

Intertidal habitat utilization patterns of birds in a Northeast Pacific estuary

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Abstract A habitat-based framework is a practical method for developing models (or, ecological production functions, EPFs) to describe the spatial distribution of ecosystem services. To generate EPFs for Yaquina estuary, Oregon, USA, we compared bird use patterns among intertidal habitats. Visual censuses were used to quantify abundance of bird groups and general species richness in: *Zostera marina* (eelgrass), *Upogebia* (mud shrimp)/mudflat, *Neotrypaea* (ghost shrimp)/sandflat, *Zostera japonica* (Japanese eelgrass), and low marsh estuarine habitats. Also assessed were (1) spatial variation within a habitat along the estuary gradient and, (2) temporal variation based on bi-monthly samples over a year at five tidal ranges. *Z. marina* was an important estuarine habitat based on

nearly all metrics of bird use, except for shorebird densities. This suggests that reductions in native eelgrass habitat may reduce the abundance and diversity of birds in Yaquina estuary. Our results suggest that a habitat based assessment approach is generally feasible for developing relative EPFs related to the presence of birds within estuarine systems.

Keywords Estuary · Bird · Seagrass · Eelgrass · Intertidal · Pacific Northwest

Introduction

Ecosystem services are the outputs from natural systems that sustain and fulfill human life (Daily 1997). One reason many ecosystems may be in decline is that they are not valued as much as the activities and products that degrade them due to lack of public awareness of their ecologic, economic, societal, and cultural value (Daily et al. 1997; Costanza et al. 1997; Cork et al. 2002). Increasingly there is an appreciation that a comprehensive framework describing the services provided by ecosystems can inform environment management and land-use decisions (National Research Council 2004; Millennium Ecosystem Assessment 2005a, b). One of the greatest limitations in the practical application of ecosystems services concepts is the need for more complete empirical data describing the relationship of services to ecosystem attributes (Batker et al. 2008) at the appropriate spatial

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scale for land management decisions (Nelson et al. 2009; O'Higgins et al. 2010). Ultimately, the implementation of this management approach depends on the development of quantitative models that describe how the provisioning of a service is linked to ecological structure or function, i.e., ecological production functions (EPFs) (Polasky 2008; Nelson et al. 2009).

Land-management decisions often occur at the local scale. However, in many systems, little is known about the variability of ecosystem service values at the spatial scale most relevant to local decision makers (Nelson et al. 2009; O'Higgins et al. 2010). Estuaries, for example, are generally considered one of the most valuable of habitat types (Costanza et al. 1997); however, the provisioning of ecosystem services varies within an estuary which has important management implications. The discrete habitats comprising an estuary appear to provide a useful framework for quantifying ecosystem services at a scale that is appropriate for many land management decisions (O'Higgins et al. 2010). Estuaries in the Pacific Northwest experience 2–3 m tides, resulting in extensive intertidal areas which comprise about 50 % of estuarine area (Lee and Brown 2009). These intertidal areas are typically composed of functionally discrete habitats such as burrowing shrimp, sea grass, and marsh. Broad faunal–habitat associations in the PNW region have been demonstrated to be reasonably consistent across space and time for abundance and species richness of sediment invertebrates (Ferraro and Cole 2007, 2011) and nekton (Ferraro and Cole 2010).

Based on this framework, O'Higgins et al. (2010) developed a standardized method that combines habitat maps and habitat–faunal associations to estimate the spatial distribution of ecosystem service values for recreational and commercial fisheries within estuaries. We used a similar approach to develop EPFs to describe bird usage among five dominant intertidal habitats found in a representative Pacific Northwest estuary, Yaquina estuary, Oregon, USA. We also expanded upon previous work by exploring within habitat variation of bird use to better understand potential sources of error when EPFs derived at local scales are extrapolated to larger spatial scales, which is a standard practice (Costanza et al. 1997).

Estuaries and the varied wetland types they contain are critical bird habitats (Baldwin and Lovvorn 1994a,

b; Buchanan 1988; Buchanan and Evenson 1997; Colwell 1993, 1994; Page et al. 1999; Warnock et al. 2002; Warnock and Takekawa 1995; Wetzel 1996; Wilson and Atkinson 1995) that provide opportunities for bird watching and waterfowl hunting, which are significant human recreational activities both in the U.S. and worldwide (U.S. Department of the Interior, Fish and Wildlife Service, U.S. Department of Commerce, U.S. Census Bureau 2007; Southwick Associates, Inc. 2008; U.S. Department of the Interior, Fish and Wildlife Service 2009). In a meta-analysis of the economic values associated with wetlands, Woodward and Wui (2001) found that bird watching was one of the highest valued services of wetlands. In Oregon, estimated expenditures on wildlife viewing exceed that from fishing, hunting and shellfishing combined (Dean Runyon Associates 2009). In addition to direct economic services, birds provide many supporting ecosystem services (i.e., those that support the production of services directly used by humans) such as pest control, pollination, seed dispersal, scavenging, and nutrient cycling (Wenny et al. 2011). The ecological status of wetland dependent bird species, particularly globally threatened species dependent on coastal wetlands, have continued to deteriorate (Millennium Ecosystem Assessment 2005a). Improved understanding of habitat utilization patterns is a key to the protection of the wetlands these species depend on.

The monitoring, protection and restoration of estuarine habitats and species is a global and national priority due to their key role in providing humans with ecosystem services such as food, safe harbors and ports, protection from floods and storms, water regulation and filtration, and sites for recreation, aesthetics, and culture (Constanza 1997; Pendleton 2009). At the international level, the “Ramsar Convention” (www.ramsar.org) provides a framework for member countries to sustainably use wetland resources of international importance. At the national level, several acts have been established to protect estuaries and associated wildlife (e.g., The Estuary Restoration Act of 2000; The Estuaries and Clean Waters Act of 2000). In regard to estuarine birds, the Western Hemisphere Shorebird Reserve Network (WHSRN, www.whsrn.org) is a conservation effort to protect key habitats throughout the Americas for shorebirds. Specifically, intertidal habitats in the Yaquina and other Pacific Northwest estuaries have been classified as important components of the Pacific Coast fly-way

for migrating and overwintering shorebirds and waterfowl (Page et al. 1999).

To describe bird utilization patterns of intertidal habitats within Yaquina estuary, Oregon, we conducted censuses to obtain bird species and abundance data for the five dominant estuarine intertidal habitats: *Zostera marina* (eelgrass), *Upogebia* (mud shrimp)/mudflat, *Neotrypaea* (ghost shrimp)/sandflat, *Zostera japonica* (Japanese eelgrass), and low marsh. EPFs were developed for the following metrics of bird use: standardized species richness; Shannon diversity; and density for the following four groups: all birds, all birds excluding gulls, waterfowl (ducks and geese), and shorebirds. To assess the uncertainties associated with using a habitat based framework to quantify ecosystem services, we also considered additional temporal and spatial variation. These data can be used by local managers to better predict how land use decisions may alter bird viewing opportunities within Yaquina estuary. Furthermore, the general approach provides a framework to assess ecosystem services in other Pacific Northwest estuaries. There was no attempt to derive economic or non economic valuation information as part of the study, but the ecological data will help define the uncertainties for such translations in future studies.

