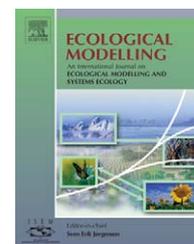


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Population dynamics of smallmouth bass in response to habitat supply

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ARTICLE INFO

Article history:

Received 31 January 2005

Received in revised form 11 August 2005

Accepted 15 November 2005

Published on line 27 December 2005

Keywords:

Smallmouth bass

Freshwater lakes

Population modelling

Habitat modelling

ABSTRACT

We have developed an age-structured, spatially explicit model to estimate smallmouth bass (*Micropterus dolomieu*) population dynamics from the readily available habitat data of a lake. Habitat suitability models were used to rank the suitability of different sites throughout a lake for smallmouth bass. Population dynamics were then linked to the habitat suitabilities via a home range mechanism, a density-dependent mechanism and the ideal-free distribution theory. The home ranges are calculated as a function of size, the density-dependent mechanism assumes that habitat suitability will decrease as the density of fish at a site increases and the ideal-free distribution theory assumes fish will seek out more suitable habitats. When all fish are distributed throughout the lake, growth is calculated as a function of temperature and density. This consequently affects the fecundity of the mature females, survival of the young-of-year (YOY) and the number of fish recruited to the population in subsequent years. Sensitivity analyses indicated that the habitat alterations that increased YOY survival (increased temperature and total nesting habitat) had the greatest impact on population dynamics and suggests that conservation or restoration efforts should focus on the nesting (YOY) habitat. When validated, the model described the population indicators, total number of nests and fish, better than the spatial distribution of fish within the study lakes. These findings suggest that in its current state, the model may be successfully used to guide smallmouth bass population and habitat management practices. Future developments of the model are also discussed.

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1. Introduction

Traditionally, the influence of habitat on fish production has been measured through assessments of habitat suitability indices (HSIs) that assume animals will concentrate in areas that optimize their survival, growth and reproduction (Hubert and Rahel, 1989; Freeman et al., 1997). Using the habitat preferences for a given species as reference, HSIs allow one to determine the relative suitability of different areas of a

lake, stream or river for that species. HSIs do not however, incorporate measures of the intensity of intraspecific interactions that may affect fish populations within any habitat. Nor do they allow one to explore how a population may be affected by changes in the supply of various habitat types. To fill this gap, recent publications have focused on the need to link habitat supply to fish population dynamics (for e.g., Minns et al., 1996; Hayes et al., 1996; McHugh et al., 2004).

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doi:10.1016/j.ecolmodel.2005.11.024

Some studies have linked habitat to population dynamics via regression models. Population density or yield may be determined as a function of habitat characteristics, such as macrophyte abundance (Maceina, 1996), landscape variables (Cross and McInery, 2005) or temperature (Shuter et al., 2002). However, these models do not incorporate population processes such as mortality rates or growth rates that influence the dynamics of fish populations. Habitat supply has also been linked to the dynamics of a particular life stage of a species (Jones et al., 2003; McHugh et al., 2004) or a particular population process such as growth rates (Brandt and Kirsch, 1993). Although these studies are informative, they do not allow one to determine how habitat changes may impact other life stages or include other processes that may be influencing the population such as mortality rates.

Another approach links HSIs to population processes using proportional relationships (Jessup, 1998). However, assumptions of proportionality do not incorporate density-dependent effects or behavioural choices that may affect the distribution of fish among habitats with different HSI scores. The distribution of fish among varying habitats can affect population processes because high densities of fish in a particular habitat may lead to slow growth (due to competition for resources) or because fish may choose sub-optimal habitats if food resources there are plentiful (Bevelhimer, 1996). This suggests that mechanisms describing habitat use should be incorporated into habitat-population models. This can be accomplished using individual-based modelling approaches whereby the individual habitat choices of a fish in a population can be linked to its growth and survival to produce more detailed estimates for the entire population (Wildhaber and Lamberson, 2004; Jepsen et al., 2005).

The objective of this study was to develop a model that links habitat to the population dynamics of smallmouth bass while incorporating density-dependent effects on habitat use, growth and survival. Empirical data were used to develop a lake-dwelling smallmouth bass model specific to Ont., Canada. Sensitivity analyses were used to learn about the population dynamics of smallmouth bass under different habitat scenarios and the model was validated to test the accuracy of its predictions.

2. Methods

2.1. General model structure

We defined two habitat sub-models based on the habitat requirements of the different life stages of smallmouth bass (Fig. 1). The first focuses on the nesting habitat and encompasses reproductive adults, eggs, hatchlings, swim-up fry and YOY (post-dispersal and for the remainder of the growing season). The second includes the juvenile and adult life stages. The adult life stage is defined as fish age ≥ 3 years because that is the age when these fish approach maturity. Due to data deficiencies, the model does not presently support density or habitat-dependent changes in the age of maturity.

Habitat suitability indices were developed for each of the habitat variables (Fig. 1). Using the habitat data, the model first maps the suitability of different sites in a lake for nesting and

for the juveniles/adults. The ideal-free distribution theory is then used to distribute nests and fish among the sites and thus calculate density estimates in each site. Fry, YOY, juvenile and adult growth is then calculated daily as a function of density and temperature. Mortality is size-dependent for the fry and YOY but is set at an annual rate for the older fish. At the end of first year the model produces the suitability of the different sites of the lake for smallmouth bass, and the growth and survival of the population. The model is then looped for several years until the population reaches equilibrium (Fig. 1). Equilibrium is assumed to be established when the population density varies by no more than 5% over a 10 year period.

2.2. Habitat suitability indices

2.2.1. Water temperature suitability for nesting

Smallmouth bass nest in the littoral zone of lakes at temperatures ranging from 12.8 to 18 °C with the average spawning temperature in Ontario being 16 °C (Edwards et al., 1983; Armour, 1993). Given that littoral water temperature data are often lacking, an offshore temperature model developed by Shuter et al. (1983) was modified to predict littoral temperatures throughout the ice-free season (Chu, 2001):

$$\text{Spring: } T = (0.48 \ln(F_{\text{eff}}) - 2.96) + [(T_{\text{max}} - 1) \times \sin(\pi d D^{-1} + 1) - 1] + (0.004d^2 - 0.09d + 4) \quad (1)$$

$$\text{Summer: } T = (0.31 \ln(F_{\text{eff}}) - 1.97) + [(T_{\text{max}} - 1) \times \sin(\pi d D^{-1} + 1) - 1] + (0.0004d^2 - 0.09d + 4) \quad (2)$$

$$\text{Fall: } T = (0.42 \ln(F_{\text{eff}}) - 2.71) + [(T_{\text{max}} - 1) \sin(\pi d D^{-1} + 1) - 1] + (0.0004d^2 - 0.09d + 4) \quad (3)$$

where spring, summer and fall represent the days from ice-out to June 21, June 21–September 21 and September 21 to temperatures of 10 °C, when smallmouth bass become inactive (Shuter et al., 1980), respectively. T is the littoral temperature (°C), d the day in the ice-free season, T_{max} the maximum of offshore surface temperature calculated as a function of mean annual air temperature and littoral depth (2 m), F_{eff} the effective fetch (m) and D is the duration of the entire ice-free season (days). Eqs. (1)–(3) therefore provide daily temperatures with the effective fetch component driving much of the variation in temperatures throughout the littoral zone.

In the nesting model, spawning occurs at 16 °C; a value that represents the mean spawning temperature in Ontario. The nesting period is treated as a single event. Re-nesting or second nesting events have been documented and typically follow either a dramatic cooling in water temperature (from ≥ 16 °C to < 12 °C) or a wind event that has led to nest destruction (Shuter et al., 1980; Armour, 1993; M. Ridgway, 1998, personal communication). However, re-nesting events have not been incorporated into the model because of their unpredictable nature and, because the long-term average smallmouth bass density in a lake is not likely to be strongly influenced by them.

