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TAXON-SPECIFIC HABITAT AND TIDAL USE BY BIRDS IN AN OYSTER CULTURE ESTUARY

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ABSTRACT Shorebirds use a variety of intertidal estuarine habitats to rest and refuel during their seasonal migrations. Birds can be found foraging on mud or sandflats, aquatic vegetation, as well as intertidal areas developed for shellfish aquaculture. In Washington State, which contributes substantially to commercial U.S. production of the Pacific oyster (*Crassostrea gigas*), little research has been published about how aquaculture habitats are used by shorebirds relative to surrounding seagrass and mudflat. Using photographic sampling, shore- and waterbird use of mudflat, seagrass, and longline oyster culture habitats was studied on an oyster farm in Grays Harbor, WA. The effect of the tidal stage (ebb, dry, or flood periods) was also evaluated. Thirteen bird taxa were identified and analyzed for effects of habitat on community composition and total bird abundance, whereas the six most common taxa were used in an analysis of habitat type and tidal stage effects on taxon abundance. Of the six focal taxa, black-bellied plover, American crow, and dunlin (*Pluvialis squatarola*, *Corvus brachyrhynchos*, and *Calidris alpina*, respectively) responded significantly to habitat type—having positive associations with eelgrass and/or longlines—whereas dunlin, dowitcher, and gulls (*C. alpina*, *Limnodromus* spp., and *Larus* spp., respectively) responded significantly to tidal stage—having positive associations with the ebb or flood periods. Total bird observations varied by habitat and through the tidal cycle, where more birds were observed in eelgrass and during ebb and flood periods. There was no strong effect of habitat type on community composition when sampling across several months. Overall, all three habitat types were used by a variety of shore- and waterbird taxa, with no evidence of a negative effect of longline oyster culture on bird abundance.

KEY WORDS: shorebirds, waterbirds, seagrass, oysters, aquaculture

INTRODUCTION

Estuaries serve as critical stopover and breeding sites for many species of waterbirds. Grays Harbor Estuary, in Washington State, has been designated as a reserve of international significance by the Western Hemispheric Shorebird Reserve Network since 1996 (US Fish & Wildlife Service), due to being an important stopover habitat for migratory birds. Tidal flats of Grays Harbor are also used commercially to farm oysters (mostly nonnative *Crassostrea gigas*). As a result, the intertidal zone is a mosaic of three main habitat types: unstructured mudflat, seagrass (native eelgrass, *Zostera marina*), and oyster aquaculture. Despite the recognized importance of the region for shorebirds, how birds interact with the habitat mosaic has not been explored in Grays Harbor, where bird activity could also vary seasonally and through the tidal cycle.

Structured habitats found nearshore, such as seagrasses, reef-forming bivalves, mangroves, and coral reefs, are well known for their ecosystem services, such as providing trophic resources and refuge, as well as their ability to host higher diversity communities than in unstructured habitats (Beck et al. 2003, Kovalenko et al. 2012, Whitfield 2017). Anthropogenic structure, in this case, shellfish culture suspended above the sediment, has been documented to have a mix of positive and negative effects on intertidal communities including sea- and shorebirds, with a consensus that the structures can provide resources and refuge (Dumbauld et al. 2009, Callier et al. 2018). In past studies of waterbird use of structures placed for oyster culture, different bird species show distinct habitat associations (Kelly et al. 1996, Caldow et al. 2003, Burger & Niles 2017), and the overall pattern may be attraction (Connolly & Colwell 2005) or avoidance (Hilgerloh et al. 2001). An advance in the current study was to include both unstructured mudflat and eelgrass as comparative habitats to longline oyster culture. With the potential for increased refuge and resource availability, increased use of structured habitats (seagrass and/or suspended oyster culture) by some shorebird taxa was predicted. Shorebird species likely vary in how they use the habitat mosaic, as seen in past studies, based on factors such as foraging strategy (Jing et al. 2007), diet, and predation risk.

Waterbird habitat use could differ over time at multiple temporal scales. Seasonally, migratory birds pass through the region twice a year as they move to and from northern breeding grounds. The physiological needs of the birds are different based on whether they are heading to breed, or returning from breeding, which can be reflected in behavioral changes like flock size, and decisions surrounding caloric intake and predator avoidance (O'Reilly & Wingfield 1995, Ydenberg et al. 2002). Other birds, such as the American crow and certain Gull species use the Grays Harbor habitat continuously throughout the year, but would still be likely to have seasonal changes that reflect pre and postbreeding, even if they do not migrate. On a much smaller temporal scale, the timing of tides influences access to intertidal flats. In the intertidal habitat mosaic studied here, habitats are exposed 0–2 times a day, depending on neap versus spring tides. Many shorebirds forage at the waterline (tide-following), where resources are emerging during an ebb tide and before infauna have burrowed down as water drains from sediment (Jiménez et al. 2015), however, tide-following may be abandoned in particularly resource-rich environments (Drouet et al. 2015). Given this, it is hypothesized that taxa that act as habitat-generalists will show strong tide-following tendencies.

