

**Species distribution model of Warmouth (*Lepomis gulosus*) in Long Point Bay, with evaluation of climate change and *Phragmites* impact scenarios**

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SPECIES DISTRIBUTION MODEL OF WARMOUTH (*LEPOMIS GULOSUS*) IN LONG  
POINT BAY, WITH EVALUATION OF CLIMATE CHANGE AND *PHRAGMITES*  
IMPACT SCENARIOS

by

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## ABSTRACT

Species distribution modeling was conducted for Warmouth at Long Point Bay to identify environmental characteristics of, and map, suitable habitat. Environmental variables, including depth, substrate, temperature, vegetation, and water quality, were used to predict the species distribution using a machine learning method within a geographic information system. The potential impact of climate change and spread of an invasive reed, *Phragmites australis*, on Warmouth habitat were also examined. Species distribution modeling identified suitable habitat at Long Point Bay for Warmouth with a high degree of statistical support. However, projections of climate change impacts were varied. If warmer temperatures are considered beneficial to Warmouth, a warmwater species, an expansion of suitable habitat is expected. If *Phragmites* colonized up to 1 m water depth, Warmouth spawning and nursery habitat would effectively be eliminated.

## RÉSUMÉ

Une modélisation de la répartition de l'espèce a été effectuée pour le crapet sac-à-lait dans la baie Long Point, afin de déterminer les caractéristiques environnementales d'un habitat convenable et de le cartographier. Des variables environnementales, notamment la profondeur, le substrat, la température, la végétation, et la qualité de l'eau, ont été utilisées pour prédire la répartition de l'espèce, à l'aide d'une méthode d'apprentissage automatique au sein d'un système d'information géographique. Les éventuelles répercussions des changements climatiques et de la propagation d'une espèce envahissante, le roseau commun, *Phragmites australis*, sur l'habitat du crapet sac-à-lait ont également été examinées. La modélisation de la répartition de l'espèce a permis d'identifier la baie Long Point comme étant un habitat convenable pour le crapet sac-à-lait, grâce à un degré élevé de soutien statistique. Toutefois, les prévisions des répercussions des changements climatiques étaient variées. Si des températures plus élevées sont considérées comme bénéfiques pour le crapet sac-à-lait, une espèce d'eau chaude, on s'attend à ce qu'il y ait une expansion de l'habitat convenable. Si les *phragmites* colonisaient jusqu'à 1 m de la profondeur de l'eau, l'habitat de frai et d'alevinage du crapet sac-à-lait serait alors éliminé.

## INTRODUCTION

Freshwater fishes have declined worldwide primarily due to habitat loss related to direct and indirect effects of human activities (Abell 2002, Jelks et al. 2008). The identification of suitable habitat is an essential step for protecting existing habitat of species at risk. The distribution of Warmouth is widespread in the United States but, in Canada, the species is restricted to a few locations on Lake Erie: Point Pelee National Park, Rondeau Bay (part of which is inside Rondeau Provincial Park), and Long Point Bay, including Turkey Point Provincial Park and Big Creek National Wildlife Area (Edwards and Staton 2009). Warmouth is assessed as 'Endangered' in Canada (COSEWIC 2015), but listed as 'Special Concern' under the *Species at Risk Act*. The species is considered nationally 'secure' in the United States (Edwards and Staton 2009).

Warmouth is thought to prefer vegetated, clear, shallow waters in streams and lakes (Edwards and Staton 2009), although the species is considered tolerant of both turbid water (Larimore 1957, McMahon et al. 1984) and low dissolved oxygen concentrations (Larimore 1957). Adults are found in water depths of 0.1-5 m, although spawning and rearing habitat is found in depths up to 2 m (Lane et al. 1996a, b, c). Habitat at all life stages consists of mud, silt, sand, or gravel substrates along with vegetation, stumps, and rocks (COSEWIC 2005). Spawning occurs in the springtime on muddy bottoms of streams and lakes at water temperatures of 18-32 °C (Edwards and Staton 2009). Edwards (1997) describes the species as a 'sit-and-wait' ambush predator that uses vegetation or debris as cover. Its large mouth allows Warmouth to consume crustaceans, crayfishes, molluscs, and small fishes, as well as aquatic insect larvae (Larimore 1957). Warmouth is a warmwater species and its current distribution in Canada may be limited by temperature. Warming conditions expected with climate change may lead to an expansion of available habitat (Edwards and Staton 2009, Mandrak 1989).

The focus of this study is the Long Point Bay population. Long Point Bay is the largest wetland in the Great Lakes system and is recognized by UNESCO as a biosphere reserve (Thomassen et al. 2013). Long Point Bay remains one of the least developed coastal wetlands in the Great Lakes. However, as Lake Erie is an unregulated lake, water-level changes associated with climate change will likely have direct and substantial impacts on nearshore habitat (Hebb et al. 2013).

Climate change is expected to have substantial impacts on aquatic ecosystems over the next century, causing both thermal changes and changes in water level due to increased evaporation rates (Magnuson et al. 1997). Water depth is predicted to decrease in the Great Lakes by as much as 1.2 m by 2050 in Lake Michigan and Lake Huron, although the prediction for Lake Erie is more modest, up to 0.83 m during summer months (Mortsch et al. 2006). Maximum water temperature is expected to increase substantially in the Great Lakes, by as much as 6.7 °C by the end of this century in Lake Superior (Trumpickas et al. 2009). However, in Lake Erie, the prediction is for 1.6 °C by mid-century and as much as 3.3 °C by the end of this century

(Trumpickas et al. 2009). Given its rarity and reliance on the nearshore habitats, Warmouth is considered highly sensitive to changes in water level (Doka et al. 2006).

Invasive species also pose a substantial threat to species at risk in Canada. In particular, the common reed, *Phragmites australis*, poses a major threat to nearshore species due to its propensity to spread into nearshore habitats and alter aquatic ecosystems (Allan et al. 2013, Bourgeau-Chavez et al. 2015). *Phragmites* can spread both through seed formation and vegetatively through rhizome growth. Seeds are dispersed in the fall and have a germination time of approximately one year (Altartouri et al. 2014). Seedling growth cannot occur underwater; however, rhizome growth can, with a rate of spread of about 1-4 m per year (Altartouri et al. 2014). Although that may not seem rapid, vegetative growth of rhizomes accounted for an increase in *Phragmites* coverage of 18% in one year along the St. Lawrence River (Hudon et al. 2005). *Phragmites australis* can have a significant impact on nearshore environments as it tends to dominate wetlands with large dense stems, outcompeting other types of vegetation (Bourgeau-Chavez et al. 2015) and converting open water to dense stands of emergent growth (Crisman et al. 2014). Although some studies suggest that *Phragmites* growth is inhibited at water depths greater than 1 m (Zhao et al. 2013), it is known to survive in water up to 2 m deep (Altartouri et al. 2014, Crisman et al. 2014). Removal efforts are underway in many aquatic environments in Ontario, but *Phragmites* requires significant effort to remove, and it often regrows via its deep system of underground rhizome growth. *Phragmites* is known to be a significant threat to aquatic habitat at Long Point Bay (Wilcox et al. 2003). The impact of *Phragmites* may be exacerbated by climate change as water level declines and periodic droughts occur, which could allow the species to invade increasingly deeper areas.

The objectives of this study were to estimate the current distribution of Warmouth and to predict impacts of climate change and continued colonization of the invasive reed *Phragmites australis* at Long Point Bay. Species habitats and distributions are increasingly modelled within a Geographic Information System (GIS) framework. A machine learning algorithm based on maximum entropy was used to predict the distribution of Warmouth; and, the future distribution under climate change was projected using thermal and water level forecasts. The potential impact of *Phragmites* invasion on available habitat was also assessed using a depth-based approach. Species distribution modelling was conducted to guide habitat protection and efforts to control the spread of *Phragmites australis*.

## METHODS

Environmental data used to conduct species distribution modelling for Warmouth were taken from a wide variety of sampling surveys at Long Point Bay. Data collection and analytical methods described here are very similar to those described for species distribution modelling of the Pugnose Shiner (*Notropis anogenus*) at Long Point Bay (McCusker 2015).

## DATA COLLECTION

### Bathymetry, water level

Bathymetry data for Lake Erie were downloaded from the National Oceanic and Atmospheric Administration ([www.ngdc.noaa.gov/mgg/greatlakes/erie.html](http://www.ngdc.noaa.gov/mgg/greatlakes/erie.html)) (National Geophysical Data Centre 1999) (Figure 1). Bathymetric sounding data were compiled over a 100-year period for navigation safety and nautical charting by the U.S. Army Corps of Engineers, the NOAA Coast Survey, and the Canadian Hydrographic Service. Spacing of data control tracklines ranged from 500 to 2500 m for the open lake and from 125 to 500 m for nearshore areas. Bathymetric contours were based on the Lake Erie low water datum, the zero-depth employed for bathymetric surveys and nautical charting. Therefore, a correction was required to bring these data in line with water levels that occurred during summer sampling periods from 2002-2014.

Average monthly water levels for Lake Erie were accessed online ([www.glerl.noaa.gov/data/dashboard/GLWLD.html](http://www.glerl.noaa.gov/data/dashboard/GLWLD.html)) for the period spanning from 1918 to the present. Average water levels for June were evaluated from 2002-2014 (the years in which fish sampling occurred) for Lake Erie and compared to the water low for the past 100 years. June water levels over the past decade have been ~1.15 m higher than average monthly water level low. Therefore, the bathymetry layer was adjusted to reflect conditions over the past decade to be consistent with the fish locality data. Water depth within the GIS layer was then compared to those from a transect study by Fisheries and Oceans Canada (DFO) from 2002-2005 (Marson et al. 2010). Based on the discrepancy between the depth layer within the GIS and depth from Marson et al. (2010), bathymetry was adjusted again by ~0.4 m. Despite these attempts to reconcile the bathymetry data with water depth during sampling, some discrepancies may remain as sampling occurred over a number of months and years with fluctuating water levels. Moreover, bathymetric sampling occurred every 125-500 m within the nearshore area, therefore, resolution of the GIS layer is limited.

