POPULATION DYNAMICS OF SMALLMOUTH BASS (*Micropterus dolomieu*) IN RESPONSE TO HABITAT SUPPLY

by

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A smallmouth bass habitat model was developed to estimate how changes in habitat may affect smallmouth bass populations. Habitat characteristics such as mean annual air temperature and substrate were used to determine the spatial distribution of nests, juveniles and adults throughout a lake. Growth is density-dependent for all life stages. Mortality is size-dependent in the young-of-the-year (YOY) but is set at a constant annual rate for older fish.

Sensitivity analyses revealed that increases in mean annual air temperature, total dissolved solids concentration and the area available for nesting increased the density of the simulatied population. Furthermore, a YOY bottleneck exists in smallmouth bass populations and the nesting habitat appears to be more important than the juvenile/adult habitat.

Model predictions were compared to data from Lake Opeongo, Ontario and Long Point Bay, Lake Erie. This revealed that the model can be applied to estimate how habitat changes influence fish density but requires modification before it can be used to predict the spatial distribution of nests and fish within a lake.

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General Introduction

In recognition of the importance of habitat to fish species, the Canadian Department of Fisheries and Oceans and United States Fish and Wildlife Service revised the Fisheries Act and the Sustainable Fisheries Act, respectively. Both acts now impose no net loss of essential fish habitat. These acts ensure that habitat degraded through anthropogenic sources will be replaced (Baird et al. 1996; USFWS 1996). However, methods to identify essential habitat and determine how habitat changes may affect fish populations are presently not available.

Conventional fisheries models fail to include habitat quality when estimating stock abundance. For example, a fundamental model in fisheries science is the Ricker (1954) stock and recruitment curve. This theory states that at low spawning stock densities, increases in the number of young produced will be positively related to increases in adult stock. However, at high densities, density-dependent compensatory factors will reduce the number of young recruited into the population. Therefore reducing the numbers of spawning adult fish will enhance the number of young produced by reducing the population density. This theory (when parameterized to a specific situation) is used to estimate allowable catch and sustain maximum yield, yet no explicit measures are taken to include habitat supply in this analysis.

One method of incorporating habitat into fisheries models has been the generation of habitat suitability indices (HSI's; example, Stanley and Trial 1995). These models are used to categorize the habitat suitability of different bodies of water (or habitat patches within them) for a fish species based on the presence or absence of certain habitat features. However, HSI's are limited because they do not incorporate intraspecific interactions that may affect stock yield. Therefore fisheries managers must aim to link population dynamics to the habitat supply and demand of fish populations (Minns et al. 1996).

The main objective of this thesis is the development of a habitat-based population model for smallmouth bass that incorporates both habitat requirements and population dynamics. The first chapter of this thesis is a literature review used to define the habitat requirements of smallmouth bass. Potential areas of future research are also highlighted for life stages where ecological data are lacking.

Chapter Two is the development of the model using data from the primary literature, government agencies and the University of Toronto. The model was programmed using Microsoft® Visual Basic®; thus it can be implemented as a user-friendly tool for fisheries managers. Once the model was constructed, sensitivity analyses were performed to determine which habitat variables are most important to smallmouth bass populations. Implications for smallmouth bass conservation and habitat rehabilitation were then discussed.

In Chapter Three the model is validated using data from smallmouth bass populations in Lake Opeongo, Ontario and Long Point Bay, Lake Erie. This was accomplished by entering the habitat characteristics of these systems into the model and comparing the model predictions to real measurements from these systems.

Chapter One

The life history of smallmouth bass, *Micropterus dolomieu*

INTRODUCTION

Smallmouth bass are endemic to eastern central North America but are now found throughout Nova Scotia along the eastern coast to Georgia, westerly to Alabama and northerly to Central Saskatchewan, southern Manitoba, Ontario and Quebec. They are also found in isolated bodies of freshwater in southern British Columbia. Globally, they are distributed in England, Europe, Russia and Africa due to introductions and stocking practices (Scott and Crossman 1973; Shuter et al. 1980).

Smallmouth bass are typically found in clear, freshwater lakes and rivers (Coble 1975; Edwards et al. 1983). They inhabitat shallow waters during the spring and deeper waters in late summer and winter. Areas with scant vegetation and rocky substrate are preferred (Hubbs and Bailey 1938; Rankin 1986). Reproduction, larval survival and adult growth are particularly dependent on water temperature (Shuter et al 1980; Serns 1982; Goff 1985; Ridgway et al. 1991b, Armour 1993; Rejwan et al. 1999).

These fish have a complex life history and exhibit male parental care. Their life stages are defined by changes in morphology, food preference, habitat and behaviour. The smallmouth bass life cycle can be divided into seven stages: eggs, hatchlings on the nest (sac-fry), swim-up or black fry when the fry are rising from the nest, young-of-the-year (YOY) between the time of dispersal from the nest and the end of the first growing season, YOY over first winter, juveniles and mature adults (Figure 1.1).

Parental care is a behavioural strategy found among 60% of freshwater fish species to improve their reproductive success and the survival rates of their young (Brown 1984). Members of the centrachid family all demonstrate a level of brood care. However, the duration of care differs. For example, rock bass (*Ambloplites rupestris*) protect their young only until the swim-up stage, whereas largemouth bass (*Micropterus salmoides*) guard their young for as long as a month after hatching (Brown 1984). Parents invest their time, energy and compromise their own survival during the developmental period of their young (Lavery and Keenleyside 1990). While defending the brood, smallmouth bass decrease their foraging time and subsist on energy reserves (Ridgway et al. 1991b; Ridway and Shuter 1994). Parental defense is strongest during the egg, hatchling and swim-up stages. If the energy reserves of the male become critically low, he may abandon his nesting effort (Hinch and Collins 1991; Ridgway et al. 1991b). Nests that are abandoned can be destroyed within 24 hours from predation (Neves 1975).

1.1. NESTING AND SPAWNING

Smallmouth bass demonstrate an inverse relationship between body size and timing of nesting (Ridgway et al. 1991b). Larger males may nest earlier in the spring than smaller males because they have more energy available for reproduction after winter. Smaller males may delay spawning and direct their energy towards growth in order to increase their chances of successfully spawning in the next year (Ridgway et al. 1991b).

Smallmouth bass males show strong nest site fidelity to their birth place and nest sites from year to year (Ridgway et al. 1991a; Gross et al. 1994). Sixty five to 85 % of returning males nest within 150 m of their previous nest site in following years (Scott and Crossman 1973; Ridgway et al. 1991a).

The nesting habitats of these fish are described for many locations in North America (Neves 1975; Shuter et al. 1980; Serns 1982; Goff 1986; Ridgway 1988; Witzel 1989; Friesen 1998; Rejwan et al. 1999). Suitable nesting areas for smallmouth bass are in the littoral zone of lakes and rivers in approximately one to two meters of water (Ridgway 1988; Goff 1986). Water temperature (Cleary 1956; Shuter et al. 1980; Serns 1982; Edwards et al. 1983; Rejwan et al. 1999), substrate (Vogele and Rainwater 1975; Hoff 1991; Wiegmann et al. 1992), wind (Turner and MacCrimmon 1970; Goff 1986; Rejwan et al. 1999), pH and dissolved oxygen (Tester 1930; Edwards et al. 1983), turbidity (Robbins and MacCrimmon 1974) and water flow rate (Lukas and Orth 1995) influence smallmouth bass nesting.

When the littoral water temperature approaches 13 °C - 15 °C, male smallmouth bass migrate to the littoral zone of lakes and rivers to build nests. Once nests are built, spawning may occur at temperatures ranging from 12.8 °C - 23.5 °C but typically occurs at 16 °C (Ridgway 1988; Armour 1993; Scott 1993).

Substrate is another important feature of the nesting habitat. Nesting is traditionally thought to occur on sand, gravel and rock substrates (Scott and Crossman 1973; Coble 1975). Wiegmann et al. (1992) found that at high densities (<10 m between nesters), the probability of mating was relatively higher (0.8 - 0.9) in sand and rock substrates as opposed to pebble, gravel and vegetation substrates (0.5). This indicates that females prefer spawning in sand and rock substrates at high nest densities. Nesting sites in Inner Long Point Bay, Lake Erie are found in areas with >50 % cover of the macrophyte, *Chara vulgaris* and sand substrates (Witzel 1989).

Turner and MacCrimmon (1970) documented that males will avoid building nests in areas with high prevailing winds. This may be due to the damaging effect of wave action on the eggs (Goff 1986). A poignant example of the detrimental effects of wind can be taken from the 1998 nesting season in Lake Opeongo, Ontario. High winds during a storm event at which gust speeds were 51 km/hr destroyed all but three of several scores of nests in the prime nesting area, Jones Bay (Ridgway pers. comm. Aquatic Ecosystems Science Section, Ontario Ministry of Natural Resources, Peterborough, Ontario; Environment Canada, unpublished data).

A water flow rate of >10 m^3/s was responsible for 85 % of the nest failures in a regulated Virginia stream (Lukas and Orth 1995). High turbidities (2,000 JTU) can also displace smallmouth bass (Edwards et al. 1983). Water flow rate and turbidity are habitat characteristics important to stream and river populations of smallmouth bass and have not been incorporated into the habitat model developed in this thesis.

The optimum pH range for all life stages of smallmouth bass is 7.9-8.1 but they occur at levels of 5.7 to 9 (Clady 1977; Edwards et al. 1983). Growth is compromised at dissolved oxygen levels < 6 mg/L and death occurs at 1 mg/L (Edwards et al. 1983).

Once a nest site has been selected by the male, he digs out a saucer-shaped nest using his pectoral and caudal fins (Ridgway et al. 1988). The nest is 4-8 cm deep and 30-100 cm in diameter (Doan 1940). Nest diameter is positively related to male size (Neves 1975).

Males mate with females of a size similar to their own (Neves 1975; Ridgway pers. comm. 1998). Rare incidences of males spawning with two females have been documented (Webster 1954; Neves 1975). The percentage of the mature male population spawning in Lake Opeongo, Ontario in any given year was estimated to be between 12 and 47% (Post 1982).

Pre-spawning behaviour is characterized by displays, rubbing and nipping (Scott and Crossman 1973; Ridgway et al. 1989). During spawning, eggs are discharged intermittently in the range of every 4 seconds to every 15 minutes for 2 to 3 hours (Scott and Crossman 1973; Neves 1975). After spawning, the male assumes parental care of the offspring. The female may remain in the littoral zone for approximately a week and then returns to deeper waters (Ridgway pers. comm.).

1.2. EGGS

Smallmouth bass ova are 1.5-2.5 mm in diameter and are light amber to grayish white in colour. They are demersal and adhere to the substrate of the nest (Scott and Crossman 1973; Coble 1975). The embryogenesis of the fertilized ova signals the onset of the first critical period of the smallmouth bass life history (Shuter et al. 1980). At this stage the eggs are extremely susceptible to temperature fluctuations (Webster 1948; Armour 1983), fungal infestations (Tester 1930; Webster 1948), wave action (Goff 1986) and predation (Neves 1975).

The most favourable temperatures for egg incubation range between 15-25 °C (Armour 1983). Sudden drops in temperature below 14 °C are lethal to the embryos and may also result in the male abandoning the nest (MacLean et al. 1981; Armour 1983).

Wave action may transfer eggs out of the perimeter of the nest, making them more vunerable to predation (Goff 1986). Predators of eggs are rock bass, yellow perch, juvenile smallmouth bass, catfishes, suckers and turtles (Coble 1975; Hinch and Collins 1991). Total mortality from the egg to the black fry stage can range from 4-90 % (Carlander 1977; Friesen 1998).

1.3. HATCHLINGS

Eggs hatch 2-10 days after deposition and the hatchlings or wrigglers are at first clear in colour and absorb nutrients from their yolk sacs. They remain on the bottom of the nest and within days develop a black pigmentation. The black-fry are 5.6-5.9 mm in length during this time and remain on the nest for 3-11 days before rising (Beeman 1924; Shuter et al. 1980; Scott and Crossman 1973). Development from black fry to swim-up is temperature-dependent (Shuter et al. 1980) and mortality has been estimated at 7.9 %/day (Friesen 1998). The hatchlings are still susceptible to adverse temperatures and fungal attacks during this time (Beeman 1924).

