Comparison of shallow-water seston among biogenic habitats on tidal flats

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Aquatic structure-formers have the potential to establish mosaics of seston in shallow water if they modify the relative amounts of deposition (or filtration) and resuspension of particles. By sampling surface water adjacent to Lagrangian drifters traveling 0.1 to 2 m above the bottom, we tested the modification of seston in water masses flowing over two marine foundation species (native eelgrass, *Zostera marina*; introduced oysters, *Magallana* [recently *Crassostrea*] *gigas*) in comparison to unstructured tidal flats. Water properties were examined at five intertidal sites in Washington State, USA, each with 27 drifts (three drifts at different stages of the tidal cycle in each of three patches of three habitat types; drift distance 116 m (109SD), duration 24 min (15SD)). At the initiation of each drift, habitat differences in water properties were already apparent: chlorophyll-*a* and total suspended solid (TSS) concentrations were greater in structured habitats than bare, and TSS was also inversely related to water depth. Water flowed more slowly across eelgrass than other habitat types. During drifts, TSS generally increased, especially in shallow water, but without habitat differences; chlorophyll-*a* showed no consistent change during drifts. At higher TSS concentrations, quality in terms of organic content declined, and this relationship was not habitat-specific. However, quality in terms of chlorophyll-*a* concentration increased with TSS, as well as being greater in water over eelgrass than over other habitat types. These results support widespread mobilization of seston in shallow water ebbing or flooding across Washington State's tidal flats, especially as water passes into patches of biogenic species.

1 Comparison of shallow-water seston among biogenic habitats on tidal flats

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11 Running head: Shallow-water seston on tidal flats

12   **ABSTRACT**

13   Aquatic structure-formers have the potential to establish mosaics of seston in shallow water if

14   they modify the relative amounts of deposition (or filtration) and resuspension of particles. By

15   sampling surface water adjacent to Lagrangian drifters traveling 0.1 to 2 m above the bottom, we

16   tested the modification of seston in water masses flowing over two marine foundation species

17   (native eelgrass, *Zostera marina*; introduced oysters, *Magallana* [recently *Crassostrea*] *gigas*) in

18   comparison to unstructured tidal flats. Water properties were examined at five intertidal sites in

19   Washington State, USA, each with 27 drifts (three drifts at different stages of the tidal cycle in

20   each of three patches of three habitat types; drift distance 116 m (109SD), duration 24 min

21   (15SD)). At the initiation of each drift, habitat differences in water properties were already

22   apparent: chlorophyll-*a* and total suspended solid (TSS) concentrations were greater in structured

23   habitats than bare, and TSS was also inversely related to water depth. Water flowed more slowly

24   across eelgrass than other habitat types. During drifts, TSS generally increased, especially in

25   shallow water, but without habitat differences; chlorophyll-*a* showed no consistent change

26   during drifts. At higher TSS concentrations, quality in terms of organic content declined, and this

27   relationship was not habitat-specific. However, quality in terms of chlorophyll-*a* concentration

28   increased with TSS, as well as being greater in water over eelgrass than over other habitat types.

29   These results support widespread mobilization of seston in shallow water ebbing or flooding

30   across Washington State's tidal flats, especially as water passes into patches of biogenic species.

32   Keywords: biogenic, ecosystem engineers, flow, oysters, seagrass, top-down control

INTRODUCTION

The shallow water on tidal flats that bathes intertidal organisms is highly variable, such that the chemical and physical properties of the water introduce temporal variability for intertidal organisms beyond that of just tidal wetting and drying (e.g., particulates and light [Ralph et al. 2007], oxygen and carbon dioxide [Duarte et al. 2013]). The amount and composition of suspended particulate matter, termed seston, has important implications for the productivity of macrophytes (de Boer 2007) and benthic suspension feeders (e.g. Kang et al. 2003). Quantifying how biogenic species influence the mobilization and removal of particles improves understanding of the feedbacks governing local heterogeneity in water properties (Widdows et al. 2000, de Boer 2007). In this study, we track water properties across tidal flats and compare unstructured habitat to two foundation species: eelgrass (*Zostera marina*) and oysters (*Magallana* [recently *Crassostrea*] *gigas*).

These two species are expected to modify water properties in different ways. As suspension-feeders, oysters remove particles, and water passing across oyster beds typically declines in chlorophyll concentration (Grizzle et al. 2006, 2008, Grangere et al. 2010, Plutchak et al. 2010, Wheat and Ruesink 2013). Away from the footprint of oysters, mixing and compensatory phytoplankton dynamics obscure this trophic effect (Dame and Libes 1993, Plutchak et al. 2010). Seagrass influences seston predominantly as a side effect of altering water motion, since more rapid flow or turbulence can lift and transport larger, denser particles (Widdows et al. 2008, Wilkie et al. 2012). Empirically, seagrass beds buffer against water motion and accumulate fine particles (Fonseca et al. 1982, Kenworthy et al. 1982). However, effects on flow velocity and turbulence within and around structure are sensitive to a variety of parameters that naturally vary in the field, including the fraction of the water column occupied

58 by structure (Moore 2004, Hasegawa et al. 2008, Luhar et al. 2008), and the density and

59 flexibility of structural elements (Adhitya et al. 2014, Houser et al. 2015). Seagrass contributes

60 tall, flexible structure, whereas oysters are stiff and typically shorter (although reefs can build up

61 from gregarious settlement and particle trapping; Walles et al. 2015). Bivalves such as hard

62 clams can intensify erosional processes and accordingly augment seston, even while drawing

63 down phytoplankton biomass overall (Porter et al. 2013). Similarly, benthic animals that

64 bioturbate sediment or graze biofilms are associated with increased erodability of sediments

65 (Widdows et al. 2000, Guizien et al 2014). However, biogenic species might block the sediment

66 surface and therefore reduce the surface area subject to resuspension. Dense seagrass in tidally

67 dominated flow regimes is expected to slow laminar flow or divert flow away from sediment

68 through skimming flow (Koch and Gust 1999, de Boer 2007), whereas oyster reefs may increase

69 turbulent flow with ancillary effects on particle transport (Colden et al. 2016).

70   On intertidal flats, the water transiting across a particular patch can vary dramatically in

71 depth and motion through the tidal cycle. The consequences for water column seston are,

72 however, difficult to predict because of covarying factors that may act in opposite directions.