Materials and methods

Study area

The Yaquina is a small (18.8 km²), tidally-dominated (mean tidal range = 2 m), drowned river mouth estuary (Lee and Brown 2009) located on the central Oregon coast, USA (44.62N, 124.06W; Fig. 1). Bird usage patterns were measured in five of the dominant estuarine intertidal habitats occurring in Pacific Northwest estuaries: *Z. marina* (eelgrass), *Upogebia* (mud shrimp)/mudflat, *Neotrypaea* (ghost shrimp)/sandflat, *Z. japonica* (Japanese eelgrass), and low marsh. Native seagrass *Z. marina* occurs typically at the lowest intertidal elevation as patches or meadows. Unvegetated mudflat habitat typically occurs at a higher intertidal elevation and consists of mud to muddy-sand, often occupied by *Upogebia pugettensis* (mud shrimp). The unvegetated sandflat habitat has well-sorted medium sized sand and is often extensively occupied by *Neotrypaea californiensis* (sand

shrimp). The nonindigenous Japanese dwarf eelgrass *Z. japonica* is present in the upper intertidal year-round, expanding in summer with significant winter die back (Kaldy 2006; Young et al. 2008). Low marsh habitat is found primarily near creek mouths and in the major bends of the estuary. Dominant marsh plants include *Deschampsia cespitosa*, *Distichlis spicata*, *Sarcocornia perennis*, *Jaumea carnosa* and *Carex lyngbyei* (Janousek and Folger 2013).

The intertidal habitats were identified based on a synthesis of three mapping efforts. *Z. marina* and *Z. japonica* habitats were classified using 2007 false color infrared aerial orthophotography acquired at extreme low tide (Clinton et al. 2007); the two shrimp habitats were identified using GPS survey (DeWitt et al. 2004); and the low marsh habitat using the Oregon tidal wetland delineation and classification (Scranton 2004). For the synthesis, *Z. marina* habitat took precedence over shrimp habitat. The intertidal boundaries were defined using 1998 false color infrared aerial orthophotography acquired at extreme low tide.

Because it was not possible to census the entire estuary within the short tide windows, the estuary was delineated into four sectors that provided unobstructed bird viewing from the observation sites: Idaho Flat, Sally's Bend, Raccoon Flat, and Upriver (Fig. 1). The habitats within each sector were further delineated with input from J. Lamberson. Based on these delineations, habitat/sector areas were calculated using arcGIS software (Table 1). Bird use data were collected and analyzed at the level of the habitat/sectors.

Count methods

Daylight censuses of all birds utilizing the five intertidal habitats were conducted by a single observer (J. Lamberson) from shoreline observation sites (Fig. 1) using 10 × 42 binoculars and a 65-mm spotting scope equipped with a 20–60× zoom eyepiece. Counts were made over a 1 year period during six bi-monthly cycles (December 2007–November 2008). During each cycle, birds were censused at five tide levels (<0.3, 0.6–0.9, 1.2–1.5, 1.8–2.4 and >2.4 m above MLLW), avoiding periods of heavy rain or when wind velocity exceeded 48 kph, due to the negative effects on viewing. Because tide levels

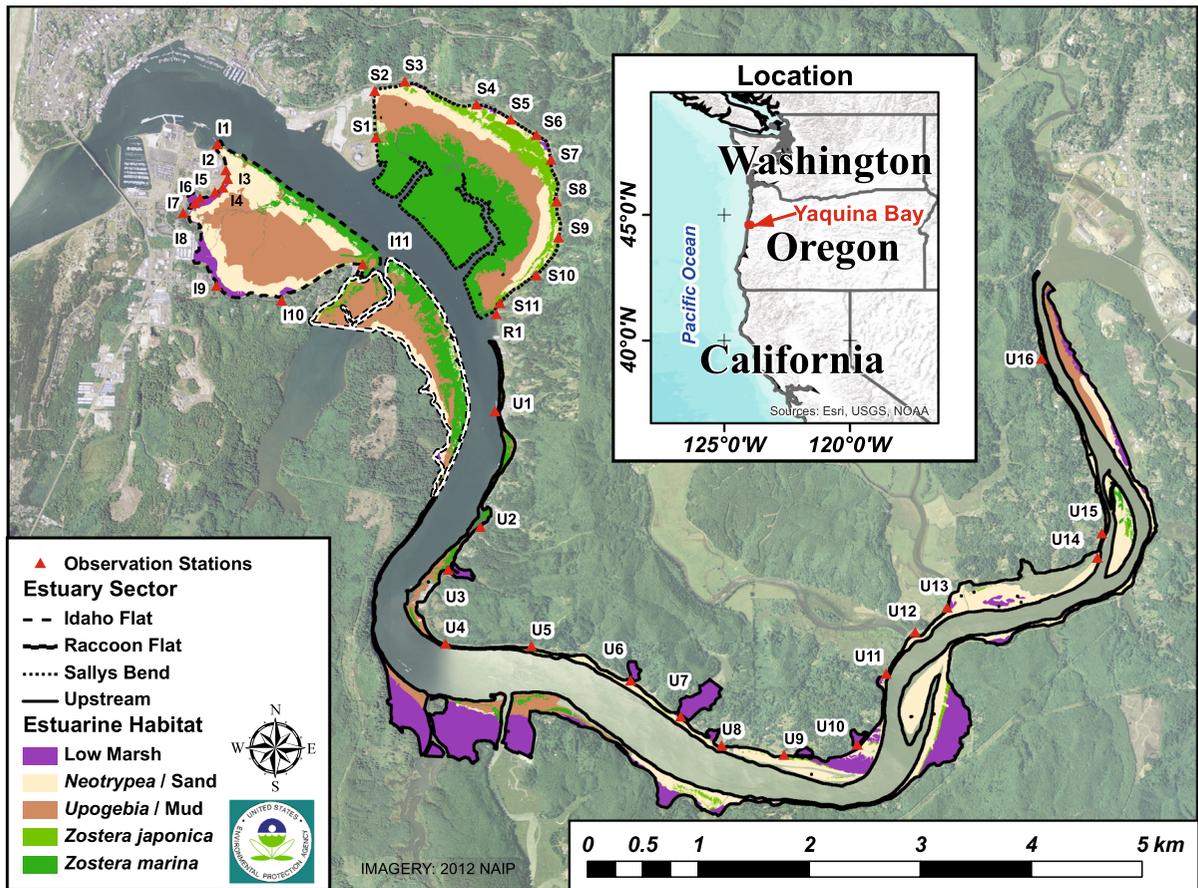


Fig. 1 Distribution of the five intertidal habitats among sectors of Yaquina estuary with observation sites

Table 1 Areas (ha) of intertidal habitats within each sector of the Yaquina estuary

Sector	<i>Z. marina</i>	<i>Upogebia</i> /Mudflat	<i>Neotrypeae</i> /Sandflat	<i>Z. japonica</i>	Low marsh	Total
Idaho Flat	14.32	59.84	43.37	0.87	8.92	127.32
Sally’s Bend	104.29	50.29	29.50	23.11	1.66	208.85
Raccoon Flat	30.62	35.61	12.07	1.88	1.58	81.76
Upriver	11.10	31.36	95.06	8.62	94.09	241.04
Total	160.33	177.10	180.00	34.48	107.06	658.97

did not exceed +2.4 m during daylight hours from April to July data were not collected at this tide level during this period.