1.4. SWIM-UP AND DISPERSAL

This stage is characterized by the rising of the wrigglers off the nest (swim-up) and the shift to exogenous feeding on zooplankton. Fry at this stage are 8.3-9.2 mm in length and are still black in colour. After rising they remain in a dense mass close to the bottom of the nest and within two days they begin to disband. Seven to nine days after rising from the nest, they metamorphose into typical smallmouth bass (Ridgway 1988). During this time habitat use is dictated by the movement of the male. The male prevents the young from straying too far and patrols the area for predators (Ridgway 1988; Sabo and Orth 1994).

As the YOY grow, they begin feeding on larger invertebrate prey (Sabo and Orth 1994), male defense declines (Ridgway 1988) and they begin to disperse further and further from the nest site during the day. They continue to aggregate into dense schools above the nest at night (Wales 1981).

1.5. YOY SUMMER GROWTH

Once the fry are 20-30 mm in length, the male reduces parental care and eventually abandons the nest (Ridgway and Friesen 1992). Desertion coincides with the dispersal of the fry from the nest site and the infiltration of new microhabitats. Two to four weeks after dispersal the YOY move in small schools to shallower waters than their nest sites but remain within 200 m of the nest. They show a preference for boulder and rock habitats, possibly to avoid predation (Serns 1982; Houpt 1991; Sabo and Orth 1994).

Throughout the summer the YOY feed on zooplankton, insects, fish and YOY crayfish (Scott and Crossman 1973). In Lake Erie, the YOY are thought to migrate from their birthplaces in Inner Bay to Outer Bay where the water temperatures cool at a slower rate. This allows them to maximize their growth period and enhances their chances of winter survival (Witzel 1989). Mortality during this time is inversely size-dependent (Hoapt 1991).

Temperatures during the first summer growing season are positively correlated with year class strength. This relationship exists because energy reserves which the young use to survive their first winter are produced in the summer when food is abundant and the water temperature is most suitable for growth (Horning and Pearson 1973; Clady 1975; Shuter et al. 1980).

1.6. YOY FIRST WINTER

As the temperature decreases in the fall, there is a noticeable decrease in YOY activity. They remain in the littoral zone around boulders and rocks (Sabo and Orth 1994). At 7°C the YOY seek shelter, stop feeding and become inactive for the winter season. This signifies the second critical stage of development where over-winter survival is dependent on energy reserves produced during the first summer of life (Shuter et al. 1980). Larger fish survive this period better since they have more energy reserves and their metabolic expenditure per gram body weight is lower (Oliver et al. 1979).

1.7. JUVENILES AND ADULTS

These two life stages have been combined since little is known about the habitat requirements and behaviour of the juvenile smallmouth bass. During a trap net study in Lake Opeongo (Lester Aquatic Ecosystems Science Section, Ontario Ministry of Natural Resources, Peterborough, Ontario unpublished data 1994) juvenile fish were captured with the adults. Therefore in the model, adult and juvenile habitats have been assumed to be the same. However, juveniles prefer warmer temperatures (26-33 °C) than their older counterparts (21-26 °C) and their diets shift from fish and insects to predominantly crayfish as adults (Bevelhimer 1996). These data indicate that the juveniles may select slightly different thermal and foraging habitats. A juvenile tracking survey would help to better define differences in their habitats.

Adults prefer temperatures ranging from 21-26 °C (Armour 1993; Bevelhimer 1996) and are typically found in the epilimnion of stratified systems (Edwards et al. 1983). They prefer rocky shorelines and submerged humps (Kraai et al. 1991). Adults establish winter and summer home ranges. Fifty-four percent of smallmouth bass displaced 8-24 km from their capture site in Oneida Lake returned to within 5 km after one year (Forney 1961). In Lake Opeongo, 83% of displaced smallmouth bass returned to the site of capture on average 11 days after capture. In this study, home range areas varied from 83-304 ha in size (Ridgway and Shuter 1996). As the temperature approaches 10 °C in the fall, adults move to deeper waters and seek shelter. At temperatures of approximately 5 °C the fish become torpid.

Sexual maturity is achieved earlier in males than females but varies from one population to another depending on the growth rate of the population. Males most commonly mature at 3-5 years and lengths of 180-330 mm whereas females mature at 4-6 years at lengths of 250-390 mm (Scott and Crossman 1973; Carlander 1977; Robbins and MacCrimmon 1977). Males and females grow at the same rate (Doan 1940; Coble 1975). Fecundity is positively related to female weight (See Chapter Two). Spawning occurs when both the male and female gonadosomatic index is at its maximum (Shuter et al. 1980).

Mortality of the adults is most likely due to angling practices since smallmouth bass are one of the top predators of the littoral zone (Coble 1975; Ridgway pers. comm.). They are also vulnerable to parasitic infections, the most common being bass tapeworm which can lead to sterility in afflicted bass (Scott and Crossman 1973).

1.8. IMPLICATIONS FOR MODEL

Based on the life history and habitat requirements of these fish, two habitat sub-models have been developed. The nesting and spawning of the reproductive adults and the development of the YOY to dispersal all occur at the nest site. Even after dispersal the YOY remain within 200 m of their nest site. Given that the habitat requirements of all these life stages are found at the nest site, they have been grouped into the nesting habitat sub-model.

Ages 1+ to 2+ represent the juveniles since maturity typically occurs at age 3+ (Coble 1975; Scott and Crossman 1973). Since little is known about the juvenile habitat they have been grouped with the adults to form the juvenile/adult habitat sub-model.

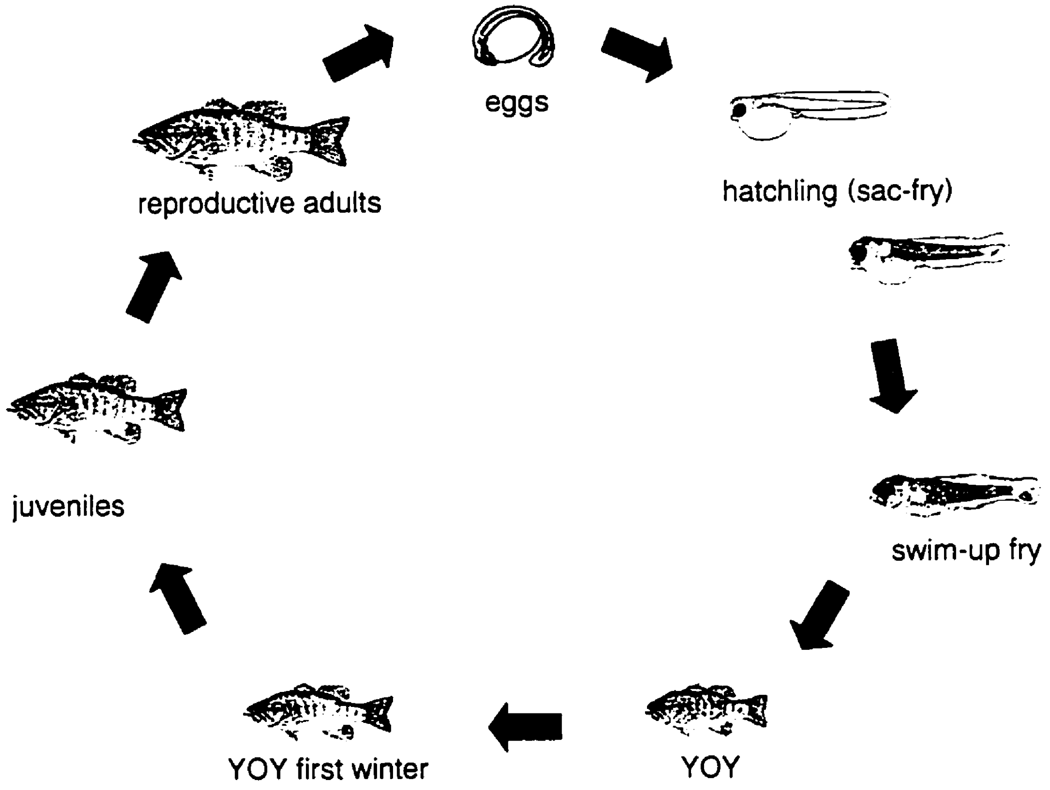


Figure 1.1: Life history stages of smallmouth bass (*Micropterus dolomieu*).
(Modified from the Early Life History Section of the American Fisheries Society (www2.ncsu.edu/elhs/))

Chapter Two

The smallmouth bass habitat model

Abstract

In recognition of the negative effects of habitat destruction on fish stocks and the lack of inclusion of habitat into conventional fisheries models, we have developed a model to estimate smallmouth bass (*Micropterus dolomieu*) population dynamics from readily available habitat data for a water body. Two habitat sub-models, nesting and juvenile/adult have been designed. The habitat variables that have been incorporated into the model include mean annual air temperature, mean monthly windspeed, effective fetch, total dissolved solids concentration [TDS], substrate composition, pH and dissolved oxygen.

Using the habitat data, the model first maps the suitability of different sites in a water body for nesting and the juveniles/adults. Nest and population distributions are then computed to provide density estimates in each site. Growth is then calculated as a function of density and habitat. Mortality is size-dependent in the nesting sub-model and is set at an annual rate for the older fish.

Sensitivity analyses were performed using habitat data from 1646 smallmouth bass lakes in Ontario. Increasing the mean annual air temperature, lake size, [TDS] and area available for nesting improved the survival of the YOY and had the greatest influences on smallmouth bass numerical density. The analyses also showed that a YOY bottleneck exists in smallmouth bass populations. To conserve or rehabilitate a smallmouth bass population, emphasis should be placed on the nesting habitat. Nesting habitat may be restored or improved by filling regions of a lake to increase the area between the 0.5 – 2.5 m depth contours that is, the area available for nesting, introducing shelters from wave action or increasing the thermal regime or [TDS] of a lake. Restoring or conserving smallmouth bass populations without manipulating habitat would involve enforcing catch and release practices, setting catch limits or shortening the smallmouth bass fishing season.

INTRODUCTION

Habitat destruction is one of the major causes for the decline of many freshwater fish stocks (Regier and Hartman 1973; Steedman and Regier 1987; Bruton 1995), and many human manipulations of fish habitat lack regulation and persist unabated (Hannah *et al.* 1994; Minns *et al.* 1999). Continuing habitat destruction has led to revisions of the Fisheries Act by the Department of Fisheries and Oceans, Canada. The act now prohibits the Harmful Alteration, Disruption and Destruction of fish habitats (Baird *et al.* 1996).

Traditionally, the influence of habitat on fish production has been expressed through assessments of habitat suitability indices (HSI's). HSI's assume that animals will concentrate in areas that optimize their survival, growth and reproduction (Hubert and Rahel, 1989; Freeman et al. 1997). Combining data from several studies, researchers can usually find consistent habitat preferences for a species. Once these preferences are incorporated into an HSI, scientists can use the habitat features of a lake, stream or river to determine its relative suitability (range from 0 – 1) for a given species.

Although HSI's allow us to recognize the most suitable fish habitat, they do not 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 linking habitat supply to fish population dynamics (example, Minns *et al.* 1996; Hayes *et al.* 1996; Minns and Bakelaar 1999).

In this chapter I construct a model linking the population dynamics of lake-dwelling smallmouth bass (*Micropterus dolomieu*) to habitat supply. This model uses empirical data to generate HSI's for the habitat variables important to different life stages of smallmouth bass (Figure 2.1). Density-dependent effects on growth and size-dependent mortality of the YOY are then incorporated to describe how the population will respond to habitat supply (Figure 2.2). This model allows researchers to estimate a lake's potential fisheries yield (adults/ha and kg (adults)/ha) from its habitat inventory. The model also helps researchers identify habitat conditions currently limiting a smallmouth bass population within a lake.