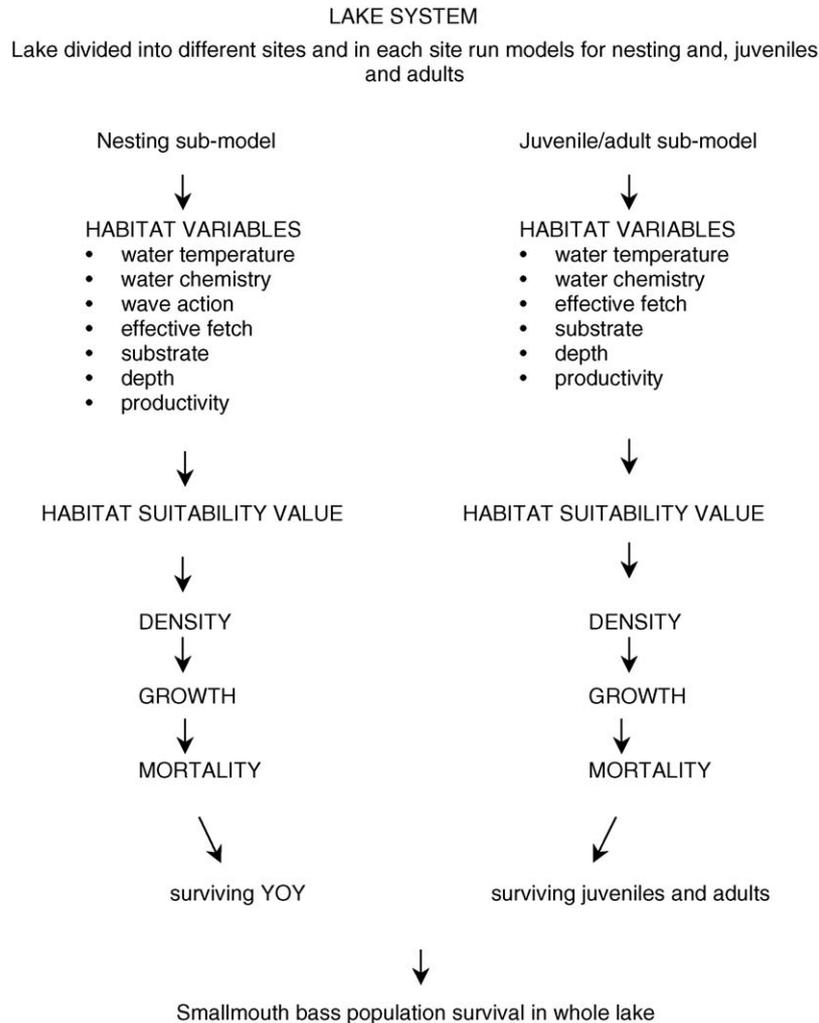


Fig. 1 – A general outline of the habitat-based population model.

2.2.2. Water temperature suitability for juveniles and adults

Smallmouth bass in Ontario prefer temperatures of are warmwater fish that prefer temperatures of 13–26 °C (Lasenby and Kerr, 2000). Within the present Canadian range of smallmouth bass, temperatures are below the preferred range for most of the season. Therefore, areas of a lake that offer warmer temperatures for a longer period of time were assumed to be more suitable for smallmouth bass than cooler areas. Temperature suitability (0–1) within a lake is calculated for different sites by standardizing the maximum temperatures to one. The site with the highest maximum temperature is typically warmest throughout the ice-free season and receives an HSI temperature value of one. The temperature suitability of the other sites is calculated by dividing their maximum temperature by the highest maximum temperature.

2.2.3. Substrate suitability for nesting

Substrate is an important component of the nesting habitat because it is the material upon which nests are built and affords cover and protection for the YOY (Goff, 1985). A sub-

strate suitability model was developed using nesting data from seven Ontario populations (Chu, 2001). Substrates composed of a combination of sand and rock tend to be preferred for smallmouth bass nesting (Eq. (4)).

$$S_N = 0.68(P_S) + 0.88(P_{SR}) + 1(P_G) + 0.79(P_R) + 0(P_W) + 0.41(P_L) \tag{4}$$

where S_N is substrate suitability for nesting, P_S the sand (more than 80% of substrate covered by particles ≤ 2 mm in diameter), P_{SR} the sand and rocks (20% or more of substrate covered by particles ≥ 140 mm, and at least 50% ≤ 60 mm), P_G the gravel (70% or more of substrate covered by particles ≤ 100 mm and at least 10% in the 20–100 mm range), P_R the rock (40% of more of substrate covered by particles > 140 mm diameter), P_W the weed (40% or more of substrate covered by aquatic plants) and P_L is litter (80% organic debris, logs, sticks and decaying plant material). These substrate categories are consistent with the categories defined during a Lakeshore Capacity Study performed by the OMNR during 1978–1981 (Harker, 1982).

2.2.4. Substrate suitability for juveniles/adults

Juveniles and adults prefer rocky substrates or submerged logs (Scott and Crossman, 1973). The substrate HSI for this life stage was modified from Edwards et al. (1983):

$$S_{JA} = 0.2(P_S) + 0.7(P_G) + 1(P_R) + 0(P_W) + 0(P_L) \quad (5)$$

where S_{JA} is the substrate suitability for juveniles and adults and $P_{SR} = P_G$. To calculate the substrate suitability of a site in a lake, percentage(s) of the different substrate types are entered into the model.

2.2.5. Water chemistry suitability

A literature review provided data to generate a habitat suitability curve for pH and dissolved oxygen (Edwards et al., 1983). HSI's for both of these parameters were used for the nesting and juvenile/adult habitat models.

$$pH_S = -0.04(pH)^2 + 0.64(pH) - 1.56 \quad (6)$$

where pH_S is the pH suitability and if $pH \leq 3$ then $pH_S = 0$, if $pH > 9$ then $pH_S = 0$.

$$dO_{2S} = 0.003(dO_2)^3 - 0.074(dO_2)^2 + 0.59(dO_2) - 0.51 \quad (7)$$

where dO_2 is the dissolved oxygen concentration (ppm), dO_{2S} is the dissolved oxygen suitability and if $dO_2 \leq 1$ ppm, $dO_{2S} = 0$, if $dO_2 > 6$ ppm, $dO_{2S} = 1$.

2.2.6. Depth suitability

Most commonly observed depths for nesting are 0.5–2.5 m (Neves, 1975; Coble, 1975; Goff, 1986). This depth range sets the boundaries of the nesting habitat. Smallmouth bass inhabit the epilimnion of lakes therefore the thermocline depth represented the lower limit of the juvenile/adult depth range. Thermocline depth (Z_T) was calculated from maximum fetch, mean depth and mean annual air temperature using a model developed by Shuter et al. (1983).

$$\ln(Z_T) = 0.22 \ln(F) + 0.21 \ln(Z) + 1.42 \quad (8)$$

where Z_T is thermocline depth (m), F the maximum fetch (km) and Z is the mean depth of the lake (m). The area between 0.5 and 2.5 m and between 0 m and the thermocline depth were used to calculate the suitable area of each site in the lake for nesting and juveniles/adults, respectively.

