NRC Research Press

ARTICLE

Transferability and scalability of species distribution models: a test with sedentary marine invertebrates

Aaron M. Eger, Janelle M.R. Curtis, Marie-Josée Fortin, Isabelle M. Côté, and Frédéric Guichard

Abstract: We found the predictive accuracy of species distribution models (SDMs) for sedentary marine invertebrates to be dependent on the methodology of their application. We explored three applications of SDMs: first a model tested at a scale smaller than at which it was trained (downscaled), second a model tested at scale larger than its training scale (upscaled), and third a model tested at the same scale but outside the extent for which it was trained (transferred). The accuracies of these models were compared with the "reference" models that were trained and tested at the same scale and extent. We found that downscaled SDMs had higher predictive accuracy than reference SDMs. Transferred and upscaled models had lower predictive accuracy than their reference counterparts but still performed better than random, making them potentially acceptable alternatives where information is lacking for imminent decisions or in cost-restricted scenarios. Our results provide insights into the techniques available for researchers and managers developing SDMs at varying scales, with different species, and with different levels of initial information.

Résumé : Nous avons constaté que l'exactitude de prévision des modèles de répartition des espèces (MRE) pour les invertébrés marins sédentaires dépendait de la méthodologie de leur application. Nous avons exploré trois applications des MRE : soit d'abord un modèle mis à l'essai à une échelle plus petite que celle à laquelle il avait été entraîné (réduction de l'échelle), deuxièmement un modèle mis à l'essai à une plus grande échelle que celle à laquelle il avait été entraîné (augmentation de l'échelle) et troisièmement, la mise à l'essai d'un modèle à l'échelle à laquelle il avait été entraîné, mais au-delà de l'étendue de son entraînement (transfert). Les exactitudes de ces modèles ont été comparées aux modèles « de référence » ayant été entraînés et mis à l'essai à la même échelle et sur la même étendue. Nous avons constaté que les MRE dont l'échelle avait été réduite présentaient une exactitude de prévision plus élevée que les MRE de référence. Les modèles ayant fait l'objet d'un transfert ou d'une augmentation de l'échelle avaient une exactitude de prévision plus faible que les modèles de référence correspondants, mais étaient quand même plus exacts que le scénario aléatoire, ce qui en fait des solutions de rechange potentiellement acceptables en cas d'information manquante pour des décisions imminentes ou de scénarios de limitation des coûts. Nos résultats fournissent de l'information sur les techniques dont disposent les chercheurs et aménageurs qui élaborent des MRE à des échelles variables, avec différentes espèces et différents niveaux d'information initiale. [Traduit par la Rédaction]

Introduction

Knowledge of the spatial distribution of species is essential to underpin a broad range of species- and community-level conservation and management planning processes, including the identification and protection of critical habitat (Gibson et al. 2004; Gregr and Trites 2001), the design of marine protected area networks (Leslie et al. 2003; Louzao et al. 2006), and the development of area-based fishery quotas (Hobday and Hartmann 2006). However, complete knowledge of a species' occurrence over large spatial scales (e.g., 1000s of km) or its entire range is rare and can be prohibitively expensive to obtain. When such data are not available, an alternative approach is to identify the biotic and abiotic variables that correlate with species presence or abundance in a given area using species distribution models (hereinafter SDMs). Such models are then used to extrapolate predicted distributions into unsurveyed areas that are still within a species' known geographic range (Loiselle et al. 2003; Elith and Leathwick 2009). By doing so, SDMs can be used to inform policy decisions, even in data-limited situations, identify major knowledge gaps in species distributions, and develop hypotheses about tolerance thresholds and responses to climate change or other shifting environmental conditions (Guisan and Thuiller 2005).

The predictive power and accuracy of SDMs depend on several factors. The availability of data on species locations and environmental characteristics, data resolution, and sampling biases all affect a model's performance (Karl et al. 2000; Gontier 2007; Guisan et al. 2007). Data collection is rarely tailored for use in distribution modeling, and even if it is, sampling biases still exist and have the potential to distort SDM predictions (Anderson and Gonzalez 2011). Therefore, biases related to sampling are mostly out of researchers' control and must be recognized and accepted as limitations. In contrast, the use and analysis of the data are explicitly at the discretion of the researcher(s). How to delineate the predicted areas, which modelling approaches to use, as well as how and over which spatial scales to apply the predictive models are issues that have to be considered when undertaking species distribution modelling. More specifically, several questions arise when a model is developed over a large region. For example,

A.M. Eger* and F. Guichard. Department of Biology, McGill University, Montreal, QC H3A 1B1, Canada.
J.M.R. Curtis. Pacific Biological Station, Fisheries and Oceans Canada, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada.
M.-J. Fortin. Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON M5S 3G5, Canada.
**I.M. Côté.** Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

Corresponding author: Aaron M. Eger (email: aeger@uvic.ca).
*Present address: Department of Biology, University of Victoria, Victoria, BC V8P 5C2, Canada.

Can. J. Fish. Aquat. Sci. **00**: 1–13 (0000) dx.doi.org/10.1139/cjfas-2016-0129

Published at www.nrcresearchpress.com/cjfas on 5 October 2016.

Pagination not final (cite DOI) / Pagination provisoire (citer le DOI)

2   Can. J. Fish. Aquat. Sci. Vol. 00, 0000

Fig. 1. Examples of upscaling (local to regional, local to provincial, and regional to provincial), downscaling (provincial to regional, provincial to local, and regional to local), transferring (local to local, regional to regional) and reference (trained and tested at the same scale and extent) species distribution models. [Colour online.]
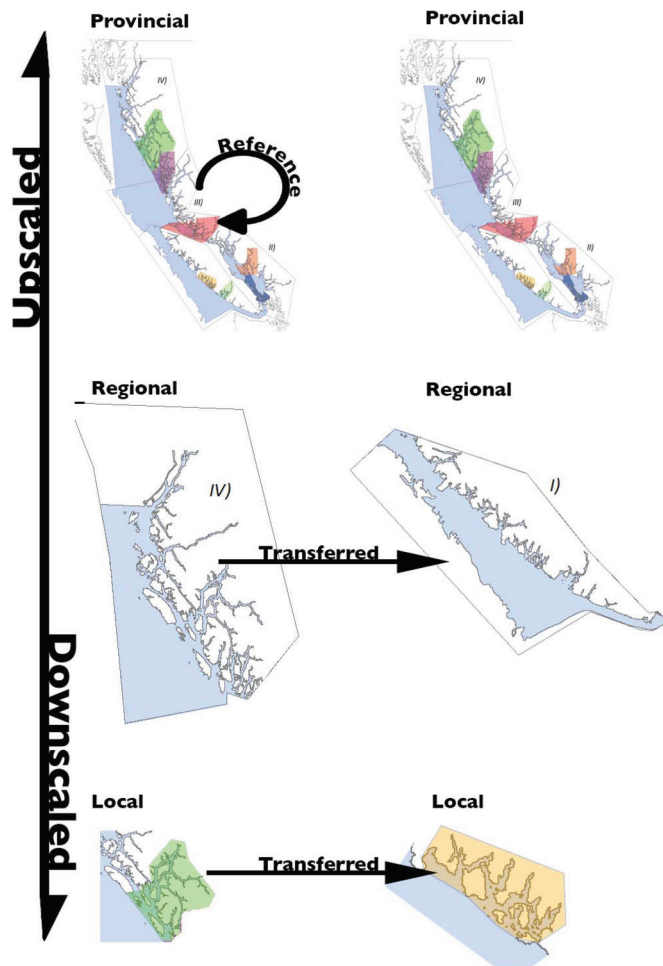
one might need to model an entire species' range to identify critical habitats for transitory or migratory species, to set area-based quotas for a harvested species, or to undertake a systematic planning process over a large area. At what spatial scale is the SDM best developed and applied? Is it most effective to model species distributions across the entire region of data availability? How can local variability in habitat associations be taken into account? To what extent can model predictions based on species distribution data from one area be transferred and applied to an unsurveyed area? Can a model from a small region be applied to a much larger one? Such questions raise the issues of scalability and transferability of SDMs and warrant further consideration in the application of SDMs (Wenger and Olden 2012).

The scalability of a model is a sought-after feature with two possible variations. Upscaling a model is the process of training a model (termed the reference model) on data from a small area and then testing that model on a larger area that encompasses the original smaller area. In contrast, downscaling uses a reference model that was trained on data from a large area to predict distribution over a smaller area nested within the larger area (Fig. 1). Upscaling SDMs is advantageous if upscaled models perform well because it saves a considerable amount of time and money that would otherwise need to be spent surveying additional areas. However, one might expect an SDM to perform poorly when upscaled if there is variability in habitat use across the larger region

that is not captured by at the smaller scale of the reference model. Downscaling would only be advantageous if it produces better results than the large-scale reference model. However, a downscaled model might be ill-suited to a subset of the original area if it cannot account for local variability in species–environment interactions and over-generalizes the relationships. For instance, if a species occupies multiple habitat types across a landscape, a global model trying to fit these trends simultaneously might predict that the species occupies an "average" of those habitat types or environmental conditions, thus failing to predict distribution accurately at either a large or small scale.

Model transferability is also desirable, because models that make accurate predictions can be extrapolated to areas with little to no survey information also still within a species' geographic range (Wenger and Olden 2012). For a model to transfer well into new areas, the relationships between species distribution and environmental variables need to be similar across areas. Yet many species exhibit local adaptations (Holt and Gaines 1992; Doebeli and Dieckmann 2003), which may cause those relationships to differ among localities. Thus far, the transferability (i.e., the extent to which a model retains its predictive power) of small-scale reference models extrapolated to other small-scale locales has been found to be poor (Randin et al. 2006; Segurado et al. 2006; Wenger and Olden 2012; Knudby et al. 2013). Note that the two main differences between scaled and transferred models are that (*i*) scaled models are trained on some survey information from the areas to which they are tested, while transferred models are not, and (*ii*) transferred models are tested at roughly the same scale (Fig. 1), while scaled models are tested at larger or smaller scales than at which they are trained.

How well a model scales or transfers might be influenced by the characteristics of the target species, specifically niche breadth and spatial variability in habitat use. Species that have narrow environmental niches with well-defined habitat boundaries can be more accurately modelled (Luoto et al. 2005; Hernandez et al. 2006; Evangelista et al. 2008). If the pattern of habitat use holds across the study region, a model built for one area is likely to transfer well to another. In contrast, species with variable habitat requirements or habitat generalists have proven more difficult to model (Brotons et al. 2004; McPherson et al. 2004; Hernandez et al. 2006), and the scaling and transferring of such models should be less successful.

