SNOOK, M. Roxanne[1, 5], MAGEROY, Jon[1, 4, 6], PITHER, Jason[1,3, 7], CURTIS, Jeff[1, 8], NIELD, Lora[2], and WALKER, Ian R.[1,3, 9]

[1]Department of Earth, Environmental and Geographic Sciences, Okanagan Campus, University of British Columbia, 3333 University Way, Kelowna, British Columbia, Canada V1V 1V7

[2]Penticton Office, Ministry of Forests, Lands, Natural Resource Operations and Rural Development (MFLNRORD), 102 Industrial Place, Penticton, British Columbia, Canada V2A 7C8. E-mail: lora.nield@gov.bc.ca

[3] Department of Biology, Okanagan Campus, University of British Columbia, 3187 University Way, Kelowna, British Columbia, Canada V1V 1V7

[4]Landscape Ecology, Norwegian Institute for Nature Research, Gaustadalléen 21, 0349 Oslo, Norway

Modeling Habitat Suitability for the Rocky Mountain Ridged Mussel (*Gonidea angulata* Lea) in Okanagan Lake, British Columbia, Canada

Running footer: Modeling Rocky Mountain Ridged Mussel Habitat Suitability

2 tables, 3 figures

[5]Author to whom correspondence should be addressed. E-mail: Roxanne@pearsonecological.com

[6]E-mail address: Jon.mageroy@nina.no

[7]E-mail address: Jason.pither@ubc.ca

[8]E-mail address: Jeff.curtis@ubc.ca

[9]E-mail address: Ian.walker@ubc.ca

Abstract

Once common throughout surface waters west of the Rocky Mountains, the Western Ridged Mussel (*Gonidea angulata* Lea) has been extirpated throughout much of its range, and is currently listed as endangered in Canada (COSEWIC 2010), where its northernmost occurrences are thought to be in Okanagan Lake within the southern interior of British Columbia. Recovery plans are legally required for listed species. For *G. angulata,* recovery planning is a substantial challenge as little is known about its habitat requirements, particularly within lakes. Consequently, we conducted snorkel surveys of more than 70 km of potential shoreline habitat within Okanagan Lake, combined our survey data with extensive ancillary habitat data, and developed habitat suitability models using two complementary classification methods based on the RandomForest algorithm. Our surveys revealed 25 local occurrences, 6 of which were previously unknown. Both classification methods ranked the top four predictor variables as effective fetch between 1 and 2.25 km, medium-high embeddedness of substrates (%), high proportion of sand in the substrate, and low slope (0-20 %). In comparison, *G. angulata* habitat in river systems have been described as having low sediment accumulation, boulders that offer refuge, low flow variability, and bank stability. The best model achieved a misclassification rate of 24.2 %, and is currently being used by government ministries to improve the species' management in the Okanagan Valley.

Keywords: *Gonidea angulata*, freshwater mussel, habitat suitability, conservation, ecological modelling

Introduction

Freshwater mussels are among the most endangered animal taxa in North America, as ca. 70% of species are either extinct or are designated under national species-at-risk legislation (Bogan 1993, Williams et al. 1993, Neves et al. 1997, Lydeard et al. 2004). *Gonidea angulata* Lea, the Western Ridged mussel (also known as the Rocky Mountain ridged mussel; family Unionidae), is an aquatic mollusc native to North America west of the Rocky Mountains. *G. angulata* is listed as Red and imperiled (S2) in the British Columbia provincial conservation priority framework (BC Conservation Data Centre 2015 a, b), nationally listed as both a species of special concern (SARA 2016) and endangered (COSEWIC 2010). There are no legal implications for the provincial listings of Red and imperiled species, no legal consequences to COSEWIC listings, and general prohibitions under SARA do not apply to species of special concern. Therefore, despite these listings, there are no legal protections which target the conservation of habitat for this species.

Once prevalent from British Columbia (BC), south to California and eastward to Idaho and Nevada, *G. angulata* has been largely extirpated from its original range for reasons including, but not limited to, human development, industrial contamination of waterways, habitat loss, invasive species, and loss of host fish (Downing et al. 2010, Jepsen et al. 2010, Stanton et al. 2012). Similar pressures have negatively impacted other freshwater mussels in North America (e.g., Bauer 1988, Dudgeon 2006, Downing et al. 2010) highlighting the need for increased efforts on the part of researchers and policy makers, alike, to devise successful conservation management strategies for mussel taxa (Fisheries and Oceans Canada 2010, 2011). This requires reliable information regarding the habitat requirements and preferences of the target species (Fisheries and Oceans Canada 2010, 2011, Stanton et al. 2012). Similar to many threatened or endangered freshwater mussel species (Salmon and Green 1983, Howard and Cuffey 2003, Harriger et al. 2009), details concerning the habitat requirements and preferences of *G. angulata* are largely unknown, especially in lakes.

Most studies of *G. angulata* habitat requirements pertain to riverine environments (e.g., Vannote and Minshall 1982, Allen and Vaughn 2009, Daraio et al. 2012, Davis et al. 2013). In river habitats, important habitat characteristics include low hydraulic variability, flow refugia (i.e., boulders), stable substrate, substrate size and distribution, and low sediment accumulation (e.g., Vannote and Minshall 1982, Allen and Vaughn 2009, Daraio et al. 2012, Davis et al. 2013). River and lake environments are inherently very different, although some of these river characteristics and their functional significance may be transferable to understanding lake environments. Overall, these attributes offer little insight regarding *G. angulata's* lacustrine distribution or habitat requirements.

It is likely there will be many key factors defining the distribution of this species in lakes, and the relative importance of each attribute is likely to vary with spatial scale. On a global scale, climate, and dispersal barriers, as well as distribution of host fish (Vaughn and Taylor 2000, Schwalb et al. 2013) likely govern freshwater mussel distributions. At somewhat smaller regional scales, these limiting factors may include hydraulic habitat, fish community structure, geology, water chemistry, cold summer temperatures, high summer temperatures, and land use (e.g., affecting water runoff) (Strayer 1983, Vaughn and Taylor 2000, Arbuckle and Downing

2002, Schwalb et al. 2013). At yet smaller local scales, within lake shorelines or stream segments, the dominant influence may be substrate size distribution and embeddedness, presence or absence of macrophytes, and flow refugia (Strayer 2014).

Unionids, including *G. angulata*, spend a large part of their lives either completely or partially buried within substrates. Fine substrates are necessary for mussels to bury in and to anchor successfully (Vannote and Minshall 1982), but oxygen must also be able to permeate this substratum. In high-energy environments where water turbulence and scouring forces increase substrate mobility, stable refugia are required to protect mussels from becoming dislodged or crushed by cobbles (Davis et al. 2013). Thus, factors which affect substrate composition and mobility (e.g., fetch, slope) will also directly or indirectly impact mussel distribution (Cyr 2009, Davis et al. 2013).

