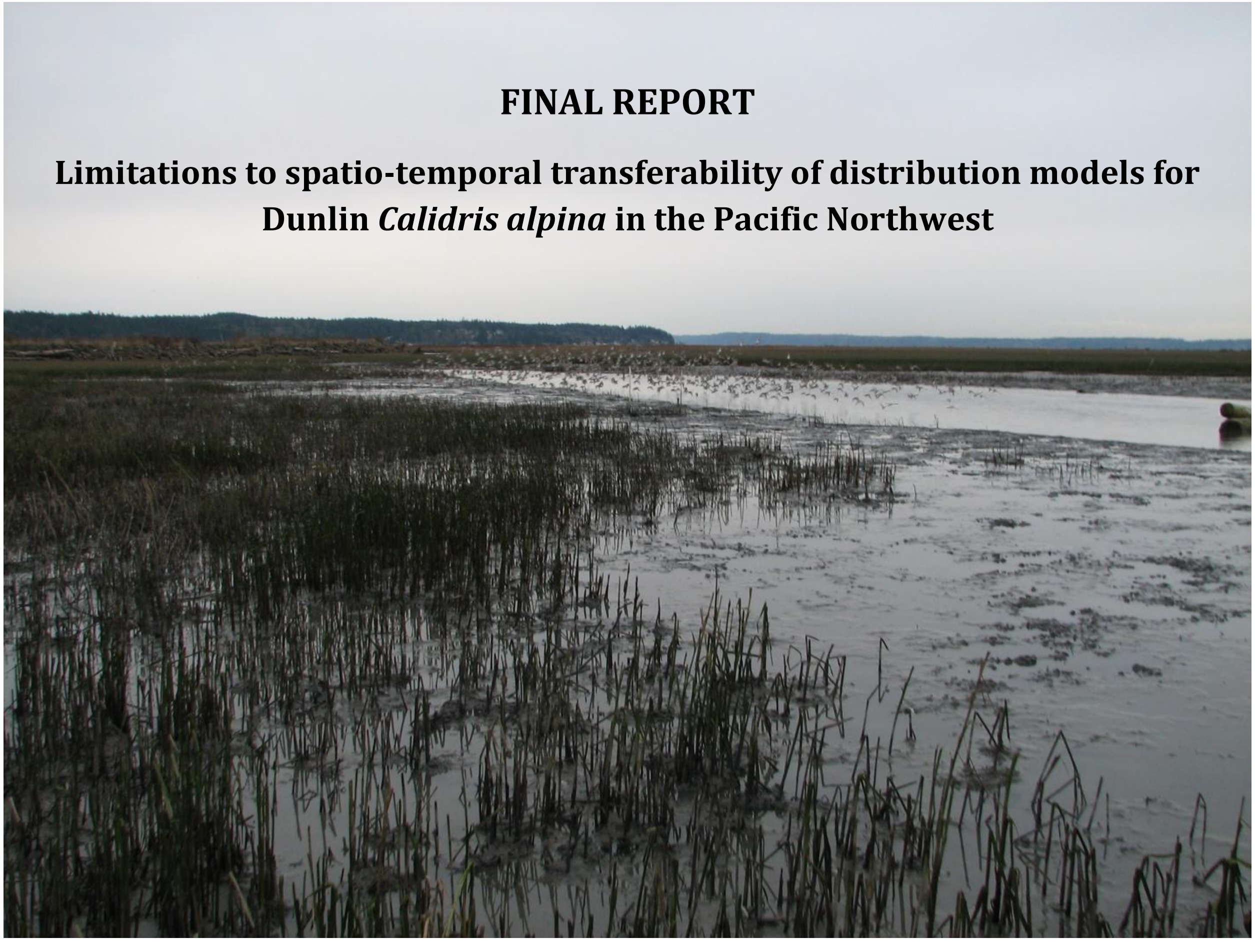
FINAL REPORT

Limitations to spatio-temporal transferability of distribution models for Dunlin *Calidris alpina* in the Pacific Northwest



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Prepared for
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Contents

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Abstract

A series of SDMs (species distribution models) have been developed for a small shorebird, the dunlin *Calidris alpina*, using intertidal mudflats at two important wintering sites in the Pacific Northwest of North America located 100 km apart, the Fraser River Delta in British Columbia, Canada and the Skagit River Delta in Washington State, USA. This report deals with the question of spatio-temporal transferability of SDMs for the dunlin, between these two sites.

Fraser models were developed using presence/absence data from a set of distinct random locations while Skagit models were based on a sample of radio-telemetry locations compared to a set of available locations (pseudo-absences). Generalized linear models (GLM) were used as the modelling tool in the exercise.

Models demonstrated a reasonable fit to the data and acceptable internal discriminatory capacity and calibration. When compared between the two sites they also included many of the same predictors that defined dunlin distribution in the intertidal zone. Dunlin showed strong preferences for organically-rich sediment, proximity to tide line and intertidal channels. Two important predictors – distance to vegetation cover (high-shore) and/or mudflat elevation, however, showed very different effects between Fraser and Skagit models. While dunlin in the Fraser selected for intermediate to maximal distances from shoreline and/or lower mudflat elevations, dunlin in the Skagit heavily used higher intertidal and adjacent saltmarsh habitats. This variation in spatial patterns of habitat use at these two sites, resulted in in poor cross-region transferability of models. While basic relationships between dunlin and their habitat remain similar in both study areas, heavy predation on dunlin and other small shorebirds by diurnal and nocturnal raptors in the Fraser Delta likely strongly skews dunlin habitat preferences away from the source of danger, the shoreline, at that site. This biotic interaction appears to be the most likely reason for poor model transferability between Fraser and Skagit deltas. Based on these results it is recommended that region-specific SDMs be used for spatially-explicit quantitative habitat modelling and visualization of intertidal distribution of the species.

In the Skagit River Delta, the habitat mosaic of unvegetated mudflats and up-shore saltmarsh provide areas of preferred habitat for dunlin. Conservation strategies that restore these habitats or that increase the amount or extent of organic-rich sediments and channel development in them should increase the quality of shorebird foraging habitat and enhance the carrying capacity of the Skagit River estuary for dunlin and likely other shorebird species.

Introduction

Contemporary conservation science and wildlife management make a broad use of species distribution models (SDMs) (Convertino *et al.*, 2011; Thaxter *et al.*, 2011; Elith & Leathwick, 2009). Such models are employed to visualize species distribution in space, explore mechanistic links between the organism in question and its environment, and to make predictions about changes in distribution when physical characteristics of the environment are altered. This latter, predictive use of SDMs is dependent on their transferability, i.e. ability to predict species distribution outside of the original model training environment (Vanreusel *et al.*, 2007; Heikkinen *et al.*, 2011; Zharikov *et al.*, 2009; Loe *et al.*, 2012). Generally, models comprised of parameters with known mechanistic links to species ecology and built on data covering broad environmental gradients of species distribution are expected to perform well (Vaughan & Ormerod, 2005; Randin *et al.*, 2006). Still, significant challenges in the development of transferable models remain (Heikkinen *et al.*, 2011; Vaughan & Ormerod, 2005), many of which are purely objective. For example, local idiosyncrasies in habitat composition and configuration, history of occupancy, biotic interactions and individual population traits may result in poor cross-region model transferability (Mcalpine *et al.*, 2008; Randin *et al.*, 2006; Zharikov *et al.*, 2007; Bamford *et al.*, 2009; Zanini *et al.*, 2009; Vernier *et al.*, 2008; Godsoe & Harmon, 2012; Fielding & Haworth, 1995). This in turn may necessitate development and application of local SDMs for management and conservation purposes.

Migratory shorebirds are a globally declining taxon (Thomas *et al.*, 2006). Many species belonging to this group are long-distance migrants nesting on the Arctic tundra and wintering in temporal to tropical estuaries and wetlands. Degradation of shorebird wintering habitat has been implicated as a likely cause of many shorebird population declines (Hicklin & Chardine, 2012; Howe & Geissler, 1989; Morrison *et al.*, 2004; Morrison, 2012). Therefore efforts have been directed at management and conservation of intertidal mudflats, estuaries, coastal wetlands and adjacent agricultural lands for the benefit of migratory shorebirds across the globe (Brown *et al.*, 2001; Donaldson *et al.*, 2000).

Shorebirds are one of the best studied avian groups (Colwell, 2010; Piersma *et al.*, 2004). Drivers of shorebird distribution within their wintering habitat are well-documented and understood, conceptually allowing for reliable prediction of their distribution in time and space at a given site (Piersma *et al.*, 1993; Pomeroy, 2006; Goss-Custard *et al.*, 2006; Yates *et al.*, 1993; Colwell *et al.*, 2003; Mouritsen, 1994; Zharikov & Milton, 2009; Nehls & Tiedemann, 1993). Many of the environmental parameters defining shorebird habitat can be digitally mapped or modeled in GIS, providing both the source of data and a platform for spatially explicit modelling and visualization of shorebird distributions (Granadeiro *et al.*, 2004; Zharikov *et al.*, 2005). Hence, there is a potential for SDMs to play an important role in coastal habitat management and conservation for the benefit of migratory shorebirds. Specifically, SDMs can be used for visualizing shorebird distributions on the landscape and predicting impacts of changes in habitat management and land-use (Zharikov *et al.*, 2009; Taft & Haig, 2006; Granadeiro *et al.*, 2004).