The goals of our study are threefold. First, we investigate the scalability of SDMs, in terms of predicting distributions both at smaller and larger scales than their respective reference models. Second, we assess the transferability of models in terms of how well they can predict distributions in areas other than the ones for which they were devised. Third, we examine species-specific differences in model performance for the reference, scaled, and transferred models. We then discuss these topics in the context of supporting management decisions.

We focus on four benthic marine invertebrates of Canada's coastal ecosystems in the northeastern Pacific Ocean: the California sea cucumber (*Apostichopus californicus*), geoduck clam (*Panopea generosa*), green sea urchin (*Strongylocentrotus droebachiensis*), and red sea urchin (*Mesocentrotus franciscanus*). All these species are widespread, abundant, and socio-economically important in British Columbia (BC). Accurately mapping their distributions has immediate management applications in terms of refining commercial fisheries management, implementing spatial management measures, including fishery closures (DFO 2013*a*, 2013*b*, 2014*a*, 2014*b*), and informing the design of a network of marine protected areas in BC.

We examine scalability and transferability across three spatial scales: local, regional, and provincial (Fig. 1). When upscaling, local reference models were scaled to the encompassing regional and provincial scales, while reference models built at the regional scale were scaled to the provincial scale (Fig. 1). Similarly, when

downscaling, provincial models were scaled to regional and local scales, while regional models were applied to local areas with them (Fig. 1). Transferred models were examined at the local and regional scale and involved applying a reference model to a different extent of the same scale (Local Area I to Local Area II, Region I to Region II). Finally, reference models were trained and tested at the same scale and extent (i.e., local-to-local, regional-to-regional, or provincial-to-provincial), and their accuracy scores were used as references for the transferred and scaled models. (Fig. 1). We predicted that models developed for a given area would be more accurate than models transferred from other areas. We also anticipated that scaling a model, especially downscaling, would reduce its accuracy, reflecting spatial variation in species habitat use. Even if they are less accurate, scaled models (notably upscaled) might still prove useful when sampling cost prohibits additional data collection. Lastly, we expected model transferability and scalability to vary with species habitat requirements and niche breadth. More specifically, because *A. californicus* and *S. droebachiensis* have relatively more generalist habits than *P. generosa* and *M. franciscanus* (see Materials and methods), the SDMs developed for the latter species might be more accurate and more easily transferred and scaled than those developed for the former.

Materials and methods

Study area

The study area comprised coastal ecosystems along the mainland of BC and surrounding Vancouver Island to a depth of 1138 m, the maximum depth of the four species. The islands of Haida Gwaii were excluded because survey data were sparse and these islands are ecologically dissimilar to the rest of the province (Zacharias et al. 1998). The provincial scale was divided into four regions (regional scale), corresponding approximately to the Shellfish Transfer Zones established by Fisheries and Oceans Canada (DFO) to manage the movement of cultured fish and shellfish along the BC coast (DFO 2014c). The four regions were (I) the west coast of Vancouver Island, (II) Strait of Georgia, (III) Queen Charlotte Sound and Queen Charlotte Strait, and (IV) North Coast of BC (Fig. 2; Table 1). Finally, at the local scale, smaller areas corresponding to DFO Pacific Fisheries Management Areas (PFMAs) — the spatial units used by DFO to assess and manage fish and invertebrates — were selected within each of the four regions (Fig. 2; Table 1). We usually chose one PFMA per species per region, although two PFMAs were sometimes combined to generate a suitable sample size (Fig. 2; Table 1). For clarity, each local area shares the same identifying number as its encompassing region (e.g., Local Area I is nested within Region I; Table 1). Our analyses thus provide opportunities to assess SDM transferability across spatial scales and areas that are recognized as relevant to the scale of species management in BC.

Sufficient data as determined by the step.gbm function in R were available for all four species to develop SDMs with all permutations of the selected parameters (see analysis) at the province-wide scale and within the four regions, except for *S. droebachiensis* and *M. franciscanus*, for which there was insufficient survey data from Region I (West Coast Vancouver Island; Table 1). With the exception of *S. droebachiensis*, there were sufficient data to develop models for each of the species at one or more local (PFMA) scales.

Study species

We focussed on four common benthic invertebrates found on the Pacific coast of North America that are widely distributed, differ qualitatively in the degree of niche specialization, and are subject to spatially managed commercial fisheries. Two species, the giant California sea cucumber (*A. californicus*) and the green sea

urchin (*S. droebachiensis*), have broad habitat preferences and environmental tolerances. *Apostichopus californicus* occurs in a variety of hard- and soft-bottom habitats at depths ranging from intertidal to 250 m (Lamb and Hanby 2005; Paltzat et al. 2008). *Strongylocentrotus droebachiensis* is also widely distributed, ranging to depths of 1138 m (Lamb and Hanby 2005), although restricted to hard substrates (Scheibling and Hatcher 2001). Both species have wide thermal tolerances that exceed the range found in BC. Similar to other sea cucumber species, *A. californicus* likely prefer stable haline environments (Stickle and Diehl 1987). Low salinities are generally detrimental to *S. droebachiensis* (Scheibling and Hatcher 2001), but some populations persist in estuarine environments (Campbell and Russell 2004). *Apostichopus californicus* is generally absent from areas of high current velocities (Hand et al. 2008), but green urchins tolerate a broad range of tidal speeds (Lauzon-Guay and Scheibling 2007).

The other two species, the geoduck clam (*P. generosa*) and the red sea urchin (*M. franciscanus*), occupy relatively narrower environmental niches. Their depth limits are 100 and 65 m, respectively (Lamb and Hanby 2005). *Panopea generosa* commonly occurs in soft sediment in discrete patches characterized by moderate to high currents, which are optimal for filter feeding (Bureau et al. 2012). *Panopea generosa* are also thought to be more abundant in areas of lower chlorophyll *a* values (Campbell et al. 1998). *Mesocentrotus franciscanus* prefer hard substrate (Lamb and Hanby 2005) with moderate to high currents, but thrive in areas with high chlorophyll *a* values and lower water temperatures (Kato and Schroeter 1985). We therefore tentatively consider *P. generosa* and *M. franciscanus* as more specialized than *A. californicus* and *S. droebachiensis*, although we recognize that this distinction is not based on a formal comparison of niche breadth.

Species surveys

Species presence and absence data were derived from subtidal surveys conducted by scientific SCUBA divers at the Pacific Biological Station (DFO; Nanaimo, BC) as part of departmental population monitoring programs for each of the four study species. The surveys were conducted using SCUBA, no deeper than 18 m, and are therefore all considered to be nearshore surveys. The species surveys cover an extensive area (Fig. S1[1]), were systematically conducted, and yielded presence–absence information, all attributes conducive to species distribution modeling.

Apostichopus californicus

The sea cucumber data used in our models were collected from 1997 to 2012 during systematic surveys within the PFMAs. When an area was surveyed more than once, the most recent data were used. The surveys were conducted along transects laid perpendicular to the coast from the surface to a depth of 15.2 m, and the number of sea cucumbers within 1 m of the transect line was recorded. Transects were set 2 km apart in five to 11 segments of coastline within each PFMA (Duprey 2011).

Panopea generosa

The majority of geoduck data used in our SDMs was obtained from 1992 to 2013 during surveys conducted in areas with soft sediment or rocky cobble substrate. These substrate types were identified as suitable habitats, as these are a known habitat requirement for geoduck populations (Bureau et al. 2012). At each site, survey effort was stratified by substrate type and surveys spanned the entirety of suitable habitats. Transects were run across suitable habitats every 150 m perpendicular to shore to a chart depth of 18 m. The number of geoducks was recorded in every one to four quadrats (5 m × 2 m) along each transect, depending on transect length (Bureau et al. 2012). Additional survey

Pagination not final (cite DOI) / Pagination provisoire (citer le DOI)

4

Can. J. Fish. Aquat. Sci. Vol. 00, 0000

Fig. 2. Map of coastal British Columbia, Canada, showing the spatial divisions used in this study, which were based on federal fisheries management area designations. Regions (delineated by solid black lines, numbered I–IV) are based on Shellfish Transfer Zones, while local areas (colour blocks) are based on Pacific Fisheries Management Areas (PFMAs) used to manage fisheries. The Arabic numbers correspond to the DFO-designated PFMA number. Multiple PFMAs within the same region indicate that different PFMAs were used for different species due to data availability (Table 1).
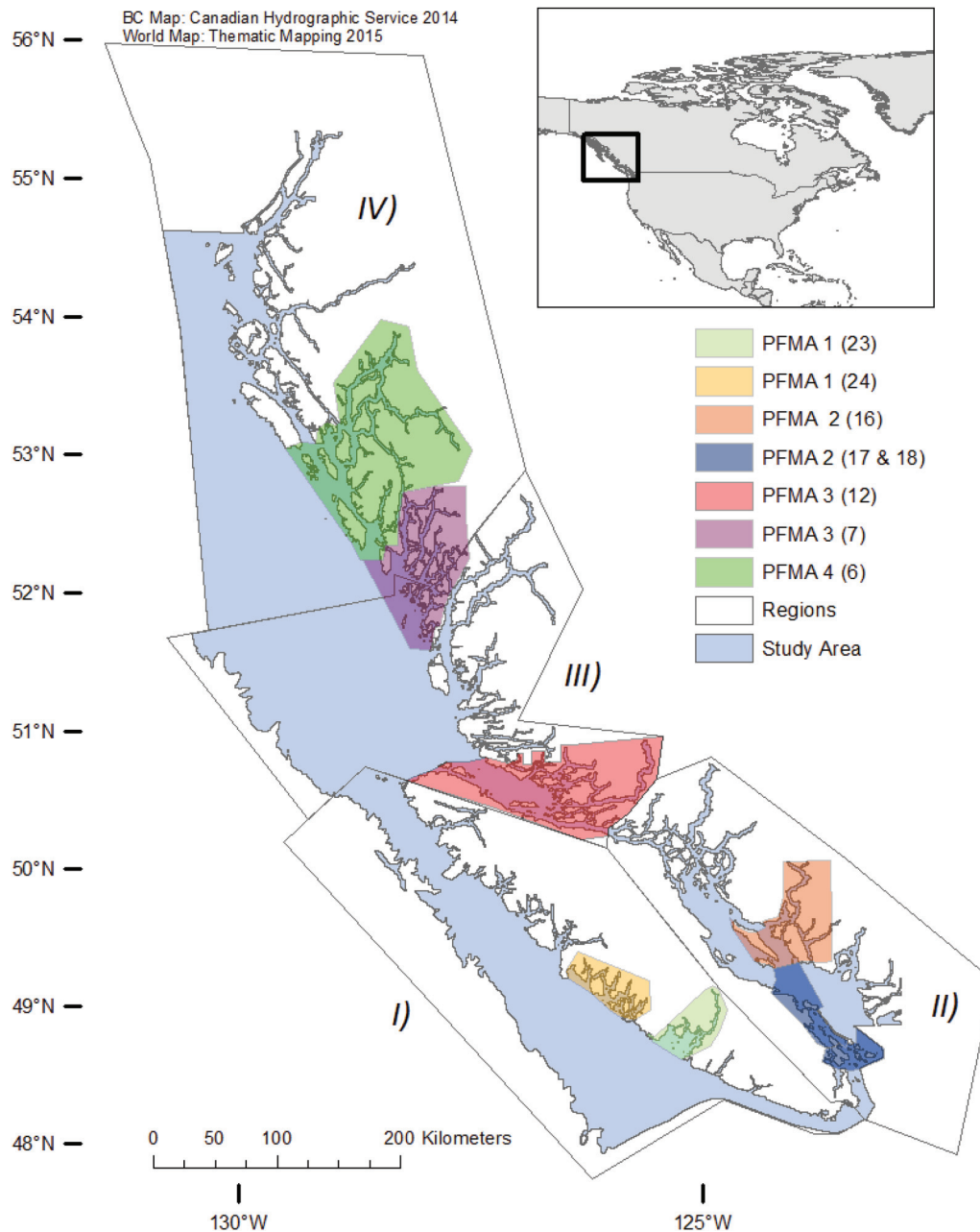
information was collected from the surveys focusing on sea cucumbers from 2009 to 2010. These were conducted using the methods described in the sea cucumber surveys but recording all geoducks visible from the transect line (Duprey 2011, 2012).

