# 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 biogenic marine species (native eelgrass, *Zostera marina*; introduced oysters, *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. As water flowed across each habitat type, TSS generally increased, especially in shallow water, but without habitat differences; chlorophyll-*a* in these surface-water samples 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.

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11    Running head: Shallow-water seston on tidal flats

12    **ABSTRACT**

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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 biogenic marine species

17    (native eelgrass, *Zostera marina*; introduced oysters, *Crassostrea gigas*) in comparison to

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

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

20    patches of three habitat types; drift distance 116 m (109SD), duration 24 min (15SD)). At the

21    initiation of each drift, habitat differences in water properties were already apparent: chlorophyll-

22    *a* and total suspended solid (TSS) concentrations were greater in structured habitats than bare,

23    and TSS was also inversely related to water depth. Water flowed more slowly across eelgrass

24    than other habitat types. As water flowed across each habitat type, TSS generally increased,

25    especially in shallow water, but without habitat differences; chlorophyll-*a* in these surface-water

26    samples showed no consistent change during drifts. At higher TSS concentrations, quality in

27    terms of organic content declined, and this relationship was not habitat-specific. However, quality

28    in terms of chlorophyll-*a* concentration increased with TSS, as well as being greater in water over

29    eelgrass than over other habitat types. These results support widespread mobilization of seston in

30    shallow water ebbing or flooding across Washington State's tidal flats, especially as water passes

31    into patches of biogenic species.

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35    **INTRODUCTION**

36    Intertidal organisms, in addition to spending time in both water and air, experience short-term

37    variation because coastal water fluctuates in such properties as dissolved gas concentrations

38    (Duarte et al. 2013) and particle loads (Ralph et al. 2007). The amount and composition of

39    suspended particulate matter, termed seston, has important implications for the productivity of

40    macrophytes via light limitation (de Boer 2007) and for benthic suspension feeders via food

41    resources (e.g. Kang et al. 2003). Quantifying how biogenic species influence the mobilization

42    and removal of particles improves understanding of the feedbacks governing local heterogeneity

43    in water properties (Widdows et al. 2000, de Boer 2007). In this study, we track water properties

44    across tidal flats and compare unstructured habitat to two dominant structure-forming species:

45    eelgrass (*Zostera marina*) and oysters (*Crassostrea gigas*).

46           These two species are expected to modify water properties in different ways. As

47    suspension-feeders, oysters remove particles, and water passing across oyster beds typically

48    declines in chlorophyll concentration (Grizzle et al. 2006, 2008, Grangere et al. 2010, Plutchak et

49    al. 2010, Wheat and Ruesink 2013). Away from the footprint of oysters, mixing and

50    compensatory phytoplankton dynamics obscure this trophic effect (Dame and Libes 1993,

51    Plutchak et al. 2010).  Seagrass influences seston predominantly as a side effect of altering water

52    motion, since more rapid flow or turbulence can lift and transport larger, denser particles

53    (Widdows et al. 2008, Wilkie et al. 2012). Empirically, seagrass beds buffer against water motion

54    and accumulate fine particles (Fonseca et al. 1982, Kenworthy et al. 1982). However, effects on

55    flow velocity and turbulence within and around structure are sensitive to a variety of parameters

56    that naturally vary in the field, including the fraction of the water column occupied by structure

57    (Moore 2004, Hasegawa et al. 2008, Luhar et al. 2008), and the density and flexibility of

58    structural elements (Adhitya et al. 2014, Houser et al. 2015). Seagrass contributes tall, flexible

59    structure, whereas oysters are stiff and typically shorter (although reefs can build up from

60    gregarious settlement and particle trapping; Walles et al. 2015). Bivalves such as hard clams can

61  intensify erosional processes and accordingly augment seston, even while drawing down

62  phytoplankton biomass overall (Porter et al. 2013). Similarly, benthic animals that bioturbate

63  sediment or graze biofilms are associated with increased erodability of sediments (Widdows et al.