2.2.7. Wave action suitability

Wave action can lead to nest destruction by displacing eggs or disturbing the substrates housing eggs (Goff, 1986). A wind storm event in Lake Opeongo, Ontario, destroyed most of the nests in the prime nesting area of the lake in 1998 (M. Ridgway, 1998, personal communication). Data regarding the gust speed during the storm (51 km h^{-1}) and the effective fetch of the area affected (2200 m) were entered into a wave height equation developed by Smith and Sinclair (1972):

$$WH_N = \left[0.003 \left(\frac{g F_{\text{eff}}}{14.17^2} \right)^{0.47} \frac{14.17^2}{g} \right] P_{GS} \quad (9)$$

where WH_N is wave height at the nesting area (m), g the gravitational constant (9.8 m s^{-2}), F_{eff} the effective fetch (m) and P_{GS} is the probability of attaining detrimental gust speeds of $\geq 51 \text{ km h}^{-1}$. Gust speed represents an index of the storm's intensity so to broaden the applicability of the model, the probability of achieving detrimental gust speeds for different mean monthly wind speeds was calculated using wind data from Environment Canada (2000) (Eq. (10)). Therefore, if gust speed data are not available for a lake being modelled, mean monthly wind speed data can be used: ($r^2 = 0.99$, $p = 0.04$).

$$P_{GS} = 0.003 (MS)^3 - 0.13 (MS)^2 + 2.11 (MS) - 10.38 \quad (10)$$

where P_{GS} is the probability of attaining $\geq 51 \text{ km h}^{-1}$ gust speeds and MS is the mean monthly wind speed (km h^{-1}). If $MS \leq 9$ then $P_{GS} = 0$, if $MS \geq 17 \text{ km h}^{-1}$ $P_{GS} = 1$. Eq. (9) produced a wave height of 0.48 m. This wave height was taken as the critical height leading to nest destruction. If the wave height produced by Eq. (9) is greater than 0.48 m then the site(s) of a lake being modelled is(are) deemed unsuitable for smallmouth bass nesting ($HSI = 0$). For other sites wave height suitability equals 1.

2.2.8. Effective fetch (m)

Effective fetch is a variable that is indirectly related to habitat suitability and is a component of the water temperature and wave height equations. The effective fetch of a site was calculated using the model developed by Scheffer et al. (1992):

$$F_{\text{eff}} = \Sigma(\cos(a)L(a))\Sigma(\cos(a))^{-1} \quad (11)$$

where F_{eff} is the effective fetch (m), a the angle of measurement (-45° , 0° and $+45^\circ$) where 0° represents the prevailing wind direction and L is the distance (m) to land across the lake along angle a .

2.2.9. Productivity and YOY

The complexities of bass-prey relationships have not been directly incorporated into the model because the model is meant to focus on how habitat supply influences bass populations. For the nesting model, the P parameter of a bioenergetics model (Shuter and Post, 1990) was linked to [TDS], a broad-based measure of material in the water and an index of lake productivity (Chu, 2001) ($r^2 = 0.81$, $p = 0.04$):

$$P = -0.0003TDS^2 + 0.03TDS + 0.45 \quad (12)$$

where P is the proportion of food consumed out of the maximum potential consumption, $TDS = [TDS]$, if $[TDS] > 40 \text{ mg L}^{-1}$ then $P = 1$. If a lake is productive, food should be abundant and one can expect the consumption and growth of smallmouth bass to be near their maximum rates therefore P would equal one. Using [TDS], P is fed into a bioenergetics model to estimate growth (see Section 2.3).

2.2.10. Prey abundance in the juvenile/adult sub-model

A similar approach (relating [TDS] to P) was attempted for the juvenile/adult model but there was no clear relationship between [TDS] and growth. Consequently, P is set to one for the juvenile/adult model. If another value of P is available

for the lake being modelled, the user can enter it, or the user may vary P from 0 to 1, to determine how it affects the population.

2.2.11. Overall habitat suitability score

The geometric mean of the HSI values for each habitat variable provides an overall HSI score for a lake site. The geometric mean is the n th root of the product of the n HSI's and is employed because the overall index is multiplicative (Zar, 1996). This process gives each habitat variable equal weight and is represented by Eq. (13) for the nesting model and Eq. (14) for the juvenile/adult model:

$$HSI_N = (T_N S_N pH_S dO_{2S} WH_N)^{0.2} \quad (13)$$

$$HSI_{JA} = (T_{JA} S_{JA} pH_S dO_{2S})^{0.25} \quad (14)$$

where pH_S and dO_{2S} are the same in both the nesting and, juvenile/adult model, T_N and S_N the temperature and substrate suitabilities for nesting model and T_{JA} and S_{JA} are the temperature and substrate suitabilities for the juveniles and adults. The overall HSI score ranges from 0 to 1 with 1 representing the most suitable habitat. Each site in the lake is assigned an overall suitability score for both nesting and the juveniles/adults.

2.3. Linking habitat to population dynamics

2.3.1. Nest distribution

To calculate the maximum number of nests possible in a site, the area between 0.5 and 2.5 m deep is divided by the minimum area of a nest, 230 m² (Scott, 1993). This value is then multiplied by the suitability of the site to determine the potential number of nests in each site.

Population data and Eq. (15) (Shuter and Ridgway, 2002) are then used to determine how many reproductive males (age 3 years and older) are available for nest building.

$$P_{\text{males}} = e^{-0.0003 \text{ males}} \quad (15)$$

where males represent the number of mature males in the population and P_{males} represents the proportion of those males who will build nests.

Individual males are then assigned to different nests using the ideal-free distribution theory. This theory states that organisms will distribute themselves across habitats of varying quality such that the degree of crowding in the best habitats will negate the premium in quality between the most and least favourable sites (Fretwell and Lucas, 1970). That is, as the density of nesters increases, the suitability of that site for nesting decreases. In nature, larger, older males attain the best nest locations (Ridgway et al., 1991b) therefore the model first assigns large males to the most suitable nests. Successively smaller fish will populate that site until the density is so high that the suitability of that site for nesting is no better than the second-most suitable site. Males are then assigned to the second-most suitable site until that site becomes less suitable than another site. This process continues until all the nests are occupied or there are no more reproductive males, whichever comes first.

2.3.2. Juvenile/adult distribution

The distribution of the juveniles and adults is also modelled using the ideal-free distribution theory. The largest fish (having the greatest mobility) will first populate the most suitable site. Each consecutive fish will then populate that site until the density is so high that due to the competition for habitat and resources, the benefit of being at that site is no greater than being at the second-most-suitable site. This process continues until all individuals are distributed throughout the different sites of the lake.

2.3.3. Egg deposition

Observations at Lake Opeongo suggest that (1) larger, older males occupy the best nest sites and (2) females mate with males of a similar size (Ridgway et al., 1991b; M. Ridgway, 1998, personal communication). Therefore, the size of a nesting male determines his mate's fecundity. Other observations suggest that most males nest with only one female (Neves, 1975; Goff, 1985). The model pairs males with females in accordance with these findings.

Fecundity is calculated as a function of weight using a linear regression (Chu, 2001) ($r^2 = 0.75$, $p < 0.001$):

$$F = 10.008 W - 381.18 \quad (16)$$

where F is the fecundity (number of eggs) and W is the weight (g). The number of eggs deposited in a nest is equal to the fecundity of a female of a weight equal to the male. The number of eggs deposited in each nest is then summed to provide an estimate of the total number of eggs deposited in each site.

2.3.4. Growth

Growth of the YOY is positively related to temperature (Shuter et al., 1980; Armour, 1993). A model developed by Shuter et al. (1980) was used to determine the time to hatch and time to rise off the nest in different sites of a lake. Once the YOY rise from the nest and begin exogenous feeding, a bioenergetics model parameterized according to Shuter and Post (1990) is used to estimate growth.