For tides <+0.3 m MLLW, all habitats were exposed; for >+2.4 m tides, all habitats including lower parts of the emergent marsh were flooded. For tides >+0.3 m, *Z. marina* habitat became mostly flooded; for +1.2–1.5 m tides, most *Upogebia*/mudflat became flooded; and for >+1.8 m, the sandflat and

Z. japonica habitats were also flooded. When habitats were exposed, birds in flooded tidal channels were included with those in the surrounding habitat. When habitats were flooded, birds were only counted if directly interacting with the habitat. For example, diving ducks and herons that foraged were counted, whereas dabbling ducks floating on the water surface without using the intertidal habitats were not. This distinction was used because it could not be

determined whether birds located over a submerged habitat were actively selecting the habitat or passively distributed by winds or tides. Tide levels were predicted from online data (<http://tbone.biol.sc.edu/tide/index.html>) and recalculated using real time, online surge tide corrections provided by NOAA's Water Level Observation Network for the South Beach, OR tide station (<http://tidesonline.nos.noaa.gov/geographic.html>). Additional variables such as bird activity, food items, and weather condition were recorded and are available in an EPA report (Lamberson et al. 2011) and online database (<http://www.epa.gov/wed/pages/models/Yaquina.htm>).

Identification of birds was made to the lowest taxonomic level possible for viewing conditions, with the exceptions that all scaup were recorded as “scaup spp.”, and Calidrid shorebirds were recorded as “sandpipers”. Large groups of gulls were not identified to species and were combined as “gulls, spp.” because their behavior and use of estuarine habitats were similar. The gull species include Bonaparte's Gull (*Chroicocephalus philadelphia*), California Gull (*Larus californicus*), Glaucous-winged Gull (*Larus glaucescens*), Herring Gull (*Larus argentatus*), Mew Gull (*Larus canus*), Ring-billed Gull (*Larus delawarensis*), Thayer's Gull (*Larus thayeri*), and Western Gull (*Larus occidentalis*), as well as hybrids between Western and Glaucous-winged Gulls. Data on individual taxa are in the online database.

For some analyses, birds were assigned to “species groups” representing broad taxonomic similarities (geese, ducks, loons/grebes, pelicans/cormorants, herons/egrets, raptors, rails, shorebirds, terns/gulls, alcids, corvids, and songbirds; Online Resource).

Statistical analyses

For analyses comparing bird use among habitats, we did not include tidal heights >2.4 m because of missing data during some of the census periods. Of the remaining surveys (N = 480), about 32 % had zero values. To analyze these data we initially attempted a generalized linear mixed effects model approach with either a negative binomial distribution or an overdispersed Poisson distribution. However, neither model could adequately accommodate the high degree of overdispersion in the data. Ultimately, we aggregated the birds observed during all 4 tidal levels (0 to +2.4 m) for each sector/habitat/bi-monthly cycle

(referred to as a “sampling period”) for a resulting sample size of 120 sampling periods. This eliminated most of the zero counts, normalized the distribution and variation of the data (when transformed as described below), and simplified the analysis. To control for variation in bird use among estuary sectors, we analyzed the data using mixed effects regression models that included sector as a random variable. Habitat analyses were, therefore, similar to a randomized block design, with each of the five habitats represented in the four sectors of the estuary. For analyses comparing bird use among tidal levels we analyzed the raw census data (N = 600) using an ANOVA design to describe the direct and interactive effects of tide level and habitat on both abundance and bird density [$\sqrt{\sqrt{(\text{number of birds ha}^{-1} \text{ census}^{-1})}}$]. For this analysis, we were less concerned with violating the assumption of normality given the large sample size, balanced design, and the relatively simple statistical test. Simulations have demonstrated that the false positive rate is not strongly affected by non-normal distributions for ANOVA analyses (e.g., Glass et al. 1972; Harwell et al. 1992), however, the *P* values from this analysis should still be interpreted cautiously.

We analyzed three indices of bird use that mitigate variation in area among habitats and sectors: bird density, Shannon diversity index, and species richness standardized for habitat/sector area. We analyzed $\sqrt{\sqrt{\text{abundance}}}$ to more equally represent abundant and rare species and to control for higher variation at high abundances (Clarke and Green 1988). Bird density [$\sqrt{\sqrt{(\text{number of birds ha}^{-1} \text{ sampling period}^{-1})}}$] was analyzed for groups of: all birds, all birds minus gulls, waterfowl (ducks and geese), and shorebirds. For analyses of bird diversity, we excluded some composite taxa (*Mergus* sp., *Calidris* spp., *Anas* spp., *Podiceps* sp., Charadriiformes unid., Emberizidae sp., and Tachycineta spp.) because they did not necessarily represent unique species. The Shannon diversity (*H'*) index using the natural log of proportional abundance (Pielou 1969) was calculated for each sampling period. For standardized species richness (number of bird species), we corrected for unequal habitat areas (Table 1) using rarefaction. Specifically, the number of individual birds predicted to occur in 5 ha was calculated, and then rarefaction (Hurlbert 1971; Oksanen et al. 2009) was used to predict the number of species. For example, if 500 birds were observed in a sampling period within an area of 100 ha, the number

of species was predicted for 25 birds (i.e., 5 ha/100 ha sample area \times 500 individuals = 25 individuals). For analyses of standardized species richness, samples from habitats/sectors with areas less than 5 ha were excluded (analyzed sample size: $N = 96$ sampling periods). Excluded samples were low marsh habitat in Sally's Bend and Raccoon sectors and *Z. japonica* habitat in Idaho Flat and Raccoon sectors.

Statistical analyses were performed in R (v. 2.8.1; R Development Core Team 2008). For analyses comparing habitat and seasonal patterns of bird use, predictor variables included: habitat, bi-monthly cycle, and \ln (area). Area was included as a predictor because it often had an effect on bird use even though the indices of bird use controlled for sample area (density and rarefaction) or were considered relatively insensitive to sample effort (Shannon Index). To control for the influence of sector on bird use we analyzed the data with mixed effects regression models, including sector as a random variable using the nlme package (Pinheiro et al. 2009). Log likelihood ratio tests were used for model selection. Comparisons of bird use among the habitats and among bi-monthly cycles were made using the pairwise Tukey's correction for multiple comparison based on the simultaneous inference methods in the "multcomp" package (Hothorn et al. 2008). The "vegan" package (Oksanen et al. 2009) was used to generate the rarefaction estimates of species richness and to calculate Shannon diversity. A two-way ANOVA (linear model) was used to analyze the direct and interactive effects of tide level and habitat on both abundance and bird density [$\sqrt{\sqrt{(\text{number of birds ha}^{-1} \text{ census}^{-1})}}$].

For analyses of average bird use, habitat and bi-monthly cycle were analyzed as factors, and as such, the estimates for these variables represent the average predicted bird use in each category; area is analyzed as a continuous variable, and thus, model estimates describe the change in the bird use variable given a one unit change in \ln area. To make the results more intuitive, all model estimates are standardized to a 30 ha plot [i.e., $\ln(\text{area}) - \ln(30)$], rather than using the model default of a zero hectare plot. For seasonal patterns, the cycle from December 2007–January 2008 was used as the reference against which the other cycles were compared. We also derived simplified EPFs that describe bird use of habitats as averaged over the entire year after controlling for habitat area (when significant).

