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

--Manuscript Draft--

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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 (Blevins et al. 2017), 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; but for G. angulata, recovery planning is a challenge as little is known about its habitat requirements, particularly within lakes. To be able to recover G. angulata throughout its historic range, we must study lentic as well as lotic habitats. We developed habitat suitability models for G. angulata in Okanagan Lake using snorkel survey data, habitat data, and two complementary classification methods based on the RandomForest algorithm. Both classification methods ranked the top four predictor variables as effective fetch between 1 and 2.25 km, medium-high embeddedness of substrates (25 - >75%), 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. These findings suggest that the drivers for G. angulata distribution in lakes are similar to those in rivers, although predictor variables themselves may vary. This is important because simply using predictor variables from lotic systems would not correctly predict G. angulata occurrence in lakes, demonstrating the importance of this lake-specific investigation.
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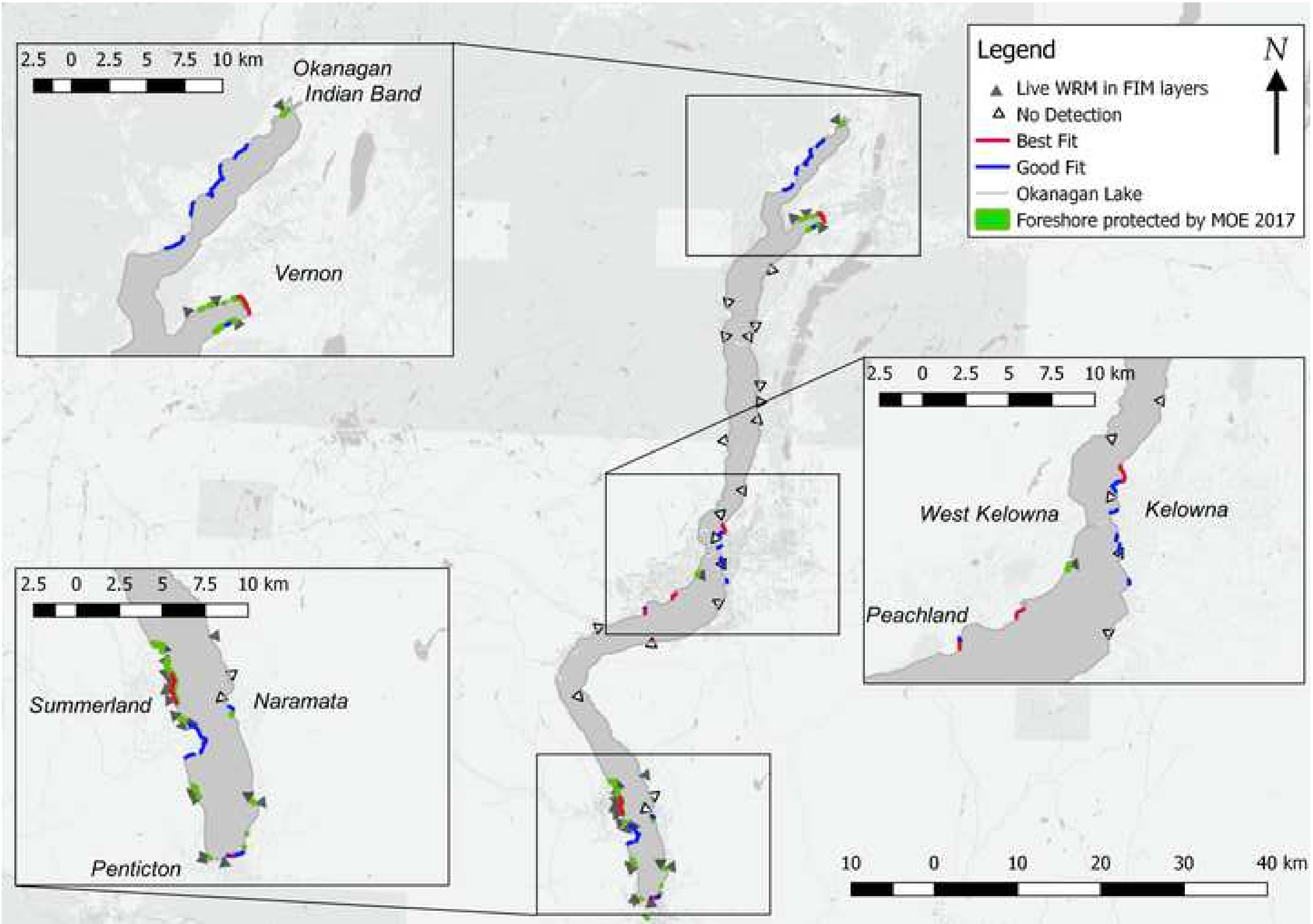
Figure 1 Click here to access/download;Figure;Figure 1 Resub WRM 3.jpeg