During early stages in their development, freshwater Unionoidea (hereafter referred to as mussels) are obligate parasites on fish (Bogan 1993, Vaughn and Taylor 2000). Field data from Okanagan Lake suggests the primary host fish for *G. angulata* in this system are sculpin (*C. asper* Richardson, 1836 and/or *C. cognatus* Richardson, 1836) (Mageroy et al. 2015), but potential host species may also include Longnose Dace (*Rhinichthys cataractae* Valenciennes, 1842), Leopard Dace (*R. falcatus* Eigenmann and Eigenmann, 1893) and Northern Pikeminnow (*Ptychocheilus oregonensis* Richardson, 1836) (Stanton et al. 2012, Mageroy 2015).

Here, we use extensive field survey data to develop a habitat suitability model for *G. angulata* in Okanagan Lake, from remnant populations (Figure 1; COSEWIC 2010, Stanton et al. 2012). Our primary objective is to inform conservation management efforts. The ability to predict which sites offer the most favorable conditions for *G. angulata* will be particularly useful for potential preservation or relocation of mussels, and will increase the effectiveness of future mussel surveys. We also seek a better understanding of *G. angulata's* ecology, and in particular the factors that influence its geographic distribution. This paper presents the first habitat suitability study of *G. angulata* in a lake environment.

Methods

Study Area

The Okanagan Valley is a semi-arid region in British Columbia, with precipitation ranging from 27.5 cm/yr in the south to 44 cm/yr in the north. Extreme high summer air temperatures reach 41°C and extreme winter cold temperatures can reach -27°C (Stockner and Northcote 1974).

Okanagan Lake (50°0'N, 119°30'W) is long and narrow, approximately 120 km long and ca. 3.5 km (average) wide (Figure 1; Stockner and Northcote 1974). Its watershed encompasses 6178 km^2 (Roed 1995). The lake has a maximum depth of 232 m and an average depth of 76 m (Stockner and Northcote 1974).

It is a warm monomictic lake (Stockner and Northcote 1974), with surface water temperatures ranging from 1.7 to 23.0°C (Mackie 2010). Lake level fluctuates annually from ± 0.5 m to ± 0.9 m (in 2009 - 2010; Stanton et al. 2012). It is an oligotrophic lake (Stockner and Northcote 1974), with high dissolved oxygen, calcium and alkalinity, and low total nitrogen and phosphorus (Mackie 2010, BC Ministry of Environment 2001). Water pH is circum-neutral to alkaline (pH 7.9 to 8.7) with specific conductance ranging from about 220 to 330 µS/cm (e.g., Pinsent and Stockner 1974). The water residence time is very long (approximately 60 to 70 years). Shoreline length is 290 km.

Site selection

Habitat suitability models are composed of explanatory variables, which can predict the occurrence of a species. While many variables may be measured, an *a priori* approach can enable data reduction for model construction. Therefore, a Delphic approach (i.e., eliminating variables based on expert opinion and scientific literature) was implemented to choose a subset of variables for site selection within Okanagan Lake. Prior to site selection and new surveys, five persons with relevant professional expertise (Jon Mageroy, Norwegian Institute for Nature Research, personal communication., Ian Walker, University of British Columbia, Kelowna, B.C., personal communication., Jeff Curtis, University of British Columbia, Kelowna, B.C., personal communication., Robert Plotnikoff, Tetra Tech. Inc., Bellevue, WA. personal communication, and Shelly Miller, Oregon Department of Fish and Wildlife, Corvallis, OR. personal communication) were consulted to identify a subset of variables likely to be key determinants of *G. angulata's* distribution in Okanagan Lake. This Delphic approach enabled a stratified random sampling design to increase the likelihood of observing this species. The sites selected were distributed throughout Okanagan Lake, to make the model inclusive of all potential habitat types.

For the model, 25 sites were included where *G. angulata* was already known to be present as of 2016. The variables identified by the expert consultation process were then used to generate 20 additional sites, selected in accordance with a stratified random design. GIS (ESRI, 2011) was used to locate these sites. This resulted in forty-five sites along Okanagan Lake that were chosen (spatially random) for this project, to gain a complete representation of the lake's habitat. Sites were selected on either side of the lake and in the north, central and southern sections of the lake.

Habitat characteristics

Most of the variables included in the model came from pre-existing Foreshore, Inventory and Mapping (FIM) data from Okanagan Lake (Schleppe and Mason 2009), and included: percentages of boulder, sand, embeddedness, and foreshore slope. To better characterize the sites, several new variables were added to supplement the FIM data. These included the biotic attribute host fish presence and several abiotic attributes. Abiotic attributes consisted of total fetch, geomorphic description (e.g., cuspate foreland, alluvial fan, crag, beach, bay, cove, breakwater, bank, and a river mouth), presence of an underwater ledge, shoreline morphometry (i.e., degree of concavity/convexity), clay, and depth of dissolved oxygen penetration into substrate.

Fetch is a measure of site exposure to predominant winds (Hakanson 1981, Callaghan et al. 2015). Effective fetch, also known as total fetch, was included in the data as a proxy for wave action, turbulence, disturbance, nutrient movement, and dissolved oxygen at each site (Hakanson 1977, Cyr 2009), and was calculated using the Wind Fetch Tool. Atmospheric data from government weather stations (www.windfinder.com) were collected for five stations bordering Okanagan Lake describing average historical wind origins. Fetch was calculated as a weighted average fetch for each season (spring, summer, autumn, and winter). The lake surface is well-mixed throughout the year and water chemistry was not incorporated into the study.

Mussel and host fish surveys

Surveys to detect previously unknown *G. angulata* populations (presence/not detected) were conducted according to standard methods for rare freshwater mussel species (Smith 2006, Mackie et al. 2008, Stanton et al. 2012). A minimum of two snorkelers swimming beside each other, made parallel sweeps along the shoreline. Sweeps progressed to greater depths once the entire length of the site was reached. Maximum survey depth was approximately 4 m. Presence/not detected data on *G. angulata* were recorded. Presence/not detected observations of primary host fish sculpin (*Cottus* spp.), were also noted during the surveys. Other fish species in Okanagan Lake were not included in our surveys, because our focus was on the primary host.

Constructing the habitat suitability model

Two classification packages using random forests (RF) in R 3.1.2 (R Core team, 2014) were used to generate a habitat suitability model; RF and Party packages. RF can be used for both classification and regression to derive habitat suitability models (Breiman 2001, Grömping 2009, Chen and Ishwaran 2012). RF can identify ecologically important variables for interpretation (Cutler et al. 2007) and can be very useful for determining ecologically important predictors. RF accounts for correlations and variable interactions, and ranks interactions between variables by importance (Chen and Ishwaran 2012). The popularity of this algorithm is attributed to its ability to incorporate large numbers of variables with small sample sizes, and in addition output a valid assessment of variable importance (Grömping 2009, Buechling and Tobalske 2011, Chen and Ishwaran 2012).