Estuarine habitats in the Pacific Northwest of North America (Oregon and Washington States in the US and British Columbia in Canada) support millions of shorebirds on migration and dozens of thousands in the winter (Vermeer *et al.*, 1994). Dunlin *Calidris alpina* is the most abundant winter resident and a common migrant using estuaries with extensive intertidal mudflats and also often adjacent agricultural fields throughout the region (Evans Ogden *et al.*, 2008; Shepherd & Lank, 2004; Slater *et al.*, 2011). A recent study successfully developed and locally tested a series of SDMs for dunlin occupying a large intertidal area in the Fraser River Delta (British Columbia, Canada) (Zharikov *et al.*, 2009). While the models performed well within their training environment on temporally independent data their transferability in both space and time remains to be evaluated.

A recent study on habitat selection and distribution of dunlin in the Skagit River Delta in Washington State (US) (see Slater *et al.,* 2011 for details) provides an opportunity to test spatio-temporal transferability of dunlin SDMs developed for the Fraser Delta (Fraser models henceforth). This test can demonstrate broad-scale applicability of the models and as a corollary – consistency of intertidal habitat selection in dunlin across the region.

Methods

Study areas

The general study areas are described in detail in Zharikov *et al*., (2009) (Robert's Bank, Fraser Delta, 49° 02' 42" N, 123° 09' 37" W) and Slater *et al.,* (2011) (Skagit Bay, Skagit Delta, 48° 19' 29" N, 122° 24' 48" W). Additional data used to update previously published dunlin SDMs were collected in 2006-2007 in Mud Bay (49° 04' 30" N, 122° 52' 24" W), Fraser Delta – a location 21 km east from the original study site described in Zharikov *et al.,* (2009) (Fig. 1). Dunlin distribution modelling in the Skagit Delta (100 km south-east from Fraser Delta) was undertaken on a 9.25 km^2 subset of the general area (test polygon henceforth) that covered a broad range of environmental conditions experienced by shorebirds foraging in the intertidal habitat (Fig. 2).

Dunlin distribution data

Methods used to collect the original data for development of Fraser models have been described in detail by Zharikov *et al.,* (2009). In brief, dunlin occurrence was recorded within 100 m radius of 242 random intertidal locations separated by at least 200 m. Surveys were conducted during day and night periods between December – April in 2005 – 2006. Concurrently, dunlin dropping occurrence was recorded with 16 m^2 plots at the same locations. These data were used to develop a series of models respectively describing the instantaneous and cumulative probability of occurrence of dunlin in the intertidal zone using a set of spatial and temporal variables. In this case instantaneous probability of use refers to the probability of dunlin occurrence at the location around mid-low tide period. The cumulative probability refers to the probability that the location had been used by the birds at any point in time starting from the moment the location emerged during the previous receding time and up to the moment of the actual observation (Mccurdy *et al.*, 1997). Ninety nine new locations sampled in Robert's Bank in December – April 2006 – 2007 were used to test the models locally (Zharikov *et al*., 2009). Additional 91 locations were sampled in Mud Bay in December – April 2006-2007 following identical methodology. In the present study these additional, previously unpublished data were combined with the 99 locations sampled in Robert's Bank in December – April 2006 – 2007 to update (re-train) the original Fraser models.

Data on dunlin distribution in the Skagit Delta were collected using radio-telemetry in the winters of 2006 – 2007, 2007 – 2008 and 2008 – 2009 (see Slater *et al.,* 2011 for details). Each location had UTM coordinates assigned to it obtained through bi- and triangulation with the spatial accuracy of ± 100 m for ground-based detections and ± 450 m for aerial detections (range 50 - 800 m) (G. Slater, pers. comm.) as well as tidal height at the nearby LaConner tidal gauge at the time of detection (obtained from http://tbone.biol.sc.edu). From this study, a subset of dunlin radio-telemetry detections that fell within the test polygon was selected. Different detections for the same individuals were separated by at least 1 calendar day (tidal cycle). Examination of geographic locations of these detections with respect to tidal height suggested that some of them should have been well underwater at the time of observations. Dunlin are known to roost on the wing, flying over the ocean during high tide to avoid predation (Ydenberg *et al.*, 2010). Therefore, some of these detections may have been of birds in flight. Others could have been due to location error, especially when birds were tracked from a plane by night when no visual fix on the flock was possible (no large pieces of woody debris, on which birds could roost during flood tides, fell within the test polygon). To minimize spatial uncertainty of locations of dunlin detections but not to be overly conservative, all detections that would have been > 0.5 m underwater based on their position and the time of observation were removed from the dataset. Following similar logic, all detections, in which the location would not become exposed by a receding tide $\leq$ 30 min after the time of detection, were also eliminated. The end result of these manipulations, which filtered out ca. 10% of raw data, were 284 georeferenced detections belonging to 88 individuals (henceforth, total testing set). On average there were 3.23 ± 2.59 (SD) detections per individual per winter. Of these, 213 detections had unique geographic coordinates (henceforth, unique testing set). Some

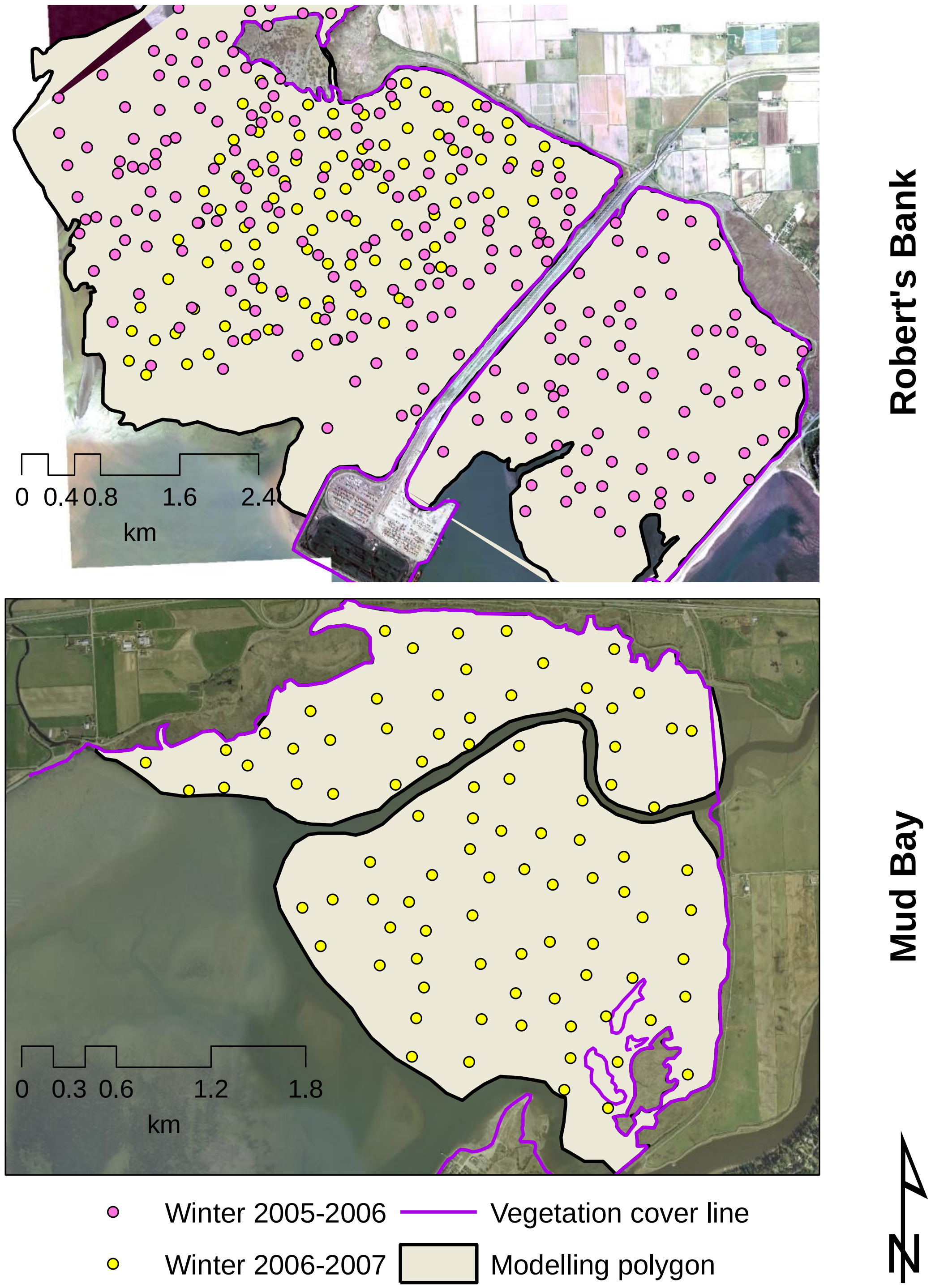

Fig. 1. *The two study areas in the Fraser Delta including locations of bird/sediment sampling stations and the definition of vegetation cover. Mud Bay is located 21 km due east from Robert's Bank.*

