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Intertidal beach habitat suitability model for Pacific sand lance (*Ammodytes personatus*) in the Salish Sea, Canada

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Abstract

Pacific sand lance (*Ammodytes personatus*) support marine food webs in the Salish Sea, yet our knowledge of intertidal spawning habitat for this species is limited. Increasing participation in community science surveys for intertidal sand lance spawning has resulted in the detection of eggs on more than 90 beaches in the Canadian Salish Sea since 2001. Using these data, we developed a MaxEnt habitat suitability model using six environmental variables. We estimate that only 5.4% of the intertidal zone of the Canadian Salish Sea has a moderate to high likelihood of providing suitable sand lance spawning habitat. This rare habitat was best predicted by its proximity to estuaries, shoreline slope, distance to predicted subtidal sand lance burying habitat, seabed substrate, and aspect. Our model could be used as the basis for a Pacific coast-wide model in areas with less available information. Identifying intertidal spawning habitat of sand lance will support conservation efforts intended to maintain forage fish species.

Résumé

Si le lançon du Pacifique (*Ammodytes personatus*) supporte des réseaux trophiques marins dans la mer des Salish, les connaissances sur l'habitat intertidal de frai de cette espèce sont limitées. La participation croissante par des citoyens scientifiques au recensement des aires de frai intertidales des lançons s'est traduite par la détection d'œufs sur plus de 90 plages dans la mer des Salish canadienne depuis 2001. À partir de ces données, nous avons mis au point un modèle MaxEnt de qualité de l'habitat qui intègre six variables environnementales. Nous estimons que seuls 5,4 % de la zone intertidale de la mer des Salish canadienne présente une probabilité modérée à élevée de fournir des habitats de frai convenables pour les lançons. Les meilleurs prédicteurs de ces habitats rares sont la proximité d'estuaires, la pente du rivage, la distance par rapport à des habitats de fouissage subtidaux des lançons et le substrat et l'aspect du fond marin. Notre modèle peut servir de base pour un modèle à l'échelle du littoral du Pacifique pour des secteurs pour lesquels peu d'information est disponible. La délimitation d'habitats de frai intertidaux de lançons appuiera les efforts de conservation visant le maintien d'espèces de poissons-fourrage. [Traduit par la Rédaction]

Introduction

Pacific sand lance (*Ammodytes personatus*) are small (<25 cm fork length), short-lived forage fish that play a key role in coastal marine ecosystems (Sisson and Baker 2017; Staudinger 2020). Sand lance support trophic structures of several culturally and ecologically important species such as salmon, seabirds, and whales, and are known prey for more than 100 predators (Robards and Piatt 1999; Zamon 2000). For example, the critically endangered southern resident killer whale (*Orcinus orca*) has a diet that is primarily composed of Chinook salmon (*Oncorhynchus tshawytscha*) (Ford et al. 2009), and between April and September sand lance comprise up to half the consumed prey of resident Chinook salmon in the southern Strait of Georgia (Osgood et al. 2016).

Despite their key role in supporting marine food webs, knowledge of intertidal sand lance habitat requirements within the Salish Sea is scarce, patchy, and not well published. This knowledge gap limits the ability of habitat managers to make conservation and management decisions that would protect essential habitat from threats and loss (Buchanan et al. 2019). Spatially explicit predictions of suitable habitat for sand lance could identify habitat for protection as well as aid managers in assessing the cumulative impacts of multiple pressures including shoreline armouring, dock installation, ship anchoring, and marina development. Recent modelling work has shown that suitable subtidal benthic habitats for sand lance in the Salish Sea are limited and patchy (Baker et al. 2021; Greene et al., in press;

Robinson et al. 2021). The objective of this study is to develop a complementary intertidal habitat suitability model to the subtidal model to predict suitable locations of intertidal spawning habitat for Pacific sand lance in the Canadian Salish Sea.

Pacific sand lance range from northern California to Alaska and are found in nearshore intertidal and subtidal environments of the northeastern Pacific Ocean (Orr et al. 2015). What may be the most notable feature of this species is their unique behaviour to bury into coarse sandy, silt-free, and well-sorted seabed sediments. Sand lance have specific adaptations that permit them to bury in the seabed such as the lack of a swim bladder, a slender tapered body, and the ability to respire in interstitial water even in low oxygen concentration (Quinn and Schneider 1991). Sand lance only bury into the top 5–10 cm when occupying sediments and when spawning, have been observed "digging" out small shallow depressions in which eggs are deposited (Quinn 1999; Robards et al. 1999; Bizzarro et al. 2016). It is thought that sand lance bury to avoid predation and to compensate for the lack of a swim bladder. Sand lance have short life cycles typically only surviving up to three years, but can live up to six (Robards et al. 1999; Matta and Baker 2020). In the spring and summer sand lance feed on zooplankton in tight schools in the water column when there is sufficient light and rest in seabed substrates at night or when taking cover from predators (Hipfner and Galbraith 2013; Sisson and Baker 2017). The number of sand lance feeding in the water column decreases at the onset of winter when individuals enter an overwinter aestivation period and bury in the seabed (Baker et al. 2019).

Most species of *Ammodytes* spawn in the winter with a few exceptions in warmer areas (Yamashita and Aoyama 1985). Along the Pacific coast, annual spawn timing varies by region, and is possibly driven by water temperature (Robards et al. 1999). In Alaska, spawning was observed from August to October, whereas further south in Puget Sound (Washington), and Baynes Sound (British Columbia), eggs have been found from November to mid-February, with peak observations occurring in December (Penttila 1995, 2007; Robards et al. 1999; Tomlin et al. 2021). No environmental cues that trigger spawning, such as sea surface temperature, tidal and lunar cycles have yet been identified. After spawning, eggs remain attached to sand grains (0.25–7 mm) for one to three months before hatching (Winslade 1974). Sand lance hatch from eggs, retaining a yolk sack and begin feeding opportunistically as free-floating larvae. From May to September sand lance undergo rapid growth periods and recruit into nearshore sediments (Robards et al. 1999).

Spawning habitats used by sand lance have specific characteristics including coarse sand, pebble, and pea gravel substrates that have uniform grain sizes ranging from 0.25 to 7 mm that can include shell fragments with very low silt content and are usually located in shallow water (<80 m) up to and including within the intertidal zone (Ostrand et al. 2005; Haynes and Robinson 2011; Selleck et al. 2015). Suitable spawning habitat is typically found where wave and current energy sort the available substrate (Penttila 2007; Greene et al. 2020). Adult sand lance do not appear to migrate or move long distances, and are thought to remain within 5 km of burying habitats, reusing the same sediment patches over time (Haynes et al. 2008; van der Kooij et al. 2008; Haynes and Robinson 2011; Jensen et al. 2011; Suca et al. 2021). Site fidelity to suitable benthic habitats tie sand lance to specific geographical areas and provide both a practical habitat-based management opportunity and heightened vulnerability to habitat loss or damage.