### Substrate and Secchi Depth

Substrate and Secchi depth data collected by Robin Churchill (Bird Studies Canada) at 300 localities in Long Point Bay were used in the model (Figure 2). Dominant substrate type was classified as either sand, sandy loam, or silt using a modified Wentworth scale (Wentworth 1922). Substrate was assessed by removing below-ground plant parts (e.g., roots, turions/tubers, and rhizomes) using a fine-mesh sieve (2 mm × 2 mm). Substrate data were collected at the same locations in 1976, 1991, 1992, and 2009, although only the 2009 data were used for this study to be consistent with fish locality data.

Substrate data were also obtained from DFO, which conducted bottom sampling along transects in July 2004, and categorized substrate using the Wentworth scale as organic, silt, and sand. These were recorded based on proportional coverage, not dominant substrate type, of sand, silt, and organic substrate types. Sand and silt were the dominant forms (Figure 2) and were inversely related to one another. Organic

substrate was generally confined to the northeast section of the Crown Marsh (Figure 2).

## **Temperature**

Temperature data were compiled from near-bottom temperature loggers monitored by Ontario Ministry of Natural Resources and Forestry (MNR) from 2007-2009 (Larry Witzel, MNR, unpublished data) (Figure 3). The near-bottom temperature records were collected during a three-year project, the Long Point Bay Ecological Assessment 2007-2009. Average, maximum, and minimum values were estimated for all sites within a given year (from June 11-August 31 in 2007; May 15-August 31 in 2008; and May 5-August 31 for 2009). Mean daytime temperatures were evaluated for all sites between the hours of 0900 and 1700. In addition, data from a temperature logger located 1.6 km west of Bait Island in the inner Bay and a gas well located near the interface between the inner Bay and outer Bay were also used. Overall, the broadest spatial coverage of temperature loggers was in 2008, therefore, only data from this year were used to build the species distribution model.

A second source of temperature data came from DFO's sampling records. These records represent point in time temperature readings, rather than average values. However, they provide better spatial coverage of the inner bay of Long Point Bay than the temperature loggers from MNR (Figure 3). The DFO temperature data were sorted by season and year, and the survey from July 2004 was used as it had the broadest spatial coverage.

## **Vegetation**

DFO collected vegetation data along sampling transects in July 2004. Percent cover of submergent, emergent, and floating vegetation, as well as open water were recorded, which sum to 100%. Each vegetation type was analyzed separately, and also combined as 'all vegetation types' (Figure 4).

## **Water quality**

Water-quality data were compiled from DFO sampling records. All records were sorted by year and season and the time period with the best spatial coverage was selected for inclusion in our study. Turbidity data were used from the summer of 2014 and conductivity data from transects conducted in July 2004 (Figure 5). Records from the summer of 2013 were used for dissolved oxygen and pH readings.

## ***Phragmites australis***

*Phragmites australis* has been mapped in Long Point Bay over different time periods. Data were collected from Bird Studies Canada on the *Phragmites* distribution from the southern shoreline of Long Point Bay in 1999, which includes both Big Creek National Wildlife Area and the Crown Marsh (Wilcox et al. 2003). Data were obtained from Nature Conservancy (Kelly Bernard, unpubl. data) which represented a visual interpretation from Google Earth in 2014. Vegetation data, including *Phragmites*, were also obtained from the entire shoreline around Long Point Bay from mapping studies

conducted by MNRF (Bourgeau-Chavez et al. 2015, Young et al. 2011). Collectively, these data were important for visualizing the extent of *Phragmites* presence on Long Point Bay, which currently extends along all shorelines of the inner bay (Figure 6). However, *Phragmites* does not currently extend very far into the water layer used in this study with the exception of some parts of the Crown Marsh and Turkey Point. Given the minimal overlap with environmental layers, we did not include *Phragmites* in a species distribution model of current distribution.

### **Warmouth sampling**

Warmouth were collected at Long Point Bay from 2012-2014, by DFO. In 2012, 46 fish were collected at 28 localities; in 2013, six fish were collected at five localities; and, in 2014, six fish were collected at five localities. The Ontario Commercial Fisheries Association also captured 82 Warmouth in 2009 using trapnets near shore. All of these data were used in species distribution modelling. In addition to these data, 11 individuals were caught by DFO inside the Big Creek National Wildlife Area from 2002-2005 (Marson et al. 2010); however, these were not included as our environmental layers did not extend into that area.

To illustrate the extent of fish sampling in general in Long Point Bay, all fish collection localities from DFO sampling records (2004-2014) as well as Warmouth localities from the Ontario Commercial Fisheries Association in 2009 were plotted with gear types indicated (Figure 7).

### **LOCALITY DATA AND DATA ANALYSIS IN ARCGIS**

Interpolations of environmental data were conducted using the “Topo to Raster” function in ArcMAP 10 with a cell size of 0.0003 (or approximately 25 m x 30 m). The geographic extent of layers was defined using water boundaries of Lake Erie from Scholars GeoPortal (<http://geo2.scholarsportal.info/>). The analysis was restricted to the inner bay of Long Point Bay as most of the fish and habitat sampling was conducted there. A small number of samples (< 5%) were moved to fit on the grid in ArcGIS (typically <100 m). If two Warmouth localities were on the same 25 m x 30 m cell, one was removed so that all localities represented different cells within ArcGIS. This ensured that training and testing sites could not involve the same cell. In total, 67 georeferenced sample localities were included.

Interpolated environmental data were collected using the ‘Extract Multi Values to Points’ function in ArcGIS (n=86 data points). Correlation analysis was conducted among environmental variables and visualized using the package ‘corrplot’ in R (RStudio Team 2015). The final model in MAXENT was run on a subset of environmental variables to reduce the chances of overfitting the model (Radosavljevic and Anderson 2014). Environmental variables were removed if they were either highly correlated with other variables or exhibited inconsistency across sampling surveys. When two variables were highly correlated, one variable was randomly removed from the analysis.

## **RUNNING MAXENT**

The distribution of Warmouth was modeled using MAXENT (Maximum Entropy Species Distributional Modeling, Version 3.3.3k), a presence-only, machine-learning method based on maximum entropy (Phillips et al. 2006). MAXENT can handle a high degree of model complexity, is relatively robust to correlated environmental variables (Elith et al. 2011), and has been shown to perform well compared to a variety of similar methods (Elith et al. 2006). Like all species distribution modeling methods, MAXENT assumes that all environmental variables have ecological importance to the species and that the species' distribution is limited by the environmental variables rather than physical barriers. Analyses were performed with the 10-fold cross-validation method, in which 10% of the data were withheld as 'test' data, and the model was built with the 90% training data. This was repeated across all 10-folds, with each fold (10% set of data) being used as the 'test' data once. The final model prediction was based on an average of the ten models. A regularization parameter of 3.5 was used to avoid over-fitting (Radosavljevic and Anderson 2014).

Model performance was evaluated by assessing the area under the receiver operating curve (AUC), a threshold-independent means of evaluating statistical support (Phillips et al. 2006). The AUC represents the fit of the model, or the ability of the model to distinguish between locations where the species was found and all other locations. Models with an AUC of 0.9 are often considered outstanding and those of 0.7 acceptable (Hosmer and Lemeshow 2000). Elith et al. (2006) suggested that an AUC value of 0.75 indicates a useful model for understanding species distributions with MAXENT. The 1-tailed binomial probability that the model predicted the test data no better than random was evaluated using the 'maximum test sensitivity plus specificity' threshold. This threshold has been found to perform well compared with other threshold approaches (Liu et al. 2005).

The role of each environmental variable was examined using the jackknife approach in MAXENT to evaluate 'test' AUC both for each variable individually and after excluding each variable in turn. Variable importance was estimated by the decrease in AUC when each parameter in turn is randomly permuted across the study site. Suitable habitat was identified in each scenario using the 'maximum test sensitivity plus specificity' threshold, which has been found to perform well compared with other threshold approaches ((Liu et al. 2005).

## **EXPECTATIONS FROM CLIMATE CHANGE AND PHRAGMITES INVASION**

Climate change is expected to decrease water levels due to increased evaporation (Mortsch et al. 2006), and to increase water temperature of the Great Lakes (Trumpickas et al. 2009). Environmental layers were created to represent future conditions. Water depth was decreased by 0.83 m (predicted by 2050 in Mortsch et al. 2006) and temperature was increased by 2 °C in relevant GIS layers. Trumpickas et al. (2009) predicted that water temperature will increase by 1.5-1.6 °C by mid-century, and by as much as 3.3 °C by the end of this century. Therefore, an increase of 2 °C is within the range of possibility.

Projected species distributions following climate change were examined using depth, temperature (using only one temperature layer per model to allow for a wide range of potential outcomes), and two substrate layers (sand and organic layers), which were the same layers used for current distribution modeling. Although relatively clear climate change predictions only exist for depth and temperature, substrate was still considered relevant as it may be relatively slow to change compared to other environmental variables.

After projecting future species distributions under climate change, all cells with water depth < 0.5 m were removed. This was done to maintain consistency between current estimates of habitat and future scenarios as the current map of Long Point Bay had shoreline depths of ~0.5 m, with very few cells having shallower depths. The colonization potential of *Phragmites* under climate change was assessed using a depth-based approach. All cells with water depth < 1 m were removed to mimic *Phragmites* invasion up to 1 m water depth (see Figure 8). This does not represent the worst-case scenario as *Phragmites* has the potential to colonize nearly everywhere within the inner bay assuming it can survive in water depths up to 2 m. In this worst-case scenario, *Phragmites* invasion up to 2 m water depth would effectively eliminate all Warmouth spawning and nursery habitat (Lane et al. 1996b, c).

## RESULTS

### CORRELATION ANALYSIS AND DATA SELECTION

Secchi-disk depth was negatively correlated with depth ( $r = -0.79$ ), and silt substrate data from DFO was negatively correlated with sand substrate data, as they were the two dominant substrate types ( $r = -0.96$ ) (Figure 8). Therefore, Secchi-disk depth and silt data were both removed from MAXENT analysis. Submerged vegetation was strongly negatively correlated with no vegetation ( $r = -0.83$ ). Submergent vegetation was retained as it was the most dominant vegetation type.

Average temperature data from 2008 was strongly correlated with both average and maximum temperature from 2007. Average and maximum temperatures from 2008 were also highly correlated with one another (Figure 9). Maximum, minimum, and average values were included in analyses to determine which was most strongly associated with Warmouth localities.