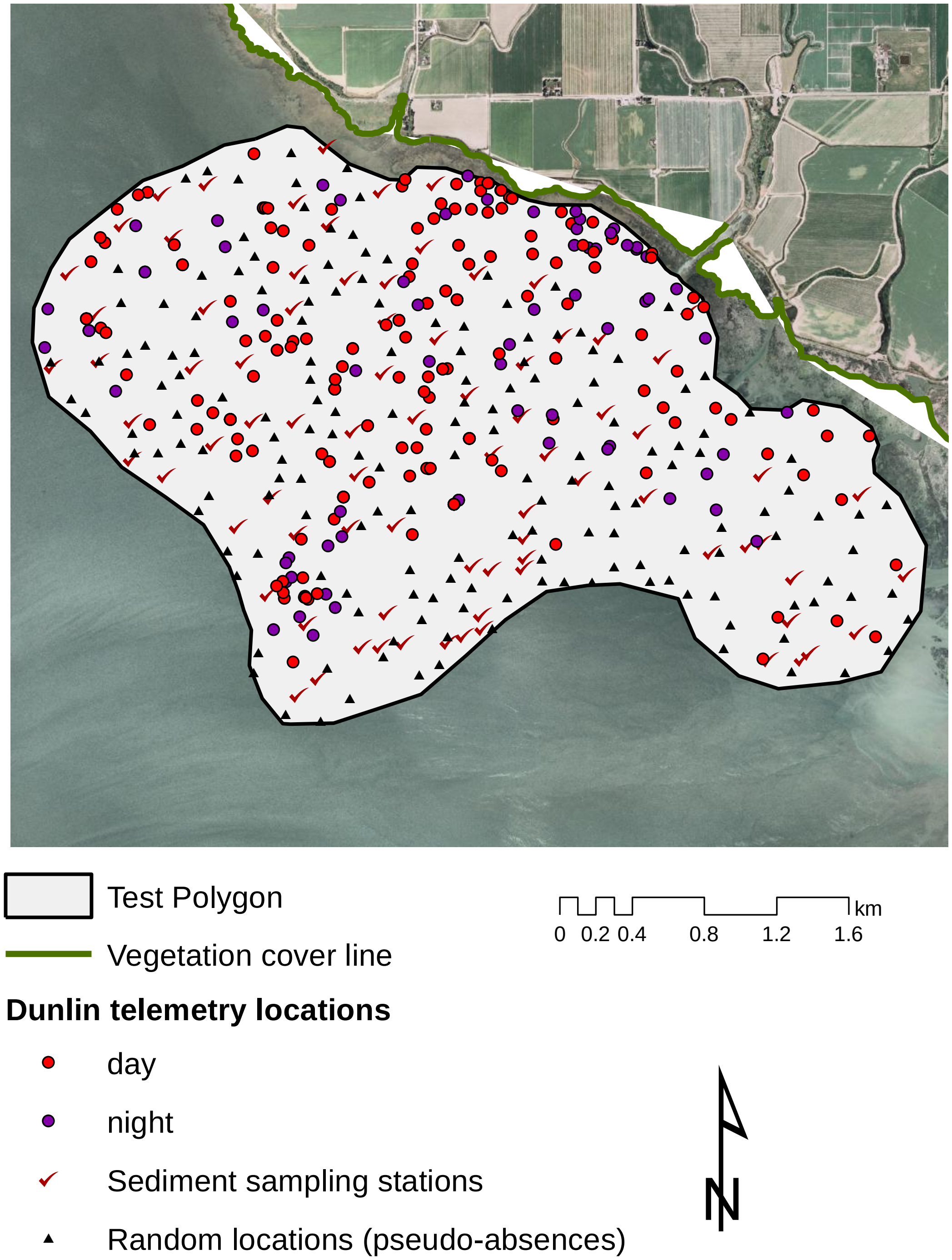

__Fig. 2.__ The Skagit Delta study area including locations of diurnal and nocturnal dunlin detections, locations of sediment sampling stations, random points (pseudo-absences) selected for the purpose of distribution modelling and the definition of vegetation cover.

detections had identical coordinates because when a flock containing several radio-tagged individuals was tracked all individuals in the flock were assigned to the same position.

Habitat data

As per Zharikov *et al.,* (2009) the following spatial and temporal predictor variables known to shape shorebird distribution in the intertidal zone were generated for the Skagit delta test polygon: (1) Mudflat elevation relative to the mean lower low water (MLLW) datum (m), (2) Distance to cover (km), (3) Distance to tidal channel (km), (4) Surface water cover (%), (5) Surface water depth (cm), (6) Sediment organic content (%), (7) Fraction of fine (<0.125 mm diameter) sediment (%, dry mass), (8) Julian date, (9) Tide at the time of observation (m), (10) Distance to tide line (m, difference between mudflat elevation and predicted tide for the LaConner tide gauge at the time of observation), (11) Time since emersion during the preceding ebbing tide (min).

Tidal channels and vegetation cover lines (edge of the tall saltmarsh, dike, or woody vegetation) were digitized from high resolution orthorectified aerial images of the study area by YZ.

All spatial data used for modelling were generated in ArcGIS 10. Spatial Analyst was used to generate distance predictors using the Euclidean distance tool. Geostatistical Analyst was employed to interpolate surface grids using ordinary kriging for surface water cover, surface water depth, sediment organic content, and fine sediment fraction. Interpolation for the test polygon was based on 82 – 90 point samples (depending on a variable) from random locations (Fig. 2) sampled for the sediment variables in May 2007 following methods described in Zharikov *et al*., (2009). Mudflat elevation was derived from a LiDAR model of the study area provided by G. Slater. All predictors were resolved at 100 m to approximately match data resolution with the special uncertainty around dunlin locations.

Modelling

All modelling was carried out on interpolated (mapped) data thus implicitly incorporating any uncertainty (error) with respect to interpolated data into the modelling process. All predictors were checked for co-linearity and distribution. Surface water depth had a strongly skewed distribution and was excluded from all analyses. If two variables were strongly inter-correlated ($r_p > 0.7$), as for example sediment organic content and fine fraction of the sediment, only one of them was included in a particular analysis (model). All modelling was carried out in the R statistical environment (http://www.r-project.org/, built 2.14.2) using libraries car, MASS, and SDMtools (updated 1 May 2012) (see Electronic Appendices[1] 1a, b for details and R code).

[1] Open J:\SkagitProject\R_files\R_WorkSpace_CombinedSkagit&FraserTests.RData in RStudio or R – this will load all the R script associated with the report

Three sets of SDMs were tested on Skagit dunlin data: (1) Fraser models published in Zharikov *et al.,* (2009); (2) updated Fraser models developed specifically for this report using additional data; (3) native Skagit models developed from the Skagit telemetry data.

Testing published Fraser SDMs

The four best performing models ("Instantaneous, day" *i* and *ii* and "Cumulative, day" *i* and *ii*, Table 2 in Zharikov *et al.,* 2009) were used to test transferability of Fraser models to Skagit Delta. Testing was done in two ways.

First. The published SDMs had been built from a set of dunlin presence and absence locations accessed around mid-low tide. Since the set of Skagit telemetry locations did not contain true absences, 170 random locations, each at least 100 m away from the nearest telemetry location and each other were generated. This was the maximum amount allowed by the size of the test polygon and spacing. These locations were assumed to represent absences analogous to the sites with no dunlin detections in the original study. This assumption is not unreasonable because random locations were not allowed to overlap with locations of positive dunlin detections, although, strictly speaking, they represent pseudo-absences and characterize available as opposed to unused habitat (Manly *et al.*, 2002; Lobo *et al.*, 2010). Interpolated spatial data were assigned to the locations in GIS. The three temporal variables used in modelling were generated for the set of random points as follows. The date and time from an instance of dunlin detection during the study period was randomly assigned to a random location such that the mudflat elevation of the random location was greater or equal to the tidal height at the time of dunlin detection. In other words the random locations were assigned to dates and times so as to be both spatially and temporally available to the birds at the time of actual fieldwork. This procedure ensured that, for example, lower-lying random locations were treated as available only when the actual tidal height was sufficiently low and also the proportion of day and night assignments among the random points was similar to that among the dunlin detections. The time of emersion was then calculated as the difference between the (randomly assigned) time from the subset of times of dunlin detections and the time when the location would have become exposed at the preceding ebb-tide.