Materials and methods

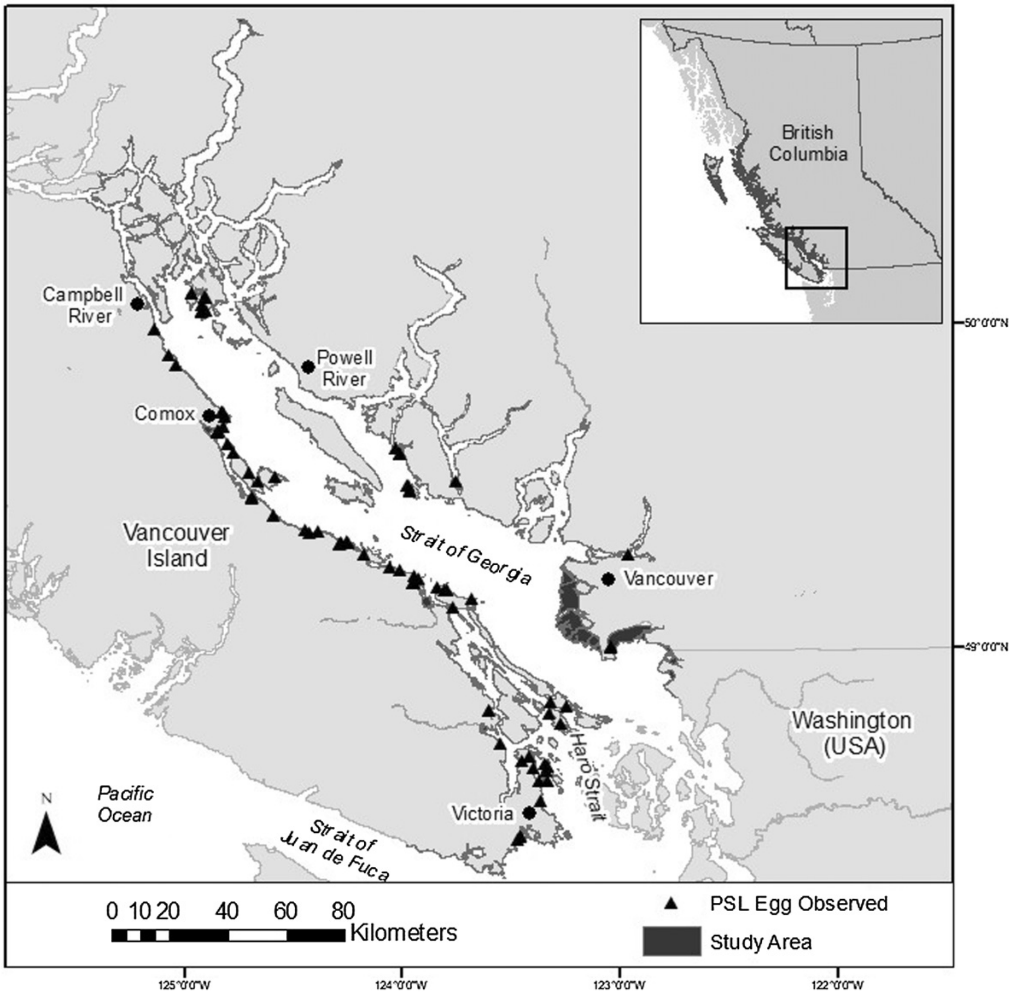
Study area

The Salish Sea is on the southwestern shore of British Columbia and north shore of Washington State, USA (Fig. 1). It is named for the ancestral home of the Coast Salish peoples and covers approximately 135 000 km^2 and 7470 km of coastline. The Salish Sea is a unique area of land and sea where several large coastal rivers, deltas, and estuaries, multiple mountain ranges, large population centers with major industrial and economic activities, culturally diverse First Nation groups and National borders converge (Islam et al. 2016). There are three major basins: the Strait of Georgia, Puget Sound, and the Strait of Juan de Fuca, and they are characterized by long channels, narrow shallow tidal passages, and sheltered embayments connecting to the Pacific Ocean (Fraser et al. 2006). The climate is temperate with significant winter precipitation inputs and strong prevailing southeasterly and north-westerly winds. Sand habitats in the Salish Sea are formed as a result of complex coastal geological and oceanographic processes, strong tidal current, surface wave action, freshwater estuarine inputs, bedform geography, depositional processes, headland erosion, and glaciofluvial processes (Rice 2006; Barrie et al. 2009; Greene et al. 2017; Earle 2019). These processes drive the occurrence of the specific suite of habitat characteristics such as grain size and uniformity that provide the essential spawning habitat for Pacific sand lance. The study area encompasses the Canadian intertidal zones of the Salish Sea as defined by the mean high-water line and the mean low water line delineated by the Canadian Hydrographic Service and accessed from the BC Data Catalogue (charts.gc.ca). There is approximately 42 576 km^2 of intertidal habitat within the Canadian Salish Sea, and approximately 493.5 km^2 or 1% of that area falls within a protected area or other effective area-based conservation measure (Government of Canada 2021).

Species observations

The presence of sand lance eggs was compiled from 1065 intertidal surveys for Pacific sand lance eggs from The Strait of Georgia Data Centre (SoGDC) repository (Curran 2020). Additional data were gathered from published reports (de Graaf 2007, 2010, 2017). Surveys were conducted by community scientists (previously termed citizen scientists), First Nations, independent biologists, and Fisheries and Oceans Canada (Thuringer 2004; de Graaf 2007, 2007). Surveys took place over a 19-year period between 2001 and 2020. Only surveys that occurred between October and April were included because this period encompasses what is thought to be the

Fig. 1. Sand lance habitat suitability modelling study area within the Salish Sea. Shaded area represents the modelling boundary; triangles are where sand lance eggs have been observed (NAD 1983). All maps were created in ESRI ArcMap 10.8.



peak spawning window for the study area. Although surveys provide coverage throughout the study area, survey effort is concentrated on the eastern shores Vancouver Island. Community scientists conducted surveys for eggs following the Washington State Department of Fish and Wildlife Marine Beach Spawning Program methodology or by similar, modified methods developed by Mount Arrowsmith Biosphere Reserve Institute (MABRRI 2018; Tomlin et al. 2021; Dionne 2015).

In brief, surveyors lay out a 30 m transect parallel to, and 1–2 m below, the most recent high tide line. Small cups (approximately 0.1 L) are used to collect a 4 L bulk sample of sand within 1 m of the transect on both the up and down slope sides, to a depth no deeper than 5 cm. The sediment is reduced using sieves ranging from 0.5 to 4 mm. The remaining sediment is further reduced using a vortex to approximately 0.5 L. Using Petri dishes the entire sample is examined under a dissecting microscope in approximately 5 mL increments. Surveyors look for eggs attached to grains of sand. All potential eggs are recorded and representative photos are collected for expert verification. Results along with meta data of survey site characteristics such as tide height, weather conditions, and backshore shading are uploaded to the SoGDC (Curran 2020).

Data preparation

Observations of the presence of sand lance eggs were aggregated to a 20 m × 20 m resolution to match the environmental data, resulting in 145 positive detections of sand lance eggs. Duplicate observations per cell were removed and the final total number of beaches with positive observations was 94. Only presence data were utilized as the likelihood of false negatives is presumed to be high due to the difficulty of detecting eggs in the samples and to the potential for a mismatch between spawn timing and survey timing.