A RF is created by hundreds to thousands of trees which branch from a bootstrap sample (approximately two-thirds) of the original data (Breiman 2001, Chen and Ishwaran 2012). The first randomized step of RF occurs when predictor variables are chosen randomly from a given number of variables denoted by the 'mtry' tuning parameter, which are then used to create a tree derived from the partitioned response variable (i.e., considering one variable at a time) (Genuer et al. 2010, Murphy et al. 2010). The second layer of randomization occurs at the nodes, where RF selects a random subset of variables in which to create the next node, rather than using the entire dataset (Chen and Ishwaran 2012). The hundreds to thousands of trees comprise the forest. Trees are then combined into a single prediction, which is used to rank variable importance (Murphy et al. 2010). The Party and RF packages were used to both create forests and rank variables by importance. The RF package was also used to visualize the effects of each variable on the probability of *G. angulata* occurrence (Figure 2).

The main tuning parameter in RF models is the ‘mtry’ function, which dictates how many “randomly preselected predictor variables” are used to create each split in a node in a classification tree (Breiman 2001, Strobl et al. 2009). Multiple models, listed below, were run as iterations with data reductions and ‘mtry’ ranging for each series from 2 (minimum mtry) to 6.

The RF package iterations were run to produce a model with the lowest average misclassification rate (Grömping 2009, Strobl et al. 2009), by tuning the mtry parameter. Each model run generated 5000 trees of 100 iterations each. The data was also run through the classification package Party, developed by Hothorn et al. (2006), to assess correlation among predictor variables and to facilitate a comparison of results between the two classification packages.

The RF package outputs were used to create variable partial dependence plots. Partial dependence plots illustrate the probability of *G. angulata* occurrence based on one predictor variable in the best model, after averaging out the effects of all other predictor variables (Cutler et al. 2007). In the partial dependence plots the y-axis is a logit function, which is the log of the odds (probability/ 1-probability). The x-axis is the independent predictor variable.

Variable importance was assessed using the mean decrease in accuracy (MDA). The MDA for each variable was determined by normalizing the difference between the classification accuracy for variable data 'observed' and the classification accuracy for the variable randomly permuted (Cutler et al. 2007). The higher the value of the mean decrease in accuracy, the more important the variable is within the classification (Cutler et al. 2007).

The optimal model was used to generate a vector map of mussel habitat distribution from FIM data using QGIS 2.18.7. Layers used within the FIM included the most favorable habitat ranges of embeddedness, slope, sand, and boulders, in addition to a 'mussels' (known presence) layer.

Results

Both classification methods (using the randomforest and party packages) consistently ranked the same four predictors as most important (listed from most important to least important): embeddedness of substrates, sand occurrence, total fetch, and foreshore slope (Table 1). Within the Party models, boulder occurrence was determined to be a correlated variable, but was an important predictor within the RF models. The probability of *G. angulata* occurrence based on each predictor variable is highest in sites with medium embeddedness, high sand, fetch between 1 - 2.5 km, and consists of a bench type slope (Figure 2). While many other variables (e.g., gravels and cobbles; fine – coarse grain sizes, aquatic vegetation, groynes, cliffs, littoral zone width, docks, etc.) were incorporated into preliminary models, these were not influential in explaining *G. angulata's* distribution in Okanagan Lake.

Discussion

Since the review and subsequent status of *G. angulata* as imperiled and a species of special concern, governments at different levels have to be aware of, and interested in, conservation of this species. Conservation should be science based, yet up to this point very little was known about *G. angulata's* lacustrine habitat requirements.

Geomorphic and Biotic controls of G. angulata

The most important habitat variables for *G. angulata*, as identified by both models, were high embeddedness (>75%), sand (>20%), followed by total fetch (>1 km and < 2.25 km), and bench or low slope. In addition, the RandomForest model included boulders as an important variable; the Party model did not. These results support our *a priori* hypotheses (i.e., that *G. angulata* is not distributed randomly; substrate type, low-moderate slope, and fetch are identified as useful predictors of *G. angulata* occurrence). Interestingly, low embeddedness was negatively associated with *G. angulata* habitat, thus this habitat characteristic was not included in the final model.

Embeddedness is often used to assess macroinvertebrate habitat (Sylte and Fischenich 2002). Our results show that medium-to- high embeddedness is a positive attribute, while low embeddedness is a negative habitat attribute for *G. angulata* in Okanagan Lake. We were surprised by the positive impact of high substrate embeddedness (70-100%). High embeddedness could result in the clogging of mussel gills; thus, it is not necessarily associated positively with *G. angulata* in river habitats (Bogan 1993, Brim Box et al. 2002). Organic matter may be included in the fine sediment components contributing to embeddedness and, through decomposition, may institute a locally hypoxic or anoxic environment in the sediments. Thus, high embeddedness often limits the areal extent of habitat within which many fish, macroinvertebrates and periphyton may live (Sylte and Fischenich 2002).

The difference in the embeddedness effect between studies might be explained by the very different hydrodynamic properties of these systems. In lotic environments, water movement enables finer sediments and organics to continually move downstream, delivering a constant supply of food to mussels. In lentic habitats, significant wind and wave action is required to transport these fine materials. Higher embeddedness in

Okanagan Lake, could be associated by higher food availability; lower embeddedness (0-20%) may be associated with lower food availability. In addition, since Okanagan Lake is exposed and well-mixed (pers. obs.), high oxygen concentrations are maintained throughout the littoral benthic environment. Thus, oxygen depletion in areas with high embeddedness may not be a problem in Okanagan Lake. The texture of the embedding materials may also be important. It would be useful to contrast sites where the embedding materials are coarse (sand) versus fine (clay/silt) sediments.

Medium or high embeddedness may also be associated with greater sediment stability in low energy environments (Brim Box et al. 2002). *G. angulata* has a well-developed siphon and individual mussels appear to maintain a mostly buried positioned where filtering functions may be little affected; thus, making them suitable inhabitants of fine sediment and sand (Vannote and Minshall 1982).

In agreement with earlier studies, in the absence of sand, there was zero likelihood of finding *G. angulata* in Okanagan Lake. Vannote and Minshall (1982) noted an increasing sand component was positively associated with *G. angulata* habitat. Sand provides a suitable medium within which *G. angulata* may bury (Vannote and Minshall 1982, COSEWIC 2003, Davis et al. 2013, Strayer 2014) without inhibiting their movement. Sand will also more readily allow oxygen to penetrate into the substrate, whereas clay or silt will impose a barrier preventing oxygen exchange with overlying water. High amounts of sand and medium embeddedness do not appear to negatively impact *G. angulata* (pers. obs.).

The positive association of mussels with boulders can be explained via their functionality, but their presence is not an essential part of suitable habitat at each site (Snook 2017a, b). The positive association with boulders may be explained by the fact that they provide micro-eddy environments beneath them, supplying oxygen and organic matter and a depositional environment suitable for anchoring the mussel (Davis et al. 2013), or possibly that they impeded the ability of invasive macrophyte management via rototilling, thus offering the mussels refuge from this activity. Boulders function as refuge from predators (and possibly rototilling), shear stress and scouring. However, boulders were found to be a highly correlated variable, adding instability to the model in RandomForest, and were not included in the Party output (Table 1) (Snook 2017a, b). The importance of boulder occurrence likely depends on site exposure. We infer that microhabitats among boulders may be more important at sites with higher effective fetch.

