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Suitable habitat model for walleye (*Sander vitreus*) in Lake Erie: Implications for inter-jurisdictional harvest quota allocations

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ABSTRACT

Models predicting habitat distributions can give insight into species–habitat requirements and anticipate how populations respond to environmental change. Despite the economic and ecological importance of walleye (*Sander vitreus*) in Lake Erie, no preferred-habitat model exists and the spatial extent of suitable habitat is poorly understood. Empirical species-habitat models for three groups of walleye (juveniles, adults, and all walleye) was developed using records from a long term gill net data base (21 years). We examined the degree to which habitat suitability varies with vertical stratum for each group and whether the new model yields different estimates of available walleye habitat when compared to the current depth-based approach. Walleye occurrence in gill nets was positively related to water temperature, negatively related to water depth and water clarity, and unrelated to dissolved oxygen concentration. A model that incorporated interaction terms among the independent variables performed better than the linear, quadratic, and cubic generalized linear models (GLMs) for all three groups. Our results indicate that the extent of suitable habitat varies spatially in Lake Erie and is greatest in the West basin. Weighted Habitat Suitability Areas (WHSA), a combination of habitat quality and quantity, differed significantly among basins and vertical strata in Lake Erie. The current quota allocation strategy for Lake Erie walleye is based on the proportional amount of preferred habitat by jurisdiction. However, the current depth-based definition of preferred habitat may not be an adequate representation of walleye suitable habitat shared by each jurisdiction.

Introduction

Walleye (*Sander vitreus*) is a primary predator and keystone species in Lake Erie and other mesotrophic North American lakes (Bowlby et al., 2010; Pierce et al., 2006). They influence the aquatic community and lake ecosystem dynamics through top-down trophic cascades (Bowlby et al., 2010; Hurley, 1986). Commercial and recreational walleye fisheries contribute millions of dollars annually to the economy of the Great Lakes region (Lichtkoppler et al., 2008; Roseman et al., 2010). To conserve and protect the ecological integrity of the ecosystem, one of Lake Erie's management objectives is to maintain a healthy walleye population (Ryan et al., 2003).

Although walleye preference for mesotrophy (i.e. cool water and moderate primary productivity) is well documented (e.g., Kerr and Puddister, 1996; Lester et al., 2004; Mosindy, 1984), the current definition of walleye habitat according to the Great Lakes Fish Commission's Standing Technical Committee for Lake Erie only includes waters less than 13 m deep (STC, 2007). This definition of habitat is used to allocate Lake Erie's annual harvest quota for walleye to each of three participating jurisdictions (Ontario, Michigan and Ohio) by the amount of shared surface area of waters less than 13 m. Because fish population growth depends upon the quality and quantity of suitable habitat, identifying the habitat requirements of a fish species over the broad region across which it is managed is a vital issue for sustainable management. To date, there is no comprehensive model describing the spatial and temporal variability of suitable habitat for Lake Erie walleye. Such a model integrating information collected during the fisheries season (i.e., excluding spawning habitat preferences) could further inform managers about the validity of the current inter-jurisdictional quota allocations. Thus the objectives of this study are to derive a habitat model if walleye occurrence in gill nets is related to certain variables and to determine if the new model yields different estimates of available walleye habitat when compared to the previous 13 m depth-based approach.

The walleye population in Lake Erie collapsed during the 1960s (Muth and Wolfert, 1986), partially due to lake eutrophication and gradually recovered through the 1980s. This recovery was likely due to a combination of improved water quality achieved through federally-mandated reductions in anthropogenic phosphorus inputs (Ludsin et al., 2001; Ryan et al., 2003) and a ban on fishing as a result of high levels of mercury in fish tissues (Vandergoot et al., 2011). Recent studies

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show that Lake Erie has undergone considerable environmental change and numerous forms of fish habitat degradation (see Ryan et al., 2003; Stepien et al., 2010). There has been a recent resurgence in primary productivity, which has been attributed to several sources (Conroy et al., 2005), and there are indications of a return to eutrophy. Lake Erie adult walleye stocks are in decline and have approached 'crisis' levels in recent years, and exploitation rates are among the lowest levels on record (WTG, 2011). Annual recruitment of juvenile Lake Erie walleye is also highly variable (Zhao et al., in press). For these reasons, it is imperative to understand species–environment relationships (ecological niche) of Lake Erie walleye across basins and life stages and to anticipate how walleye distribution may respond to potential degradation in environmental conditions.

The concept of an ecological niche has been used extensively for developing habitat suitability models by relating observed presence/absence of a species to the environmental characteristics of the location at which samples are collected (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000; Thuiller et al., 2010). Although environmental variables are often treated discretely, it is also important to consider that habitat is a multidimensional space (Chase and Leibold, 2003) within which individuals of a given species tend to cluster according to specific combinations of habitat variables (Brown et al., 1995). Predictions from habitat models are generally good indicators of habitat suitability and of species' performance (Thuiller et al., 2010). The habitat suitability for a species in an area can be expressed as the probability of occurrence of the species, and the total amount of suitable habitat supply for the species in an area can be calculated by summing over all its sub-areas weighted by their suitability indices. In general, when habitats of different levels of quality are available, a species will choose the highest quality of habitat first; this indicates that more suitable habitats attract more frequent visits of a species (see, Albert and Thuiller, 2008; Thuiller et al., 2010) and result in greater probability of species presence in that habitat. Thus, establishing the species–environment relationship (presence/absence information), by using data collected over a wide range of values of individual habitat variables, will provide the information to estimate such suitability.

In this study, we examined a 21-year sampling record (1989–2009) of walleye occurrence in gill nets and water quality information concurrently collected during late summer/autumn to derive a species–environment relationship for walleye in Lake Erie using a generalized linear model (GLM). We used dissolved oxygen, water temperature, light attenuation, and depth to derive the species–environment relationship, because these variables are often used to describe optimal fish habitat (e.g., Jackson et al., 2001; Lester et al., 2004). Specifically, we used a logistic regression model to describe species presence or absence as a binary response variable. Logistic regression is a robust technique for predicting animal distribution from habitat variables and has been extensively used for many species (see, e.g., Austin, 2007; Brotons et al., 2004; Douglas et al., 2009; Elith et al., 2006; Pandit et al., 2010; Pearce and Ferrier, 2000a,b; Thuiller, 2003), including fish catch allocation (Venables and Dichmont, 2004). We then applied the estimated species–environment relationship to develop a habitat suitability model that predicts the probability of walleye occurrence, a proxy of habitat quality (Thuiller et al., 2010), and estimated the distribution and the extent of walleye habitat in Lake Erie.

Because juvenile fish may respond to environmental variation differently from adults, we compared the estimated habitat requirements and habitat suitability models between juvenile walleye, adult walleye, and a combination of both (all walleye). In addition, the morphometry of Lake Erie's three basins differs substantially in depth as the mean and median depths gradually increase from the warm, un-stratified West basin and the cool, dimictic Central basin to the cold, dimictic East basin. We postulated that suitable walleye habitat would vary vertically among deeper portions of the lake because of thermal stratification and potential hypoxia. Thus, we further examined the degree to which the spatial distribution of habitat suitability varies with vertical stratum (i.e., depth within water column). Lastly, we compared the amount of suitable habitat based on the definition of walleye habitat by the Standing Technical Committee of Lake Erie (i.e. all waters less than 13 m deep) to the amount estimated from the species–habitat models developed in this study.