Existing work has largely occurred in California and New Jersey (Kelly et al. 1996, Hilgerloh et al. 2001, Caldow et al. 2003, Connolly & Colwell 2005, Burger & Niles 2017, Burger 2018); this study is the first to examine the use of oyster aquaculture habitat by waterbirds in Washington State, a dominant

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region of commercial oyster production in the United States. This study is also unique in that it compares both bare and eelgrass habitats outside of culture, whereas past studies in other regions have primarily compared inside versus outside of shellfish aquaculture (a single control habitat), or shellfish reefs versus aquaculture (Burger & Niles 2017, Burger 2018). The oyster culture featured in the current study is a type of intertidal off-bottom culture known as "longlines," where clusters of oysters are strung on lines (Fig. 1). Including both eelgrass and oyster longlines as two structured habitats in the study allows for differentiation between simply the presence of structure versus no structure and possible differences based on *type* of structure; i.e., does type of structure matter, or will waterbirds respond to eelgrass and longline habitats similarly? The aims of this study were to determine:

(1) Temporal differences in waterbird abundance on an intertidal flat in Grays Harbor through the spring and fall migration periods,
(2) How bird taxa respond to habitat type and tidal stage, and
(3) How bird community composition responds to habitat type.

MATERIALS AND METHODS

Field Methods

Surveys of waterbirds were performed at an intertidal site with a mosaic of habitat types in Grays Harbor, WA (46.8667 N, 124.0697 W). Three focal habitat types were oysters on longlines, eelgrass, and adjacent bare mudflat habitat, and in patches of approximately 100 m at equivalent tidal elevation (mean lower low water). There was no eelgrass within the longline habitats (Fig. 1). The design included two true replicates, each of which was a block consisting of three patches (one of each habitat type). Blocks were separated by 1 km. Bird presence was surveyed in the field of view (approximately 7 m diameter) of cameras that captured one image per minute when habitat patches were exposed during a daytime low tide, on average 4.4 h. Surveys were carried out every two weeks in spring (mid-March to late-May 2020) and in fall (late August to mid-October 2020). Each spring survey consisted of two sampling days, but fall surveys were done on a single day. These 2-wk intervals coincided with spring tides of relatively high tidal amplitude. In most cases, each patch was surveyed with two cameras. Cameras occasionally failed, resulting in only one camera per patch for that day. Also during mid and late-March surveys, only longline and eelgrass habitats were surveyed (three cameras per patch per day; Table 1). Fall surveys were limited at the end of the migration period by low tides no longer occurring during daylight hours, and birds appearing around the farm later than anticipated from their migratory season.

Figure 1. Example of photo survey in oyster longline habitat.

Cameras (GoPro Hero3 + Silver Edition) were placed roughly 60 m apart in each patch and 1 m above the substrate, with a bamboo stake placed 7 m from the camera to determine the frame of view for data collection. CamDo intervalometers were used to take photos at a 1-min interval. Cameras were deployed during daylight ebb tides and retrieved during the following flood tide. Sites were accessed by kayak, and camera deployment and retrieval occurred in shallow water, except on some occasions when the timing was misjudged, or the authors were constrained by daylight and had to do the final approach to camera position on foot. Photographs were displayed on a computer screen, and birds were identified to species and counted in all images between 5 min before the water ebbed past each camera and then 5 min after the water passed again during the flood. The total interval was divided into equal thirds to create tidal stages: ebb, dry, and flood. Some species were combined into taxa groups due to the inability to distinguish species in the photos; for example, all gull species were grouped into "Gull spp.," and long- and short-billed dowitchers were combined into "dowitchers."

Species-specific Abundance and Habitat-use

Samples consisted of all images from each camera per habitat patch and tidal stage on 1 day. The sum of birds per species for each camera was divided by the number of images examined, providing an index of relative abundance (birds/min). Any bird that appeared in a frame of view multiple times was counted each time; individuals were unable to be distinguished to overcome this potentially repeated counting. Two analyses were carried out with respect to the six most common bird taxa, addressing Aims 1 and 2:

TABLE 1.