Our results show that a fetch between ca. 1 km and 2.25 km is most favorable for *G. angulata,* while the probability of *G. angulata* occurrence decreases at shorter and longer fetches (Figure 2). This suggests a moderately energetic environment is most suitable for these mussels.

Due to the spatial generalizations involved in converting between raster and vector formats during the implementation of the wind fetch tool, fetch could not be calculated for twelve sites (Munshaw 2016). These sites are classified as unknown for how they fit the model. Of these sites, five contain top predictor categories, suggesting they may offer suitable habitat for *G. angulata* (Table 2, Figure 3).

Fetch may also serve as a proxy for longshore current velocities. Elsewhere, *G. angulata* is principally a riverine species (Frest and Johannes 1995, Taylor 1981, Nedeau *et al.*2005); lentic populations may be associated with exposed sites where wind and waves yield analogous conditions. Longshore currents are expected to be stronger, and waves action greater, both at the surface and internally (in the thermocline), at the most exposed sites (greatest fetch).

Currents and wave action also shape the patterns of erosion and sediment redistribution in lakes, and thus the embeddedness and substrate composition at each site. A very long fetch can contribute to scouring, bed shear stress, excess turbulence, and removal of the fine sediments necessary for burying mussels, ultimately promoting substrate instability (Hakanson 1977, Cyr 2009). Mussels, especially the juvenile mussels, may be eroded and transported away from exposed sites during scouring events (Cyr 2009, Davis et al. 2013) or crushed by the large, mobile substrate elements (Strayer 1999).

Rocky shorelines, boulders and cobbles are expected to prevail at exposed sites; fine sediments and organic matter will accumulate in lower energy environments (Hakanson 1977). Exposed, high energy sites (large fetch) may enhance the delivery of food (plankton), nutrients, and dissolved oxygen to littoral benthic communities (e.g., Cyr 2009). It is likely these effects explain the relationship between fetch and *G. angulata* occurrence in Okanagan Lake (Figure 2). At a fetch lower than 1 km, the lower probability of *G. angulata* occurrence may be attributable to a reduced supply of food (plankton), nutrients, and dissolved oxygen. Very few sites exist in Okanagan Lake with fetch lower than 1 km (10 sites exist), which may also explain why it is unlikely mussels are found at these locations. At exposures greater than 2.25 km increased turbulence results in removal of fine substrates, substrate instability and, potentially, direct damage to and/or dislocation of the mussels. In Okanagan Lake, the "Goldilocks" zone in terms of fetch appears to lie between 1 and 2.25 km, where fetch is sufficient to supply food, oxygen and nutrients, without excessive scouring of the shoreline.

We found that a bench feature or low slope was positively associated with *G. angulata* occurrence (e.g., bench vs. slope > 60%). The importance of 'bench' and 'low' gradient sites for *G. angulata* occurrence may be linked to the turbulence arising from waves as they interact with the lake bottom. Wind and waves interact differently at sites with different littoral slopes. At steeper sites no fine material is deposited (Hakanson 1977). At lower slopes waves tend to break farther offshore, and macrophyte beds may increase substrate stability. In addition, *G. angulata* need an environment where anchorage is accessible (i.e., fine material is present within an optimal fetch range), food is available, and oxygen is delivered to the benthic community.

Surprisingly, we found no impact of sculpin presence/absence on the occurrence of *G. angulata*. Unionid distribution is passive and generally limited by host fish movement (Kat 1984). Therefore, host fish presence and movement potentially have important implications for *G. angulata*. In Okanagan Lake *G. angulata* glochidia have been found to encyst on several species of fish (Stanton et al. 2012, Mageroy 2015). However, prevalence (i.e., of a fish species) and intensity (i.e., number of encysted glochidia on gills) data suggest that sculpin (*Cottus* spp.) are the most important hosts. Currently, since sculpin occur at all sites surveyed, there is no evidence that host fish availability is limiting *G. angulata* in Okanagan Lake.

Management implications

Sites with the top four predictor variables for *G. angulata* occurrence are considered the best fit with this model, and top priority for conservation within Okanagan Lake (Table 2, Figure 3; Red). Of these ten sites, three sites are known to contain *G. angulata* (located in Summerland, BC). Note that all the sites within Okanagan Lake, with the exception of one site (in Penticton, date of occurrence unknown), are recent (2005-2015) records (Snook 2017a). There are existing foreshore segments which are currently protected (Figure 3), and overlap with many, but not all of the occurrences of *G. angulata*.

Like most animals, these mussels have ranges within these important habitat characteristics that are tolerable. For example, even though a medium embeddedness measure at a site is the best predictor for this species, high embeddedness sites also positively predict mussel occurrence (Figure 2). Therefore, sites with appropriate categorical and fetch values should also be considered a good model fit, and high priority habitat for ground-truthing for this mussel. Sites that contain combinations of these ranges (Figure 2) Medium-High embeddedness, Medium and Very High sand, fetch > 1.0 km and < 2.25 km, with Low slope are considered good model fit and high priority habitat (Table 2). Sites that were not ranked as best fit, good fit, or unknown were listed as low priority for the rest of Okanagan Lake.

Sites which contain the most favorable ranges of important variables (i.e., are ranked as best and good model fit), are recommended for ground-truthing of this species (Table 2). These sites are situated throughout the length of the lake (Figure 3). Additionally, it is recommended that the sites of unknown fetch values (Table 2) should be considered potentially suitable habitat and should be surveyed for *G. angulata*. Sites with the best model fit are recommended as locations for preservation, while the new occurrences of *G. angulata* should be included in the protected foreshore.

Acknowledgments

Extensive field work was conducted by Steven Brownlee (University of British Columbia, Okanagan; UBCO) and Jerry Mitchell (BC Ministry of Environment; MOE). Editing and comments were provided by Sean MacConnachie (Fisheries and Oceans Canada; DFO) and Greg Wilson (MOE). We thank MOE for sharing the Wind Fetch Tool data for fetch values for the entire circumference of Okanagan Lake. Robin Munshaw (Simon Fraser University) was the Geographic Information Systems technician who implemented the wind fetch tool in GIS 10.0. Financial support was provided by BC Ministry of Forests, Land, Natural Resource Operations, and Rural Development; MFLNRORD, the Pacific Northwest Shell Club, and the University of British Columbia.

Author contributions include snorkel surveys, literature review, and writing the statistical models (Roxanne), snorkel surveys and manuscript edits (Jon Mageroy), manuscript edits and scientific advice (Jeff Curtis), in addition to those, both Ian Walker and Jason Pither provided lab and office space. Jason Pither wrote the sensitivity analysis code. Lora Nield taught us how to identify freshwater mussels, provided technical advice for snorkel surveys, and advised the project for the entire duration.

Literature Cited

Allen, D.C. and C.C. Vaughn. 2009. Burrowing behavior of freshwater mussels in experimentally manipulated communities. *Journal of the North American Benthological Society* 28: 93–100. doi:10.1899/07-170.1.