Methods

For this study, we used data sets collected in Lake Erie by the Ontario Ministry of Natural Resources (OMNR) and the Ohio Department of Natural Resources (ODNR). The sampling designs are presented in detail as follows:

Partnership index gillnet program (OMNR)

The Ontario data used for this study were collected annually from August through November from 1989 to 2008 by the partnership index gill netting program conducted by the Ontario Ministry of Natural Resources and the Ontario Commercial Fisheries Association. In this program, standard gangs of monofilament gill net consisting of different mesh sizes were fished in two distinct manners: suspended (canned) and bottom sets. One gang (or strap) of gill nets consists of 14 mesh sizes (i.e., 32, 38, 44, 51, 57, 64, 70, 76, 89, 102, 114, 127, 140, and 152 mm stretched). Each panel was 15.2 m long, and we used duplicate panels of each mesh from 51 to 152 mm in a gang. Thus, a single gang consisted of 25 panels and was 380 m long. Panel order was randomly selected and remained the same through the survey. Nets were fished for 24 h.

Each year, a stratified random sampling design was used for the Canadian waters of all basins (West, West-Central and East-Central, and East basins) and on the Pennsylvania Ridge (which divides the Central from the East basins). Depth strata classification varied among basins, reflecting the geo-morphometric differences among them. Specifically, in the West basin (maximum depth of about 18 m), the surface area was stratified into 2 depth strata (0–10, and >10 m). The West-Central and East-Central regions, which have a maximum depth of about 26 m, were partitioned into 3 depth strata (0–15, 15–20, and >20 m). The surface areas of the Pennsylvania Ridge and the East Basin, with a maximum depth of about 64 m, were partitioned into 3 depth strata (0–15, 15–30, and >30 m). Within each stratum, the number of sampling sites was decided based on the surface area. Locations were randomly selected from one of 4 quadrants within predefined 5-minute sampling grids.

Ohio Department of Natural Resources (ODNR)

The ODNR data were collected from overnight sets (average 16 h) of suspended and bottom gill nets deployed from May through November in each year from 1990 to 2009 in the Ohio waters of Lake Erie. Of all nets, more than half (56%) were comprised of thirteen 30.5 m long, 1.8 m tall panels of randomly-ordered multifilament mesh that ranged from 5 to 12.7 cm (2–5 in. at 0.64 cm (0.25 in. increments (total gang area = 396 m long × 1.8 m high). The remaining nets consisted of twelve 15.2 m long panels of randomly-ordered monofilament mesh ranging in size from 3.2 to 7.6 cm by 0.64 cm increments, and 7.6 to 12.7 cm at 1.27 cm increments. Suspended nets were fished at depths from 0.9 to 20.7 m below the water surface. Most of these (85%) were suspended less than 3 m from the surface. Four suspended nets were set at each transect annually. In the Central basin, one suspended net was set at each depth stratum (0–5, 5–10, 10–15, and >20 m). In the West basin, one net was set at each depth stratum (0–5 m and 5–10 m) while 2 nets were spatially distributed across the 10–15 m stratum. Only one bottom net was set for every 1–2 transects annually. Transects were distributed somewhat evenly (a longitudinal distance of 11–19 km between transects) from the Michigan state line at the westernmost portion of Lake Erie to the Pennsylvania state line. More sampling detail can be found in Vandergoot et al. (2011).

Fish catch and abiotic data

Fish catch in both subsurface (suspended) and bottom gill nets was recorded by age (age 0, age 1, age 2, age 3, etc.) for each net in the OMNR survey, whereas in the ODNR survey, catch was recorded by age class (age 0, age 1, age 2+) for each net. In the ODNR survey, a gender-based age key (Isermann and Knight, 2005) was used to assign ages to fish that were not aged by examination of otoliths or scales. Site depth, fishing depth (i.e., distance between the water surface and the top of the net), and geographic coordinates were recorded for all sampling sites for both surveys. Limnological data at each site were most often collected on the set day. For the ODNR data, temperature, dissolved oxygen, and Secchi disk readings were collected at most sites or were interpolated from the values collected at surrounding sites (i.e., the same depth stratum, site, and date sampled) or from a concurrent limnological survey. For the ODNR nets that were suspended mid-water column during stratification, the temperature and dissolved oxygen values at the net depths were interpolated from limnological profile data. In this study we used 3690 of 4943 OMNR catch records and 910 of 1162 ODNR catch records due to incomplete limnological information (i.e., missing measurements of all or one of Secchi disk, temperature or dissolved oxygen) and the presence of outliers (i.e., obvious instrument or entry error; e.g. DO >15 mg/L) for some records. Fig. 1 depicts the spatial layout of all catch records used from 1989 to 2009.

In general, these nets were set either overnight (ODNR — 16 h) or for an entire day (OMNR, 24 h) and thus there might have an issue of potentially collecting fish in suboptimal habitat while walleye were moving between preferred habitats since walleye sometime engage in diel movement (Knight et al., 1993). However, some of the previous studies demonstrated that these movements were associated with specific combinations of abiotic and biotic components. For example, we have had higher catches offshore in some years where walleye did not move to nearshore shoals (reefs), especially when gizzard shad (*Dorosoma cepedianum*) abundance was low in Lake Erie (ODNR unpublished data). The sampling programs in Lake Erie were aware of these issues and used a range of multifilament mesh size that were randomly-ordered as well as stratified random sampling techniques to reduce the biases in catchability. Using a long term dataset (20+ years) further reduces the bias if such bias exists.

Biological and environmental variables

We developed species–environment relationships (SERs) using a logistic regression in which only species presence/absence was used. Our objective was to develop the models for walleye as well as different age groups, because we expected that walleye may respond to their environment differentially by age. We first assessed whether gill net sampling bias has been associated with a different age group of walleye captured and found that a group of individuals comprised of ages 0 and 1 made up ~25% of the total catch (see Supplementary information (SI), Appendix 1). Since the mesh size of the gill nets were able to capture Lake Erie Walleye of a wide range of sizes, we built SERs for each of the following age classification: juveniles (≤1 year old), adults (>1 year old), and all walleye (regardless of age, sex, and length).

For environmental modeling (SER), we assessed the effects of water temperature (degrees C), dissolved oxygen concentration (DO, mg/L), light attenuation (Secchi depth, m), and depth (gear depth or distance between the water surface and top of the sample gear, m). These variables were also readily available in our database. We selected these variables because they were often used to describe optimal walleye habitat (see Christie and Regier, 1988; Jackson et al., 2001; Lester et al., 2004). Substrate type is also a potentially important measure of habitat suitability. However, because we did not classify substrate at each sample and because the existing substrate maps are of much coarser resolution than our survey, we excluded substrate type from our analyses. We tested for multi-collinearity among the variables because strong correlations among explanatory variables (i.e., $R^2 \geq 0.80$ for at least one of variables) can result in biased estimates and inferences from the model (Menard, 1995). A preliminary screening showed that there was little correlation among the four independent variables across the time series. Water temperature and depth had the strongest correlation, although it was weak ($R^2 = 0.262$, $p < 0.01$, sample size $(n) = 3690$) according to Menard (1995).