Mesocentrotus franciscanus

The red sea urchin data were obtained during surveys carried out from 2000 to 2011. Most transects were run every 1 km along several stretches of coastline of each PFMA to a chart depth of 10 m (Dan Leus, Fisheries and Oceans Canada, Nanaimo, BC, personal communication). Along these transects, 1 m² quadrats were placed every 2 m (Leus et al. 2014) and the number of red sea urchins noted.

Additional survey information was collected from the surveys focusing on sea cucumbers from 2009 to 2010 (Duprey 2011; Duprey 2012).

Strongylocentrotus droebachiensis

Green sea urchin data were collected from 1995 to 2013 during surveys that were conducted in areas with existing fisheries and in areas known to contain green urchins. Subtidal transects were run from nonsystematically predetermined locations on shore to a gauge depth of 10 m (Waddell et al. 1997). All green sea urchins within 1 m of the transect line were recorded (Waddell and Perry 2007). Additional survey information was collected from the surveys focusing on sea cucumbers from 2009 to 2010 (Duprey 2011, 2012).

Table 1. Modeling areas, their correspondence to Shellfish Transfer Zones (STZs) and Pacific Fisheries Management Areas (PFMAs) (see Fig. 2), their respective sizes, and the number of surveys of each of the four study species included in each model.

				No. of surveys			
Scale	STZ	PFMA	Total area (km²)	AC	SD	MF	PG
Province	2, 3, 4, 5	1–29, 104–111	100 621	4 630	532	1 366	4 627
Region I	5	—	25 258	244	—	—	556
Local I	—	AC: 24	815	151	—	—	—
		PG: 23 and 24	1 374	—	—	—	304
Region II	4	—	10 872	1 382	168	463	1 316
Local II	—	AC and PG: 16	4 305	496	—	—	396
		MF: 17 and 18	2 730	—	—	219	—
Region III	3 and southern part of 2	—	29 417	1 238	104	321	1 048
Local III	—	12	9 428	532	—	246	435
Region IV	Northern part of 2	—	35 074	1 766	260	582	1 707
Local IV	—	AC and PG: 6	3 507	734	—	—	621
		MF: 6 and 7	7 571	—	—	243	—

Note: AC, *Apostichopus californicus*; SD, *Strongylocentrotus droebachiensis*; MF, *Mesocentrotus franciscanus*; PG, *Panopea generosa*.

Table 2. The environmental variables considered in the distribution models for four species of benthic invertebrates on the British Columbia coast, with associated metadata.

Variable	Resolution	Year	Source	Mean	Min.	Max.
Chlorophyl *a* (mg·m⁻³)	500 m	2003–2006	BCMCA (unpub.)[a]	11.46	0.50	29.17
Current speed (m·s⁻¹)						
East–west summer	100 m near shore	2008	Foreman et al. 2008	0.00	−6.15	4.90
East–west winter	100 m near shore	2008	Foreman et al. 2008	−0.01	−3.56	4.01
Mean summer	100 m near shore	2008	Foreman et al. 2008	0.08	0.00	14.89
Mean winter	100 m near shore	2008	Foreman et al. 2008	0.09	−0.00	8.66
North–south summer	100 m near shore	2008	Foreman et al. 2008	−0.01	−14.13	3.68
North–south winter	100 m near shore	2008	Foreman et al. 2008	0.01	−8.23	3.29
Salinity (psu)						
Fall	100 m near shore	2008	Foreman et al. 2008	30.91	14.58	34.19
Year-round maximum	100 m near shore	2008	Foreman et al. 2008	31.41	18.02	34.31
Year-round minimum	100 m near shore	2008	Foreman et al. 2008	30.12	1.41	33.95
Year-round range	100 m near shore	2008	Foreman et al. 2008	1.29	0.04	19.90
Spring	100 m near shore	2008	Foreman et al. 2008	30.59	2.47	34.24
Summer	100 m near shore	2008	Foreman et al. 2008	30.78	15.18	34.11
Winter	100 m near shore	2008	Foreman et al. 2008	30.84	15.18	34.30
Temperature (°C)						
Fall	100 m near shore	2008	Foreman et al. 2008	8.79	4.28	11.85
Year-round maximum	100 m near shore	2008	Foreman et al. 2008	9.61	5.18	18.09
Year-round minimum	100 m near shore	2008	Foreman et al. 2008	7.29	3.95	9.97
Year-round range	100 m near shore	2008	Foreman et al. 2008	2.32	0.04	11.11
Spring	100 m near shore	2008	Foreman et al. 2008	8.31	3.96	14.32
Summer	100 m near shore	2008	Foreman et al. 2008	9.11	4.73	18.08
Winter	100 m near shore	2008	Foreman et al. 2008	7.49	4.22	10.34
Tidal						
Speed (m·s⁻¹)	100 m near shore	2008	Foreman et al. 2008	0.07	0.00	2.14
Direction (°)	100 m near shore	2008	Foreman et al. 2008	98.96	1.07	179.39
Bathymetry						
Slope (°)	100 m	1999	Benthic terrain modeller (ArcGIS)	1.95	0	32.65
Benthic position index (regional measure of slope)	100 m	1999	Benthic terrain modeller (ArcGIS)	1.45	−407	419

[a]BCMCA, British Columbia Marine Conservation Analysis.

Environmental variables

We compiled data on primary production, salinity, temperature, bathymetry, and current from several different sources (Table 2). These variables are known to influence marine species distributions (Whitlatch 1981; Degraer et al. 2008; Tyberghein et al. 2012). All data pertained to 2003 to 2008 (see Table 2) and were recorded at a resolution of 500 m. To our knowledge these were the most comprehensive and accurate data sets publicly available for our study area at the time of analysis. Environmental data did not overlap with species surveys for all years, which is an oft-encountered limitation of SDMs. The environmental point data were interpolated using the inverse distance weighting technique in ArcGIS 10.2. Any land was masked from the interpolation and the boundary was set to the 1138 m depth contour. Substrate composition was not considered, as a robustly verified data set was not available for the entire study area.

6

Can. J. Fish. Aquat. Sci. Vol. 00, 0000

Data limitations

The survey data were collected over a range of years, and older samples could potentially not represent current distribution if conditions have changed. Furthermore, survey data were not collected randomly at all locations; some surveys specifically targeted areas predicted to harbour the species. The results could be skewed if certain environments were not sampled or were oversampled. These problems are commonplace in SDMs and likely to be encountered by other researchers on similar projects. Nevertheless, the surveys used here covered a broad area, were likely to be representative of the study region, with perhaps the exception of Local Area I (Table 1), and were collected in a consistent manner over time. Finally, certain environmental variables such as pH, depth, nitrates, and substrate type were not considered because reliable data sets could not be obtained across our study region. While depth was used to demarcate the study area, it was not included as a predictor variable because there was little difference in depth across our survey locations (all less than 18 m). Instead, we used slope and bathymetric position index (BPI, a regional measure of slope; Lundblad et al. 2006) as habitat variables.

Analysis

Boosted regression trees

We used the boosted regression tree method (BRT) to model the distribution of the four marine invertebrate species. The BRT approach is a machine learning method that can deal with skewed data and with both quantitative and qualitative predictors. BRTs have strong predictive capabilities (Elith et al. 2008) and are tailored for presence–absence data. All BRT models were created using the packages gbm (version 2.1; Ridgeway 2006) and dismo (version 0.9–3; Hijmans et al. 2011) in R (version 3.1.0; R Core Team 2013). The raster prediction layers were created and examined using the packages raster (version 2.2–31; Hijmans and van Etten 2012) and rgdal (version 0.8–1.6; Keitt et al. 2011).

We converted all survey data into presence–absence (i.e., occurrence) data because assuming a binomial distribution facilitates testing for congruency in predictions among models. For each of the nested models developed for each of the four species, the presence–absence data were randomly and evenly split in two data sets, one set for training the model and one set for testing it. Optimal parameter settings were then determined by running the gbm.step function 100 times for each set. Each run was done with a unique combination of the basic BRT parameters and values regularly used in optimization practices (Elith et al. 2008). Said factors were tree complexity (TC), learning rate (LR), and bag fraction (BF). The ranges of values for TC were 1, 3, 5, 7, and 10; for LR were 0.01, 0.005, 0001, and 0.0005; and for BF were 0.2, 0.4, 0.6, 0.8, and 0.9. The optimal iteration was deemed to be the one that minimized deviance in the form of cross-validation deviance. Cross-validation refers to the gbm.step function, which creates nine subtraining sets to be tested against the 10th set. This is performed 10 times and all 10 models are used to build the final training model. This process also determines the optimal number of trees to be used in the testing model.