There has been to our knowledge, only one empirical study looking at the effects of density on YOY growth (Friesen, 1998) and this study ceased once the YOY dispersed from the nest site. Therefore, another approach was used to incorporate density-dependent effects on YOY growth. Density was incorporated following the model used by Minns et al., (1996) for northern pike. In this model, density-dependent growth is a function of the area required by a population versus the area that is available. If a fish has an optimal home range area to forage, one can expect its growth rate to be at the maximum allowed by the temperatures observed. The equation used to calculate the optimal home range area required by a fish is (Minns, 1995):

$$HR = 2.746 L^{1.52} \quad (17)$$

where HR is the home range (m²) and L is the total length (mm). The home range model was developed for lake-dwelling fish ranging in length from 170 to 830 mm. Although this spans the size range of older smallmouth bass, we assumed the same relationship for fish smaller than 170 mm because data were

not available to develop a small fish home range model. The home range required by a YOY is multiplied by the number of YOY in a site to produce the total area required by all individuals. Maximum growth is calculated daily using temperature and the bioenergetics model. For each site, the maximum growth estimates, home range estimates and site area are entered into Eq. (18) (modified from Minns et al., 1996) to calculate the actual daily growth of the YOY:

$$G_{ACT} = \frac{G_{MAX}(AA^{0.96})}{AA^{0.96} + 0.0101(THR^{0.96})} \quad (18)$$

where G_{ACT} is the actual growth (mm), G_{MAX} the maximum growth expected in site (mm), AA the area available (nesting or juvenile/adult area (m^2)), THR the total home range required for the population (m^2), 0.0101 represents a scaling coefficient that ensures G_{ACT} is close to G_{MAX} when the area required by the population is equal to the habitat area available to the population, 0.96 is a scaling coefficient that ensures G_{ACT} is close to $0.5(G_{MAX})$ at high densities (Fig. 2). The $0.5(G_{MAX})$ was chosen by Minns et al. (1996) to represent the recorded reductions in growth of northern pike at different population densities. If the area available is close to the total area required, growth is close to maximum. The model calculates growth daily until temperatures reach $10^\circ C$, the temperature at which YOY stop feeding, seek shelter and remain dormant over winter (Shuter et al., 1980).

The juvenile/adult growth model operates in a similar fashion. After the model determines the spatial distribution of the juveniles and adults, maximum growth is calculated for each age class in a site using daily temperatures and a bioenergetics model (Hanson et al., 1997). The model then calculates the home range required for each fish based on its size and then sums each home range to produce the total home range required by all fish in a site. This total, the maximum daily growth for each age class and the area of the site is entered into Eq. (18) to calculate the daily actual growth of each age class in a site. The actual growth estimates for each age class are then summed across the entire growing season when water temperatures are greater than $10^\circ C$ (Armour,

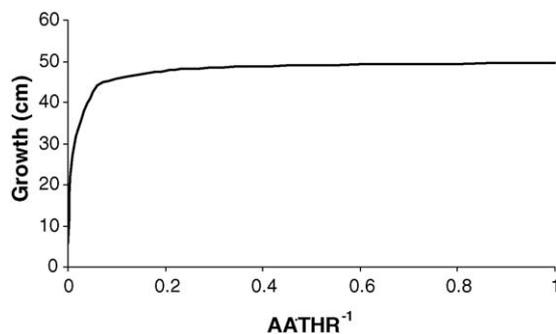


Fig. 2 – Schematic of Eq. (18) used to describe density-dependent effects on growth of smallmouth bass. AA represents the habitat area available to a life stage of the population and THR represents the total home range area required by a life stage. The maximum growth potential of 50 cm is realized at low densities that is, when the $AA = THR$.

1993) to calculate the annual growth of each age class in a site.

2.3.5. Mortality

YOY daily mortality on the nest was set at 12.3% during the embryonic stage, 7.9% after hatch and 16% during swim-up prior to metamorphosis in accordance with Friesen (1998). After metamorphosis, mortality is calculated daily as a function of size. The empirical size-dependent mortality equation was developed for YOY smallmouth bass by Houpt (1991):

$$M = 0.2e^{-0.04L} \quad (19)$$

where M is the mortality ($\%day^{-1}$) and L is the length (mm). The growth component of the model provides daily estimates of the length of each fish therefore survival is calculated daily as:

$$N_{YOY} = N_0(1 - M100^{-1}) \quad (20)$$

where N_{YOY} is the number of YOY, N_0 the number of YOY at beginning of day and M is the mortality ($\%day^{-1}$). Once water temperatures fall below $10^\circ C$, over-winter survival is calculated using a model developed by Shuter et al. (1980). The basic idea being larger YOY survive winter because they have more energy reserves than smaller YOY. Annual juvenile and adult mortality is set at 25% for each age class. This estimate is based on a literature review of natural smallmouth bass mortality (Carlander, 1977; Shuter et al., 1987).

2.3.6. Model outputs

Our model outputs the suitability of each site for nesting and the juveniles/adults, the distribution of nests, juveniles and adults and, an equilibrium population with mean length and weight at age, numerical density (adults ha^{-1}) and adult biomass density ($kg ha^{-1}$). Equilibrium is assumed when the mean number of adults (age ≥ 3 years) varies by no more than 5% over a 10-year period. If not, another 40-year simulation is performed until equilibrium is established.

2.4. Sensitivity analyses

Sensitivity analyses of the model were performed to determine which model parameters most influenced smallmouth bass density. Realistic ranges of the model parameters were defined using a habitat database that included data from 1646 smallmouth bass lakes in Ontario (Dodge et al., 1984). A hypothetical lake, hereafter referred to as the control lake, was designed using the median values of the habitat variables (Fig. 3, Table 1). Median values were chosen because the ranges of some of the habitat variable values were not normally distributed. The control lake was arbitrarily divided into six sub-sections (sites). The effective fetch of each site was calculated using Eq. (11) with the assumption that the prevailing wind directions in Ontario are from the west (Environment Canada, 2000). The habitat characteristics of the control lake were entered into the smallmouth bass habitat model and run for 40 years to produce an equilibrium population that represented the starting population for all further sensitivity analyses.

