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A predictive model for water clarity following dreissenid invasion

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Abstract Optical transparency, or water clarity, is a fundamental property of lake ecosystems which influences a wide range of physical, chemical and biological variables and processes. The establishment of non-native dreissenid mussels in lake and river ecosystems across North America and Europe has been associated with often dramatic, but highly variable, increases in water clarity. The objective of this study was to develop a predictive model for water clarity (Secchi depth, m) in lakes following the establishment of dreissenids. We compiled water clarity data before and after dreissenid invasion from North American lakes that varied in size and nutrient status. An AIC model averaging approach was used to generate post-invasion water clarity predictions based on pre-invasion water clarity and lake morphometric characteristics from a 53 lake dataset. The accuracy of the model was verified using cross-validation. We then extended this model to existing empirical models of lake mixing depth and Walleye (*Sander vitreus*) yield, to demonstrate that increased water clarity associated with dreissenid invasion may have far-reaching physical and ecological consequences in lakes, including deeper thermoclines and context-dependent changes in fish yields.

Keywords Dreissena · Mussel · Transparency · Thermal stratification · *Sander vitreus* · Ecological modelling

Introduction

Optical transparency, or water clarity, is one of the most widely reported indicators of ecosystem condition for freshwater ecosystems and is considered a state variable, defining the vertical distribution where short wave radiation is absorbed and long wave radiation is emitted and stored as heat. Variations in optical transparency can drive changes in surface temperature, heat budgets, and thermocline depth and stability in small lakes (<500 ha; Mazumder et al. 1990; Fee et al. 1996). A similar, but more variable effect is seen in large lakes, where wind and Coriolis effects are increasingly important in determining thermocline depth and the importance of DOC diminishes (Fee et al. 1996). Water clarity is of direct importance to biota: defining the depth to which potentially damaging UV radiation penetrates and the

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maximum depth at which photosynthesis can occur (Kirk 1994), determining how primary and secondary production is partitioned between benthic and pelagic energy pathways, especially in small and shallow lakes that are prone to regime shifts (Mazumder et al. 1990; Vadeboncoeur et al. 2008; Higgins et al. 2014), and influencing predation and reproduction for fish populations that use visual cues (Ryder 1977). Changes in the concentration of suspended particles through the process of eutrophication or the grazing action of herbivores (like dreissenids) can have a large effect on water clarity and lake mixing depths.

The translocation and establishment of *Dreissena polymorpha* (zebra mussel) and *D. rostriformis bugensis* (quagga mussel) across Eurasia and North America has been associated with often dramatic, but highly variable, changes in suspended particle concentrations and water clarity (Higgins and Vander Zanden 2010). Such changes are associated with two processes: a ‘fast’ (minutes to days) process where high dreissenid densities and filtration rates directly reduce particle concentrations and improve water clarity, and a ‘slow’ (months to years) process where nutrients are redistributed from the pelagic zone to the littoral zone, and eventually buried within the sediments, further reducing pelagic plankton growth and biomass but increasing nearshore production (Hecky et al. 2004). This redistribution of energy and matter affects a variety of physical, chemical and biological properties, including water clarity, that are sustained for decades or longer (Higgins 2013). Effects of dreissenid induced changes in water clarity on aquatic ecosystems may induce changes in physical processes such as mixing depth (Fee et al. 1996; Yu and Culver 2000) and can alter patterns of habitat use and energetics of fishes (Rennie et al. 2009, 2012, 2013, 2015).

The effect of dreissenids on water clarity is a function of their filtration rate, ecosystem size, hydrodynamics (i.e. horizontal and vertical mixing), particle renewal rates and other factors such as sediment resuspension (Strayer et al. 1999; Vanderploeg et al. 2002). However, because dreissenid population densities at the ecosystem scale are not routinely estimated and hydrodynamics of most systems are poorly understood, it has remained challenging to develop robust mechanistic models including all of these important parameters and processes. However, in the absence of more complex mechanistic models, the development of statistical-based models that incorporate at least some of the important mechanisms would be useful to understand how the establishment of dreissenids might influence a wide range of physical, chemical, and biological processes in water bodies at high risk of invasion. For example, such models could be used to predict changes in thermocline depth, stability and heat content, photosynthesis (Higgins et al. 2014), and could be combined with fisheries models (Lester et al. 2004) to estimate potential changes in yield as a consequence of dreissenid invasion.

The primary objective of our study was to define a predictive model for water clarity (as Secchi depth, m) following dreissenid invasion based on commonly available limnological parameters that are likely to be included in most monitoring programs. As a secondary objective we apply the predictive water clarity model to existing limnological and fisheries models to demonstrate the value in extending our model to describe the potential for dreissenids to influence physical lake processes and biota. Walleye (*Sander vitreus*) production models were used as this species is among the most sought-after commercial and recreational species in North America (Kinnunen 2003; Fisheries and Oceans Canada 2010), and has been shown to exhibit light sensitivity (Lester et al. 2004).

Methods

Data compilation

Data were compiled from various sources including the Environmental Protection Agency (EPA) Storet database, Cornell University Knowledge Network for Biocomplexity (KNB) database, Minnesota Pollution Control Agency (MPCA), the Michigan and Wisconsin Departments of Natural Resources, Ontario Ministry of the Environment and Climate Change (OMOECC), the Ontario Ministry of Natural Resources and Forestry (OMNRF) and the scientific literature. Grand mean values for some Great Lakes and other freshwater lakes were obtained from published literature on dreissenid effects on water clarity (Higgins and Vander Zanden 2010). All data came from mid-continental North America (Iowa, Michigan, Minnesota, New York, Vermont, Wisconsin, and Ontario) and covered a wide range of lake morphometric characteristics (Table 1). Dates of invasion are based on those listed on the USGS website (http://nas.er.usgs.gov/taxgroup/mollusks/zebramussel/) for American lakes and on published invasion dates for Canadian lakes, which were cross-referenced with peer reviewed literature where available. Though over 600 freshwater lakes were identified as being invaded by dreissenids (Benson 2013), a total of 62 North American lakes were found with sufficient data to permit an analysis of water clarity in lakes invaded by dreissenids ("Appendix 1").

Data were constrained to include Secchi depth measured during the ice-free period at multiple pelagic sampling stations in a lake. Following the methodology of similar analyses (Higgins and Vander Zanden 2010; Higgins et al. 2011; Cha et al. 2013) data had to conform to the following criteria to be included: (1) data were available for both the pre- and post-invasion periods, (2) pre-invasion data were from up to 15 years before invasion and post-invasion data within 25 years since invasion, (3) individual data points were within ±2 standard deviations (SD) from annual mean value (to avoid the influence of outlier values), (4) data were from the summer "ice-free" season (April–November) and (5) data were from stations chosen to represent a central location in the lake, or, where data were available, by averaging across multiple stations. Lakes with more than three data points per year were included when calculating annual mean and SD values, and lakes with at least three annual mean data points in both the pre- and post-invasion periods were included when calculating grand mean and SD values.

For lakes that did not have reported thermocline depths or available temperature profile data, thermocline presence and depth was estimated from lake surface area using the equations of Hanna (1990). Equations in Hanna (1990) can over predict mixing depth for very large temperate lakes because they do not account for the Coriolis effect (Fee et al. 1996) so maximum mixing depth was set to 20 m for temperate lakes with surface area >4000 ha that had no reported thermocline depth. Lakes with greater than 80 % of lake area above mixing depth were defined as "mixed", and those with <80 % were defined as "stratified" (sensu Higgins and Vander Zanden 2010).