Bauer, G. 1988. Threats to the freshwater pearl mussel *Margartifera margartifera* L. in central Europe. *Biological Conservation* 45: 239-253.

B.C. Conservation Data Centre. 2015b. Species Summary: *Gonidea angulata*. B.C. Minist. of Environment. Available: http://a100.gov.bc.ca/pub/eswp/ (accessed Oct 25, 2017).

BC Ministry of Environment. 2001. Environment Protection Division, accessed December, 2014: http://www.env.gov.bc.ca/wat/wq/objectives/okphosphorus/okphosphorus.html

BC Ministry of Forests, Land, Natural Resource Operations, and Rural Development; MFLNRORD. 2017. Rocky Mountain Ridged Mussel foreshore protection layers.

Bogan, A.E. 1993. Freshwater Bivalve Extinctions (Mollusca: Unionoida): A search for causes. Amer. Zool 33: 599–609.

Breiman, L. 2001. Random Forests. Machine Learning 45: 5–32. doi:10.1023/A:1010933404324.

Buechling, A. and C. Tobalske. 2011. Predictive habitat modeling of rare plants species in Pacific Northwest forests. *Western Journal of Applied Forestry* 26: 71–81.

Brim Box, J., R.M. Dorazio and W.D. Liddell. 2002. Relationships between streambed substrate characteristics and freshwater mussels (Bivalvia: Unionidae) in Coastal Plain streams. *Journal of the North American Benthological Society* 21: 253– 260. doi:10.2307/1468413.

Burrows M.T., R. Harvey and L. Robb. 2008. Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. *Marine Ecology Progress Series* 353: 1-12. doi: 10.3354/meps07284

Callaghan, D.P., J.X. Leon and M.I. Saunders. 2015. Wave modelling as a proxy for seagrass ecological modelling: Comparing fetch and process-based predictions for a bay and reef lagoon. *Estuarine, Coastal and Shelf Science* 153: 108-120. doi:10.1016/j.ecss.2014.12.016

Chen, X. and H. Ishwaran. 2012. Random forests for a genomic data analysis. *Genomics* 99: 323-329.

Conservation Data Centre. 2015a. Conservation Status Report: *Gonidea angulata*. B.C. Minist. of Environment. Available: http://a100.gov.bc.ca/pub/eswp/ (accessed Oct 25, 2017).

COSEWIC 2003. COSEWIC assessment and status report on the Rocky Mountain Ridged Mussel *Gonidea angulata* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vi + 29 pp. http://www.sararegistry.gc.ca/default_e.cfm

COSEWIC. 2010. COSEWIC assessment and status report on the Rocky Mountain Ridged Mussel *Gonidea angulata* in Canada. In *Committee on the Status of* 78 *Endangered Wildlife in Canada.* a. Ottawa. x + 56 pp. www.sararegistry.gc.ca/status/status_e.cfm BC Conservation Data Centre 2015 a, b

Cutler, D.R., T.C. Edwards, Jr., K.H. Beard, A. Cutler, K.T. Hess, J. Gibson and J.J Lawler. 2007. Random forests for classification in ecology. *Ecology* 88: 2783–2792.

Cyr, H. 2009. Substrate and fetch affect the emergence of freshwater mussels from lake sediments. *Journal of the North American Benthological Society* 28: 319–330. doi:10.1899/08-133.1.

Daraio, J.A., L.J. Weber, S.J. Zigler, T.J. Newton and J.M. Nestler. 2012. Simulated effects of host fish distribution on juvenile unionid mussel dispersal in a large river. *River Research and Applications* 28: 594–608.

Davis, E.A., A.T. David, K.M. Norgaard, T.H. Parker, K. Mckay, C. Tennant, T. Soto, K. Rowe, and R. Reed. 2013. Distribution and abundance of freshwater mussels in the Mid Klamath Subbasin, California. *Northwest Science* 87: 189–206.

Department of Fisheries and Oceans. 2011. Recovery potential assessment for rocky mountain ridged mussel (*Gonidea angulata*) 1-13 pp. In. *Canadian Science Advisory Secretariat Science Advisory Report*. Rep. 2011/053.

Downing, J.A., P.V. Meter and D.A. Woolnough. 2010. Suspects and evidence: a review of the causes of extirpation and decline in freshwater mussels. *Animal Biodiversity and Conservation* 33.2: 151–185.

Dudgeon D., A. Arthington, M. Gessner, Z. Kawabata, D. Knowler, C. Leveque, R. Naiman, A. Prieur-Richard, D. Soto, M. Stiassny and C. Sullivan. 2006. Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews* 81:163–182, ISSN 1469-185X.

ESRI. 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, California

Fisheries and Oceans Canada. 2010. Management Plan for the Rocky Mountain Ridged Mussel (Gonidea angulata) in Canada [Final]. Species at Risk Act Management Plan Series. Fisheries and Oceans Canada, Vancouver. iv + 52 pp.

Geist, J. and K. Auerswald. 2007. Physicochemical stream bed characteristics and recruitment of the freshwater pearl mussel (*Margaritifera margaritifera*). *Freshwater Biology* 52: 2299–2316.

Genuer, R., J.M. Poggi and C. Tuleau-Malot. 2010. Variable selection using random forests. *Pattern Recognition Letters* 31: 2225-2236. doi:10.1016/j.patrec.2010.03.014

Grömping, U. 2009. Variable importance assessment in regression: Linear regression versus Random Forest. *The American Statistician* 63: 308–319. doi:10.1198/tast.2009.08199.

Hakanson, L. 1977. The influence of wind, fetch, and water depth on the distribution of sediments in Lake Vanern, Sweden. *Canadian Journal of Earth Sciences* 14: 397–412.

Hakanson, L. 1981. *A Manual for Lake Morphometry*. Springer-Verlag, Berlin-Heidelberg-New York: ix + 78 pp.

Harriger, K., Moerke A., and P. Badra. 2009. Freshwater Mussel (Unionidae) Distribution and Demographics in Relation to Microhabitat in a First-Order Michigan Stream. Michigan Academician xxxix, 149–162.

Hill, N., Pepper, A. R., Puotinen, M. L., Hughes, M. G., Edgar, G. J., Barrett, N. S., Stuart-Smith R. D., and R. Leaper. 2010. Quantifying wave exposure in shallow temperate reef systems: applicability of fetch models for predicting algal biodiversity. *Marine Ecology Progress Series* 417: 83-95.

Hothorn, T., K. Hornik, and A. Zeileis. 2006. Party: A laboratory for Recursive Partytioning.

Howard, J. K., and K. M. Cuffey. 2003. Freshwater mussels in a California North Coast Range river: Occurrence, distribution, and controls. *Journal of the North American Benthological Society* 22:63–77.

Jepsen, S., C. Labar and J. Zarnoch. 2010. Species profile: Western Ridged Mussel (*Gonidea angulata*). The Xerces Society. http://www.xerces.org/western-freshwater-mussels. Accessed May, 2014.

Kappes, H. and P. Haase. 2011. Slow, but steady: Dispersal of freshwater molluscs. *Aquatic Sciences* 74: 1–14. doi:10.1007/s00027-011-01876.