Water-quality data were evaluated for correlations among data types and for consistency across years (Figure 10). Conductivity was the most consistent across years (average value of  $r = 0.7$ ), although pH ( $r = 0.6$ ), and turbidity ( $r = 0.6$ ) also demonstrated consistency. Dissolved oxygen was the least consistent ( $r = 0.2$ ) across years.

### SPECIES DISTRIBUTION MODELLING

Species distribution modelling identified suitable habitat for Warmouth in the northwestern portion of the inner bay and within the Crown Marsh (Figure 11). The environmental variables used to build the model in MAXENT included depth, substrate, temperature, submergent vegetation, and three water quality variables (conductivity,

turbidity, pH). The average AUC value across test replicates for the final model was 0.98, with most individual variables showing strong statistical support (Figure 12). The 1-tailed binomial probability that the model predicted the test data no better than random was highly significant ( $p < 0.001$ ) using the 'maximum test sensitivity plus specificity' threshold.

Permutation importance showed that depth was by far the most important parameter, accounting for 74% of 'importance', followed by Churchill's dominant substrate type (9%), conductivity (8%), and minimum temperature (7%). The model indicated that preferred habitat was characterized by shallow depths, abundant submergent vegetation, silt substrate, high conductivity (particularly  $>350 \mu\text{S/cm}$ ), and low turbidity.

## **SPECIES DISTRIBUTION MODELING- PROJECTING FUTURE SCENARIOS**

A key, but highly uncertain, factor for predicting future distributions under climate change was the influence of temperature. Different temperature layers showed different patterns with respect to probability of suitable habitat (Figure 13), and these different thermal preferences led to starkly different predictions with climate change (Figure 14). Models based on DFO 2004 temperature data and minimum temperature logger data from 2008 both predicted higher probability of Warmouth presence with warmer water (Figure 13). Based on either of these temperature layers, the distribution of suitable habitat for Warmouth under climate change was predicted to expand, possibly to a large extent, within Long Point Bay (Figure 14). Given the abundance of suitable habitat in either of these scenarios, the impact of *Phragmites australis* colonization was not examined. However, using the average temperature logger data as an environmental predictor within the model, the amount of suitable habitat would decrease to 15% of the current amount following climate change (Figure 14), and no suitable habitat following *Phragmites australis* colonization to 1 m water depth (Figure 15). With the maximum temperature 2008 layer, the amount of suitable habitat following climate change would decrease to 31% of the current amount (Figure 14), and to 3% of current levels following *Phragmites australis* colonization (Figure 15).

## **DISCUSSION**

Species distribution modeling of Warmouth at Long Point Bay produced a habitat model with very high statistical support. Environmental characteristics of suitable habitat were consistent with expectations based on the literature, including shallow depth, silt substrate, vegetation, and low turbidity (COSEWIC 2005, Edwards and Staton 2009). However, projecting future scenarios under climate change contains far more uncertainty. Future projections varied widely from one another depending on which temperature layer was used and whether warmer temperatures were considered favourable or unfavourable in the resulting model. Given that Warmouth is a warmwater species and is widely distributed in the United States, warmer temperatures brought about by climate change are more likely to be beneficial than detrimental for this species. Some authors have speculated that the northern edge of the species' range

may be limited by temperature, suggesting that climate change could lead to range expansion for Warmouth in Canada (Edwards and Staton 2009, Mandrak 1989).

Warmouth was identified as a species at risk with high sensitivity to climate change due to its reliance on nearshore habitat and its limited distribution in Canada (Doka et al. 2006). Reductions in water depth in the inner bay of Long Point Bay may present a risk to Warmouth. A reduction of 0.83 m to the water level of Lake Erie will have a pronounced influence on the extent and location of aquatic habitat at Long Point Bay. In this study, substrate was assumed to remain unchanged in climate change scenarios, and vegetation and water quality parameters were not used to project future distributions as they were difficult to predict. How higher temperatures and lower lake levels will affect substrate, vegetation, and water quality are sources of uncertainty, which could negatively impact the extent of suitable habitat in the future. Another source of uncertainty is *Phragmites australis* colonization. The impact of *Phragmites australis* explored in this study (colonization up to 1 m water depth) is not the worst case scenario for this invasive weed. *Phragmites* has been documented growing in water depths of up to 2 m (Altartouri et al. 2014, Crisman et al. 2014). If this were to occur, Warmouth spawning and nursery habitat would be largely eliminated (Lane et al. 1996b, c).

Barring a large increase in the spread of *Phragmites australis*, Warmouth may be able to expand its range and increase its population size at Long Point Bay as the climate changes; however, this assumes that higher water temperature would be beneficial to the species. Warmouth has a large mouth for its body size and consumes small fishes as prey (Scott and Crossman 1998). This raises an additional concern about what effect an increasing population size of Warmouth might have on other species at risk. Warmouth has similar habitat preferences to many of southern Ontario's freshwater species at risk (e.g., Pugnose Shiner, Spotted Gar) and expansion may be detrimental for other species that share the same habitat.

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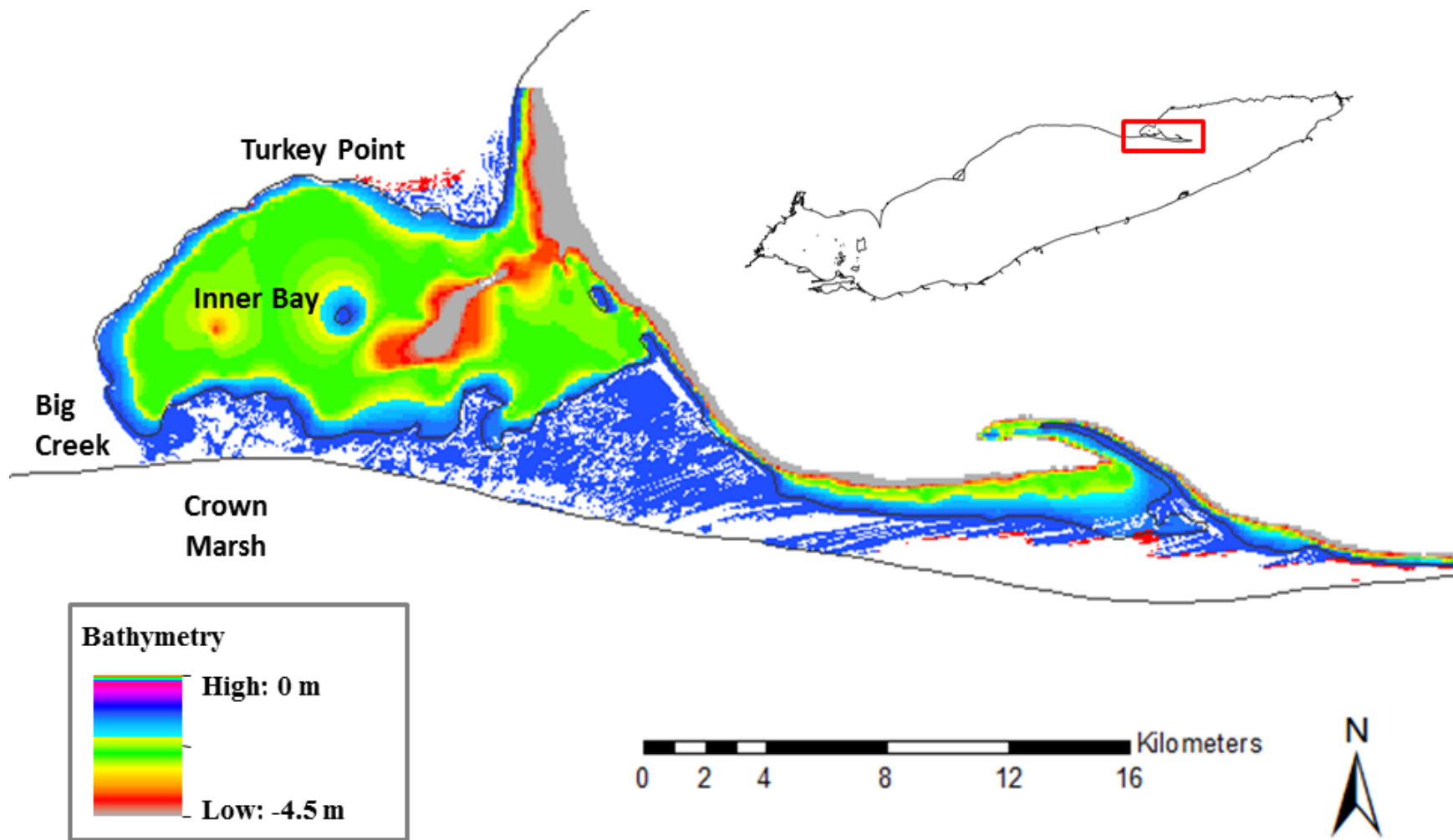


Figure 1. Long Point Bay on the northern shore of Lake Erie (top left), illustrating the inner bay, surrounding marshes, and the long spit of land jutting into Lake Erie. Bathymetry data were downloaded from the National Oceanic and Atmospheric Administration National Geophysical Data Center and adjusted to reflect conditions during summer sampling over the past decade. Water depth for our study area (inner bay and surrounding marshes) is estimated to range approximately 0-4.5 m deep.