Probability of G. angulata Presence [logit (probability of presence)]/2
Embeddedness
0.6
0.4
0.2
0.0
-0.2
-0.4
Low
Med
High
Sand
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
None
Low
Med
High
Very High
Fetch
0.6
0.0
-0.5
-1.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
Km
Slope
0.6
0.4
0.2
0.0
Bench
Low
Moderate
Steep
Very Steep

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

Running footer: Modeling Western Ridged Mussel Habitat Suitability

1 table, 2 figures

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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 (Blevins et al. 2017), 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; but for *G. angulata*, recovery planning is a challenge as little is known about its habitat requirements, particularly within lakes. To be able to recover *G. angulata* throughout its historic range, we must study lentic as well as lotic habitats. We developed habitat suitability models for *G. angulata* in Okanagan Lake using snorkel survey data, habitat data, and two complementary classification methods based on the RandomForest algorithm. Both classification methods ranked the top four predictor variables as effective fetch between 1 and 2.25 km, medium-high embeddedness of substrates (25 - >75%), 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. These findings suggest that the drivers for *G. angulata* distribution in lakes are similar to those in rivers, although predictor variables themselves may vary. This is important because simply using predictor variables from lotic systems would not correctly predict *G. angulata* occurrence in lakes, demonstrating the importance of this lake-specific investigation.

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

Introduction

Gonidea angulata Lea, the Western Ridged mussel (also known as the Rocky Mountain ridged mussel; family Unionidae) is among the most endangered animal taxa in North America (Bogan 1993, FMCS 2016). For conservation efforts to be successful for this species, all habitat types and requirements must be understood. All studies regarding this species' habitat, thus far, have been conducted in river environments, but much of its population occurs in lakes in British Columbia (B.C.), Canada. In the Okanagan Valley, B.C., *G. angulata* occurs in four lakes and the river connecting them, the Okanagan River. This paper presents the first habitat suitability study for *G. angulata* in a lake environment.

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). Of the various North American species of freshwater mussels, *G. angulata* is considered at most risk of extinction in many places (Blevins et al. 2017), yet very little is known about its habitat requirements. Management strategies require reliable information regarding the habitat requirements and preferences of the target species (Fisheries and Oceans Canada 2010, 2011, Stanton et al. 2012). Conservation should be science based, yet up to this point very little was known about *G. angulata's* lacustrine habitat requirements.

Most studies of *G. angulata* habitat requirements pertain to riverine environments; of all of the twenty-eight papers we reviewed in the literature, none of them focused on *G. angulata* in lakes. In river environments, 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). Although some of these river characteristics and their functional significance may be transferable to understanding lake environments, river and lake environments are inherently very different.

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* are sculpin (*C. asper* Richardson, 1836 and/or *C. cognatus* Richardson, 1836) (Mageroy et al. 2015), along with a few other potential host species (Stanton et al. 2012, Mageroy 2015). Because sculpins are very widely distributed in Okanagan Lake, host fish are unlikely to be a factor limiting *G. angulata* in this system.