Model development and selection

Prior to establishing the species–habitat relationships, we split the OMNR data into a training dataset and an evaluation or reference data set using a ~75:25 ratio (Fielding and Bell, 1997). These data subsets

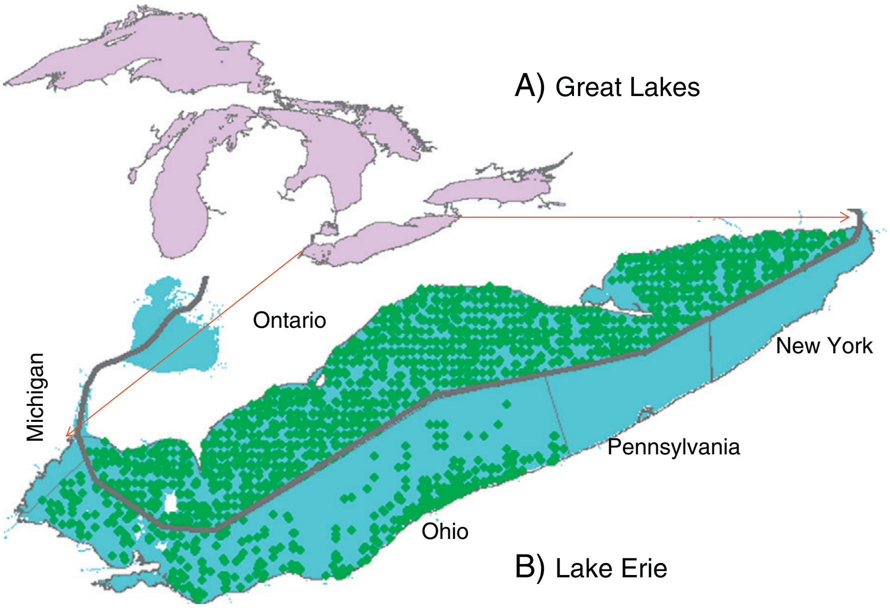

Fig. 1. The Great Lakes (A) and the location of observation sites in Lake Erie (B). Each point in Lake Erie represents one gill net set. A total of 4649 sets were conducted in Ontario waters by OMNR (1989–2008) and in Ohio waters by ODNR (1990–2009).

were created by randomly assigning 'training' or 'reference' to each of the 3690 observation sites. Using this procedure, a subset consisting of 2752 net records (~75% of the total data set), was designated for model development (training data), and the remaining 938 records (~25% of the total data set) were used for statistically-independent cross-validation in the subsequent accuracy assessment. The ODNR data set (910 observation sites) was used only for accuracy assessment (described in the next section) because the data set is completely independent from the OMNR training data set in terms of sampling design and operation.

To assess the species–environment relationship, we applied a logistic regression model which, is one of the generalized linear models (GLM; McCullagh and Nelder, 1989), including linear (asymptotic, LR-L), quadratic (unimodal, LR-Q), cubic (multimodal, LR-C), and interaction (LR-I) configurations of the model. The general form of the model was:

$$\mathrm{Log}[p/(1-p)] = \beta + f(E_i)$$

where p is the probability of walleye occurrence (i.e., habitat suitability), ß represents the intercept constant, $f(E_i)$ is a function comprised of each independent variable E_i ($i = 1,2,3,\ldots k$). The $f(E_i)$ can be $\sum_{i=1}^{i=k} \beta_i E_i$, $\sum_{s=1}^{s=2} \sum_{i=1}^{i=k} \beta_{i,s} {E_i}^s$ and $\sum_{s=1}^{s=3} \sum_{i=1}^{i=k} \beta_{i,s} {E_i}^s$ (where β is the coefficient and i is number of the independent variables) for linear, quadratic, and cubic functions, respectively. For the interaction function, we only tested the main variables and the first order interactions between any two independent variables. We used 4 environmental variables (water temperature, dissolved oxygen concentration, light attenuation, and depth) as the independent variables to relate to walleye occurrence in a backward-selected logistic regression procedure ($p < 0.05$). This analysis was performed using the statistical software, SYSTAT 7.2 for Windows (Systat Software, Inc, Chicago, IL). To select the best fitting model configurations, we used an evidence (weight) ratio that was derived from the Quasi-likelihood Akaike Information Criterion adjusted for over-dispersion (QAIC). Over-dispersion was adjusted in AIC by dividing the residual deviance (-2 log likelihood) with an over-dispersion factor calculated from the full model as the sum of the squared Pearson residuals divided by the number of degrees of freedom of the full model (see Mysterud et al., 2007). We did not correct for sample size in QAIC because the ratio of sample points and parameters in the full model was relatively large and AIC tends to yield the same conclusion as sample size corrected AICc. To select the best model among the four model configurations (LR-L, LR-Q, LR-C, and LR-I) for each group, we used an evidence ratio derived from the QAIC weight ratio between the best fit model and other models (see, Burnham and Anderson, 2002; Wagenmakers and Farrell, 2004).

We further tested whether the best model captured spatial autocorrelation in the observed distribution. We calculated Pearson residuals from the best model as the standard residual of the observation points (observation, 0 or 1, minus the model prediction, $0 < \text{prob} < 1$) divided by the standard deviation of the standard residuals (see Diebel et al., 2010; Mysterud et al., 2007). The statistical significance of residual spatial autocorrelation was assessed using Moran's I statistics. The values of Moran's I statistics being $+1$, 0 and -1 to indicate complete clustering, random and completely dispersed patterns, respectively. The analysis was performed separately for each group of individuals (all walleye, juvenile walleye only, adult walleye only) in ArcMap 9.3 (ESRI, Redlands, CA, USA, 2008).

Accuracy assessment

To test the accuracy of walleye occurrence probability or Habitat Suitability Index (HSI), predicted by the selected best model, we used a threshold independent measure — the area under the receiver operating characteristics (ROC) curve (AUC; for detail, see Fielding and Bell, 1997; Phillips et al., 2006). For each group, the overall predictive success of the model was assessed using ROC curves by plotting the predicted HSI values yielded from the best selected model against the independent reference data (938 records of OMNR and 910 records of ODNR) reserved for this purpose. These plots represented the true positive rate (sensitivity; Y-axis) versus the false positive rate (1-specificity; X-axis) at all possible thresholds. Sensitivity was the fraction of all 'presences' correctly classified as 'present'. Specificity is the fraction of all 'absences' correctly classified as 'absent'. ROC analyses were performed using MedCalc for Windows, Version 11.2.1.0 (MedCalc Software, Mariakerke, Belgium).

Model implementation and Habitat Suitability Index (HSI)

To create an HSI over the entire area of Lake Erie, it was necessary to create a continuous surface for each of the environmental variables. Interpolating observed environmental values is a common method for creating a continuous surface or raster. However, in our case, annual lakewide data were collected from May to November and covered a relatively wide range of environmental conditions (for example surface water temperature in our data set in each year spanned the range 11–21 °C), restricting our ability to interpolate the observed environmental variables across the entire lake. Therefore, we selected only those sampling areas where the environmental variables were collected during the same month of each year and where the variations were relatively small. The data collected by the OMNR started chronologically from the East basin to West basin. The sampling schedule for both basins was relatively consistent for each year. For example, in 2008, samples were collected in the East basin from September 2-8 and in the West from September 11–18. In 2007, data were collected between August 25–30 in the East and September 4–9 in the West. Because the sampling area and schedule varied annually in the central basin, we focused only on data from the West and East basins to illustrate how to apply the model and how to examine the degree to which the spatial distribution of habitat suitability varies with vertical stratum.

We created maps for each year (2006–2008) at a 50 m × 50 m resolution: two layers for bottom or epibenthic and subsurface each for dissolved oxygen, temperature, Secchi depth (light penetration), and water depth (assuming a minimal inter-annual change in water depth). The Secchi depth and water depth were the same for both the bottom and subsurface layers. The detailed procedures of creating the environmental layers are described in the Supplementary information Appendix 2.

Using the selected best model and the aforementioned environmental layers, we generated the HSI or the probability of species presence for the East and West basins (Canadian side) for the epibenthic and subsurface layers for each year (2006–2008) and for each age group. The probability of species presence is used as a proxy of habitat suitability (see, Thuiller et al., 2010). The suitability is depicted as a HSI ranging from 0 (zero probability of occurrence) to 1 (certainty of occurrence), representing "poor" to "good" habitat quality, respectively.