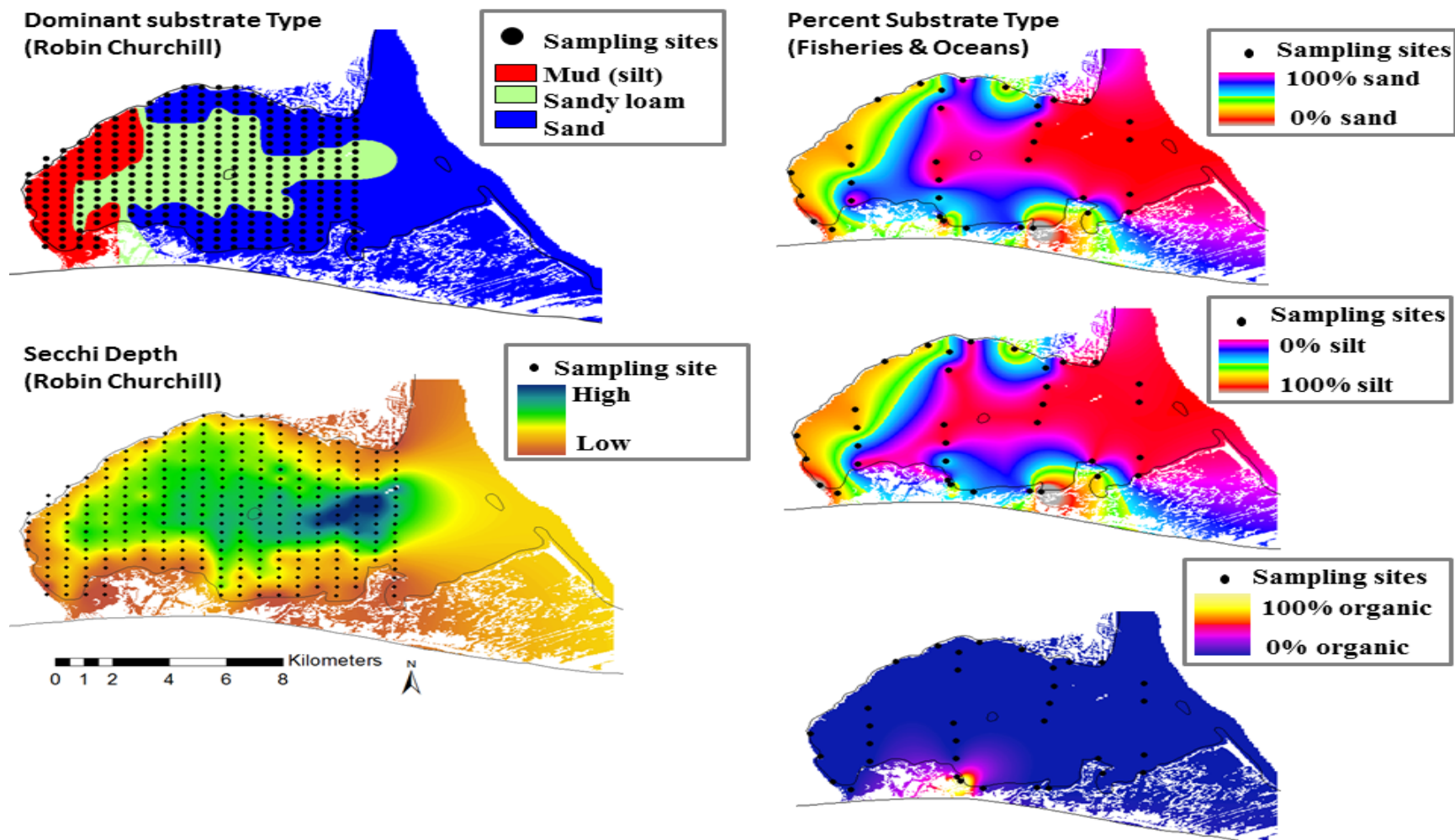


Figure 2. Substrate and Secchi depth data collected by Churchill in 2009 (left) and substrate type collected by Fisheries and Oceans Canada in 2004 (right).

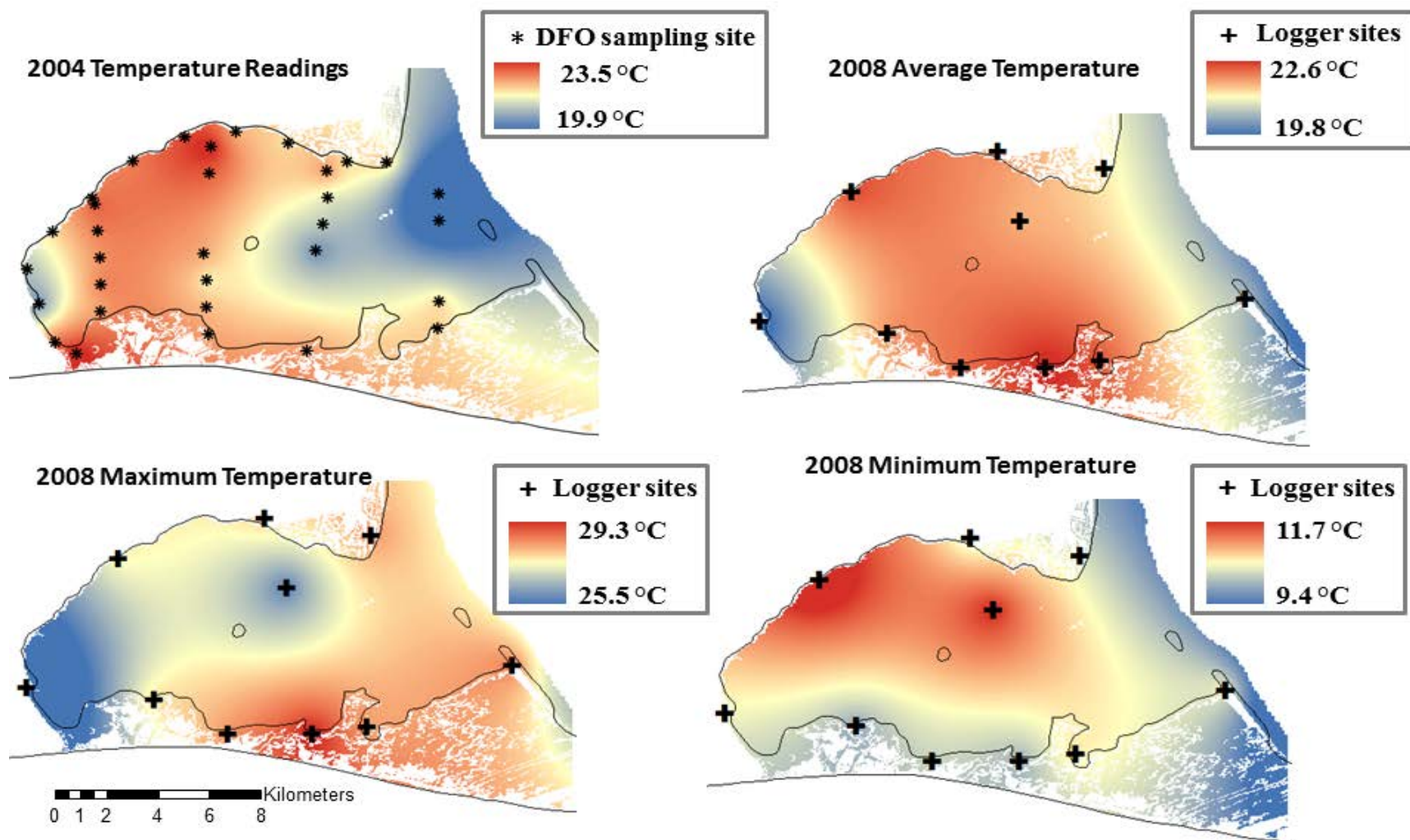


Figure 3. Interpolated temperature based on sampling transects of the inner bay by Fisheries and Oceans Canada in the summer of 2004 (top left), and near bottom temperature loggers set by the Ministry of Natural Resources and Forestry in 2008. Average (top right), maximum (bottom left) and minimum (bottom right) daily temperature readings were collected hourly and averaged across summer months (May-August). See Figure 2 for an appropriate scale.

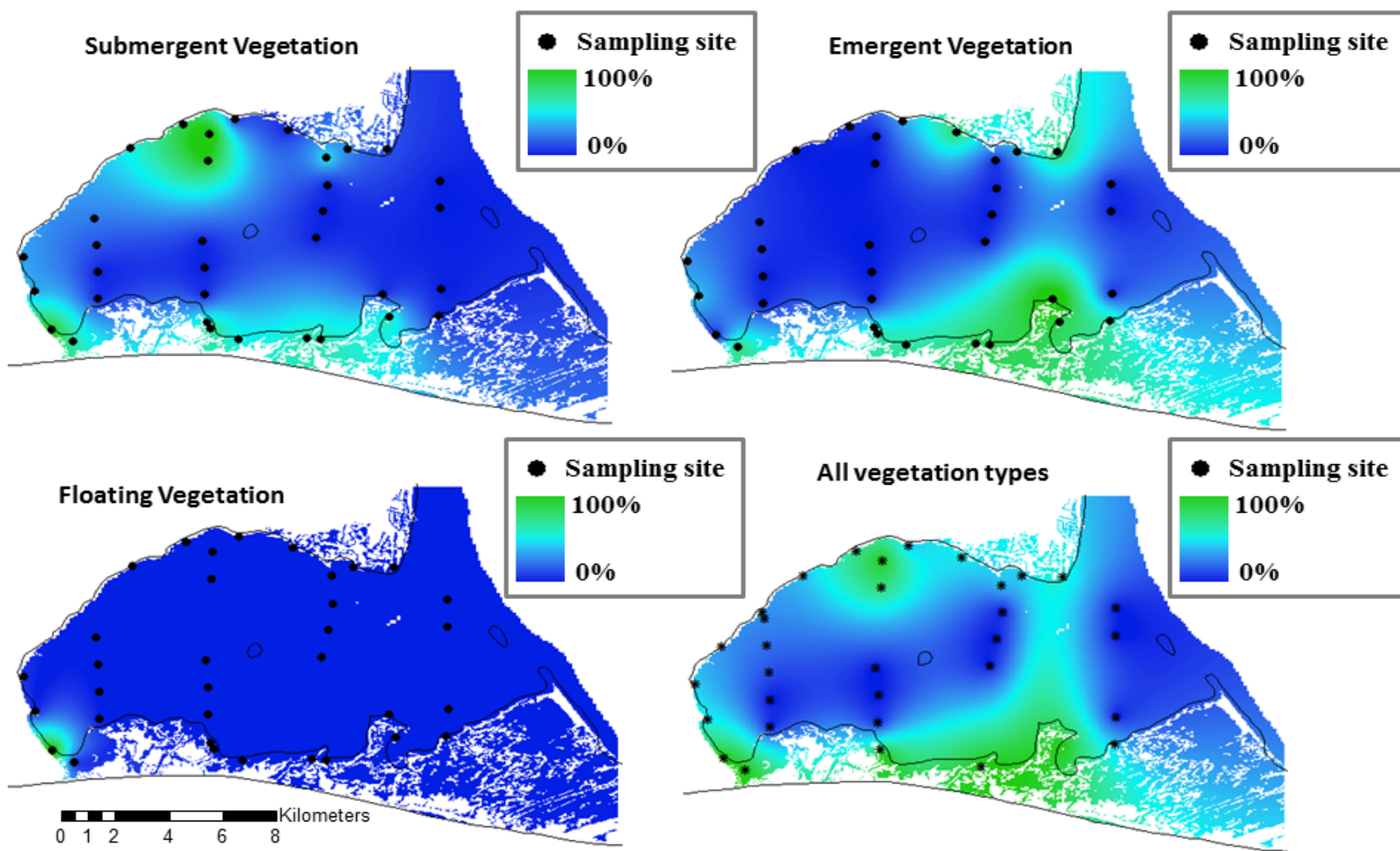


Figure 4. Interpolated vegetation (submergent, emergent, floating, all) based on sampling transects of the inner bay by Fisheries and Oceans Canada in the summer of 2004.