Predicted probability scores were calculated for both dunlin telemetry locations and pseudo-absences using reverse logistic transformation $p = 1/(1+ \mathrm{Exp}(-logit))$ where *logit* refers to the linear part of the model. Then estimates of the area under the curve (AUC) of the receiver operating curve's (ROC) were calculated for each model (McPherson *et al,* 2004). The AUC value relates the true positive classification rate from the model with a binary response to the false positive classification rate across the full range of predicted probabilities. The AUC describes model's discriminatory ability and is interpreted as the probability of a random positive (presence) case receiving a greater probability score than a random negative (absence/random) case across the full range of probabilities. Models with AUC > 0.7 are considered useful in habitat suitability modelling applications (Heikkinen *et al.*, 2011; Mcpherson *et al.*, 2004).

In this analysis the subset of dunlin locations with unique coordinates (n = 213) obtained on different days (low-tide periods) was used to minimize spatial pseudo-replication. It is important to note here that the analysis assumes statistical independence of the telemetry locations even when they came from the same individuals, which would not be correct in many telemetry studies where animals sequentially move from location α to location α+1 (Koper & Manseau, 2009). In the present case, however, this assumption is not unreasonable because wintering dunlin are broadly ranging, non-territorial birds without stable social or geographic association (Conklin & Colwell, 2008; Sanzenbacher & Haig, 2002). They also have to vacate the intertidal area at high tide and retreat to roost sites. Consequently their habitat use during different low tides is likely to be driven more by prevailing environmental conditions and habitat availability and properties then by the previous position of the individual (Conklin & Colwell, 2008), i.e. not be autocorrelated.

Second. As per Zharikov *et al.,* (2009) a surface of predicted probabilities of occurrence was built for the test polygon using reverse logistic transformation in ArcGIS Raster Calculator for each of the four models. The surface was then reclassified into 10 quantiles – equal area classes of predicted probability of occurrence. The sum of radio-telemetry locations falling within each class was tabulated. It was expected that the quantiles representing higher probabilities of occurrence would contain more (i.e. higher density) individual locations. Following (Apps *et al.*, 2004) each telemetry location was given a weight of 1/*n* where *n* = number of location per individual (here all 284 locations were used). This method describes model calibration. For well-calibrated models the rank correlation between the ranked probability and sum of individual weights is expected to be $r_s > 0.7$. While good discrimination does not necessarily imply good ranking (Vaughan & Ormerod, 2005; Vernier *et al.*, 2008), when discrimination is poor, ranking will also be poor.

All selected dunlin locations were used to test transferability of the “cumulative” models since they reflect dunlin distribution during all tidal stages. Locations detected at predicted tidal height <= 2.4 m, i.e. when much of the intertidal zone would be available, were used to test the “instantaneous” models since they approximate dunlin distribution around mid-low tide.

Developing and testing updated Fraser SDMs

Since more data became available to calibrate Fraser models (Mud Bay and additional Robert’s Bank data collected in 2006 - 2007) the entire model building exercise was re-run on the combined dataset using modified, arguably improved and more objective procedures. Data were assembled as per Zharikov *et al*. (2009) and tested for co-linearity and normality of distribution. Predictors were standardized by subtracting from each value the variable's overall mean and dividing by the standard deviation. Standardization puts all predictors on the same scale and allows for easier interpretation of the relative importance of model parameters. Day and night data were analyzed within the same model by introducing interaction terms between *day/night* and all continuous predictors. First, a full model including continuous predictors and their second-order polynomial terms and all *day/night* interactions was fitted using a generalized linear model with binomial link function (*glm* routine in MASS package). Then residuals were examined and cases with unduly strong leverage on the model were identified based on Cook's distance and automatically excluded from the dataset. The full model was re-run and the most parsimonious model was selected based on the Aikaike Information Criterion (AIC, *stepAIC* routine in MASS package) without any subjective manual removal of predictors or interaction terms by the researcher. The final model automatically produced by the procedure was retained and evaluated for its fit (% deviance explained) and discriminatory performance (AUC score) using relevant routines in the SDMTools package.

Developed models were then tested on the Skagit data using the two methods described above. If the updated Fraser models "work" in the Skagit Delta, AUC and r_s scores similar to those produced by the models in their native environment (0.7-0.8) are expected. As above, cumulative models were applied to the entire set of locations and instantaneous models only to the subset of dunlin data obtained at predicted tidal height <= 2.4 m.

Developing and testing Skagit SDMs

Finally, the Skagit data were used to build local models predicting dunlin distribution in the intertidal zone – the most important foraging habitat for the birds (Slater *et al.,* 2011). Generalized linear models with binomial link function were used on the subset of geographically unique detections and random points following the steps described for the updated Fraser SDMs. These models are analogous to the cumulative models since they reflect dunlin distribution across the tidal cycle from the time the mudflat begins to emerge on a receding tide to its complete flooding 12 – 13 hours later. As discussed above this approach assumes independence of individual dunlin telemetry locations obtained on different days. Therefore application of GLM in this case seemed appropriate (Loe *et al.*, 2012). It was not possible to use, for example, generalized estimating equations to account for potential non-independence among detections belonging to the same individual, as suggested by Koper and Manseau (2009, 2012), because of uneven number of detection per individual dunlin. Models' discriminatory capacity was assessed on the entire Skagit dataset (partially independent data) as well as on the entire Fraser dataset (fully independent data) using AUC score as above.

The model calibration test was modified as follows. Because strictly speaking the Skagit models were based not on presence/absence but on presence/availability data they described relative, not absolute habitat selection (Manley *et al.,* 2002). Therefore, random (available) locations had to be used in the calculation of model calibration as well dunlin detections. As above, surfaces of predicted probability of occurrence were reclassified into 10 quantiles. Each telemetry location was given a weight of 1/*n* where *n* = number of location per individual. Each random location was given a weight of one. Sums of positive and random locations were tabulated for each quantile and the relative use per quantile was expressed as: *sum of dunlin weights / (sum of dunlin weights + sum of random location weights)*.

Here preferred habitats would display relative use values > 0.5 whereas avoided habitats would receive values < 0.5. For well-calibrated models the correlation between the ranked probability and relative use is expected to be $r_s > 0.7$.

Mapping

Predicted distribution of dunlin in the test polygon was visualized by implementing SDMs in ArcGIS Raster Calculator using reverse logistic transformation (see Electronic Appendix 2 for Raster Calculator code). Separate distributions maps were generated for day/night as appropriate. Time of exposure (min) had to be modeled as function of mudflat elevation (m) for a given tidal height (m) to generate a surface grid for predictive mapping using the following parameter coefficients from an ordinary linear model:

	Estimate (SE)	t value	Pr(>|t|)
Intercept	71.00(15.72)	4.518	< 0.0001
Elevation^2	108.04(18.74)	5.765	< 0.0001
Elevation^3	-26.81(7.60)	-3.527	0.0005
Tide	-78.04(11.64)	-6.705	< 0.0001
Tide^2	-79.24(14.78)	-5.360	< 0.0001
Tide^3	34.65(4.92)	7.046	< 0.0001

Residual standard error: 73.97 on 448 degrees of freedom, $R^2 = 0.422$, $F_{5,448} = 65.37$, $p < 0.0001$

The average tidal height at the time of observation for the set of dunlin locations was 1.15 ± 0.86 m (n = 284, range – 0.65 – 2.99 m). Also, the lowest mudflat elevation within the test polygon was 1.01 m (Table 1). Consequently, the tidal height of 1.0 m was used for all visualizations. With this regard it should be noted that the mapped (visualized) distribution represents a pattern predicted for a given point in time, in this case mid-low tide with the tidal height of 1.0 m.

Results

Modelling environments

The range of values for the spatial and temporal predictors was similar and largely overlapping between the two Fraser Delta sites and Skagit Delta (Table 1). A noticeable difference was the generally lower sediment organic content at Skagit, where organic-rich sediments were concentrated in or at the high-intertidal saltmarsh. Also the average distance from cover was considerably shorter at the two Fraser sites due to their convoluted shoreline and/or artificial structures protruding far into the intertidal zone (*cf* Figs 1 and 2). The difference in tidal height at the time of observation (detection) was methodological as Fraser observations were limited to mid-low tide period on days with the low tide ≤ 2.4 m whereas Skagit data were collected throughout a tidal cycle.