Spatial variation of habitat suitability area (habitat supply)

To compare the area of suitable walleye habitat (habitat supply) between the two basins or the two vertical strata (subsurface and epibenthic layers), we first calculated the suitable walleye habitat area as the area weighted by habitat suitability (WHSA). WHSA is the combination of habitat quality and quantity and was calculated as: WHSA $= \sum_{i=1}^{n} P_i \times a$; where P_i is the suitability index pertaining to each grid (i) and a is the area of the grid i (2500 m^2). Using these procedures, we computed WHSAs for the subsurface and the bottom layers of the lake for each basin (West and East). Because the surface areas of the selected basins differ, we divided the WHSA by the area of each basin. This resulted in a weighted suitability per unit area (Weighted Habitat Suitability Area Index, WHSAI) with values ranging from 0 to 1. A total of 12 WHSAIs for each group were calculated: one for each of three years

(2006–2008) for two basins (East and West) at two vertical strata (subsurface and epibenthic). We then used these 12 WHSAIs in an analysis of variance (with a randomized block design ANOVA) with "year" treated as a block to determine whether the habitat supply varied among vertical strata.

Results

Of the 3690 OMNR samples collected over 21 years, walleye were present in 2488 sample sites (67% of the observation sites). The range of temperature, depth, Secchi depth (water clarity), and DO of the

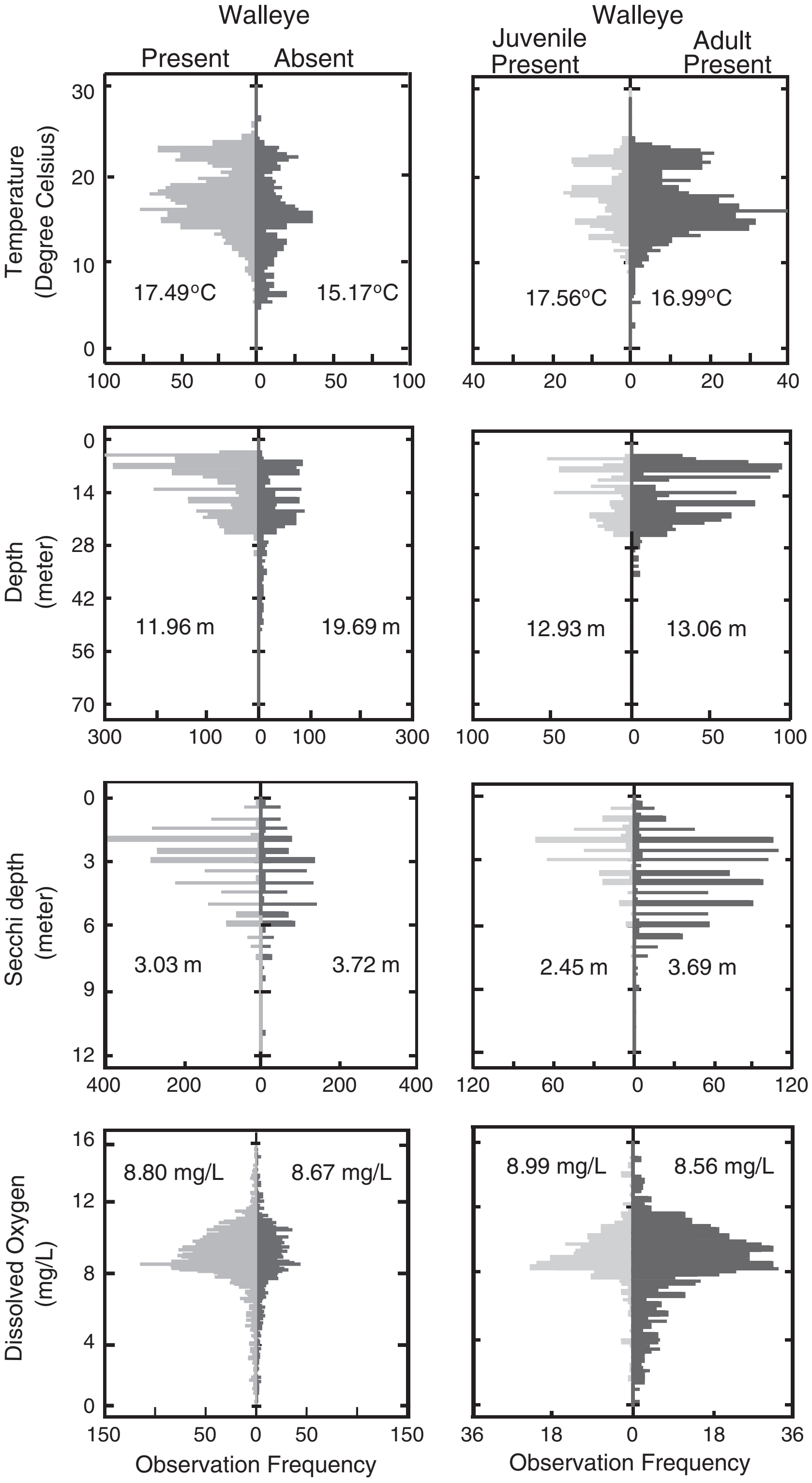

Fig. 2. The frequency of observations from the OMNR gill nets (1990–2008) with respect to water temperature, gear depth, Secchi depth (light attenuation) at the net set depth. Leftmost panels are data for all walleye absent (black; number of sample size, n = 1202) or present (gray; n = 2488) while rightmost panels are for juveniles only (gray, n = 399) and adults only (black, n = 983). The value in each box is the average value of temperature, depth, Secchi depth, and DO of the sites where walleye were present and absent and at the sites where only juveniles and only adults were present.

observation sites where walleye were present was from 2.7 to 25.0 °C, 3 to 51 m, 0.25 to 11.0 m and 0.2 to 15.0 mg/L, respectively (Fig. 2). On average, sites at which walleye were present were significantly warmer (ANOVA, $F_{1,3688} = 271.85$, $p < 0.001$), shallower ($F_{1,3688} = 74.81$, $p < 0.001$), and more turbid (i.e., Secchi depth, ANOVA, $F_{1,3688} = 174.13$, $p < 0.001$) than sites where walleye were absent (Fig. 2). There was a marginally significant difference in mean DO concentration between sites where walleye were present (8.80 mg/L) and where walleye were absent (8.67 mg/L; ANOVA, $F_{1,3688} = 3.815$, $p = 0.05$).

Adults were present at 1726 sites, whereas juveniles were only present at 1142 observation sites. At 983 sites, only adults were present, while at 399 sites only juveniles were observed. Sites at which only juveniles were present were on average significantly warmer (ANOVA, $F_{1,1380} = 7.49$, $p = 0.006$), more turbid (ANOVA, $F_{1,1380} = 174.127$, $p < 0.001$) and had higher DO concentration (ANOVA, $F_{1,1380} = 12.56$, $p < 0.001$) than sites where adults were present (Fig. 2). There was no significant difference in mean depth (± standard error) between sites where only juveniles were present (12.93 ± 0.32 m) and where only adults were present (13.06 ± 0.22 m; ANOVA, $F_{1,1380} = 0.097$, $p = 0.755$).

Estimated coefficients and the statistics from each of the models (LR-L, LR-Q, LR-C, and LR-I) for juvenile, adult, and all walleye are summarized in Table 1. The linear model (LR-L) for all groups (all walleye, adult walleye and juvenile walleye) identified a positive relationship between potential suitable habitat and temperature. Potential suitable habitat was negatively related to water depth and water clarity, but the level of DO within the observed range in this study did not influence walleye habitat preferences for juvenile and all walleye. Surprisingly, the level of DO within the observed range in this study did negatively influence the habitat preferences of adult walleye.