73 Specifically, shallow water near low tide may allow orbital motion of small waves to resuspend

74 sediment, a process that no longer interacts with the bottom as depth increases (Green 2011). Yet

75 current speed could be increasing from slack low tide to mid-tide, increasing resuspension even

76 as depth increases (Widdows et al. 2000, Orvain et al. 2014). At the same time, given evidence

77 of vertical gradients of some particle types in shallow water (Judge et al. 1993, Guizien et al.

78 2014), benthic effects on water sampled at the surface may decline as depth increases simply due

79 to distance from the bottom. As water depth increases, seagrass occupies a smaller fraction of the

80 water column and its effects on surface water decline (Koch 2001, Luhar et al. 2008). Similarly,

81   deeper water depths dilute the effects of suspension-feeders on a per-volume basis. Thus surface

82   water properties might be expected to become more homogeneous across a mosaic of habitat

83   types as water depth increases; that is, depth × habitat interaction.

84   To empirically demonstrate the spatio-temporal heterogeneity of water properties on tidal

85   flats, we sampled surface water over different habitat types, at multiple water depths experienced

86   through the tidal cycle. We expected that water velocity would increase from low to mid-tide

87   depths and that eelgrass would baffle currents. We expected water depth × habitat interactions

88   for seston in which structured habitats influenced water properties at shallower depths, but

89   heterogeneity was reduced among habitat types as surface water was farther from the sediment.

90   For water properties of total suspended solids and chlorophyll-*a*, we evaluated both the static

91   differences among habitat types based on point samples and the dynamic changes as water

92   transited over bare tidal flat, eelgrass, or oysters.

93

94   **METHODS**

95   **Study sites**

96   The study took place at five low intertidal sites in Washington State, where eelgrass (*Zostera*

97   *marina*), oysters (*Magallana gigas*), and unstructured bare mudflat co-occur near mean lower

98   low water. The sites occupied distinct bays: Willapa Bay on the outer coast (46.5°N, 124.0°W),

99   Samish Bay in north Puget Sound (48.6°N, 122.5°W), Case Inlet in south Puget Sound (47.3°N,

100   122.8°W), Port Gamble (47.8°N, 122.6°W) and Dabob Bay (47.8°N, 122.8°W) in Hood Canal,

101   which is a natural fjord connected to Puget Sound (Fig. 1A). These tidal flats are exposed to air

102   on extreme low tides and experience a mean tidal range of 2.1 m (Samish Bay, Willapa Bay) to

103   3.1 m (Case Inlet). Sediment type spans a range of sandy to muddy conditions (1-4% organic

104   content, Richardson et al. 2008, unpublished data). The bays were selected to be representative

105   of the diversity of eelgrass and oyster habitats in Washington State, so site was considered a

106   random effect in all analyses. Recruitment of *M. gigas*, which is non-native, rarely occurs in

107   Samish Bay and Case Inlet, so at these sites in particular, habitat patches of oysters were the

108   product of aquaculture activities. Although these oysters can form vertical reefs, we focused on

109   places where they occurred in clusters over large areas, consistent with the dimensions of other

110   habitat patches. Each site was sampled over four days of spring tides in 2014 (Port Gamble 14-

111   17 May, Case 26-29 May, Dabob 11-15 Jun, Willapa 25-28 Jun, Samish 10-14 Jul).

112

113   **Study design**

114   The study design was nested, with measurements at three subsites in each of five sites. Each

115   subsite consisted of patches of each of three habitats (bare, eelgrass, oysters), for a total of nine

116   habitat patches per site. Thus, habitat type had three true replicates (i.e., distinct, interspersed) in

117   each of the five sites. A patch had to exceed 20 m in its minimum dimension in order to be

118   selected for study, and most were an order of magnitude larger than this. Each patch was

119   sampled three times at different water levels, including upstream (initial) and downstream (final)

120   paired samples. Overall, the design emphasized habitat type and water level as main effects.

121   Across all five sites, we sampled 45 patches (evenly divided among bare, eelgrass, and oyster),

122   with each patch sampled upstream and downstream at three water levels during the tidal cycle.

123

124   **Benthic sampling**

125   Each of the 45 patches was surveyed at low tide, by placing 10 (0.25 m^2) quadrats at random

126   intervals along a 50-m transect. In each quadrat in oyster habitat, we counted all live oysters and

127   measured the first 10 for shell height (nearest 0.5 cm). In each quadrat in eelgrass, we counted

128   eelgrass shoots and collected above-ground material of eelgrass. Eelgrass across these sites

129   shows several ecotypic growth forms: smallest in Case Inlet (0.2 m average shoot length),

130   intermediate in Port Gamble and Dabob Bay (0.3-0.6 m), and longest in Willapa Bay and Samish

131   Bay (0.8-1.2 m). In quadrats in all habitats, we assessed shell cover and collected any

132   macrophytes to assess biomass. Above-ground material of eelgrass and other macrophytes was

133   dried separately (60°C for 5 days) and weighed. Biomass of oysters was estimated from density

134   and size-frequency based on the length-weight relationships of Kobayashi et al. (2007), first at

135   the quadrat level and then calculated per patch. Each of the 45 patches was described by the

136   mean (n=10 quadrats) and variation in above-ground biomass of primary producers and

137   suspension-feeding oysters (Fig. 1B, C).

138

139   **Water sampling**

140   To assess changes in water properties across patches, we tracked parcels of water with neutrally

141   buoyant Lagrangian drifters consisting of a PVC frame at the surface of the water and a circular

142   skirt, 80 cm in diameter and extending 10 cm into the water (Fig. 2, also used in Wheat and

143   Ruesink 2013). This approach enables sampling the same water over time, clarifying what was

144   "upstream" and "downstream" at any particular time, and accounting for potentially variable

145   initial conditions. We restricted our sampling to periods of light winds, since wind can decouple

146   the drifter from strictly tracking the water (pers. obs.). These light-wind conditions limited the

147   development of surface waves, and water transport during sampling was driven by tidal currents.