Table 1. *Means, standard deviations and ranges of the predictors used for modelling dunlin distribution in the Fraser (updated models) and Skagit deltas. Temporal variables were summarized based on the field observations. Spatial variables were summarized based on the interpolated surfaces.*

Predictor mean (SD), range	**Robert's Bank**	**Mud Bay**	**Skagit Bay**
Mudflat elevation (m)	1.59 (0.88), 0.00-3.91	2.15 (1.16), -0.36-3.90	1.54 (0.25), 1.01-2.76
Distance to cover (km)	0.90 (0.68), 0-2.92	0.57 (0.42), 0-1.62	1.82 (0.71), 0-3.22
Distance to tidal channel (km)	0.32 (0.29), 0-1.60	0.34 (0.35), 0-1.80	0.37 (0.46), 0-2.00
Surface water cover (%)	62 (32), 0-100	31 (6), 17-55	63 (31), 0-100
Sediment organic content (%),	2.3 (0.8), 0.0-5.9	2.3 (0.8), 1.3-5.0	1.4 (0.5), 0.9-3.4
Fraction of fine (<0.125 mm diameter) sediment (%, dry mass)	35.3 (25.1), 0-100	39.6 (27.5), 0-100.0	23.7 (18.7), 0-65.8
Tide at the time of observation (m)	1.28 (0.38), 0.3-2.15	1.30 (0.39), 0.1-2.15	0.78 (0.74), -0.65-2.99
Distance to tide line (m)	0.70 (0.57), 0-2.39	1.19 (0.69), 0-3.21	0.81 (0.60), 0-2.52
Time since emersion at the receding tide (min)	163.5 (123.1), 0-535	190.2 (104.4), 0-405	138.1 (96.7), 0-573

Testing published Fraser SDMs

Based on AUC calculations none of the four published Fraser models could reliably discriminate between dunlin and random locations in the Skagit test polygon. Cumulative models performed slightly better than instantaneous model but still below an acceptable accuracy of 0.7. Likewise predicted probability did not rank well with the actual frequency of occurrence of radio-tagged dunlin in the Skagit Delta (Table 2). The distribution pattern predicted by the models generally mimicked the distribution pattern in the Fraser Delta (cf. Figs 2a and c in Zharikov *et al.*, 2009), which in this case did not represent the pattern of distribution in the Skagit Delta. Fraser models of instantaneous probability of use were associated with lower percent surface water cover, intermediate distance from shore (vegetation line), higher sediment organic content, and closer distance to tide-line. The cumulative models predicted a distribution pattern associated with intermediate distances from vegetation cover, increased proportion of fine sediment, lower surface water cover, greater time since emersion and proximity to tide-line. Disagreements between predicted and actual occurrences appeared mostly due to the models' classifying a heavily used saltmarsh (high-intertidal) area in the north-central part of the Skagit test polygon as low-probability habitat because of its proximity to vegetation cover (Fig.3). The published models also did not capture well the relatively heavy use of the lower extreme of the intertidal zone by Skagit dunlin.

Table 2. *Results of application of the published Fraser models to data on dunlin distribution from the Skagit Delta*

Model	Predictors	AUC	r_s
Instantaneous, day, *i*	Sediment organic content, surface water cover, distance to tide line, distance to cover	0.556	<0.7, ns
Instantaneous, day, *ii*	Sediment organic content, surface water cover, distance to tide line, tidal height, distance to cover	0.503	<0.7, ns
Cumulative, day, *i*	Fraction of fine sediment, surface water cover, distance to cover	0.633	<0.7, ns
Cumulative, day, *ii*	Fraction of fine sediment, surface water cover, distance to tidal line, distance to cover, time since emersion	0.569	<0.7, ns

Developing and testing updated Fraser SDMs

Four Fraser models were retrained using additional data collected in 2006 – 2007 (Fig. 1). Instantaneous occurrence models (based on bird observations) and cumulative occurrence models (based on observation of droppings) just for Robert's Bank (RB) and for Robert's Bank and Mud Bay combined (full) retained the expected predictors and displayed a reasonable, for a binomial response, model fit and predictive performance (Table 3). None of the models were overdispersed.

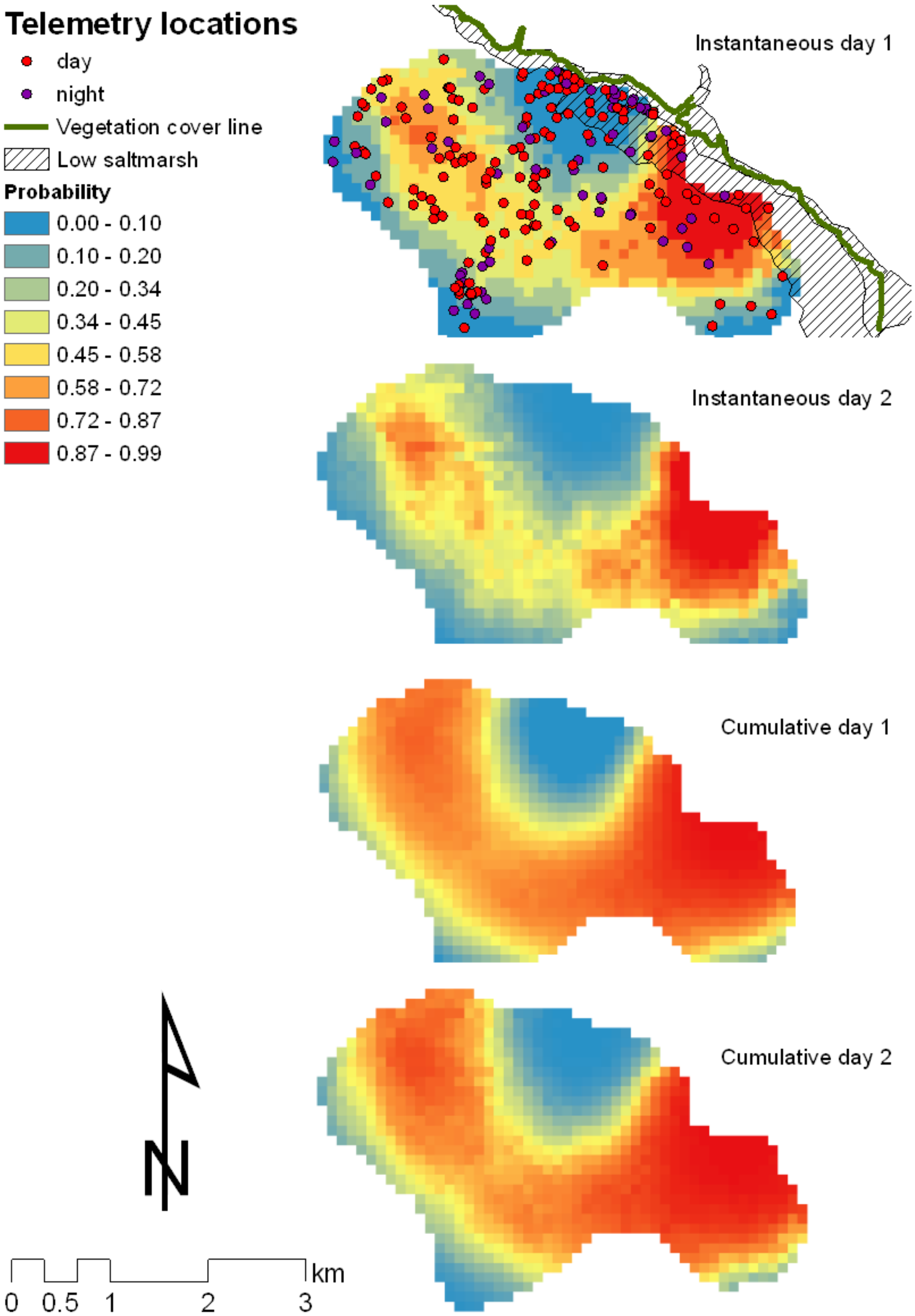

Fig. 3. *Dunlin telemetry detections overlaid on predicted distribution maps of dunlin in the Skagit Delta study area based on models from Zharikov* et al., 2009 (*at a 1.0 m tide)*.

The instantaneous probability of occurrence (i.e. probability of detecting a dunlin around mid-low tide) was positively associated with sediment organic content and was negatively associated with the duration of sediment exposure (to air), mudflat elevation, distance from a tidal channel, tidal height (i.e. birds were more likely to be detected when the tide was higher up-shore), distance to tide line (i.e. birds tended to follow the tide line) and proportion of sediment covered by water (RB model only). The birds were more likely to be detected at intermediate distances from vegetation cover. The effects of tidal height, mudflat elevation and water cover (RB model) differed between day and night (diurnal period itself did not have a clear effect on the probability of occurrence). Both instantaneous models suggested that probability of occurrence decreased with incoming tide by day, but increased by night (i.e. dunlin tended to avoid crowding into smaller areas on a rising tide during daylight hours). The full Fraser model suggested that by day, all else equal, there was no selection for mudflat elevation, whereas at night probability of occurrence was lower at higher mudflat elevations (closer to shore).

Finally, the Robert's Bank model suggested that probability of occurrence increased with percent water cover by night and decreased by day. Based on absolute values of parameter coefficients sediment surface water cover, organic content and distance to tide line had the greatest influence on the instantaneous probability of dunlin occurrence.