With optimal parameters defined, a test model was built for each species using predict.gbm function with the relevant tuned training model. The test model was evaluated using the area under the curve (AUC) of the receiver operator curve, a well-established method for testing and comparing SDMs (Phillips et al. 2006; Hirzel et al. 2006). The AUC score is obtained by plotting the area under the curve of the true positive (a positive occurrence that is correctly classified as positive) rate plotted against the false positive (a negative occurrence that is incorrectly classified as positive) rate. AUC scores range from 0 to 1. The values can be roughly interpreted as follows: 1–0.9 = excellent; 0.9–0.8 = good; 0.8–0.7 = fair; 0.7–0.6 = poor; and 0.6–0.5 = random or unacceptable (Luna-Herrera et al. 2003). An AUC score was obtained for each area (provincial, re-

gional, and local) and was considered the reference model for that corresponding area. As a post hoc cross-check for the influence of sample size, we ran models for *A. californicus*, the species with the most data points at the provincial scale, with 100%, 75%, 50%, 25%, and 10% of the available data and compared their AUC scores.

Scaling and transferring

We tested both the transferability and scalability of SDMs for each of the four species. After a species-specific model was built for a given area (i.e., a reference model), we scaled it up to the area(s) it was nested in and (or) down to the area(s) nested within it. We also assessed how models built for a specific area performed when transferred (i.e., applied to other areas of the same scale). The performance of scaled and transferred models was compared with that of the reference models with the AUC metric. The difference of the AUC score of a scaled or a transferred model compared with the reference model's AUC was tested against the hypothesis that such a difference should be less than zero, thus indicating a worse performance in comparison with the reference model (($AUC_{scale\ or\ transfer} - AUC_{Reference}) < 0$). These tests were conducted using one-tailed t tests ($a = 0.05$). Differences in AUC scores among species and scenarios were tested using one-way ANOVAs, and pairwise differences between groups were assessed using Tukey's tests.

Results

Predictive accuracy of reference SDMs

Across all scales, the predictive accuracy of the reference models for the four invertebrate species examined was variable, ranging from mean AUC of 0.67 for *S. droebachiensis* to 0.88 for *P. generosa* (Fig. 3; Table S1[1]). There were significant differences among species in mean AUC ($F_{[3,25]} = 4.92$, $p = 0.008$). Reference models developed for *P. generosa* performed significantly better than models developed for *A. californicus* and *S. droebachiensis*; models developed for *M. franciscanus* also performed better than those developed for *S. droebachiensis*, their more generalist counterparts (Fig. 3). There was little difference between models built for *A. californicus* at the provincial scale with 100%, 75%, 50%, or 25% of the available data. Only at 10% of the sample size did the model's accuracy significantly decline from AUC values of between 0.73–0.75 to 0.53 (Table S2[1]).
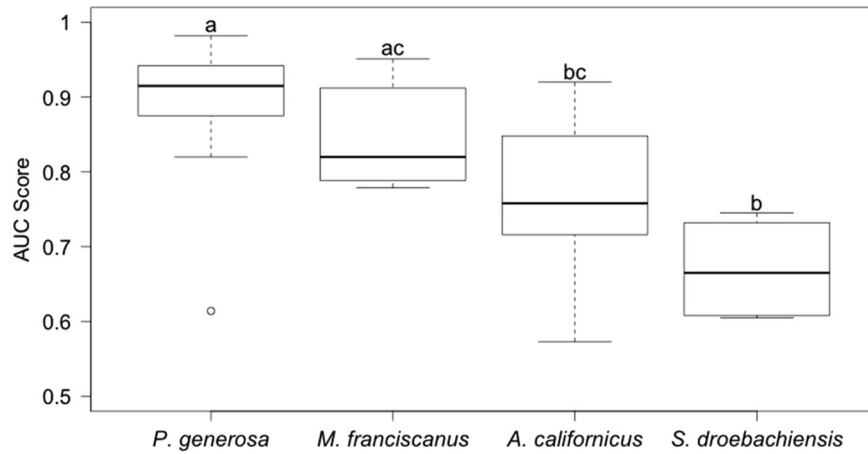
Scalability of SDMs

In nine out of the 10 comparisons between downscaled and corresponding reference models, the differences in AUC scores were significantly positive ($p < 0.05$; Fig. 4), meaning that downscaled models had significantly better accuracy. The one exception was for *P. generosa* when comparing regional with local scales. Mean absolute AUC scores for downscaled models were 0.94, 0.93, 0.94, and 0.87 for *P. generosa*, *M. franciscanus*, *A. californicus*, and *S. droebachiensis*, respectively (Fig. 4).

In contrast, the upscaled models performed significantly worse ($p < 0.05$) in seven out of 10 comparisons ($p < 0.05$; Fig. 5). The exceptions were the local to regional applications for *P. generosa* and *M. franciscanus*, as well as regional to provincial application for *S. droebachiensis* (Fig. 5). Mean absolute AUC scores for upscaled models were 0.70, 0.69, 0.65, and 0.73 for *P. generosa*, *M. franciscanus*, *A. californicus*, and *S. droebachiensis*, respectively (Fig. 5).

There were significant differences among species in predictive accuracy of upscaled ($F_{[3,32]} = 6.026$, $p = 0.002$) and downscaled ($F_{[3,25]} = 6.711$, $p < 0.001$) models. In pairwise comparisons, upscaled models for *P. generosa* performed significantly better than those of *A. californicus* and of *S. droebachiensis* (Table 3). In contrast, the downscaled models for *S. droebachiensis* performed significantly better than those of the three other species (Table 3).

Fig. 3. Area-under-the-curve (AUC) scores indicating predictive accuracy of species distribution models of four species of sedentary benthic invertebrate species in British Columbia. Higher AUC represent more accurate model predictions. The thick horizontal line represents the mean; the bottom and top of the box are the lower and upper quartile values, and whiskers are the minimum and maximum values. Means with the same letter are not significantly different from each other ($p > 0.05$).

Fig. 4. Scalability of species distribution models: downscaling. Data include absolute AUC scores (left axis, solid circles) and the difference in predictive accuracy (right axis, open circles), as measured by the difference in AUC scores between downscaled and reference models, for distribution models of four benthic invertebrate species on the coast of British Columbia. Positive differences mean that a downscaled model was more accurate than its reference. An asterisk (*) indicates AUC differences that were statistically different from zero ($p < 0.05$). Scales: L = local, R = regional, BC = provincial.
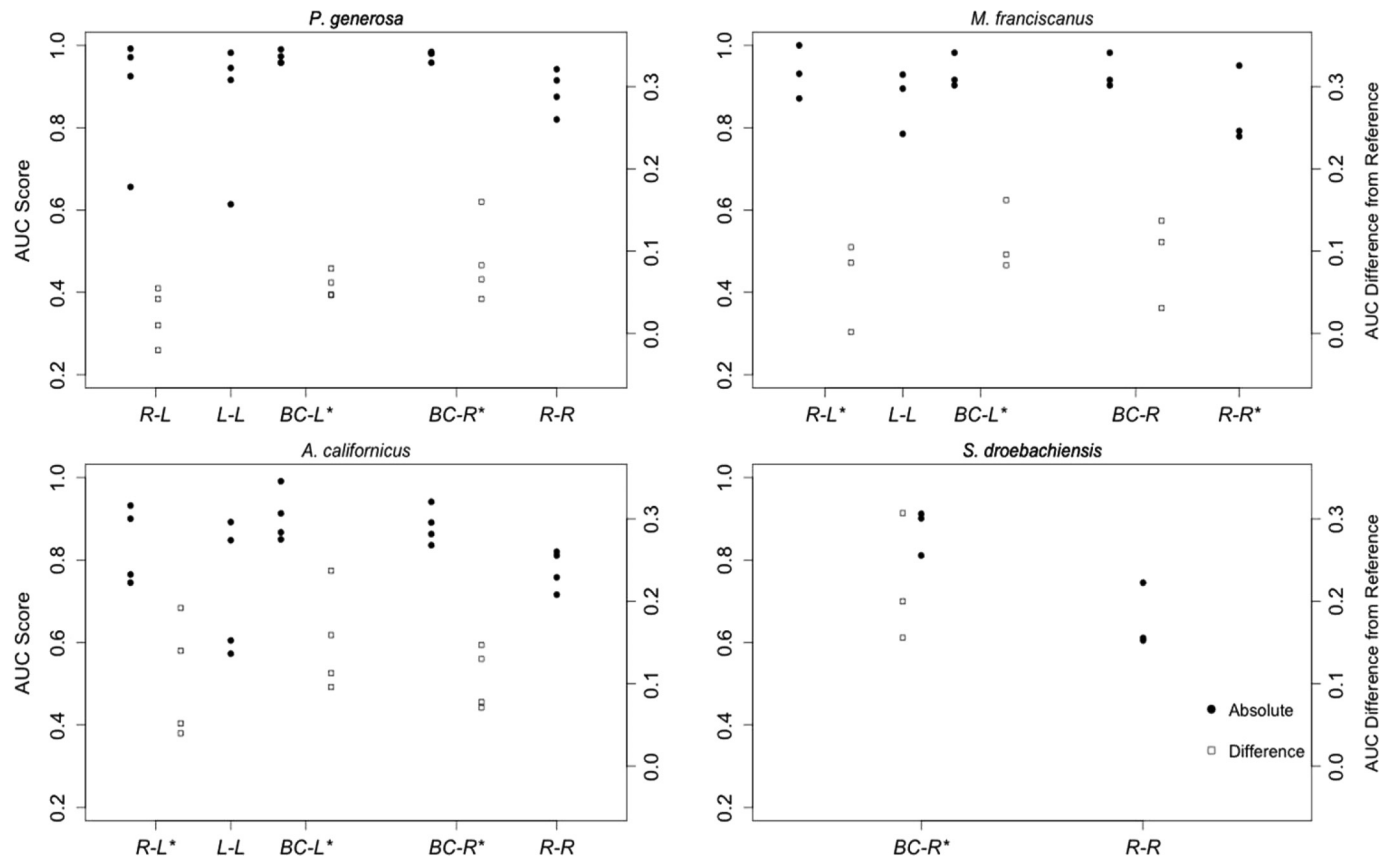

Transferability of SDMs

Overall, model performance decreased when transferred to other areas at the same scale. In almost all cases, except for models of *S. droebachiensis*, transferring SDMs resulted in a decrease in AUC scores (Fig. 6). The changes in AUC scores were similar for transfers among localities and among regions for *P. generosa* and *A. californicus* ($p > 0.05$ in both cases), but models for *M. franciscanus* transferred at the local scale resulted in a significantly greater decline in mean AUC than transfers among regions (Fig. 6). While transfers resulted in declines in AUC scores, they still averaged