Total observations of birds on each sampling date.

Dates	Habitat types surveyed	Cameras per habitat in each of two blocks	Total bird observations per day (including potential repeats)
3/16/20, 3/18/20	Eelgrass, longlines	3	114, 89
3/31/20, 4/2/20	Eelgrass, longlines	3	206, 183
4/13/20, 4/14/20	Eelgrass, longlines, bare	2	103, 246
4/30/20, 5/1/20	Eelgrass, longlines, bare	2	205, 390
5/15/20, 5/17/20	Eelgrass, longlines, bare	2	29, 46
5/30/20, 5/31/20	Eelgrass, longlines, bare	2	20, 1
8/22/20	Eelgrass, longlines, bare	2	47
9/5/20	Eelgrass, longlines, bare	2	26
9/20/20	Eelgrass, longlines, bare	2	40
10/3/20	Eelgrass, longlines, bare	2	18
10/18/20	Eelgrass, longlines, bare	2	81

(1) Seasonality: relative abundance (birds/min on each day) was determined in each block and visualized over time
(2) Habitat type (eelgrass, longlines, and bare) and tidal stage (ebb, dry, and flood) relative abundance was determined for each habitat patch and tidal stage within a block on days when the species was present (at least one individual sighted at either block).

Generalized linear mixed effects modeling was performed for each taxon (glmmTMB package, R version 4.1.3; R Core Team 2022) to test whether relative abundance (birds/min on each day) differed by habitat type (eelgrass, longlines, and bare) or tidal stage (ebb, dry, and flood). The data were not well described by typical distributions due to the preponderance of zero values and large variability in numbers when birds were present. A tweedie distribution (Smyth 1996, Shono 2008) applied to these data resulted in suitable residual distribution (DHARMa package, R) and was used in linear mixed models. Date and block were included as random effects, with camera position (two or three cameras per habitat per block) as a nested random effect. For dowitchers, dunlin, and black-bellied plovers, only spring dates were used due to their limited presence during fall sampling, and May 31, 2020, was excluded from all models, due to sampling a single bird. Confidence intervals were extracted and visualized with the effect estimates. An additional generalized linear mixed effects model was fit to test the effect of habitat and tidal stage on total bird abundance with date and block as random effects (with camera position nested as before). This model also used tweedie distribution and was tested for fit using residual analysis (glmmTMB, DHARMa packages). All observed taxa were combined (total birds/min, no taxa removed), to have a value for each habitat per day and block.

Bird Community Composition

Abundance standardized by time (birds/min) was calculated for each habitat per block per day, removing taxa that were present in fewer than 5% of the samples, resulting in 11 remaining taxa (Table 2), and one taxon removed (willet, *Tringa semipalmata*). Rows [birds/day, taxa, tidal stage, habitat, and block, averaged across 2–3 cameras (see Table 1)] that did not have bird sightings were excluded. Including all sampling dates, a distance matrix was calculated (labdsv package, R) using Bray-Curtis distance measures. Permutational analysis of variance was performed (vegan package, R) to test the effect of habitat type (eelgrass, longlines, and bare) on shorebird community composition, and visualized using nonmetric multidimensional scaling. For the permutational analysis of variance, "date" was used as strata to account for the 17 sampling days across several months. Similarity percentages analysis (vegan package, R) was used to further analyze differences in community composition.

TABLE 2.

Total observations of each taxon included in community analysis.

Species	Common name	Total observations
Corvus brachyrhynchos	American crow	104
Pluvialis squatarola	Black-bellied plover	152
Limnodromus scolopaceus & griseus	Dowitcher spp. (long-billed and short-billed)	457
Anas platyrhynchos	Mallard duck	31
Calidris alpina	Dunlin	459
Ardea herodias	Great Blue Heron	6
Larus spp.	Gull spp.	207
Calidris canutus	Red knot	12
Arenaria interpres	Ruddy turnstone	6
Numenius phaeopus	Whimbrel	71
Tringa melanoleuca & T. flavipes	Yellowlegs spp. (greater and lesser)	8

RESULTS

Taxa Presence Over Time

Abundance (birds/min) over time revealed temporal differences in bird presence (Fig. 2). Dunlin (*Calidris alpina*) and dowitchers (*Limnodromus* spp.) were most frequently observed among the six focal taxa. Dunlin and black-bellied plovers (*Pluvialis squatarola*) were most abundant in surveys 2 and 3 (March and April), whereas dowitchers and whimbrels (*Numenius phaeopus*) were most abundant in survey 4 (end of April and beginning of May). Gulls (*Larus* spp.) were present throughout all surveys, but were most prevalent in the fall, when other taxa were primarily absent. American crows (*Corvus brachyrhynchos*) were present throughout the surveys, at relatively constant abundance.