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 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 cobble (Davis et al. 2013). Thus, factors which affect substrate composition and mobility (e.g., wave action, slope) also directly or indirectly impact mussel distribution (Cyr 2009, Davis et al. 2013). It is likely there will be many key factors defining the distribution of this species in lakes. 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).

This paper presents the first habitat suitability study of *G. angulata* in a lake environment. Here, we use extensive field survey data to develop a habitat suitability model for *G. angulata* in Okanagan Lake, based on recent presence/not detected populations (Figure 1; COSEWIC 2010, Stanton et al. 2012). We also seek a better understanding of *G. angulata's* ecology, and in particular the factors that influence its geographic distribution. Our *a priori* hypotheses are: *G. angulata* are not distributed randomly, and useful predictors of its distribution include substrate type and embeddedness, low shoreline slope, and site exposure.

Methods

Study Area

The Okanagan Valley is located in south-central British Columbia and is surrounded by three mountain ranges: the Columbia Mountains lie to the east, the Cascade Mountains lie to the south-west, and the Coast Mountains are found to the west. Following a north-south fault, the Okanagan Valley was deeply carved into bedrock by recent successive glaciations. The valley is occupied by a series of lakes, the most northern one, Okanagan Lake, being the focus of our study. Okanagan Lake drains south into the Okanagan River, which connects a series of lakes at the southern end of the valley, before continuing on to join the Columbia River in the U.S.A.

This valley is part of the Montane Cordillera Ecozone. It is a semi-arid region 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 3.5 km (average) wide (Figure 1; Stockner and Northcote 1974). Its watershed encompasses 6178 km^2 (Roed 1995), with a maximum depth of 232 m and an average depth of 76 m (Stockner and Northcote 1974). Lake level fluctuates annually from ± 0.5 m to ± 0.9 m (in 2009 - 2010; Stanton et al. 2012). Shoreline length is 290 km. The majority of the watershed surrounding Okanagan Lake is forested, with some adjacent communities and cities.

Okanagan Lake is a warm monomictic lake (i.e., stratified in summer, and ice-free in winter) (Stockner and Northcote 1974), with surface water temperatures ranging from 1.7 to 23.0°C (Mackie 2010). 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).

Explanatory variables

We used an *a priori* approach to select relevant variables for habitat suitability model construction. Based on scientific literature and expert opinions, we included the following variables in our predictive models: percentages of boulder, sand, embeddedness, and foreshore slope. These variables were chosen based on previous significance in mussel occurrence studies. For example, boulders can provide refuge and microhabitats important for mussels, while sand grain sizes allow for mussel anchorage in the substrate (Strayer 2014), and low embeddedness is related to low sediment accumulation, which is significant in river environments with *G. angulata* present (Allen and Vaughn 2009). The slope of a site can explain interactions between lake bottom and wave action, and subsequent sediment accumulation and substrate composition (Hakanson 1977). Most of the identified variables included in the model came from pre-existing Foreshore, Inventory and Mapping (FIM) data from Okanagan Lake (Schleppe and Mason 2009). In this methodology, shore zone is defined as the deep water regions of the lake to 30 to 50 m past the high water level, reaching into the upland/riparian zone (Schleppe and Mason 2009).

To better characterize the sites, several new variables were added to supplement the FIM data. These included several abiotic attributes: 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 (e.g., by depth of oxidization on rebar stakes).

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).

Geomorphic characterizations of sites have been effective in mussel studies (e.g., Vannote and Minshall 1982, Gangloff and Feminella 2006), and may have been useful in predicting mussel occurrence in certain bathymetric and topographical features in this lake. During field surveys, an underwater ledge was observed in many of the sites surveyed. This lead to the hypothesis that perhaps this feature played a role in predicting mussel presence. The degree of shoreline morphology, explained in part by interactions with wind and longshore currents (e.g., Burrows et al. 2008), may have illustrated at what, if any, specific threshold mussel habitat exists in certain shoreline shapes. Clay substrate has very low permeability for oxygen. Lake bottom which is clay dominant near the upper layers was hypothesized to be unsuitable for mussels, since clay would cut off oxygen supply to buried mussels. Furthermore, experimental data on depth of oxygen permeation into the substratum was included, as shallow oxygen permeation is likely a limiting factor for mussel occurrence.