Statistical analysis

Observed patterns of water clarity changes after dreissenid invasion were examined in 62 lakes and compared graphically against a 1:1 line representing no change, and a paired *t* test to evaluate change among lakes, We also evaluated the potential effects of the dreissenid community present in a lake (zebra mussels only versus zebra and quagga mussels together) in order to determine whether this played a significant role in our results. The comparison was evaluated using a two sample *t* test (with a Welch correction on the degrees of freedom to account for differences in variance between groups). Residuals were examined to ensure the satisfaction of assumptions of homogeneous variance and normality. All statistical procedures were carried out using R (version 2.15.2, R Development Core Team 2012).

Standardized *Z*-scores were used to graphically display long-term Secchi depth changes in a subset of lakes where raw data over multiple years were available ($n = 42$, see "Appendix 1"). As in Higgins (2013), mean annual parameter values for each year's growing season (April–November) were used to calculate the pre- and post-dreissenid invasion period grand means. *Z*-scores were calculated as:

$$Z = \frac{\mu\mathrm{A} - \mu\mathrm{Pre}}{\mathrm{SD\ Pre}} \quad (1)$$

where μ_A is the post-invasion annual mean, μ_{Pre} is the pre-invasion grand mean, and $\mathrm{SD}_{\mathrm{Pre}}$ is the pre-invasion grand standard deviation.

Table 1 Morphometric characteristics of 62 North American lake ecosystems used in this study to evaluate zebra and quagga mussel effects on water clarity

Characteristic	Units	Range	Mean	Median
Surface area	ha	43.3–5 959 600.0	170,745.8	448.0
Maximum depth	m	2.7–244.0	32.0	18.3
Mean depth	m	1.5–88.6	12.3	6.4

Model development and selection

Biologically meaningful parameters were chosen to be included in models and various combinations of these parameters were investigated using model selection criteria (Burnham and Anderson 2002). We evaluated models to predict Secchi depth in lakes invaded by dreissenids as a function of pre-invasion Secchi depth, lake size and mean depth, and pre-invasion thermal stratification. While dreissenid densities in most invaded ecosystems are not known, previous meta-analyses have demonstrated that the magnitude of dreissenid impacts on particle concentrations generally decline with increases in the volume of the surface mixed layer (Higgins et al. 2011), and we include such variables within our model evaluation process. The model parameters examined were deemed biologically relevant based on their interaction with dreissenids reported in previous research (Cha et al. 2013; Higgins and Vander Zanden 2010) and the contribution of other factors such as lake size and mean depth in dictating water clarity (Fee et al. 1996). However, the inclusion of mean depth as a variable reduced the number of lakes in our model selection exercise from 62 to 53.

The relationship, which would be traditionally fit with a log–log transformation, was described with a multiplicative generalized linear model (GLM) to avoid issues in back-transformation in the interpretation and application of the model. In a GLM, the response variable remains untransformed. When the variables in the linear predictor are log transformed, the GLM's log-link defines a multiplicative model between the response and the predictors. The expected value of "y" is calculated from the linear predictor through the inverse link function; in the case of the log-link this is exponentiation. For a single predictor, the model fit for the mean response of our GLM would be:

$$y = e^{(a+b*\log(X))} \tag{2}$$

which simplifies to:

$$y = e^{a} * X^{b} \tag{3}$$

The coefficients a and b are estimated using likelihood-based methods in the GLM. See Zuur et al. (2013) for additional details on the use of GLM's in ecological analysis.

Akaike's Information Criterion (AIC) was used to determine which models best described Secchi depth following dreissenid invasion. Models were compared using the second-order Akaike's Information Criterion for smaller sample sizes (AIC_c, Burnham and Anderson 2002). Measures used to determine strength of evidence for each model include $\Delta\text{AIC}_\text{c}$ (the difference between the AIC for model i and AIC of the "best" model) and Akaike weights ($w\text{AIC}_\text{c}$). $\Delta\text{AIC}_\text{c}$ values <2 indicates empirical support for the model (Anderson 2008) and the $w\text{AIC}_\text{c}$ of each model indicates the probability that it is the best model among the set (Burnham and Anderson 2002). The model which produced the smallest AIC value (AIC_{min}) was determined to be the "best" model (Akaike 1973). In cases where no model has overwhelming support, AIC model averaging is used where individual model parameter estimates (of post-invasion water clarity, in this case) are generated and weighted based on their $w\text{AIC}_\text{c}$, then are summed to generate a single model-averaged estimate across all models. Models with a $\Delta\text{AIC}_\text{c} < 7$ (which is a common threshold in wildlife literature for similarity among models, Arnold 2010) were chosen as having similar explanatory power from in the model selection process, as the remaining models with varying parameter combinations contributed relatively little to the model averaging process (i.e. $w\text{AIC}_\text{c}$ values too low to make any meaningful additional contribution of explained variance relative to the top four models).

The null model, which consists of only the intercept and no predictor variables, was included in model comparisons as an indicator of the relative performance of the remaining models.

In order to determine the predictive efficacy of our models, leave-one-out cross validation (LOOCV) was used to assess model fits when applied to independent data and is commonly used on small datasets with a predictive outcome (Wong 2015). We estimated the predictive accuracy of the model using a cross-validation r^2 (Xr^2, sensu Rennie et al. 2005):

$$Xr^2 = 1 - \frac{\Sigma\left[\text{y\_i}_{\text{observed}} - \text{y\_i}_{\text{predicted}}\right]^2}{\text{SS}_\text{T}} \tag{4}$$

where $\text{y}_{\text{observed}}$ is the observed value of post-invasion Secchi depth from the lake excluded from model generation, $\text{y}_{\text{predicted}}$ is the value of post-invasion Secchi depth predicted from the subset of data from which the observed values were excluded, i is the lake excluded from parameter estimation in the LOOCV iteration and SS_T is the total sum of squares estimated as the variance of post-invasion Secchi depth times $n-1$, where n is the number of observations used to generate the model (Rennie et al. 2005). Cross-validation r^2 calculation was based on that of traditional r^2 values (e.g. Sokal and Rohlf 1995) with the exception that we used independent data in the leave-one-out procedure, versus observed values included in the model, to estimate the statistic.

Applications

The water clarity model developed above was then applied to a suite of lakes in the province of Ontario, Canada using lake morphometric information and Secchi depths of uninvaded lakes (or pre-invasion measures of invaded lakes) reported by Lester et al. (2004, "Appendix 2") in order to estimate Secchi depth following a hypothetical dreissenid invasion. We then extended this model to examine how these predicted Secchi depth values affect (1) thermal structure of lakes and (2) Walleye yield, using models defined in the literature, as described below. These particular variables were chosen because both have published predictive models linking these responses to water clarity and they represent ecologically and limnologically important parameters in freshwater ecosystems that could potentially be affected by dreissenid invasion.

Hypothetical effects of dreissenids on mixing depths in 49 Walleye lakes in Ontario (Lester et al. 2004) were assessed using an empirical model by Fee et al. (1996) that relates the mixing depth to lake area and water clarity.

Estimated mixing depth (z_{mix}) was determined from percent light transmission per meter (T%) following relationships presented in Fee et al. (1996), which combine and simplify to:

$$z_{mix} = -0.08 + 0.0607 \times A_o^{0.25} + 0.80 \times e^{0.022T\%} \tag{5}$$

where A_o is lake surface area (m^2). T% was estimated as:

$$T\% = 100 \times e^{-k} \tag{6}$$

where k is the estimated light extinction coefficient (Fee et al. 1996). k was estimated from Secchi depth (z_{sec}, m) using the equation (Wetzel 2001):

$$k = \frac{1.7}{z_{sec}} \tag{7}$$

This procedure was applied to both the pre-invasion (reported) and post-invasion (estimated) water clarity in order to predict the change in estimated thermocline depth as a result of increased water clarity due to dreissenid establishment.