Kat, P.W. 1984. Parasitism and the Unionacea (Bivalvia). *Biological Reviews of the Cambridge Philosophical Society* 59: 189–207.

Lydeard, C., R.H. Cowie, W.F. Ponder, A.E. Bogan, P. Bouchet, S.A. Clark, K.S. Cummings. 2004. The global decline of nonmarine mollusks. *BioScience* 54: 321-330.

Mackie, G., T.J. Morris, and D. Ming. 2008. Protocol for the detection and relocation of freshwater mussel species at risk in Ontario- Great Lakes area (OGLA). *Canadian Manuscript Report of Fisheries and Aquatic Sciences* No. 2790.

Mackie, G.L. 2010. Risk assessment of water quality in Okanagan Lake, British Columbia, to Zebra/Quagga Mussel infestations: 6.

Mageroy, J., Snook, R., Nield, L., and Walker, I. 2017. Impact of Control Methods for Eurasian Watermilfoil on Western Ridged Mussel: Does Rotovation Harm the Mussel? Northwest Science 91(2): 186-197.

Mageroy, J. 2015. Rocky Mountain ridged mussel (*Gonidea angulata*) in the Okanagan Valley, BC: Final report on juvenile recruitment, host fish field sampling, and the impact of rototilling against Eurasian watermilfoil (*Myriophyllum spicatum*). Report. University of British Columbia, Kelowna, British Columbia.

Mageroy, J., Brownlee, S., Mitchell, J., Snook, R., Nield, L., Walker, I. 2015. Host Fish Use among Western Ridged Mussels (*Gonidea angulata*) in the Okanagan Valley, B.C.: Field Studies. BC Ministry of Forests, Lands, and Natural Resource Operations. Draft.

Ministry of Forests, Lands, Natural Resource Operations, and Rural Development; MFLNRORD. 2017. Mussel Habitat Zones Okanagan Region

Morales, Y., L.J. Weber, A.E. Mynett and T.J. Newton. 2006. Effects of substrate and hydrodynamic conditions on the formation of mussel beds in a large river. *Journal of the North American Benthological Society* 25: 664–676. doi:10.1899/0887-3593(2006)25[664:EOSAHC]2.0.CO;2.

Munshaw, R. 2016. Writeup for Wind Fetch Tool methodology of Okanagan Lake *G. angulata* habitat, in Snook, R. 2017b. Habitat suitability model for the Rocky Mountain Ridged Mussel (*Gonidea angulata*) in Okanagan Lake, BC. BC Ministry of Environment.

Murphy M.A., J.S. Evans and A. Storfer. 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. Ecology 91: 252–261.

Neves, R.J., A.E. Bogan, J.D. Williams, S.A. Ahlstedt, and P.D. Hartfield. 1997. Status of aquatic mollusks in the southeastern United States: A downward spiral of diversity. pp. 43–86. In G.W. Benz and D.E. Collins (Eds.) (1998) *Aquatic Fauna in Peril: The Southeastern Perspective.* Special Publication No. 1, Southeast Aquatic Research Institute, Lenz Design and Communications, Decatur, GA.

O'Brien, C., D. Nez, D. Wolf and J. Brim Box. 2013. Reproductive biology of *Anodonta californiensis, Gonidea angulata,* and *Margaritifera falcata* (Bivalvia : Unionoida) in the Middle Fork John Day River, Oregon. *Northwest Science* 87: 59–72.

Pinsent, M. E., and J. G. Stockner (eds.). 1974. Technical Supplement V to the Final Report: The Limnology of the Major Okanagan Basin Lakes. Office of the Study Director, Canada-British Columbia Okanagan Basin Agreement, Penticton, BC.

Roed, M.A. (Ed.). 1995. Geology of the Kelowna Area and Origin of the Okanagan Valley British Columbia. Kelowna Geology Committee, Kelowna, B.C.

Salmon, A., and R. H. Green. 1983. Environmental determinants of unionid clam distribution in the Middle Thames River, Ontario. *Canadian Journal of Zoology* 61:832–838.

Schleppe, J. and B. Mason. 2009. Standard methods for completion of Foreshore Inventory and Mapping Projects. *Prepared by: Ecoscape Environmental Consultants Ltd. and The Community Mapping Network*

Schwalb, A.N., T.J. Morris, N.E. Mandrak and K. Cottenie. 2013. Distribution of unionid freshwater mussels depends on the distribution of host fishes on a regional scale. *Diversity and Distributions* 19: 446–454.

Smith, D.R. 2006. Survey design for detecting rare freshwater mussels. *Journal of the North American Benthological Society* 25: 701–711. doi:10.1899/0887-3593(2006)25[701:SDFDRF]2.0.CO;2.

SARA: Species at Risk Act, public registry. Rocky Mountain Ridged Mussel. (accessed December 2016) Available: http://www.registrelep-sararegistry.gc.ca/species/speciesDetails_e.cfm?sid=791

Snook, R. 2017a. Information in support of the identification of critical habitat for the Rocky Mountain Ridged Mussel (*Gonidea angulata*). DFO Can. Sci. Advis. Sec. Res. Doc. 2017/nnn. viii + 55 p

Snook, R. 2017b. Habitat suitability model for the Rocky Mountain Ridged Mussel (*Gonidea angulata*) in Okanagan Lake, BC. BC Ministry of Environment.

Spring Rivers. 2007. Reproductive timing of freshwater mussels and potential impacts of pulsed flows on reproductive success. California Energy Commission. PIER Energy-Related Environmental Research Program. CEC-500-2007-097.

Stanton, L., R. Lauzier, S. Macconnachie, L. Nield, S. Pollard, J. Heron and S. Davies. 2012. Exploratory surveys and directed studies of Rocky Mountain Ridged Mussel (*Gonidea angulata* Lea, 1839) in British Columbia. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* No. 3003.

Stockner, J.G. and T.G. Northcote. 1974. Recent limnological studies of Okanagan Basin lakes and their contribution to comprehensive water resource planning. *J. Fish. Res. Board Can* 31: 955-976.

Strayer, D.L. 2014. Use of flow refuges by unionid mussels in rivers. *Journal of the North American Benthological Society* 18: 468–476.

Strobl, C., J. Malley and G. Tutz. 2009. An introduction to recursive partitioning: rationale, application, and characteristics of classification and regression trees, bagging, and Random Forests. *Psychological Methods* 14: 323–348. doi:10.1037/a0016973.

Sylte, T. and C. Fischenich. 2002. An evaluation of techniques for measuring substrate embeddedness. *Watershed Management Bulletin* 10:1-25. http://oai.dtic.mil/oai/oai?verb=getRecord&metadataPrefix=html&identifier=ADA434902.

Vannote, R.L. and G.W. Minshall. 1982. Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds. *Proceedings of the National Academy of Sciences of the United States of America* 79: 4103– 4107.

Vaughn, C.C. and C.M. Taylor. 2000. Macroecology of a host-parasite relationship. *Ecography* 23: 11–20. doi:10.1111/j.1600-0587.2000.tb00256.x.