Taxa Response to Habitat and Tidal Stage

Taxa varied in their response to habitat type. Black-bellied plovers, dunlin, and American crows had significant responses to habitat type, where black-bellied plovers were positively associated with eelgrass and longlines, whereas American crows were positively associated with longlines and dunlin with eelgrass (Fig. 3, Table 3). Dunlin, dowitcher, and gulls were all significantly affected by the tidal stage, where dowitchers were positively associated with the ebb period, whereas dunlin and gulls were associated with both the ebb and flood periods (Fig. 3, Table 3). When all taxa were combined, there was a significant positive effect of eelgrass relative to bare habitat as well as ebb and flood relative to dry periods on total bird abundance (Fig. 4, Table 4). There was no significant effect of longlines on total bird abundance relative to bare.

Community Response to Habitat

Community composition was not significantly affected by habitat type as a main effect, although a relatively low P value (0.069) indicates this may be a result of not having enough data and large variability across dates (as assemblages change). Pairwise post hoc comparisons across habitats indicate that the greatest community differences may be between bare and eelgrass habitats, although bare and longline habitats were the most similar. The similarity of composition across habitat types is corroborated by the nonmetric multidimensional scaling visualization (Fig. 5), showing a large overlap of all habitat types. Lastly, similarity percentages analysis revealed that gulls, dowitchers, and dunlin were primary drivers of the minimal community differences in all pairwise comparisons (Table 5), however, none of these were statistically significant.