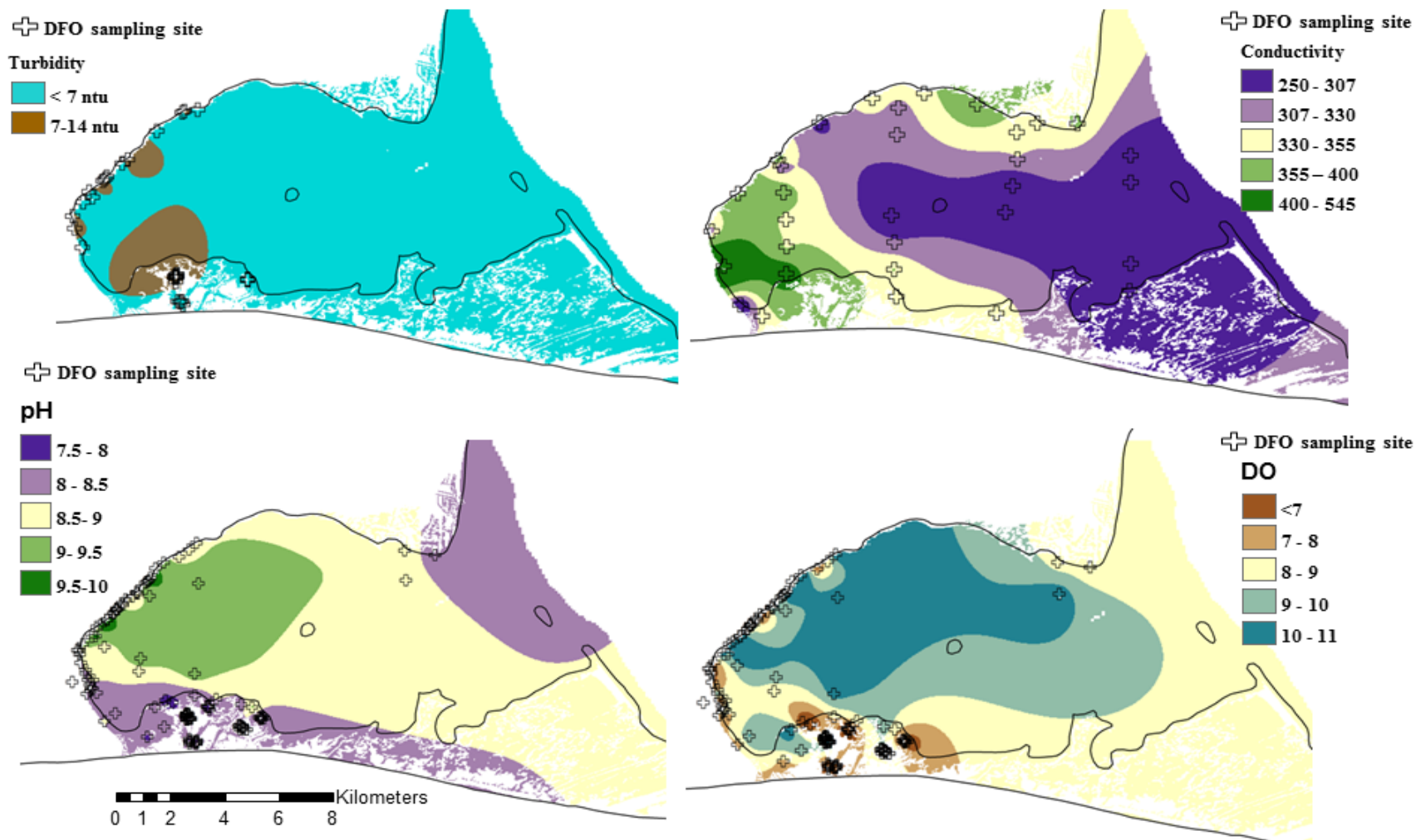


Figure 5. Interpolated water quality data collected by Fisheries and Oceans Canada in the inner bay of Long Point Bay. Data were organized by season and year and the time period with the broadest spatial coverage of sampling sites was used for analysis. Turbidity data (top left) were collected in the summer of 2014; conductivity data were collected in the summer of 2004 (top right); and pH (bottom left) and dissolved oxygen (bottom right) were collected in the summer of 2013.

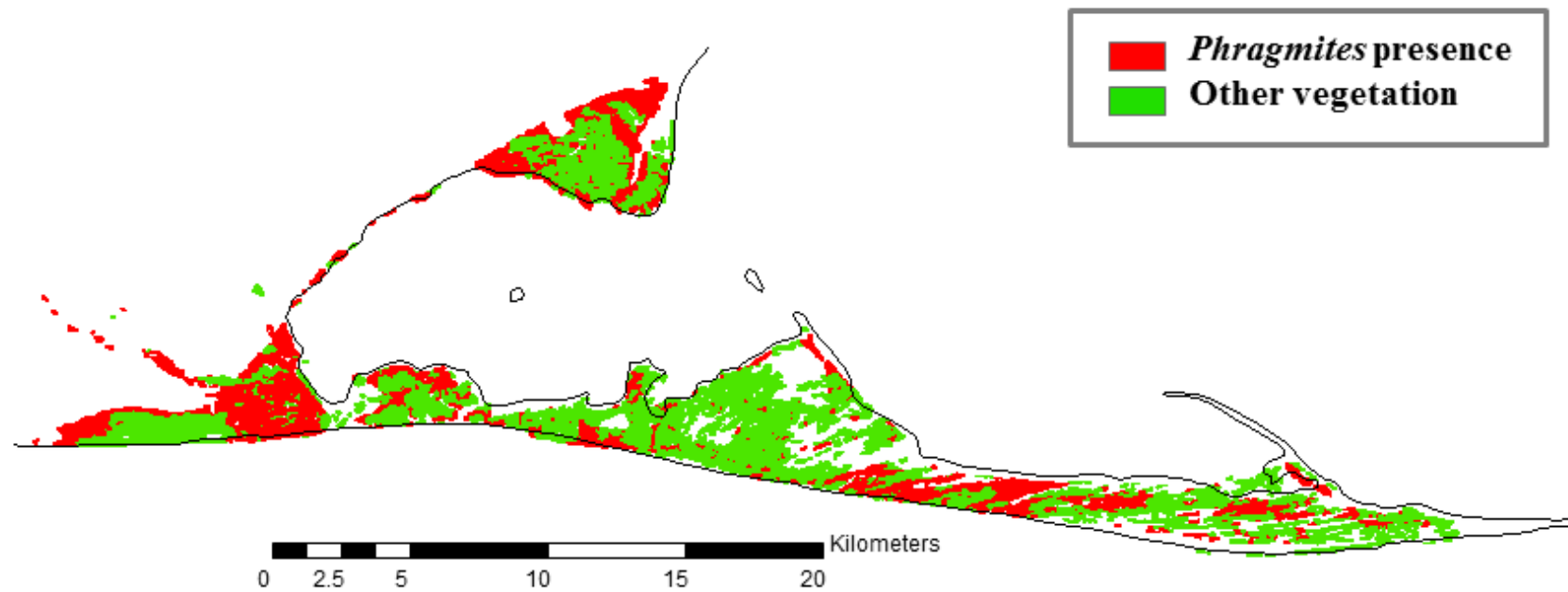


Figure 6. *Phragmites australis* and vegetation mapping of Long Point Bay carried out as part of the Ontario *Phragmites* Monitoring project conducted by MNRF (data courtesy of Adam Hogg, MNRF).