Effects of predicted post-dreissenid invasion Secchi depth on Walleye yield were investigated using equations presented in Lester et al. (2004). Lester et al. (2004) estimate Walleye yield via available juvenile-adult Walleye habitat based on a number of parameters, including water clarity ("Appendix 3"). Estimates of yield were generated and compared under scenarios with and without dreissenids present to represent the potential impacts of dreissenid-induced water clarity changes on Walleye yield in this suite of Ontario lakes. In predicting post-invasion Walleye yield, we varied the parameters relating to light limitation (z_{sec}, "Appendix 3"). However, because the model also incorporates mixing (thermocline) depth in defining the habitat used by Walleye, we ran a second set of predictions allowing both water transparency (z_{sec}) and mixing depth (z_T) to change, where changes in mixing depth as a consequence of changes in water transparency were estimated as described above.

Finally, we evaluated error propagation from the predicted values from our equations through both the mixing depth and Walleye yield models. The parameter estimates (Table 2) and variance–covariance matrices from each of the four final water clarity models were used to generate 1000 sets of predicted post-dreissenid Secchi depth using a multivariate normal distribution for each model. Predictions from each model were then averaged using the AIC_c weights, and passed through each of the mixing and Walleye models. Predicted changes in Walleye yield due to dreissenid invasion were examined against post-invasion Secchi depth and thermocline depth.

Results

Among all lakes included in our survey ($n = 62$), Secchi depth was highly variable across systems, ranging from 0.5 to 12.7 m pre-invasion (mean ± SD, 3.0 ± 1.8 m) and 0.3 to 14.8 m (3.6 ± 2.2 m) post-

Table 2 Predictive model coefficients and fits of post-dreissenid invasion Secchi depth (m) for 53 North American lakes

Model	Predictor variables								
	Intercept	Log (Pre-invasion secchi) (m)	Log (mean depth) (m)	Log (area) (m^2)	Stratification (1 = mixed, 2 = stratified)	AICc	ΔAIC_c	$wAIC_c$	Adj.R^2
1	0.186 (0.078)	0.788 (0.076)	0.106 (0.046)			121.56	0.00	0.58	0.903
2	0.143 (0.096)	0.873 (0.060)		0.023 (0.011)		122.92	1.36	0.29	0.896
3	0.283 (0.071)	0.904 (0.062)				125.46	3.89	0.08	0.876
4	0.265 (0.073)	0.870 (0.073)			0.077 (0.088)	126.91	5.34	0.04	0.876
5[a]	1.310 (0.084)					217.80	96.24	0.00	0.000

Models are listed in order of AIC rank, with the top model listed first. The top four models were used in model averaging to generate predicted values using $wAIC_c$ as weighting factors in averaging the predictors. Values in parentheses are standard errors of the coefficient estimates

[a] Indicates the null model

invasion. Secchi depth changes following dreissenid invasion were also highly variable across lakes, ranging from a decrease of 0.85 m in North Lake, WI to an increase of 3.49 m in Lake Ontario, ON. Increases in Secchi depth following dreissenid invasion were found in 79 % of lakes analyzed (Fig. 1), with a statistically significant mean increase of 0.53 m (95 % CI 0.36, 0.71; $t_{\text{paired}} = 5.14$, $df = 61$, $p < 0.0001$).

For lakes with long term datasets available (n = 42), our results indicate increased water clarity after dreissenid invasion persists up to 20 years post-invasion (Fig. 2). Variation in z-scores was high but the trend of an overall increase among systems is seen in the post-invasion period, with some annual post-invasion values being >6 SD's above the pre-invasion mean.

Of the 62 lakes with sufficient data, 8 had both zebra and quagga mussels present. Analyzing the difference between these two categories, without constraining lake morphometric variables, demonstrated lakes with both species present showed a higher degree of increase in water clarity than those with only zebra mussels ($t = 3.1, df = 7.6, p < 0.05$). Mean absolute change of Secchi depth for lakes where only zebra mussels had invaded was 0.37 ± 0.61 m (mean ± SD, $n = 54$) compared to an increase of 1.68 ± 1.16 m ($n = 8$) when both species of dreissenids were present (Fig. 3).

We performed model selection on lakes with complete observations only; removing lakes without mean depth estimates reduced our total sample size to 53. The 53 North-American lakes included in model development spanned a wide range of size, depth and trophic status ("Appendix 1").

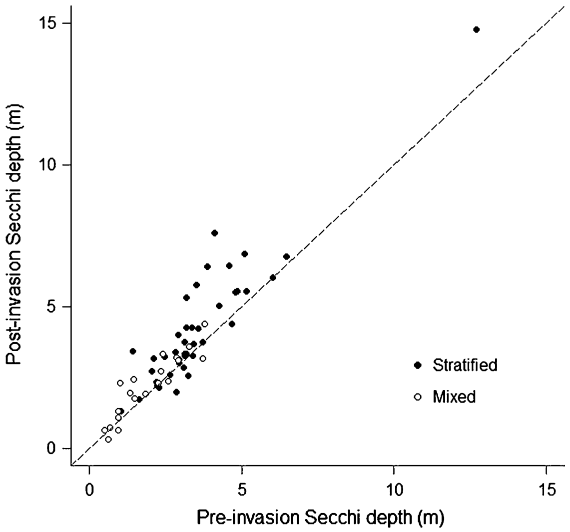

Fig. 1 Observed Secchi depth (m) showing changes in water clarity (deviation from the 1:1 line) following the invasion and establishment of zebra mussels in 62 North American lakes. Closed circles represent lakes that stratify during summer months and open circles represent non-stratified (mixed) lakes. Values above the 1:1 line (*solid line*) indicate an increase in water clarity over the invasion period

As there was no single model among the top four rankings with substantial support (Table 2), these four models were averaged using an AIC_c model averaging approach. The model averaged parameter estimate generated by these four models explained 91 % of the variance in post-invasion Secchi depth and the predicted values were very similar to the observed

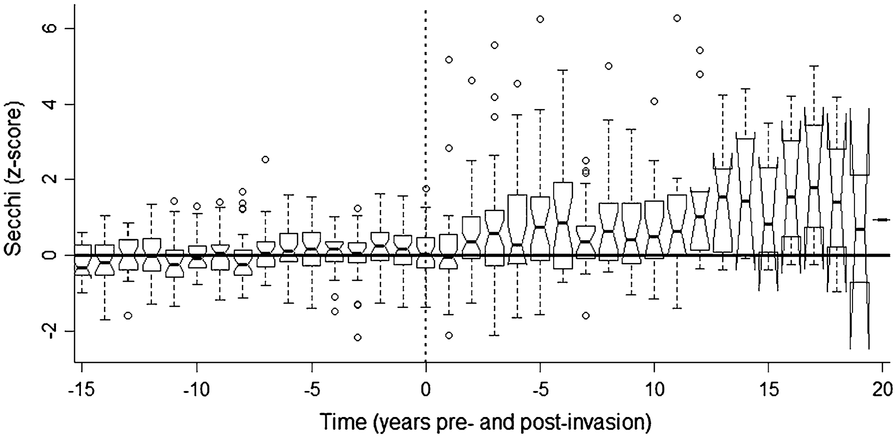

Fig. 2 Time series effects of dreissenids on water clarity in 42 lake ecosystems with annual data available. *Solid horizontal line* represents the mean pre-invasion Secchi depth value, *broken vertical line* represents year of invasion. *Box* represents the range of 1st to 3rd quartile, with the median as the *solid black line*. Whiskers represent 1.5 × Interquartile Range (IQR, where data extend that far), open circles represent data outliers. Notches extend to ± 1.58 IQR/$\sqrt{}$(n) and effects between the two time periods were considered significant where notches of boxes did not overlap between the two periods (i.e. strong evidence their medians differ). Notches overlap boxes in the last 10 years because few data points exist in that time period