148   Eelgrass, oyster and unstructured tidal flat habitats were sampled concurrently. A waterproofed

149   GPS (Garmin GEKO) was secured at the center of each drifter to ride on the water surface. Three

150   drifts were carried out for each of the 45 habitat patches (27 drifts per site), spanning a range of

151   water depths as depth changed during the tidal cycle. Water depth ranged from 0.1 m to ~2 m

152   (94% of drifts occurred at water depths <2 m), which represented about half of the tidal

153   amplitude during the sampling periods of spring tides. Drifts generally lasted half an hour, but

154   duration was constrained by patch size and water velocity (Fig. 3). At the beginning of a drift,

155   starting near a patch edge where water was flowing in to the patch, a person in a kayak collected

156   water samples at ~0.3 m below the surface (or less in shallower water). Effort was made to

157   collect water samples as close to the drifter as possible without disturbing its motion or the

158   bottom. Water depth was evaluated by holding the paddle vertically and checking the water level

159   at 0.1 m increments. As the drifter exited the patch, water samples were collected again. Each

160   water sample collection consisted of three 300 ml Nalgene bottles for pigment analysis and one

161   1-L bottle for total suspended solids (TSS). All bottles were kept cold and dark and were filtered

162   through 47 mm glass fiber filters (GF/F, 0.7 μm pore size) within three hours. Samples for

163   pigment analysis were placed in 10 ml of 90% (W/V) acetone and kept frozen and dark. At the

164   end of the field season, these samples were measured for chlorophyll-*a* (Chl) via standard

165   acidification procedure on a Turner Designs AU-10 fluorometer (Welschmeyer 1994). Samples

166   for TSS were filtered through pre-weighed filters, dried to determine mass of material, and

167   combusted at 500°C for three hours to determine organic content by loss-on-ignition. A few of

168   these samples dried incompletely, generating large values for TSS (including some water) and

169   for organic content (also including some water), and we censored nine values (eight drifts) with

170   proportion organic <0 or >0.5. The time of collection of initial and final samples was recorded

171   by the kayaker, which enabled later extraction of geo-positions from GPS units recording at 10 s

172   intervals. The absolute distance between initial and final positions (in m, accounting for non-

173   parallel longitude), divided by the duration of the drift, defined drift velocity.

174

175   **Data analysis**

176   Five water properties were tested for depth and habitat differences. Two of these water properties

177   were TSS and Chl collected at the initiation of each drift. Two were the change in TSS and Chl

178   during each drift, using samples collected initially and finally in calculations of

179   $\ln(TSS_{final}/TSS_{initial})$ and $\ln(Chl_{final}/Chl_{initial})$. The fifth response variable was drift velocity. Each

180   of these response variables was used in a linear mixed effects model, with fixed effects of habitat

181   type, ln(water depth), and their interaction, and random effects of site and subsite in site. Three

182   Chl samples collected simultaneously were averaged prior to analysis.

183   Quality of seston was evaluated through relationships of organic content and Chl to TSS.

184   In these analyses, all samples from both initial and final collections for each drift were used.

185   Response variables of ln(Chl) and ln(proportion organic) were used in linear mixed effects

186   models, with fixed effects of habitat type, ln(TSS), and their interaction, and random effects of

187   site and subsite in site. In all these analyses, any significant habitat effect was followed up by

188   similar analyses using subsets of the data to determine which biogenic species were different

189   from bare tidal flat: bare vs. eelgrass, and bare vs. oyster samples.

190   Residuals in all analyses were examined visually for normality, and TSS and Chl required

191   ln-transformation. Following Zuur et al. (2009), we tested for optimal random effects structure,

192   which included random intercepts in all models. Statistical significance of predictors was set at

193   $\alpha=0.05$, but $\alpha=0.025$ whenever habitat was significant, and subsets of data were tested for

194   pairwise habitat differences. However, when linear mixed effects models generate P-values near

195   the border of significance, this provides weak evidence of their importance (Zuur et al. 2009).

196   Linear mixed effects models were re-run with only significant factors in order to find coefficients

197   for best-fit lines in visual display of data. Linear mixed effects analyses were carried out with

198   *nlme* (Pinheiro et al. 2016) in R (R Core Team 2015). Characteristics of each of the 135 drifts

199   have been archived at Ruesink J (2018), "Data from: Comparison of shallow water seston among

200   biogenic habitats (eelgrass, oysters, bare) on tidal flats", Mendeley Data, v1

201   http://dx.doi.org/10.17632/9y8xrhvhmy.1.

202

203   **RESULTS**

204   **Benthic composition of patches**

205   Eelgrass patches contained 38-120 gDW m^{-2} in above-ground biomass of eelgrass (Fig. 1B), with

206   an overall moderate coefficient of variation (CV = SD/mean = 0.32, n = 15 patches). Oyster

207   patches were more variable in estimated live oyster biomass (10-270 gDW m^{-2}, CV = 0.84, Fig.

208   1C) and ranged from 8 to 97% shell cover (mean 49%, CV = 0.53, n=15, also positively

209   correlated with live oyster biomass, r=0.52). For both foundation species, these densities are

210   categorized as functionally dense, since fluid dynamics for sparse structure typifies cover <10%

211   (Bouma et al. 2007). Other primary producers, in particular macroalgae, were present in some

212   patches, averaging 2 gDW m^{-2} in bare and eelgrass patches, but 20 gDW m^{-2} in oyster patches,

213   possibly reflecting the availability of hard surface for anchoring.

214

215   **Water properties at the initiation of drifts**

216   Based on initial samples from each drift, the analysis of TSS revealed significant main effects of

217   habitat and water depth, while Chl responded only to habitat type (Table 1). Higher

218 concentrations of TSS and Chl were present in both biogenic habitats than over bare tidal flat,

219 although the oyster-bare comparisons had P-values close to $\alpha=0.025$ that should be interpreted

220 cautiously in linear mixed effects models. TSS declined as water depth increased, but Chl did not

221 (Fig. 4, Table 1). The depth-related differences for TSS were in keeping with predictions of

222 increased resuspension in shallow water, but the lack of depth × habitat interactions meant that

223 the heterogeneity in surface water properties across habitat types was not muted as water level

224 rose.

225

226 **Water properties during drifts**

227 Based on initial and final samples from each drift, the analysis of $\ln(TSS_{final}/TSS_{initial})$ revealed a

228 significant effect of water depth, but no factors were significant for $\ln(Chl_{final}/Chl_{initial})$ (Table 1).

229 Specifically, TSS continued to increase during drifts in shallow water but not when more water

230 covered these patches (Fig. 5). No habitat differences or habitat × depth interactions emerged in

231 analyses of changes in water properties during drifts (Table 1). Accordingly, distance to the

232 sediment was important for the dynamics of TSS, but neither eelgrass nor oysters cleared the

233 water of particles, regardless of water depth.

