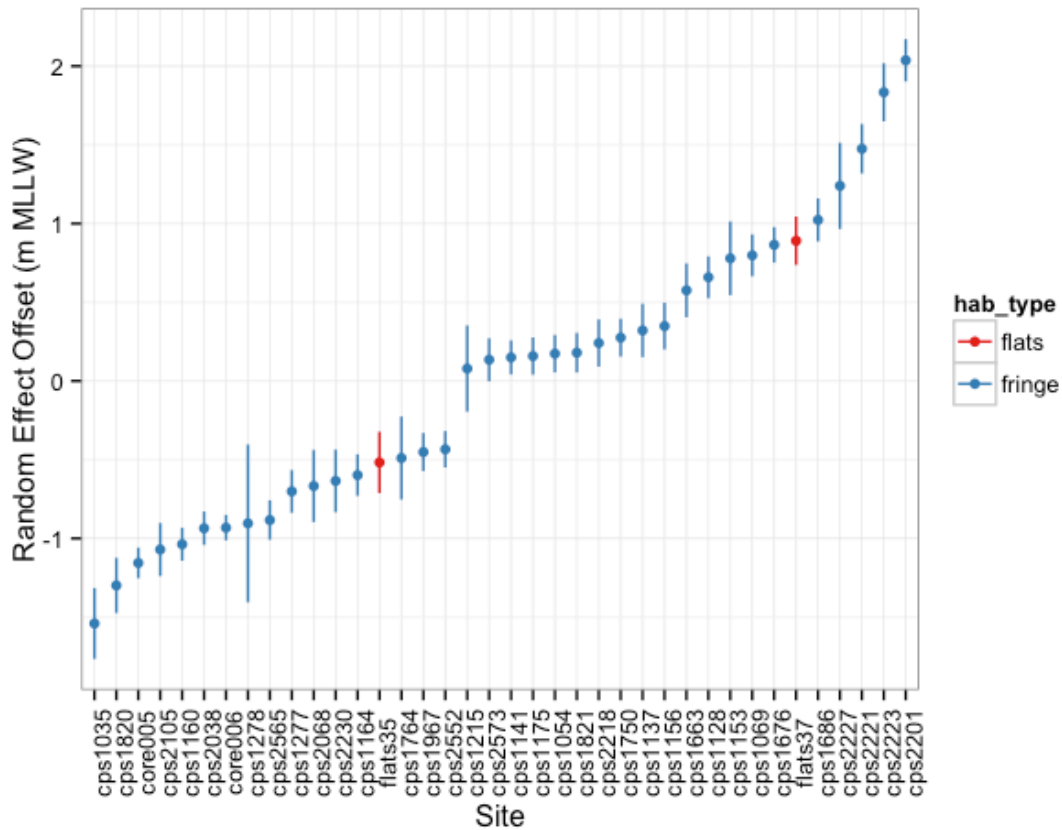


Fig A-3.7 Site-to-site variability in depth range in the CPS region as function of habitat type, as estimated by linear mixed effects models. Error-bars and random-effects estimates are conditional on the fixed-effects estimates, that is, they do not account for uncertainty in the estimation of the fixed effects.

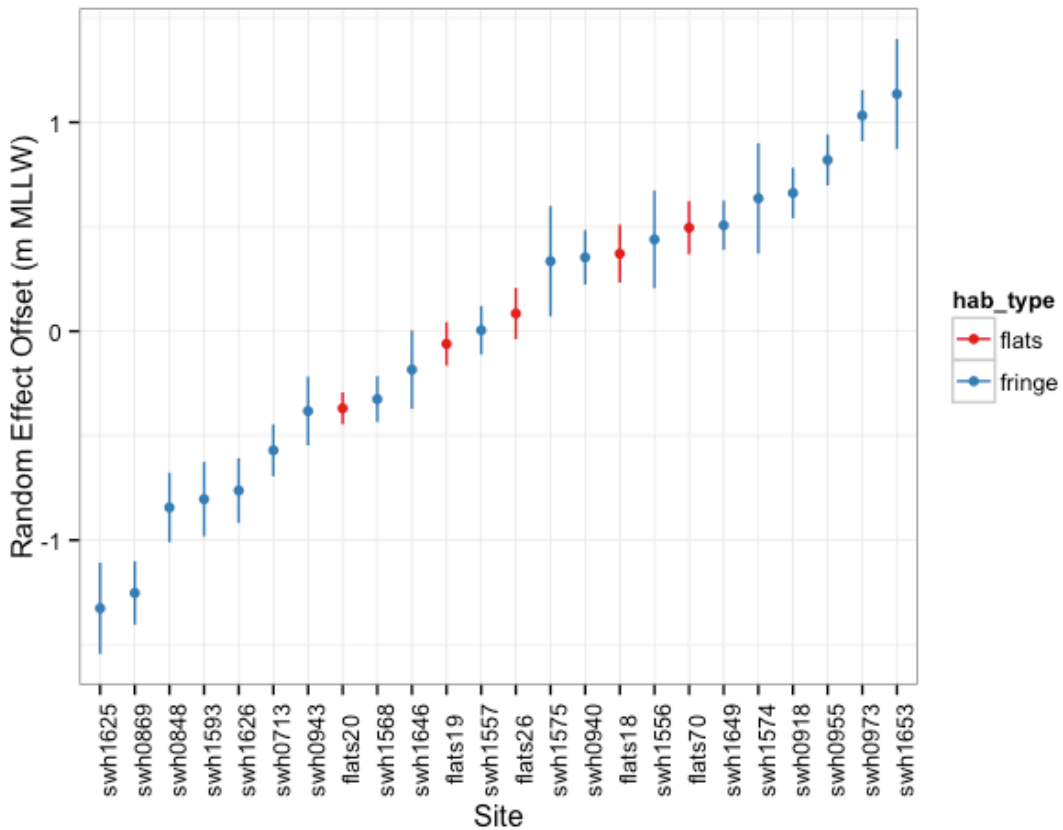


Fig A-3.9 Site-to-site variability in depth range in the SWH region as function of habitat type, as estimated by linear mixed effects models. Error-bars and random-effects estimates are conditional on the fixed-effects estimates, that is, they do not account for uncertainty in the estimation of the fixed effects.

9 Appendix 4: Extreme Low Water Data

Tide Station	Extreme Low Water (m below MLLW)	
	50% AEP ¹	10% AEP
Neah Bay	0.9	1
Port Angeles	1	1.2
Port Townsend	1	1.2
Seattle	1.1	1.3
Friday Harbor	0.9	1.1
Cherry Point	1	1.1

1. Annual Exceedance Probability: The probability of a more extreme water level in any year.

Table A-4.1 Extreme water levels at NOAA tide gauges in the study area. Data from NOAA: http://tidesandcurrents.noaa.gov/est/est_states.shtml?region=wa