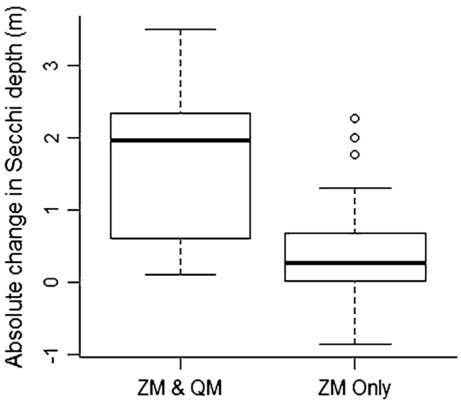

Fig. 3 Absolute change in Secchi depth (m) pre- and post-dreissenid invasion within 53 North American lakes. ZM, lakes invaded by zebra mussels ($n = 45$); QM, lakes invaded by quagga mussels ($n = 8$). *Box* represents the range of 1st to 3rd quartile, with the median as the solid black line. Whiskers represent 1.5 × Interquartile Range (where data extend that far), *open circles* represent data outliers

values in those analyzed invaded systems (Fig. 4). LOOCV model validation produced an Xr^2 value of 0.98, suggesting a good fit of our models against independent data.

To extend our models for the purpose of predicting physical and biological characteristics of lakes that depend on mixing depth, we applied our models to an independent set of 49 Ontario lakes (Table 2 in Lester et al. 2004). Were dreissenids to invade this set of lakes, we predicted that Secchi depth would increase on average by 0.465 m (95 % CI 0.431, 0.500), similar to our observed effects in the original dataset where dreissenids had in fact invaded the lakes. Applying these predicted changes in water clarity due to a hypothetical dreissenid invasion in this lake set to the mixing depth model (Eqs. 5–7), we predicted consistent increases (deepening) of thermocline depth

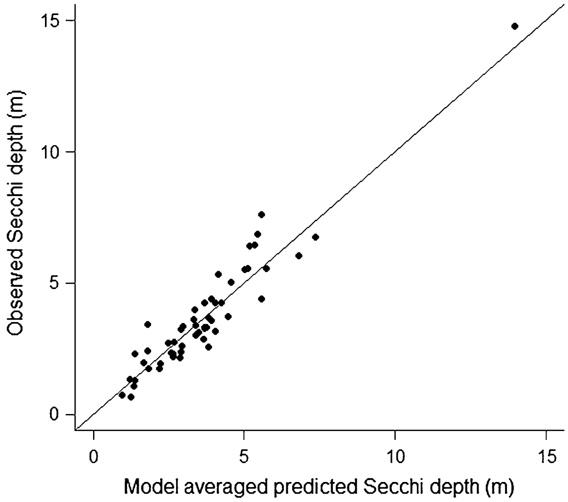

Fig. 4 Observed versus predicted values of post-invasion Secchi depth (m) from cross-validated averaging four models using AIC model averaging ($n = 53$). *Solid line*, 1:1 line

among all stratified lakes. There was a significant increase in predicted mixing depth following hypothetical dreissenid invasion of 0.33 m (95 % CI 0.30, 0.36; $t_{\text{paired}} = 20.8$, $df = 44$, $p < 0.0001$) which is a 5 % increase on average (relative to pre-invasion conditions) with a maximum predicted increase of 0.5 m in mixing depth due to increased light penetration consistent with the effects of dreissenid invasion (Fig. 5). Using our error propagation procedure, we found that simulations were equally distributed around model predictions (Fig. 5). Using 1000 simulations, the mean increase in Secchi depth following hypothetical dreissenid invasion was 0.33 m, with a maximum simulated increase of 0.7 m. Only 1.1 % of all simulated values were less than or equal to zero, indicating that predictions of increased mixing depth following dreissenids were robust in the face of uncertainty derived from our water clarity model.

On average, Walleye yield was estimated to decline by 5 % following a hypothetical increase in water clarity of a magnitude that is consistent with dreissenid invasion ($t_{\text{paired}} = -2.94$, $df = 48$, $p < 0.01$). However, there was a large range of predicted Walleye response to dreissenids from an estimated decrease in yield of −20 % to an increase of 50 %. In general, predicted Walleye yields in lakes with an initial Secchi depth <2 m tended to increase, whereas predicted Walleye yields in lakes with an initial Secchi depth >2 m tended to decrease (Fig. 6a). There appeared to be a tendency for lakes with shallower mixing depths to have negative predicted impacts on Walleye yield, and positive predicted effects with deeper mixing depths, as revealed by linear regression of the predicted change in yield on mixing depth ($F_{1,47} = 8.76$, $p = 0.005$, Fig. 6b). When we allowed mixing depth to deepen in our lakes by the amount predicted in the mixing depth model, the results were the same but changes in predicted Walleye yield were not as great; average yield declined by 3 % on average ($t_{paired} = -2.54$, $df = 48$, $p < 0.05$) but the trend of change in Walleye yield with predicted post-invasion mixing depth was nearly identical ($F_{1,47} = 7.83$, $p = 0.007$, Fig. 6b).

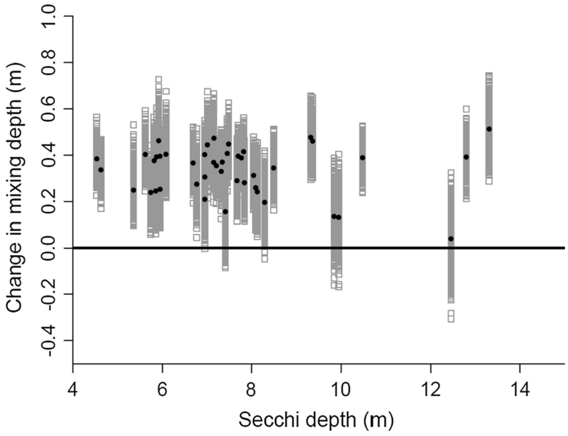

Fig. 5 Predicted magnitude of change in mixing depth (m) in stratified lakes after a hypothetical dreissenid invasion event associated with lake Secchi depth (m) in Ontarian lakes ($n = 44$). *Black circles* are estimates of change in mixing depth using water clarity parameter estimates from models 1–4 and predictions from each were averaged using AICc weights; these model averaged predictions were then applied to the mixing depth model (Fee et al. 1996; see text). *Grey squares* are simulated predictions generated from 1000 generated values using a multivariate normal distribution, the parameter estimates and the model variance covariance matrix, with AIC_c weighting applied to generate a final prediction set for application to the mixing depth model

Error propagation from our initial model describing post-dreissenid invasion Secchi depth appeared much wider in the Walleye yield model versus the mixing depth model (Figs. 5, 6). As the initial secchi depth increased, the hypothetical response to simulated error around predicted post-invasion Secchi depth became larger (Fig. 6). Overall, error propagation around predicted Walleye yield following hypothetical dreissenid-induced changes in Secchi depth appeared to be larger when declines were predicted than when increases were predicted and increased in both positive and negative directions as the Secchi depth of lakes was either smaller than 1 m or larger than 3 m (Fig. 6).

Walleye yield was predicted to decline following hypothetical water clarity increases consistent with dreissenid invasion in 38 lakes where initial Secchi depths ranged from 1.7 to 10.7 m. Among these lakes, the change in Walleye yield based on hypothetical dreissenid invasion was never predicted to be greater than zero in 32 lakes, and increase or be equal to zero <5 % of the time in 36 lakes. In two lakes, 30–40 % of the simulated predictions were equal to or greater than zero.