Environmental variables

The selection of environmental variables to include in the habitat suitability model came from knowledge of the species ecology and previous studies (Quinn et al. 2012; Robinson 2013). Nine environmental variables (Table 1) that may potentially influence the presence of intertidal sand lance habitat were developed or obtained and realigned to a 20 m × 20 m

Table 1. Environmental variables used to model Pacific sand lance intertidal habitat in the Salish Sea and their native resolutions, the resolution of the data from the original source.

Variable	Unit	Native resolution	Source (calculation tool)
Aspect (northness/eastness)	—	20 m^2	Lecours et al. 2017; Fields et al. 2020
Fetch	—	20 m^2	Fields et al. 2020
Seabed substrate	See Table 2	—	Gregr et al. 2013; Gregr 2016
Distance to estuaries	km	20 m^2	Pacific Birds Habitat Joint Venture 2020
Distance to terrestrial sand features (bluffs)	km	20 m^2	DFO Pacific Region, unpublished data
Slope	degrees	20 m^2	Bathymetric derivative (BTM Toolbox); Fields et al. 2020
Tidal current	$cm \cdot s^{-1}$	Variable	Foreman et al. 2008
Distance to predicted subtidal habitat	m	50 m^2	Robinson et al. 2021

spatial resolution raster grid covering the intertidal zone of the Canadian Salish Sea.

Rationale for environmental predictor selection

A habitat suitability model for Pacific surf smelt (*Hypomesus pretiosus*), a species thought to use similar intertidal habitats as sand lance, found that aspect and fetch were important predictors of egg abundance on beaches (Quinn et al. 2012). Observations of sand lance eggs are known to be restricted to habitats with coarse (0.25–2.0 mm), silt free sand or shell hash sediments, as such we assumed this would be a strong driver of habitat suitability (Wright et al. 2000; Haynes et al. 2007). A substrate layer was developed by combining existing grain size (Gregr 2016) and bottom patch (Gregr et al. 2013) models to produce a substrate classification composed of nine classes. However, due to the sample size constraints (i.e., not all sediment substrate classes contained sufficient observations), the nine classes were reclassified into four composite classes grouping together similar surface types including hard (including bedrock and boulder dominated substrates), mixed (including soft surface and patchy distributions of large particles such as cobble), soft (including sand/shell and soft sediments covering hard surfaces), and mud.

Due to imperfect knowledge of the distribution of substrate, we also considered additional, proxy environmental variables that would capture geophysical processes that influence the formation of sandy beaches. We created a layer quantifying the distance to estuaries and to terrestrial sand sources, many of which are originally derived from glacial deposits, as they are known to contribute sediment to intertidal beaches and spits and drive water circulation in the Salish Sea (Peterson et al. 1984; Mason et al. 2018; Earle 2019; Robin et al. 2020). A layer of shoreline slope was created as increases in slope are correlated with increases in sediment grain size. As such, we predict there would be an optimal slope range in which suitable sand lance habitat would occur (McFall 2019). Tidal currents play a strong role in spit formation (Robin et al. 2020), a shoreline feature where sand lance eggs are frequently observed.

It is likely that intertidal spawning habitat is located near subtidal burying habitat (Haynes and Robinson 2011; Laugier et al. 2015). A layer representing the proximity to predicted suitable subtidal habitat (from Robinson et al. 2021) was created by calculating the distance of each raster cell from the closest neighbouring cell where predicted subtidal habitat suitability from Robinson et al. (2021) was 0.54 or greater.

Modelling approach

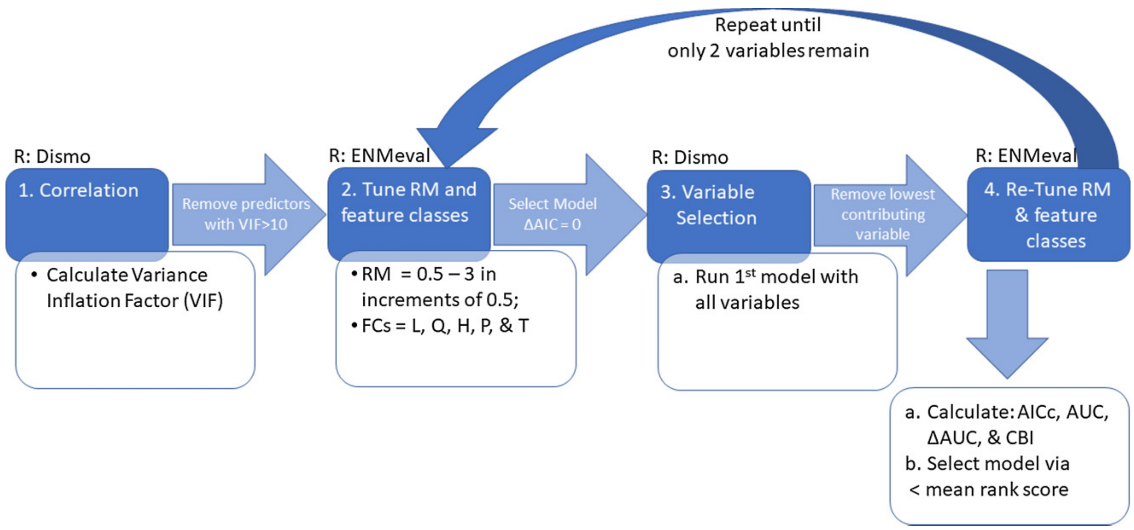
Habitat suitability modelling (HSM) is a method for predicting the suitability of a location for a species based on their observed relationship with environmental conditions (Guisan and Zimmermann 2000; Elith et al. 2006). Maximum entropy (MaxEnt) HSM is well suited to presence-only, small sample size data sets (Phillips et al. 2004; Elith et al. 2006). They do not require absence observations, and instead rely on background points. Background points are randomly selected points throughout the study area and are intended to represent all the conditions that could occur within the study area, including both suitable and unsuitable habitats.

MaxEnt is based on the concept of the ecological niche, where species distributions can be defined by the environmental characteristics required by that species to persist (Hutchinson 1957). MaxEnt models assess the range of the environmental predictors at the species presences, compared to the range at random background locations within a given geographic space, characterizing the spread, or maximum entropy, of the environment while penalizing the results for complexity to reduce overfitting (Merow et al. 2013). To build the model, we used the MaxEnt algorithm from the “dismo” package in R (version 1.3–3; 2008) (Hijmans et al. 2017). We randomly selected 10 000 background points as suggested by Phillips and Dudik (2008).

Cross-validation

To evaluate model predictive performance, data used to create a model (training data) should be independent from data used to test the model (testing data) (Hijmans 2012). As no independent data were available for testing in this study, we partitioned the full data set into training and testing data sets using five-fold spatial blocking cross-validation. This approach is considered best practice for partitioning training and testing data because the spatial independence of the training and testing data are improved, thereby improving the accuracy of model performance estimates (Roberts et al. 2017; Araújo et al. 2019; Nephin et al. 2020). We used the range of spatial autocorrelation in the environmental

Fig. 2. Workflow of the parameter and variable selection in MaxEnt habitat suitability model based on variable importance, correlation, and AIC. RM is regularization multiplier, FCs are feature classes that include L (linear), Q (quadratic), H (hinge), P (product), and T (threshold). [Colour online.]



predictor data to determine the optimal block size as calculated by the "blockCV" package (version 2.1.1; Valavi et al. 2019) in R. Blocks were then iteratively (n = 2000) and randomly assigned to folds. The block arrangement with the most even distribution of presence and pseudoabsence observations across folds was selected as the final configuration. We sequentially fit the model on four data folds and tested the resulting model against the fifth fold. Spatial predictions and model performance metrics were made for each of the five folds and then averaged across the five folds.