This *a priori* variable selection approach also informed site selection, by enabling a stratified sampling design to increase the likelihood of observing *G. angulata* within the lake. The strata included the entire range of the selected variables. For example, although low substrate embeddedness was hypothesized to be a predictor for presence of this species, sites with medium and high embeddedness were also included in the model. This was the case for substrate embeddedness, boulders, slope, and sand. In stratified random sampling, locations within the strata are themselves randomly selected.

Site selection

The sites selected were distributed throughout the littoral zone of Okanagan Lake, to include all potential habitat types and to avoid distance-related interactions between sites. No sites were located in the middle of the lake.

For the model, all 19 sites in Okanagan Lake where *G. angulata* had been reported (between 2005 – 2012) were included. The variables identified by the expert consultation process were then used to target 26 additional sites, selected in accordance with a stratified sampling approach to increase the likelihood of encountering this inconspicuous species. A random number generator was used in GIS (ESRI, 2011) to locate these sites. Thus, this model is based on stratified random sampling. This resulted in a total of forty-five survey sites along the shoreline of Okanagan Lake. Selected sites included north, central, and southern sections of the lake. Sites not accessible by road were accessed by boat. This study was limited to 45 sites due to effort constraints, while still maintaining a sufficient sample size.

Mussel and host fish surveys

Surveys to detect *G. angulata* populations (presence/not detected) at all 45 sites were conducted according to standard methods for rare freshwater mussel species (Smith 2006, Mackie et al. 2008, Stanton et al. 2012). Snorkel surveys were conducted at every site included in this model between June – August in 2014. 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, with a maximum survey depth of approximately 4 m. Sites with steep slopes generally limited the distance from shore the parallel snorkelers could survey, since depths of 4 m occurred quicker at these gradients than at more moderately sloped sites. The length of the selected sites varied greatly, from 110 m to 6250 m. This was a limitation of the existing FIM database, where site lengths were pre-determined based on foreshore type, categorized by Schleppe and Mason (2009). Presence/not detected data on *G. angulata* were recorded at every site. Although it is possible mussels may occur deeper than 4 m, we were not able to observe them at depths greater than this, even while diving below the surface.

A presence/not detected design was implemented as it answered the main questions of this study: which variables predict occurrence of this species? Far fewer sites could have been studied if we had chosen to look at abundance or density of mussels. These types of studies are later discussed for future research.

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 accounts for correlations and variable interactions, and ranks interactions between variables by importance (Chen and Ishwaran 2012). A tuning parameter, 'mtry', is altered within the RF package; denoting the number of predictor variables chosen to create a tree derived from the partitioned response. High classification accuracy has been shown in presence-absence ecological data using RF (Cutler et al. 2007).

The RF package iterations were run multiple times with data reductions, to produce a model with the lowest average misclassification rate (Grömping 2009, Strobl et al. 2009). Each model run generated 5000 trees of 100 iterations each in a sensitivity analysis, with 'mtry' ranging for each series from 2 (minimum) to 6. The data were also run through the classification package Party, developed by Hothorn et al. (2006), to assess correlation among predictor variables and to facilitate a comparison and validation of results between the two classification packages.

Variable importance was assessed using the mean decrease in accuracy (MDA), which 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).

Results

Mussel Surveys

Mussel surveys resulted in six new occurrence sites for *G. angulata*. One of these new sites had only 1 live *G. angulata* observed in the 4 km shore length, as well as 1 shell. *G. angulata* are distributed in the north, central, and south of Okanagan Lake, as well as on both the east and west sides of the lake. Additionally, *Anodonta*, another native freshwater mussel was observed throughout the lake, and *Margaritifera falcata* was observed in Mission Creek, a tributary of Okanagan Lake. Sculpin (*Cottus* sp.), the primary host fish for *G. angulata*, were observed at all 45 sites.