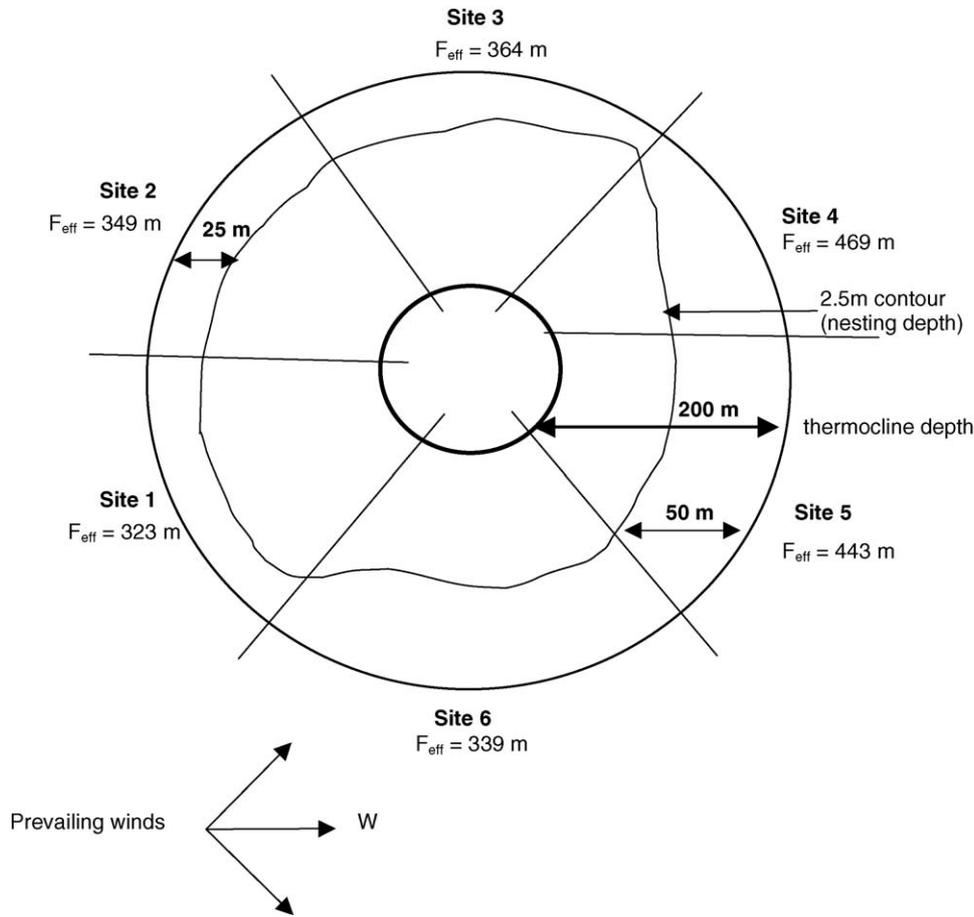


Fig. 3 – Morphometry of the control lake, the outer circle represents the perimeter of the lake (3750 m), inner circle represents the thermocline depth. Double arrows represent the distance from shore to the nesting and thermocline depth contours. F_{eff} represents the effective fetches for each site.

Where applicable, the 10th and 90th percentile values of each habitat variable were used to perform the sensitivity analyses (Table 2). The 90th percentile value (150 mgL^{-1}) for [TDS] was not included as a scenario because $[\text{TDS}] > 40 \text{ mgL}^{-1}$ have P values of 1. The nesting and juvenile/adult habitat supply were altered on a linear scale, that is, the habitat supplies were increased or decreased by 50% (Table 2). Fishing mortality was incorporated into the scenarios by increasing the mortal-

ity of fish age 3 years and older from 25 to 50% and 75%. Age 3 represents the average age of harvest of smallmouth bass in Canada (Carlander, 1977).

2.5. Model validation

The accuracy of the model was evaluated using data for smallmouth bass populations in Lake Opeongo, Ontario and Long

Table 1 – Physical characteristics of 1646 smallmouth bass lakes in Ontario			
Variable	Median	10th	90th
Lake surface area (ha)	112	16.9	990.5
Mean depth (m)	5.7	2.1	13.1
Perimeter (m)	3750		
Maximum fetch (m)	1194		
Mean annual air temperature (°C)	4.36	1.8	7.12
Thermocline depth (m)	6.32	5.2	6.3
Mean windspeed during the month of spawning (km h^{-1})	14	7	20
pH	7		
Dissolved oxygen (mgL^{-1})	10		
Total dissolved solids (mgL^{-1})	38	21	150

The median represents the data used to develop a hypothetical smallmouth bass lake.

Table 2 – Data used to perform the sensitivity analyses of the model

Variable	Control	Lower value or 10th percentile	Upper value or 90th percentile
Temperature (°C)	4.36	1.8	7.12
Total dissolved solids (mgL ⁻¹)	38	21	150
Substrate (percent composition)			
Sand	11	42	51
Sand and rock	9	0	0
Gravel	5	0	12
Rock	47	0	27
Weed	15	52	5
Litter	14	6	4
Available nesting habitat area (m ²)	139060	69530	208590
Available juvenile/adult habitat area (m ²)	624860	312430	937290
Lake size (ha)	112	16.9	990.5
P in bioenergetics model	1	0.75, 0.5	0.25
Mortality (%)	25	50	75

Point Bay, Lake Erie. Lake Opeongo (45°42'N, 78°22'W) is located in Algonquin Park, Ontario. It has a surface area of 5860 ha with a maximum depth of 52 m and a mean depth of 14.8 m. Whole lake nest maps, trap net and mark-recapture data were available for the Lake Opeongo population (M. Ridgway, 1998, unpublished data).

Long Point Bay (42°37'N, 80°10'W) is located along the north shore of Lake Erie. The bay is divided into two distinct regions, Inner and Outer Bay. Inner Bay is 7900 ha in surface area with a mean depth of 1 m and a maximum depth of 3.05 m (MacGregor and Witzel, 1987). Outer Bay is approximately 27 500 ha and is deeper than Inner Bay with a mean depth of approximately 15 m (Witzel, 1989). Less than 1% of the Inner Bay is deeper than 2.5 m so the entire area of the bay was assumed to have suitable depths for nesting. Nesting, index netting, creel surveys and trawl data were available for this population (Witzel, 1989).

Lake Opeongo was divided into 34 sections and Long Point Bay was divided into 23 sites. For each site, the areas available for nesting and for juveniles/adults were obtained from digitized maps using Scion Image software (Scion Corporation, Beta 3b). Mean annual air temperatures were 4°C in Lake Opeongo and 7.9°C in Long Point Bay, and were estimated using the 30-year mean annual air temperature for each region (Environment Canada, 2000). The substrate compositions of the different sites in each lake were determined from substrate maps (M. Ridgway, 1998, unpublished data; C. Bakelaar, 1999, unpublished data). [TDS] in Lake Opeongo, 29 mgL⁻¹, and Long Point Bay, 175 mgL⁻¹, were taken from Dodge et al., (1984) and Timmermans and Craigie (2003), respectively. Mean monthly wind speeds for each lake were taken from the weather station closest to the lake (Environment Canada, 2000). Directional wind data for Lake Opeongo came from a study conducted in 1970–1974 (Finlay et al., 2001). In Long Point Bay, prevailing winds are from the west and southwest. Effective fetches for each of the sites were calculated using Eq. (11) (Chu, 2001).

Annual mortality for fish age 5 years and older was estimated at 53% in Lake Opeongo (Coble, 1975; Shuter et al., 1987) and set at 25% annually for fish age 1–4 years. Mortality

estimates were not available for Lake Erie so data from lakes Huron and Michigan were used. This produced a mean mortality estimate of 55% (Coble, 1975). Mortality for the Long Point population was set at 35% for age 1 and 2 years according to MacGregor and Witzel (1987) and Witzel (1989), and 55% for fish age 3 years and older.

Simulation results were compared to available nesting and catch data for the lakes. Site-specific observed nest densities were compared to predicted densities, and whole lake nest and population estimates were also compared to the model predictions. In Lake Opeongo, site-specific catch data (fish trapnet⁻¹) were compared to the predicted densities of juveniles/adults in each site. Site-specific juvenile/adult catch data were not available for Long Point Bay.

3. Results

The nest densities in the control lake ranged from 0.01 to 0.36 nests 100 m⁻². Smallmouth bass numerical density in the control lake was 9.68 adults ha⁻¹ with a biomass density of 5.12 kg ha⁻¹. Mean length at age was within the range recorded for Ontario (Fig. 4).

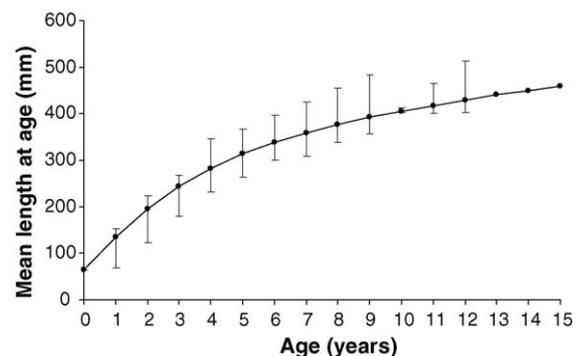


Fig. 4 – Mean length at age of the simulated control population (●) and range of lengths recorded for each age in Ontario (error bars) (Carlander, 1977).