Walleye yield was predicted to increase following hypothetical water clarity increases consistent with dreissenid invasion in 11 lakes where initial secchi depths ranged from 0.3 to 2.3 m. Among these lakes, the simulated change in Walleye yield based on

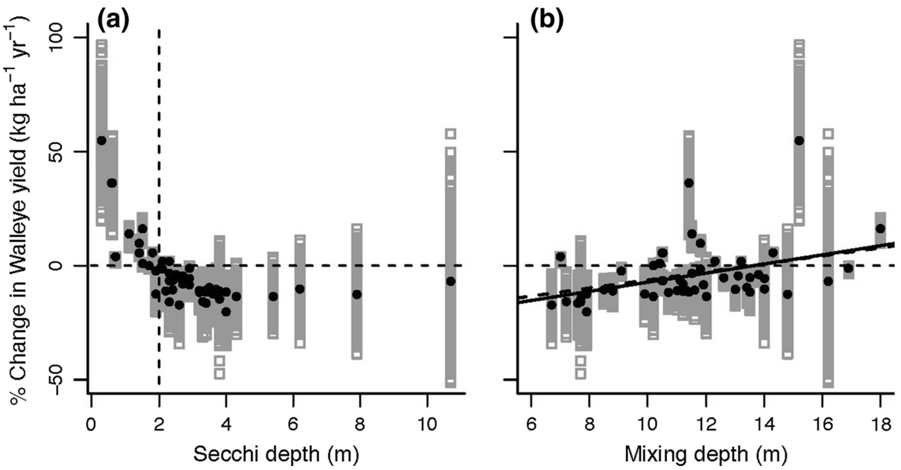

Fig. 6 Predicted % change in yield of Walleye associated with **a** Secchi depth and **b** mixing depth in Ontario lakes (n = 49). *Black circles* are estimates of change in Walleye yield using water clarity parameter estimates from models 1–4 and predictions from each were averaged using AICc weights; these model averaged predictions were then applied to the Walleye yield model (Lester et al. 2004; "Appendix 3"). *Grey squares* are simulated predictions generated from 1000 generated values using a multivariate normal distribution, the parameter estimates and the model variance covariance matrix, with AIC$_c$ weighting applied to generate a final prediction set for application to the Walleye yield model. Panel **a** *vertical dashed line* at 2 m indicates optimal Secchi depth for Walleye (Lester et al. 2004) and region where increased water clarity changes from net positive to net negative effects on Walleye yield. Panel **b** *solid trendline* demonstrates significant relationship between lake mixing depth and predicted change in Walleye yield, *dashed line* is significant relationship between predicted post-invasion mixing depth (based on equations used in Fig. 5) and corresponding predicted change in Walleye yield

hypothetical dreissenid invasion was never predicted to be less than 0 in 10 lakes, and only 1.1 % of observations were below zero in the remaining lake.

Discussion

Predictive capacity

We were successful in generating models capable of accurately predicting post-dreissenid invasion Secchi depth using limited but readily available ecosystem parameters. We found that model averaging across four GLM models which incorporated pre-invasion Secchi depth, mean lake depth, lake surface area and presence of thermal stratification generated accurate predictions of post-invasion Secchi depth in North American lakes after invasion by dreissenid mussels. Further, we demonstrate the utility of using these basic limnological characteristics to estimate potential changes in water clarity across a broad range of ecosystems in predicting hypothesized changes in mixing depth and Walleye yield in lakes following dreissenid invasion. Such applications should prove useful for investigators and resource managers alike, who wish to forecast potential effects of these invasive species on aquatic ecosystems through their impact on water quality.

In accordance with results from previously published papers and meta-analyses (see Higgins and Vander Zanden 2010), increases in water clarity were a near ubiquitous feature of dreissenid invaded lakes. The lakes in our dataset range in size, depth and trophic status, and represent a broad range of north-temperate lake types in the Great Lakes basin, many occurring on the Canadian Shield. Despite the reported reduction in dreissenid density (both zebra and quagga mussels) over time due to density dependence (Karatayev et al. 2015), our results support a meta analysis of long-term monitoring studies (Higgins 2013) that demonstrated dreissenid effects on water clarity increases were lasting and showed no signs of diminishing after two decades of dreissenid establishment. This long-term impact highlights the engineering and restructuring effect that dreissenids have on the ecosystem beyond simply density dependence as discussed by Hecky et al. (2004) and Bootsma and Liao (2013).

Ecosystem responses

We observed a greater increase in water clarity among lakes invaded with both zebra and quagga mussels as opposed to those invaded with zebra mussels alone. While the zebra mussel colonizes in great numbers in the littoral area, quagga mussels tend to be found in deeper, colder water of lakes (Vanderploeg et al. 2002) in addition to the littoral areas. While it is generally difficult to separate the effects of these two species, a review by Karatayev et al. (2015) described that quagga mussels tend to occur in both littoral and profundal habitats of the lake and in larger populations, therefore the total dreissenid filtering capacity in lakes with both species present may be higher than with zebra mussels alone and could have led to a higher water clarity increase in those systems, which our findings reflect (Fig. 3).

Though zebra mussel densities and subsequent impacts on Secchi depth would be expected to vary spatially in a lake, especially littoral zones (e.g. Higgins and Vander Zanden 2010), our models are intended to represent effects on pelagic zones. Water quality data included in this exercise were limited to offshore stations, and though littoral areas will inevitably experience greater impacts in the short term due to the presence of dreissenids in the littoral zone, hydrodynamic mixing will incorporate this effect into a pelagic component as well. Other analyses have shown that dreissenid effects on water clarity are greatest near shore, increasing ~50–78 % of pre-dreissenid values in the littoral zone, and less-pronounced in the pelagic zone with increases of 31–49 % of pre-dreissenid values (Yu and Culver 2000; Higgins and Vander Zanden 2010). As such, our models represent a conservative estimate of dreissenid effects on water clarity of lakes; effects on water clarity in littoral zones are expected to be higher.

Dreissenid-induced water clarity responses can differ among lakes depending on the management strategies in place. If dreissenid establishment occurs concurrently with phosphorus loading reductions, which arguably was the case in Lake Erie (Phosphorus Management Strategies Task Force 1980), there may well be a greater increase in water clarity than due solely to the filtering ability of the mussels. However, the majority of lakes used in our model development were small inland lakes with no known phosphorus reduction strategies in place that could be contributing to observed increases in clarity that we attribute to dreissenids ("Appendix 1").

Optical transparency of natural waters is a function of both particulate and soluble (i.e. color) components though dreissenid effects are predominantly associated with the reduction of particle concentrations (MacIsaac 1996). As described by Higgins and Vander Zanden (2010), the relationship between dreissenid induced reductions in particle concentration and resulting effects on water clarity is non-linear.We attempted an evaluation of these parameters in our models but too few lakes had TSS or turbidity data to permit a robust analysis. The non-linear response between suspended particles and water clarity may partially explain why some systems do not show a strong water clarity response to dreissenids, and we encourage other investigators to collect and report such information for a more detailed analysis. Further, as dreissenid effects on dissolved organic carbon (DOC) are considered negligible (MacIsaac 1996), lakes with high DOC or highly variable DOC (e.g. in response to climate change) are likely to either minimize dreissenid effects on water clarity or confound our ability to detect them. However, as our results and models are based on empirical responses among >50 natural systems across a broad geographical region, they likely also represent natural variation in DOC concentration among lakes.

Extensions of dreissenid effects and implications to ecosystems and management

The ability to predict water clarity with reasonable accuracy for lakes invaded, or likely to be invaded, by dreissenid mussels expands our ability to better understand and predict the potential consequences to additional properties of lake ecosystems. For example, coupling our predictive water clarity model to empirical models in the scientific literature, we demonstrated the capacity of changes in dreissenid-induced water clarity of a magnitude and direction capable of significant influences on other ecosystem parameters, including mixing depth and Walleye yield.