Results

Abundance and density patterns

A total of 49,015 birds consisting of 79 species and 10 composite taxa were recorded over the one year study period. Gulls and terns (41.5 %), ducks (32.1 %), shorebirds (10.5 %), corvids (4.7 %), geese (2.8 %), herons/egrets (2.9 %), rails (i.e., coots) (1.9 %), and pelicans/cormorants (1.8 %) comprised about 98 % of all birds observed. The remaining 1.8 % consisted of songbirds, loons/grebes, raptors and alcids. The complete list of taxa and their abundances by habitat, census period, and estuary sector is available in Lamberson et al. (2011).

Total annual bird abundance showed marked spatial variation across habitat and sector (Fig. 2). Birds were most abundant nearer the mouth of the estuary in mid and lower intertidal habitats and generally less abundant in the Upriver sector. Total abundance in *Upogebia*/mudflat and *Z. marina* habitats was more than 10 \times greater than in *Z. japonica*, while *Neotrypaea*/sandflat and low marsh habitats had intermediate values (Online Resource). However, comparisons of absolute abundance are complicated by the variation in areal extent among habitats both within and across sectors (Table 1).

After converting abundance to density values, habitats and sectors with the highest bird density were *Z. marina*, low marsh, and *Upogebia*/mud habitats in Idaho Flat, and low marsh in the Sally's Bend sector (Fig. 3; Table 2). Habitat usage comparisons based on bird density increased the importance of low marsh habitats within the lower estuary sectors relative to absolute bird abundance. However, the bird densities among the habitats could still be misleading because habitat area varied dramatically among the estuary sectors and bird density was shown to vary among the sectors of the estuary.

After statistically controlling for both sector and area with a mixed effects regression model, there were significant differences among habitats in bird density for the four bird groups examined (Fig. 4). For all birds (Fig. 4a), *Z. marina* ($P = 0.003$) and possibly *Upogebia*/mudflat ($P = 0.070$) habitats supported significantly greater bird densities than *Z. japonica*; whereas low marsh and *Neotrypaea*/sandflat were intermediate and statistically indistinguishable from all other habitats. This pattern persisted when gulls

Fig. 2 Total abundance of birds by habitat and sector in the Yaquina estuary observed during censuses conducted at five tidal levels and six bi-monthly cycles throughout the year

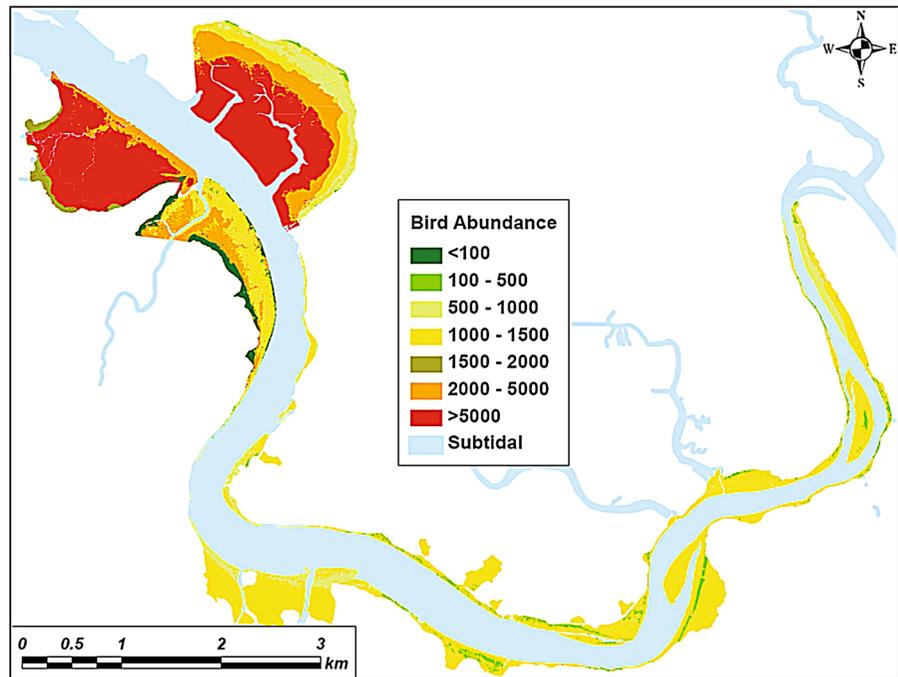
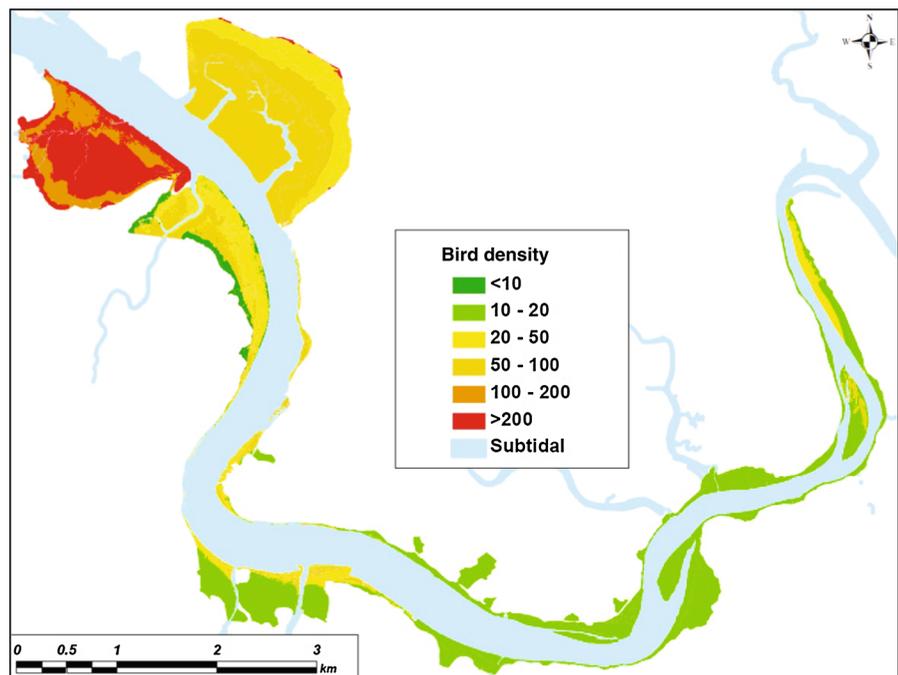


Fig. 3 Total bird density (abundance ha^{-1}) by habitat and sector in the Yaquina estuary, calculated by dividing total abundance (Fig. 2) by habitat/sector area (Table 1)



were excluded (Fig. 4b), indicating the general pattern was not driven by gulls even though this group accounted for a large proportion of observed birds. For waterfowl (Fig. 4c), *Z. marina* had significantly

greater densities than *Upogebia*/mudflat ($P = 0.020$), *Neotrypa*/sandflat ($P < 0.001$), and *Z. japonica* ($P < 0.001$); low marsh had intermediate bird densities and was statistically indistinguishable from all other

Table 2 Bird density (ha^{-1}) by bi-monthly cycle and estuary sector in five intertidal habitats