64  2000, Guizien et al 2014). However, biogenic species might block the sediment surface and

65  therefore reduce the surface area subject to resuspension. Dense seagrass in tidally dominated

66  flow regimes is expected to slow laminar flow or divert flow away from sediment through

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

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

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

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

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

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

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

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

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

76  vertical gradients of some particle types in shallow water (Judge et al. 1993, Guizien et al. 2014),

77  benthic effects on water sampled at the surface may decline as depth increases simply due to

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

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

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

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

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

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

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

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

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

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

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

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

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

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

92

93    **METHODS**

94    **Study sites**

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

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

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

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

99    122.8°W), Port Gamble (47.8°N, 122.6°W) and Dabob Bay (47.8°N, 122.8°W) in Hood Canal,

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

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

102   3.1 m (Case Inlet). Sediment type spans a range of sandy to muddy conditions (1-4% organic

103   content, Richardson et al. 2008, Yang et al. 2013). The bays were selected to be representative of

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

105   effect in all analyses. Recruitment of *C. gigas*, which is non-native, rarely occurs in Samish Bay

106   and Case Inlet, so at these sites in particular, habitat patches of oysters were the product of

107   aquaculture activities. Although these oysters can form vertical reefs, we focused on places where

108   they occurred in clusters over large areas, consistent with the dimensions of other habitat patches.

109   Each site was sampled over four days of spring tides in 2014 (Port Gamble 14-17 May, Case 26-

110   29 May, Dabob 11-15 Jun, Willapa 25-28 Jun, Samish 10-14 Jul).

111

**Study design**

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

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

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

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

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

118    three times at different water levels, including upstream (initial) and downstream (final) paired

119    samples. Overall, the design emphasized habitat type and water level as main effects. Across all

120    five sites, we sampled 45 patches (evenly divided among bare, eelgrass, and oyster), with each

121    patch sampled upstream and downstream at three water levels during the tidal cycle.

122

**Benthic sampling**

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

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

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

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

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

129    in Port Gamble and Dabob Bay (0.3-0.6 m), and longest in Willapa Bay and Samish Bay (0.8-1.2

130    m). In quadrats in all habitats, we assessed shell cover and collected any macrophytes to assess

131    biomass. Above-ground material of eelgrass and other macrophytes was dried separately (60°C

132    for 5 days) and weighed. Biomass of oysters was estimated from density and size-frequency

133    based on the length-weight relationships of Kobayashi et al. (2007), first at the quadrat level and

134    then calculated per patch. Each of the 45 patches was described by the mean (n=10 quadrats) and

135    variation in above-ground biomass of primary producers and suspension-feeding oysters (Fig. 1B,

136    C).

137

138    **Water sampling**

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

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

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

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

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

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

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

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

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

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

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

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

151    (94% of drifts occurred at water depths <2 m), which represented about half of the tidal

152    amplitude during the sampling periods of spring tides. Most (85%) of drifts occurred on ebb

153    tides. Drifts generally lasted half an hour, but duration was constrained by patch size and water

154    velocity (Fig. 3). At the beginning of a drift, starting near a patch edge where water was flowing

155    in to the patch, a person in a kayak collected water samples at ~0.3 m below the surface (or less

156    in shallower water). Effort was made to collect water samples as close to the drifter as possible

157    without disturbing its motion or the bottom. Water depth was evaluated by holding the paddle

158    vertically and checking the water level at 0.1 m increments. As the drifter exited the patch, water

159    samples were collected again. Each water sample collection consisted of three 300 ml Nalgene

160     bottles for pigment analysis and one 1-L bottle for total suspended solids (TSS). All bottles were

161     kept cold and dark and were filtered through 47 mm glass fiber filters (GF/F, 0.7 μm pore size)

162     within three hours of collection. Samples for pigment analysis were placed in 10 ml of 90%

163     (W/V) acetone and kept frozen and dark. At the end of the field season, these samples were

164     measured for chlorophyll-*a* (Chl) via standard acidification procedure on a Turner Designs AU-

165     10 fluorometer (Welschmeyer 1994). Samples for TSS were filtered through pre-weighed filters,

166     dried to determine mass of material, and combusted at 500°C for three hours to determine organic

167     content by loss-on-ignition. A few of these samples dried incompletely, generating large values

168     for TSS (including some water) and for organic content (also including some water), and we

169     censored nine values (eight drifts) with proportion organic <0 or >0.5. The time of collection of

170     initial and final samples was recorded by the kayaker, which enabled later extraction of geo-

171     positions from GPS units recording at 10 s intervals. The absolute distance between initial and

172     final positions (in m, accounting for non-parallel longitude), divided by the duration of the drift,

173     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 of

180     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. The study design was

183     unbalanced for any test of whether patterns differed between ebb and flood tides, or as a function

184   of water residence time in a habitat patch. In exploratory analyses, these correlates explained

185   little of the residual variation and were not considered further.

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

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

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

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

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

191   planned contrasts testing bare vs. eelgrass, and bare vs. oyster.