Parameterization

MaxEnt default settings of the feature class combinations (FCs) and regularization multiplier (RM) have been shown to sometimes produce overfit and inappropriate models (Radosavljevic and Anderson 2014; Morales et al. 2017). To avoid model overfitting and maximize performance, the optimal combination of model settings were selected for in the ENMeval package (Muscarella et al. 2014). The RM was varied from 0.5 to 3 in increments of 0.5 and all of the possible FCs and combinations of FCs were considered: linear (L), quadratic (Q), product (P), hinge (H), and threshold (T) (Fig. 2, Box 2). Models with sequentially varying RM and FC parameters were compared, and the settings resulting in the lowest Akaike Information Criterion (corrected for small sample sizes; AIC_c) were selected (Warren and Seifert 2011; Morales et al. 2017). All models were constructed with clamping to reduce large variations outside the range of training data (Elith et al. 2011). Clamping is an extrapolation option that allows users to constrain the modelling process to only predict into the environmental variables within the range of values that exist in the training data so as to reduce uncertainty about novel environments (Elith et al. 2011).

Variable selection and model evaluation

Collinearity between environmental predictors can lead to problems when training models and when making predictions across space and time. Collinearity was assessed using variance inflation factor (VIF) and a correlation matrix was created using the "usdm" R package (Guisan et al. 2002; Dormann et al. 2013; Naimi et al. 2014). VIF values of 10 or less indicate a predictor is not highly correlated with other predictors. No predictors had VIF values > 3; therefore, all variables were included in model development (Table 2).

Models that are too complex are often the result of having more environmental variables than necessary, either from the initial inclusion of too many environmental predictor layers, or from the lack of assessing the default parameters during model fitting (Li et al. 2020). To reduce model complexity and determine the best performing set of environmental predictors we followed a sequential, backwards stepwise elimination of unimportant variables (Fig. 2, Boxes 3 and 4) (Rooper et al. 2019). We first created a global model with all nine environmental predictors. Using a jackknife approach in the MaxEnt algorithm, we determined the contribution of each variable (Efron and Stein 1981; Hilborn 1985; Wu 1986; Phillips et al. 2006). The variable contributing the smallest amount of explanatory power to the model was removed and the model was refit. This process was repeated until only a single environmental predictor remained.

We evaluated each model produced using the area under the curve (AUC) of the receiver operating characteristic (ROC), Akaike's information criterion corrected for small sample size (AIC_c), and the Continuous Boyce Index (CBI) (Boyce et al. 2002; Elith et al. 2006; Warren and Seifert 2011). AUC is a commonly used metric for evaluating model performance (Warren and Seifert 2011). AUC scores less than 0.5 indicate a model that performs no better than chance, values ranging between 0.5 and 0.7 have low accuracy, values ranging from 0.7 to 0.9 indicate adequate accuracy, and values greater than

Table 2. Correlation matrix and variance inflation factor for each predictor layer.

Variable	Slope	Tidal current	Northness	Eastness	Fetch	Seabed substrate	Distance to predicted subtidal habitat	Distance to estuaries	Distance to terrestrial sand	Variance inflation factor
Slope	1	—	—	—	—	—	—	—	—	1.41
Tidal current	0.187	1	—	—	—	—	—	—	—	1.11
Northness	0.093	0.048	1	—	—	—	—	—	—	1.16
Eastness	−0.047	−0.094	−0.084	1	—	—	—	—	—	1.3
Fetch	−0.406	−0.201	−0.192	−0.300	1	—	—	—	—	2.27
Seabed substrate	−0.066	−0.045	−0.152	0.321	−0.387	1	—	—	—	1.43
Distance to predicted subtidal habitat	−0.087	0.031	−0.030	−0.085	−0.052	0.086	1	—	—	1.05
Distance to estuaries	0.324	0.212	0.082	0.286	−0.568	0.158	−0.033	1	—	1.59
Distance to terrestrial sand	0.295	0.134	−0.084	−0.023	−0.239	−0.037	0.070	0.167	1	1.17

0.9 show very high accuracy of the predicted output of the model (Swets 1988). CBI has been proposed as a better evaluation metric for presence-only data sets which can be biased due to low sample size (Hirzel et al. 2006). CBI values range from 0 to 1, similar to AUC and follow the same scale. CBI was calculated using the Ecospat Package (version 3.2) (Cola et al. 2017). We ranked the models based on AUCtest, deltaAUC, AIC_c, and CBI and calculated a mean rank for each model and selected the model with the lowest mean rank value as the best combination of environmental variables for predicting suitable sand lance intertidal habitat. We constructed variable response curves from the best-fitting model to investigate how environmental predictors affected the predicted probability of habitat suitability, by changing the variable of interest while holding the other variables constant (at their mean). To quantify overfitting, we calculated the difference between training AUC and testing AUC. Overfit models generally perform well on training data but poorly on testing data resulting in larger differences (Warren and Seifert 2011). Additionally, we calculated the omission rate for the 10th percentile presence (OM10), a common threshold-dependent metric for evaluating overfitting, where values greater than 0.10 indicate overfitting (Radosavljevic and Anderson 2014).

The best-fitting model was used to generate a prediction surface of the probability of suitable intertidal sand lance habitat on a 20 m × 20 m raster grid for each cross-validation fold. From the five-fold cross-validation rasters, we stacked them and calculated an average, and a standard deviation for each grid cell. To avoid selecting a binary habitat presence/absence threshold, which is known to be problematic, particularly for presence only data (Merow et al. 2013), we used natural boundaries in the steps defined in the predicted to expected (P/E) ratio curve from the CBI calculation to create four likelihood of habitat presence categories (Hirzel et al. 2006). These include: highly unlikely where P/E values fall below 1, indicating areas where the model is predicting fewer presences than expected by chance; unlikely where the occurrence of a presence is random and likely, where there is a distinct change in the slope, and highly likely, at the highest suitability values, where the slope is the most steep (Hirzel et al. 2006).

To evaluate novel combinations of environmental conditions within the study area where the model might be less reliable, we created a multivariate environmental similarity surface (MESS) (Elith et al. 2010). In the MESS, negative values indicate regions that are environmentally dissimilar from the reference region and positive values are within the range of the modelled environmental predictors. Modelled predictions in areas with negative values in the MESS surface should be regarded with caution.

Results

Model selection

Distance to estuaries was found to be the most important predictor of habitat suitability for sand lance for all model iterations, followed by slope, distance to predicted subtidal habitat, fetch, northness, and seabed substrate (Table 3). For the MaxEnt model with the best performing set of environmental predictors, the model with the lowest AIC_c had a regularization multiplier of 3 and included linear, quadratic, product, and hinge feature classes. Details and results of model parameterization can be found in the Supplementary Information (Table S1). The cumulative contribution or importance of distance to estuaries to the best-fitting model was estimated at 61.8%. The probability of intertidal sand lance spawning habitat decreased as the distance to estuaries increased (Fig. 3). The probability of suitable habitat increased for low shoreline slopes up to 4°, once slopes became steeper than 4°, the suitability gradually decreased. Similar to the effect of estuaries, habitat suitability had a negative relationship with the distance to predicted subtidal buying

Table 3. Estimates of relative contributions of the environmental predictors in the global model and the best-fitting model.