Though the predicted changes in mixing depth were estimated to be relatively small (0.33 m on average, a 5 % deepening), changes of this magnitude in lakes can represent a significant volume of water depending on lake size. Variations in mixing depth have considerable influence over a variety of lake properties including: the availability of nutrients in the surface mixed layer (Diehl 2002), particle loss rates and the efficiency of nutrient recycling in the surface layer (Fee 1979; Ptacnik et al. 2003), the vertical distribution of biota in the water column and sediments (Schindler et al. 1996; Kelly et al. 2016), and the habitat availability for cold water stenotherms (Schindler et al. 1996). For example, deepening thermoclines may negatively influence the available oxythermal habitat for cold water species like Lake Trout (Plumb and Blanchfield 2009) and Lake Herring (Jacobson et al. 2012), species which are already at risk of habitat loss due to climate change (sensu Jansen and Hesslein 2004).

Walleye are an important commercial and recreational fishing species in Canada and the United States. This species has been shown to exhibit movements associated with light transmission and thus are highly susceptible to changes in water clarity (Ryder 1977) which may affect foraging behaviour and reproductive capability. Though Walleye yield was predicted to decline on average across all of our lakes, and predicted to decline in more than 75 % of lakes studied, our study also indicates that water clarity effects on Walleye may be context specific and not always negative. Increases in Walleye yield were predicted in systems with low initial water clarity as they move toward an “optimum Secchi depth” which (depending on the bathymetry of the system) is near 2 m (Lester et al. 2004). However, in systems where optimal habitat is already constrained by high water clarity, further increases are expected to lead to reductions in yield. Further, our analysis suggests that lakes that can support mixing layers deeper than 14 m (and therefore more optimal thermal habitat for Walleye) may be more likely to demonstrate an increase in yield following dreissenid-induced changes in water clarity. As Walleye are economically significant for both commercial and recreational fisheries (Kinnunen 2003; Fisheries and Oceans Canada 2010), the predictions of dreissenid impacts to water clarity (e.g. Lake Winnipeg) are highly relevant to fisheries management and provide an ‘early warning’ of potential changes in the fishery. Empirical monitoring approaches for assessing dreissenid impacts on Walleye could take years before impacts are detected due to long lifespan of the species, natural variation, errors in population estimates and the influence of multiple stressors. Through the application of predictive models, fisheries resource managers may be able to better predict the Walleye fisheries that are most vulnerable to dreissenid-induced changes in order to inform adaptive management frameworks.

In summary, this study provides a predictive model for estimating water clarity in lakes following dreissenid invasion with reasonable accuracy, based on few commonly measured limnological variables and was successfully applied to lakes across a large range in size and trophic status. Because the water clarity of lakes is a state variable influencing a wide range of other ecosystem components, we demonstrate ways in which our water clarity model can be coupled with existing ecosystem models to understand the broader impacts of water clarity changes associated with dreissenids. While we provided examples of such model linkages with empirical models for mixing depth and Walleye habitat, we recognize that dreissenid effects on some ecosystem components (e.g. Walleye yield) are likely to be impacted by additional factors (e.g. changes in food web) and a more complex analysis would require an assessment of these factors. However, our results suggest that the influence of dreissenids on water clarity have the potential for cascading effects on a wide range of ecosystem properties, The water clarity model proposed here provides researchers with an important means of incorporating predictions into other models, and forecasting other effects as a means to understand the wider implications of dreissenid establishment.

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Appendix 1

See Table 3.

Table 3 List of freshwater lakes (n = 62) included in analysis of dreissenid effects

Lake	Data source	Location	Mixing status	Year invaded	Area (ha)	Max. depth (m)	Mean depth (m)	Species present	↓ [P]	No. of secchi readings
Beulah[i]	EPA Storet[a]	WI, USA	Stratified	1999	337.5	17.7	5.2	Z	N	299
Big Cedar[i]	EPA Storet	WI, USA	Stratified	2002	377.2	32.0	10.4	Z	N	382
Brophy	EPA Storet	MN, USA	Mixed	2009	118.4	13.4		Z	N	271
Butte des Morts	EPA Storet	WI, USA	Mixed	1999	3472.6	2.7		Z	N	369
Carlos[i]	EPA Storet	MN, USA	Stratified	2009	1051.6	49.7	14.0	Z	N	398
Cedar[i]	EPA Storet	WI, USA	Mixed	2001	57.46	6.4	2.74	Z	N	407
Champlain[i]	EPA Storet	NY/VT, USA	Stratified	1993	112,664.5	121.9	19.5	Z	N	9502
Clear[i]	EPA Storet	IA, USA	Mixed	2005	1500.0	9.1	3.0	Z	N	49
Cowdrey[i]	EPA Storet	MN, USA	Stratified	2009	98.2	15.9	6.7	Z	N	365
Crystal[i]	EPA Storet	WI, USA	Stratified	2001	52.2	18.6	6.1	Z	N	542
Darling[i]	EPA Storet	MN, USA	Stratified	2009	424.9	18.9	5.8	Z	N	597
Dunmore[i]	EPA Storet	VT, USA	Stratified	1999	419.7	32.0	33.5	Z	N	518
Erie (Central)	Higgins[b,h]	CAN/USA	Stratified	1989	1,618,400.0	29.0	18.3	B	Y	n/a
Erie (East)	Higgins[h]	CAN/USA	Stratified	1990	615,600.0	64.0	24.0	B	Y	n/a
Geneva[i]	EPA Storet	MN, USA	Stratified	2009	258.9	19.2		Z	N	635
Geneva	EPA Storet	WI, USA	Stratified	1995	2117.0	41.2	18.6	Z	N	263
Golden[i]	Higgins[h]	WI, USA	Stratified	2003	101.1	14	6.4	Z	N	n/a
Green[i]	EPA Storet	WI, USA	Stratified	2001	2972.8	71.9	31.7	Z	N	1163
Gull[i]	MPCA[c]	MN, USA	Stratified	2010	4025.4	24.4	8.8	Z	N	1313
Hunters[i]	EPA Storet	WI, USA	Mixed	2002	54.0	11.0	1.5	Z	N	348
Huron	Higgins[h]	CAN/USA	Mixed	1990	5,959,600.0	229.0	59.0	B	Y	n/a
Lac La Belle[i]	EPA Storet	WI, USA	Stratified	1999	471.0	13.7	3.4	Z	N	638
Le Homme Dieu	EPA Storet	MN, USA	Stratified	2009	728.8	25.9		Z	N	588
Leelanau	Higgins[h]	MI, USA	Stratified	1997	3483.0	36.9	13.1	Z	N	n/a
Little Muskego[i]	EPA Storet	WI, USA	Stratified	1999	204.7	19.8	4.3	Z	N	223
Little Rock	EPA Storet	MN, USA	Mixed	2009	530.4	7.0		Z	N	376
Lizzie	MPCA	MN, USA	Stratified	2011	1632.9	20.1		Z	N	64
Long[i]	Higgins	WI, USA	Stratified	2002	170.0	14.3	6.7	Z	N	224
Lower Prior	EPA Storet	MN, USA	Stratified	2009	386.9	18.3		Z	N	825
Machinakee[i]	EPA Storet	WI, USA	Mixed	2002	180.0	6.4	1.8	Z	N	94
Margaret[i]	MPCA	MN, USA	Mixed	2008	89.8	7.9	3.2	Z	N	1178
Mary[i]	EPA Storet	WI, USA	Stratified	2002	120.0	10.1	2.7	Z	N	260
Metonga[i]	EPA Storet	WI, USA	Stratified	2001	824.8	24.1	7.6	Z	N	174
Mille Lacs[i]	EPA Storet	MN, USA	Mixed	2005	51,891.3	12.8	6.4	Z	N	997
Minnetonka[i]	MPCA	MN, USA	Stratified	2010	5960.8	34.4	8.5	Z	N	8745
Nagawicka[i]	EPA Storet	WI, USA	Stratified	1998	397.0	27.4	11.0	Z	N	168
North[i]	EPA Storet	WI, USA	Stratified	2002	178.0	23.8	11.3	Z	N	171
Oconomowoc[i]	EPA Storet	WI, USA	Stratified	1999	331.0	18.3	9.8	Z	N	294
Oneida[i]	KNB[d]	NY, USA	Mixed	1991	20,670.0	16.8	6.8	B	Y	4395
Onondaga	Higgins[h]	NY, USA	Stratified	1992	1200.0	19.5	10.9	B	N	n/a