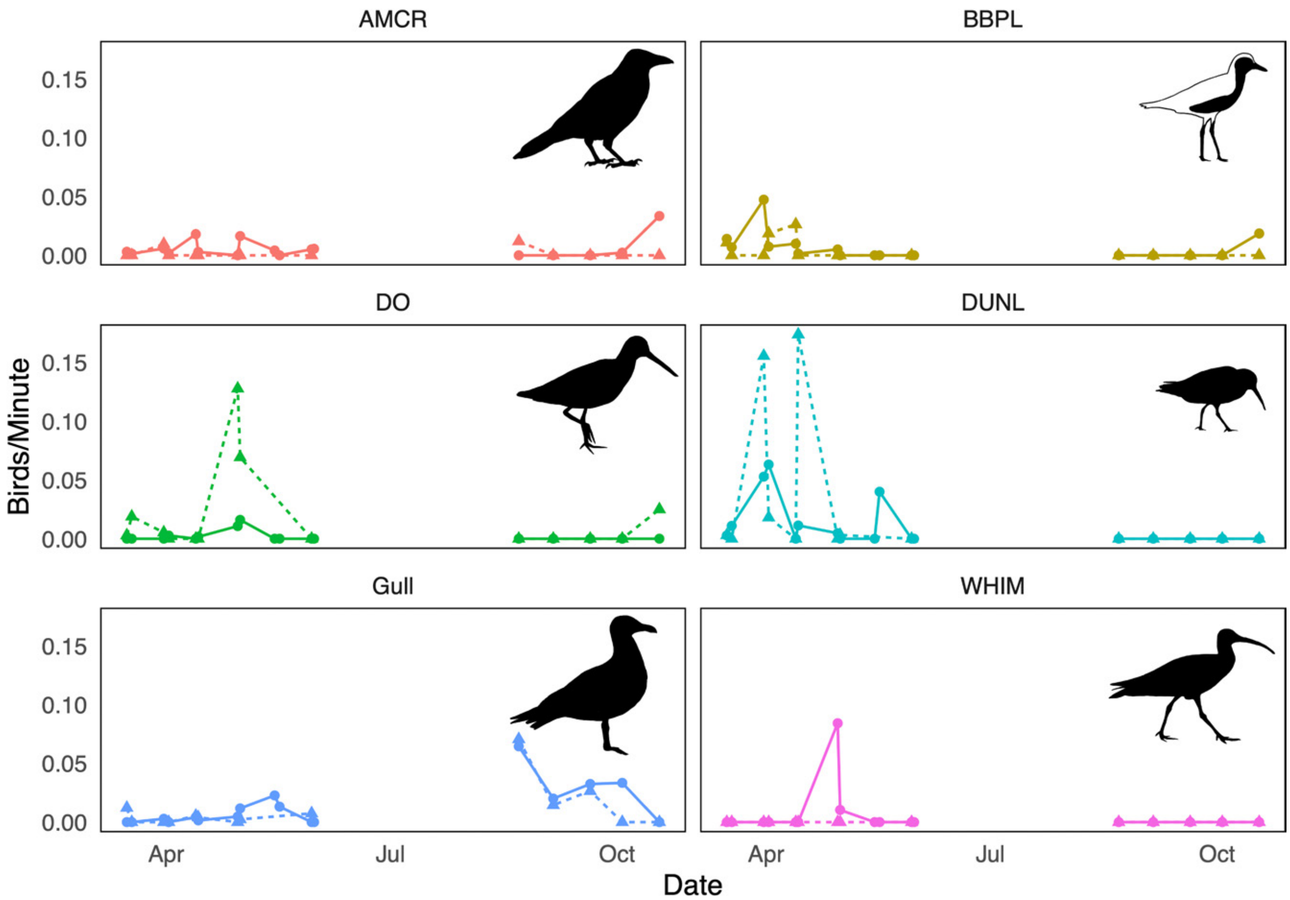

Figure 2. Standardized abundance (birds/min) of the six most prevalent waterbird taxa using intertidal habitat in Grays Harbor, WA, in 2020. Dotted lines represent the western site and filled lines represent the eastern site. No data was collected during June or July.

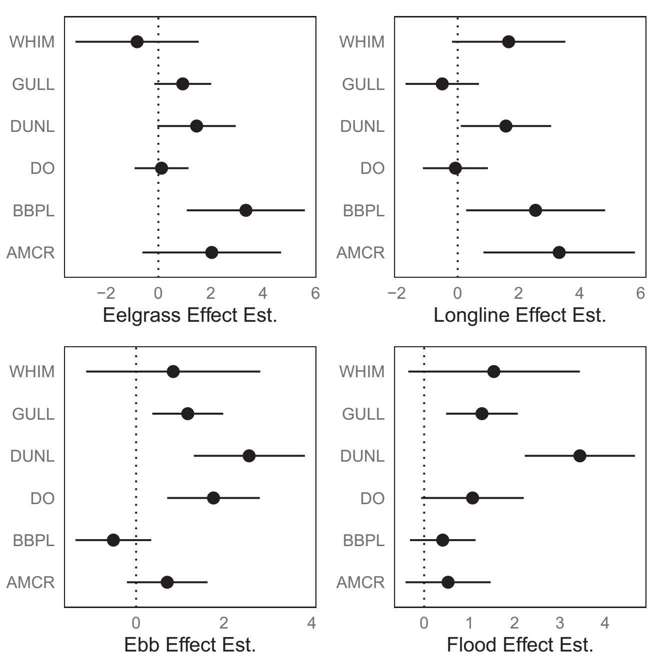

Figure 3. Coefficients and 95% confidence intervals of fixed effects on bird taxa.

DISCUSSION

Waterbirds respond to both tidal stage and habitat type. The responses are taxon-dependent, where some taxa respond to habitat type, whereas others respond more to tidal stage. In the individual analysis of six focal taxa, black-bellied plovers, dunlin and American crows responded to habitat type. Black-bellied plovers were positively associated with eelgrass and longlines, whereas dunlin and American crow were positively associated with longlines (Fig. 3, Table 3). Gulls, dunlin, and dowitcher all responded significantly to the tidal stage and were positively associated with either ebb or flood periods.

Species-dependent responses to habitat are a common outcome of studies on waterbird habitat use in other regions (Kelly et al. 1996, Hilgerloh et al. 2001, Caldow et al. 2003, Connolly & Colwell 2005, Burger & Niles 2017). In Humboldt Bay, CA, in comparisons of eelgrass habitats with and without longlines, whimbrels and dowitchers were more abundant in longline plots than adjacent control plots, whereas black-bellied plovers were more abundant on eelgrass-containing control plots; three additional species, including dunlin, used the habitats differently depending on the site (Connolly & Colwell 2005). This is only mildly consistent with the current study, where black-bellied plovers were positively associated with both eelgrass and longlines, dunlin were associated with longlines, and dowitchers

TABLE 3.

Results from six generalized linear mixed effects models of birds/min of each focal taxon as a function of habitat type and tidal stage.