Predictor	Global model		Best-fitting model	
	Percent contribution	Permutation importance	Percent contribution	Permutation importance
Distance to estuaries	45.4	20.4	61.8	38.8
Shoreline slope	16.5	20.2	18.3	18.7
Distance to predicted subtidal habitat	10.3	11.1	11.3	23.4
Fetch	6.9	24	5.8	15.9
Northness (aspect)	6.6	4.5	1.3	2.3
Seabed substrate	6.3	8	1.4	0.9
Eastness (aspect)	4	4.7	Not included	Not included
Distance to terrestrial sand source features	3.2	3.7	Not included	Not included
Tidal current	0.8	3.6	Not Included	Not included

habitat and this may be due to the interconnected nature of the lower shoreface with the upper shoreface and beach (Anthony and Aagaard 2020). Increasing fetch was associated with increases in the probability of suitable intertidal spawning habitat. Beaches with soft sediments had the highest habitat suitability with mud and hard beaches having the lowest. South-facing beaches (where values are close to −1) had the highest habitat suitability, closely followed by east- and west-facing beaches (values close to 0). Three variables, eastness, distance to terrestrial sand source features, and tidal current contributed little and were removed from the best-fitting model (Table 4). It was surprising that the distance to terrestrial sand source features (glacial deposits) and tidal current did not contribute significantly as both of these are thought to contribute to other sand lance habitats (Barrie et al. 2009; Greene et al. 2020, 2021). It may be that correlations among variables masked individual variable impacts. For example, substrate composition can be determined by tidal current strength, such as when high current speeds can sweep rocky substrates clean of sediment and low tidal current speed can result in sediment deposition. In the model, this may have resulted in the significant contribution from substrate type and a minimal contribution of tidal current speed. This is an area for future investigation and may be of value to explore as new environmental predictor data sets become available.

Performance

The testing AUC values or predictive power for all models ranged from 0.813 to 0.902, signifying good performance overall and indicating strong underlying relationships between the environmental predictors and presence observations of sand lance eggs (Table 4). The training AUC or explanatory power for all models ranged from 0.870 to 0.957. The testing AUC of the best ranked model (D) was 0.857, the training AUC was 0.911, and this model had a high Spearman's rank from the CBI of 0.969. On both of these metrics, model (D) had the best performance of all the models considered. The predicted to expected (P/E) ratio curve from the CBI calculations shows a classic staircase configuration with a steep curve at the end (Fig. 4). It did have the highest and therefore poorest omission rate (OM10) of 0.38, which may indicate overfitting; however, it did have the second lowest difference between the training AUC (0.911) and testing AUC (0.857) of 0.054. The difference between the training and testing AUC is very low and is an indication that the model performs well and predicts new data well (Warren and Seifert 2011). The number of presence points where the habitat suitability values were less than 0.500 ranged from 10% to 26.5% for all models and was 14.8% for the best model indicating low sensitivity (or false negative predictions).

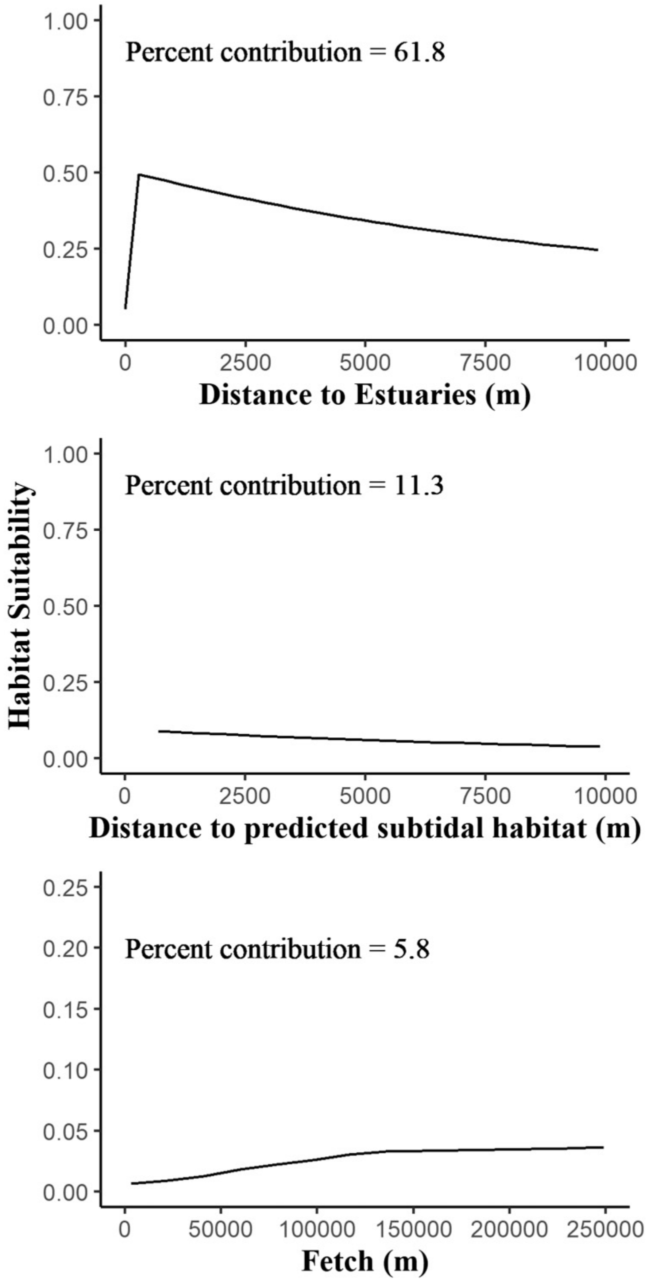
When the best-fitting model was classified into categories of predicted presence of suitable habitat using the P/E ratio, the highly unlikely category had habitat suitability values between 0 and 0.42 (Fig. 4). Habitat presence is expected to be unlikely at habitat suitability values ranging from 0.421 to 0.70, where the P/E ratio rises above 1 and before there is a noticeable change in the slope. Habitat suitability is expected to be likely at values between 0.71 and 0.89 before the curve steps into a steeper slope where habitat is highly likely at values between 0.89 and 0.93.

Spatial distribution and uncertainty

We estimated that approximately 1.4% of the intertidal zone in the Salish Sea is highly likely to be composed of suitable sand lance spawning habitat and 5.4% is composed of both habitat that is likely or highly likely to be present (Table 5). We estimated the area of the intertidal zone of the Salish Sea from the CHS mean high water line to the mean low water line (chart datum) to be 522.05 km^2 and approximately 2.4 km^2 falls within a protected area. The best-fitting MaxEnt model predicted a high likelihood of suitable intertidal habitat in many regions of the Canadian Salish Sea, specifically in Victoria and Esquimalt in the Juan de Fuca Strait, Sidney and James Islands in Haro Strait, Goose Spit near Comox, and around Marina, Cortes, Hernando, Savary, and Thormanby Islands in the northeastern Strait of Georgia (Fig. 5).