Williams, J.D., M.L. Warren, Jr., K.S. Cummings, J.L. Harris and R.J. Neves. 1993. Conservation status of freshwater mussels of the United States and Canada. *Fisheries* 18: 6–22. doi:10.1577/15488446(1993)018<0006:CSOFMO>2.0.CO;2.

WindFinder.com, GmbH & Co. KG. Germany, accessed June, 2014

TABLE 1. Habitat suitability model results for important habitat variables

Package[a]	Most important variables, ranked from most to least important	Main tuning parameter (mtry[b])	Description
Random Forest*	Fetch Sand Embeddedness Boulder Slope (Snook unpubl. data 2016)	4 (with lowest misclassification rate of 24.2%)	Ranked 5 most important variables for explaining distribution of *G. angulata* in Okanagan Lake, B.C.
Party*	Embeddedness Sand Fetch Slope (Snook unpubl. data 2015)	2, 3, 4, 5, 6,	Each iteration determined the top 4 predictor variables. Boulder occurrence was determined to be correlated with other variables, and is not in itself explanatory of *G. angulata* distribution

*Code is available upon request from the primary author.

a Classification packages implemented in R: both of which utilize random forests (Snook 2017a)

b Number of variables used to create the tree

TABLE 2. Sites with their rank of how well they fit this model of top four predictor variables, and variable ranges within tolerance of this species. For example, the best model fit has the most common variable ranges of high embeddedness, high sand, a mean fetch of 1.88 km, and low slope. All sites that did not fit as best, good, or unknown, are ranked as a poor fit. Fetch could not be calculated for some sites and are subsequently listed as "?" below, and are categorized as an unknown fit for this model. The number of sites represented by each rank are listed as a comparison to the 314 total sites within the foreshore of Okanagan Lake.

Model Fit	Embeddedness	Sand	Fetch (km)	Slope	Sites	Sites with mussels (%)	Foreshore Length (km)
Best	H	H	1.88	L	10	30	5.695
Good	M	VH or M	1.64	L	20	0	14.557
Unknown	H	VH	?*	L	5	Unkn.	1.020
Poor	M	N or L	2.18	L	279	8	268.040

Abbreviations: Very High (VH), High (H), Medium (M), Low (L), None (N), Unknown (Unkn.)

*Of the twelve sites of unknown fetch, five of these contain variables with best model fit

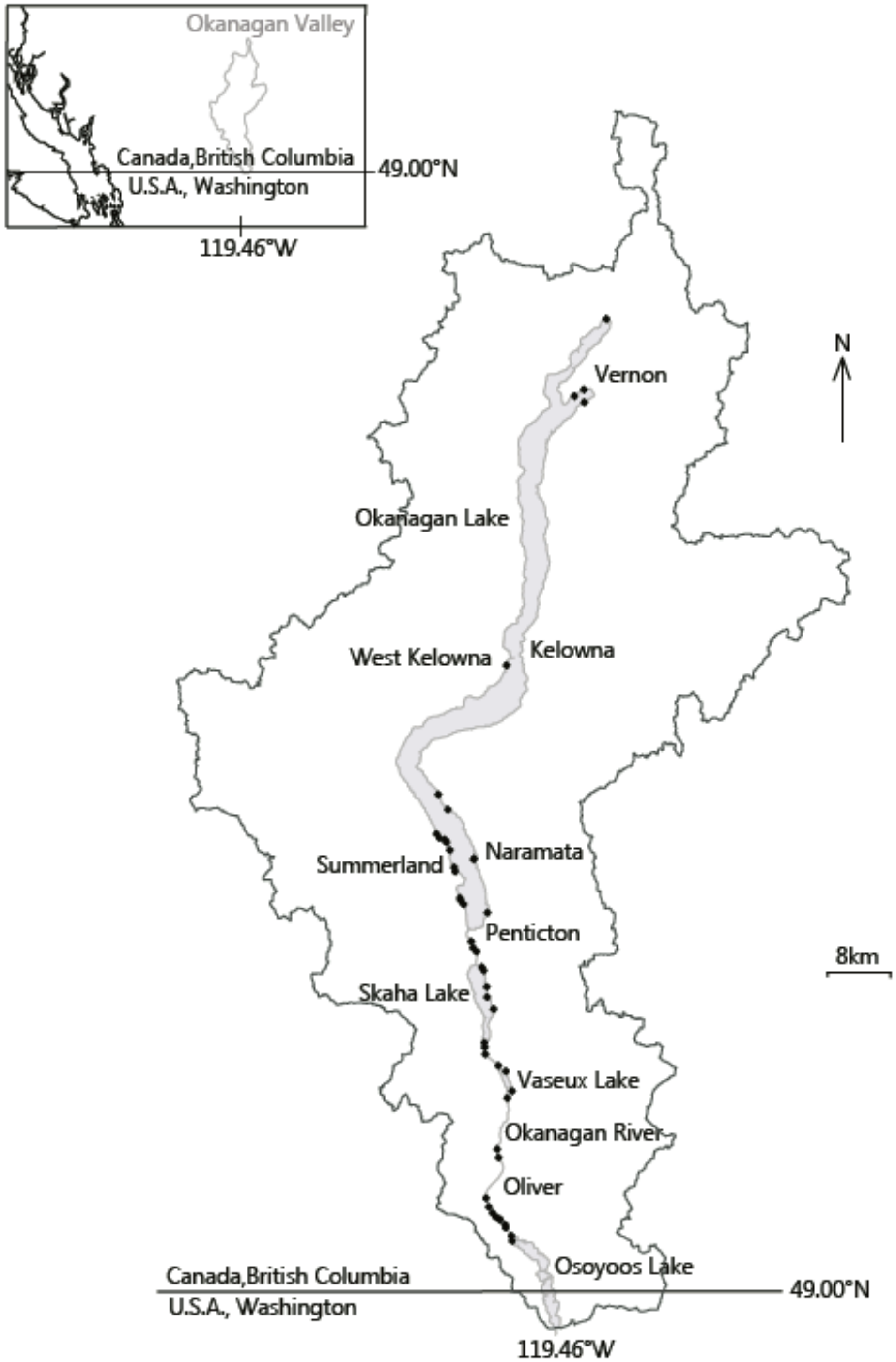

Figure 1. Canadian distribution of *G. angulata* (black dots), located within the Okanagan River watershed in British Columbia (Mageroy et al. 2017, used with permission).