Taxon	Fixed effect	Estimate	SE	*z*-value	Pr(>|*z*|)
Dowitcher	(intercept)	−6.6389	1.1554	−5.746	9.14e-09
	Eelgrass	0.1211	0.5251	0.231	0.81760
	Longlines	−0.0747	0.5438	−0.137	0.89073
	Ebb	**1.7605**	**0.5372**	**3.277**	**0.00105**
	Flood	1.0670	0.5783	1.845	0.06502
Black-bellied plover	(intercept)	−8.3949	1.1858	−7.080	1.45e-12
	Eelgrass	**3.3371**	**1.1494**	**2.903**	**0.00369**
	Longlines	**2.5530**	**1.1605**	**2.200**	**0.02781**
	Ebb	−0.5172	0.4393	−1.177	0.23900
	Flood	0.4099	0.3697	1.108	0.26765
Dunlin	(intercept)	−8.6407	0.9350	−9.242	<2e-16
	Eelgrass	1.4563	0.7638	1.907	0.0566
	Longlines	**1.5813**	**0.7554**	**2.093**	**0.0363**
	Ebb	**2.5749**	**0.6446**	**3.995**	**6.48e-05**
	Flood	**3.4391**	**0.6209**	**5.539**	**3.04e-08**
Gull spp.	(intercept)	−7.1462	0.6515	−10.968	<2e-16
	Eelgrass	0.9311	0.5538	1.681	0.09272
	Longlines	−0.5055	0.6131	−0.824	0.40966
	Ebb	**1.1746**	**0.4118**	**2.853**	**0.00434**
	Flood	**1.2772**	**0.4039**	**3.162**	**0.00157**
American crow	(intercept)	−10.2156	1.3862	−7.370	1.71e-13
	Eelgrass	2.0364	1.3502	1.508	0.13151
	Longlines	**3.3241**	**1.2654**	**2.627**	**0.00862**
	Ebb	0.7078	0.4676	1.514	0.13008
	Flood	0.5289	0.4795	1.103	0.26997
Whimbrel	(intercept)	−7.1068	1.0858	−6.545	5.94e-11
	Eelgrass	−0.8110	1.1989	−0.676	0.4987
	Longlines	1.6701	0.9463	1.765	0.0776
	Ebb	0.8443	1.0105	0.836	0.4034
	Flood	1.5447	0.9666	1.598	0.1100

"Bare" habitat and "dry" tidal stage are used as reference variables. Bold values indicate effects with *P*-values < 0.05.

were found to be primarily tide followers. Whimbrels did not respond significantly to habitat or tidal factors in this study but were only present for a brief period of observation.

The current study is unique in that eelgrass is a separate habitat type, and not a continuous variable in control and aquaculture plots, allowing us to differentiate the effects of two types of structured habitats. In another California-based study, Western Sandpipers (*Calidris mauri*) and dunlin in Tomales Bay avoided suspended bags of oysters, whereas Willets (*Tringa semipalmata*) were attracted to them (Kelly et al. 1996). Here, dunlin and black-bellied plovers were found to be attracted to oyster longline habitats relative to bare, and none of the focal taxa had negative associations with longlines. There was a significant positive effect of eelgrass on total bird observations, but no effect of longline habitat relative to bare was found. Other studies (Kelly et al. 1996, Burger & Niles 2017, Burger 2018) have found positive or negative effects of shellfish aquaculture on bird observations. Differences among studies could come down to factors such as resource distribution, aquaculture type and disturbance amount, surrounding habitats at a landscape scale (e.g., habitat connectivity) (Farmer & Parent 1997), seasonal (and thus behavioral) variation among studies, and even the significance of neighboring stopover sites (Warnock et al. 2004).

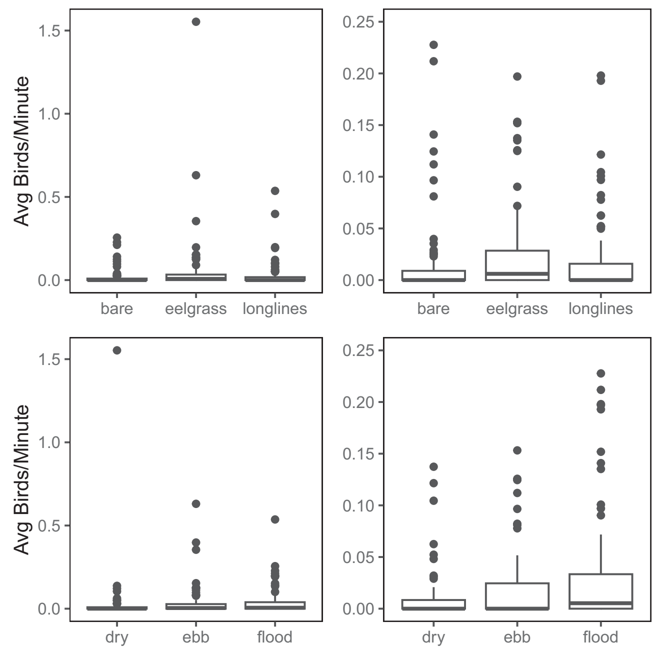

Figure 4. Box plots showing average birds/min (averaged across cameras within habitat patch/block) in different habitat types and tidal stages. Panels on the left show the entire distribution of data and panels on the right range to *y* = 0.25 to better view trends.