Table 3 continued

Lake	Data source	Location	Mixing status	Year invaded	Area (ha)	Max. depth (m)	Mean depth (m)	Species present	↓ [P]	No. of secchi readings
Ontario (offshore)	Higgins[h]	CAN/USA	Stratified	1989	1,896,000.0	244.0	86.0	B	Y	n/a
Ossawinnamakee[i]	MPCA	MN, USA	Stratified	2003	279.5	19.2	6.4	Z	N	877
Pawaukee[i]	EPA Storet	WI, USA	Stratified	2001	1009.0	13.7	4.6	Z	N	259
Pelican[i]	MPCA	MN, USA	Stratified	2009	3386.1	31.7	6.4	Z	N	785
Pike[i]	EPA Storet	WI, USA	Mixed	2003	211.2	13.7	4.1	Z	N	217
Pleasant	EPA Storet	MN, USA	Stratified	2007	236.7	17.7		Z	N	197
Poygan[i]	EPA Storet	WI, USA	Mixed	2000	5675.3	3.4	1.8	Z	N	222
Rice	EPA Storet	MN, USA	Mixed	2005	130.5	7.6	3.0	Z	N	79
Rice	OMNRF[e]	ON, CAN	Mixed	1994	9183.5	13.4	2.6	Z	N	24
Rose	MPCA	MN, USA	Stratified	2011	485.8	41.8		Z	N	88
Seneca[i]	J.D. Halfman[f]	NY, USA	Stratified	1992	17,320.6	198.4	88.6	B	N	1402
Shawano[i]	EPA Storet	WI, USA	Mixed	2001	2500.0	12.0	2.7	Z	N	147
Silver	Higgins[h]	WI, USA	Stratified	1994	190.0	13.1	4.8	Z	N	127
Simcoe[i]	OMOECC[g,h]	ON, CAN	Stratified	1994	72,200	44	14	B	Y	33
St.Clair	Higgins[h]	CAN/USA	Mixed	1988	110,000.0	6.4	3.0	Z	N	n/a
Upper Nemahbin[i]	EPA Storet	WI, USA	Stratified	1998	112.1	18.3	9.0	Z	N	129
Upper Phantom[i]	Higgins[h]	WI, USA	Mixed	2002	43.3	8.8	3.4	Z	N	n/a
Upper Prior[i]	EPA Storet	MN, USA	Stratified	2009	136.4	13.7	3.4	Z	N	1026
Victoria	EPA Storet	MN, USA	Stratified	2009	168.8	18.3	10.7	Z	N	887
Wabusee[i]	Higgins[h]	WI, USA	Mixed	1999	52.2	22.9	5.79	Z	N	n/a
Wind	EPA Storet	WI, USA	Mixed	2002	372.0	14.3	3.1	Z	N	86
Winnebago[i]	EPA Storet	WI, USA	Mixed	1999	53,393.8	6.4	4.6	Z	N	989

Z indicates presence of zebra mussels only, *B* indicates both zebra and quagga mussels. ↓[P] indicates known phosphorus reduction efforts. Only lakes with estimates of mean depth (n = 53) were used in model development

[a] EPA Storet database, available at: http://www.epa.gov/storet/, [b] Higgins Vander Zanden (2010), [c] MPCA, 520 Lafayette Road N, St. Paul, MN 55155–54194, [d] KNB database, available at: https://knb.ecoinformatics.org/, [e] OMNRF, 300 Water Street, Peterborough, ON K9J 8M5, [f]Hobart and William Smith Colleges, 300 Pulteney St., Geneva, NY, 14456, [g] OMOECC, 125 Resources Road, Etobicoke, ON M9P 3V6, [h] indicates pre-calculated grand Secchi depth (m) means. [i] indicates lakes included in *Z*-score analysis

Appendix 2

See Table 4.

Table 4 Table 2 from (Lester et al. 2004)

Lake	N years (range)	Surface area (Ha)	GDD (°C)	TDS (mg/L)	Depth			
					Maximum	Mean	Secchi	Estimated Thermocline
Angling								
Balsam	4 (1982–94)	4665	1825	78	14.9	5	3.6	9.9
Bennett	4 (1977–90)	481	1999	116	12.2	4.4	3.3	7.2
Buckhorn	3 (1981–92)	3191	1937	121	9.4	2.1	2.3	7.7
Chemong	3 (1981–92)	2280	1986	148	6.7	2.4	2.6	
Dalhousie	3 (1977–90)	590	2000	67	16.8	5.2	3.4	7.6
Eagle	4 (1972–90)	27,691	1500	38	33.5	6.8	2.9	14
Esnagi	4 (1972–89)	4586	1246	47	22	4.7	3.7	11.6
Lac des Mille Lacs	6 (1971–81)	24,101	1385	33	24.4	6.8	1.8	14.3
Lower Tweed	9 (1983–91)	361	1251	82	12	5.6	1.9	9.1
Mississippi	4 (1981–94)	2351	2000	109	9.2	2.7	3.8	7.7
Nagagami	4 (1975–86)	5363	1232	110	27.5	7.5	2.7	13.1
Nipissing	11 (1982–92)	87,325	1690	50	52	4.5	2.5	13.8
Oba	3 (1974–90)	2455	1246	57	13.1	3.9	1.5	10.4
Pigeon	5 (1981–89)	5349	1939	120	17.4	3	2.2	8.8
Pike	3 (1979–88)	317	2000	83	38.4	8.2	4	7.9
Rice	5 (1979–95)	10,018	2068	130	7.9	2.6	1.9	
Scugog	5 (1977–93)	6374	2038	156	7	1.8	0.7	
Seul	3 (1985–92)	140,943	1493	60	47.2	9.5	1.5	18
Temagami	2 (1986–89)	20,972	1612	49	110	18.2	10.7	16.2
Wakwayowkastic	9 (1983–91)	221	1254	39	18	5.3	2.4	8.5
White	8 (1961–83)	5889	1251	77	48.8	8.7	2.7	13.5
Commercial								
Abitibi	48	90,972	1386	63	15.2	3.5	0.3	
Atikwa	15	5388	1499	29	59.5	13.2	4	13.5
Ball	13	2915	1500	60	30.5	9.5	1.4	11.8
Basket	35	4267	1473	27	19.8	5.9	3.8	11.2
Lake of Bays	43	4415	1375	42	25.9	11.1	2.3	13.2
Berens	20	2790	1375	35	11.6	4.7	1.4	10.5
Churchill	15	4179	1350	32	22.6	5.2	3.4	11.3
Clay	32	3088	1499	60	21.9	7.9	0.6	11.4
Confusion	10	1426	1500	77	42.7	11.6	3.4	11.4
Deer	26	14,677	1222	25	67.7	14.8	2.9	16.9
Dogtooth	19	2723	1500	27	42	10.8	5.4	12
Gullrock	26	6420	1500	44	17.7	7.8	2.1	12.3
Hooker	11	2113	1375	32	32.3	5.9	3.2	10.7