Fig. 5. Scalability of species distribution models: upscaling. Data include absolute AUC scores (left axis, solid markers) and the difference in predictive accuracy (right axis, open circles), as measured by the difference in AUC scores between upscaled and reference models, for distribution models of four benthic invertebrate species on the coast of British Columbia. Negative differences mean that an upscaled model was less accurate than its reference. An asterisk (*) indicates AUC differences that were statistically different from zero ($p < 0.05$). Scales: L = local, R = regional, BC = provincial.
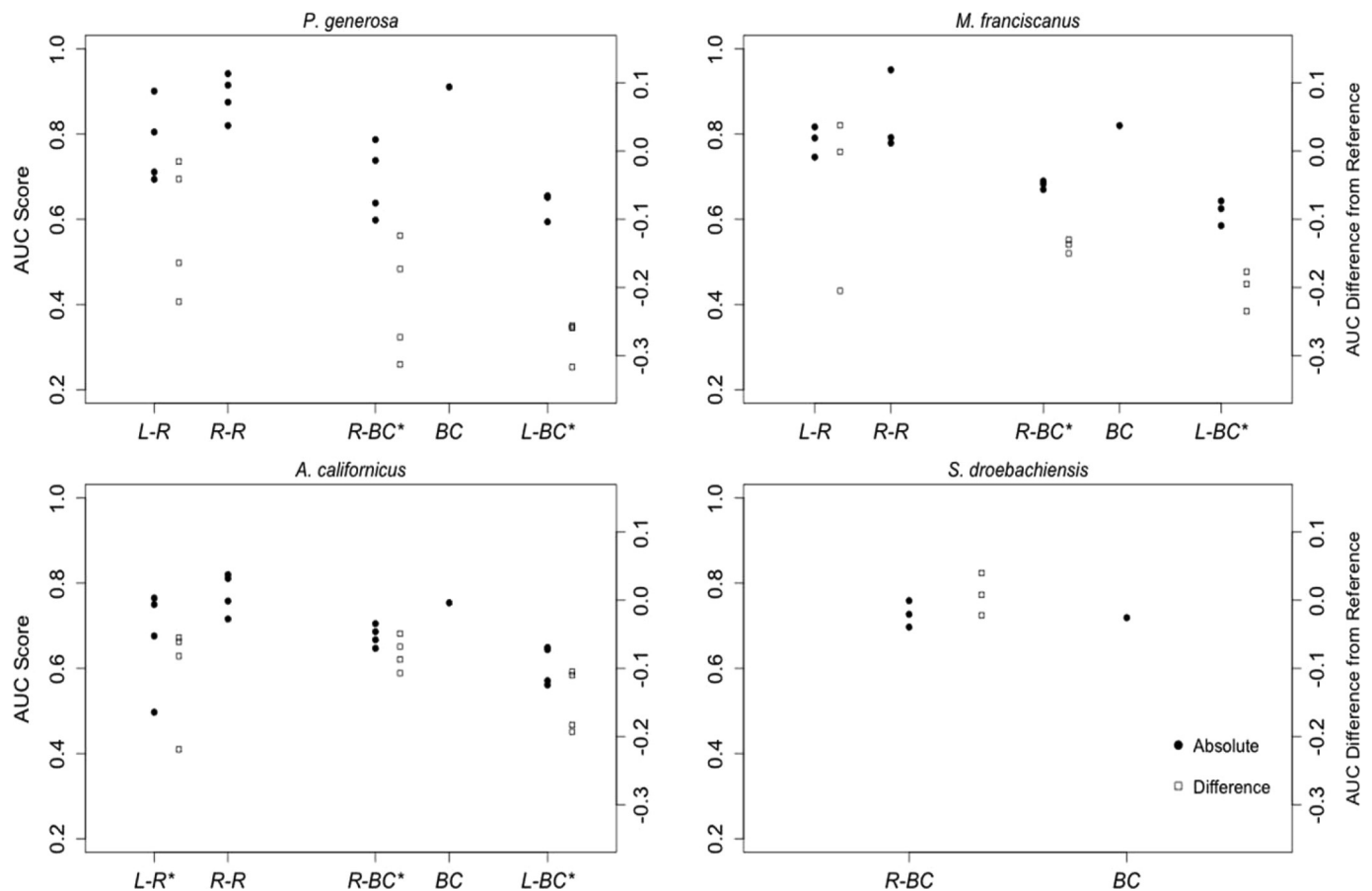
Table 3. Significance (p values associated with Tukey's tests) of pairwise differences between benthic invertebrate species in average change in AUC between the reference distribution model and either upscaled or downscaled models.

Species pair	Upscaling p value	Downscaling p value
PG–AC	0.05*	0.27
SD–AC	0.14	0.007*
MF–AC	0.92	0.99
SD–PG	0.002*	0.001*
MF–PG	0.25	0.33
MF–SD	0.07	0.008*

Note: PG, *Panopea generosa*; AC, *Apostichopus californicus*; SD, *Strongylocentrotus droebachiensis*; MF, *Mesocentrotus franciscanus*. An asterisk (*) indicates a significant ($p < 0.05$) difference between species.

above random predictive accuracy, with mean AUC scores of 0.59, 0.57, 0.58, and 0.68 for *P. generosa*, *M. franciscanus*, *A. californicus*, and *S. droebachiensis*, respectively (Fig. 6).

There were significant differences among species in transferability of SDMs ($F_{[3,62]} = 8.80$, $p < 0.001$). Transferability was significantly better (i.e., lower decline in AUCs) for distribution models of *S. droebachiensis* than for those of *M. franciscanus* and *P. generosa*. Models of *A. californicus* also had significantly better transferability than those of *P. generosa* (Fig. 7).

Discussion

We found clear patterns of scalability and transferability of SDMs. In all but one instance, downscaled models performed better than the reference model built specifically for that smaller scale. By contrast, upscaled models performed worse in seven out of 10 instances. Transferring SDMs either at the local or regional scale led to a decrease in their predictive accuracy. In almost all instances (61/66), the reference models performed better than transferred models. Although their accuracy was lower than reference models, upscaled and transferred models still tended to have higher-than-random predictive accuracy. Moreover, upscaled models had higher average predictive accuracy than transferred models. Though we found species-specific differences in the predictive accuracy and transferability of SDMs, the results were not consistently associated with patterns of species niche breadth. Together, these results raise important and testable hypotheses on the scale dependence of species–habitat relationships and have direct implications for fisheries management and conservation of marine coastal ecosystems.

Scalability and transferability

Contrary to our prediction, downscaling models significantly improved SDM predictions. In nine of 10 downscaling scenarios, the downscaled model performed better than the reference model. On average, downscaled models increased the performance of SDMs by a full increment on the performance scale. In other words, downscaling regularly turned an acceptable prediction (AUC > 0.7)

Fig. 6. Transferability of species distribution models: local-to-local and region-to-region. Data include absolute AUC scores (left axis, solid markers) and the difference in predictive accuracy (right axis, open markers), as measured by the difference in AUC scores between transferred models of reference models at the same scale, for distribution models of four benthic invertebrate species on the coast of British Columbia. Negative differences mean that a transferred model was less accurate than its reference. An asterisk (*) indicates AUC differences that were statistically different from zero for both local-to-local and region-to-region ($p < 0.05$).
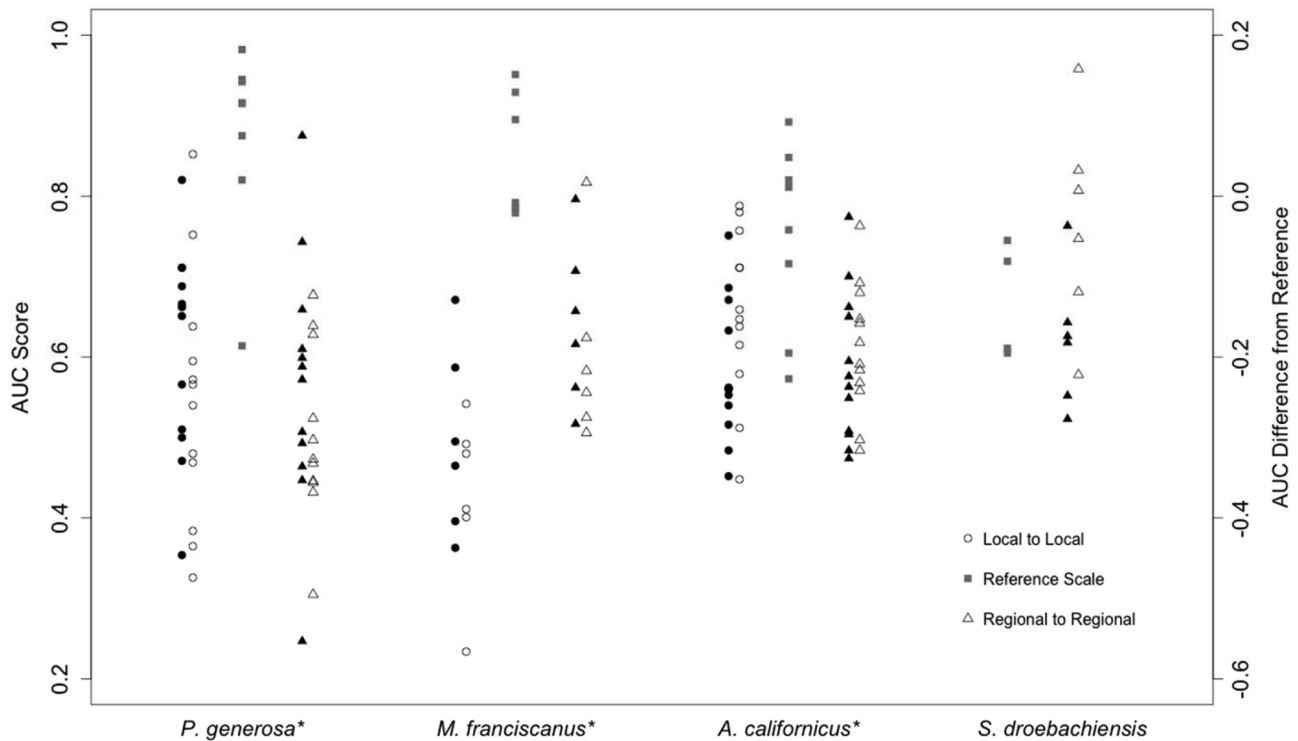

into a good one (AUC > 0.8), or a good one into an excellent one (AUC > 0.9) (see Table S1[1]). In only one scenario did a downscaled model perform worse than its reference counterpart, and in this example (Region II to Local Area II for *P. generosa*), only marginally so (change in AUC = −0.02). Such results indicate that downscaled models have the potential to provide significantly better results than developing and applying SDMs at their reference scale. At the very least, downscaled models provided results with the equivalent accuracy of their reference model. In contrast, as we had predicted, scaling models up from smaller to larger areas resulted in losses in predictive accuracy in seven out of 10 scenarios. The accuracy of upscaled models averaged around 0.7, which is acceptable, but this roughly represents a decline of one to two steps on the SDM performance scale in comparison with the reference models.