Of the four models (LR-L, LR-Q, LR-C, and LR-I), the best model selected by the QAIC to describe the presence–absence relationships of walleye for all three groups (juveniles, adults, and all walleye) was the model that included the interactions among the independent environmental variables (LR-I; Table 2). The evidence ratio derived from the QAIC weight (between the best fit model and other models) showed that the probability occurrences generated by the best model were more than 7.5×10^{13}, 6.6×10^{7} and ~134 times as likely as the second best model for all walleye, adults only and juveniles only, respectively (Table 2), indicating that interaction model best described the species–environmental relationships. Based on such strong evidence, we report only the results from the best model, i.e., interaction model (LR-I), for all three groups.

Table 2

Summary of the fit and selection statistics for the four models for three groups of individuals (all, adult, and juvenile). Model selection was based on Quasi-likelihood Akaike's Information Criterion adjusted for over-dispersion (QAIC). The model with the lowest QAIC value is considered 'best'. Δi is the difference in QAIC values between each model and the low-QAIC model. W_i is the Akaike model weight (the likelihood of the current model to the other model considered). Evidence ratio is the strength of evidence in favor of one model over the other.

Groups	Models	QAIC	Δ_i	W_i	Evidence ratio
Juveniles	Interaction (LR-I)	2736.70	0.00	0.9926	1
	Cubic (LR-C)	2746.50	9.80	0.0074	134.2897
	Quadratic (LR-Q)	2782.70	46.00	<0.0001	9.7×10^{9}
	Linear (LR-L)	2846.50	109.80	<0.0001	6.9×10^{24}
Adults	Interaction (LR-I)	3424.20	0.00	0.9999	1
	Cubic (LR-C)	3460.20	36.00	<0.0001	6.6×10^{7}
	Quadratic (LR-Q)	3465.60	41.40	<0.0001	9.8×10^{8}
	Linear (LR-L)	3494.20	70.01	<0.0001	1.6×10^{15}
Walleye	Interaction (LR-I)	2993.30	0.00	1.0000	1
	Cubic (LR-C)	3057.20	63.90	<0.0001	7.5×10^{13}
	Quadratic (LR-Q)	3083.30	90.00	<0.0001	3.49×10^{19}
	Linear (LR-L)	3105.40	112.10	<0.0001	2.2×10^{24}

In the LR-I model, depth and DO were negatively related to habitat suitability for all three groups of walleye. However, association of the environmental variables in determining the suitable habitat of juveniles and adults varied. Lower turbidity (greater water clarity) was negatively related to the presence of adults but there was no association for juveniles. Temperature was the driving variable in the interaction model for all three groups of walleye individuals, indicating that its selective effect or absence of effect depended on the values of the other independent variables. Various interactions of environmental variables were important (Table 1) for both groups (juvenile and adult), including DO × temperature (positive association), water clarity × temperature (negative association), and temperature × depth (positive association). However, some of the environmental variables were significant for juveniles but not for adults and vice versa. For example, two interactions, i.e., water clarity × depth (positive association) and depth × DO (positive association) were significant for adults but not juveniles, while DO × water clarity (positive association) was significant for juveniles

Table 1

Estimated parameters of the best fitting generalized linear response models (Linear, LR-L; Interaction, LR-I; Quadratic LR-Q; and Cubic, LR-C) for juvenile, adult and all walleye. Parameters included water temperature (Temp), dissolved oxygen (DO), light attenuation (Secchi) and the fishing depth of the sample gear from surface (Depth). Only the estimated coefficients of environmental variables that were retained in the final model are reported (the estimated coefficients, SE and P value are given in the Supplementary information Appendix 4). The superscripts indicate the second (^{2}) coefficients for the quadratic model and the third (^{3}) coefficient for the cubic model. Interaction coefficients between parameters are given at the bottom of the table.

Parameters	Juvenile				Adult				All walleye			
	LR-L	LR-I	LR-Q	LR-C	LR-L	LR-I	LR-Q	LR-C	LR-L	LR-I	LR-Q	LR-C
Constant	−1.315	2.818	−9.570		1.082	2.808	−2.510	−2.396	0.784	2.551	−2.147	
Depth	−0.040	−0.171	−0.047	−0.272	−0.071	−0.322	−0.098	−0.224	−0.071	−0.291	−0.070	−0.275
Temp	0.148		0.826	−1.344	0.031		0.501	0.510	0.086		0.440	
Secchi	−0.491			0.838		0.726			−0.127	0.669		0.658
DO		−0.678	0.581	0.560	−0.086	−0.310	−0.082			−0.226		
Depth^2				0.016			0.001	0.008				0.011
Temp^2			−0.020	0.109			−0.014	−0.014			−0.011	0.019
Secchi^2			−0.076	−0.356				−0.092			−0.014	−0.188
DO^2			−0.036	−0.035				−0.005				
Depth^3				0.000				0.000				0.000
Temp^3				−0.002								−0.001
Secchi^{3}				0.026								0.013
DO^3												
Depth: DO						0.008						
Secchi: DO		0.088										
DO:Temp		0.030				0.007				0.016		
Secchi:Temp		−0.074				−0.047				−0.060		
Depth: Secchi						0.009				0.013		
Depth:Temp		0.008				0.007				0.011		

only. Relationships for all walleye and adults only were similar except for depth × DO which was significant for adults but not for all walleye.

There was no spatial clustering in the residuals (observed-predicted value of species distribution) for any of the three groups of individuals (juveniles: Moran's $I = 0.17$, $z = 0.10$, $p = 0.460$; adults: Moran's $I = 0.65$, $z = 0.60$, $p = 0.274$; and all walleye: Moran's $I = -0.03$, $z = -0.40$, $p = 0.345$).

Model accuracy

The AUC values (mean ± standard error) in Fig. 3 demonstrate a high degree of accuracy between the reference data and the predicted presence/absence of walleye from the selected LR-I models. These accuracy values range from 74.5% (0.745 ± 0.018) using the OMNR reference dataset (Fig. 3a) to 84% (0.842 ± 0.017) for all walleye using the ODNR independent dataset (Fig. 3b). Similarly for adult walleye, the area under the AUC curve (mean ± standard error) was 0.661 ± 0.018, and 0.700 ± 0.024, for the OMNR reference data and ODNR independent reference data, respectively. For juvenile walleye, the AUC curve was 0.772 ± 0.026 and 0.743 ± 0.016 for the OMNR reference data and ODNR independent reference data, respectively.

Spatial and temporal variations of habitat supply

For all three groups, habitat supply (potential suitable habitat) varied geographically and vertically (across depth stratum) (Figs. 4 and 5, Table 3, and Supplementary information Appendix 3). The West basin had a greater WHSAI (mean ± standard error) than the East for all walleye (West: 0.959 ± 0.01, East: 0.614 ± 0.009), juveniles (West: 0.799 ± 0.0138, East: 0.266 ± 0.014), and adults (West: 0.71 ± 0.005, East: 0.47 ± 0.004). Subsurface waters had greater WHSAIs than epibenthic waters for all walleye (subsurface: 0.859 ± 0.01, epibenthic: 0.715 ± 0.009), juveniles (subsurface: 0.562 ± 0.014, epibenthic: 0.503 ± 0.0138), and adults (subsurface: 0.643 ± 0.005, epibenthic: 0.540 ± 0.004). The interaction between basin and vertical stratum was significant (see Table 3 and Fig. 4) for each group indicating that the difference of weighted suitable habitat per unit area between the surface and bottom layers varied between two basins. In the West basin, WHSAI was not significantly different for any of three groups (ANOVA, $F_{1,5} = 0.865$, $p = 0.405$ for all walleye; $F_{1,5} = 0.006$, $p = 0.942$ for juveniles; and $F_{1,5} = 1.993$, $p = 0.231$ for adults) whereas in the eastern basin it was significant different (ANOVA, $F_{1,5} = 217.812$, $p < 0.001$ for all walleye; $F_{1,5} = 14.504$, $p = 0.019$ for juveniles; and $F_{1,5} = 262.42$, $p < 0.001$ for adults).