2.1. MODEL STRUCTURE

Based on the habitat requirements of different life stages of smallmouth bass (Chapter 1), two habitat sub-models have been defined (Figure 2.3). The first focuses on the nesting habitat and encompasses reproductive adults, eggs, hatchlings, swim-up fry, YOY (post-dispersal and for the remainder of the growing season) and YOY first winter

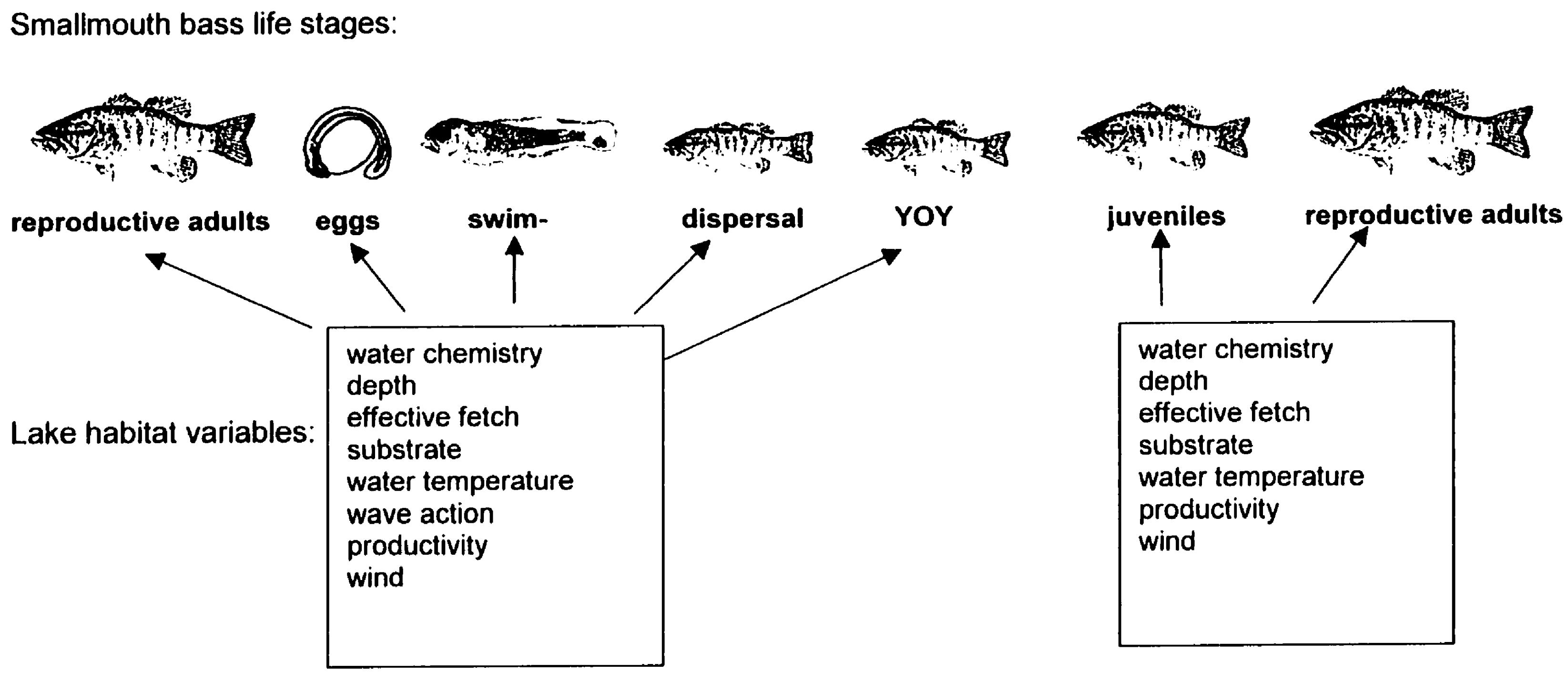


Figure 2.1: A schematic representation of the habitat variables important to smallmouth bass life stages.

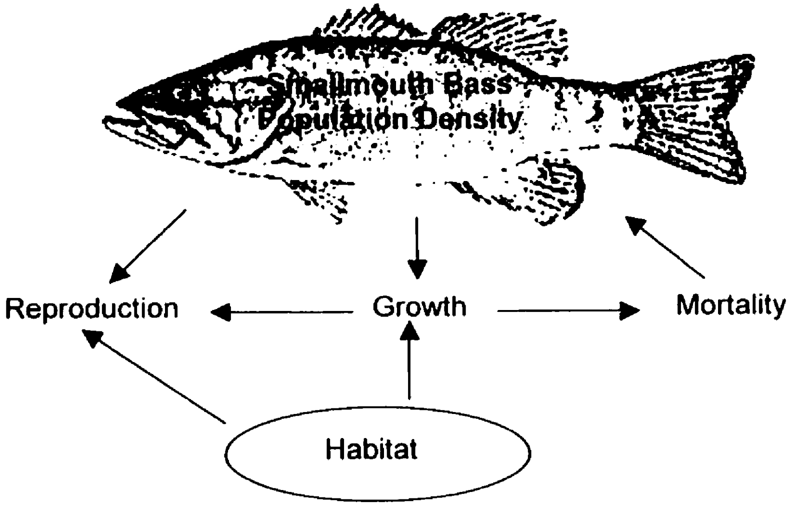


Figure 2.2: A schematic representation of how habitat and density influence smallmouth bass

survivors. The second includes the juvenile and adult life stages. The adult life stage is defined as ≥age 3 since that is the age when fish approach maturity. The model does not presently support density or habitat-dependent changes in the age of maturity.

Habitat suitability indices (HSI's) were developed for each habitat variable. Calculating the geometric mean of the HSI values for all the habitat variables provides an overall HSI score for a lake site being modelled (Figure 2.3). 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 also gives each habitat variable equal weight. The overall HSI score ranges from 0 -1 where 1 represents the most suitable habitat.

The model uses the surface area within a suitable depth range to determine the number of nests, juveniles and adults that can be supported. Individual bass nests, juveniles and adults are assumed to distribute themselves across the available habitat according to the ideal free distribution (See 2.4.1. Distribution). After the nests, juveniles and adults are distributed throughout the lake, growth is determined as a function of temperature, productivity (total dissolved solid concentration [TDS]) and density. Mortality is incorporated to determine how many YOY, juveniles and adults survive one season. For the first year of life, mortality is negatively related to size and is therefore density-dependent because growth is. The model may then be repeated for several years until the population approaches equilibrium (Figure 2.3). Equilibrium is assumed when the number of adults (age 3+) varies no more than 5% over a ten year period. This model has been programmed in Microsoft® Visual Basic® 6.0 Professional Edition and is an interactive application allowing the user to input habitat data and make decisions about the type of output the model will produce.

2.2. DEVELOPING HABITAT SUITABILITY INDICES

A literature review and analyses of data from the Ontario Ministry of Natural Resources and University of Toronto provided the foundation for the development of suitability models for each habitat variable. A brief synopsis of how each habitat variable relates to smallmouth bass presence/absence, reproduction and growth will be discussed, followed by a description of the suitability models.

2.2.1. Water temperature

Water temperature is one of the most important factors driving the reproduction and growth of aquatic organisms (Armour, 1993; Matuszek and Shuter 1996). However, littoral

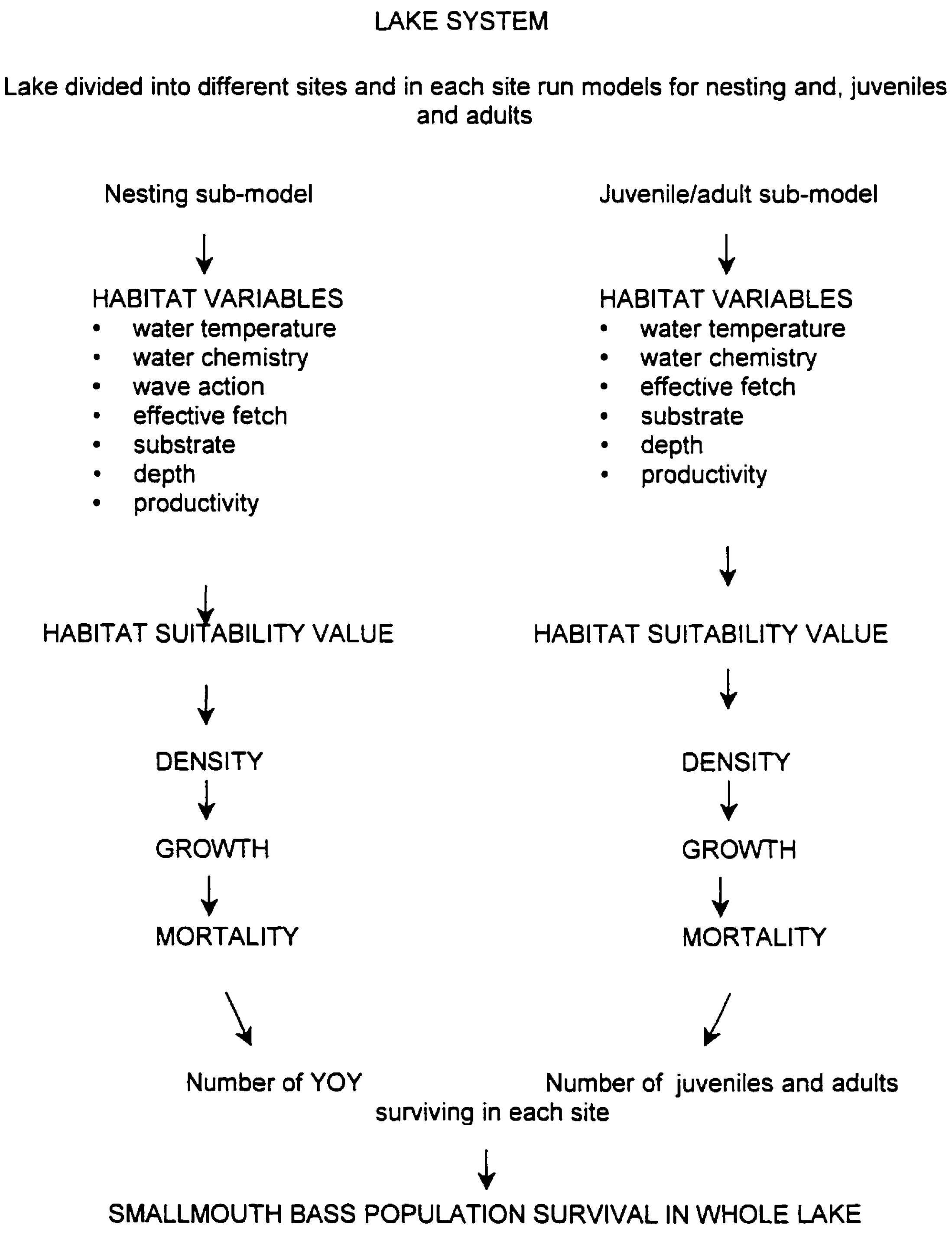


Figure 2.3: A general outline of the habitat model.

water temperature data are rarely available. We used littoral water temperature data from Lake Opeongo, Ontario in combination with an existing surface water temperature model (Shuter et al. 1983) to develop an empirical model that predicts the temperature in different littoral sites of a lake (Appendix A). This model predicts littoral water temperatures at 2 m depth throughout the ice-free season for any site in a lake as a function of mean annual air temperature (°C) and effective fetch (m).

Water temperature suitability for nesting

Smallmouth bass begin nesting in the littoral zone of lakes and rivers at temperatures ranging from 12.8 °C – 25 °C (Turner and MacCrimmon 1970; Scott and Crossman 1973; Shuter et al. 1980; Edwards 1983 and Armour 1993). However, spawning mostly occurs at temperatures of 15.6 °C – 18.3 °C (Scott and Crossman 1973; Armour, 1993). For the model, spawning is set to occur at 16 °C, a value that represents the mean spawning temperature in Ontario and the northern United States.

Different littoral areas of a lake warm up at different rates and since nest selection and spawning are temperature dependent, areas that warm up sooner than others will be first occupied for spawning (Rejwan et al. 1999). In the model, sites that warm to 16 °C before the mean littoral temperature reaches either it's maximum temperature or 25 °C (the upper limit for spawning) are suitable for nesting. The remaining sites in the lake are assumed to be too cold during the spawning period and are therefore given a water temperature suitability of zero. The day when spawning begins in different areas of the lake can be predicted from the littoral temperature model.

For the model, 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; Ridgway, pers. comm.). These 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.