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

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

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

195   $\alpha=0.05$. However, when linear mixed effects models generate P-values near the border of

196   significance, this provides weak evidence of their importance (Zuur et al. 2009). Linear mixed

197   effects models were re-run with only significant factors in order to find coefficients for best-fit

198   lines in visual display of data. Linear mixed effects analyses were carried out with *nlme* (Pinheiro

199   et al. 2016) in R (R Core Team 2015). Characteristics of each of the 135 drifts have been archived

200   (Ruesink 2018).

201

202   **RESULTS**

203   **Benthic composition of patches**

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

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

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

207   1C) and ranged from 8 to 97% shell cover (mean 49%, CV = 0.53, n=15, also positively

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

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

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

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

212　possibly reflecting the availability of hard surface for anchoring.

213

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

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

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

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

218　although the oyster-bare comparisons had P-values closer to α=0.05 that should be interpreted

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

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

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

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

223　rose.

224

225　**Water properties during drifts**

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

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

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

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

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

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

232    water of particles, regardless of water depth.

233

234    **Water velocity**

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

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

237    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.

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

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

240    with currents through the tidal cycle (Fig. 6). Across all drifts, 62% were slower than 0.1 m s$^{-1}$,

241    and the 49 that were faster than this included all 27 drifts in Samish Bay (Fig. 3).

242

243    **Seston quality**

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

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

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

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

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

249    (Table 2).

250

251    **DISCUSSION**

252    In our measurements of material carried by surface water across tidal flats, TSS was inversely

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

254    Such increases in particle loads in water flowing across tidal flats have been documented

255  previously in the field (Guizien et al. 2014), and resuspension often governs shallow water

256  properties, in terms of both the amount and characteristics of seston (Gacia and Duarte 2001,

257  Newell and Koch 2004). Resuspension increases with current speed (up to a point) in flume

258  studies, while the water velocity able to lift particles is contingent on bottom properties

259  (Widdows et al. 2000, Ovain et al. 2014). Thus, TSS in our surface water samples was affected

260  more by vertical water motion (depth or distance to sediment) than by horizontal water motion

261  (current speed), which acted in an opposite direction to observed results. That is, as more water

262  covered the tidal flat, it traveled faster (Fig. 6) and carried less TSS at the surface (Fig. 4, 5).

263  Contrary to expectations, no water depth × habitat interactions were apparent in TSS and Chl.

264  Regardless of depth, highest TSS and Chl concentrations were observed over eelgrass, where

265  reduced water velocity was expected to lead to particle settling (Fig. 4). We found little evidence

266  of top-down control by oysters, given that change in Chl over oysters was similar to that in other

267  habitat types (Fig. 5).

268      Both biogenic species acted as seston-mobilizers based on comparisons of initial drift

269  values (Fig. 4), but this effect was not apparent for changes during drifts (Fig. 5, Table 1).

270  Specifically, in initial samples, surface water over eelgrass and oysters contained twice the

271  concentration of TSS relative to bare: 38.0 (7.9 SE), 36.9 (9.8 SE), and 19.3 (1.5 SE) mg L$^{-1}$,

272  respectively. This habitat-specificity in initial values was also apparent in Chl: 6.4 (0.8 SE), 4.7

273  (0.6 SE), and 3.7 (0.3 SE) μg L$^{-1}$. The finding that biogenic habitats did not further influence

274  seston differentially with respect to bare suggests that the mosaic of intertidal water properties is

275  established at patch borders, for instance because erosional processes tend to be enhanced at

276  leading edges of structured habitats (Adams et al. 2016). Factors expected to result in build-up of

277  effects during drifts, such as suspension feeder activity, may not differ among habitats as

278    expected from oysters alone, given that we did not sample for infaunal suspension-feeders (i.e.

279    Peterson and Black 1987).

280         Despite the absence of predicted water depth × habitat effects, differential responses to

281    water depth for surface TSS and Chl can help infer causes of spatio-temporal heterogeneity over

282    these tidal flats. TSS was inversely related to depth in terms of both concentration and change

283    during drifts, but the amount and dynamics of Chl were unrelated to water depth (Figs. 4, 5, Table

284    1). Evidently, resuspension of material on these tidal flats predominantly mobilized non-

285    photosynthetic material, thus augmenting TSS without changing Chl. This explanation is

286    supported by the negative relationship between proportion organic and TSS in analyses of seston

287    quality (Fig. 7). Although Chl was positively related to TSS, the slope of this relationship was

288    small, given ca. 50% increase in Chl over a range of TSS spanning two orders of magnitude (Fig.