Table 3 – Results of sensitivity analyses in the control lake

Simulation	Fish density (adults ha ⁻¹)	Biomass density (adults kg ha ⁻¹)	Percent of numerical density	Percent of biomass density	Trend
Control	9.68	5.12			
Temperature 1.8 °C	0.00	0.00	0	0	↓
Temperature 7.12 °C	24.67	12.09	255	236	↑
TDS 21 mgL ⁻¹	1.26	0.71	13	14	↓
Nesting habitat = 50%	3.54	1.98	37	39	↓
Nesting habitat = 150%	14.33	7.27	148	142	↑
JA habitat = 50%	7.78	3.92	80	77	↓
JA habitat = 150%	9.98	5.40	103	105	–
Mortality = 50%	3.01	1.11	31	22	↓
Mortality = 75%	0.70	0.22	7	4	↓
Substrate composition A	7.01	3.78	72	74	↓
Substrate composition B	8.34	4.35	86	85	↓
P = 0.75	8.85	3.68	91	72	↓
P = 0.5	4.84	1.59	50	31	↓
P = 0.25	2.16	0.52	21	10	↓
17 ha	10.00	5.31	103	104	–
990 ha	9.86	5.22	102	102	–

An increase or decrease of more than five percent was considered significant for these simulations. Substrate composition A is predominantly sand and weeds, substrate B is largely sand, rock and gravel.

3.1. Sensitivity analyses

The numerical and biomass densities increased with increased mean annual air temperature and a 50% increase in nesting habitat supply (Table 3). Temperature had the greatest effect on numerical and biomass densities of the simulated population. A mean annual air temperature of 7.12 °C increased the population 2.5-fold whereas 1.8 °C caused the population to go extinct. Increasing the temperature also increased the mean length of the YOY (age 0 years) and 1-year old fish but decreased the mean length of fish age 2 years and older. This difference decreased as the fish aged (Fig. 5). Increasing the nesting habitat supply caused a decrease in mean length at age of the simulated population (Fig. 5).

Smallmouth bass densities decreased with decreased [TDS], nesting and juvenile/adult habitat supplies, increased mortality, altered substrate composition and decreases in P (Table 3). Of these scenarios, decreased juvenile/adult habitat supply and P decreased mean length at age; the other scenarios increased mean length at age (Fig. 5). Changing the substrate to predominantly sand and weeds (substrate composition A) decreased the suitabilities of the sites while introducing more sand, rock and gravel generally increased the suitability of the individual sites (Fig. 6). Site 4 was not suitable for nesting or the juveniles/adults with substrate composition A because it was composed of 100% weeds. Interestingly, both

substrate scenarios decreased the numerical and biomass densities of the simulated population (Table 3). Decreasing the bioenergetic parameter P caused a greater decrease in the biomass densities than the numerical densities, and had the greatest negative impact on mean length at age (Table 3, Fig. 5).

Increasing the juvenile/adult habitat supply and altering lake size had no significant effect on the population densities (Table 3). Mean length at age remained the same with changes in lake size and increased by less than 5 mm when juvenile/adult habitat supply increased.

3.2. Model validation

The model predicted the spatial distribution of nests better than juveniles/adults in Lake Opeongo (Fig. 7). Predicted and observed nest densities were significantly different than the 1:1 line ($F_{0.05(1),1,32} = 19.04, r^2 = 0.37, p < 0.001$). Juvenile/adult catch and predicted distribution data were also significantly different from the 1:1 line ($F_{0.05(1),1,32} = 3.45, r^2 = 0.10, p = 0.07$). Site-specific data were not available for the juveniles/adults in Long Point Bay. Of the sites for which observed nest densities were available, observed nest densities were higher than predicted (Fig. 8) ($F_{0.05(1),1,8} = 4.08, r^2 = 0.34, p = 0.08$). The model correctly estimated the total number of nests and juveniles/adults in both systems (Table 4). The model

Table 4 – Observed population vs. predicted population parameters for Lake Opeongo and Long Point Bay, Lake Erie

Lake	Nesting population			Juvenile/adult population	
	Observed	Predicted		Observed	Predicted
Opeongo	920–1130	1019	Age 1–4 years	15000–23500	15016
			Age 5 years and older	1400–3300	2057
Long Point Bay	25000–50000	25613	Age 2 years and older	322000–332000	331168
			Age 4 years and older	96600–99600	54583

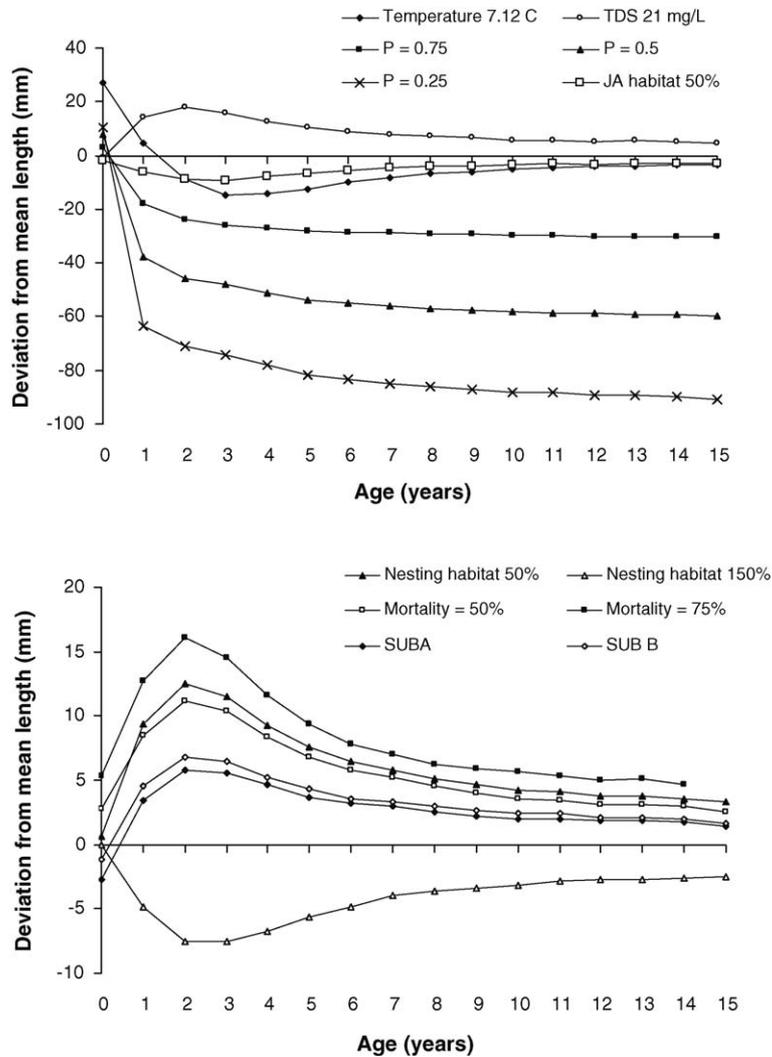


Fig. 5 – Deviations of different scenarios from mean length at age of the control population (note difference in scale of the two graphs).

underestimated the number of fish age 4 years and older in Long Point Bay. In both systems, predicted mean length at age was within the range of lengths recorded for most of ages but tended to overestimate the length of the juveniles and young adults (<6 years), and underestimate the lengths of the older fish (Figs. 8 and 9).