234

235 **Water velocity**

236 Drift velocity showed main effects of habitat type and water depth but no interaction (Table 1).

237 Dropping one fast outlier, velocity averaged 0.128 m s^{-1} (SD 0.126, n=43) across bare tidal flats,

238 0.115 m s^{-1} (SD 0.114, n=43) over oysters, and 0.085 m s^{-1} (SD 0.096, n=44) over eelgrass (Fig.

239 3). Drifts over eelgrass were 33% slower relative to bare tidal flats, but this effect did not depend

240 on water depth. Drifts increased in velocity when more water was over habitat patches,

241 consistent with currents through the tidal cycle (Fig. 6). Across all drifts, 62% were slower than

242 0.1 m s^{-1}, and the 49 that were faster than this included all 27 drifts in Samish Bay (Fig. 3).

243

244 **Seston quality**

245 Proportion organic was significantly related to TSS, whereas Chl additionally differed by habitat

246 type. Chl was positively related to TSS, rising from 4 to 6 µg/L across a range of TSS that varied

247 by two orders of magnitude (5 to 500 mg/L; Fig. 7, Table 2). Across this same range of TSS,

248 organic content declined, shifting from 30% to 10% (Fig. 7). Seston characteristics differed by

249 habitat for Chl, which was higher for a given amount of TSS in eelgrass relative to bare tidal flat

250 (Table 2).

251

252 **DISCUSSION**

253 In our measurements of material carried by water across tidal flats, TSS was inversely related to

254 water depth and tended to increase further during transit in shallow water (Fig. 4, 5). Such

255 increases in particle loads in water flowing across tidal flats have been documented previously in

256 the field (Guizien et al. 2014), and resuspension often governs shallow water properties, in terms

257 of both the amount and characteristics of seston (Gacia and Duarte 2001, Newell and Koch

258 2004). Resuspension increases with current speed (up to a point) in flume studies, while the

259 water velocity able to lift particles is contingent on bottom properties (Widdows et al. 2000,

260 Ovain et al. 2014). Thus, TSS in our surface water samples was affected more by vertical water

261 motion (depth or distance to sediment) than by horizontal water motion (current speed), which

262 acted in an opposite direction to observed results. Contrary to expectations, no water depth ×

263 habitat interactions were apparent in TSS and Chl. Regardless of depth, highest TSS and Chl

264   concentrations were observed over eelgrass, where reduced water velocity was expected to lead

265   to particle settling (Fig. 4). We found little evidence of top-down control by oysters, given that

266   change in Chl over oysters was similar to that in other habitat types (Fig. 5).

267   The conclusions regarding control of seston in biogenic habitats differed for comparisons

268   of initial drift values (Fig. 4) and for changes during drifts (Fig. 5, Table 1). Overall, the habitats

269   were more distinct in the concentrations of seston than in the dynamics of how water properties

270   changed between the initial and final measurements. Specifically, TSS and Chl were already

271   higher over eelgrass than over bare tidal flat at the initiation of each drift, but any changes during

272   drifts were not habitat-specific. One interpretation is that the mosaic of intertidal water properties

273   is established at patch borders, rather than building up during transit over different biogenic

274   habitat types, for instance because erosional processes tend to be enhanced at leading edges of

275   structured habitats (Adams et al. 2016).

276   The conclusions regarding control of seston by water depth differed for TSS, which was

277   inversely related to depth in terms of both concentration and change during drifts, and Chl,

278   whose amount and dynamics were unrelated to water depth (Figs. 4, 5, Table 1). Evidently,

279   resuspension of material on these tidal flats predominantly mobilized non-photosynthetic

280   material, thus augmenting TSS without changing Chl. This explanation is supported by the

281   negative relationship between proportion organic and TSS in analyses of seston quality (Fig. 7).

282   Although Chl was positively related to TSS, the slope of this relationship was small, given ca.

283   50% increase in Chl over a range of TSS spanning two orders of magnitude (Fig. 7), and

284   insufficient to drive identical depth-related patterns for particulates as a whole and for Chl. In

285   other studies, benthic microalgae were found to be lifted into the water column under conditions

286   of lower water energy than can mobilize mineral particles (Orvain et al. 2014) and to distribute

287 without much gradient in the water column (Guizien et al. 2014). Due to evidence in our study

288 that primarily inorganic particles were resuspended in shallow water, we interpret this to mean

289 that benthic microalgae were already mobilized under the full range of drift velocities and

290 depths, or that populations of benthic microalgae were not well developed on these tidal flats.

291   In retrospect, a large gap in our study is that we do not have coupled measurements of

292 sediment properties for all drift locations. It is reasonable to expect that eelgrass and oysters

293 could influence sediment properties, although in some past work we have found no consistent

294 differences in the sediment of these habitat types relative to bare tidal flat (Richardson et al.

295 2008). However, we cannot test how much of the variation in seston among drifts is a function of

296 the sediment type over which the water passes, therefore precluding an assessment of this

297 potential mechanism underlying the heterogeneity in shallow water properties that we

298 documented.

299   Attenuation of water movement by seagrass has been observed in many field and lab

300 studies and is largely dependent on the current speed (Fonseca et al. 1982), driver of water

301 motion (e.g. wind vs. tide, Koch and Gust (1999)), habitat configuration (patch vs. continuous,

302 Worcester 1995), and seagrass density and shoot length (Moore 2004, Hasegawa et al. 2008). In

303 our study, water velocity was reduced over eelgrass relative to other habitat types (Fig. 6, Table

304 1). Thus, all combinations of canopy height and water depth represented conditions suitable for

305 modifying surface flow. It may be necessary to include drifts at still deeper water depths

306 associated with extreme high tides to see evidence of any habitat × depth interaction, which

307 should emerge because flow reduction extends only to a factor of two of canopy height (Luhar et

308 al. 2008).