289    7), and insufficient to drive identical depth-related patterns for particulates as a whole and for

290    Chl. In other studies, benthic microalgae were found to be lifted into the water column under

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

292    distribute without much gradient in the water column (Guizien et al. 2014). Due to evidence in

293    our study that primarily inorganic particles were resuspended in shallow water, we interpret this

294    to mean that benthic microalgae were already mobilized under the full range of drift velocities

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

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

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

298    could influence sediment properties, and that a source of seston could be biodeposits in the case

299    of oysters and locally-produced organic matter in eelgrass. However, in some past work we have

300    found no consistent differences in the sediment of these habitat types relative to bare tidal flat

301    (Richardson et al. 2008). In the present case, we cannot test how much of the variation in seston

302    among drifts is a function of the sediment type over which the water passes, therefore precluding

303   an assessment of this potential mechanism underlying the heterogeneity in shallow water

304   properties that we documented.

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

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

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

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

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

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

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

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

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

314   al. 2008).

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

316   water column in eelgrass? Instead, we speculate that eelgrass on these tidal flats may increase

317   water turbulence and/or surface area hosting fragile microalgal epibionts. Seagrass biomass tends

318   to be concentrated off-bottom, and the near-bottom material is gathered into leaf sheaths.

319   Accordingly, reduced drag may enable faster near-bottom flow that fosters erosional rather than

320   depositional processes (Madsen et al. 2001, Koch et al. 2006). Key tests in flumes have been

321   carried out on small, dense morphotypes of eelgrass (e.g., 1000 shoots $m^{-2}$ of ~20 cm length;

322   Fonseca and Koehl 2006), whereas most eelgrass morphotypes found in Washington State are

323   larger, sparser, and therefore more likely to result in resuspension. The second possibility is

324   contribution to seston from the microalgae and trapped sediments on the surface area of the

325   eelgrass leaves. This layer of fine fuzz can represent almost as much dry mass as the eelgrass

326   itself during summer months (Nelson and Waaland 1997, Ruesink 2016). Mobilization of

327   epiphytes into the water column could underlie the higher quality (as Chl) of seston in eelgrass

328    relative to other habitats in our study (Fig. 7). Specifically, 50 mg $L^{-1}$ of TSS is associated with

329    about 5 µg $L^{-1}$ of Chl (Fig. 7), but 50 mg of material scraped from eelgrass leaves contains 100

330    µg of Chl, yet a moderate organic content (13%, Ruesink 2018). Overall, suspended materials in

331    water moving through eelgrass may depend on morphologically-mediated differences in bottom

332    turbulence resuspending benthic particles or picking up materials from the large surface area of

333    eelgrass leaves.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

351    Ruesink 2013). Also, our baseline condition of "bare" tidal flats contained unknown numbers of

352    infaunal suspension-feeders. Because seston did not decline during drifts in any habitat type, our

353    data point towards resuspension as a factor that may complicate assessments of the filtration

354    capacity of shellfish. Other researchers have noted rapid variation in processing speed in response

355    to food quality and quantity (Barillé et al. 1997) and filtration failing to scale with abundance due

356    to the collective consequence of reef structure (Colden et al. 2016). The accumulation of

357    empirical evidence regarding filtration as an ecosystem service is essential to understanding the

358    conditions under which bivalves can improve water quality, and by how much.

359

360    **CONCLUSIONS**

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

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

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

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

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

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

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

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

369    examination of seston in surface water passing across tidal flats revealed spatial heterogeneity

370    that mapped on to habitat mosaics and shifted during the tidal cycle. Potential food resources

371    were elevated in eelgrass, as has been demonstrated in other species of seagrass as well (Judge et

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

373    environment, which may help explain why resuspension appeared as a primary driver of seston.

374    The habitat-specific mosaic that we documented may be a feature of summer sampling, given

375    seasonally high biomass of eelgrass, although also providing a best-case temperature scenario for

376    oysters to feed (Ren and Ross 2001). The relative rates of deposition, filtration, and resuspension

377   deserve further scrutiny across sediment types, more extreme water depths, and morphologies

378   and epiphyte loads of eelgrass, which could be additional factors involved in the spatial transfer

379   of resources in coastal environments.

380

381   **Acknowledgements**

384

385   **References**

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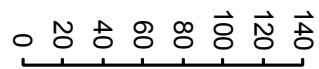
**Figure 1**(on next page)

Biogenic species across study sites.

(A) Study sites in Washington State, USA. (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.