The standard deviation between the five spatial CV folds exhibited similar patterns of spatial uncertainty to one

Fig. 3. Response curves characterizing how each environmental variable affected the MaxEnt predictions for the best performing model.



another. Areas with the highest uncertainty values were areas in muddy bays and in inlets. In the MESS analysis that highlights areas of extrapolation, the highest uncertainty corresponded to areas the bottom patch model predicts are hard substrates. Uncertainty was generally low in areas where habitat suitability values were higher.

Discussion

Our habitat suitability model provides a spatially explicit prediction surface for intertidal Pacific sand lance spawning habitat in the Canadian Salish Sea. Suitable spawning habitat is limited and patchy across the Salish Sea with less than 5.4% of the intertidal zone in the Canadian portion of the Salish Sea likely or highly likely to have suitable sand lance spawning habitat. This result complements the findings of 2.6% of subtidal areas predicted to have highly suitable burying habitat (Robinson et al. 2021). In this subtidal burying habitat model, authors also used similar predictors including slope, distance to estuaries, distance to terrestrial sand (bluffs), and substrate. In our intertidal model, the most important environmental variable across all model iterations predicting the presence of suitable intertidal habitat for sand lance was distance to estuaries. This layer was also a key variable in the subtidal model (Robinson et al. 2021). Estuaries are major sources of terrestrial sand and the freshwater

Table 4. Performance metrics for each model evaluated from the backwards stepwise environmental variable selection process.

Predictor suite	RM	FC	AUC test	AIC_c	CBI	ΔAUC	OM10	Low sensitivity	Ave. rank
Estuaries, slope, subtidal, fetch, northness, sediment, eastness, bluffs, current (A)	0.5	LQ	0.836	2157.2	0.957	0.121	0.31	19	4.25
Estuaries, slope, subtidal, fetch, sediment, northness, eastness, bluffs (B)	0.5	LQ	0.834	2268.7	0.967	0.120	0.28	25	4.50
Estuaries, slope, subtidal, fetch, sediment, northness, eastness (C)	0.5	LQ	0.848	2263.3	0.966	0.101	0.23	25	3.50
Estuaries, slope, subtidal, sediment, fetch, northness (D)	**3.0**	**LQHP**	**0.857**	**2260.8**	**0.969**	**0.054**	**0.38**	**14**	**1.50**
Estuaries, subtidal, slope, fetch, sediment (E)	3.0	LQHPT	0.841	2341.8	0.889	0.053	0.31	10	4.25
Estuaries, subtidal, fetch, slope (F)	1.0	LQHPT	0.823	2362.7	0.952	0.081	0.30	19	5.50
Estuaries, subtidal, fetch (G)	1.5	LQHPT	0.815	2454.0	0.948	0.068	0.28	11	6.25
Estuaries, subtidal (H)	1.5	LQHPT	0.813	2482.9	0.949	0.057	0.30	10	6.25

Note: Variables are listed in order of estimated relative percent contribution. Metrics include Continuous Boyce Index (CBI), Spearman's rank correlation, OM is omission rate (false negative rate), low sensitivity is the number of presence points with a habitat suitability value < 0.5. The predictor suite with the lowest average rank is highlighted in bold.

Fig. 4. Predicted to expected ratio by habitat suitability values from CBI calculation for the best-fitting model calculated from the mean of the cross-validation folds. The black circles represent the values from the mean model, and the gray ribbon represents the minimum and maximum P/E values from each of the five cross-validation folds. Spearman's rank correlation of this model was 0.969.

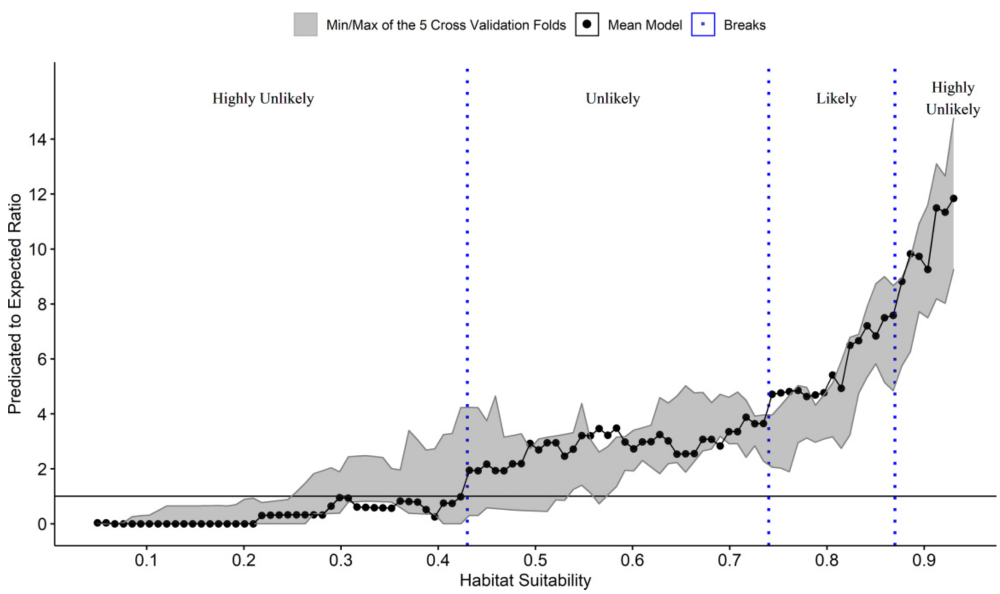
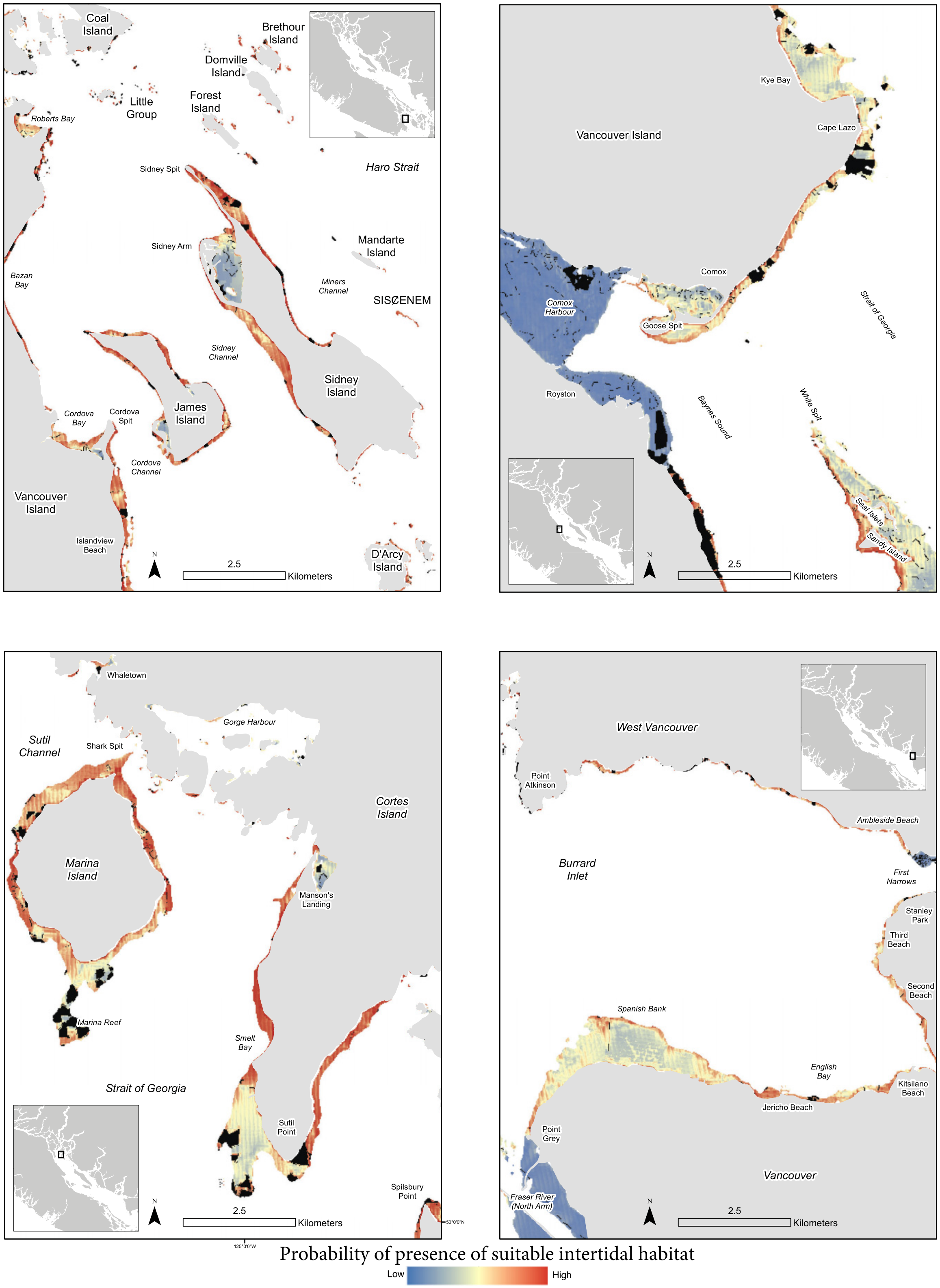