309   Why, then, did this slower flow not lead to deposition of particles and a clearing of the

310   water column in eelgrass? We propose two explanations, which are not mutually exclusive, the

311   first related to shoot architecture and the second to epibionts. Seagrass biomass tends to be

312   concentrated off-bottom, and the near-bottom material is gathered into leaf sheaths. Accordingly,

313   reduced drag may enable faster near-bottom flow that fosters erosional rather than depositional

314   processes (Madsen et al. 2001, Koch et al. 2006). Key tests in flumes have been carried out on

315   small, dense morphotypes of eelgrass (e.g., 1000 shoots m^{-2} of ~20 cm length; Fonseca and

316   Koehl 2006), whereas most eelgrass morphotypes found in Washington State are larger, sparser,

317   and therefore more likely to result in resuspension. The second possibility is contribution to

318   seston from the microalgae and trapped sediments on the surface area of the eelgrass leaves. This

319   fragile material can represent almost as much dry mass as the eelgrass itself during summer

320   months (Nelson and Waaland 1997, Ruesink 2016). Mobilization of epiphytes into the water

321   column could underlie the higher quality (as Chl) of seston in eelgrass relative to other habitats

322   in our study (Fig. 7). Specifically, 50 mg L^{-1} of TSS is associated with about 5 μg L^{-1} of Chl

323   (Fig. 7), but 50 mg of material scraped from eelgrass leaves contains 100 μg of Chl, yet a

324   moderate organic content (13%, unpublished data from Willapa Bay in 2012). Overall,

325   suspended materials in water moving through eelgrass may depend on morphologically-mediated

326   differences in bottom turbulence resuspending benthic particles or picking up materials from the

327   large surface area of eelgrass leaves.

328   One other issue regarding water velocity is worth noting here, which is the rapid flow in

329   Samish Bay (Fig. 3), where the bathymetry has a shallow grade. Eelgrass in Washington State

330   exhibits two spatial configurations: flats (areas with extensive broad shallows such as river deltas

331   and pocket beaches) and fringes (areas with linear eelgrass distribution due to steep bathymetry;

332 Berry et al. 2003). Samish Bay was our only site where sampling overlapped eelgrass flats.

333 There, the bathymetry was conducive to both extensive eelgrass and rapid flow, resulting in drift

334 durations similar to other sites. Overall, the flat vs. fringe dichotomy needs further examination

335 for the engineering of water properties by biogenic species. In this study, with one "flat" and four

336 "fringes", it was necessary to consider site a random effect.

337 Many studies of water properties directly over shellfish beds have documented

338 measurable depletion of water column resources (Grizzle et al. 2006, 2008, Grangere et al. 2010,

339 Plutchak et al. 2010, Wheat and Ruesink 2013). Downstream concentrations of Chl are typically

340 lower than upstream concentrations, but not as different as would be expected from scaling up

341 filtration rates measured in the laboratory (Grizzle et al. 2008, Wheat and Ruesink 2013). Here

342 we found little evidence of oyster filtration reducing Chl or particle loads above patches (Table

343 1). This weak effect may be due to overall low oyster biomass, that is, averaging <100 gDW m^{-2}

344 relative to 400 gDW m^{-2} where drawdown has been documented in Washington State (Wheat

345 and Ruesink 2013). Our data also point towards resuspension as a factor that may complicate

346 assessments of the filtration capacity of shellfish. Other researchers have noted rapid variation in

347 processing speed in response to food quality and quantity (Barillé et al. 1997) and filtration

348 failing to scale with abundance due to the collective consequence of reef structure (Colden et al.

349 2016). The accumulation of empirical evidence regarding filtration as an ecosystem service is

350 essential to understanding the conditions under which bivalves can improve water quality, and by

351 how much.

352

353 **CONCLUSIONS**

354   Ecological interest in resuspension processes in shallow water has been motivated by

355   understanding food web linkages and subsidies among habitats. Sediment resuspension has a

356   number of potential ecological feedbacks to the biogenic species considered in this study.

357   Resuspension provides a potential benefit to suspension-feeders as they may use benthic

358   microalgae or other organic particles in their diet (Kang et al. 2003, Herman et al. 2000, van

359   Oevelen et al. 2006). In contrast, for seagrass, resuspension contributes to light attenuation and

360   provides a mechanism whereby alternative stable states can occur, when seagrass clears its own

361   water (Ralph et al. 2007, De Boer 2007), which was not the case in our study. Our empirical

362   examination of seston in water passing across tidal flats revealed spatial heterogeneity that

363   mapped on to habitat mosaics and shifted during the tidal cycle. Potential food resources were

364   elevated in eelgrass, as has been demonstrated in other species of seagrass as well (Judge et al.

365   1983, LeBreton et al. 2011). We worked at particularly low water levels in a dynamic tidal

366   environment, which may help explain why resuspension could modify water properties

367   dramatically and over such a wide observed range. These different patterns deserve further

368   scrutiny across sediment types, more extreme water depths, and morphologies and epiphyte loads

369   of eelgrass, which could be additional factors involved in the spatial transfer of resources in

370   coastal environments.

371

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377

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Study sites and benthic composition of habitat patches in Washington State, USA

A) Map showing study sites. B) Dry above-ground biomass of eelgrass (*Zostera marina*) in three habitat patches per site. C) Estimated dry meat weight of oysters (*Crassostrea gigas*) from length-frequency distribution in three habitat patches per site. Error bars show SE of 10 quadrats per patch.