Sector	Cycle	<i>Z. marina</i>	<i>Upogebia</i> /mud	<i>Neotrypaea</i> /sand	<i>Z. japonica</i>	Low marsh	Sector grand total	
Idaho	Dec/Jan	153.9	50.4	30.1	92.0	22.4	53.5	
	Feb/Mar	11.0	22.3	23.0	0.0	39.6	22.3	
	Flat	Apr/May	6.2	14.5	11.8	0.0	7.5	12.1
	Jun/Jul	6.4	4.5	20.7	0.0	10.8	10.6	
	Aug/Sep	11.8	28.8	25.8	0.0	23.5	25.3	
	Oct/Nov	81.1	81.1	17.2	0.0	100.9	60.2	
Idaho subtotals		270.4	201.6	128.6	92.0	204.7	183.9	
Raccoon	Dec/Jan	5.5	19.6	0.0	0.0	0.0	10.6	
	Feb/Mar	6.2	12.4	0.0	0.0	0.0	7.7	
	Flat	Apr/May	2.4	3.6	0.0	0.0	0.6	2.4
	Jun/Jul	3.7	19.2	0.2	0.0	0.0	9.8	
	Aug/Sep	14.5	6.9	0.0	0.0	1.9	8.5	
	Oct/Nov	10.6	33.2	0.9	0.5	0.6	18.6	
Raccoon subtotals		42.9	94.9	1.1	0.5	3.2	57.6	
Sally's	Dec/Jan	12.4	12.0	20.8	23.8	159.0	15.9	
	Feb/Mar	6.4	8.2	11.9	0.5	1.2	6.9	
	Bend	Apr/May	9.7	36.5	4.2	0.4	29.5	14.5
	Jun/Jul	4.7	4.7	4.3	1.9	8.4	4.4	
	Aug/Sep	13.4	17.8	4.3	9.3	20.5	12.8	
	Oct/Nov	37.3	18.8	2.9	5.1	1.8	24.2	
Sally's subtotals		83.9	98.1	48.4	41.0	220.5	78.6	
Upriver	Dec/Jan	28.1	5.7	1.9	0.0	3.6	4.2	
	Feb/Mar	16.8	2.2	3.6	0.7	1.7	3.2	
	Apr/May	5.2	2.0	2.9	0.6	1.9	2.4	
	Jun/Jul	4.1	1.8	1.0	1.9	1.7	1.5	
	Aug/Sep	24.9	7.0	0.6	3.8	1.3	3.0	
	Oct/Nov	13.3	3.4	3.1	8.5	4.1	4.2	
Upriver subtotals		92.5	22.1	13.2	15.4	14.2	18.5	
Habitat density		93.3	119.0	46.0	33.7	33.1	74.4	
Habitat relative use		2.8	3.6	1.4	1.0	1		

Sector and habitat grand totals were calculated by dividing the total bird abundance in a given habitat or sector by the total area of the habitat/sector within the estuary. Relative use values for the habitats were calculated by dividing each habitat grand total by the value of the least used habitat

habitats. Shorebirds displayed a different distributional pattern (Fig. 4d). For this group, estimated mean density was lowest in *Z. marina* habitat, and densities in *Z. marina* were significantly lower than all other habitats except *Z. japonica*, and marginally non-significant in *Upogebia*/mudflat ($P = 0.059$).

Even for a given habitat type, bird density varied among the sectors of Yaquina estuary. Models that included a random sector effect were generally better supported than models without this variable (Likelihood

ratio tests, $P < 0.001$; except for shorebirds $\chi^2 = 2.95$, $df = 1$, $P = 0.086$; Fig. 3; Table 2). Sector differences cannot be formally compared using this model, but Idaho Flat had the highest observed total bird densities, likely due to the ducks that used this sector during the winter (Online Resource; Lamberson et al. 2011, Appendix C). The Raccoon and Upriver sectors had relatively low bird densities. There was also a significant interaction between sector and habitat on total bird density (Likelihood ratio test: $\chi^2 = 29.21$, $df = 14$,

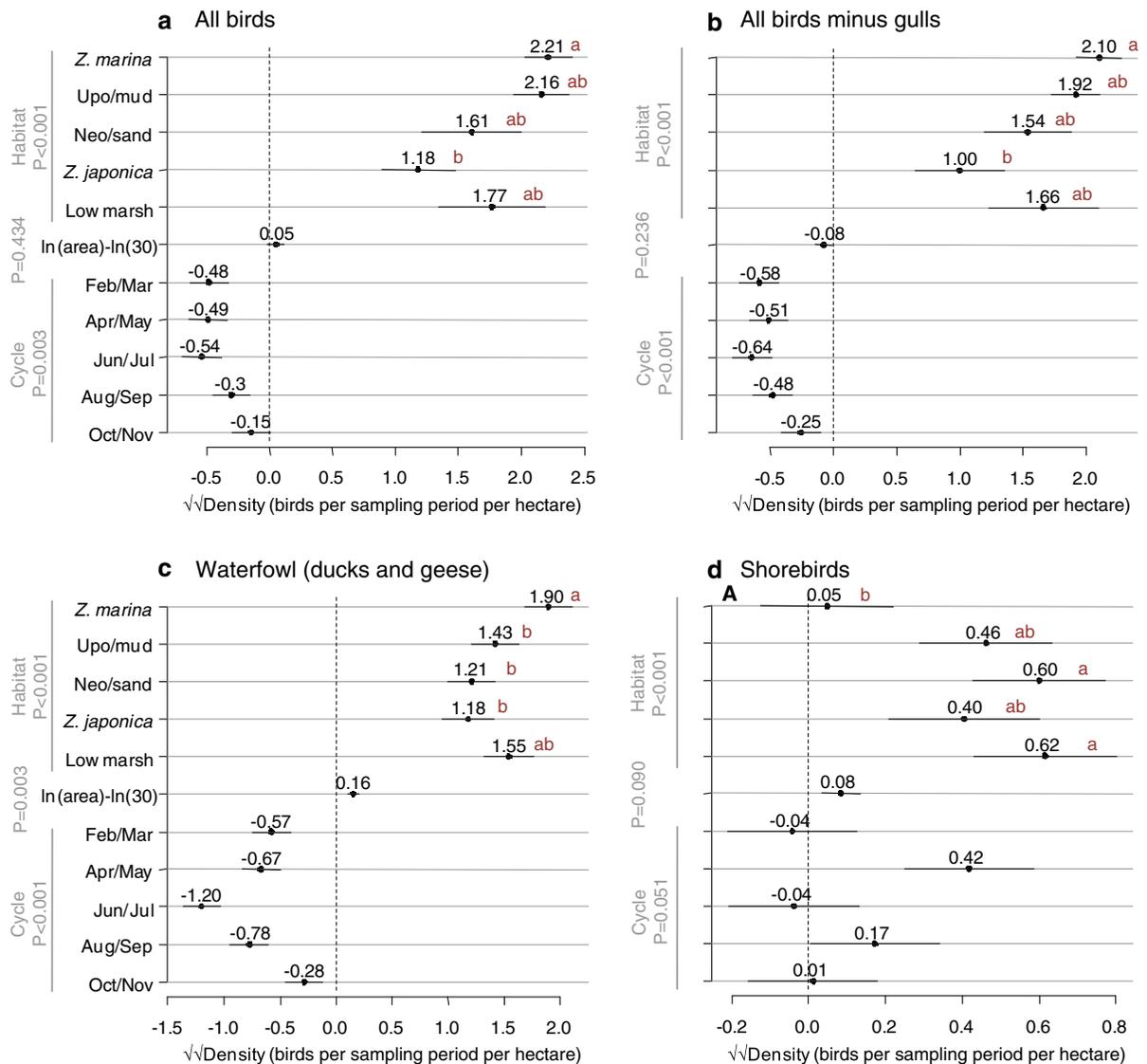


Fig. 4 Model predictions for mean bird density ($\sqrt{\sqrt{\text{birds sample period}^{-1} \text{ ha}^{-1}} \pm \text{standard error bars}$) for habitat, area, and bi-monthly cycle for: **a** all birds, **b** all birds minus gulls, **c** waterfowl (ducks and geese), and **d** shorebirds. Means are referenced to the baseline prediction for a 30 ha area sampled in