Random Forest model

The use of four predictor variables yielded the lowest misclassification rate (Out-of-bag error; OOB) of 24.2 %, with ‘mtry’ tuned to 2 (using the randomForest function for package RandomForest). In comparison, ‘mtry’ tuned to 3 had a higher misclassification rate of 25.8 % with the top four predictor variables in the RandomForest package. While many other variables (e.g., substrate grain sizes: fines (< 0.06 mm), fine gravel (2 – 16 mm), coarse gravel (16 – 64 mm), fine cobble (64 – 128 mm), coarse gravel (128 – 256 mm), aquatic vegetation, groynes (i.e., any perpendicular structure to shoreline impacting regular sediment drift), cliffs, littoral zone width, docks, etc.) were incorporated into preliminary models, these were not influential in explaining *G. angulata’s* distribution in Okanagan Lake. With 38 variables (chosen based on the expert consultation process), the OOB error was 23.26%. Many of these variables were eliminated based on the MDA measures of variable importance, which ranked significantly lower than the top ranked predictor variables. Top predictors MDA were greater or equal to 18, while all other variables consistently ranked less than 8.

The variable importance function 'varimp' in the Party package supported the RandomForest results, which illustrated variables with lower MDA were correlated and added no meaning to the rest of the model.

Geomorphic and Biotic controls on G. angulata

The RF package outputs were used to create variable partial dependence plots (Figure 2). 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).

The most important habitat variables for *G. angulata*, as identified by both models, were high embeddedness of substrates (>75%), sand (0.06 – 2 mm) occurrence (>20%), followed by total fetch (>1 km and < 2.25 km), and bench or low slope.

Within the Party models, boulder (> 256 mm) occurrence was determined to be a correlated variable, but was an additional important predictor within the RF models. 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). Low embeddedness of substrates was negatively associated with *G. angulata* habitat, thus this habitat characteristic was not included in the final model.

Constructing the habitat suitability model

We applied these results, from the 45 sites analyzed in the RF packages, to the rest of the Okanagan Lake foreshore. The optimal model was used to generate a vector map of mussel habitat distribution from FIM data using QGIS 2.18.7 (Figure 1). 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. Sites were ranked as best, good, and poor model fit, based on the presence of top predictor variables.

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 out of the entire circumference (314 sites) of Okanagan Lake (Munshaw 2016). Their fetch was then calculated by averaging the fetch for adjacent sites. Of these sites, five contain top predictor categories, suggesting they may offer suitable habitat for *G. angulata* (Table 1, Figure 2). One site was included as a best model fit, while four were included as good model fits.

Throughout the circumference of the lake (314 sites, 290 km), 27.3 percent (n = 3) of the sites with best model fit have known *G. angulata* occurrences (Table 1). Best model fit represents a mere 11 sites throughout the lake, and 5.99 km. No sites of Good fit (15.2 km) contain *G. angulata*, while 8 percent (n = 22) of Poor fit sites do. The majority of Okanagan Lake represent Poor model fit for *G. angulata* habitat; 268 km.

Discussion

Mussel surveys

Importantly, in our study, sites with over 300 *G. angulata* are weighted the same as a site with only 1 mussel found. All sites with a minimum of 1 mussel are considered occurrence sites. Since mussels spend the majority of their lives either completely or partially buried, we assumed sites with only 1 mussel observed likely contained many more individuals that were not found. Conversely, sites with no mussels found may also have been occurrence sites. This is a limitation of our presence/not detected study design.

Geomorphic and Biotic controls of G. angulata

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). Mussels tend to inhabit interstitial spaces in streambed (and littoral zone) substrate; areas with high embeddedness levels subsequently decrease space between substrates, and therefore decrease available habitat.