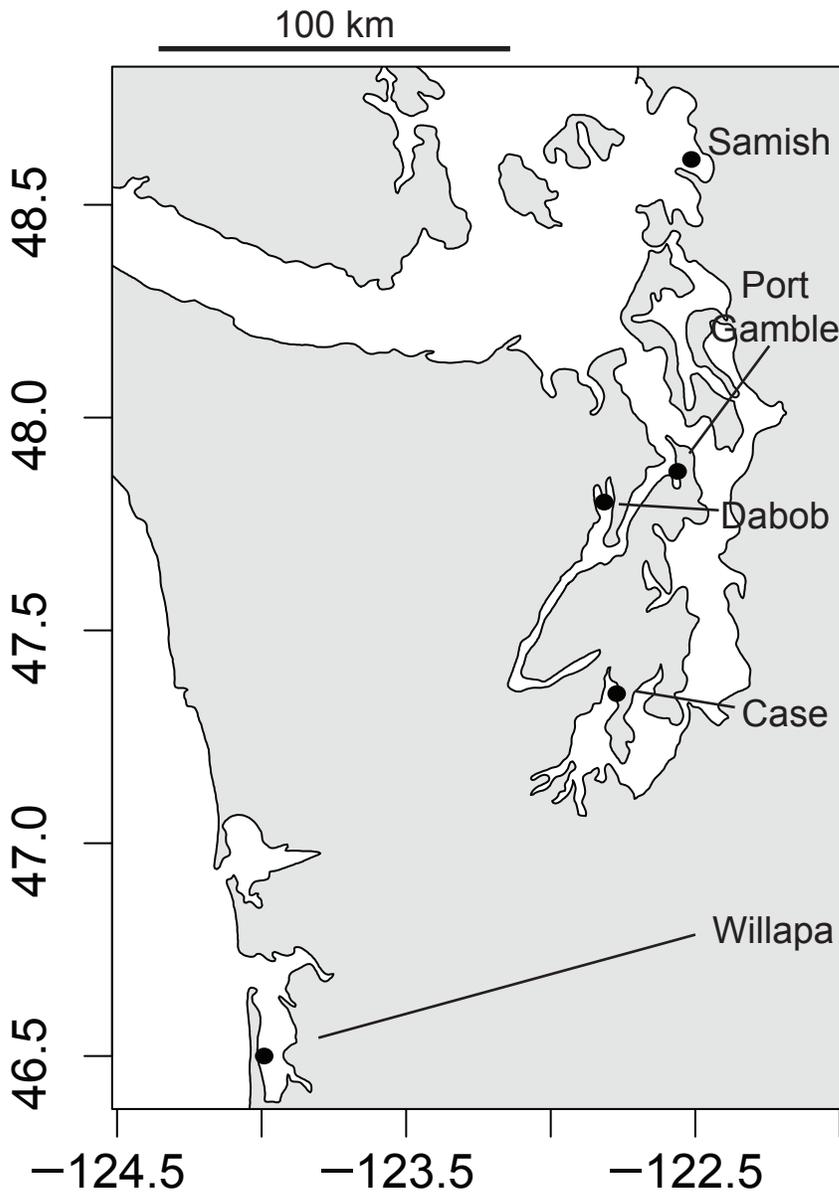
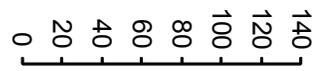
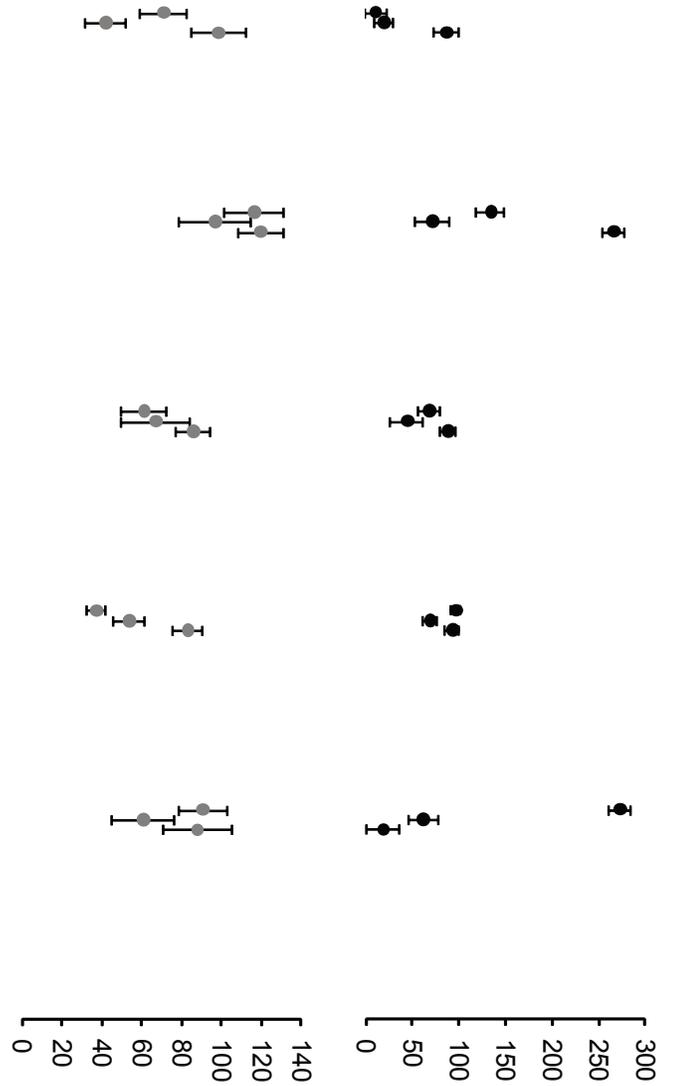
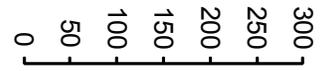
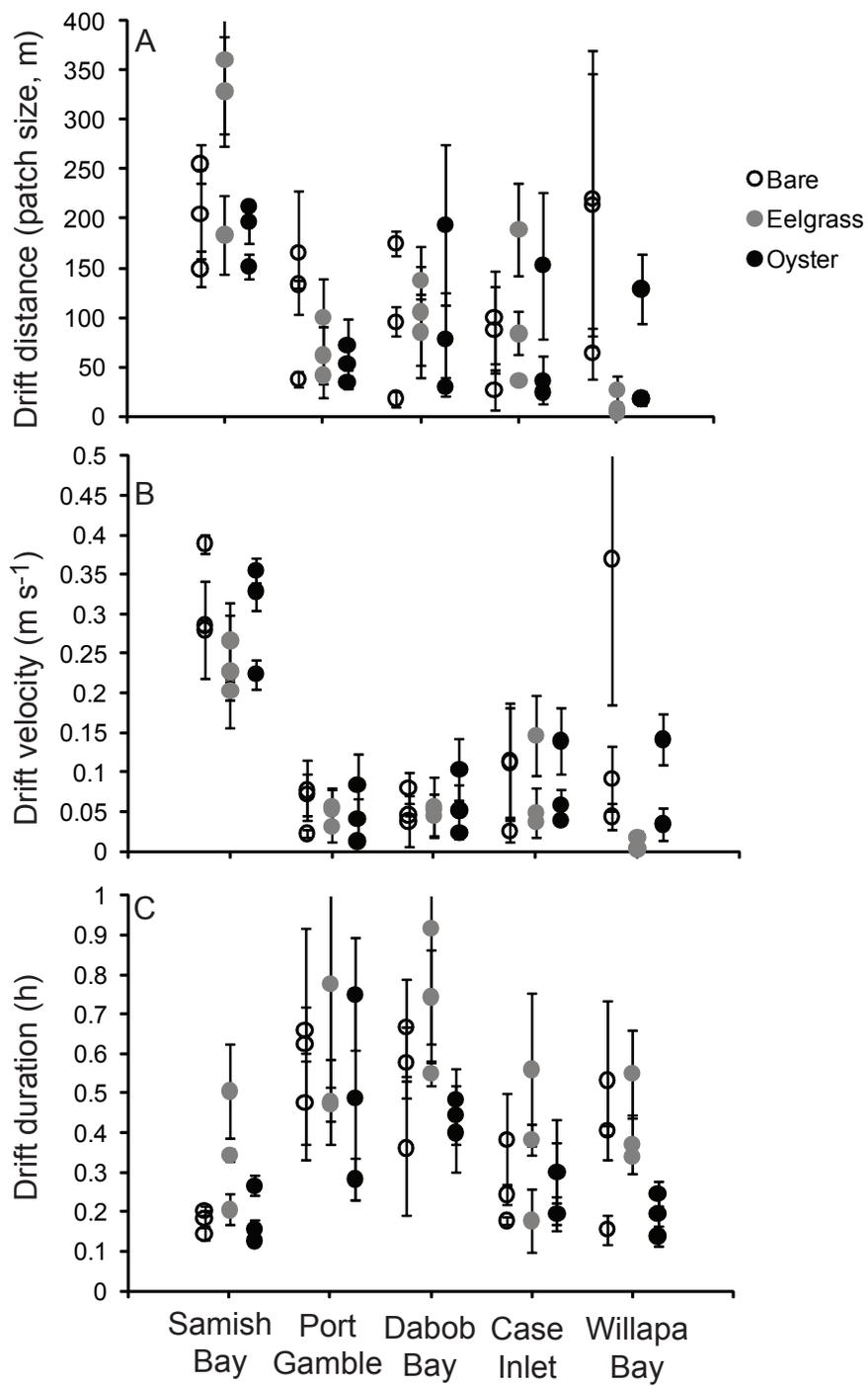
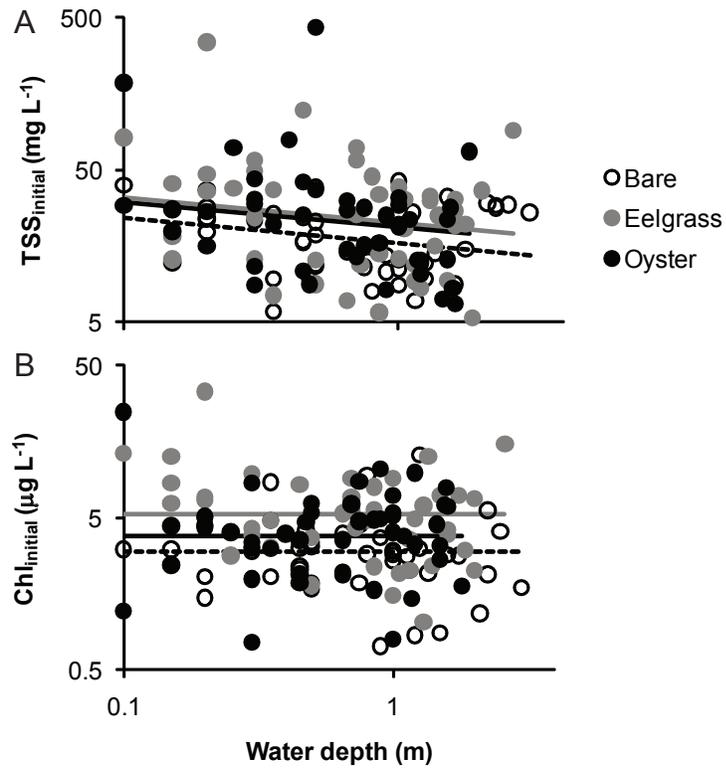