Downscaled models could be more accurate than reference models for a number of reasons. One is sample size; increasing sample size tends to increase AUC values (Stockwell and Peterson 2002; Hernandez et al. 2006; Wisz et al. 2008), and our downscaled models had larger sample sizes than their reference. However, the relationship between sample size and accuracy is a decelerating curve, with the point of diminishing returns usually reached at sample sizes of 10s to 100s (Stockwell and Peterson 2002; Hernandez et al. 2006; Wisz et al. 2008). This was supported by our analysis of sample size that showed that only models built with the smallest sample sizes (10% of the available data, *n* = 463) had lower accuracy (Table S2[1]). Our sample sizes for models developed at the smaller (local, provincial) scales were typically much larger than the 10% subsamples from data sets used to build models at larger (provincial, regional) scales. Another potential reason for increased accuracy in downscaled models relates to the geography of the species distribution (Morris 1987; Saab 1999). If a species' distribution is better predicted from information gathered at a larger scale than

the data it is tested with, it might be because the larger area contains a more accurate representation of the species' variable habitat use patterns. Conversely, the smaller area may contain a poor or biased subsample of that species' distribution. For example, in a heterogeneous environment, species surveys conducted over a small area, and the resultant models, are more likely to over-sample and over-predict occurrence at one tail of the habitat-occurrence probability distribution. Sampling a larger area provides more representative information and allows models to better predict the species' true habitat use (Leftwich et al. 1997; Boyce 2006). While we did not encounter a limit to downscaling, there should be a point where including information from outside the study area is no longer beneficial. This point is likely to vary from species to species and should be a focus of further research. Finally, the improved performance of our downscaled models could also result from scale-dependent ecological processes directly affecting the strength of habitat-distribution correlations across spatial scales. As we did not test the influence of our predictor variables, we cannot provide further insight, but future work should be aimed at understanding whether habitat factors having variable levels of influence at varying scales. Whether our results are truly an indication of scale dependence in habitat patterns is yet to be determined. Though the influence of scale in ecological processes has long been recognized (e.g., Levin 1992), our results provide a set of nonmutually exclusive and testable hypotheses to disentangle the causes of SDM scalability. Future research could, for example, test for scale dependence in habitat use for each species. If little variance is found between scales, SDM scalability could instead be best explained by sampling and (or) modeling processes. Regardless of the exact mechanism, our results provide an intriguing consideration for the application of SDMs.

Fig. 7. Transferability of species distribution models: specific differences. Data show species-specific differences in predictive accuracy (AUC scores) of distribution models of four species of benthic invertebrates when tested on same-scale geographic areas other than the ones for which they were built. Negative differences indicate a decrease in predictive accuracy compared with the reference model. The boxes are as described in Fig. 3. Groups with the same letters are not significantly different from one another (*p* > 0.05).
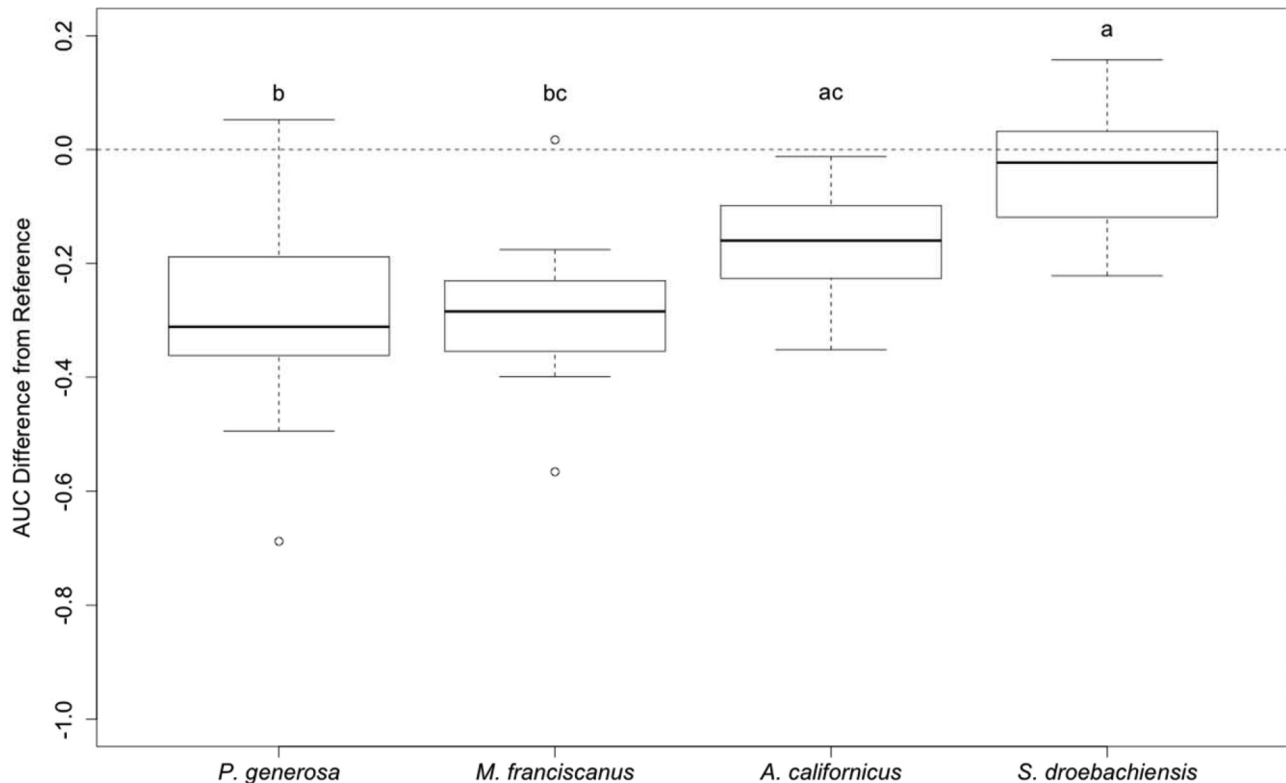
As expected, transferring SDMs to an area that had contributed no survey information resulted in decreased predictive accuracy (Randin et al. 2006; Segurado et al. 2006; Wenger and Olden 2012; Knudby et al. 2013). On average, transferred models had AUC scores of approximately 0.6, which is considered poor predictive accuracy although still slightly better than random. Nearly all same-scale transfer scenarios, whether region-to-region or local-to-local, resulted in declines in predictive accuracy compared with the corresponding reference model. The limited transferability between areas suggests that habitat usage patterns in one region cannot be assumed to be identical in another region (Fodrie and Mendoza 2006; Vasconcelos et al. 2010; García-Roger et al. 2013). Further research could test the relationship between transferability and distance of separation between areas with the expectation that SDMs should transfer better to closer areas compared with geographically distant areas.

Species-specific differences

As more consideration is being given to managing multiple species concurrently (e.g., Zipkin et al. 2010), it is worthwhile considering the similarities and differences of results among our study species. We had predicted that SDMs developed for more specialist species (*P. generosa* and *M. franciscanus*) might be more accurate and easier to transfer and scale than those developed for generalist species (*A. californicus* and *S. droebachiensis*). Our results only support this prediction for species-specific differences in performance of the reference models. Predictive accuracy was poor for *S. droebachiensis* and acceptable for *A. californicus* — the two "generalists" — but good for *P. generosa* and *M. franciscanus*, the two species with qualitatively narrower environmental niches. Our results agree with the past finding that the well-defined and consistent habitat requirements of specialists are easier to identify and to model than those of generalists, which can contain more variability (Brotons et al. 2004; McPherson et al. 2004; Luoto et al. 2005; Hernandez et al. 2006; Evangelista et al. 2008).

The SDMs of specialist species, however, did not consistently perform better than reference models when scaled up or down or when transferred to other geographic areas. While the models for *P. generosa* performed better than those of all other species when upscaled, those of *S. droebachiensis* gained the most accuracy when downscaled and showed better transferability than those of specialist species *P. generosa* and *M. franciscanus*, which had more accurate reference models. The models for *S. droebachiensis* were built using the lowest sample size and might have thus benefited the most from an increase in sample size. Our sample size analysis suggests that model prediction scores can drop significantly when samples are close to those used for the *S. droebachiensis* model at the provincial scale. While past research suggests that our sample sizes were sufficient (Stockwell and Peterson 2002; Hernandez et al. 2006; Wisz et al. 2008), it seems likely that sample size played some role in the low scores for *S. droebachiensis*. Interestingly, the species with the highest AUC scores for reference models (*P. generosa* and *M. franciscanus*) had the largest losses in model performance when transferred. This could indicate that the models of specialist species are less suited to being transferred due to the specialized habitat requirements or that the models built for *P. generosa* and *M. franciscanus* simply had more to lose due to their higher initial AUC scores. To our knowledge, ours are the first comparisons of both scalability and transferability among species in all systems. Further investigation using a broader range of taxa is needed to understand the reasons for species-specific differences in these two important features of SDMs.

Towards improved SDM-based management decisions

Decision-makers must often act without all available information (Soulé 1985). Species distribution models are one tool that

allows managers to extrapolate or interpolate existing occurrence data more quickly and cheaply than by conducting additional surveys. Our study of scalability and transferability of SDMs generates two novel insights that can contribute directly to fisheries management.

We draw two management-relevant conclusions from the scaling results. First, while it is indeed possible to build accurate SDMs for an area as large as the coast of BC, the accuracy of those results might improve by crafting downscaled models. This holds true when taking information from the province-wide level (>100 000 km²) and applying it to fisheries management zones at the local level (800–9000 km²) or at a regional level (25 000–34 000 km²). It also holds true when applying the regional-scale information to the local level. Second, it is not advisable to upscale a model, as much more accurate results can be obtained with reference or downscaled models.