Comparison of the available suitable habitat based on the existing 13 m rule and the new model

We compared the proportional distribution of habitat by basin using the existing (depth-based) and new models for the area for three groups of walleye. The model comparison in the West basin showed somewhat similar results for the new models of available suitable habitat based on WHSA (0.95 for all walleye, 0.77 for adults, and 0.75 for juveniles) and depth-based model (1.00) (Table 4). However, only 20% (0.2) of the East basin is considered habitat in the depth model, while the new models suggest that 63%, 43%, or 37% of the East basin is considered suitable for all walleye, adults, and juveniles, respectively.

Discussion

The study shows that the habitat suitability model using walleye occurrence in gill nets and observed temperature, dissolved oxygen, depth, and water clarity information is able to predict the value of an observation response with a high degree of accuracy. In general, the results of our linear model (LR-L) show an increased likelihood of occurrence of walleye in warm and shallow waters, which is consistent with previous research (Colby et al., 1972; Hokanson, 1977; Mosindy, 1984) documenting a preference for shallow water (depths less than 10 m) and warm temperatures (from 20 to 23 °C). Additionally, our linear model for walleye showed that walleye preferred turbid water. In fact, walleye develop a negative phototactic retinal response at around age-1 (Ryder, 1977; Vandenbyllaardt et al., 1991), and thus prefer water that is turbid (Secchi depth <2 m). Generally, the feeding behavior of walleye reflects the differences in water transparency (light). In clear lakes, adult walleye are primarily crepuscular or nocturnal feeders (Ali and Anctil, 1977), but in turbid environments they forage diurnally (Ryder, 1977). For these reasons, light is considered an important environmental variable that determines the temporal and spatial feeding dimensions of walleye (Ryder, 1977).

Surprisingly, dissolved oxygen was not a significant component in the LR-L models. Inspection of the data indicated that over 98% of the observed DO levels in our data set were above the critical threshold (~3 mg/L). DO concentration may have been a significant component in the model if more sampling had occurred in areas with instances of lower dissolved oxygen (for example the hypolimnial region of Lake

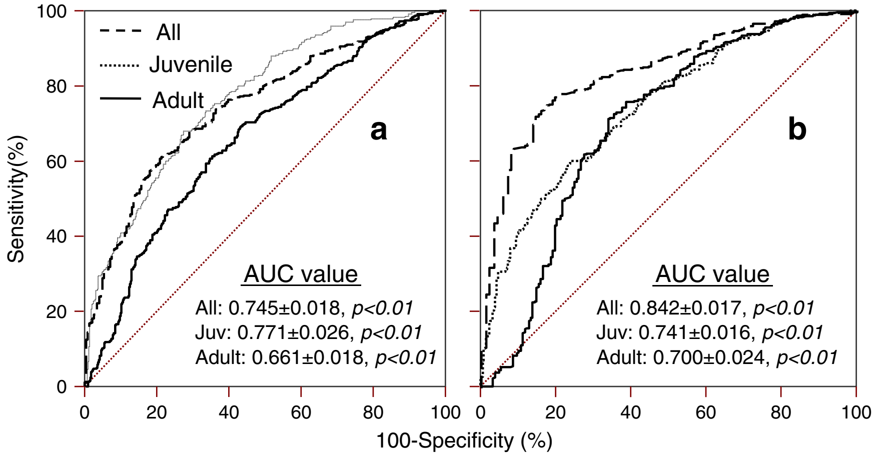

Fig. 3. Area under the receiver operating characteristic (ROC) curve or area under curve (AUC) using: a) OMNR reference data and the predicted values derived from the Logistic Regression-Interaction (LR-I) model, b) ODNR data and the predicted values derived from the LR-I model. The values in the graphs are the AUC value ± and its standard error (SE) with *p* for all walleye (All), juvenile walleye (Juv), and adult walleye (Adult).

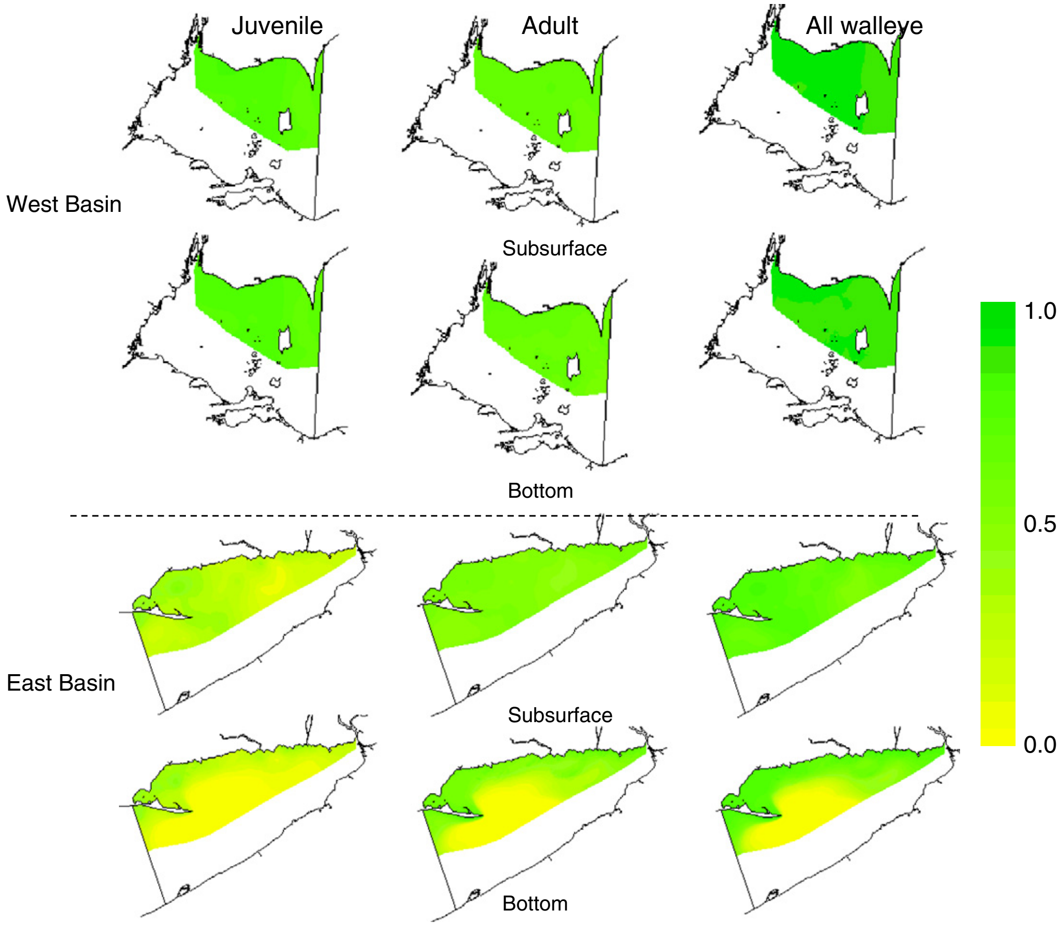

Fig. 4. Potential suitable habitat for walleye. Map of Habitat Suitability Indices (HSI, derived from the LR-Interaction response model) of juvenile, adult and all walleye in Lake Erie at subsurface (i.e., at 6 m below the water surface) and bottom of the West and East basin of the Canadian waters of Lake Erie (boundary delineating the two countries is approximate since the border line was digitized manually). The maps represent the average value of HSI index of three years (2006–2008). Indices and shading range from 0 (unsuitable) to 1 (suitable).