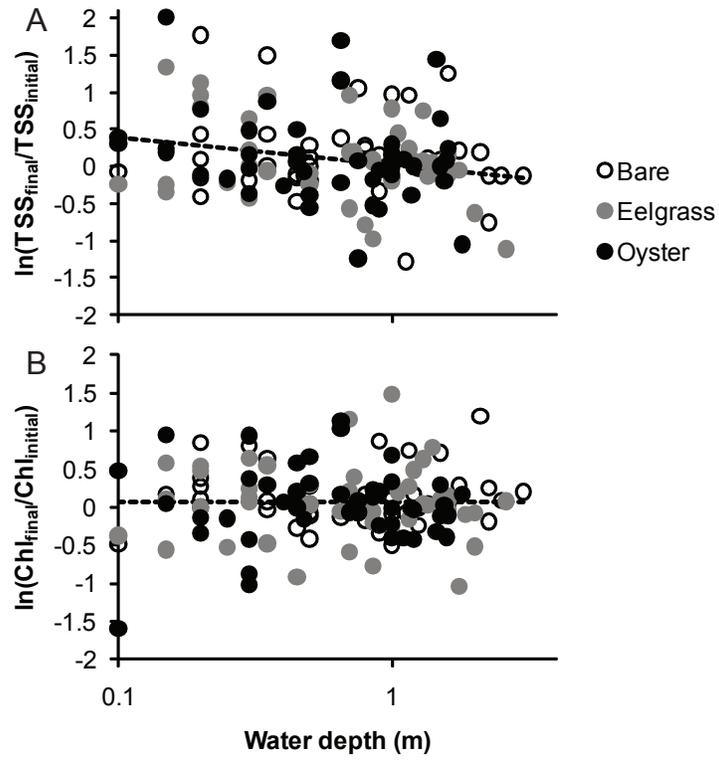
Figure 2

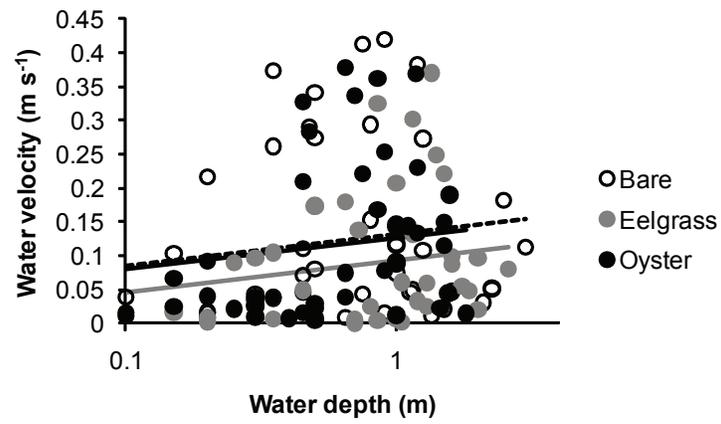
Neutrally buoyant Lagrangian drifter (diameter 0.8 m), with GPS unit at center