Downscaled models could become a useful tool for management. We have demonstrated that the benefits from downscaled models can be great; in our study the benefit was an increase in AUC of 0.1 on average, up to a maximum of around 0.3, and a minimum accuracy on par with the reference model. The increase in accuracy was maximized when the reference AUC score was low. Therefore, the most appropriate situations in which to apply downscaled models are likely to be those that have the largest room for improvement. The applicability of downscaled models will also largely depend on the costs of additional resources required to survey species over larger scales. Such cost–benefit analysis would have to be conducted on a case-by-case basis.

While upscaled and transferred models had AUC scores that were lower than those of the respective reference models, they still tended to have better than random accuracy (AUC = 0.5). Using either a transferred or upscaled model could allow managers to make relatively informed decisions about the distribution of species in unsurveyed areas. The upscaled models performed, on average, better than the transferred models (approximate average AUC of 0.7 versus 0.6) and could be considered a preferable choice. All due precautions should be taken when applying these transferred or upscaled predictions, but they provide a possible tool to managers when an immediate decision is required and time or money cannot be spent gathering further information.

Data limitations

The main limitations of the data used in our models were the absence of substrate as a predictor variable and the inclusion of nonrandom surveys in our training and testing data sets. Substrate characteristics are known to influence the predictions of species distribution models for aquatic benthic invertebrates (Whitlatch 1981; Jowett et al. 1991; Degraer et al. 2008). Including substrate data in our models might therefore have improved the performance of reference, scaled, and transferred models. Many of the species surveys used in our models were stratified according to known habitat preferences and substrate composition (e.g., soft sediment for geoducks and hard rock for urchins), but substrate data were not collected for all surveys. However, we believe that our models are still appropriate, given the coarse sampling resolution and the use of habitat types for the design of surveys. Substrate was highly likely to be heterogeneous within a cell at the resolution we used (500 m × 500 m) and therefore misrepresented by a single value per cell. Other large-scale modeling projects have also not included substrate (Tittensor et al. 2009) or relied on proxies (e.g., BPI, slope) similar to those used in our study (Wilson et al. 2007). Given that some surveys were biased towards suitable substrates, habitat variables would not provide independent predictors and introduce further biases. Finally, a number of our reference models had very high AUC scores, which suggests that the exclusion of substrate did not hamper our ability to make accurate predictions (most notably for *P. generosa* and *M. franciscanus*). The inclusion of stratified survey data are not

ideal, as it lowers the potential applicability of our models when interpolated or extrapolating into unsurveyed areas. Unfortunately, completely randomized survey data were not available within the same region to test for this potential bias. However, if they were, it would be of great interest to compare species distribution models built with data from random and nonrandom surveys.

We applied large-scale SDMs of four commercially important marine invertebrate species with acceptable and even high levels of accuracy. By building and comparing SDMs using different techniques, at different scales, and with different species, we were able to provide several insights into future SDM applications. The benefits of downscaled models, as well as the accuracy of transferred and upscaled models, should be of particular interest to fisheries and wildlife managers who may encounter similar situations as the ones we examined. Typically, the desired modeling technique will depend on available data, available resources, as well as geographic and biological details. Nevertheless, our results provide immediate information to help make management decisions and suggest further investigation into the mechanisms underpinning the results and their applicability to other species and ecosystems.

Acknowledgements

References

Anderson, R.P., and Gonzalez, I. 2011. Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. Ecol. Model. **222**(15): 2796–2811. doi:10.1016/j.ecolmodel.2011.04.011.

Boyce, M.S. 2006. Scale for resource selection functions. Divers. Distrib. **12**(3): 269–276. doi:10.1111/j.1366-9516.2006.00243.x.

Brotons, L., Thuiller, W., Araújo, M.B., and Hirzel, A.H. 2004. Presence–absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography, **27**: 437–448. doi:10.1111/j.0906-7590.2004.03764.x.

Bureau, D., Hand, C.M., and Hajas, W. 2012. Stock assessment framework for the British Columbian Geoduck Fishery, 2008. Can. Sci. Adv. Sec./Sec. Can. de Con. Sci. **1**: 121.

Campbell, A.R., Harbo, R.M., and Hand, C. 1998. Harvesting and distribution of Pacific geoduck clams, *Panopea abrupta*, in British Columbia. *In* Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management, National Research Council of Canada, Ottawa, Ont. pp. 349–358.

Campbell, J., and Russell, M.P. 2004. Acclimation and growth response of the green sea urchin *Strongylocentrotus droebachiensis* to fluctuating salinity. *In* Proceedings from International Conference on Sea Urchins Fisheries and Aquaculture. Puerto Varas, Chile, 25–27 March 2003. DEStech Publications, Villanova, Pa. pp. 110–117.

Degraer, S., Verfaillie, E., Willems, W., Adriaens, E., Vincx, M., and Van Lancker, V. 2008. Habitat suitability modelling as a mapping tool for macrobenthic communities: an example from the Belgian part of the North Sea. Cont. Shelf Res. **28**: 369–379. doi:10.1016/j.csr.2007.09.001.

DFO. [Pacific Region.] 2013a. Pacific Region integrated fisheries management plan, green sea urchin, September 1, 2013 to August 31, 2016 [online]. Fisheries and Oceans Canada, Ottawa, Ont. Available at http://www.dfo-mpo.gc.ca/Library/348894.pdf.

DFO. [Pacific Region.] 2013b. Pacific Region integrated fisheries management plan, red sea urchin, August 1, 2013 to July 31, 2016 [online]. Fisheries and Oceans Canada, Ottawa, Ont. Available at http://www.dfo-mpo.gc.ca/Library/348758.pdf.

DFO. [Pacific Region.] 2014a. Pacific Region integrated fisheries management plan, sea cucumber by dive, October 1, 2014 to September 30, 2015 [online]. Fisheries and Oceans Canada, Ottawa, Ont. Available at http://www.dfo-mpo.gc.ca/Library/356289.pdf.

DFO. [Pacific Region.] 2014b. Pacific Region integrated fisheries management plan, geoduck and horse clam, January 1 to December 31, 2015 [online]. Fisheries

Pagination not final (cite DOI) / Pagination provisoire (citer le DOI)

12   Can. J. Fish. Aquat. Sci. Vol. 00, 0000

and Oceans Canada, Ottawa, Ont. Available at http://www.dfo-mpo.gc.ca/Library/355041.pdf.

DFO. [Pacific Region.] 2014c. Shellfish Aquaculture License under the Pacific Aquaculture Regulations [online]. Fisheries and Oceans Canada, Ottawa, Ont. Available at http://www.pac.dfo-mpo.gc.ca/aquaculture/licence-permis/docs/licence-cond-permis-shell-coq-eng.pdf.

Doebeli, M., and Dieckmann, U. 2003. Speciation along environmental gradients. Nature, 421: 259–264. doi:10.1038/nature01274. PMID:12529641.

Duprey, N.T. 2011. Sea cucumber biomass estimations from surveys completed June 2009 to May 2010 [online]. Can. Manuscr. Rep. Fish Aquat. Sci. 2954. Available at http://www.dfo-mpo.gc.ca/Library/344269.pdf.

Duprey, N.T. 2012. Sea cucumber biomass estimations from surveys completed June 2009 to May 2010 [online]. Can. Manuscr. Rep. Fish Aquat. Sci. 2960. Available at http://www.dfo-mpo.gc.ca/Library/346266.pdf.

Elith, J., and Leathwick, J.R. 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40: 677–697. doi:10.1146/annurev.ecolsys.110308.120159.

Elith, J., Leathwick, J.R., and Hastie, T. 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77: 802–813. doi:10.1111/j.1365-2656.2008.01390.x. PMID:18397250.

Evangelista, P.H., Kumar, S., Stohlgren, T.J., Jarnevich, C.S., Crall, A.W., Norman, J.B., and Barnett, D.T. 2008. Modelling invasion for a habitat generalist and a specialist plant species. Divers. Distrib. 14: 808–817. doi:10.1111/j.1472-4642.2008.00486.x.

Fodrie, F.J., and Mendoza, G. 2006. Availability, usage and expected contribution of potential nursery habitats for the California halibut. Estuar. Coast. Shelf Sci. 68(1–2): 149–164. doi:10.1016/j.ecss.2006.01.017.

Foreman, M., Crawford, W., Cherniawsky, J., and Galbraith, J. 2008. Dynamic ocean topography for the northeast Pacific and its continental margins. Geophys. Res. Lett. 35(22). doi:10.1029/2008GL035152.

García-Roger, E.M., Sánchez-Montoya, M.D.M., Cid, N., Erba, S., Karaouzas, I., Verkaik, I., Rieradevall, M., Gómez, R., Suárez, M.L., Vidal-Abarca, M.R., and DeMartini, D. 2013. Spatial scale effects on taxonomic and biological trait diversity of aquatic macroinvertebrates in Mediterranean streams. Fund. Appl. Limnol. 183(2): 89–105. doi:10.1127/1863-9135/2013/0429.

Gibson, L.A., Wilson, B.A., Cahill, D.M., and Hill, J. 2004. Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. J. Appl. Ecol. 41: 213–223. doi:10.1111/j.0021-8901.2004.00896.x.

Gontier, M. 2007. Scale issues in the assessment of ecological impacts using a GIS-based habitat model: a case study for the Stockholm region. Environ. Impact Assess. Rev. 27: 440–459. doi:10.1016/j.eiar.2007.02.003.

Gregr, E.J., and Trites, A.W. 2001. Predictions of critical habitat for five whale species in the waters of coastal British Columbia. Can. J. Fish Aquat. Sci. 58(7): 1265–1285. doi:10.1139/f01-078.

Guisan, A., and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8(9): 993–1009. doi:10.1111/j.1461-0248.2005.00792.x.

Guisan, A., Graham, C.H., Elith, J., and Huettmann, F. 2007. Sensitivity of predictive species distribution models to change in grain size. Divers. Distrib. 13: 332–340. doi:10.1111/j.1472-4642.2007.00342.x.

Hand, C., Hajas, W., Duprey, N., Lochead, J., Deault, J., and Caldwell, J. 2008. An evaluation of fishery and research data collected during the phase 1 sea cucumber fishery in British Columbia, 1998 to 2007. Can. Sci. Adv. Sec./Sec. Can. de Cons. Sci. 65: 1–108.

Hernandez, P.A., Graham, C.H., Master, L.L., and Albert, D.L. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography, 29: 773–785. doi:10.1111/j.0906-7590.2006.04700.x.

Hijmans, R.J., and van Etten, J. 2012. raster: geographic analysis and modeling with raster data. R package version 2.0–12.