4. Discussion

The nest densities in the control lake ranged from 0.01 to 0.36 nests 100 m⁻². In Ontario nest densities can range from 0.01 to 0.43 nests 100 m⁻² (Harker, 1982; Witzel, 1989; Scott, 1993). Smallmouth bass numerical density in North America ranges from 0.74 to 164 adults (age 3 and older) ha⁻¹ with biomass densities of 0.52 to 82.90 kg (adults) ha⁻¹ (Carlander, 1977). Smallmouth bass numerical density in the control lake was 9.68 adults ha⁻¹ with a biomass density of 5.12 kg ha⁻¹. These results suggest that the model is not producing abnormal densities.

The sensitivity analyses indicated that temperature had the greatest effect of any habitat alteration. This is consistent with other studies that have found strong correlations between temperature and smallmouth bass biogeography and year class strength (Shuter et al., 1980; Shuter and Post, 1990; Casselman, 2002). Shuter and Post (1990) attributed the northern distribution limit of smallmouth bass populations to the shorter growing seasons and longer starvation periods of northern climates. In these environments YOY must store enough energy throughout their first summer to survive their first winter.

In eastern Lake Ontario, smallmouth bass year class strength has been positively correlated with warmer summer temperatures (Casselman, 2002). This study found a 6.0× increase in year class strength for a 2°C increase in temperature. In our hypothetical system, a 2.76°C increase in temperature led to a 2.5× increase in adult densities. This suggests that the model is operating correctly and warmer temperatures do result in higher recruitment.

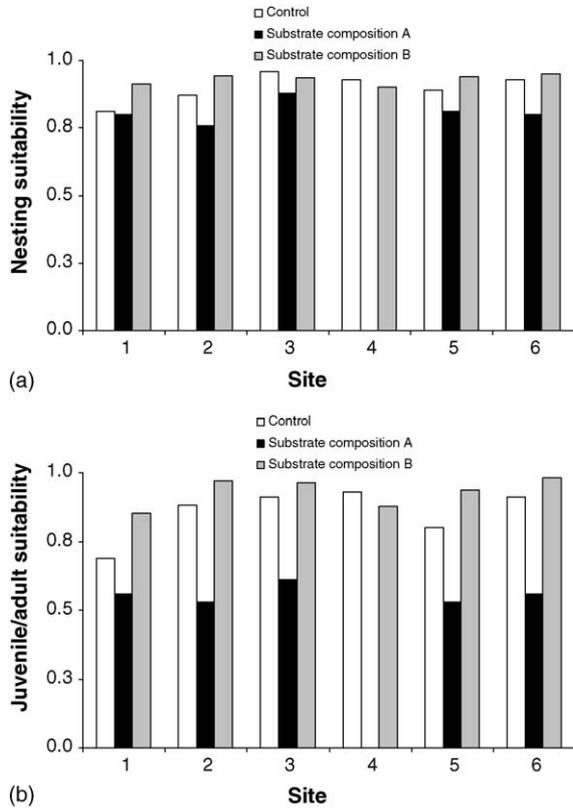


Fig. 6 – Suitability of different sites in the control lake for (a) nesting and (b) juvenile/adults.

The mean length at age results of the temperature scenarios highlight a potential amendment that may be made to a future version of our model. In nature, southern populations are larger than their northern counterparts (Carlander, 1977). This suggests that the model is overestimating density-dependent effects on growth at higher temperatures and Eq. (18) should be modified. A preliminary investigation of this revealed that modifying Eq. (18) from

$$G_{ACT} = \frac{G_{MAX}(AA^{0.96})}{AA^{0.96} + 0.0101(THR^{0.96})}$$

to

$$G_{ACT} = \frac{G_{MAX}(AA^{0.5})}{AA^{0.5} + 0.0101(THR^{0.5})}$$

that is, decreasing the 0.96 scaling coefficient to 0.5, reduced the density-dependent effects on growth and produced mean lengths that are characteristic of populations in warmer climates.

Increasing the nesting habitat supply (area between 0.5 and 2 m deep) increased the densities of the simulated population while increasing the juvenile/adult habitat supply had little impact on population densities. These findings and the substrate scenarios have implications for habitat management. Currently, rocky substrates are deposited in lakes to improve fish habitat (Pitcher and Seaman, 2000). Our findings suggest that if these practices result in more total habitat available between 0.5 and 2 m, smallmouth bass populations will benefit. However, our substrate scenarios caution that although

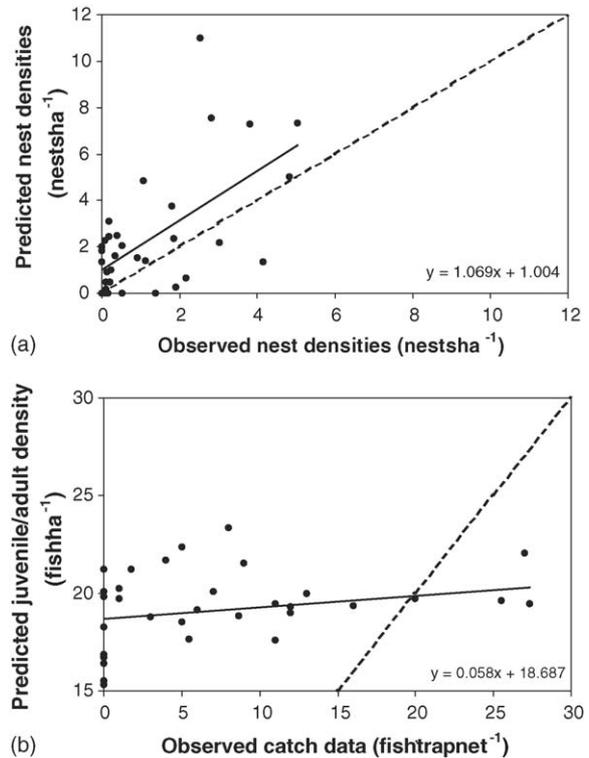


Fig. 7 – Observed and predicted (a) nest and (b) juvenile/adult densities for the 34 modelled sites of Lake Opeongo, (–) represents the 1:1 line.

introducing more rocks and gravel (preferred substrate for smallmouth bass) improves the overall suitability of the system, density-dependent effects on YOY growth may decrease potential recruitment. This suggests that our model may be used by habitat managers to determine if recruitment could be improved by increasing nesting habitat quality (substrate composition), quantity (total area between 0.5 and 2 m) or both.

Decreasing the [TDS] and P parameter decreased the numerical and biomass densities through different mechanisms. Decreasing the [TDS] reduced YOY growth rates, increased YOY mortality and directly reduced recruitment. Decreasing the P parameter reduced the biomass of each fish in the population and consequently reduced fecundity and recruitment.

The temperature, nesting habitat and [TDS] scenarios suggest that smallmouth bass densities are largely determined by YOY survival. This is consistent with previous studies (Shuter et al., 1980; MacLean et al., 1981) and suggests that conservation or restoration efforts should focus on improving or protecting the nesting and consequently YOY habitat. In conjunction with a habitat inventory, our model may be used to quantify suitable nesting habitat, identify what habitat conditions may be limiting a population, and determine what potential habitat changes may benefit a population.