TABLE 4.

Results from generalized linear mixed effects model of total bird abundance as a function of habitat type and tidal stage.

Fixed effect	Estimate	SE	*z*-value	Pr(>|*z*|)
(intercept)	−5.0582	0.4033	−12.541	<2e-16
Eelgrass	**0.8165**	**0.2531**	**3.227**	**0.00125**
Longlines	0.3405	0.2652	1.284	0.19913
Ebb	**0.7474**	**0.2392**	**3.125**	**0.00178**
Flood	**0.9621**	**0.2300**	**4.183**	**0.0000287**

Bold values indicate effects with *P*-values < 0.05.

The lack of significant response to habitat type is not to say that those taxa *do not* respond to habitat type, as responses may vary at the individual level and therefore would not be captured in this study. Shorebird responses to habitat type are likely to vary with seasonal behavioral changes (related to life history), body condition, and age. Migratory shorebirds are often faced with a trade-off between food availability and predation risk. Birds migrating north during the spring (in preparation for breeding) have been found to travel in larger flocks, seeking refuge from predators at the cost of increased competition for food. Conversely, shorebirds traveling south in autumn travel in smaller groups, prioritizing food over predation avoidance (O'Reilly & Wingfield 1995). Similarly, south-migrating Western sandpipers responded to the feeding-predation risk tradeoff based on body condition, whereas individuals in more desperate need of food forage in riskier, high-fattening sites (Ydenberg et al. 2002). With the seasonal variability of bird behavior and physiology, as well as the foraging-predation risk trade-off, habitat use by migrating shorebirds is dynamic and

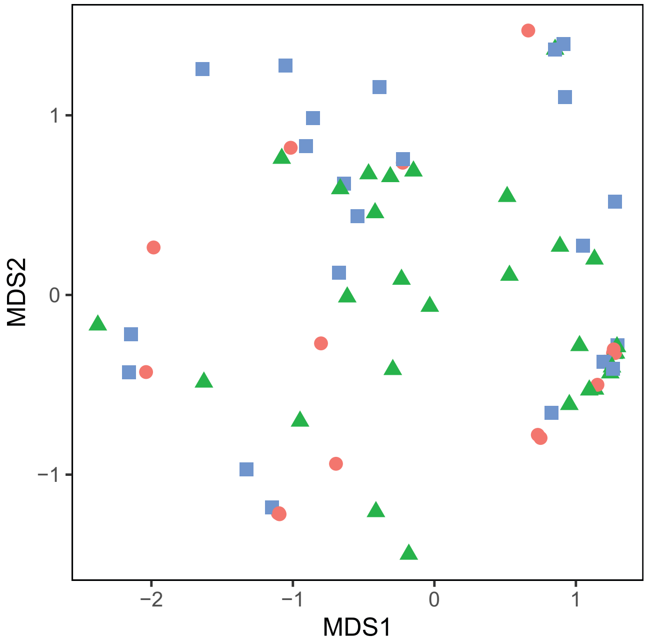

Figure 5. Nonmetric multidimensional scaling (NMDS) plot showing community composition grouped by different habitat types. Each point represents one block per day and habitat type. Bare = red circles, eelgrass = green triangles, longlines = blue squares.

TABLE 5.

Permutational analysis of variance results of community composition.

Source of variation	DF	SS	R^2	F	P
Habitat	2	1.274	0.04902	1.6751	0.069
Bare vs. eelgrass	–	–	–	–	0.174
Eelgrass vs. longlines	–	–	–	–	0.288
Bare vs. longlines	–	–	–	–	0.537
Residual	65	24.717	0.95098	–	–
Total	67	25.991	1.00000	–	–

Pairwise comparisons include Bonferroni correction.

variable, making it difficult to study. Although including both spring and fall was attempted in this study, the late arrival of birds and the shift of low tides out of daylight hours prevented the study from fully capturing seasonal dynamics at these tidal elevations.