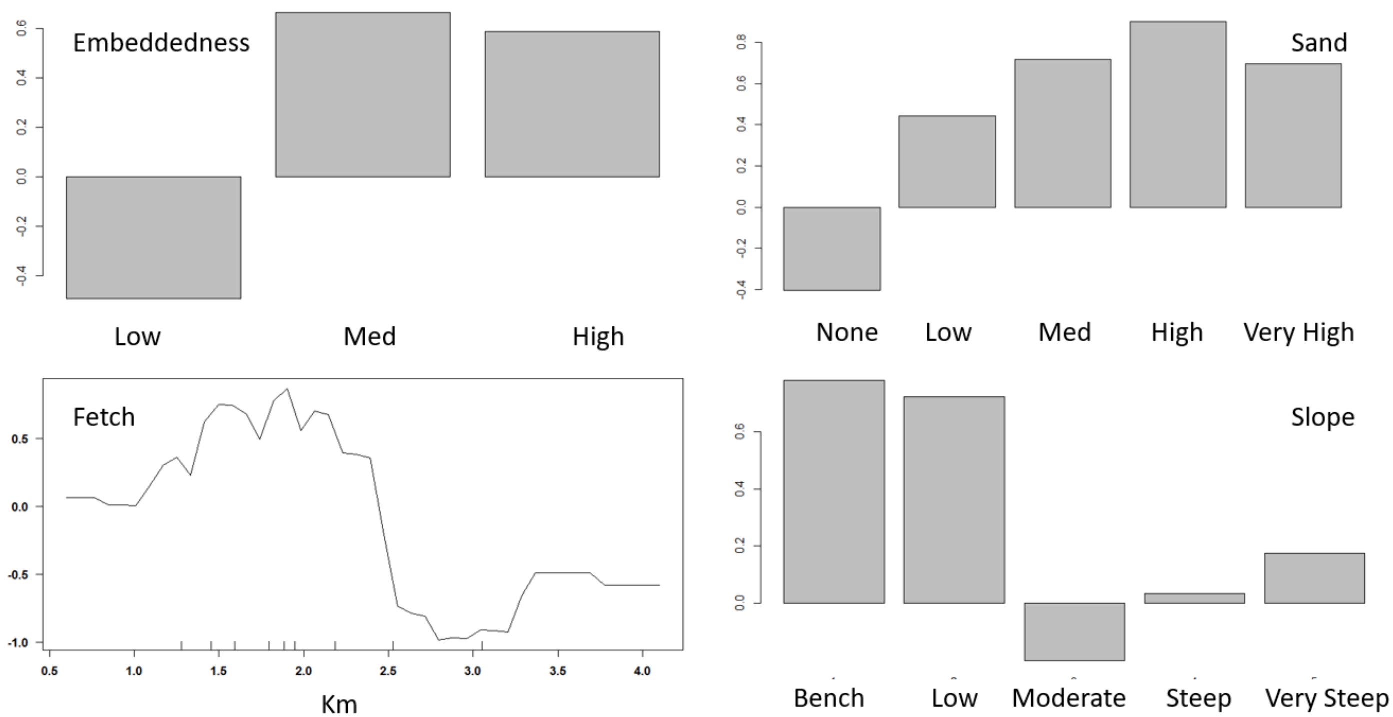

Figure 2. Partial dependence plots of each variable. Plots indicate probability of *G. angulata* occurrence based on each predictor variable in the best models after averaging out the effects of all other predictor variables in the model. Embeddedness is an ordinal variable including low (0-25%), medium (25-75), and high (>75%) categories. Total fetch (effective fetch, km) is a continuous measure. Sand is an ordinal variable including none, low (1-20%), medium (25-40%), high (45-60%), and very high (70-100%). Slope is an ordinal variable including categories bench, low (0-5), moderate (5-20), steep (20-60), and very steep (60+).

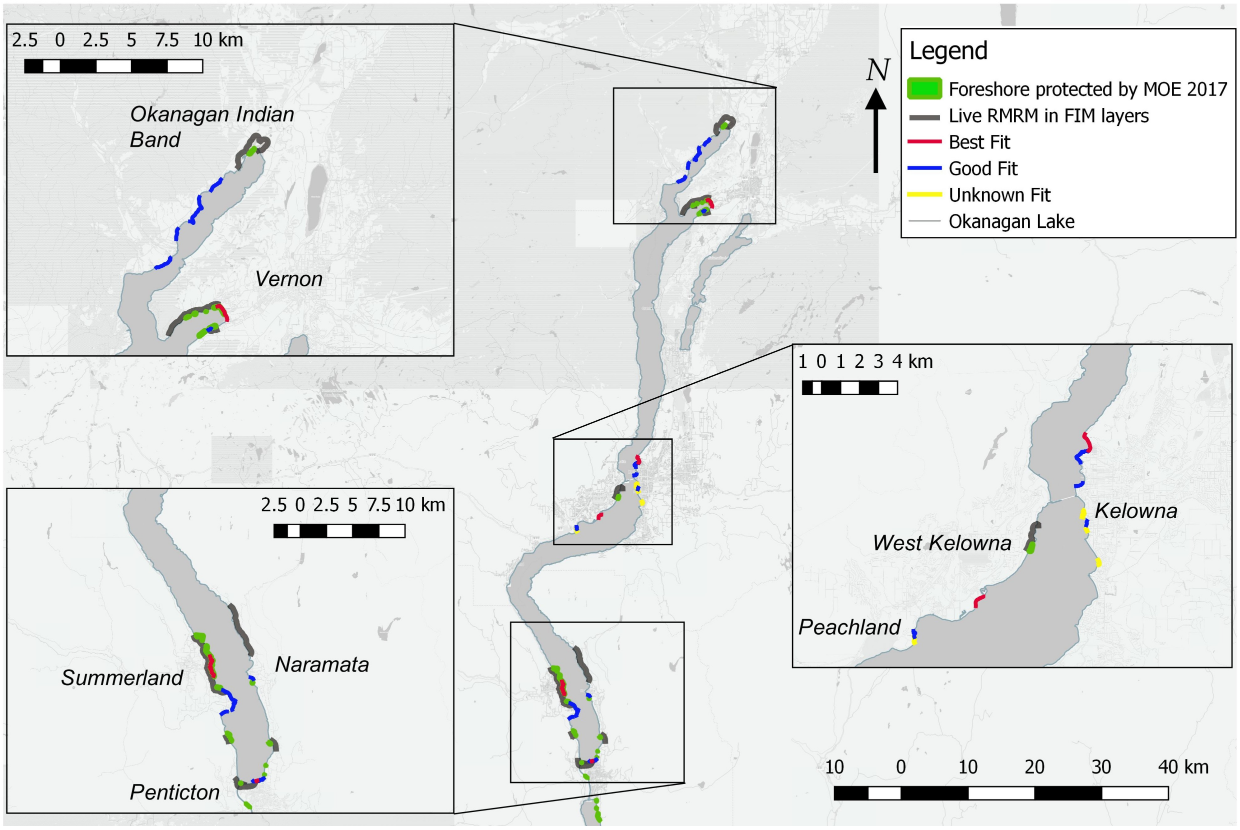

Figure 3. Map of Okanagan Lake and sites with their associated fit for this model's habitat suitability for *G. angulata* (Table 2). The best fitted sites with this model are illustrated in red, while sites with a good fit are blue, and foreshore of Okanagan Lake that is currently protected are illustrated with a green buffer (data from MFLNRORD, 2017). Sites of unknown habitat ranking are illustrated in yellow. Sites with known occurrence of *G. angulata* are included in black (image from Snook 2017b, modified and used with permission).