Erie's central basin; Burns et al., 2005). Fitz and Holbrook (1978) also suggested that walleye preferred temperatures at or near the thermocline in stratified lakes, even those with less than optimal DO levels. This would allow them to forage and/or avoid strong light conditions, which supports the hypothesis that walleye can overcome “critical” dissolved oxygen concentrations if other environmental conditions are suitable. This suggests that walleye may briefly inhabit less preferred or even unsuitable habitat for foraging. The LR-I response shows that the presence of walleye is positively associated with the interaction between DO and temperature, indicating that they prefer areas of higher DO under conditions of higher temperature. Because warmer water is less oxygen-soluble, the influence of temperature on the presence of walleye may simply dominate that of DO, especially considering the range of dissolved oxygen conditions sampled in this study. During

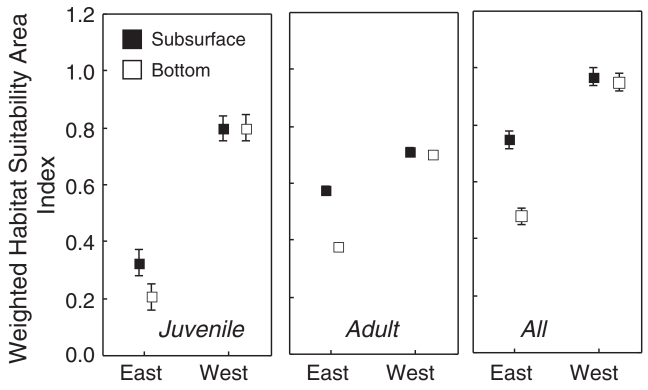

Fig. 5. WSHAI (weighted suitable habitat per unit area or index) at the subsurface and bottom for juvenile walleye, adult walleye, and all walleye for the East and West basins (Canadian site) of the Lake Erie. The solid squares indicate values of WSHAI from the subsurface (i.e., taken at 6 m from the water surface) over the three years (2006–2008); while open squares indicate the epibenthic (bottom) layer. Vertical bars denote 95% confidence interval of the mean.

Table 3
Summary statistics of randomised block design with ‘Year’ treated as a block for the variation of the WHSAI among the basins (western and eastern) and vertical stratum (V. strata) of lake (surface and bottom) in Lake Erie for juvenile walleye, adult walleye and all walleye. SS — sum of squares, df — degrees of freedom, MS — mean squares. Significant effects are in bold type.

Group	Sources	SS	df	MS	F	*p*
Juvenile	Basins	0.851	1	0.851	1057.280	<**0.001**
	V. strata	0.010	1	0.010	12.881	**0.017**
	Year (Block)	0.004	2	0.002	2.679	0.147
	Basins × V. strata	0.011	1	0.011	13.684	**0.015**
	Error	0.009	6	0.001		
Adult	Basins	0.159	1	0.159	826.243	<**0.001**
	V. strata	0.032	1	0.032	0.167.851	<**0.001**
	Year (Block)	0.000	2	0.000	0.061	0.942
	Basins × V. strata	0.027	1	0.027	137.943	<**0.001**
	Error	0.001	6	0.000		
Walleye	Basins	0.358	1	0.358	727.584	<**0.001**
	V. strata	0.062	1	0.062	126.927	<**0.001**
	Year (Block)	0.001	2	0.001	1.427	0.311
	Basins × V. strata	0.048	1	0.048	96.635	<**0.001**
	Error	0.004	6	0.001		

Table 4
Comparison of suitable habitat based on the current depth-based definition (<13 m, A) and the new, Weighted HSAI (B) for three groups of individuals in the study area (the selected area of the East and West basins of Lake Erie).

Basin	Total area (km^2)	≤13 m depth		Weighted HSA (km^2)			
		Area	HSI (A)	Subsurface	Epibenthic	Average	HSI (B)
1. All walleye							
East	3651.71	726.32	0.2	2854.84	1730.62	2292.7	0.63
West	1655.04	1651.52	1	1604.08	1550.64	1577.4	0.95
2. Adult walleye							
East	3651.71	726.32	0.2	2017.89	1155.17	1586.5	0.43
West	1655.04	1651.52	1	1276.01	1264.47	1270.2	0.77
3. Juvenile walleye							
East	3651.71	726.32	0.2	1684.8	999.85	1342.3	0.37
West	1655.04	1651.52	1	1304.27	1274.48	1289.4	0.78

the summer, hypoxia (DO < 2.0 mg/L in the hypolimnion) is common in Lake Erie (Brandt et al., 2011), especially in the central basin. Reduced oxygen availability has the potential to affect fish physiology, their vertical and geographic distribution, and prey–predator relationships, and these effects are species and life-stage dependent (e.g., Roberts et al., 2009; Vanderploeg et al., 2009). As a top predator, walleye may actually benefit from hypoxia in Lake Erie because of the increase in spatial overlap with prey fish species, which become trapped by low-oxygenated waters (Roberts et al., 2009; Vanderploeg et al., 2009). For these reasons, additional work under more severe hypoxic conditions is necessary to better quantify the relationship between walleye occurrence and hypoxia. This will be especially important when the model is applied to the central basin.

Although results from our linear model are statistically significant, are primarily consistent with the literature, and are commonly used in species–habitat modeling (see example, Embling et al., 2010; Hooker et al., 1999; Parnell et al., 2006), we selected the interaction response model over the linear model for our HSI. The interaction model not only performed better statistically but also allows us to understand how environmental variables act in an interactive manner rather than independently to shape walleye habitat. That is, we can examine how the effects of one variable on walleye habitat depend on the level of other variables as well. Unfortunately, the possibility of interactive effects of environmental variables was seldom considered, in order to avoid complexity, until recently (Gibson et al., 2004). Our LR-I model indicates that the suitability of walleye habitat increases with increasing water temperature only when the water is turbid. Under less turbid conditions, the habitat suitability is not influenced solely by water temperature. Scherer (1976) also demonstrated interactive effects in that a walleye's preference for depth was related to light intensity. In his study, walleye tended to stay near the bottom of the water body under high light conditions (275–245 lx), in mid-water column under intermediate light conditions (25 to 32 lx), and near the surface at low light levels (3.3 to 2.6 lx). Our study detected a negative interaction between Secchi depth and temperature in the LR-I model which suggests that the occurrence of walleye, including juveniles, increases as temperature increases in areas with lower water clarity (high turbidity or lower Secchi depth). A positive association of temperature and depth with species presence indicates that walleye prefer deeper waters if temperature is suitable, which is consistent with Ryder (1977) and Scherer (1976).