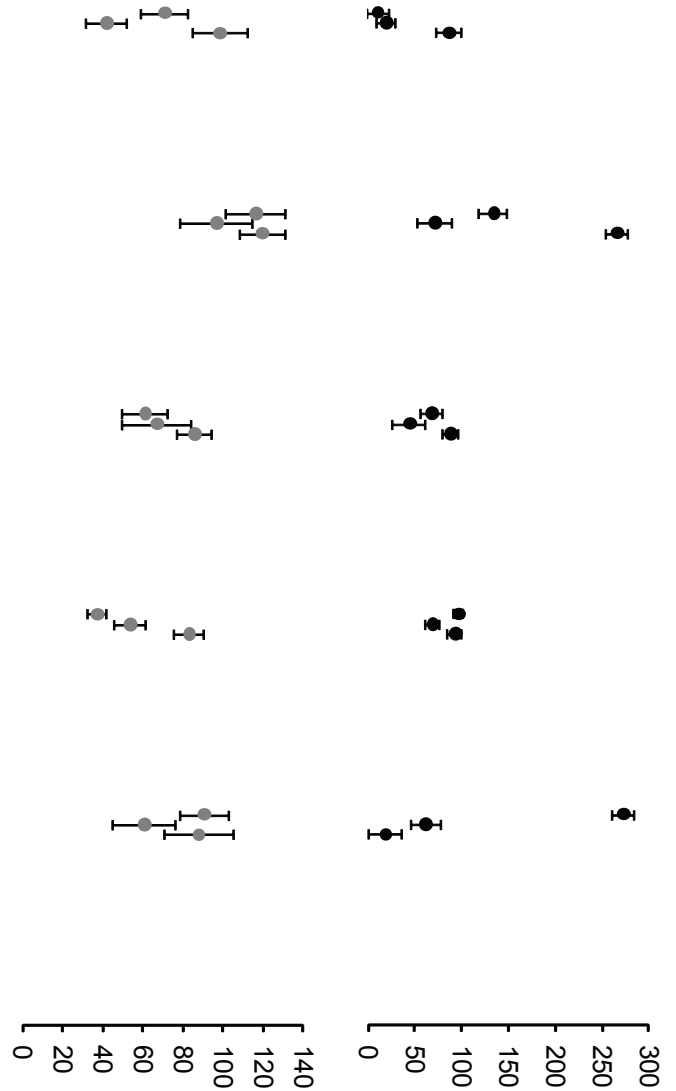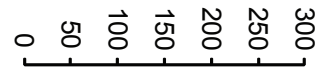A) Site locations
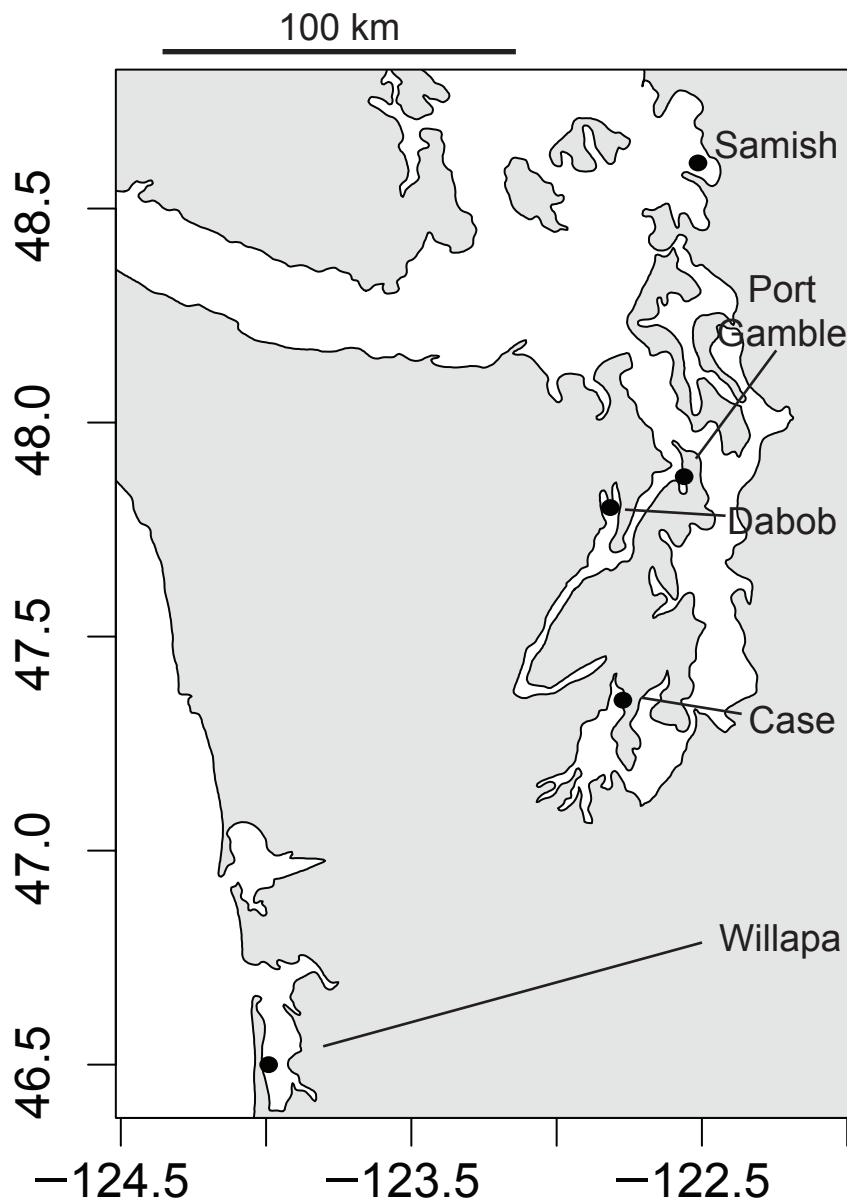
B) Eelgrass (g DW m$^{-2}$)