Hijmans, R.J., Phillips, S., Leathwick, J., and Elithc, J. 2011. dismo: species distribution modeling. R package version 0.7–23.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C., and Guisan, A. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecol. Model. 199: 142–152. doi:10.1016/j.ecolmodel.2006.05.017.

Hobday, A.J., and Hartmann, K. 2006. Near real-time spatial management based on habitat predictions for a longline bycatch species. Fish. Manage. Ecol. 13: 365–380. doi:10.1111/j.1365-2400.2006.00515.x.

Holt, R.D., and Gaines, M.S. 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. Evol. Ecol. 6: 433–447. doi:10.1007/BF02270702.

Jowett, I.G., Richardson, J., Biggs, B.J., Hickey, C.W., and Quinn, J.M. 1991. Micro-habitat preferences of benthic invertebrates and the development of generalised Deleatidium spp. habitat suitability curves, applied to four New Zealand rivers. N.Z. J. Mar. Freshw. 25(2): 187–199.

Karl, J.W., Heglund, P.J., Garton, E.O., Scott, J.M., Wright, N.M., and Hutto, R.L. 2000. Sensitivity of species habitat-relationship model performance to factors of scale. Ecol. Appl. 10: 1690–1705. doi:10.1890/1051-0761(2000)010[1690:SOSHRM]2.0.CO;2.

Kato, S., and Schroeter, S.C. 1985. Biology of the red sea urchin, Strongylocentrotus franciscanus, and its fishery in California. Mar. Fish. Rev. 47: 1–20.

Keitt, T.H., Bivand, R., Pebesma, E., and Rowlingson, B. 2011. rgdal: bindings for the geospatial data abstraction.

Knudby, A., Kenchington, E., and Murillo, F.J. 2013. Modeling the distribution of Geodia sponges and sponge grounds in the Northwest Atlantic. PloS ONE, 8(12): e82306. doi:10.1371/journal.pone.0082306. PMID:24324768.

Lamb, A., and Hanby, B.P. 2005. Marine life of the Pacific Northwest: a photographic encyclopedia. Harbour Publishing, Madeira Park, B.C., Canada.

Lauzon-Guay, J.S., and Scheibling, R.E. 2007. Seasonal variation in movement, aggregation and destructive grazing of the green sea urchin (Strongylocentrotus droebachiensis) in relation to wave action and sea temperature. Mar. Biol. 151: 2109–2118. doi:10.1007/s00227-007-0668-2.

Leftwich, K.N., Angermeier, P.L., and Dolloff, C.A. 1997. Factors influencing behavior and transferability of habitat models for a benthic stream fish. Trans. Am. Fish. Soc. 126(5): 725–734. doi:10.1577/1548-8659(1997)126<0725:FIBATO>2.3.CO;2.

Leslie, H., Ruckelshaus, M., Ball, I.R., Andelman, S., and Possingham, H.P. 2003. Using siting algorithms in the design of marine reserve networks. Ecol. Appl. 13: 185–198. doi:10.1890/1051-0761(2003)013[0185:USAITD]2.0.CO;2.

Leus, D., Campbell, A., Merner, E., Hajas, W.C., and Barton, L.L. 2014. Framework for estimating quota options for the Red Sea Urchin (Strongylocentrotus franciscanus) fishery in British Columbia using shoreline length and linear density estimates. DFO Can. Sci. Adv. Sec./Sec. Can. de Con. Sci. 94.

Levin, S.A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. Ecology, 73: 1943–1967. doi:10.2307/1941447.

Loiselle, B.A., Howell, C.A., Graham, C.H., Goerck, J.M., Brooks, T., Smith, K.G., and Williams, P.H. 2003. Avoiding pitfalls of using species distribution models in conservation planning. Conserv. Biol. 17: 1591–1600. doi:10.1111/j.1523-1739.2003.00233.x.

Louzao, M., Hyrenbach, K.D., Arcos, J.M., Abelló, P., Sola, L.G.D., and Oro, D. 2006. Oceanographic habitat of an endangered Mediterranean procellariiform: implications for marine protected areas. Ecol. Appl. 16: 1683–1695. doi:10.1890/1051-0761(2006)016[1683:OHOAEM]2.0.CO;2. PMID:17069363.

Luna-Herrera, J., Martinez-Cabrera, G., Parra-Maldonado, R., Enciso-Moreno, J.A., Torres-Lopez, J., Quesada-Pascual, F., Delgadillo-Polanco, R., and Franzblau, S.G. 2003. Use of receiver operating characteristic curves to assess the performance of a microdilution assay for determination of drug susceptibility of clinical isolates of Mycobacterium tuberculosis. Eur. J. Clin. Microbiol. 22: 21–27. doi:10.1007/s10096-002-0855-5.

Lundblad, E., Wright, D.J., Miller, J., Larkin, E.M., Rinehart, R., Battista, T., Anderson, S.M., Naar, D.F., and Donahue, B.T. 2006. A benthic terrain classification scheme for American Samoa. Mar. Geod. 29(2): 89–111. doi:10.1080/01490410600738021.

Luoto, M., Pöyry, J., Heikkinen, R.K., and Saarinen, K. 2005. Uncertainty of bioclimate envelope models based on the geographical distribution of species. Glob. Ecol. Biogeogr. 14: 575–584. doi:10.1111/j.1466-822X.2005.00186.x.

McPherson, J., Jetz, W., and Rogers, D.J. 2004. The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? J. Appl. Ecol. 41: 811–823. doi:10.1111/j.0021-8901.2004.00943.x.

Morris, D.W. 1987. Ecological scale and habitat use. Ecology, 68: 362–369. doi:10.2307/1939267.

Paltzat, D.L., Pearce, C.M., Barnes, P.M., and McKinley, R.S. 2008. Growth and production of California sea cucumbers (Parastichopus californicus, Stimpson) co-cultured with suspended Pacific oysters (Crassostrea gigas, Thunberg). Aquaculture, 275: 124–137. doi:10.1016/j.aquaculture.2007.12.014.

Phillips, S.J., Anderson, R.P., and Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190: 231–259. doi:10.1016/j.ecolmodel.2005.03.026.

R Core Team. 2013. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/.

Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M., and Guisan, A. 2006. Are niche-based species distribution models transferable in space? J. Biogeogr. 33: 1689–1703. doi:10.1111/j.1365-2699.2006.01466.x.

Ridgeway, G. 2006. Gbm: generalized boosted regression models. R package version 1.5-7 [online]. RAND Statistics Group, Santa Monica, California. Available from https://github.com/harrysouthworth/gbm.

Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecol. Appl. 9: 135–151. doi:10.1890/1051-0761(1999)009[0135:IOSSTH]2.0.CO;2.

Scheibling, R., and Hatcher, B. 2001. The ecology of Strongylocentrotus droebachiensis. Dev. Aquacult. Fish. Sci. 32: 271–306. doi:10.1016/S0167-9309(01)80018-1.

Segurado, P., Araújo, M.B., and Kunin, W.E. 2006. Consequences of spatial autocorrelation for niche-based models. J. Appl. Ecol. 43: 433–444. doi:10.1111/j.1365-2664.2006.01162.x.

Soulé, M.E. 1985. What is conservation biology? A new synthetic discipline addresses the dynamics and problems of perturbed species, communities, and ecosystems. BioScience, 35(11): 727–734.

Stickle, W.B., and Diehl, C.J. 1987. Effects of salinity on echinoderms. Echino. Stud. 2: 235–285.

Stockwell, D.R., and Peterson, A.T. 2002. Effects of sample size on accuracy of species distribution models. Ecol. Model. 148: 1–13. doi:10.1016/S0304-3800(01)00388-X.

Tittensor, D.P., Baco, A.R., Brewin, P.E., Clark, M.R., Consalvey, M., Hall-Spencer, J., Rowden, A.A., Schlacher, T., Stocks, K.I., and Rogers, A.D.

2009. Predicting global habitat suitability for stony corals on seamounts. J. Biogeogr. **36**(6): 1111–1128. doi:10.1111/j.1365-2699.2008.02062.x.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., and De Clerck, O. 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Glob. Ecol. Biogeogr. **21**: 272–281. doi:10.1111/j.1466-8238.2011.00656.x.

Vasconcelos, R.P., Reis-Santos, P., Maia, A., Fonseca, V.F., França, S., Wouters, N., Costa, M.J., and Cabral, H.N. 2010. Nursery use patterns of commercially important marine fish species in estuarine systems along the Portuguese coast. Estuar. Coast. Shelf Sci. **86**: 613–624. doi:10.1016/j.ecss.2009.11.029.

Waddell, B.J., and Perry, R.I. 2007. Survey results of green sea urchin (*Strongylocentrotus droebachiensis*) populations in Queen Charlotte Strait, British Columbia, October, 2006 [online]. Canadian Technical Report of Fisheries and Aquatic Sciences 2742. Available from http://www.dfo-mpo.gc.ca/Library/330497.pdf.

Waddell, B.J., Perry, R.I., Scharf, G., Ross, G. 1997. Surveys on green sea urchin (*Strongylocentrotus droebachiensis*) populations in Queen Charlotte Strait, British Columbia, October 1995 and March 1996. Canadian Technical Report of Fisheries and Aquatic Sciences 2143.

Wenger, S.J., and Olden, J.D. 2012. Assessing transferability of ecological models:

an underappreciated aspect of statistical validation. Methods Ecol. Evol. **3**: 260–267. doi:10.1111/j.2041-210X.2011.00170.x.

Whitlatch, R.B. 1981. Animal-sediment relationships in intertidal marine benthic habitats: some determinants of deposit-feeding species diversity. J. Exp. Mar. Biol. Ecol. **53**: 31–45. doi:10.1016/0022-0981(81)90082-4.

Wilson, M.F., O'Connell, B., Brown, C., Guinan, J.C., and Grehan, A.J. 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Mar. Geod. **30**: 3–35.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., and Guisan, A. 2008. Effects of sample size on the performance of species distribution models. Divers. Distrib. **14**: 763–773. doi:10.1111/j.1472-4642.2008.00482.x.

Zacharias, M.A., Howes, D.E., Harper, J.R., and Wainwright, P. 1998. The British Columbia marine ecosystem classification: rationale, development, and verification. Coast. Manage. **26**: 105–124. doi:10.1080/08920759809362347.

Zipkin, E.F., Royle, J.A., Dawson, D.K., and Bates, S. 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. Biol. Conserv. **143**: 479–484. doi:10.1016/j.biocon.2009.11.016.