Table 5. Spatial summary of habitat suitability values of suitable spawning habitat in the estimated intertidal zone (from Canadian Hydrographic Service mean high water mark to low water mark) in the Salish Sea.

Likelihood of habitat presence	Habitat suitability value	Area (km^2)	Cell count (20 m × 20 m)	% of intertidal zone	Cumulative % intertidal zone	Protected area (km^2)
Highly unlikely	0–0.43	333.43	833 574	0.639	0.801	207.770
Unlikely	0.431–0.74	56.76	141 911	0.109	0.163	6.159
Likely	0.741–0.87	21.01	52 522	0.040	0.054	1.628
Highly likely	0.871–1.00	7.17	17 927	0.014	0.014	0.728
Estimated total intertidal zone	522.05	1 305 118	1.000	—	493.5	—

Note: Habitat presence likelihood categories were created based on Continuous Boyce Index (CBI) plot results.

Fig. 5. Predicted surface of intertidal habitat used for spawning and burying by Pacific sand lance (*Ammodytes personatus*) in the Canadian Salish Sea (NAD 1983). Areas shaded in red show higher suitability, medium in yellow, and lower in blue. Blank areas indicate unsuitable habitats due to steep, thin intertidal terrain. Black areas indicate areas were MESS (Multivariate Environmental Similarity Surface; values are less than 0). Additional, and larger figures can be found in Figs. S1–S11 in the supplementary information. [Colour online.]



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input contributes to water and sediment circulation in the Salish Sea (Peterson et al. 1984; Mason et al. 2018; Earle 2019). Within the estuary itself, silt content is high, which is not suitable for sand lance because fine particles are thought to clog their gills (Wright et al. 2000).

In the best-fitting model, slope is estimated to contribute 18.3%, the second most to the model. Research comparing beaches across the world found a positive correlation between increasing beach slope and increasing sediment size (McFall 2019). The response curve between suitable habitat and slope indicates that the most suitable slopes range from approximately 4° to 10°. Slopes below this range are too low as they allow the accumulation of silts, and slopes above this range gradually decrease in suitability as slopes that are too steep do not retain suitable sand grains (Fig. 3) (McFall 2019).

The distance to predicted suitable subtidal habitat was also identified as an important variable, where the closer suitable subtidal burying habitat is, the more likely there is to be suitable intertidal spawning habitat. We suspect sand lance are using habitat in both areas for spawning and burying, but more research is needed to understand if these zones are used at different frequencies or for different life stages or purposes.

Derived seabed sediment only contributed 6.8% to the best-fitting model, and this is lower than would be expected, as sediment is thought to be an important feature of sand lance habitat (Penttila 1995). The subtidal model found that derived seabed sediment contributed the most to three of the four models tested (Robinson et al. 2021). The layer may have had a low contribution to the model because of difficulty in obtaining spatially accurate data for intertidal sediments. The intertidal zone is difficult to study as it is highly dynamic (Prodger et al. 2016) and it is rarely captured continuously across broad geographic areas. Sediment surveys across the Salish Sea are composed of surveys from multiple years, at different times of the year, some areas are from multiple decades prior (Gregr et al. 2013; Lerner and Gregr 2018). Investigations comparing spatial coverage of each environmental predictor layers to the MESS show that areas of lower certainty (negative MESS values) overlap seamlessly with the hard category of the bottom patch model. This is likely due to the fact that there are no samples collected in this type of habitat as areas where the sediments are hard (bed rock or boulders), sand is not typically present and therefore no sand can be collected.

Higher fetch values were associated with lower likelihoods of suitable habitat. We assume this relationship exists because the more exposed a shoreline is, the greater potential there is that waves that can build up over the longer distances, resulting in higher amounts of energy removing smaller sediments including suitable sediments from shorelines. Our analysis found that shorelines that face south, east, and west are slightly more likely to have suitable habitat than north-facing shorelines. According to the jackknife, this predictor contributes less than 2% of explanatory power, and may only have a weak relationship with the presence of suitable intertidal habitat for sand lance. This is contrary to the findings by Quinn et al. (2012) on surf smelt spawning beaches on Camano Island in nearby Puget Sound where northerly aspects were more likely to have suitable habitat for surf smelt. Quinn et al. (2012) as well as Nakashima and Taggart (2002) suggests that processes affecting spawning beach usage are similar among species and locations. However, it is possible that aspect, a proxy of sun exposure, is not as important to sand lance whose main spawning window occurs in the winter rather than throughout all months of the year like surf smelt. Alternatively, aspect may be an important predictor because it relates to the dominant wind patterns. In the Salish Sea, strong southeasterly winter systems dominate and bring strong winds driving waves and currents that rework shoreline sediments, potentially influencing the presence of sandy beaches (Jackson et al. 2010; Gemmrich and Pawlowicz 2020). Beaches that face southeast, particularly those with greater fetch values, would receive the strongest winds and waves.