Overall, we found slight differences in habitat preference between juvenile and adult walleye. Juveniles are more likely to be found in waters that are warmer (similar to Hokanson, 1977), shallower, more turbid (lower Secchi readings), and have more dissolved oxygen than adults. The ability of young walleye to utilize more turbid environs, which are not typically preferred by other species in Lake Erie, may assist them in avoiding predation or reducing competition with other piscivorous species (Vandenbyllaardt et al., 1991). Because young walleye are adapted to a turbid and scotopic environment (Vandenbyllaardt et al., 1991), they are able to exploit dimly-lit environments not used by other predators. Juveniles are also found within a narrower range of temperatures and turbidity values than the adults, indicating that habitat is more limiting for young fish. Overall, the probability of juvenile occurrence was greater in shallower water, which may provide benefits with respect to predator avoidance at the smallest sizes or for foraging. However, the study shows if temperature is suitable, juveniles can move to deeper waters which may have higher levels of dissolved oxygen and, generally, lower turbidity.

The fact that our models include the data collected from a variety of mesh sizes, multi- and monofilament gill net material, and suspended and bottom nets helps to reduce size biases. About one fourth of the total catch consists of walleye ≤age-1 in our data set, which is a good representation of the age group. In the lake, length at age for age-1 walleye does differ by location; the fish in the East tend to be larger and in better condition at a given age than those in the West. Therefore, they were more likely to recruit to the gear in a given year, which would result in a higher probability (i.e. more suitable habitat) in the East than the West if there were size biases from gillnet sampling. The results of our habitat model actually show the opposite to be true, so recruitment to the gear is not likely biasing the results of our habitat model between juveniles and adults. If anything, it may support the notion that the variables associated with more suitable habitat are producing fish in better condition (i.e. that are more likely to recruit to the gear).

Once we found lower probability of walleye occurrence in less turbid conditions, we also became concerned that this may be a result of net avoidance by walleye under clearer water conditions. To address this issue, we examined the relationship between catch and water clarity and found no significant relationship between the two variables. Similarly, in our study, we found no spatial autocorrelation of the residuals of the best model indicating there was no bias in fitting the model. In fact, our selected model is an interaction model and thus may have no significant autocorrelation since previous studies (Diniz-Filho et al., 2003; Kűhn, 2007; Zuur et al., 2007) showed that, in general, spatial autocorrelation of residuals decreased to non significant levels when several environmental variables or their interaction terms are included in the model.

The prediction power of our selected best model (accuracy of the model) is relatively high for all three groups of individuals. It is fairly common in species distribution/habitat models to have some predictive error (Pandit et al., 2010), and these could be caused by sampling error, accidental omission of other important environmental variables in the model, a mismatch in the resolution of environmental and biological data, or any combination of the above (Pandit et al., 2009, 2010; Pandit and Kolasa, 2012). For example, bottom substrate (clay or sand or gravel, etc.) could be an important attribute of walleye habitat. We decided to exclude this information from our model, because the spatial resolution of the bottom substrate data available for Lake Erie is too coarse to provide accurate information at the resolution of the biological information used in this study. Furthermore, short-term variation in physicochemical factors may have escaped our monitoring regime, which included sampling abiotic factors when the nets were set, but affected species presence/absence later (i.e. during the subsequent 16–24 h while the net fished).

In fact, the use of logistic regression on presence/absence data is common for this type of habitat suitability modeling and has been shown to perform similarly to abundance models (Lamouroux et al., 1999; Pearce and Ferrier, 2001). Because walleye populations undergo high levels of inter-annual variability, developing a probability of occurrence model is more effective than estimating abundance for understanding the distribution of suitable habitat. Because some of the variation in abundance is not driven by environmental (habitat) variables, using abundance to estimate the habitat suitability is expected to increase significantly the uncertainties. In this study, the surveys have sampled a broad range of each environmental variable and collected sufficient information on walleye presence and absence. Thus, we believe our models provide reliable estimates of walleye habitat suitability.

In this study, the habitat model was developed using a long term data set; and the model accuracy was high between the Ontario and Ohio reference data sets. To evaluate how suitable habitat in Lake Erie varies spatially and temporally for the entire lake, we needed a dataset collected over a short time period; however the data were not collected over a consistent time frame lakewide. We thus focused our analyses on the Canadian waters of the East and West basins during late summer. This time–space combination provided the highest resolution for abiotic data available, and it gave a general overview of how the habitat varied temporally, spatially, and vertically. The model predicted that, in the Canadian waters of Lake Erie, there is more suitable habitat for adult walleye (50% of the surface area) than for juvenile walleye (~40%). In general, the area of suitable habitat is higher in the West basin than the East basin for both adults and juveniles, despite marked differences in the sizes of the two basins. Suitable habitat supply for walleye also varies by vertical stratum in Lake Erie. Subsurface waters provide more suitable habitat than bottom waters do, but this depends upon the basin. For example, the West basin is relatively shallow and isothermal throughout the year, and consequently the difference in the amount of suitable habitat for walleye between subsurface and bottom layers of the lake is minimal. During summer, Lake Erie's Central and East basins stratify, resulting in great differences in the amount of walleye habitat by vertical stratum. Our study highlights the importance of depth in determining the amount and location of suitable habitats for fish species. This suggests that refined, 3-dimensional analyses are needed in stratified lakes in order to improve the estimates of suitable habitat.

Fisheries management application

The proportional amount of habitat by jurisdiction using the present (≤13 m depth-based) and new WHSA Index are slightly different. According to the current habitat definition for quota allocation (≤13 m depth-based), the West basin of this study has a probability of 1.0 (100%) of having suitable walleye habitat because the entire area is less than 13 m deep, and this is similar (Figs. 4 and 5) to our model for all walleye (0.95). When age groups are separated, our model suggests there may be almost 25% less habitat than the present depth-based model. There is also disparity between the new and existing model (≤13 m depth) in the East basin; the new model suggests there may be up to three times more habitat than the current model estimates. Therefore, the 13 m depth-based model may be overestimating the West basin habitat and under-estimating the East basin habitat.

Our spatial models have not yet been developed based on the exact bounds of the walleye management units because of the limitations of the available abiotic data. As that dataset is compiled, lakewide versions of our WHSA maps will provide a valuable tool for managers. Although portions of the East are not presently managed under this strategy, recent increases in East basin recruitment, recent warming trends which invoke more easterly summer migrations, and better understanding of walleye movement using acoustic telemetry, reinforce that our knowledge of lakewide habitat is essential to the future of walleye management in the lake.

This research has direct implications for the sustainable management of Lake Erie walleye. Currently, annual quota allocation for recreational and commercial walleye fisheries is determined based on the proportion of surface areas of 'preferred habitat' shared by each jurisdiction and walleye habitat is defined as the surface area of waters less than 13 m deep (STC, 2007). Results from our study demonstrate that water depth is not the only driving factor in the species–habitat relationship; other environmental factors (and their interactions) are also essential in determining the occurrence of walleye. This clearly indicates that fish resource managers are faced with limited and uncertain ecological information for their management decisions. Results from our work could be used to refine the definition of walleye habitat and reassess the present quota-sharing allocation formula. Our study further shows that suitable habitat for juvenile walleye is mostly located in the West basin compared to the East basin. Therefore, in order to maintain its recruitment, it might be important to protect some areas of the West basin.

In summary, this study showed that the relationship between walleye occurrence and environmental factors (temperature, depth, dissolved oxygen and water clarity) can be better described by an interaction response model than by an additive, independent effects model of single factors with linear, quadratic, or cubic response function. Using the probability of walleye occurrence as a surrogate for a walleye habitat suitability index, we determined that walleye prefer warm, turbid waters and that they may adjust their distribution horizontally (i.e., nearshore or offshore) or vertically (within the water column) to search for desired conditions. Habitat preference varied by both age group and vertical stratum. These findings may lead to more precise criteria by which to determine the quota allocation protocol for walleye in Lake Erie.

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Appendix A. Supplementary information

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2013.09.011.

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