The cumulative probability of dunlin occurrence (i.e. the probability that a location had been used by dunlin at any time after its emergence and up to the time of observation) was most strongly affected by the diurnal cycle (it was considerably lower at night), had a U-shaped relationship with surface water cover, expectedly increased with the length of time sediment had been exposed, increased with sediment organic content, all else equal - decreased with elevation (full model only), had a bell-shaped relationship with distance to cover line, increased with proximity to channel (weak effect), and was moderately greater closer to tide line. The effect of tidal height itself was uncertain and this parameter was kept simply because it was automatically selected by the software. The tendency for the cumulative probability of occurrence to increase with proximity to tidal channels was only true at night.

The distribution pattern projected by the updated models generally aligned with the pattern projected by the published models (Fig. 4), which in itself is not surprising since the updated dataset was still dominated by 2005 – 2006 Robert's Bank data.

When applied to the Skagit dataset (unique geographic locations) none of the models predicted dunlin occurrence well relative to the random locations based on AUC values. Models predicting cumulative probability of occurrence performed slightly better than the instantaneous models but still had AUC values < 0.7 (Table 3). Likewise none of the updated Fraser models predicted dunlin distribution in the Skagit Delta well in terms of correct habitat ranking (r_s). Similar to the published models the central up-shore saltmarsh area received low probability scores resulting in a poor correspondence between the predicted and observed distribution of dunlin in the Skagit Delta (Fig. 4). The usage of the mid-intertidal zone of the study area was predicted reasonably well.

Table 3. *Updated Fraser models of instantaneous and cumulative probability of occurrence of dunlin including the final model structure based on AIC selection, model fit expressed as percent deviance explained and model discriminatory performance represented by internal AUC. Model performance on the Skagit data in terms of AUC and r_s coefficients is given in parentheses.*

Model	Model Structure	Estimate (SE)	z	Pr(>|z|)	Deviance Explained	AUC^{int} (AUC^{Skagit}/r_s)
Instant. (full)	Intercept	-0.182(0.205)	-0.89	>0.10	13.9%	0.736 (0.516 / <0.7, ns)
	Day.Night	0.067(0.234)	0.28	>0.10		
	Time exposed	-0.272(0.148)	-1.83	0.066		
	Tide	-0.563(0.206)	-2.73	0.0065		
	Elevation	-0.092(0.317)	-0.29	>0.10		
	Organics %	0.700(0.152)	4.62	<0.0001		
	Distance channel	-0.369(0.123)	-3.01	0.0025		
	(Dist cover)^2	-0.406(0.105)	-3.85	0.0001		
	Distance tide	-0.396(0.271)	-1.46	>0.10		
	Day.Night:Tide	0.850(0.257)	3.31	0.0009		
	Day.Night:Elev	-0.568(0.247)	-2.30	0.0215		
Instant. (RB)	Intercept	0.233(0.265)	0.88	>0.10	15.7%	0.754 (0.524 / <0.7, ns)
	Water cover %	-0.784(0.231)	-3.39	0.0007		
	Day.Night	-0.520(0.277)	-1.87	0.0606		
	Tide	-0.372(0.225)	-1.65	0.09		
	(Tide)^2	-0.172(0.119)	-1.44	>0.10		
	Elevation	-0.520(0.323)	-1.61	>0.10		
	Organics %	0.644(0.172)	3.76	0.0002		
	Distance channel	-0.254(0.137)	-1.86	0.063		
	(Dist cover)^2	-0.392(0.116)	-3.36	0.0008		
	Dist tide	-0.601(0.330)	-1.82	0.07		
	Day.Night:Water %	0.924(0.262)	3.53	0.0004		
	Day.Night:Tide	0.721(0.284)	2.54	0.0111		
Cumulative (full)	Intercept	0.181(0.267)	0.68	>0.10	17.3%	0.766 (0.527 / <0.7, ns)
	Water over %	-0.368(0.145)	-2.54	0.0111		
	Day.Night	-1.215(0.252)	-4.82	<0.0001		
	(Water cover%)^2	0.280(0.149)	1.87	0.06		
	Time exposed	0.547(0.159)	3.439	0.0006		
	Tide	0.191(0.130)	1.47	>0.10		
	Elevation	-0.869(0.195)	-4.45	<0.0001		
	Organics %	0.665(0.161)	4.12	<0.0001		
	Distance channel	-0.043(0.198)	-0.22	>0.10		
	Distance cover^2	-0.270(0.115)	-2.34	0.0192		
	Distance tide^2	-0.205(0.133)	-1.54	>0.10		
	Day.Night:Channel	-0.438(0.266)	-1.65	0.10		
Cumulive (RB)	Intercept	0.329(0.294)	1.12	>0.10	21.5%	0.796 (0.532 / <0.7, ns
	Water cover %	-0.490(0.173)	-2.84	0.0045		
	Day.Night	-1.537(0.289)	-5.30	<0.0001		
	(Water cover%)^2	0.429(0.172)	2.49	0.0127		
	Time exposed	0.638(0.180)	3.54	0.0004		
	Tide	-0.155(0.221)	-0.70	>0.10		
	Organics %	0.572(0.193)	2.96	0.0030		
	Distance channel	-0.258(0.151)	-1.71	0.08		
	Distance cover	0.649(0.260	2.49	0.0127		
	(Dist cover)^2	-0.518(0.156)	-3.32	0.0009		
	Distance tide	-0.614(0.224)	-2.74	0.0062		
	Day.Night:Tide	0.508(0.294)	1.73	0.08		

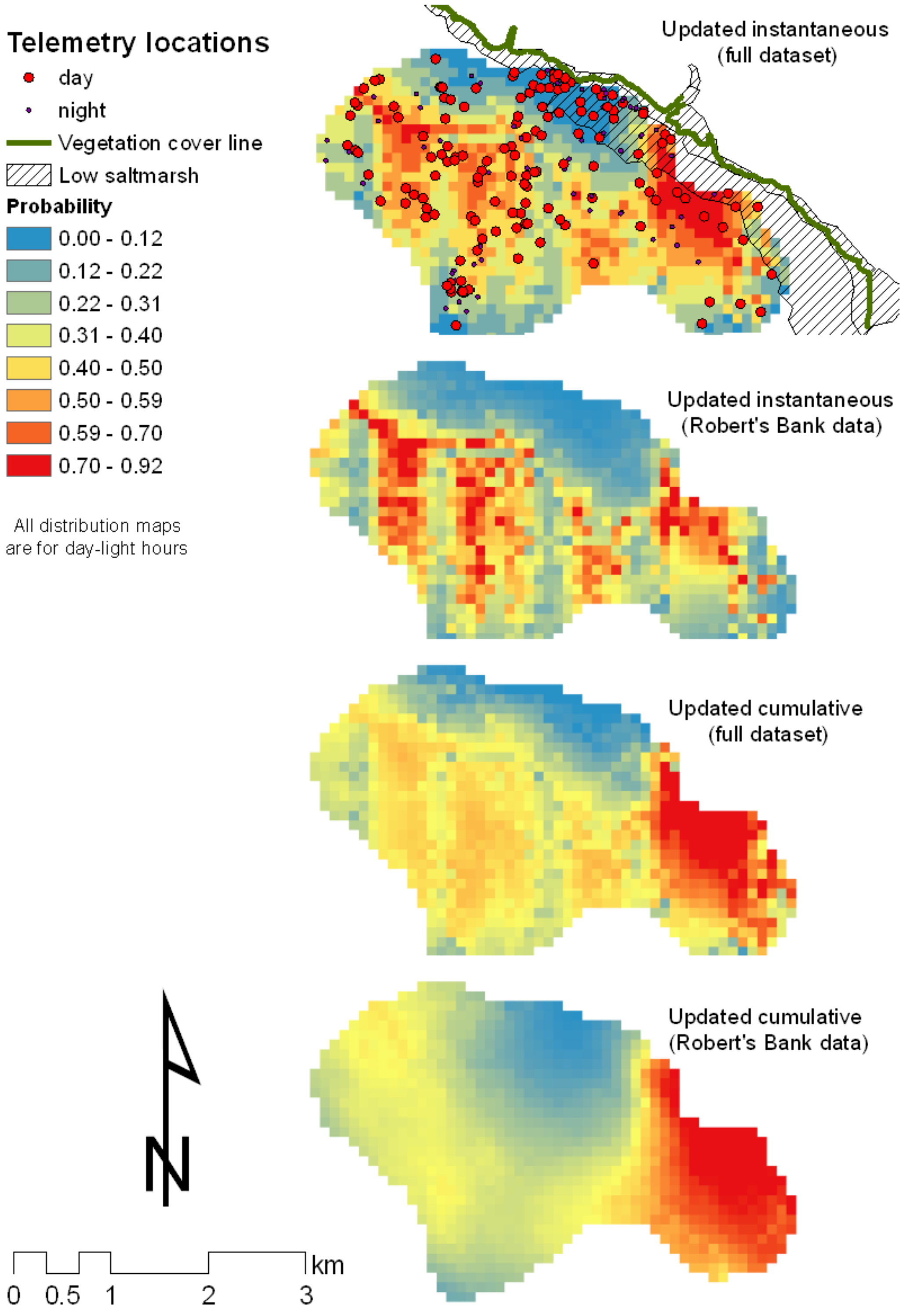

Fig. 4. *Dunlin telemetry detection overlaid on predicted distribution maps of dunlin in the Skagit Delta study area based on updated Fraser models (at a 1.0 m tide).*