Water temperature suitability for juveniles and adults

Laboratory experiments and field studies provide estimates of the thermal preferences of juvenile and adult smallmouth bass. Suitable temperatures range from 21°C

-33 °C (Doan 1940, Scott and Crossman 1973, Edwards et al. 1983, Armour 1993). Within the present North American range of smallmouth bass, water temperatures almost never exceed the upper limit, and in much of the range, 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 are more suitable for smallmouth bass. 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 value of one. The temperature suitability of the other sites is calculated by dividing their maximum temperature by the highest maximum temperature. For example, a cooler site with a maximum temperature of 23.5°C in a lake where the warmest site has a maximum temperature of 27°C will have a suitability of 0.87. In practice this means that the temperature suitability will not commonly range to 0.

2.2.2. Substrate

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 (Turner and MacCrimmon 1970; Goff 1984; Houpt 1991). Juveniles and adults prefer rocky substrates or submerged logs probably as protection from predators. In the case of larger adults, these coarse substrates may offer a predatory advantage (Turner and MacCrimmon 1970; Scott and Crossman 1973; Edwards et al. 1983; Bevelhimer 1996).

Substrate suitability for nesting

A substrate suitability model was developed from historical observations of substrate preference. Nesting data from seven Ontario populations (Billings, Davis, Four Mile, Long, Mountain, Opeongo and Tock Lakes) revealed that substrates composed of a combination of sand and rock (20% or more of substrate covered by particles ≥140 mm, and at least 50% ≤60 mm) tend to be preferred for smallmouth bass nesting (Appendix B). These findings are consistent with other studies (Edwards et al. 1983; Weigmann et al. 1992). This study produced equation 1, whose coefficients describe the relative suitabilities of six different substrate types for nesting.

$$S_N = 0.75(P_S) + 1(P_{SR}) + 0.64(P_G) + 0.75(P_R) + 0.20(P_W) + 0.26(P_L) \qquad (1)$$

S_N= substrate suitability for nesting

p_S = sand (more than 80% of substrate covered by particles ≤2 mm in diameter)

p_{SR} = sand and rocks (20% or more of substrate covered by particles ≥140 mm, and at least 50% ≤60 mm)
p_G = gravel (70% or more of substrate covered by particles ≤100 mm and at least 10 % in the 20 –100 mm range)
p_R = rock (40% of more of substrate covered by particles >140 mm diameter)
p_W = weed (40% or more of substrate covered by aquatic plants)
p_L = litter (80% organic debris, logs, sticks and decaying plant material)

These substrate categories are consistent with the categories defined during the Lakeshore Capacity Study performed by the Ontario Ministry of Natural Resources during 1978-1981 (Harker, 1982). To calculate the overall substrate suitability of an area of a lake, percentage(s) of the different substrate types are input into the model.

Substrate suitability for juveniles and adults

The substrate HSI for this life stage was modified from Edwards et al. (1983) according to the equation:

$$S_{JA} = 0.2(P_S) + 0.7(P_G) + 1(P_R) + 0(P_W) + 0(P_L) \qquad (2)$$

S_{JA} = substrate suitability for juveniles and adults
$p_{SR} = P_G$

As with the substrate model for nesting, the user inputs the percentage(s) of the different substrates in the site being modelled.

2.2.3. Water chemistry

A literature review provided data to generate a habitat suitability curve for pH and dissolved oxygen. Both HSI's were used for the nesting and, the juvenile/adult habitat models. Smallmouth bass are tolerant of pH within the range of 3 – 9 but the optimal range is 7.9 - 8.1 (Edwards et al. 1983). Suitable dissolved oxygen levels are concentrations greater than 6 mg/L. Death occurs quickly at concentrations approaching 1 mg/L (Edwards et al. 1983). These data were plotted to produce the habitat suitability indices for these variables (Figure 2.4 and 2.5) and are incorporated into the model using a polynomial regression (pH: $r^2 = 1$, p=0.000; dissolved oxygen: $r^2 = 0.99$, p=0.003) to produce the following equations.

$$pH_S = -0.04(pH)^2 + 0.6402(pH) - 1.5604 \qquad (3)$$

If pH ≤ 3 then $pH_S = 0$
If pH >9 then $pH_S = 0$
pH_S = pH suitability

$$dO_{2S} = 0.0031(dO_2)^3 - 0.0739(dO_2)^2 + 0.585(dO_2) - 0.514 \qquad (4)$$

dO_2 = dissolved oxygen (ppm)
If $dO_2 \leq 1$ ppm, $dO_{2S} = 0$
If $dO_2 > 6$ ppm, $dO_{2S} = 1$
dO_{2S} = dissolved oxygen suitability

2.2.4. Depth

Depth suitability for nesting

Most commonly observed depths for nesting are 0.5 to 2.5m (Neves 1975; Coble, 1975; Goff 1984). This depth range sets the boundaries of the nesting habitat for input into the model.

Depth suitability for juveniles and adults

Smallmouth bass is a warmwater species that inhabitats the epilimnion of lakes (Edwards et al. 1983). To calculate the thermocline depth and hence the lower limit of the smallmouth bass depth range, a model developed by Shuter et al. (1983) was employed (5):

$$Z_T = \frac{FT^{0.22} * Z^{0.213}}{e^{(0.0263 * TEMP - 1.55)}} \qquad (5)$$

Z_T = thermocline depth (m)
FT = fetch (km) (maximum distance)
Z = mean depth (m)
TEMP = mean annual air temperature (°C)

The area above the thermocline depth represents the habitat available for juveniles and adults in a lake. Areas with depths > Z_T have juvenile/adult suitabilities of zero.

2.2.5. Wave action

Wave action can lead to nest destruction by displacing eggs or disturbing the substrates housing eggs (Goff, 1986) and is therefore important to consider in the nesting sub-model. A wind storm event in Lake Opeongo, Ontario destroyed almost all the nests in the prime nesting area of the lake in 1998 (Ridgway pers. comm.). Data regarding the gust speed during the storm (51 km/h) and the effective fetch of the area affected (2,200 m) were entered into a wave height equation developed by Smith and Sinclair (1972). The gust-speed represents an index of the storm's intensity.

$$WH_N = 0.0026 \bullet (g^* F/w^2)^{0.47} \bullet w^2/g \qquad (6)$$

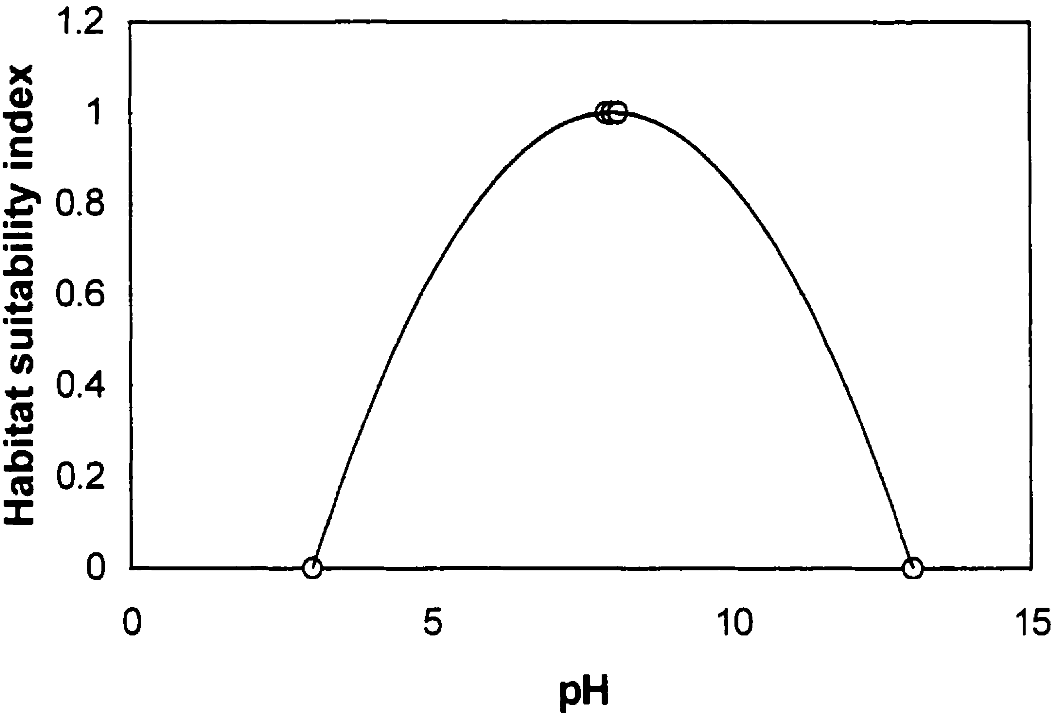


Figure 2.4: Habitat suitability index for pH optimal values range from 7.9-8.1.

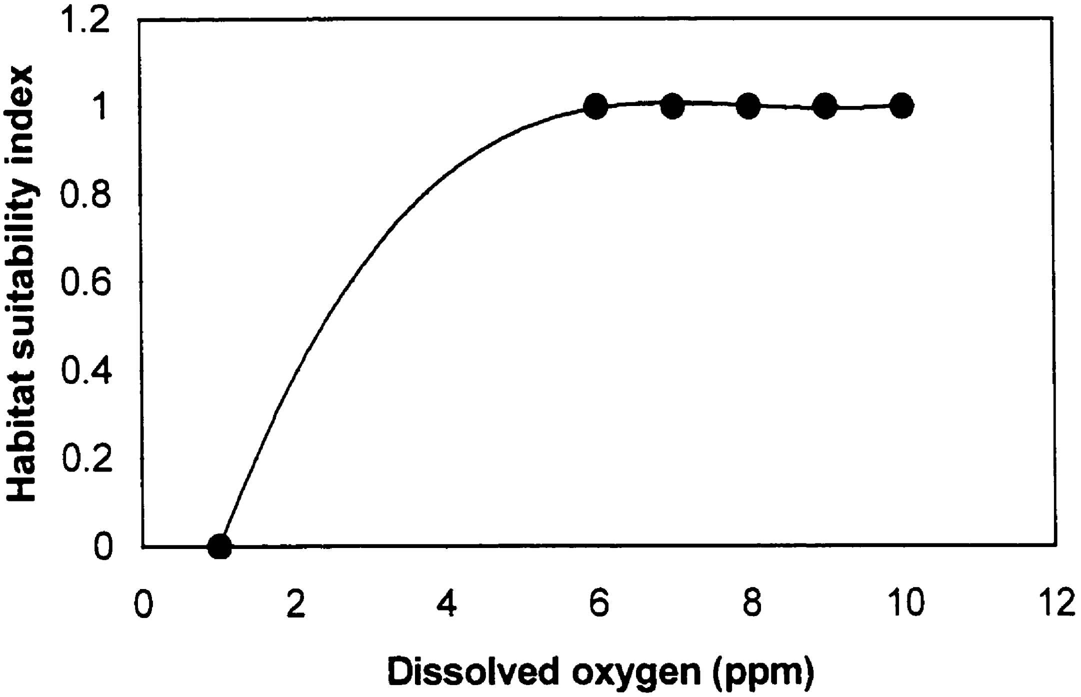


Figure 2.5: Habitat suitability index for dissolved oxygen.

WH_N= wave height (m)
g = gravitational constant 9.8 (m/s^2)
F= effective fetch (m)
w = windspeed – 14.167 (m/s)

This produced a wave height of 0.48 m that was taken as the critical wave height leading to nest destruction.

To improve the applicability and flexibility of the habitat model, the probability of attaining a detrimental gust speed given the mean monthly windspeed was modelled using data from Environment Canada. The detrimental gust speed was set at 51km/h since this was the gust speed recorded during the storm in Lake Opeongo. The probability of the occurrence of speeds equal to or greater than 51km/h was calculated for different mean monthly windspeeds (Figure 2.6). A third-order polynomial fit ($R^2 = 0.996$, $p=0.041$) to the data produced an equation representing the probability of achieving detrimental gustspeeds for different mean monthly windspeeds (Equation 7).

$$P_{GS} = 0.0027(MS)^3 - 0.1306(MS)^2 + 2.1091(MS) - 10.378 \qquad (7)$$

If $MS \leq 9$ then $P_{GS} = 0$
If $MS \geq 17$km/hr $P_{GS} = 1$

P_{GS} = probability of attaining gust speed ≥ 51 km/hr
MS = mean monthly windspeed

The wave height equation therefore became:

$$WH_N = [0.0026 * (g * F/14.167^2)^{0.47} * 14.167^2/g] * P_{GS} \qquad (8)$$

This equation calculates wave height as a function of the mean monthly windspeed, the probability of attaining a detrimental gust speed and effective fetch. Therefore if wind data are not available for a lake being modelled, mean monthy windspeed data from the nearest weather station can be used in the model. If the wave height produced by equation (8) is greater than 0.48 m then the area(s) of a lake being modelled is(are) deemed unsuitable for smallmouth bass nesting (HSI = 0). For other areas wave height suitability is taken as 1.0.