Our mortality scenarios demonstrate that the model can be readily used by fisheries managers to determine how different fishing mortality levels may affect a population. A sustainable fishing mortality may be estimated and catch limits, size limits

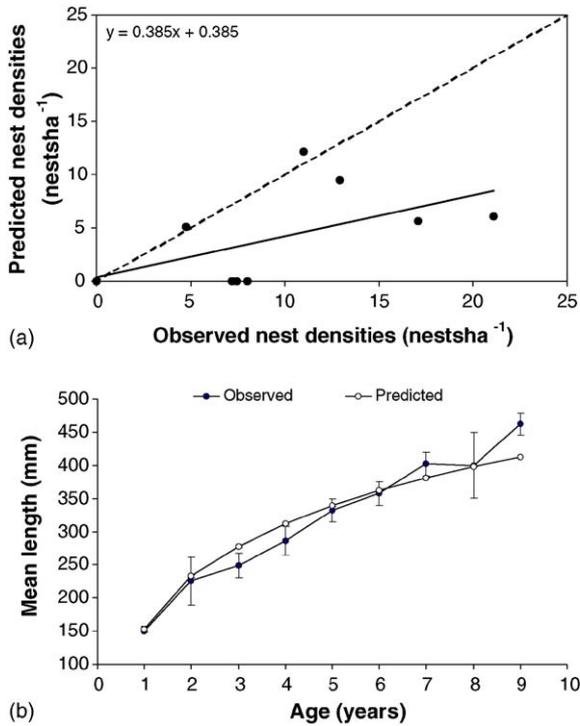


Fig. 8 – Predicted and observed (a) nest densities and (b) predicted and observed of mean lengths at age in Long Point Bay, Lake Erie. (–) represents the 1:1 line and the error bars around the observed and predicted values represent the range of lengths recorded for each age in Long Point Bay.

and catch and release practices may then be implemented accordingly.

The mediocre success of the model at accurately predicting the spatial distributions of nests and fish in Lake Opeongo and Long Point Bay suggests two things (1) other factors may be dictating smallmouth bass distribution within the two systems and (2) the model may not be accurately reflecting habitat use and behaviour.

Rejwan et al. (1999) found that shoreline reticulation was significantly and positively correlated with nest densities.

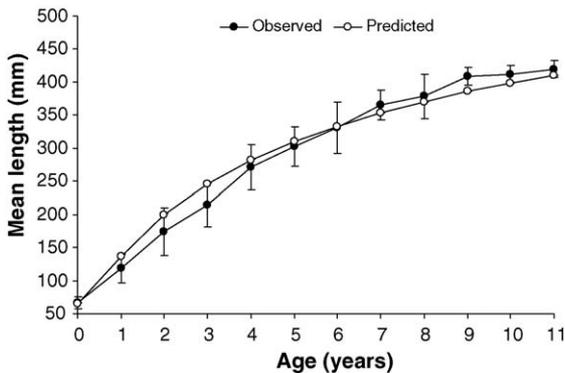


Fig. 9 – Predicted and observed mean length at age of the Lake Opeongo population. The error bars represent the range of sizes recorded for fish at each age.

This suggests that adding shoreline reticulation to the nesting sub-model may improve its predictive ability. The juvenile/adult sub-model may be improved by directly incorporating prey density or prey distribution. Laboratory experiments have demonstrated that smallmouth bass stayed in less suitable temperatures when prey were limited to cool waters but retreated to more suitable temperatures when prey were abundant (Weidel et al., 2000). These findings suggest that prey distribution should be included in a future version of the model and may improve the predicted distribution of fish.

To better reflect habitat use and behaviour, our model could incorporate nest site and home range fidelity. Our model currently assigns fish to different sites using the ideal-free distribution theory. Previous studies have found both nest site and adult home range fidelity in smallmouth bass populations (Ridgway et al., 1991a; Ridgway and Shuter, 1996). With nest site fidelity, sites that successfully produce many YOY have high nest densities in subsequent years. Conversely sites with low YOY survival have fewer nests in subsequent years. This phenomenon may be incorporated into the model by increasing the suitability of sites with high YOY survival each subsequent year. A run, for example, of the Opeongo simulation with this modification may produce a spatial pattern similar to what occurs in nature; extremely high nest densities in site 8 (4.14 nests ha⁻¹) and relatively lower densities (1.14 nests ha⁻¹) throughout the rest of the lake. This same approach may be used to incorporate home range fidelity into the juvenile/adult sub-model and possibly improve the predicted spatial distribution of the fish.

Although the model can be further modified to better predict the site-specific distribution of nests and fish, it does accurately predict the total number of nests and juveniles/adults in both systems. This suggests that the model is accurate enough to capture the population dynamics of the whole system. We examine why this is so using our nesting sub-model because smallmouth bass year class strength is largely determined by YOY growth and survival (Shuter et al., 1980; MacLean et al., 1981). In our model, warm sites were conducive to faster YOY growth and produced higher densities of YOY than cooler sites. In Lake Opeongo, site 8 and 9 have the greatest number of nests and produce the most YOY, in our model site 8, 16 and 9 had the most nests and produced the most YOY. The same is true for Long Point Bay sites 23, 13, 6 and 1 had the highest observed and predicted nest densities. These results suggest that the model is correctly identifying productive versus less productive regions of the lake. Therefore, the differences between the observed and predicted nest distributions were not enough to cause significantly different population densities than those observed.

The underestimation of the age 4 years and older fish in Long Point Bay may be attributed to the mortality rate chosen for that study area. Specific mortality data were not available for Long Point Bay so an average (55%) of data from lakes Huron and Michigan was used. The results suggest that a 55% mortality rate is too high for the Long Point population and the model estimates may be improved if and when more specific data become available.

Mean length at age was greater than observed for the juveniles and young adults (age <6 years) but less than observed for fish older than 6 in Lake Opeongo and Long Point Bay. Ridgway

et al. (2002) suggest that density-dependent effects on growth decrease as smallmouth bass age. In our model, density-dependent effects on growth are constant for all ages. Therefore, to better improve the model's performance, the density-dependent effects on growth may be scaled to decrease as the fish age. Mortality is also set at a constant rate for juvenile and adult fish but YOY survival changes as a function of length and indirectly, habitat supply. A similar mechanism may exist in the juvenile and adult life stage, and should be explored in a future version of the model.

5. Conclusion

Our model is a comprehensive method of linking habitat to smallmouth bass population dynamics because it includes a complete life cycle, incorporates several habitat variables, models the spatial distribution of the different life stages and quantifies density-dependent effects on the population. However, this work represents a contribution to our understanding of smallmouth bass ecology and is by no means inclusive of all of the factors that may affect smallmouth bass populations. Interspecific interactions may also influence smallmouth bass population dynamics. Smallmouth bass may compete with walleye, northern pike, largemouth bass, yellow perch and rock bass for resources in systems where they co-exist (Lasenby and Kerr, 2000). As predators, smallmouth bass reduce the abundance and alter the habitat use of small-bodied fishes; their primary prey base (MacRae and Jackson, 2001). These interspecific interactions directly affect the growth and mortality of smallmouth bass populations and should be included in a future version of the model.

Although this model may be improved to better predict the distribution of nests and fish, it does accurately estimate the total nest and juvenile/adult population size. This suggests that the model may be used to estimate lake-wide population changes and answers the demonstrated need for more habitat-based population models (Hayes et al., 1996; Minns et al., 1996; McHugh et al., 2004). This model provides a foundation upon which new knowledge of smallmouth bass populations may be implemented (for e.g., quantified relationships for density-dependent effects on growth) and more complex ecosystem models may be developed.

Acknowledgements

We thank M. Ridgway, M. Jones, D. Hayes, J. Netto, P. Ryan, L. Witzel, C.K. Minns, S. Doka, B. Henderson, R. Szabo, H. Cyr, E. Dunlop and J. Cook who provided valuable data and advice in developing various components of the model. Two anonymous reviewers provided valuable insights that improved this manuscript. This project was funded by the Great Lakes Fishery Commission.

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