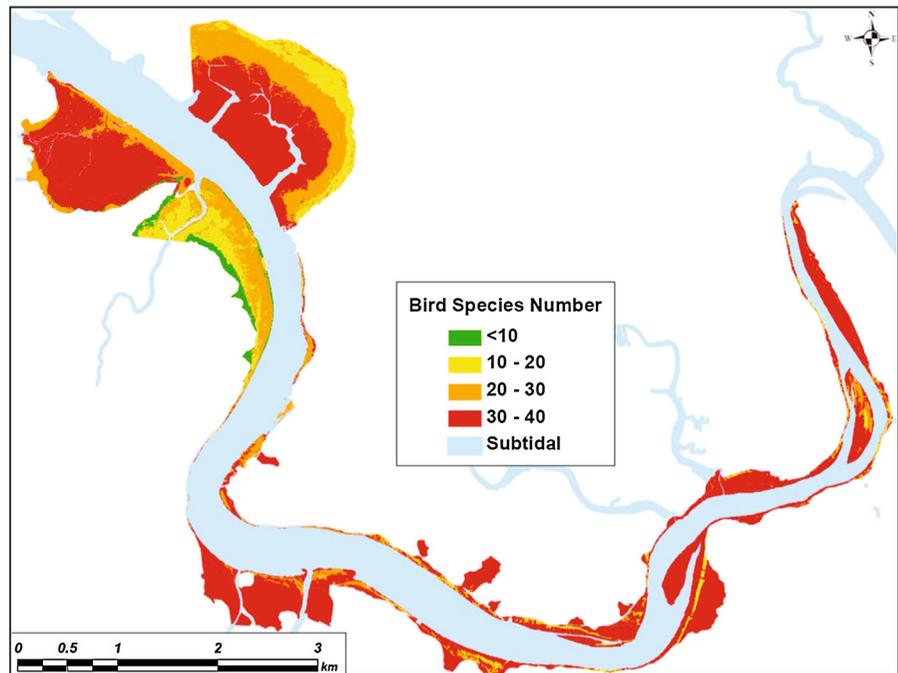
Dec/Jan and are averaged over all estuary sectors. Habitats with the same letters were not significantly different based on pairwise comparisons. Densities were calculated from the cumulative number of birds observed in censuses conducted at four tidal levels

$P = 0.01$) and marginal support for an interaction on total density excluding gulls (Likelihood ratio test: $\chi^2 = 23.40$, $df = 14$, $P = 0.05$). Qualitatively, *Z. marina* and *Upogebia*/mudflat were valuable habitats regardless of location within the estuary, whereas low marsh quality depended on sector. For marsh habitat, bird densities were very high in the Sally's Bend and

Idaho Flat sectors but very low in the Raccoon Flat sector.

Density metrics of bird use did not always fully correct for differences in habitat area. Larger habitat areas were associated with higher densities of waterfowl ($P = 0.003$, Fig. 4c). The relationship between shorebird density and habitat area was marginally non-

Fig. 5 Total number of bird species by habitat and sector in the Yaquina estuary observed during censuses conducted at five tidal levels and six bi-monthly cycles throughout the year



significant ($P = 0.090$, Fig. 4d), suggesting a similar response for these taxa.

Species richness and diversity patterns

The spatial distribution pattern of total annual bird species richness (Fig. 5) differed from that of total abundance, particularly in regard to the relatively high richness values recorded in the Upriver sector. During the course of the study 45–53 species were observed in all of the habitats, except *Z. japonica*, where only 23 species were recorded. However, as for abundance, differences in habitat area among the estuary sectors influenced richness patterns.

To control for the variation in area and sector, we used a mixed effects regression model to compare richness (standardized for habitat area using rarefaction) and Shannon diversity among the intertidal habitats. There were significant differences among the habitats for both species richness ($P < 0.001$, Fig. 6a) and Shannon diversity ($P < 0.001$, Fig. 6b). Model results indicate that, on average, significantly more bird species (nearly 2×) were observed during a sampling period in *Z. marina* habitat than for any other habitat (Fig. 6a). Based on the Shannon diversity index (Fig. 6b), *Z. marina* had significantly greater diversity than all other habitats ($P < 0.05$) except low

marsh ($P = 0.781$), which although higher than the other habitats, was only significantly greater than *Z. japonica* ($P = 0.033$). Habitats with larger areas had significantly greater bird diversity based on the Shannon index ($P < 0.001$, Fig. 6b).

Models that included a random sector effect provided better estimates of species richness (Likelihood ratio test: $\chi^2 = 22.47$, $df = 1$, $P < 0.0001$) and Shannon diversity (Likelihood ratio test: $\chi^2 = 38.7$, $df = 1$, $P < 0.0001$). Idaho Flat had the highest average number of species observed during a sampling period (means: Idaho Flat = 7.16, Upriver = 5.5, Sally's Bend = 5.27, Raccoon Flat = 3.36). For the Shannon diversity index, the Upriver sector had the highest mean values during the course of a sampling period (means: Upriver = 1.65, Sally's Bend = 1.01, Idaho Flat = 0.98, Raccoon Flat = 0.41). The Raccoon Flat sector had the lowest diversity for both metrics. There were no statistically significant interactions between sector and habitat on bird richness and diversity.

Seasonal patterns

Total bird abundance peaked in the winter months (Oct/Jan) with nearly 4× the summer (Jun/Jul) abundance (Online Resource; Lamberson et al. 2011