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 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. 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 (Hyatt and Stockwell 2003), 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.

Medium or high embeddedness may also be associated with greater sediment stability in low energy environments (Brim Box et al. 2002). *Gonidea 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, increasing sand at a site is positively associated with *G. angulata* habitat (Vannote and Minshall 1982) in Okanagan Lake. 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.

The positive association of mussels with boulders can be explained via the refuge and stability they offer, but their presence are not an essential part of suitable habitat at each site. 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. Invasive macrophytes are partially managed in Okanagan Lake by rototilling. Live *G. angulata* were present in 25% of the rotovation polygons in the Okanagan Valley, B.C., in a recent experimental study (Mageroy et al. 2017).
Boulders function as refuge from predators, shear stress and scouring. However, boulders were found to be a highly correlated variable with the other predictor variables, adding instability to the model in RandomForest, and were not included in the Party output. The importance of boulder occurrence likely depends on site exposure. In more exposed sites, boulders provide the low energy microhabitat that aggrades sand, which we have demonstrated is important to *G. angulata* in Okanagan Lake. We infer that microhabitats among boulders may be more important at sites with higher effective fetch.

Our results show that a fetch between 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. Fetch may also serve as a proxy for longshore current velocities. In Canada, *G. angulata* occur in two additional lakes within this watershed south of Okanagan Lake (i.e., Skaha Lake and Vaseux Lake), as well as historically in Osoyoos Lake. The dimensions of these lakes are narrow, like Okanagan Lake, but are much shorter, i.e., each lake has a shorter fetch than Okanagan Lake. Vaseux Lake is arguably an extension (a wide section) of Okanagan River, in terms of its hydrodynamic properties. 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 wave 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) or crushed by large, mobile substrate elements (Strayer 1999).

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 out of 314), which may also explain why no mussels are found in this habitat type. 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 (i.e., less than 5% gradient) was positively associated with *G. angulata* occurrence (e.g., bench vs. steeper slopes > 60%). A bench shoreline is one that rises, typically very steeply, has a flat area typically greater than 15 horizontal meters, then becomes steep or very steep again (Schleppe and Mason 2009). In Okanagan Lake, foreshores with categorical bench slopes are uncommon (4 such sites exist), while 132 have low slope. 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, mussel anchorage may be possible in a fine material depositional environment, within an optimal fetch range.

Management implications

We applied our results, from the 45 sites analyzed and discussed above, to the entire Okanagan Lake shoreline. 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 1, Figure 1; Red). Of these ten sites, three are known to contain *G. angulata* (located in Summerland, BC). Note that all the *G. angulata* sites within Okanagan Lake, with the exception of one site (in Penticton, date of occurrence unknown), are recent (2005-2015) records. There are existing foreshore segments which are currently protected (Figure 1), 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, for future surveys, 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 < 3.28 km, with Low slope are considered good model fit and high priority habitat (Table 1). Sites that were not ranked as best or good fit were listed as low priority for the rest of Okanagan Lake.

Sites which contain the most favorable ranges for important variables (i.e., are ranked as best and good model fit), are recommended for ground-truthing of this species (Table 1). These sites are situated throughout the length of the lake (Figure 1). 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.

This novel work is important for understanding the relationships between this species' occurrence and its lake-specific habitat requirements. In large systems, such as Okanagan Lake, where survey effort is often limited by time and financial constraints, and by the characteristically patchy distribution of mussel populations, targeting sites for ground-truthing and conservation is invaluable.

Future research

This study outlines the framework for building a habitat suitability model for this species. Habitat suitability models based on presence/not detected data are built with the assumption that sites where the species is undetected (i.e., "no detection" sites) are sites where the mussels are truly absent; a difficult claim to make, especially for inconspicuous species which are buried for the majority of their lives. For a greater understanding of this species' habitat preferences and habitat suitability, exploring *G. angulata* abundance, density, and/or population age structure at these sites is required. The usefulness of this model is reflected by the number of sites where *G. angulata* were correctly predicted to exist, in a very large system. Similar models characterising habitat requirements for other mussel species can be built using this approach.