Developing and testing Skagit SDMs

The final step of the modelling exercise was to develop and test SDMs based on Skagit data alone. Two models were generated using the same methods as for the updated Fraser models. The two models built had one of the two alternative correlated predictors included into the initial set of predictors: sediment organic content or fine fraction of sediment (Table 4). These models were based on dunlin detections with unique coordinates from all tidal stages and therefore were analogous to the cumulative occurrence models developed for the Fraser Delta. The final Skagit cumulative model based on sediment organic content (strong positive effect) also retained mudflat elevation (positive effect, i.e. higher probability of occurrence up-shore), sediment water cover (strong positive effect, i.e. wetter, less drained sediment), time exposed (positive effect, i.e. the longer a location was available to the birds the more likely it was to be used at some point), proximity to the tide line (strong negative effect, i.e. dunlin tended to follow the tidal front), and distance to a tidal channel (U-shaped effect, i.e. dunlin tended to be detected either close to or far from tidal channels). The model with the fine fraction of sediment had essentially the same predictors with the same directions and relative strengths of effect. It additionally included the distance from cover (negative effect) reflecting the large number of detections from the saltmarsh habitat located close relative to vegetation cover. The fine sediment fraction itself was not retained in the final model following an automated model-selection process. The model based on sediment organic content (model 1) projected a pattern of heavy habitat use in both the saltmarsh and lower intertidal area with little preference for mid-intertidal areas. The model that initially included sediment fine fraction (model 2) projected a northeast to southwest wedge of preferred habitat protruding from saltmarsh across the mudflats and into the lower intertidal (Fig. 5).

The models demonstrated a reasonable fit and accepted discriminatory capacity based on both internal data test and application to the (partially independent) complete set of Skagit dunlin detections. The models fit particularly well for high-shore (saltmarsh) and lower intertidal areas (Fig. 5). Several attempts to remodel the data either keeping the outliers or adding interaction terms between pairs of continuous predictors to potentially improve model performance resulted in essentially the same projected distribution patterns and model fit.

The models displayed good calibration (Table 4, Fig. 6) suggesting that predicted probability of occurrence ranked well with the actual use of the habitat by dunlin relative to its availability on the mudflat. The models did not transfer well to Fraser Delta, although compared to the Fraser-to-Skagit test, the AUC scores were slightly better.

Table 4. *Skagit models of (cumulative) probability of occurrence of dunlin including the final model structure based on AIC selection, model fit expressed as percent deviance explained and model discriminatory performance represented by internal AUC. Model performance on the full Skagit data in terms of AUC and r_s coefficients and Fraser data (in parentheses) is given in a separate column (model calibration was not tested on Fraser data).*

Model	Model Structure	Estimate (SE)	z	$Pr(>\lvert z\rvert)$	Deviance Explained	AUC^{full}/r_s (AUC^{Fraser})
Model 1 (AUC^{int} = 0.748)	Intercept	-0.055(0.217)	-0.26	>0.10	18.5%	0.722 / 0.81, $p < 0.01$ (0.618)
	Water cover	1.199(0.288)	4.17	<0.0001		
	Time exposed	0.443(0.186)	2.38	0.0174		
	Elevation	0.568(0.203)	2.80	0.0051		
	(Elevation)^2	0.336(0.181)	1.85	0.0641		
	Organic %	1.033(0.256)	4.04	<0.0001		
	Distance channel	-0.887(0.342)	-2.60	0.0094		
	(Dist channel)^2	0.290(0.141)	2.06	0.0393		
	Distance tide	-0.713(0.180)	-3.97	<0.0001		
Model 2 (AUC^{int} = 0.730)	Intercept	-0.339(0.205)	-1.65	0.0988	15.9%	0.725 / 0.79, $p < 0.01$ (0.600)
	Water cover	0.556(0.167)	3.33	0.0009		
	(Water cover)^2	0.385(0.139)	2.77	0.0057		
	Time exposed	0.377(0.183)	2.06	0.0399		
	Elevation	0.432(0.207)	2.08	0.0372		
	(Elevation)^2	0.409(0.165)	2.49	0.0129		
	Distance cover	-0.638(0.203)	-3.15	0.0016		
	Distance tide	-0.580(0.172)	-3.38	0.0007		

Discussion and Recommendations

Patterns of habitat use by dunlin in Fraser and Skagit deltas

Overall variables included into the final Skagit models were similar to those contained in both published and updated Fraser models. Differences mainly lay in the relative strength of effects, their shape (linear versus second order polynomial) and in some cases the direction of effect (negative versus positive), which will be discussed below.

Both Fraser and Skagit models suggested consistent preferences for organically-rich sediment, proximity to tidal channels, and proximity to tidal line, all of which are intertidal habitat features known to be associated with higher density and/or availability of invertebrate prey for small shorebird in general and dunlin in particular (Lourenço *et al.*, 2005; Yates *et al.*, 1993; Piersma *et al.*, 1993; Zwarts & Wanink, 1993; Mouritsen, 1994; Nehls & Tiedemann, 1993). Expectedly, the probability of cumulative use at both Skagit and Fraser also increased with the duration of mudflat exposure. This reflects the basic pattern of shorebirds' congregating at higher densities on the upper mudflat as the tide begins to recede (Piersma *et al.*, 2004; Nehls & Tiedemann, 1993) and then following the tide-line, as both the preferred foraging location (Boates & Smith, 1989) and as a route for accessing other parts of the mudflat.

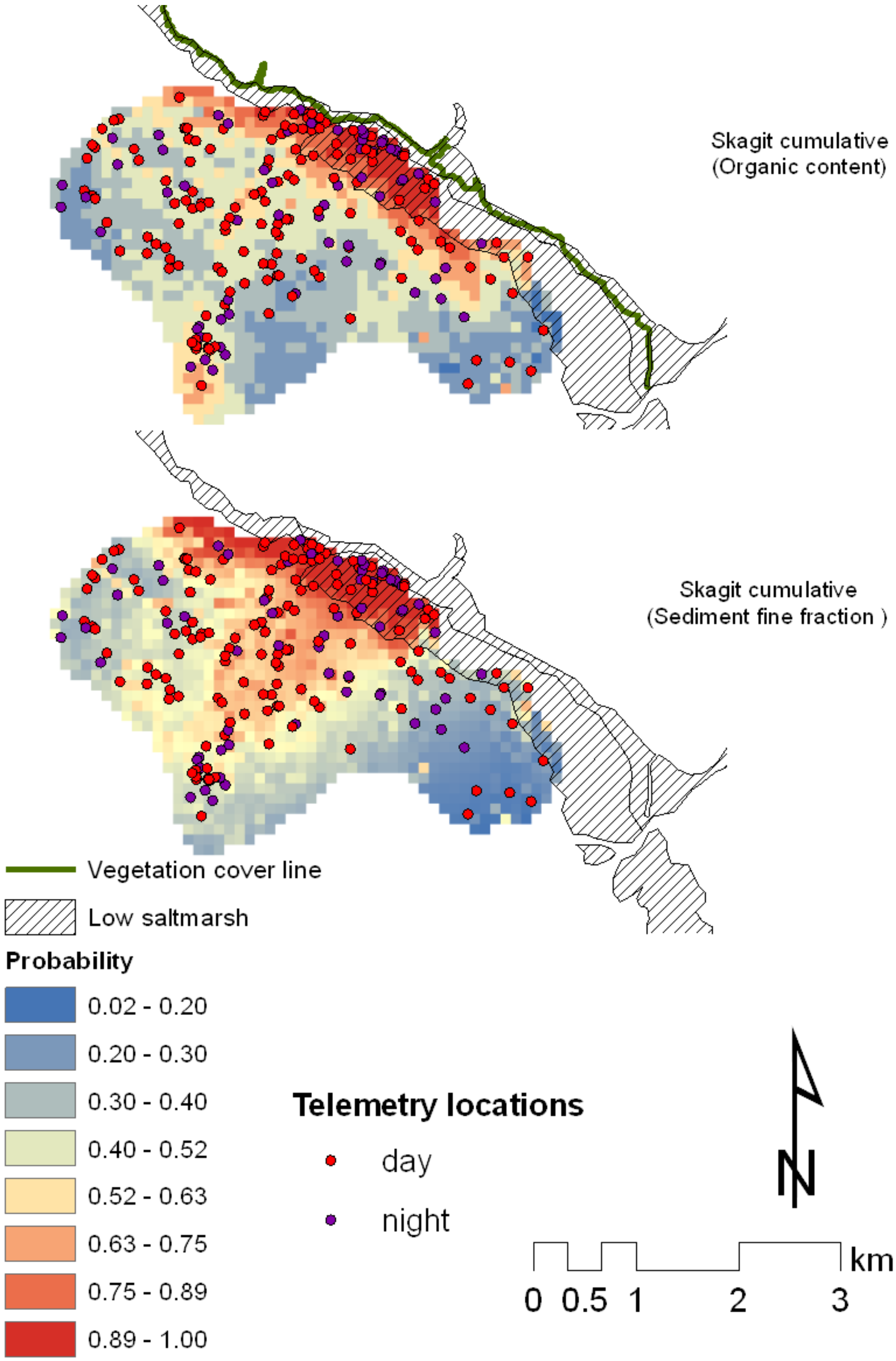

Fig. 5. *Dunlin telemetry detection overlaid on predicted distribution maps of dunlin in the Skagit Delta study area based on native Skagit models (at a 1.0 m tide).*