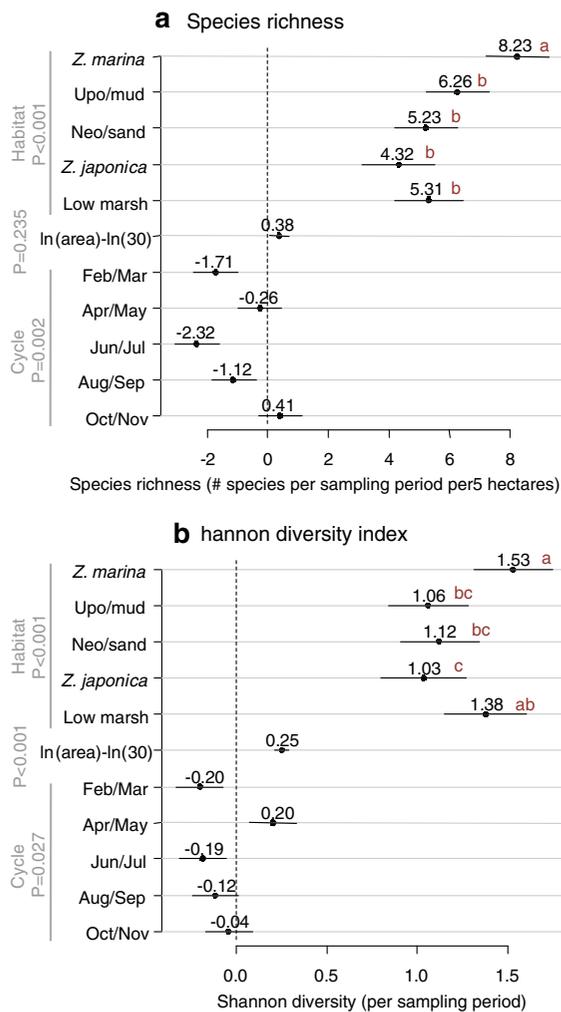


Fig. 6 Model predictions for mean **a** species richness (rarefied to 5 ha standardized area), and **b** Shannon diversity for habitat, area, and bi-monthly cycle. Means are referenced to the baseline prediction for a 30 ha area sampled in Dec/Jan and are averaged over all estuary sectors. Habitats with the same letters were not significantly different based on pairwise comparisons. Diversity metrics were calculated from the cumulative number of species observed in censuses conducted at four tidal classes. Species richness analysis does not include the low marsh habitat in Sally's Bend and Raccoon sectors and *Z. japonica* habitat in Idaho Flat and Raccoon sectors due to their small areas

Appendix C). Total bird species richness peaked in Apr/May with 52 total observed species, versus a range of 35–42 for other months (Lamberson et al. 2011).

There was a statistically significant relationship between bi-monthly cycle and total bird density

($P = 0.003$, Fig. 4a), total density excluding gulls ($P < 0.001$, Fig. 4b), and waterfowl density ($P < 0.001$, Fig. 4c). The average densities of these groups generally peaked around Dec/Jan. Densities declined during spring months to summer lows (Jun/Jul), and then increased again in the fall. Peak densities corresponded to a period when waterfowl were present, gulls were abundant, and foraging crows, and overwintering flocks of shorebirds were common (Online Resource; Lamberson et al. 2011, Appendix C).

The seasonal pattern of shorebird abundance differed from other taxonomic groups, peaking during spring migration in Apr/May (Online Resource). However, the overall model effect of bi-monthly cycle was marginally non-significant (Fig. 4d, $P = 0.051$).

Seasonal patterns of modeled species richness and Shannon diversity were more complex (Fig. 6). The analysis results suggest two yearly peaks in diversity, one around Oct/Jan and a second around Apr/May. For Shannon diversity, Apr/May had significantly greater diversity than either Feb/Mar or Jun/Jul. Interestingly the period of high diversity in Apr/May corresponded to a period of relatively low bird abundance. Similar to density, both modeled species diversity metrics were relatively low in Jun/Jul.

Tide level patterns

Two-way ANOVA found a highly significant interaction between tide and habitat on both bird abundance and $\sqrt{\sqrt{\text{density}}}$ ($P < 0.001$), indicating that bird response to tide height varies among habitats. Within each habitat, relative bird use tended to be highest as the tide approached or receded from the habitat (Fig. 7). Bird abundance in most habitats, except low marsh, tended to decline markedly when the habitat was flooded. Descriptions of tide level distribution patterns for each taxonomic group are provided in Lamberson et al. (2011).

Calculating ecological production functions

The EPFs describing bird use among habitats are provided by the model estimates in Figs. 4 and 6. For example, the average predicted $\sqrt{\sqrt{\text{density}}}$ of waterfowl (Fig. 4c) occurring in a 10 ha plot of *Z. marina* during Apr/May is calculated as:

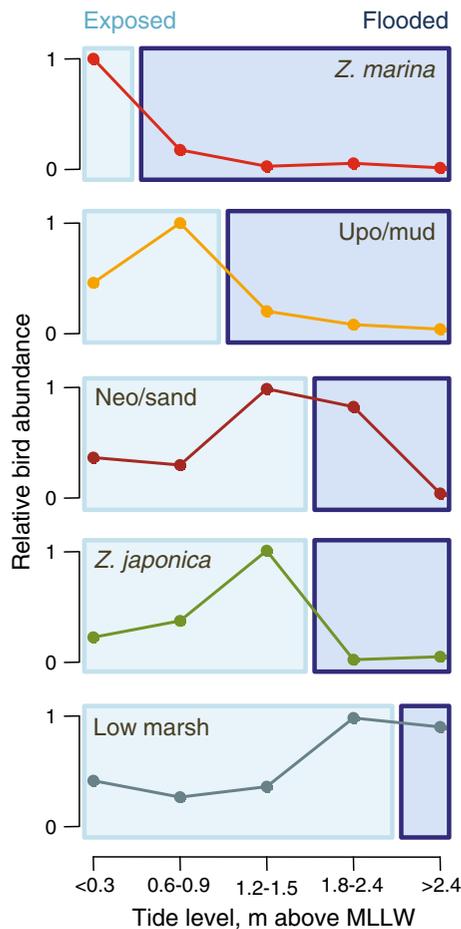


Fig. 7 Comparison of relative bird abundance versus tide level for five intertidal habitats. Points in light blue areas indicate tide levels during which the habitat tended to be exposed, and dark blue areas indicate flooded habitat

$$\begin{aligned} \sqrt{\sqrt{\text{density}}} &= \text{habitat} + 0.16 \times [\ln(\text{area}) - \ln(30)] \\ &\quad - \text{bi-monthly cycle} \\ &= 1.9 + 0.16 \times [\ln(10) - \ln(30)] - 0.67 \\ &= 1.05 \end{aligned}$$

where, density = number of birds per sampling period per hectare; the sampling period represents the total birds observed in censuses taken at 4 tide levels, habitat = estimate for *Z. marina*, Upo/mud, Neo/sand, *Z. japonica*, or low marsh, area = area of plot in hectares (should be excluded when area effect is not statistically significant), ln = natural log, bi-monthly cycle = estimate for Feb/Mar, Apr/May, Jun/Jul, Aug/Sep, Oct/Nov (Dec/Jan estimate is 0).

These estimates represent the average predicted bird use across the estuary, with each sector

weighted equally. This is a simplification because bird use within a habitat varied along the estuary gradient. We also provide similar annualized EPFs in Table 3 that describe bird use averaged over the entire year.

Discussion

A principal aim of the current study was to determine whether intertidal habitats provide a useful framework for describing the spatial distribution of ecosystem services within an estuary. Such an approach is appealing because the habitats comprising estuarine systems are relatively discrete and can be readily mapped using remote sensing and ground based approaches. This information may be used to predict how changes in habitat area may alter the suite of services we obtain from estuarine ecosystems, and may facilitate land-management decisions at the estuary scale. In this study, we developed EPFs to describe how bird use varied among intertidal habitats for six metrics of potential management relevance (Table 3). Besides habitat, we quantified several other variables, including estuary sector, tidal cycle, and season that affect bird use. These variables should be considered when assessing the provisioning of ecosystem services in estuarine environments.