C) Oysters (g DW m$^{-2}$)

# Figure 2

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

Photo credit: Micah Horwith

**PeerJ**

**Figure 3**(on next page)

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.
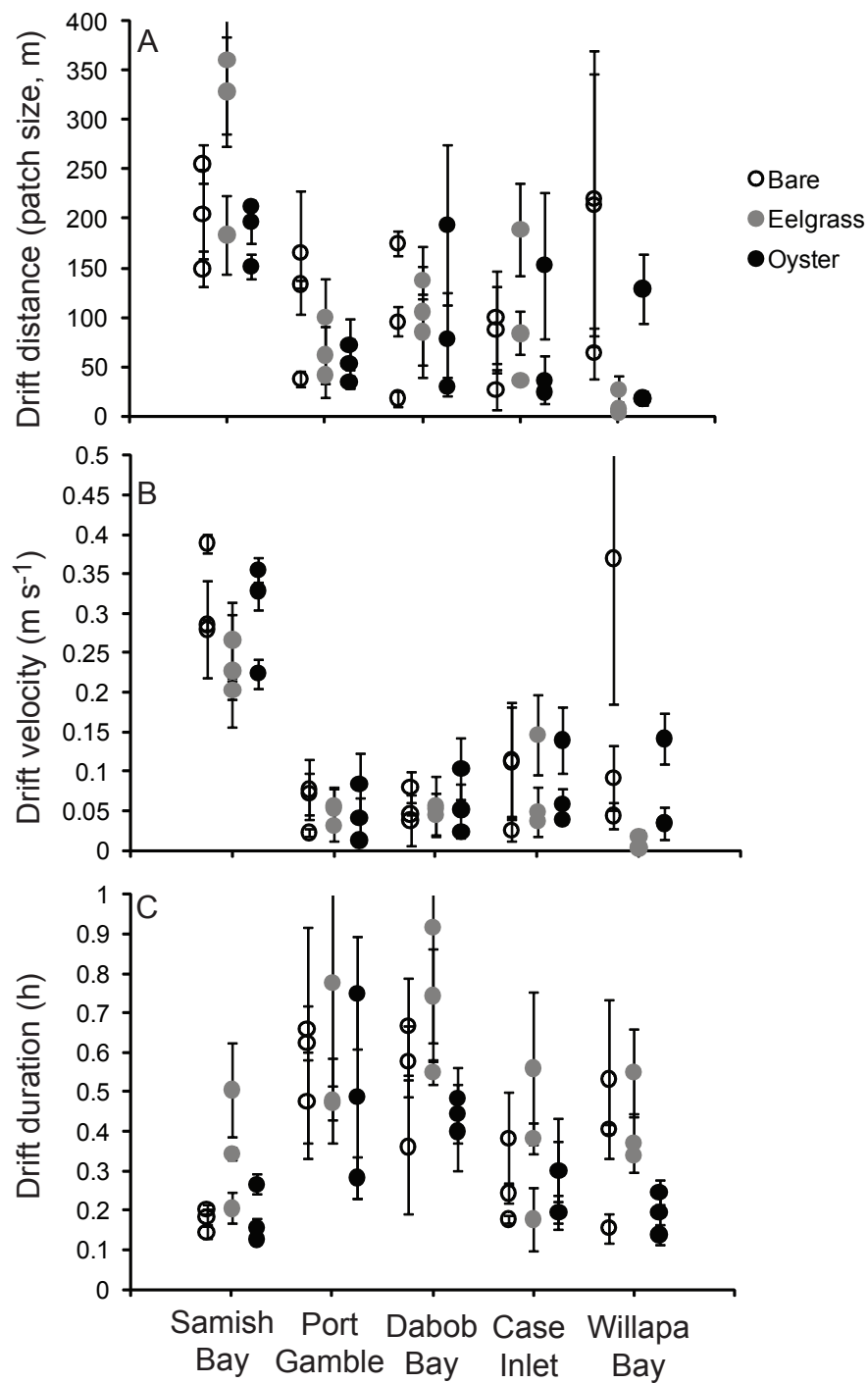
**Figure 4**(on next page)