Threats

There is limited empirical data outlining the anthropogenic threats faced by coarse, silt free sand habitats used by Pacific sand lance. However, sea-level rise, ocean temperature warming, shifting weather patterns, and other impacts of climate change along with coastal development and climate adaptation strategies are expected to intensify in the Salish Sea in coming decades, and could cause unprecedented ecological impacts on these unique low-lying coastal habitats that are particularly at risk to damage or loss (Rice 2006; Johannessen and Macdonald 2009). We estimate that approximately 2.4 km^2 (8.5%) of intertidal sand lance habitat categorized as likely or highly likely falls within a protected area as identified in the Canadian Protected and Conserved Areas Database (Government of Canada 2021).

Of particular concern is the threat of shoreline armouring (Dethier and Berry 2010; Dethier et al. 2016). Throughout Burrard Inlet (Fig. 5), where Canada's largest port (Port of Vancouver) is located, suitable habitat is predicted throughout the shorelines of West Vancouver and Vancouver, and east of the First Narrows. However, west of the First Narrows, little habitat is predicted. This is likely due to the almost complete hard armouring of the shorelines for ship docking and industrial facilities. Regions with a low likelihood of suitable habitat include areas where there is little coarse sand and high percentage of fine silts in the sediment, such as areas with cliffs and rocky shores (e.g., Lasqueti and Texada Islands) and directly within estuaries (e.g., K'ómoks Estuary), bays or inlets (e.g., Northwest Sidney Island).

As the impact of sea level rise and shoreline erosion increases, armouring has become a common climate adaption strategy. Armouring along naturally shallow, soft-sediment beaches can create deep, rocky waterfronts that become absent of fish that select for softer substrate (Munsch et al. 2017). In other studies, loss of habitat resulting from coastal armouring was associated with significant impacts to mid- and upper-beach zone widths, macroinvertebrates, foraging shorebirds, and roosting gulls and seabirds on open coast beaches (Dugan and Hubbard 2010). Current Canadian and British Columbia land development practices and the laws in place allow shoreline armouring up to the mean high-tide line leaving intertidal forage fish habitat at risk of negative impacts or loss altogether (Buchanan et al. 2019).

Study limitations

This study focused on modelling methods for identifying intertidal sand lance spawning habitat. As with all modelling exercises, there are several limitations that must be considered. First, modelling in the intertidal zone presents several challenges including appropriate delineation and access to high-resolution data (Gregr et al. 2013). For our modelling purposes areas with cliffs or steep slopes were particularly challenging to work with as the straight distance measured between the high- and low-tide mark lines results in a narrow intertidal band. In some regions, the intertidal zone is narrower than our cell resolution (20 m × 20 m) resulting in a lack of raster cells over these areas, suggesting there is no intertidal zone when in fact there is. Related to this, the process of creating raster layers at a resolution of 20 m × 20 m, a high resolution by most modelling standards, could be considered too coarse as some small beaches, colloquially known as pocket beaches, are missed and subsequently are not captured by the model. Improvements to environmental data resolution could resolve this challenge.

Second, accurate geospatial identification of occupied habitat is challenging due to the dynamic nature of beach processes and the small size of eggs (Prodger et al. 2016). Previous surveys found that spawning is most dense 2–3 m above the mean low water level but often eggs, anchored only by a few individual grains of sand, accumulate at the high-water line in the "swash" zone (Robards et al. 1999; Thuringer 2004; Penttila 2007). We have assumed the area in which adults choose to spawn is likely very close to where eggs are observed; however, it is possible that spawning may be occurring some unknown distance away and washing up.

Similar to beaches in Newfoundland, sediment density, coverage, and size at suitable spawning beaches have been observed to change annually by season, potentially from changing predominant wind patterns (Nakashima and Taggart 2002). Some beaches, such as Departure Bay near Nanaimo and Patricia Bay Beach near Saanich, have been observed becoming coarser (at all times of the year), we suspect this to be from a change in the flow of sediment or energy reaching the shoreline. We attempted to use the best available information for the environmental predictors; however, due to the dynamic nature of the study area, the predicted sediment type and tidal current layers may not always reflect conditions at the time of sampling. Our model should be validated with independently collected data confirming that the fish are actually using high probability habitat. This data could be produced by dedicated scientific surveys, an expansion of the community science data collections, or through the application of new technologies, such as environmental DNA (eDNA). Related are the biases that come from working with community science groups as areas sampled are easily accessed, not randomly selected, spatially diverse locations and they often overlap with developed areas. This model is intended to be a "living process" and future updates could include model validation using a random stratified design.

Throughout the world, most species of *Ammodytes* are thought to spawn in the same subtidal habitat that adults use for burying (Wright and Bailey 1996; Munk et al. 2009); however, in Washington, British Columbia, and Alaska, little evidence for subtidal spawning has been observed, although some have speculated it is possible, even likely (Penttila 1995; Robards et al. 1999; Thuringer 2004). In Japan and the East China Sea, sand lance (*Ammodytes personatus*) are known to spawn in subtidal habitats and eggs have not been found in the intertidal zone (Yamada 2009). Three studies report specifically investigating subtidal spawning in the eastern Pacific, none found conclusive evidence of subtidal spawning. However, it is important to note that these studies were not systematic and limited in their spatial and temporal coverage (Penttila 1995; Hrushowy 2010; Greene et al. 2011). Preliminary field work in the winter of 2019 and 2020 found 16 sand lance eggs in a grab sample from the subtidal zone (approximately 20 m deep; J. Huard and C. Robinson, 2019, unpublished data). In other species that use both intertidal and subtidal zones for spawning, subtidal spawning typically occurs later in the year than intertidal spawning, as seen in Atlantic Capelin for example (Penton et al. 2012; Davoren 2013). Late, subtidal spawning in Pacific sand lance could explain the curious observations in the east Pacific of late winter gonadal condition of adult sand lance and the presence of late summer larvae (Robards et al. 1999; Doyle and Mier 2012; Robinson 2013). This highlights a lack of full understanding of spawning strategies for this species. Investigations into subtidal spawning could contribute to further understanding on how sand lance populations might fare in the face of climate change and increasing coastal development pressure.

Conclusion

Approximately 5.4% of the intertidal zone in the Salish Sea (28.18 km^2) is predicted to have suitable habitat for Pacific sand lance, of which 8% (2.36 km^2) falls within a protected area. The maps and spatial information generated from our habitat suitability model can help inform marine and terrestrial conservation planning and for assessing risks posed by nearshore anthropogenic activities that may negatively alter or remove sand lance intertidal habitat. Model results are also potentially useful in understanding predator–prey relationships and developing endangered species recovery strategies such as the federally endangered marbled murrelets (*Brachyramphus marmoratus*), baleen whales, and Chinook salmon, which all forage on sand lance. At this time, no British Columbia coast-wide mapping or models exist for identifying sand lance spawning habitat, and hence the application of our MaxEnt spatial model could be used to develop habitat models for other nearshore coastal regions to help manage and reduce anthropogenic impacts to the habitats of this key coastal forage species.

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Data availability statement

Sand lance observations utilized in this study are available from the Strait of Georgia Data Centre (link: 904a8e86-7992-424a-9b68-40906852f4e9) and from cited, publicly available reports.

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Contribution statement

JH, TGM, and CLKR designed the study. JH performed the analysis with assistance from BP and CR. JH, TGM, and CLKR drafted the paper. All authors contributed to editing the paper.

Competing interests statement

The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2021-0335.

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