Three of the six taxa—dunlin, gulls, and dowitcher—responded to tidal stages, with higher abundances during the ebb or flood periods relative to dry (low water) conditions. Glaucous-winged gulls (*Larus glaucescens*) are known to forage in the lowest intertidal zone available, suggesting they act as tide followers (Irons et al. 1986). This is consistent with the current findings, where gulls were mostly captured as the tide crossed the cameras during ebb and flood, and would have been foraging at a lower tidal elevation during the lowest part of the tide. Similarly, dunlin were most abundant during flood periods. In the Fraser River Estuary, British Columbia, dunlin were found to follow the tide, whereas Western Sandpipers foraged in the upper intertidal where the microphytobenthos (MPB) was greatest (Jiménez et al. 2015). In the presence of high MPB in Borgneuf Bay, France, dunlin were found to switch from tide-following behavior to foraging in high MPB areas (Drouet et al. 2015). This suggests that the tide following behavior is plastic, and responds to resource availability for maximum foraging efficiency. This strategy may also interact with the predator risk aversion behavior, in which case an individual may opt for a foraging spot with lower-density prey in exchange for increased refuge.

For community composition, there is overall a very weak, if any, effect of habitat type. Despite being one of two taxa that responded significantly to habitat type, black-bellied plovers did not play a major role in shaping community composition. Whereas the species-specific analyses included only dates when that species was present, the community-level analyses included all dates. This resulted in taxa that were around for a longer duration having a greater effect on community composition, such as the American crow, dowitchers, and gulls (Table 6). Several of the taxa who were present in the greatest numbers or longest durations did not have a strong response to habitat type or used *both* longline and eelgrass more than bare habitats, resulting in an overall weak effect of habitat on community (Fig. 5, Tables 4 and 6). As mentioned previously, response to habitat on an individual basis is important to consider, as well as possible habitat effects on taxa that were present for only short times (whimbrels, red knots, and greater and lesser yellow legs). This result is likely dependent on the specific bird assemblage present and could have a different outcome if measured elsewhere. The authors also acknowledge that combining gull and dowitcher species into single taxa may affect community composition findings.

The data indicate that there are species-dependent responses to habitat type and tidal stage, and that habitat type has a weak effect, if any, on community composition of waterbirds. Three of the focal taxa were associated with structurally complex eelgrass or longline habitats relative to bare, whereas three focal taxa were more affected by the tidal stage, utilizing the ebb or flood periods; only dunlin were affected by both habitat type and tidal stage. How birds select habitat likely interacts with factors such as season, life-history behavior/physiology, predation risk, body condition, and resource availability, making trends in small-scale habitat use difficult to detect. The current findings also show that all three habitat types are used by the focal taxa, suggesting that all of the habitat types provide functional value. In fact, having a mosaic of intertidal habitat types in close proximity is likely beneficial by providing robust habitat options for foraging.

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TABLE 6.

Similarity percentages analysis results showing the percent contribution ("average") of each taxon to dissimilarity between habitat types, the ordered cumulative sum of contributions, and whether each contribution is statistically significant from permutation.

Habitat	Average	SD	Ratio	ava	avb	Cumulative sum	P
Eelgrass vs. longlines							
DUNL	0.193970	0.248610	0.780500	0.007622	0.014767	0.227	0.114
Gull	0.179340	0.215900	0.830600	0.008379	0.002793	0.438	0.672
DO	0.176790	0.300070	0.589200	0.030274	0.009735	0.645	0.945
AMCR	0.094960	0.159910	0.593800	0.002288	0.003121	0.756	0.075
Eelgrass vs. bare							
DO	0.281910	0.356600	0.970600	0.020698	0.020274	0.329	0.073
Gull	0.232050	0.259600	0.893900	0.007915	0.008379	0.599	0.063
DUNL	0.126760	0.194500	0.651700	0.001783	0.007622	0.747	0.934
BBPL	0.084380	0.150500	0.560600	0.001008	0.004156	0.845	0.549
Longlines vs. bare							
DO	0.267850	0.350500	0.764500	0.020698	0.009735	0.304	0.165
Gull	0.181470	0.264700	0.685500	0.007915	0.002793	0.510	0.601
DUNL	0.168340	0.255100	0.659800	0.001783	0.014767	0.701	0.534
AMCR	0.082260	0.174200	0.472300	0.0000	0.003121	0.794	0.431

Ava and avb are the average abundances per group. AMCR, American crow; BBPL, black-bellied plover; DO, dowitcher; DUNL, dunlin.

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