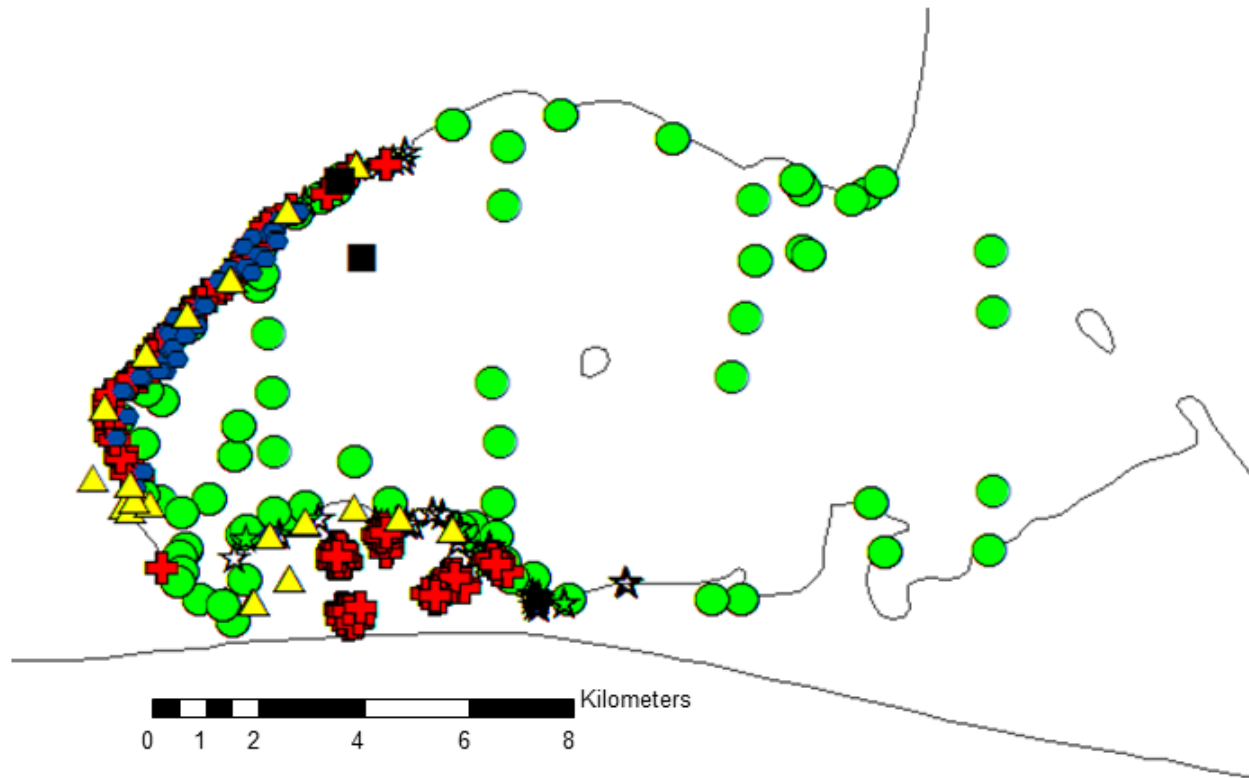


Figure 7. All fish collection localities (all species from Fisheries and Oceans Canada sampling records (2004-2014) as well as Warmouth collection localities from the Ontario Commercial Fisheries Association from 2009, with gear type indicated. Green circles represent the electrofishing boat ('Kingfisher'); stars represent hoopnets (small, 1/4" mesh, 3' diameter hoop); red plus signs represent bag seine (1/8" bag mesh, 1/8" wing mesh); blue circles are trap nets (largely set by the Ontario Commercial Fisheries Association), yellow triangles represent mini fyke nets (1/8" ace mesh, 1/8" ace mesh); and, black squares represent trammel nets (10' deep, 200 yds length, 3" bar mesh, 18" outer walls).

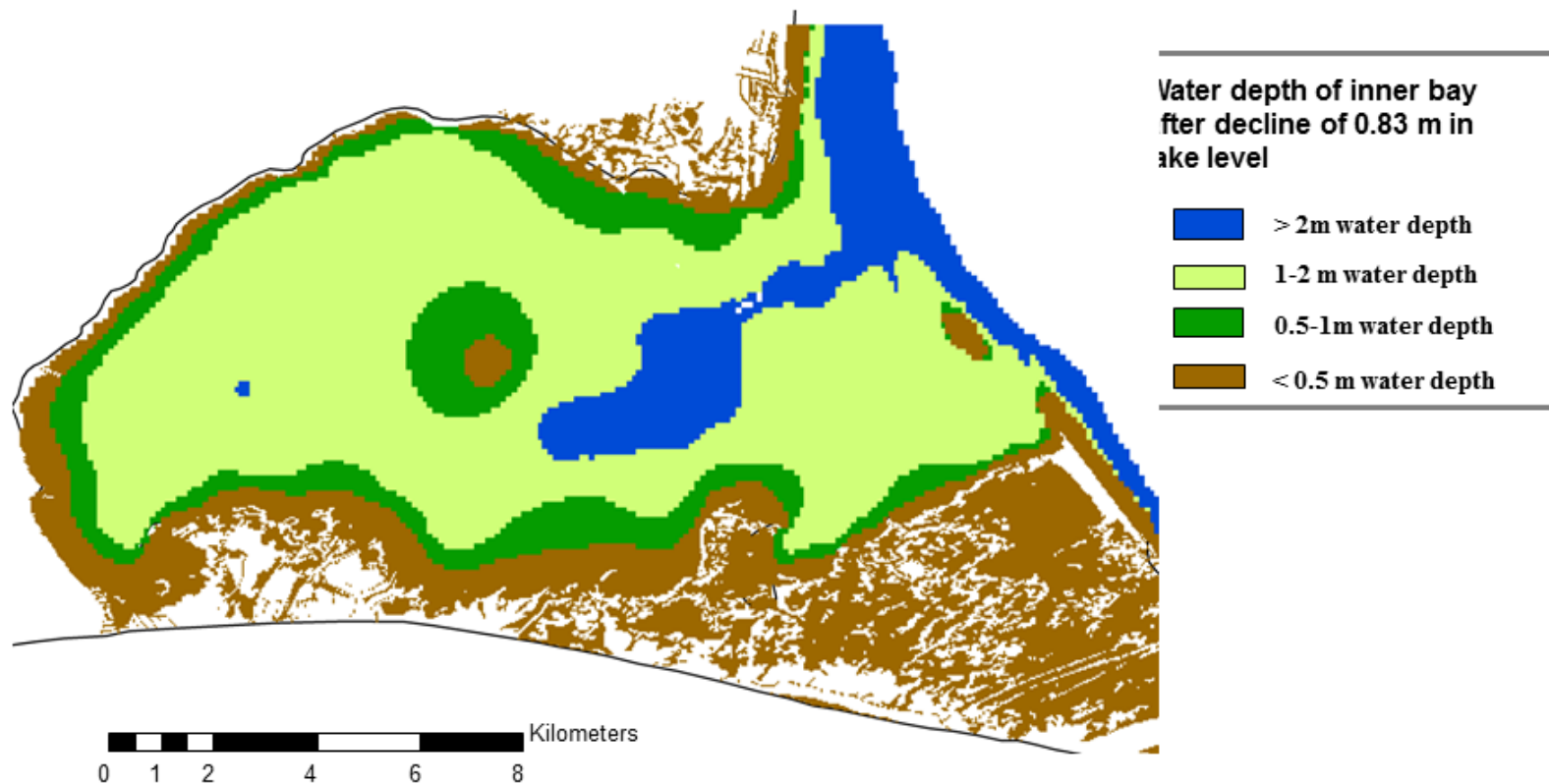


Figure 8. Water depth layers of inner bay after a reduction in lake level of 0.83 m. Dark green areas represent depths that *Phragmites australis* will likely be able to colonize (up to 1 m water depth). Light green areas represent water depths of 1-2 m, which *Phragmites australis* has the potential to colonize.

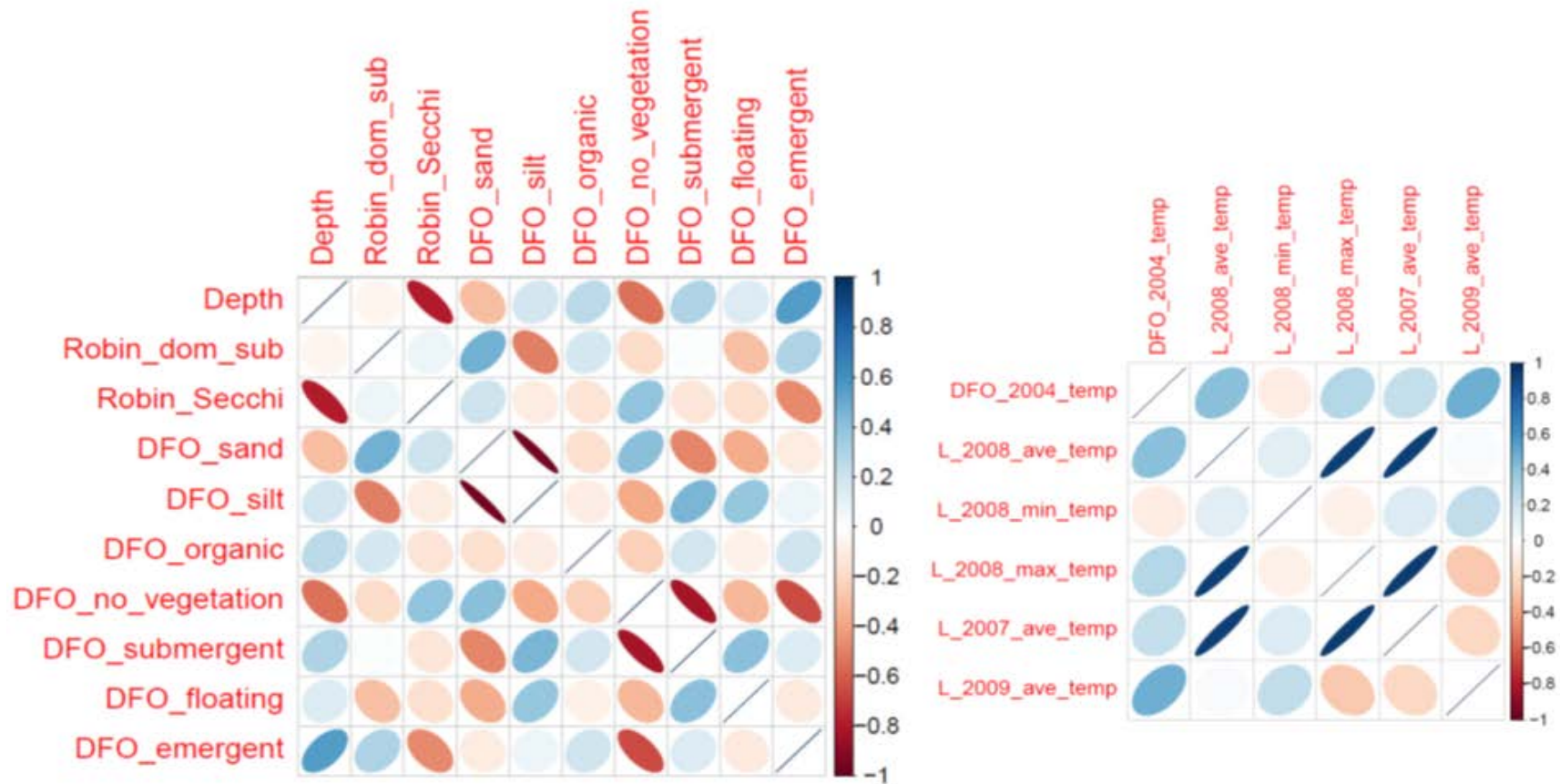


Figure 9. Correlations among depth, substrate, and vegetation (left) and among temperature layers (right). Substrate is presented by Robin Churchill's dominant substrate later as well as individual substrates layers from a Fisheries and Oceans Canada survey in 2004. Secchi depth was collected by Robin Churchill. Individual vegetation layers are from a Fisheries and Oceans Canada survey in 2004 of percentage coverage of different vegetation types. Temperature correlations illustrate similarity across the study site of a transect survey conducted by Fisheries and Oceans Canada in 2004 and data from bottom loggers in 2007, 2008 and 2009 conducted by MNRF. The strength of the correlation is indicated by color in legends shown on the right of both graphs.