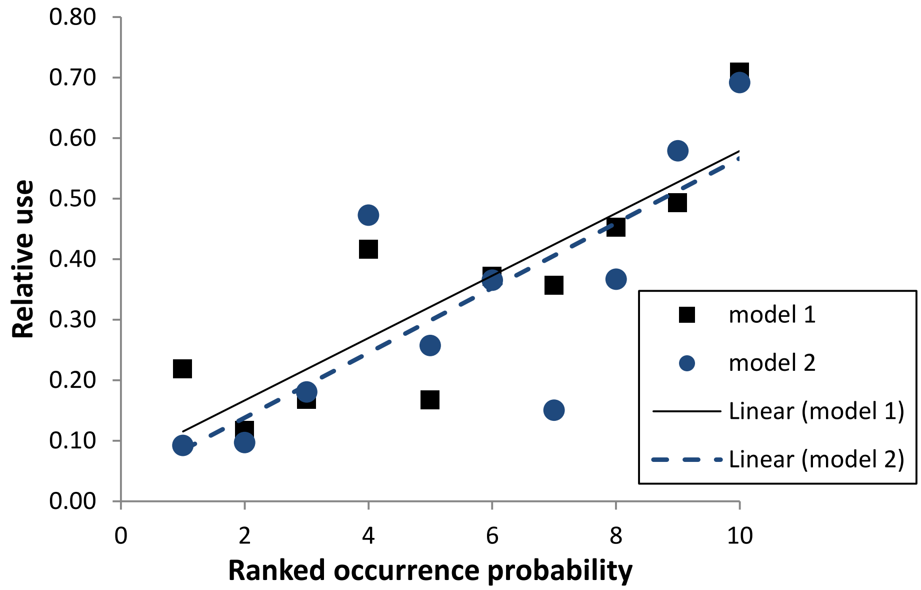

Fig. 6. *Relationship between relative use of the habitat by dunlin and the ranked probability of occurrence predicted for the Skagit study area by two local distribution models.*

The distance from cover and/or mudflat elevation were the two important predictors that differed strongly between the two sites in the direction of their effect. The general tendency for the Fraser dunlin was to select for intermediate distances from cover (and/or lower mudflat elevations) while at Skagit dunlin tended to heavily use both high-shore and lower intertidal zones. Similar to most other smaller shorebirds, dunlin actively follow the movements of receding/advancing tide but will also consistently use preferred habitats (sections of the intertidal flat) throughout a tidal cycle (Mouritsen, 1994; Nehls & Tiedemann, 1993; Piersma *et al.*, 2004). In the absence of predators or at low predation pressure dunlin habitat preferences will be mostly defined by food availability (Yates *et al.*, 1993; Zwarts & Wanink, 1993; Lourenço *et al.*, 2005; Piersma *et al.*, 1993) and in some cases also thermoregulatory considerations (Wiersma & Piersma, 1994; Kelly *et al.*, 2001). Saltmarsh is clearly one of the more productive intertidal habitats in terms of abundance and diversity of macroinvertebrates (Rader, 1984; Angradi *et al.*, 2001), available through much of a tidal cycle due to its high-shore position and the one that in the winter would also provide considerable thermoregulatory benefits to dunlin by allowing protection from the wind (Wiersma & Piersma, 1994). From purely energetic considerations therefore saltmarsh is clearly an important habitat for dunlin and this is what the results from Skagit demonstrate.

The saltmarsh, one the other hand, is located closer to upland vegetation (or other cover) and, due to its own vegetation and channelization it affords reduced visibility at the ground level relative to the more open intertidal mudflats (Cresswell & Whitfield, 1994). These conditions make the saltmarsh a preferred hunting habitat for diurnal and nocturnal predators that can launch successful surprise attacks targeting shorebirds (Dekker & Ydenberg, 2004; Zharikov *et al.*, 2009; Cresswell & Whitfield, 1994). Predation danger, thus, can drive shorebirds away from this otherwise productive high-shore habitat. The Fraser Delta accommodates large wintering populations of diurnal (peregrine falcon *Falco peregrinus*, merlin *F. columbarius*, northern harrier *Circus cyaneus*, short-eared owl *Asio flammeus*) and nocturnal (snowy owl *Bubo scandiacus*, great-horned owl *Bubo virginianus*) predators actively hunting wintering and migrating shorebirds (Ydenberg *et al.*, 2010; Zharikov *et al.*, 2009; Dekker *et al.*, 2012). Shorebirds respond to this pressure by trying to select mudflat sections that would minimize their exposure to predators while still allowing for profitable foraging conditions (Pomeroy, 2006).

Reasons for lack of transferability between Skagit and Fraser SDMs

To-date no clear pattern has emerged with respect to cross-regional transferability of SDMs. There are numerous instances of both high spatial transferability (Vanreusel *et al.*, 2007; Heikkinen *et al.*, 2011; Vernier *et al.*, 2008) and cases of failure of models to transfer between regions (Fielding & Haworth, 1995; Mcalpine *et al.*, 2008; Vernier *et al.*, 2008). Different authors highlighted different reasons for the lack of transferability including differences in habitat composition and configuration (Vernier *et al.*, 2008; Mcalpine *et al.*, 2008), different population traits (Randin *et al.*, 2006), history of occupation (Fielding & Haworth, 1995) and biotic interactions (Godsoe & Harmon, 2012) among others. All of these effects may superimpose themselves on the basic species-environment relationships projecting different distribution patterns in different regions of the species distribution range.

In our case, both Fraser and Skagit deltas offer very similar environments in terms of their abiotic characteristics (Table 1). Also dunlin propensity to select for softer, muddier intertidal habitats, drainage channels and to follow tidal fronts has been established by several studies (Lourenço *et al.*, 2005; Mouritsen, 1994; Nehls & Tiedemann, 1993; Dierschke *et al.*, 1999). It appears, however, that predation pressure on wintering shorebirds is higher at Fraser than at Skagit and this biotic interaction results in different distribution patterns between the two sites and therefore poor cross-region model transferability.

Modelling and habitat management recommendations

Based on these results it is recommended that region-specific SDMs be used for spatially-explicit quantitative habitat modelling and visualization of intertidal distribution of the species. It should be noted though that while Fraser models have been locally tested on two independent datasets (Zharikov *et al.*, 2009), i.e. datasets obtained completely separately from the training data, (Vaughan & Ormerod, 2005). Such a local test still remains to be conducted for the Skagit models and should be a subject of future research.

It is clear from the study that both the saltmarsh and sections of the adjacent intertidal flats provide areas of preferred foraging habitat for the dunlin. Reductions in the area of tidal flats, for example due to marine facility construction, or of the adjacent saltmarsh due to reclamation or erosion, can decrease the carrying capacity of Skagit Bay for the dunlin by reducing the total foraging area (Yates *et al.*, 1996; Goss-Custard *et al.*, 2003; Goss-Custard *et al.*, 2002). Our results also suggest that small-scale modifications to the tidal flats, such as reduction in channelization or sediment characteristics may influence their quality as shorebird foraging habitat and, consequently, their carrying capacity, even if the intertidal area is not reduced (Lourenço *et al.*, 2005).

Saltmarsh is a key ecological feature of intertidal systems providing nutrient input into lower-lying mudflats, facilitating development and maintenance of drainage networks and stabilizing up-shore habitats. Thus ecological integrity of the entire intertidal system as a wintering habitat for shorebirds will to a large degree depend on the extent and quality of the adjacent saltmarsh (Galbraith *et al.*, 2002; Goss-Custard & Yates, 1992). To maintain Skagit Bay as a viable shorebird wintering site, habitat managers of the estuarine system should strive to maintain habitat mosaic of unvegetated mudflats and up-shore saltmarsh and where possible work to reverse historic saltmarsh losses due to coastal erosion, land reclamation for agriculture and development (Hughes & Paramor, 2004; Pye, 1992; Kirwan & Murray, 2008).

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