2.2.6. Effective fetch (m)

Effective fetch is a variable that is indirectly related to the suitability of different habitats for smallmouth bass. As aforementioned it is a component of the water temperature and wave height equations. To calculate the effective fetch of a site in a lake, only a map

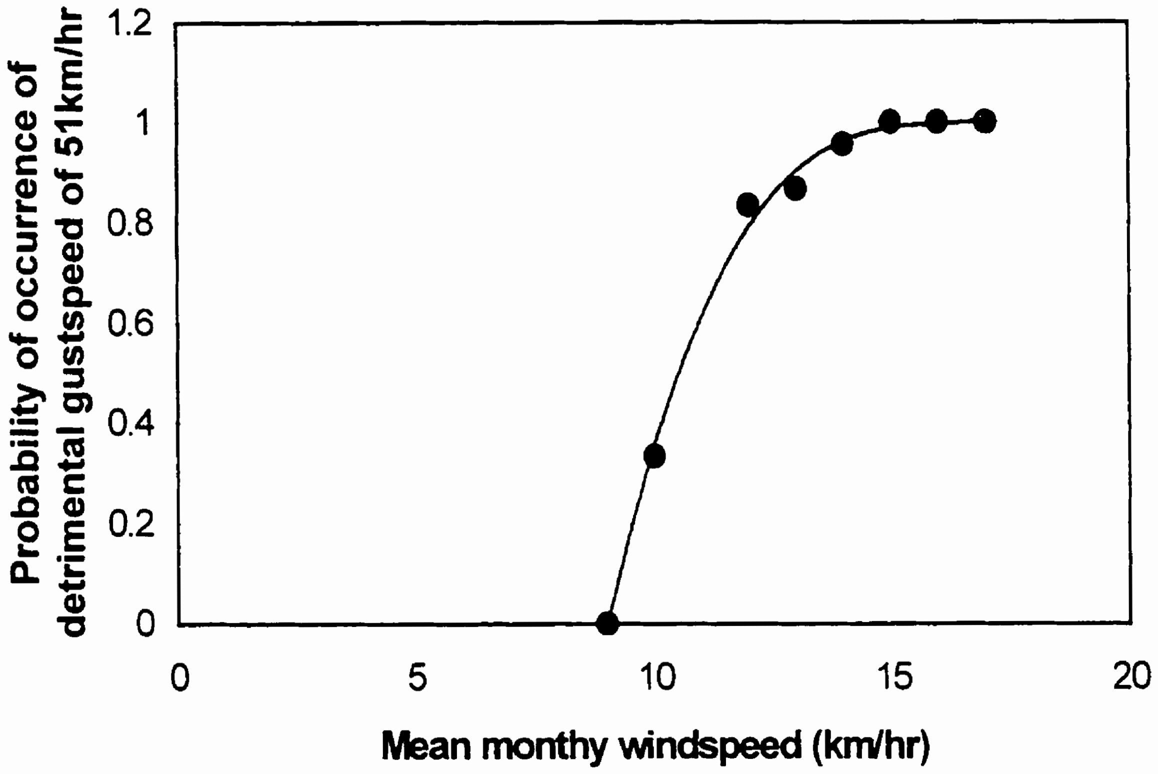


Figure 2.6: Probability (number of times gustspeed greater than 51 km/h / number of months) of detrimental gust speed of 51 km/h at different mean monthly windspeeds. For mean monthly windspeeds of 9, 10, 11, 12,13, 14, 15. 16, 17 km/h, n=3, 3, 11, 17, 14, 21, 18, 15 and 10, respectively.

and knowledge of the prevailing wind direction(s) are required. Effective fetch is calculated using the model developed by Scheffer et al. (1992) and is described in Appendix A.

2.2.7. Productivity and Prey abundance

The model focuses on how habitat supply influences smallmouth bass populations; the complexities of bass-prey relationships have not been incorporated. Instead simple models have been developed linking the P parameter in the bioenergetics model (Shuter and Post 1990) to an index of lake productivity. P is the proportion of the maximum potential consumption rate that is actually achieved. 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 possible at the given modelled water temperature. Therefore P would equal one.

Prey abundance for nesting

Prey abundance is important to the nesting model after the initiation of exogenous feeding. For the nesting model, we sought an empirical relationship between productivity and food availability with [TDS]. Shuter and Post's model (1990) of YOY smallmouth bass growth was used to calculate expected growth at the end of the growing season in six Ontario lakes using temperature data in Doan 1940; Turner and MacCrimmon 1970; Houpt 1991; Demers 1996 and Friesen 1998. If food is not limiting, growth in each lake should be close to that predicted by the smallmouth bass YOY bioenergetics model with P set to one (Shuter and Post, 1990).

Ratios of the observed to predicted growth rates provided an estimate of P, the ratio of food consumed over maximum consumption for each lake. The ratios thus produced for all of the lakes were then plotted against [TDS] and a third order polynomial was fitted to describe the relationship between [TDS] and P (Figure 2.7), ($r^2 = 0.991$, $p = 0.096$), equation (9).

$$P = -0.0003*TDS^2 +0.0257*TDS +0.447 \tag{9}$$

P = P (proportion food consumed / maximum consumption)
TDS = [TDS]

In the bioenergetics model, the activity multiplier was set constant at 2. A value this high was chosen because soon after first feeding smallmouth bass swimming speeds increase 120% and swimming speed is positively related to body size in YOY (Friesen 1998). This implies that the YOY are actively foraging. After metamorphosis agonistic behaviours also

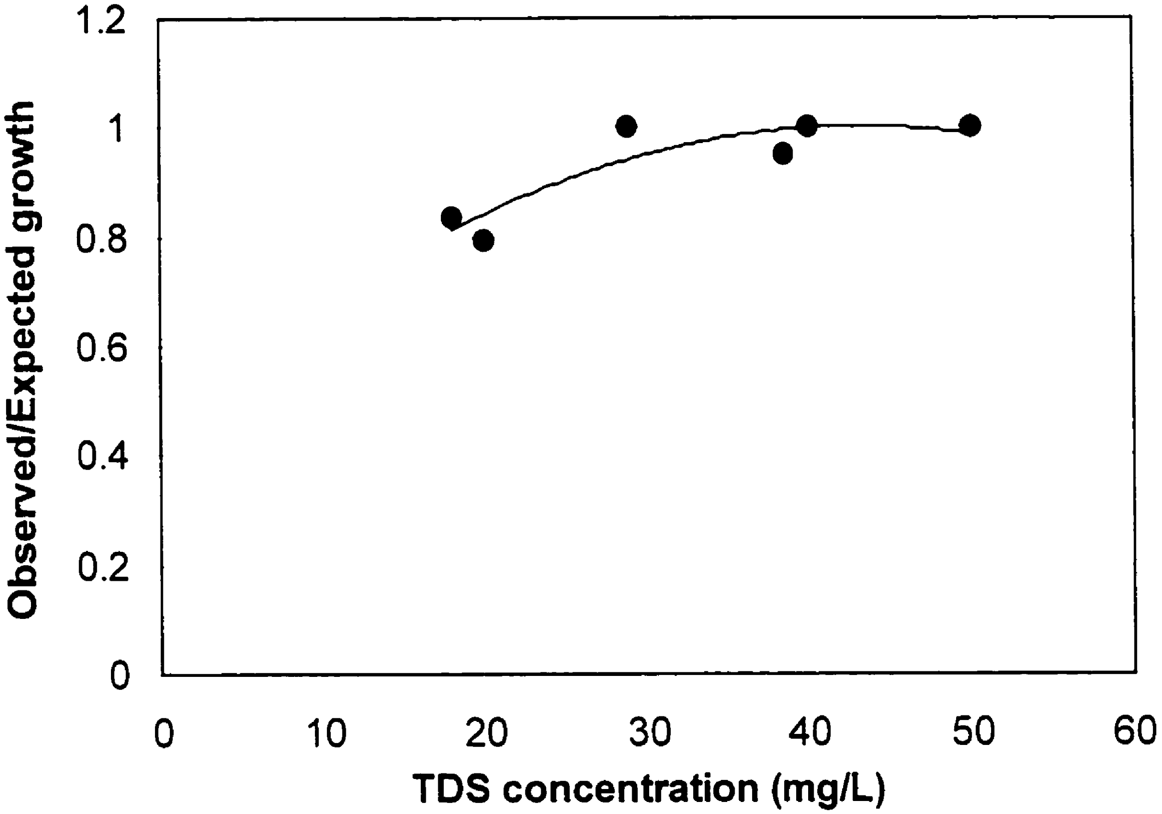


Figure 2.7: Relationship between observed/expected growth and total dissolved solids concentration (mg/L) in Cache, Canoe, Mouse, Nipissing, Tadenac and Opeongo Lake.

increase, which should further add to activity costs.

Prey abundance in the juvenile/adult model

A similar approach (relating [TDS] to P) was attempted for the juvenile/adult model but there was no clear relationship between [TDS] and observed/predicted growth. This may be due to the between lake differences in diets of the juveniles and adults. YOY feed on zooplankton and benthos in all lakes, whereas adults may feed on any combination of crayfish, forage fish, insects, frogs and tadpoles (Scott and Crossman 1973). 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 influences equilibrium model output.

2.2.8. Overall habitat suitability score

The geometric mean of all the habitat suitability values for water temperature, pH, dO_2, wave height and substrate composition provides an overall HSI score for nesting in each site of a lake being modelled. This is represented by the equation:

$$HSI_N = (T_N * S_N * pH_S * dO_{2S} * WH_N)^{1/5} \tag{10}$$

The equation for the juvenile/adult model is:

$$HSI_{JA} = (T_{JA} * S_{JA} * pH_S * dO_{2S})^{1/4} \tag{11}$$

pH_S and dO_{2S} are the same in both the nesting and, juvenile/adult model
T_N = temperature for nesting model •
T_{JA} = temperature for juveniles and adults

Once HSI scores have been assigned to different sites of a lake, population information is incorporated to link habitat to smallmouth bass population dynamics.

2.3. LINKING HABITAT TO POPULATION DYNAMICS

2.3.1. Distribution

Nest distribution

To calculate the maximum number of nests that could be expected in a site of a lake, the area between 0.5 - 2.5 m deep is divided by the minimum area of a nest. The minimum area of a nest was calculated to be the area of a circle with the radius of 8.5 m.

Eight and a half metres is half the minimum distance ever recorded between two nests in a natural population by Scott (1993). Therefore the minimum nest area was calculated to be 230 m^2. The maximum possible number of nests in an area is then multiplied by the HSI for that area. The number of nests is represented by the equation:

$$NN = (A_N * HSI^{TF})/230 \tag{12}$$

NN = number of nests
A_N = area between 0.5 and 2.5m (m^2)
TF = HSI transformation factor

The relationship between the number of nests and habitat suitability is not known. However, based on field observations we can predict what the maximum density in a site may be (Figure 2.8). We use a shape factor (TF) to model a range of scenarios. For example, if nesting habitat were severly limited in a lake, nest densities may be high even in low suitability areas. This may be modelled by setting TF to less than 1 (Figure 2.8). Conversely, if the most suitable habitats were abundant, nesting may not occur in less suitable areas. This may be modelled by setting the TF to greater than 1 (Figure 2.8). This is simply an exploratory component of the model and no criteria have been established to determine the value of the TF.