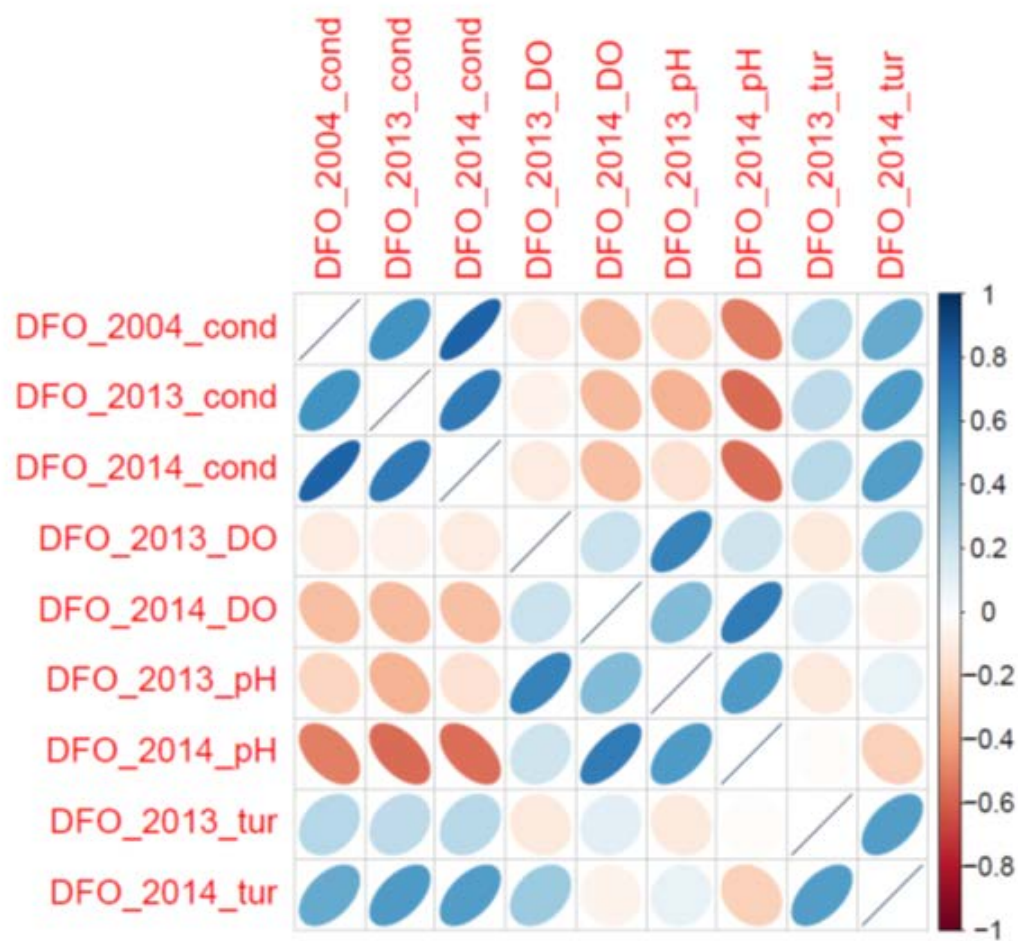


Figure 10. Correlations among interpolated water quality data from surveys conducted by Fisheries and Oceans Canada in 2013 and 2014, as well as conductivity from a transect survey in 2004. The strength of the correlation is indicated by color in legends show on the right.

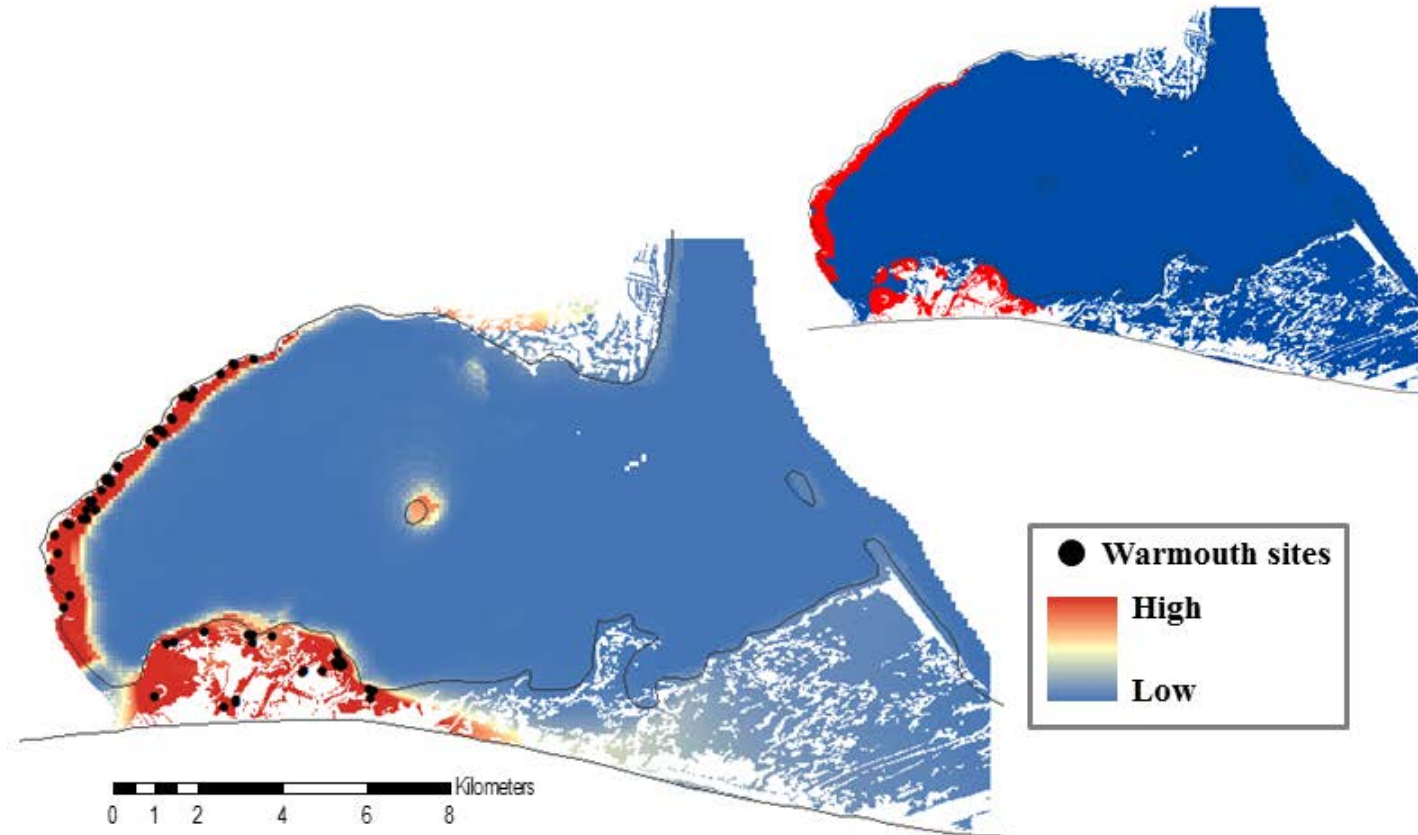


Figure 11. Predictions of suitable habitat based on MaxEnt species distribution modelling showing continuous probabilities (centre). Predictions were converted to a binary 'suitable' (red) versus 'unsuitable' (blue) map using the maximum test sensitivity plus specificity threshold of 0.32 (top right).