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.
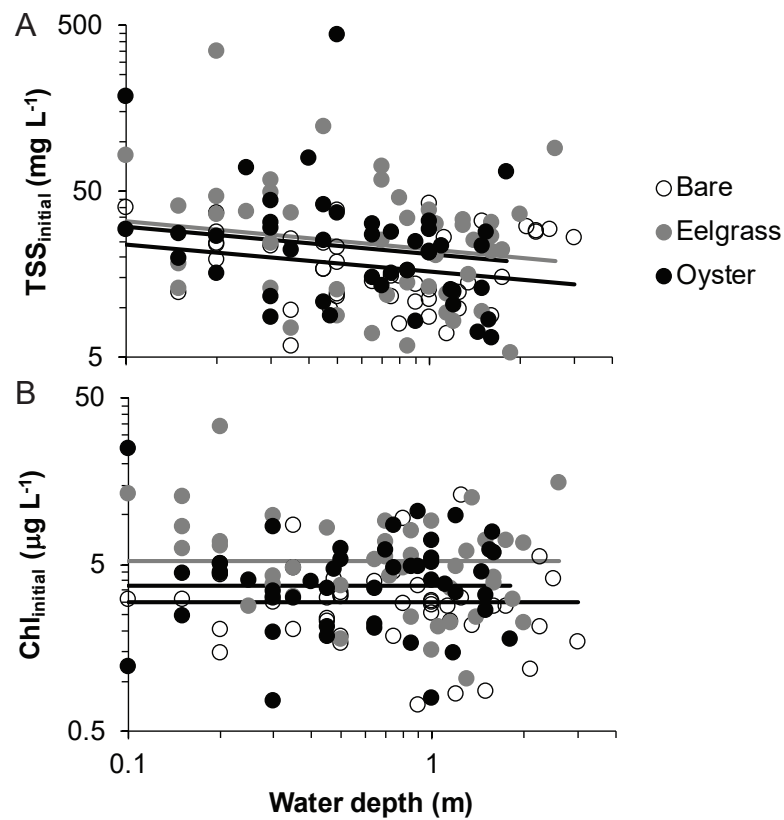
**Figure 5**(on next page)

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 $\alpha < 0.05$; habitat was not significant in these models, so a single relationship is shown.
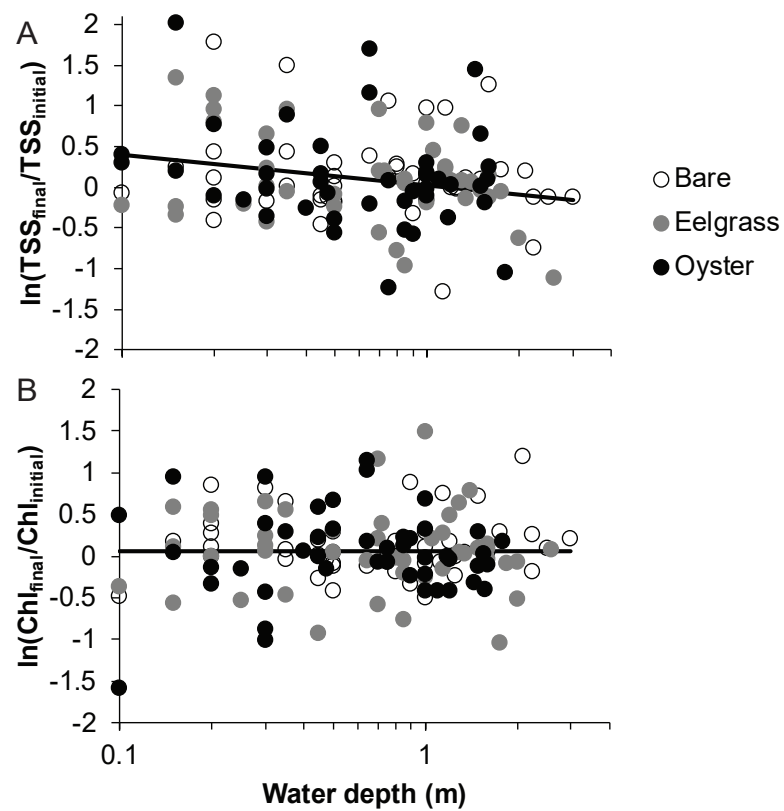
## Figure 6(on next page)