Once the potential number of nests in each site is calculated. Population data are used to determine how many reproductive males are available for nesting. Individual males are then assigned to different nests using the ideal free distribution. 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, since high densities will lead to more competition between the YOY as they emerge from the nest and may attract more predators. With this in mind, the model has been programmed so that each male will assess the trade-off between habitat suitability and density in each site. This has been programmed by first ordering the sites in descending suitabilities. 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 next most suitable site. This

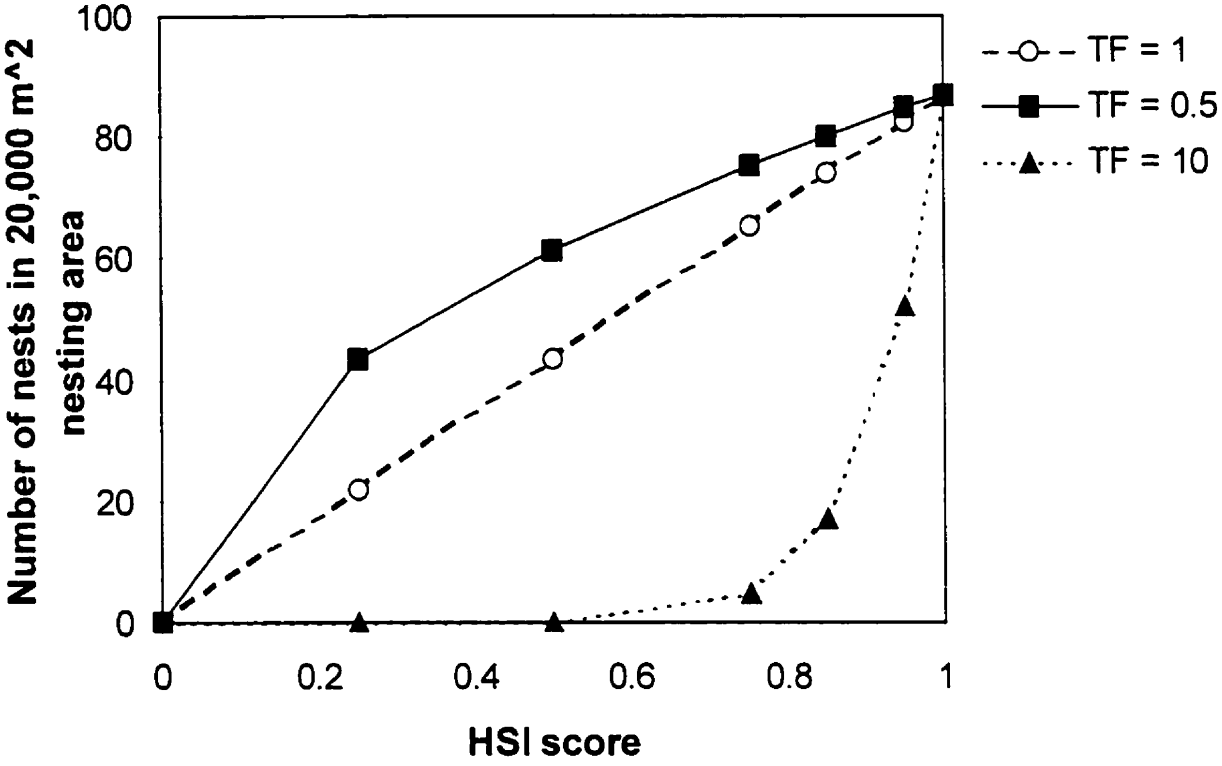


Figure 2.8: Number of nests when habitat suitability index transformation factor (TF) is equal to 1, 0.5 and 10.

process continues until all nests are occupied or there are no more reproductive males, whichever comes first.

Juvenile/adult distribution

The user can enter the number of individuals in each age class, the age-length and the length-weight relationship of the population into the program. If this information is not available, a default population with typical smallmouth bass age distribution, age-length and length-weight relationship is included.

The distribution of the juveniles and adults is also modelled using the ideal free distribution theory. The model has been programmed so that each fish in the population will assess the trade-off between habitat suitability and density-dependent reductions in growth in different sites of the lake being modelled. 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 a lake.

The ideal free distribution has been programmed by first ordering the sites in descending suitabilities. The growth potential (mm) of a one year old individual in each site is calculated using the Shuter and Post (1990) bioenergetics model with temperature and P as inputs. These growth potentials are then used as an index of the potential benefits of being at each of the sites.

Once the growth potential has been calculated for each site, an individual from the oldest age class (the largest fish) is assigned to the most suitable site. The program then loops to the next fish and the growth potential in that site is recalculated taking into account the presence of both fish using equation 18 (See Juvenile/adult growth). This new growth potential is then compared to the growth potential in the next-most suitable site and if the growth potential in the next site is greater than the growth potential in the first, the fish is assigned to the next site. Conversely, if the growth potential is greater in the more suitable site, the fish is assigned to that site. This procedure is repeated until each fish in the population is assigned to a site. The absolute growth for each fish is calculated once the population has been distributed and the densities in different sites are known (See Juvenile/adult growth).

Egg deposition

Once all the occupied nests are distributed throughout the spawning areas, data on female fecundity and abundance are used to determine the number of eggs deposited in each nest. 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. 1991; Ridgway pers. comm.). Therefore the size of a nesting male determines his mate's fecundity. Other observations suggest that 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 on combined data from South Branch Lake, Maine, Wilson Dam, Tennesee, two New York lakes and Nebish Lake, Wisconsin (Neves 1975; Hurbert 1976; Carlander 1977; Serns 1984). Linear regression (Figure 2.9, $r^2 = 0.746$, $p<0.001$) indicates:

$$F = 10.008(W) - 381.18 \tag{13}$$

F= fecundity (number of eggs)
W = 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.

2.3.2. Growth

YOY Growth

Growth of the YOY is positively related to temperature (Shuter et al. 1980; Witzel 1989; 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 areas of a lake (equations 14 and 15).

$$H = 83.2e^{-0.1606TEMP} \tag{14}$$

H= time to hatch (days)
TEMP = water temperature (°C)

$$R = 134e^{-0.1606TEMP} \tag{15}$$

R = time to rise (days)

Once the YOY rise from the nest and begin exogenous feeding, the YOY bioenergetics model (Shuter and Post, 1990) is used to estimate growth as a function of temperature and

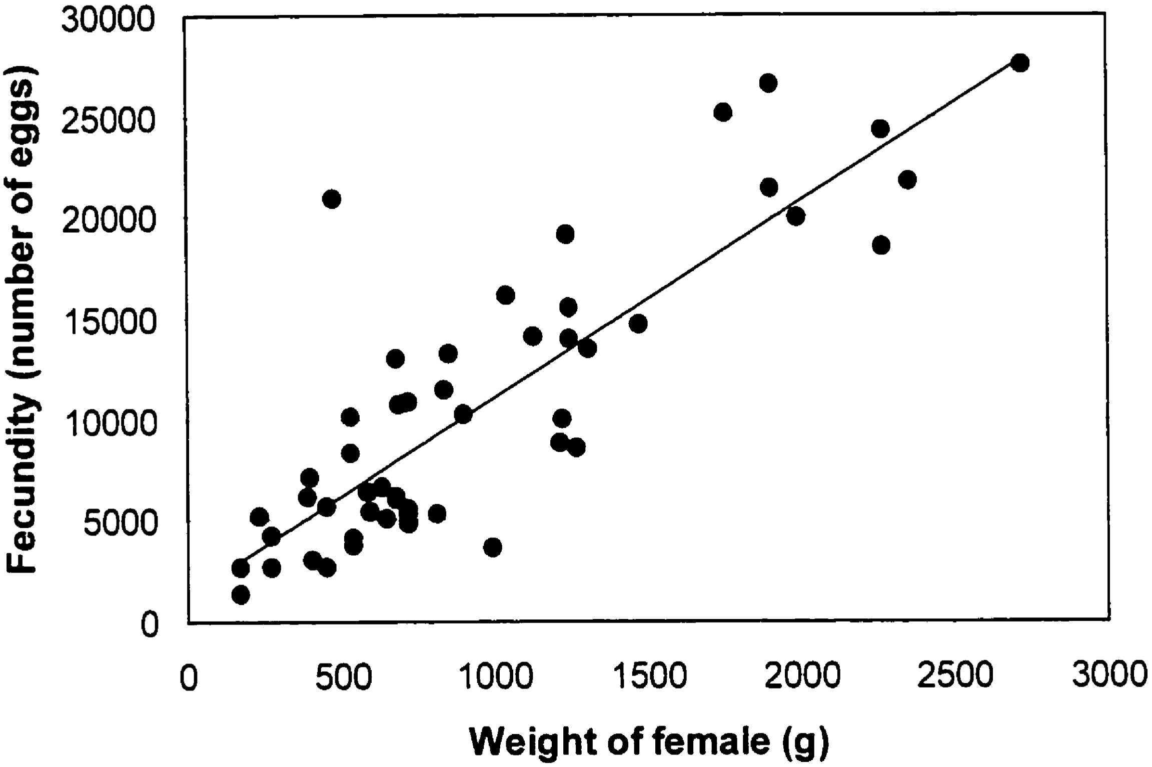


Figure 2.9: Fecundity – weight relationship using several populations of smallmouth bass.

the bioenergetic parameter P. As aforementioned, [TDS] can be used to estimate P in the YOY bioenergetics model (Equation 9).

There has been 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 the optimal home range area to forage, one can expect that the growth rate will be the maximum allowed by the temperatures observed. Minns et al., (1996) found that northern pike can still maintain a high proportion (90%) of their maximum growth rate with less than 20% of their required home range. A general equation used to calculate the home range area required by any fish as a function of its size is (Minns et al. 1996):

$$HR = 2.746 * L^{1.52} \qquad (16)$$

HR = home range (m^2)
L = total length (mm)

From the spatial distribution of nests, total egg deposition, and mortality (2.4.3 Mortality) predicted by the model, the number of YOY rising off the nest is calculated. Therefore the total area required by all individuals is:

$$THR = HR * YOY \qquad (17)$$

THR = total home range required by all individuals at nest area (m^2)
YOY = number of YOY

If the nest area available (See 2.2.4. Depth) is greater than or equal to the area required by all the YOY in the site being modelled, maximum growth is achieved and there are no overlapping home ranges. Maximum growth is calculated using the bioenergetics model. The equation used to incorporate density into smallmouth bass growth is:

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

G_{ACT} = actual growth (mm)
G_{MAX} = maximum growth expected in area (mm)
AA = area available (nesting or juvenile/adult area (m^2))
THR = total home range (m^2)

0.96 = coefficient which results in $G_{ACT} = 0.5(G_{MAX})$ for any fish species at typical densities in lakes in North America (Minns et al. 1996)
0.0101 = scaling coefficient which ensures that $G_{ACT} = 0.99(G_{MAX})$ when AA = THR

YOY growth and mortality are calculated on a daily basis. As the lengths of the fish increase throughout the season their home ranges increase but since mortality is calculated daily, density decreases.

Juvenile/adult Growth

The juvenile/adult model also employs a bioenergetics model to estimate growth (Shuter and Post 1990). P is an input variable that ranges 0 -1 and can be changed by the user of the model (See Prey abundance in the juvenile/adult model). Density-dependent effects on growth are incorporated using equation 18 after the spatial distribution of juveniles and adults is determined by the model (See Juvenile/adult distribution). The model 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. This total is then compared to the area available for the juveniles and adults (See 2.3.4. Depth) to calculate the growth of each individual (Equation 18).

2.3.3. Mortality

Mortality for nesting model

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 and for the remainder of the season mortality was calculated daily as a function of size. The empirical size-dependent mortality equation was developed for YOY smallmouth bass by Houpt (1991):

$$M = 0.2e^{-0.04*L} \tag{19}$$

M = mortality (%/d)
L = length (mm)

The growth component of the model provides daily estimates of the length of each fish after metamorphosis until low temperatures stop growth.

Survival after each day is calculated using:

$$N_{YOY} = N_0*(1-M/100) \tag{20}$$

N_{YOY} = number of YOY
N_0 = number of YOY at beginning of day
M = mortality (%/d)

Once water temperatures fall below 10 °C, YOY stop feeding, seek shelter and remain dormant over winter (Keast 1968; Shuter et al. 1980).