Habitat was a strong predictor of all bird use metrics, and consequently habitat alterations in Yaquina estuary will likely affect bird use; however the magnitude of the habitat effect depends upon the metric of bird use. One conclusion of this study is that EPFs may need to be developed for different bird groups to fully understand the effects of habitat alteration. For example, *Z. marina* habitat in Yaquina estuary was, overall, an important bird habitat and consequently, reductions in the area of this habitat are predicted to reduce the overall abundance and diversity of birds, reducing viewing opportunities. However, if *Z. marina* populations decline, shorebird populations are predicted to be less affected than waterfowl.

Bird usage within a habitat was not constant across the spatial extent of the estuary, and thus location should be considered in ecosystem services assessments. In general the two sectors nearest the mouth of the estuary had the highest observed bird densities (Idaho Flat and Sally's Bend). For species richness,

Table 3 EPFs describing average bird use among intertidal habitats, with each sector weighted equally, in Yaquina estuary, OR, USA

Metric	Bird group	Habitat	Habitat effect	Area effect
$\sqrt{\sqrt{\text{Density}}}$ (# birds per sampling period per hectare)	All birds	<i>Z. marina</i>	1.88	$+0.16 \times [\ln(\text{area, hectares}) - \ln(30)]$
		<i>Upo/mud</i>	1.85	
		<i>Neosand</i>	1.29	
		<i>Z. japonica</i>	0.76	
		Low marsh	1.29	
	All birds (minus gulls)	<i>Z. marina</i>	1.70	
		<i>Upo/mud</i>	1.48	
		<i>Neosand</i>	1.12	
		<i>Z. japonica</i>	0.74	
		Low marsh	1.36	
	Waterfowl	<i>Z. marina</i>	1.32	
		<i>Upo/mud</i>	0.84	
		<i>Neosand</i>	0.63	
		<i>Z. japonica</i>	0.60	
		Low marsh	0.96	
Shorebirds	<i>Z. marina</i>	0.12		
	<i>Upo/mud</i>	0.58		
	<i>Neosand</i>	0.70		
	<i>Z. japonica</i>	0.33		
	Low marsh	0.58		
Species richness (# species per sampling period per 5 ha)	All birds	<i>Z. marina</i>	7.35	$+0 (P < 0.05)$
		<i>Upo/mud</i>	5.56	
		<i>Neosand</i>	4.45	
		<i>Z. japonica</i>	3.08	
		Low marsh	4.51	
Shannon diversity (per sampling period)	All birds	<i>Z. marina</i>	1.47	$+0.25 \times [\ln(\text{area, hectares}) - \ln(30)]$
		<i>Upo/mud</i>	1.00	
		<i>Neosand</i>	1.06	
		<i>Z. japonica</i>	0.98	
		Low marsh	1.32	

Estimates represent the average predicted bird use across the estuary, and thus do not describe variation in use within a habitat along the estuary gradient

the Idaho Flat and Upriver sectors tended to have the highest diversity. It is likely that unmeasured variables associated with different regions of the estuary, such as human development (McKinney et al. 2006), distance from estuary mouth, etc., influence bird use. Wetzel (1996) noted that human activities on the water and on the shore adjacent to eelgrass beds in Yaquina estuary were a major influence on the use of these habitats by Brant.

Temporal fluctuations in bird use due to changing tides and seasons will greatly complicate the logistics

for developing habitat based EPFs for mobile species such as birds in the intertidal zone (Connors et al. 1981; Connors 2008; Moore and Black 2006; Wetzel 1996). Bird density typically was highest as the tide approached or receded from a habitat and decreased when the habitat was flooded, although responses varied somewhat by bird group. When fully flooded, most bird groups either rested or foraged in non-flooded portions of exposed marsh, or moved to upland locations, while diving ducks continued to feed in flooded habitats. Strong seasonal variation in bird

abundance and diversity resulted from variation in the temporal presence of various groups (e.g., shorebirds in spring migration). Large seasonal variation is typical for estuarine bird populations on the west coast (Buchanan 1988; Buchanan and Evenson 1997; Merrifield 1998, 2001; Page et al. 1999; Shuford et al. 1989). Consequently, comparisons of bird habitat usage based on a single index period will be inadequate; instead an integrated sample over the tidal and annual cycle will better reflect habitat usage.

Another complexity is the relationship of bird use to the area of the habitat being sampled. Even when we attempted to correct bird use metrics for differences in area among the habitats, the effect of area was statistically evident in some cases. On a per hectare basis, larger patches were more valuable than smaller patches of habitat based on waterfowl and (possibly shorebird) densities and Shannon diversity. For example, our model predicts that a 60 ha plot of *Z. marina* will have about 40 % more waterfowl per hectare than a 30 ha area. A similar pattern was observed by Benoit and Askins (2002) for the relationship between habitat area and the abundance and distribution of specialized tidal marsh birds in Connecticut. Benoit and Askins observed that responses to habitat area were species specific. Salt marsh Sparrow and Willet were found in higher abundance in larger marshes, especially those exhibiting lower levels of fragmentation, while other species such as Virginia Rail, Marsh Wren and Swamp Sparrow showed no response to marsh area.

An example of how relative habitat based EPFs may be used to support management decisions relates to the issue of whether the introduction of the non-native species *Z. japonica* will negatively affect bird use of intertidal habitat in estuaries, particularly for shorebirds. Although this study was not designed to address this question, it can provide a preliminary evaluation of the issue. The *Z. japonica* beds were used primarily by ducks (mostly mallards), coot, and geese foraging on *Z. japonica* blades either at mid-tide levels (0.6–1.5 m) when *Z. marina* beds were flooded, or at high tide (>1.8 m) when the *Z. japonica* was flooded but shallow (Lamberson et al. 2011). In late winter, the aboveground biomass of this eelgrass species died and plants were largely reduced to stubble, and shorebirds foraged both within this habitat and in the adjacent *Neotrypaea*/sandflat habitat without apparent regard to the presence of the stubble. In the Yaquina estuary, *Z. japonica* is most likely to

supplant the *Neotrypaea*/sand habitat. There were no significant differences between *Z. japonica* and *Neotrypaea*/sand habitat for any metric of bird use. Thus, there was no evidence that birds will be negatively impacted by the presence of this non-native species in Yaquina estuary. Baldwin and Lovvorn (1994b) have shown that *Z. japonica* is readily fed on and is an important food source for Brant and a variety of dabbling ducks including American Wigeon, Northern Pintail, and Mallard.

Conclusions

This study demonstrates that a habitat-based assessment approach is generally feasible for developing EPFs to describe bird use within an estuarine system. However assessments based on this framework must consider multiple sources of variation to obtain a complete and unbiased description of how bird use varies among habitats, including: (1) differences among bird groups in usage patterns; (2) the value of a particular habitat may not be consistent across the estuary; (3) tidal and seasonal variation; (4) larger habitats may be more valuable on a per area basis. Given the additional sources of spatial variation driving bird use patterns (beyond habitat), uncertainty will greatly increase when using EPFs derived at local scales to extrapolate to larger spatial scales in estuarine environments. In this study, we made no attempt to derive economic or non economic valuations, however, these data will help define the uncertainties for such translations in future studies. Ultimately, economic and social scientists will need to develop models to translate metrics of bird use into ecosystem service values by taking into account a variety of factors such as human valuation of abundance/diversity and opportunities for viewing and hunting.

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