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 $\alpha < 0.05$. 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.
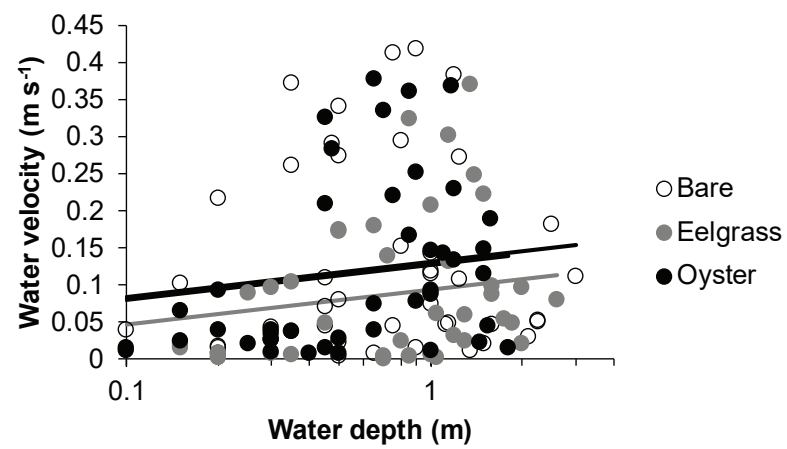
**Figure 7**(on next page)

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.
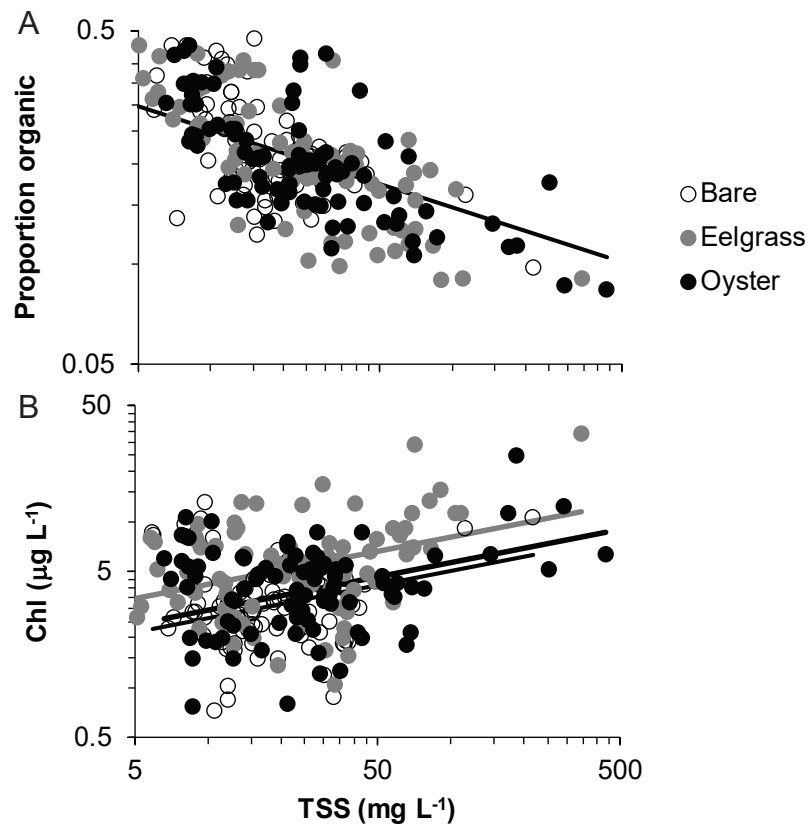
**Table 1**(on next page)

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 planned contrasts 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.

| | ln(TSS$_{initial}$) n=132 | ln(Chl$_{initial}$) n=136 | Response 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 | | |

1

2

**Table 2**(on next page)

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 planned contrasts 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. The interaction effect (habitat × ln(TSS)) was close to P=0.05 in this mixed effects model, therefore interpreted cautiously.

| | 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 | |

1