Over-winter survival is calculated using a model developed by Shuter et al. (1980). They found that larger YOY smallmouth bass have more stored energy reserves and can survive without food longer than smaller fish. Equation 21 describes energy reserves as a function of length. When these reserves are depleted to the level calculated by equation 22, a fish starves to death.

$$A_R = 10^{-7\ 073} * L^{3\ 724} \tag{21}$$

A_R = energy reserves (g)
L = length of fish (mm)

$$A_S = 10^{-7\ 418} * L^{3\ 7236} \tag{22}$$

A_S = energy reserves depleted to the point of starvation (g)
L = length of fish (mm)

Energy reserves are depleted at a constant rate

$$R = 0.6 * 10^{-7}(L)^{2\ 4} \tag{23}$$

R = rate of depletion (g/day)
L = length of the fish (mm)

Combining equations 21-23 produces an estimate of the length of time a fish can survive the winter season.

$$LWS = \frac{A_R - A_S}{R} \tag{24}$$

LWS = length of the winter survival (days)

The duration of the winter period can be calculated by substracting the length of the ice-free season (Appendix A) from 365 days. By comparing the length of the winter season to the length of winter survival for each fish, the model determines which YOY survive the winter.

Mortality in the juvenile/adult sub-model

For our model, annual juvenile and adult natural mortality is set at 25% for each age class. This estimate is based on age distribution averaged across years from long-term creel data from Lake Opeongo (Shuter et al. 1987).

2.4. SUMMARY OF SMALLMOUTH BASS HABITAT MODEL

The user divides his/her study lake into several subsections/sites and generates a habtiat inventory for each site. This is entered into the model and a map of the suitability of the different sites for nesting and juvenile/adult smallmouth bass is generated. Population data are then used to calculate the densities of nests, juveniles and adults in each site. Growth is calculated as a function of density and habitat. Mortality is size-dependent for the YOY and set to a constant annual rate in the older fish. The model then produces the number and size of the individuals in each age class surviving to the next year (Figure 2.10). The model is then looped for 40 years. Outputs of the model include equilibrium population density (all ages/ha), numerical density (adults/ha) and biomass density (kg (adults)/ha.

2.5. SENSITIVITY ANALYSIS OF MODEL

Sensitivity analysis is the process by which the factors most strongly influencing model output are identified. This involves varying each parameter individually and examining the pattern of change in model outputs (Dreschsler 1998). Because different model parameters have different units and vary naturally over different ranges, simply varying model parameters by a constant percentage or absolute range may produce a distorted picture of relative sensitivity. Therefore sensitivity analyses must somehow take into account both the slope of the response-versus-parameter relationship, and the natural range of parameter values found in the population of lakes to which the model is being applied. After identifying the most important variables, the precision of the model can be maximized by most accurately measuring these variables (McCarthy et al. 1995).

To test the sensitivity of the smallmouth bass habitat model, a hypothetical lake was designed and used as a control for comparison with other simulations. The simulations used to test the sensitivity of the model are described in Section 2.5.2. The results and conclusions of these simulations are then described in Section 2.5.3. and 2.5.4.

2.5.1. Control Lake

Data from the Ontario Ministry of Natural Resources and Environment Canada provided the range of habitat variable values found in 1646 smallmouth bass lakes in Ontario. A hypothetical control lake was designed using the median habitat values of these smallmouth bass lakes. Median values were chosen since the range of some of the habitat variable values did not follow a normal distribution. A list of the habitat variable values can

LAKE SYSTEM

Lake is divided into different site and in each site program runs models for nesting and, juveniles/adults

	Nesting sub-model	Juvenile/adult sub-model
Water temperature (Appendix A)	sites which warm to 16°C before mean littoral temperature reaches 16°C are most suitable for spawning	suitability is determined by how warm they are throughout the ice-free season
Substrate	$S_N = 0.75(P_S) + 1(P_{SR}) + 0.64(P_G) + 0.75(P_R) + 0.20(P_W) + 0.26(P_L)$ **(1)**	$S_{JA} = 0.2(P_S) + 0.7(P_G) + 1(P_R) + 0(P_W) + 0(P_L)$ **(2)**
pH	$pH_S = 0.04(pH)^2 + 0.640(pH) - 1.560$ **(3)** If $pH \le 3$ then $pH_S = 0$ If $pH > 9$ then $pH_S = 0$	
Dissolved oxygen	$dO_{2S} = 0.0031(dO)^3 - 0.0739(dO)^2 + 0.585(dO) - 0.514$ **(4)** If $dO_2 \le 1$ ppm, $dO_{2S} = 0$ If $dO_2 > 6$ ppm, $dO_{2S} = 1$	
Depth	0.5 – 2.5m	0m to thermocline depth $Z_T = FT^{0.220} \bullet Z^{0.213} / e^{(0.0263 \bullet TEMP - 1.55)}$ **(5)**
Wave action	$WH_N = 0.0026 * (g * F/(14.167)^2)^{0.47} * (14.167)^2/g$ **(8)**	
Effective fetch	Appendix A	
Productivity and prey abundance	$P = 0.00001{*}TDS^3 - 0.0017{*}TDS^2 + 0.0712{*}TDS - 0.000$ **(9)** If TDS > 50mg/L then P = 1	$P = 0 - 1$
HABITAT SUITABILITY SCORE	$HSI_N = (T_N * S_N \bullet pH_S * DO_{2S} \bullet WH_N)^{1/5}$ **(10)**	$HSI_{JA} = (T_{JA} * S_{JA} \bullet pH_S \bullet DO_{2S})^{1/4}$ **(11)**
DISTRIBUTION	$NN = (A_N * HSI^{IF})/230$ **(12)** ideal free distribution	ideal free distribution
DENSITY AND GROWTH	$G_{ACT} = G_{MAX}(AA^{0.96}) / (AA^{0.96} + 0.0101(THR^{0.96})$ **(18)**	
MORTALITY	$M = 0.2e^{-0.04*L}$ **(19)**	25%

Number of YOY, juveniles and adults surviving in each site

↘ ↓ ↙

SMALLMOUTH BASS POPULATION SURVIVAL IN WHOLE LAKE

Figure 2.10: Summary of smallmouth bass habitat model, a list of the abbreviations is provided in Appendix D.

Table 2.1a: Control lake habitat characteristics, representing the median values for smallmouth bass lakes in Ontario.

Habitat Variable	**Median**	**10 %**	**90%**
Lake size	112 ha	16.9 ha	990.5 ha
Mean depth	5.7 m		
Perimeter	3.75 km		
Maximum fetch	1194 m		
Mean annual air temperature	4.36 °C	1.8 °C	7.12 °C
Thermocline depth	6.32 m		
Mean windspeed during the month of spawning	14 km/h	7 km/h	20 km/h
pH	7		
Dissolved oxygen	10 mg/L		
Total dissolved solids	38 mg/L	21 mg/L	150 mg/L

Table 2.1b: Substrate composition and effective fetches of the six sites in control lake.

Site	Substrate composition for nesting habitat (Z = 0.5-2.5 m)						Substrate composition for juvenile and adult habitat (Z_T < 6.3m)					Effective fetch (m)
	sand	sand /rock	gravel	rock	weed	litter	sand	gravel	rock	weed	litter	
1	0.33	0	0	0.17	0.50	0	0.33	0	0.17	0.50	0	220
2	0	0.10	0	0.50	0.40	0	0	0.10	0.50	0.24	0	254
3	0.16	0.28	0.28	0.28	0	0	0.16	0.56	0.28	0	0	357
4	0.20	0	0	0.75	0.05	0	0.20	0	0.75	0.05	0	384
5	0	0	0	0.55	0	0.45	0	0	0.55	0	0.45	349
6	0	0.13	0	0.63	0	0.24	0	0.13	0.63	0	0.24	267

be found in Table 2.1. Once the morphometry and habitat variable values were determined the control lake was divided into six sites (Figure 2.11). The number of sites was arbitrarily chosen to exercise the capability of the model to allow the user to decide the number of subsections used to describe a lake. The effective fetch of each site was calculated using the method described in Appendix A. Prevailing wind directions in Ontario are from the west (Environment Canada 2000) but their exact occurrence is not known. Since we know the westerly directions are prevailing their probability of occuring is at least 50%. Therefore each westerly direction NW, W, SW was given a probability of occurence of 16.6%. The other directions (N, NE, E, SE, S) were given equal probabilities of 10% each. These values were then used to calculate the effective fetch of each site.

The substrate composition throughout the control lake was determined using substrate data from a Lakeshore Capacity Study conducted by the Ontario Ministry of Natural Resources on twelve Central Ontario lakes (Harker 1982). For each lake an overall substrate suitability score was calculated as the sum of the proportions of each substrate type multiplied by their respective suitability values for smallmouth bass nesting (Table 2.2). Once these overall scores were calculated for each lake, the substrate composition of the lake with the median score was used to represent the substrate composition of the control lake. The median substrate score was 0.607, therefore the mean proportions of substrates in Four Mile (substrate score 0.610) and Essox (0.603) lakes were used as the substrate composition of the control lake.

After determining the substrate composition of the control lake, the substrates were distributed among the six sites using the following method. The proportions of each substrate type were multiplied by the perimeter length of the lake (3751 m). The resulting values were then divided by the length of the least abundant substrate (Table 2.3). For the control lake, gravel was the least abundant substrate occupying only 75 m of the shoreline length. All perimeter lengths for the other substrate types were divided by 75 m to produce the number of 75 m segments each substrate type would occupy along the perimeter of the lake. The control lake perimeter was then divided into 75 m segments, and a substrate type was randomly assigned to each segment by drawing from the stock of substrate segments defining the overall substrate composition for the lake (Figure 2.12).

Control Population

The habitat characteristics of the control lake were entered into the smallmouth bass habitat model and run for forty years to produce an equilibrium population that represented

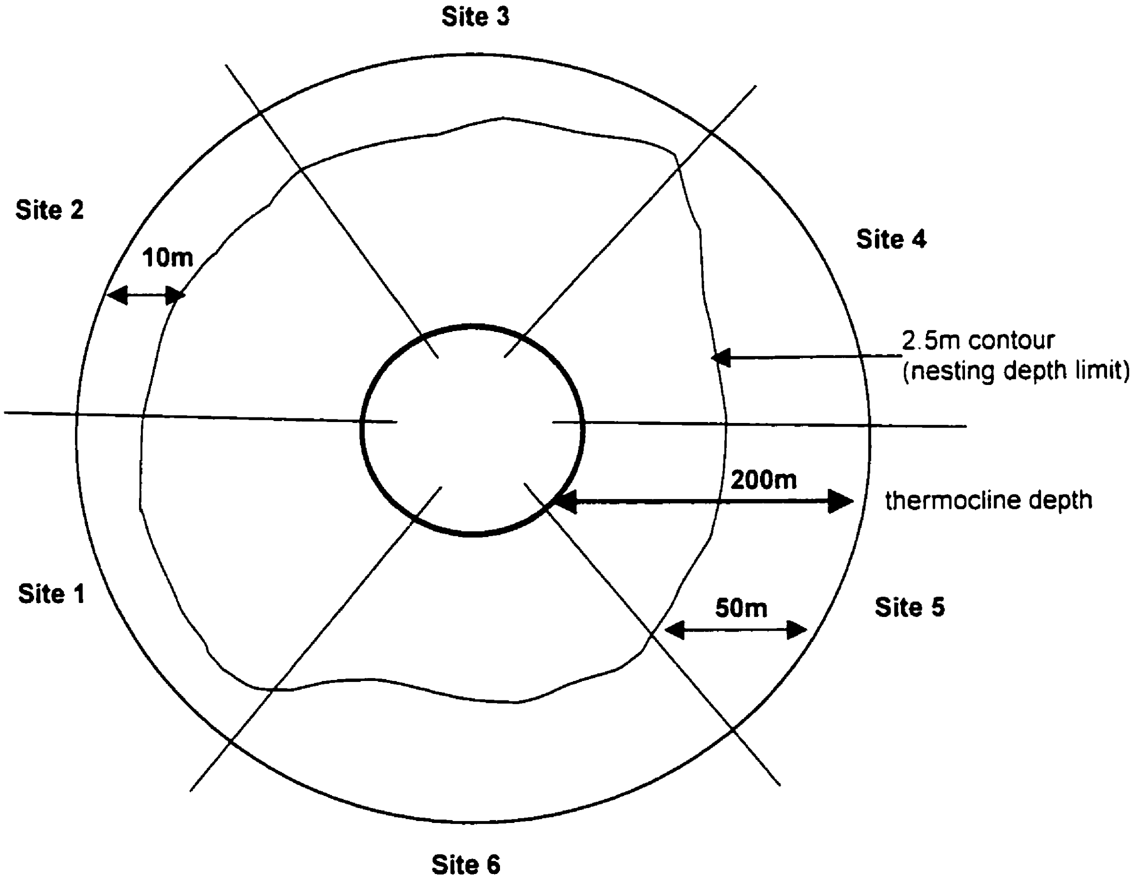


Figure 2.11: Morphometry of control lake. Outer circle represents the perimeter of the lake (3.75km), inner circle represents the thermocline depth. Double arrows represent the distance from shore to the nesting and thermocline depth contours.