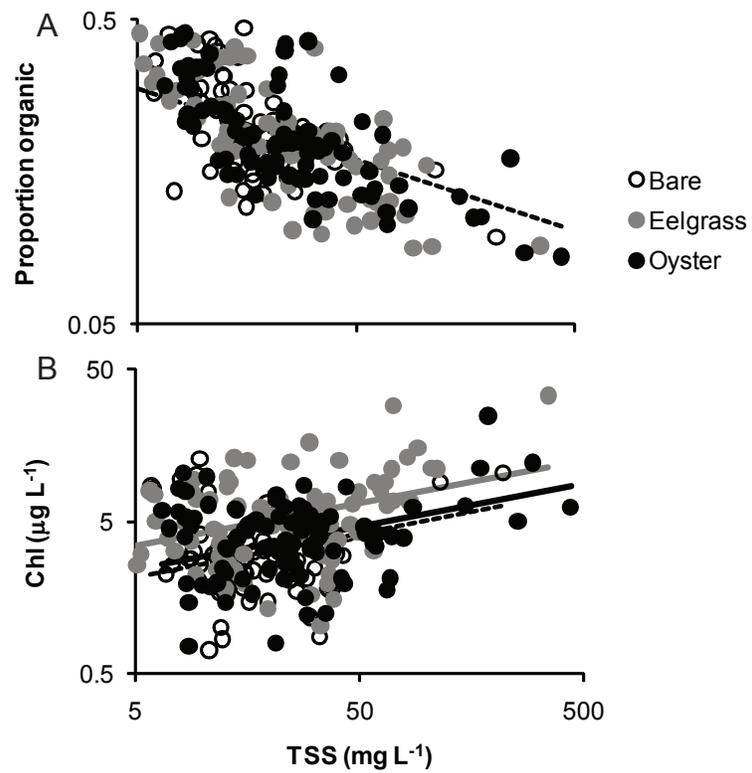
Characteristics of 135 drifts in shallow water across a mosaic of habitat types occupying intertidal flats in Washington State, USA

Each point refers to one patch, with mean and standard errors calculated from the three drifts across that patch. (A) Distance from the start to end of each drift, demonstrating the dimension of each habitat patch. (B) Surface water velocity during drifts. (C) Duration of drifts.

Water properties at the initiation of each drift when water was at different depths over three intertidal habitat types at five sites in Washington State, USA

(A) Total suspended solids. (B) Chlorophyll-*a*. Lines are plotted from the coefficients of linear mixed effects models including factors significant at α<0.05.

Change in water properties during drifts when water was at different depths over three intertidal habitat types at five sites in Washington State, USA

(A) Change in total suspended solids, based on the log-ratio. (B) Change in chlorophyll-*a*, based on the log-ratio. Lines are plotted from the coefficients of linear mixed effects models including factors significant at α<0.05; habitat was not significant in these models, so a single relationship is shown.

Water velocity during drifts when water was at different depths over three intertidal habitat types at five sites in Washington State, USA

Lines are plotted from the coefficients of a linear mixed effects model including factors significant at α<0.05. Although the residuals in this plot appear to violate assumptions of normal distributions, the distributions were suitable for analysis in the linear mixed effects model, which accounted for site and subsite as random effects.

Quality of seston in shallow water during drifts over three intertidal habitat types at five sites in Washington State, USA

(A) Organic content, and (B) Chlorophyll-*a* concentration in water varying in total suspended solids. Samples include both initial and final measurements for each drift. Lines are plotted from coefficients of linear mixed effects models including factors significant at a<0.05. Accordingly, a single relationship is shown for proportion organic, where habitat was not significant, but separate lines for chlorophyll-*a* due to water over eelgrass containing higher concentrations than over bare.

Results of linear mixed effects models of water properties during each drift at five sites in Washington State, USA, in summer 2014

Each column presents one of five water properties. Each row provides F value (P value) for main effects of habitat and depth, for their interaction, and for pairwise tests between biogenic habitats (eelgrass, oyster) and bare when habitat was significant. Random effects were site, and subsite in site. TSS = total suspended solids, mg L^{-1}. Chl = chlorophyll-a, µg L^{-1}. Samples were not used in analysis of TSS unless 0< proportion organic <0.5. Some samples were not available for calculation of water velocity due to GPS malfunction.

			Response		
	$\ln(TSS_{initial})$ n=132	$\ln(Chl_{initial})$ n=136	Water velocity n=130	$\ln(TSS_{final}/TSS_{initial})$ n=127	$\ln(Chl_{final}/Chl_{initial})$ n=136
Habitat	4.56 (0.013)	14.9 (<0.0001)	4.97 (0.009)	0.02 (0.98)	0.42 (0.66)
ln(Depth)	8.14 (0.005)	3.61 (0.06)	9.20 (0.003)	7.58 (0.007)	0.41 (0.52)
Habitat x ln(Depth)	0.56 (0.57)	0.70 (0.50)	0.88 (0.42)	0.07 (0.93)	0.17 (0.84)
Bare vs. Eelgrass	E>B P=0.003	E>B P<0.0001	E<B P=0.009		
Bare vs. Oyster	O>B P=0.013	O>B P=0.019	O=B P=0.47		

Results of linear mixed effects models of water properties using initial and final samples for each drift at five sites in Washington State, USA, in summer 2014

Each column contains a distinct water property: chlorophyll-*a* (Chl), and proportion organic. Each row provides F value (P value) for main effects of habitat and total suspended solids (TSS), for their interaction, and for pairwise tests between biogenic habitats (eelgrass, oyster) and bare when habitat was significant. Random effects were site, and subsite in site. Samples were not used in analysis unless $0<$ proportion organic <0.5. In pairwise tests for ln(Chl), no significant habitat × ln(TSS) interactions appeared.

	Response	
	ln(Chl) n=261	ln(proportion organic) n=262
Habitat	24.2 (<0.0001)	0.10 (0.90)
ln(TSS)	57.3 (<0.0001)	146.1 (<0.0001)
Habitat x ln(TSS)	3.16 (0.044)	0.49 (0.61)
Bare vs. Eelgrass	E>B P<0.0001	
Bare vs. Oyster	O=B P=0.03	