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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.

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. Ministry of Environment. Available: http://a100.gov.bc.ca/pub/eswp/ (accessed October 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. Integrative and Comparative Biology 33:599–609.

Breiman, L. 2001. Random Forests. Machine Learning 45:5–32.

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.

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.

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.

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.

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.

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. Ministry of Environment. Available online at http://a100.gov.bc.ca/pub/eswp/esr.do?id=15739 (accessed 25 Oct 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.

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.

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.

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. Van 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 of the Cambridge Philosophical Society 81:163–182.

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.

FMCS (Freshwater Mollusk Conservation Society). 2016. A national strategy for the conservation of native freshwater mollusks. Freshwater Mollusk Biology and Conservation 19:1–21.

Gangloff, M. M. and J. W. Feminella. 2006. Stream channel geomorphology influences mussel abundance in southern Appalachian streams, U.S.A. Freshwater Biology 52:64–74.

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.

Grömping, U. 2009. Variable importance assessment in regression: Linear regression versus Random Forest. The American Statistician 63:308–319.

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.

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.

Hyatt, K. D. and M. M. Stockwell. 2003. Analysis of seasonal thermal regimes of selected aquatic habitats for salmonid populations of interest to the Okanagan Fish and Water Management Tools (FWMT) project. Canadian Manuscript report of Fisheries and Aquatic Sciences 2618:26 p.

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.

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.

Magerøy, 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 91:186-197.

Magerøy, 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.

Magerøy, 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.

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.

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.

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.

SARA: Species at Risk Act, public registry. Rocky Mountain Ridged Mussel. Available online at http://www.registrelep-sararegistry.gc.ca/species/speciesDetails_e.cfm?sid=791 (accessed 1 December 2016).

Snook, R. 2017. 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. Journal of the Fisheries Research Board of Canada 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.

Sylte, T. and C. Fischenich. 2002. An evaluation of techniques for measuring substrate embeddedness. Watershed Management Bulletin 10:1-25.

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.

WindFinder.com, GmbH & Co. KG. Germany. Available online at https://www.windfinder.com/contact/weatherdata.htm (accessed 30 June 2014).

Figure 1. Map of Okanagan Lake and sites with their associated fit for this model's habitat suitability for *G. angulata* (Table 1); based on the 45 sites surveyed and analyzed in this study design, which are then extrapolated across the lake's entire shoreline. 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 with known occurrence of *G. angulata* are illustrated by black triangles, while sites surveyed without their detection* are empty triangles (image from Snook 2017, modified and used with permission).

*Additional sites may exist.

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 (a shoreline that rises, typically very steep, has a flat area typically greater than 15 horizontal meters, then becomes steep), low (0-5 %), moderate (5-20 %), steep (20-60 %), and very steep (60+ %).

TABLE 1. Sites ranked in accordance with how well they fit this model, using the top four predictor variables. Also provided are variable ranges reflecting the tolerance of this species. For example, for best model fit the most common variable ranges comprise high or medium embeddedness, high sand, a mean fetch of 1.89 km, and low slope. All sites that did not fit as best, or good, are ranked as poor fit. The number of sites represented by each rank are listed for comparison to the 314 total sites on the foreshore of Okanagan Lake.

Model Fit*	Embeddedness	Sand	Fetch (km)	Slope	Sites	Sites with *G. angulata* (%)	Foreshore Length (km)
Best	H or M	H	1.89	L	11	27.3	5.992
Good	H or M	VH or M	1.64	L	24	0	15.280
Poor	M	N or L	2.18	L	279	8	268.040

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

*Model fit is based on the variable partial dependence plots illustrated in Figure 2, from the model with the lowest misclassification rate of 24.2%. Sites containing the most to least predictive category of each variable are ranked from highest (best) to lowest (poor).