Table 4 continued

Lake	N years (range)	Surface area (Ha)	GDD (°C)	TDS (mg/L)	Depth			
					Maximum	Mean	Secchi	Estimated Thermocline
Kagianagami	28	7588	1253	84	45	8.9	6.2	14
Kukukus	23	4129	1375	31	19.5	5	2.4	11.1
Lawrence	14	1871	1500	29	76.2	22.2	3.5	13.4
Marchington	12	3596	1374	31	33.5	7.4	2.9	11.9
Miniss	13	6314	1264	28	39	6	2.5	12.6
Nungesser	13	6278	1386	21	15.2	5.5	2.1	11.8
O'Sullivan	19	4293	1250	129	45.7	8.4	3.7	13
Oak	34	4183	1500	64	32.9	7.2	1.1	11.5
Penassi	15	1441	1375	27	27.1	6.6	2.3	10.5
Press	35	3618	1375	30	22	5.6	2.7	11.2
Raggedwood	11	1118	1375	64	29.3	6.6	4.3	10.2
St. Raphael	10	4027	1367	33	27.5	4.8	3.2	11
Sowden	10	3719	1374	23	18.3	6.3	2.3	11.5
Sydney	31	5868	1500	22	70.1	19.7	7.9	14.8
Wintering	28	1708	1375	31	15.9	5.3	1.7	10.2

Lake	EB area (proportion)	EB maximum depth (m)	EB mean depth (m)	EB shape	Relative secchi	Yield	
						Observed	Predicted
Angling							
Balsam	0.89	9.9	4.2	1.35	0.49	1.42	1.21
Bennett	0.81	7.2	3.2	1.5	0.59	1.41	1.4
Buckhorn	0.99	7.7	2.3	0.88	0.51	2.01	1.77
Chemong	1	6.7	2.4	1.09	0.58	2.08	1.81
Dalhousie	0.74	7.6	3.3	1.43	0.59	1.39	0.96
Eagle	0.84	14	5.3	1.18	0.3	0.59	0.73
Esnagi	0.89	11.6	4.3	1.13	0.47	1.46	0.61
Lac des Mille Lacs	0.88	14.3	5.7	1.24	0.18	2.95	0.62
Lower Tweed	0.87	9.1	4.6	1.79	0.25	0.48	1.16
Mississippi	0.98	7.7	2.7	1.05	0.76	0.84	1.02
Nagagami	0.8	13.1	5.4	1.31	0.28	0.8	1.05
Nipissing	0.89	13.8	4.9	1.08	0.28	1.16	0.97
Oba	0.97	10.4	3.8	1.11	0.22	1.01	0.93
Pigeon	0.91	8.8	3.1	1.06	0.39	2.27	1.94
Pike	0.6	7.9	3.2	1.29	0.7	0.8	0.71
Rice	1	7.9	2.6	0.99	0.38	3.72	2.29
Scugog	1	7	1.8	0.75	0.19	2.01	2.68
Seul	0.81	18	6.9	1.19	0.12	0.93	0.67
Temagami	0.62	16.2	6.2	1.19	0.95	0.1	0.19
Wakwayowkastic	0.77	8.5	3.6	1.37	0.38	0.59	0.66
White	0.76	13.5	5.2	1.2	0.29	1.47	0.84
Commercial							
Abitibi	1	15.2	3.7	0.75	0.04	0.15	0.37

Table 4 continued

Lake	EB area (proportion)	EB maximum depth (m)	EB mean depth (m)	EB shape	Relative secchi	Yield	
						Observed	Predicted
Atikwa	0.62	13.5	5.5	1.31	0.41	0.54	0.47
Ball	0.66	11.8	5.3	1.48	0.15	1.68	0.76
Basket	0.84	11.2	4.6	1.32	0.47	0.66	0.55
Lake of Bays	0.63	13.2	6.7	1.83	0.21	0.45	0.58
Berens	0.99	10.5	4.5	1.38	0.18	0.47	0.79
Churchill	0.86	11.3	4.3	1.18	0.43	0.52	0.57
Clay	0.74	11.4	5.2	1.55	0.07	0.67	0.53
Confusion	0.58	11.4	4.9	1.43	0.39	0.6	0.8
Deer	0.66	16.9	6.9	1.29	0.24	0.32	0.37
Dogtooth	0.63	12	5.1	1.38	0.6	0.33	0.33
Gullrock	0.83	12.3	6.1	1.73	0.21	0.63	0.84
Hooker	0.8	10.7	4.1	1.18	0.43	0.85	0.57
Kagianagami	0.76	14	5.5	1.22	0.63	0.37	0.52
Kukukus	0.88	11.1	4.3	1.2	0.31	0.67	0.68
Lawrence	0.4	13.4	6.1	1.53	0.33	0.45	0.36
Marchington	0.76	11.9	4.7	1.25	0.34	0.5	0.58
Miniss	0.83	12.6	4.6	1.14	0.29	0.52	0.54
Nungesser	0.94	11.8	4.9	1.34	0.24	0.83	0.59
O'Sullivan	0.75	13	5	1.2	0.41	0.67	1
Oak	0.76	11.5	4.6	1.25	0.13	1.31	0.84
Penassi	0.76	10.5	4.3	1.29	0.31	0.56	0.58
Press	0.85	11.2	4.4	1.24	0.34	0.59	0.63
Raggedwood	0.75	10.2	4.1	1.26	0.59	0.76	0.61
St. Raphael	0.86	11	4.1	1.13	0.43	0.56	0.6
Sowden	0.85	11.5	5	1.41	0.26	0.33	0.58
Sydney	0.48	14.8	6.6	1.48	0.69	0.86	0.18
Wintering	0.87	10.2	4.3	1.36	0.22	0.78	0.71

Appendix 3

Predictive equations of thermal-optical habitat area and walleye yield based on (Lester et al. 2004).

This Appendix describes the formulae developed by Lester et al. (2004) to estimate walleye thermal-optical habitat area (TOHA, ha) and yield (kg/ha/yr).

Walleye thermal-optical habitat area

TOHA was approximated as

$$\mathrm{TOHA} = (\mathrm{GDD} - 623)^{0.73}\,\mathrm{Area}\;\mathrm{P_T}\mathrm{z_{rel}}\mathrm{e}^{-\mathrm{z_{rel}}/0.12w} \quad (8)$$

where GDD = growing degree days (°C), Area = lake surface area (ha), $\mathrm{P_T}$ = proportion of lake area above the thermocline, $\mathrm{z_{rel}}$ = relative Secchi depth of the epibenthic zone (m) and w = water clarity parameter (set to 2.12, Lester et al. 2004).

Relative Secchi depth of the epibenthic zone ($\mathrm{z_{rel}}$) is calculated as

$$\mathrm{z_{rel}} = \frac{\mathrm{z_{sec}}}{\mathrm{z_T}(1 - \mathrm{e}^{-s})} \quad (9)$$

where $\mathrm{z_{sec}}$ = Secchi depth (m), $\mathrm{z_T}$ = thermocline depth, or maximum depth of the epibenthic zone (m) and s = basin shape parameter of the epibenthic zone.Basin shape (s) of the epibenthic zone is calculated as

$$s = \frac{3r + (r^2 + 8r)^{0.5}}{4(1 - r)} \tag{10}$$

where $r = \frac{z_E}{z_T}$, where z_E = mean depth of the epibenthic zone (m) and z_T = thermocline depth (m). In mixed lakes, $z_T = z_{max}$ or maximum depth.

Walleye yield

Yield was approximated as

$$\text{Yield} = 0.011\frac{\text{TOHA}}{\text{Area}}\,\text{TDS}^{0.534} \tag{11}$$

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