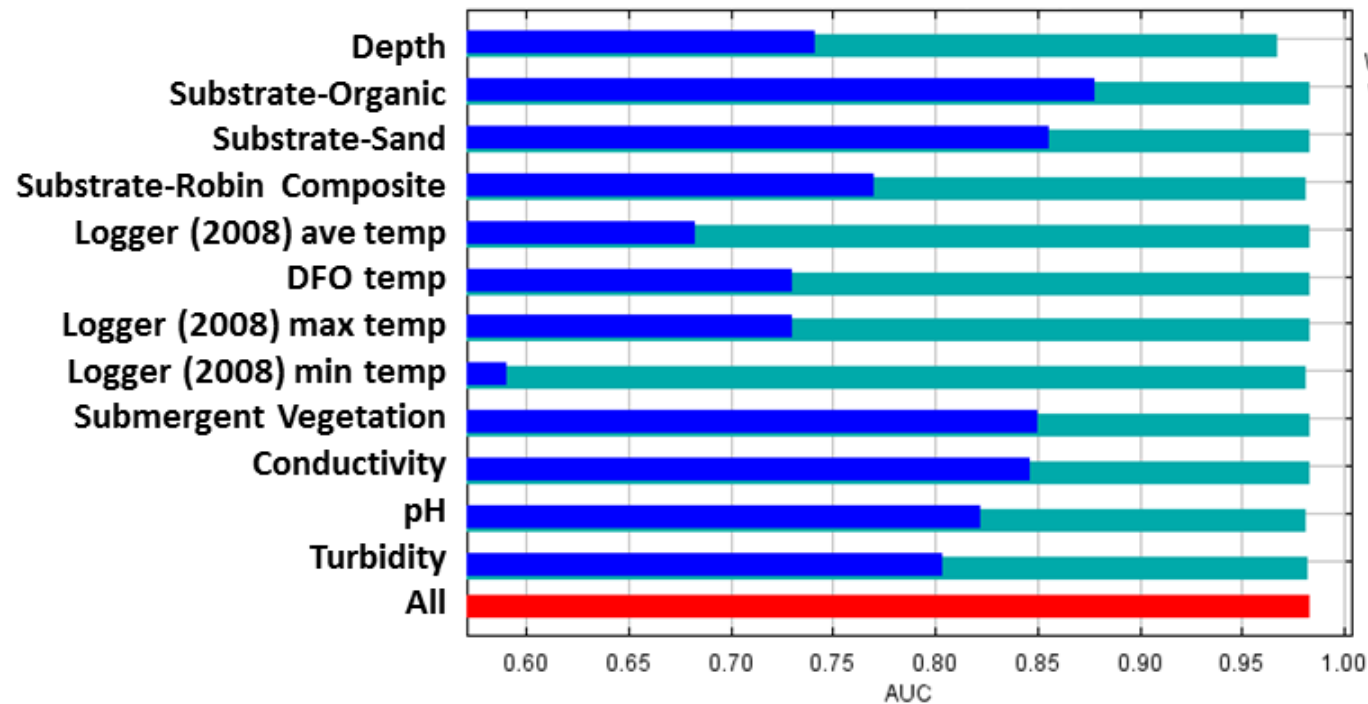
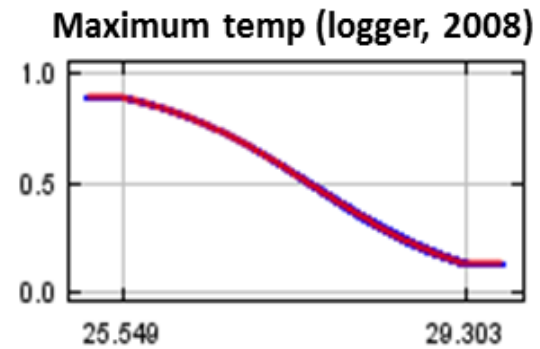
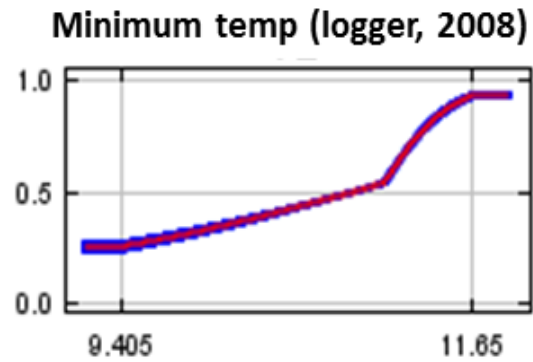
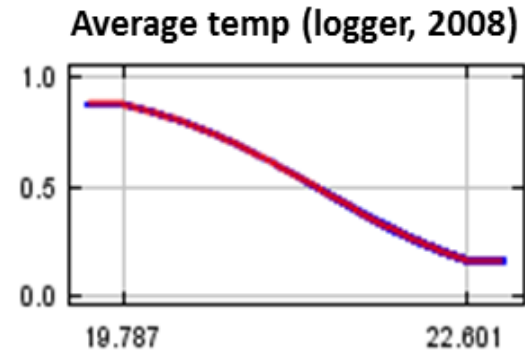
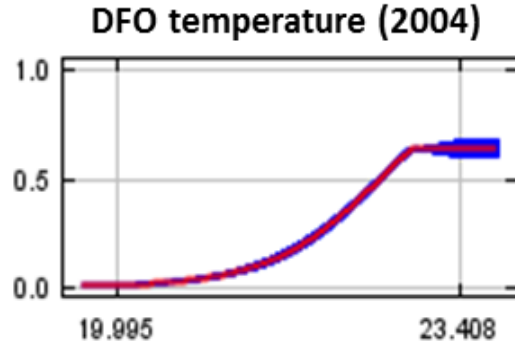


Figure 12. Statistical support ('test' AUC values) for the species distribution model using MaxEnt. The support for the model based on all variables (red bar) is very strong. Support for models based on a single variable (dark blue bars) and all variables other than that variable (light blue bars) illustrates which parameters were most predictive of Warmouth presence. An AUC value of 0.5 indicates the model predictions are no better than random.



*Figure 13. These plots represent predicted suitability of habitat based on a single environmental variable. These are the results of MaxEnt models created using only the corresponding variable.*

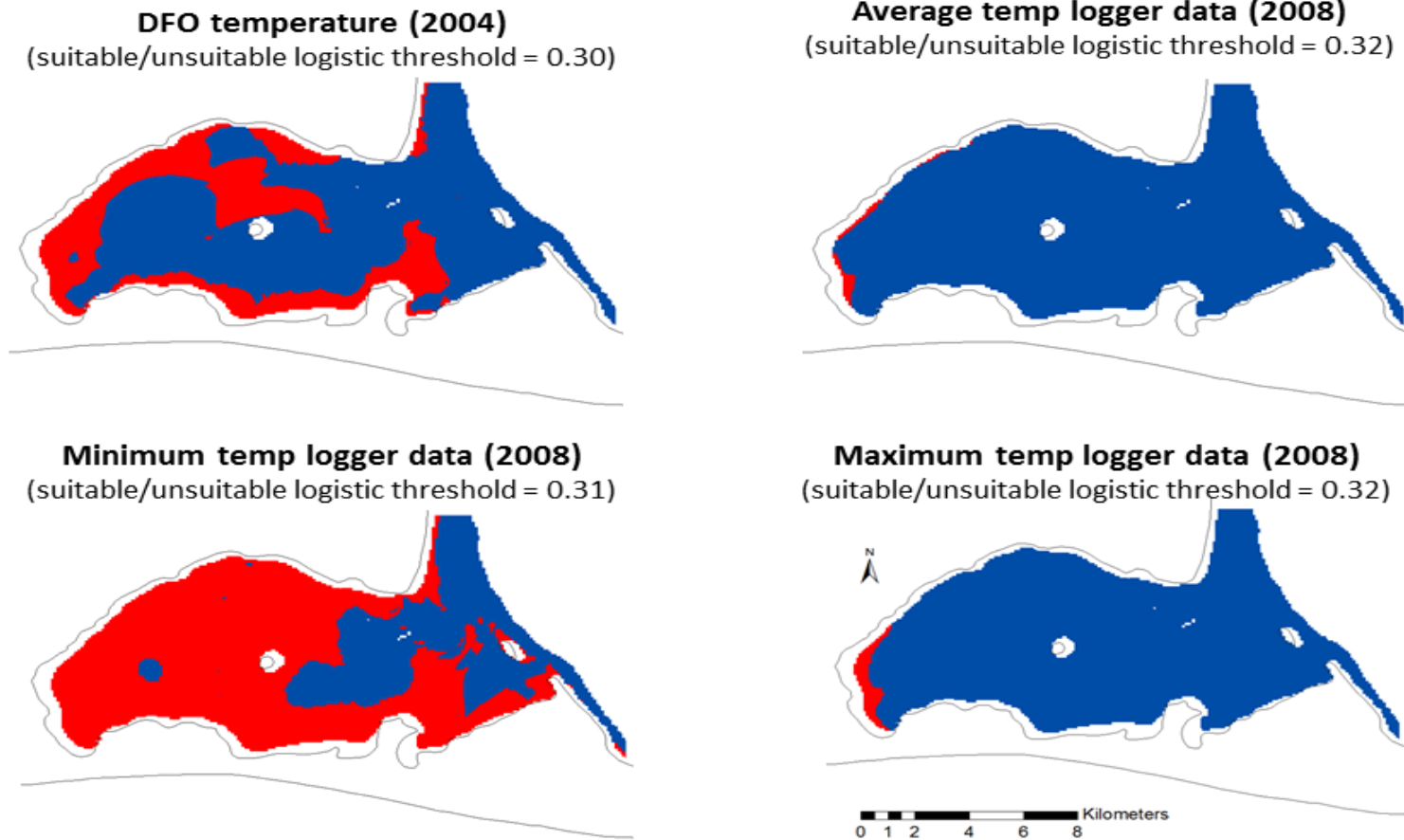


Figure 14. Projections of species distributions under climate change based on depth, substrate (silt and organic layers), and temperature data. Temperature was modeled using Fisheries and Oceans Canada survey data from 2004 (top left) and average (top right), minimum (bottom left), and maximum (bottom right) daily temperatures from bottom loggers in 2008. Suitable (red) and unsuitable (blue) habitat was based on maximum test sensitivity plus specificity threshold values. Water depth layers < 0.5 m removed.

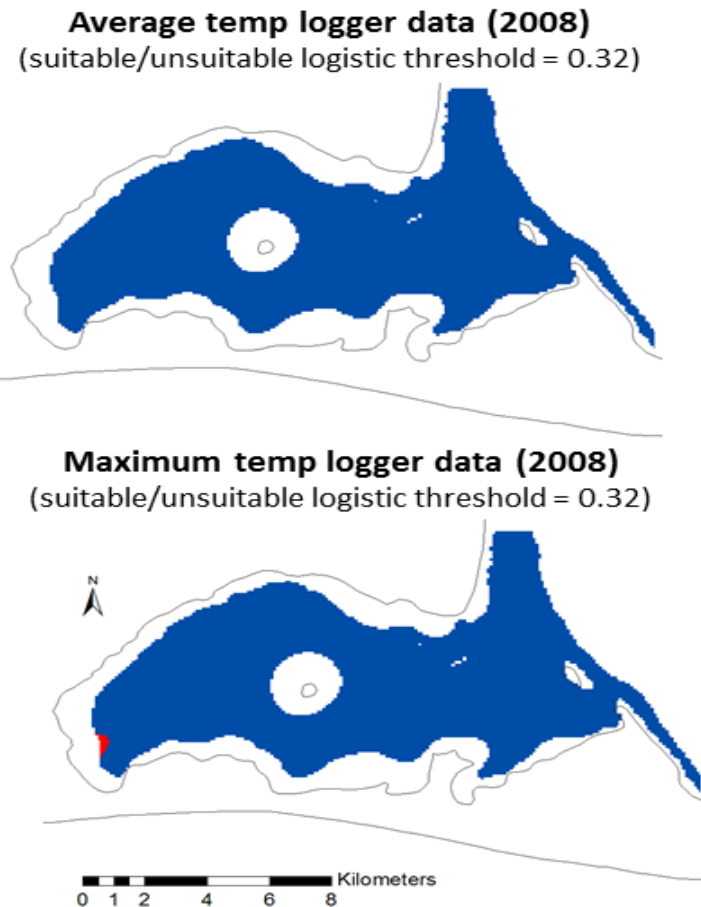


Figure 15. Projections of species distributions under climate change and following *Phragmites australis* invasion up to 1 m water depth. Only average and maximum temperature data were used to illustrate potential worst-case scenarios as other models predicted an abundance of habitat. Suitable (red) and unsuitable (blue) habitat was based on maximum test sensitivity plus specificity threshold values.