Table 2.2: Substrate composition and overall HSI scores for nesting habitat in twelve lakes found in Central Ontario.

LAKE	SAND	SAND/ ROCK	GRAVEL	ROCK	LITTER	WEED	SCORE
Four Mile	0.067	0.255	0.048	0.269		0.359	0.610
Boshkung	0.508		0.124	.273	0.041	0.052	0.687
Maple	0.421				0.056	0.523	0.434
Mountain	0.27	0.401	0.037	0.209	0.081		0.806
Misty	0.087		0.111	0.515	0.281	0.005	0.597
Essox	0.098			0.602	0.298	0.001	0.603
Glamour	0.119		0.009	0.746	0.108	0.016	0.686
Tock	0.372		0.106	0.353	0.054	0.114	0.648
Billings	0.206		0.212	0.105	0.149	0.326	0.473
Davis	0.444		0.066	0.281	0.082	0.126	0.632
Long	0.303		0.160	0.136	0.188	0.212	0.523
Gullfeather	0.213		0.062	0.097	0.509	0.117	0.428

Table 2.3: Method used to distribute the six different substrate types throughout the control lake.

Substrate Type	Substrate code for random number generator	Substrate composition	Length of lake perimeter (m)	Number of segments with each substrate type
Sand	1	0.08	0.08*3751=263	263/75=3.5
Sand/rocks	2	0.13	488	6.5
Gravel	3	0.02	75	1
Rock	4	0.43	1612	21.5
Weed	5	0.15	563	7.5
Litter	6	0.18	675	9
				Total = 49

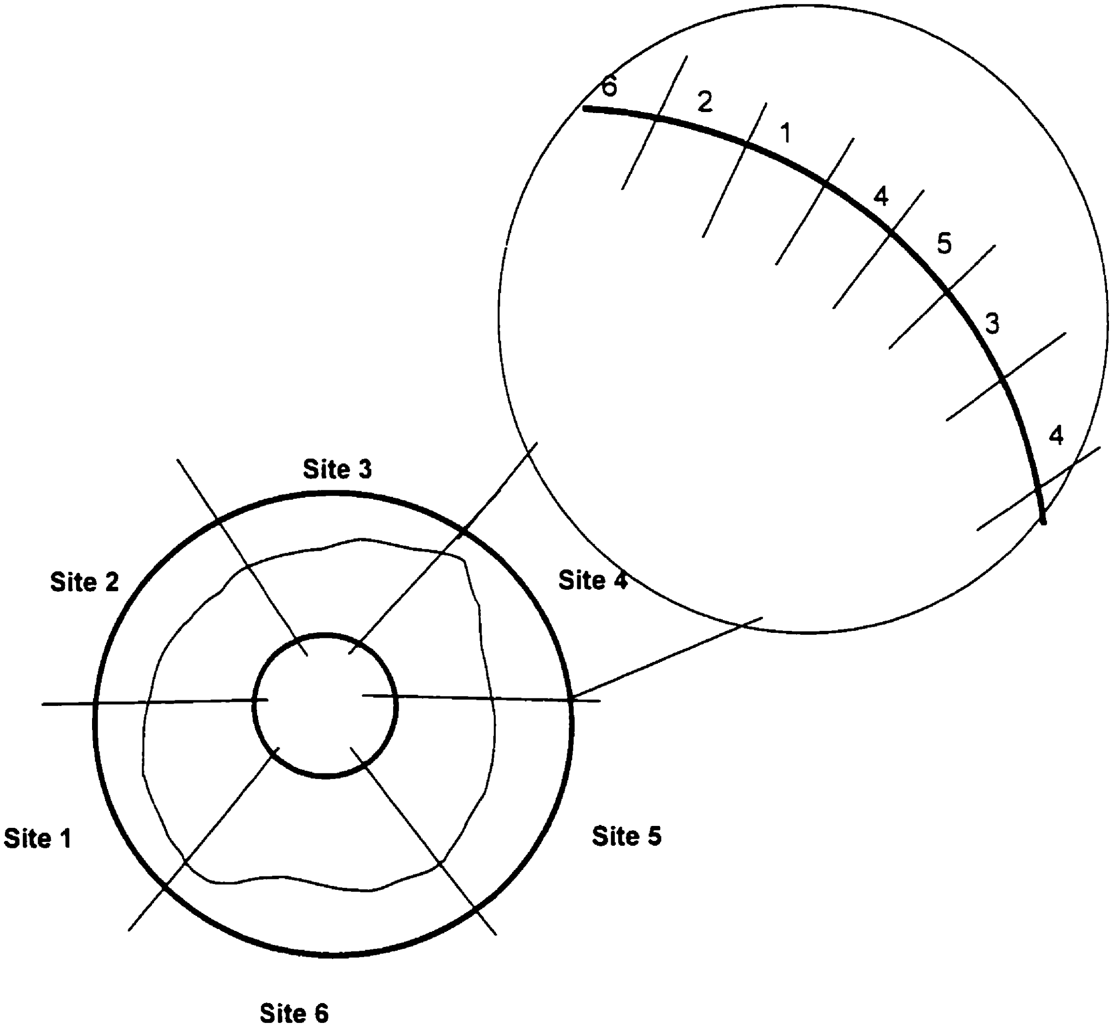


Figure 2.12: Method used to distribute substrates throughout the control lake. The lake is divided into forty-nine segments, each segment is randomly assigned a substrate type by drawing from the stock of substrate types defined by the median substrate composition among twelve Central Ontario lakes.

the starting population for all further simulations. To determine if the population had reached equilibrium, the mean number of adults was calculated for the last ten years of the forty year simulation. If the number of adults in each of the last ten years of the simulation fell within ± 5% of the mean for that 10 year period, the population was considered to be at equilibrium. If not, another forty year simulation was performed and equilibrium status was reassessed.

2.5.2. Simulation scenarios

Different simulations were performed to test the sensitivity of the model to habitat variable inputs. Where applicable, data from the smallmouth bass lakes in Ontario were used for the sensitivity analyses. These involved using the 10th and 90th percentile values for the different habitat variables among the 1646 smallmouth bass lakes in the OMNR database. The 10th and 90th values were chosen because they encompass the majority of the smallmouth bass lakes in Ontario. Each simulation using altered parameter values was run for forty years or until the population met the criteria for equilibrium.

Mean annual air temperature

Water temperature strongly influences smallmouth growth and reproduction. In the model, water temperature is a function of the mean annual air temperature and effective fetch. Increasing the mean annual air temperature will therefore increase the water temperature of the control lake. The range of mean annual air temperature values in Ontario was used to measure the relative importance of temperature to smallmouth bass populations. The 10th percentile value is 1.8 °C, the median is 4.36°C and the 90th percentile value is 7.12°C.

Substrate composition

Gravel and rock substrates are traditionally thought to be the most suitable nesting substrate for smallmouth bass. The substrate composition in our subject group of twelve Ontario lakes varied from 82% sand, litter and weed in Gullfeather Lake to 87% sand and rock in Mountain Lake. The 10th and 90th percentiles for overall substrate scores were the substrates found in Maple and Boshkung lakes, respectively (Table 2.2). These substrates were distributed throughout the control lake using the method described in 2.5.1.

Total dissolved solids concentration

Total dissolved solids concentration [TDS] is positively related to the growth of the YOY. In Ontario, [TDS] range from 6 to 450 mg/L. Two simulations were performed using the 10th and 90th percentile values of 21 mg/L and 150 mg/L.

TF value

The TF is a transformation factor that changes the number of nests relative to the habitat suitability (Figure 2.8). Low TF values increase the level of preference for nesting in sites with high suitability and produce more crowding in these areas. At high TF values the opposite is true and sites with high suitabilites receive relatively fewer nests. To assess this variable's effects, values of 0.1 and 10 were used in the model. The default in the model is one. Upon closer inspection of the TF results, an error in the programming of the ideal free distribution was detected. This error is discussed in detail in Chapter Three and preliminary analysis has shown that it does not affect the overall density of smallmouth bass in the lake. Therefore the results and discussion of the sensitivity analysis are still valid in spite of this error.

Lake size

Smallmouth bass lakes in Ontario range from 0.1 ha to 24,955 ha in size. The sizes associated with the 10th and 90th percentiles of lakes in Ontario are 16.9 ha and 990.5 ha, respectively. To investigate the influence of lake size on smallmouth bass populations, three simulations were performed using circular surface areas of 16.9 ha, 112 ha and 990.5 ha.

Mean depth

In Ontario, the mean depths of lakes can range from 0.1 m to 41.2 m. Mean depth is positively related to the thermocline depth in lakes (See 2.2.4 Depth). In the model the thermocline represents the lower limit of the smallmouth bass habitat, therefore changing the thermocline depth will influence the area of habitat available for juvenile/adult smallmouth bass in the control lake. To investigate the influence of mean depth on smallmouth bass populations, simulations were performed using the 10th and 90th percentile values of 2.1 m and 13.1 m.

Mean monthly windspeed

Windspeed influences the suitability of a lake for nesting. As lake size increases lower windspeeds can have a detrimental effect of smallmouth bass nesting (See 2.2.5. Wave action). Therefore smaller lakes would require greater windspeeds to negatively impact smallmouth bass nesting suitability. Mean monthly windspeed data for Ontario spanning 1930-1991 were gathered from Environment Canada. These were used to determine the 10th and 90th percentile values of 7 and 20 km/h, respectively. Nine simulations were performed combining the three different size lakes and the three different windspeeds. Table 2.4 is a summary of the values used for these simulations.

P value

P is a component of the bioenergetics model and represents the ratio of food consumed to the ad libitum consumption. For the control lake P is set to its maximum value of one. To examine its influence, P is set to 0.75, 0.5 and 0.25 in three simulations.

Amount of nesting and juvenile/adult habitat area available

For these simulations, the nesting habitat area and the juvenile/adult habitat area were varied at increments of 25% between 25% to 150% of the control (Table 2.5).

Annual mortality

Simulations were performed with the annual mortality of the juveniles and adults set to 10%, 25%, 40%, 50% and 60%.

2.5.3. Sensitivity analyses results

Control lake simulation results

The different outputs generated by the model are described using the control lake simulation. Using the control lake habitat characteristics (Table 2.1), the model first calculates the suitability of the different sites first for nesting and then for the juveniles/adults. For the control lake, suitability values for nesting in the six sites were related with their suitability for the juveniles and adults (Figure 2.13).

The number of nests each site could support was calculated using Equation 12. Nest densities in the different sites ranged from 0.37 to 0.41 nests/100 m^2. In Ontario nest densities can range from 0.01 to 0.43 nests/100m^2 (Witzel unpublished data 1989; Harker 1982).

Table 2.4: Effective fetch values for circular 16.9 ha, 112ha and 990.5 ha lakes used to study effects of mean monthly windspeed on smallmouth bass densities.

Site	16.9 ha–effective fetch (m)	112 ha–effective fetch (m)	990.5 ha–effective fetch (m)
1	141	323	858
2	164	349	745
3	146	364	957
4	169	469	1215
5	172	443	1244
6	153	339	1066

Table 2.5: Values for area of shoreline for nesting and area available for juveniles and adults when habitat supply is represented as 25%, 50%, 125% and 150% of the control.

	Area of shoreline available for nesting (m^2)					Area available for juveniles and adults (m^2)				
Site	**25%**	**50%**	**C**	**125%**	**150%**	**25%**	**50%**	**C**	**125%**	**150%**
1	3839	7677	15354	19192	23031	26036	52072	104143	130178	156216
2	3739	7577	16354	18192	22031	22036	51072	102143	128178	154216
3	3939	7777	17354	20192	24031	30036	53072	106143	132178	158216
4	7500	15001	30001	37501	45001	24036	50072	100143	126178	150216
5	7300	14001	28001	30501	44001	28036	54072	108143	134178	162216
6	7700	16001	32001	44501	46001	26036	52072	104143	130178	156216

C = control

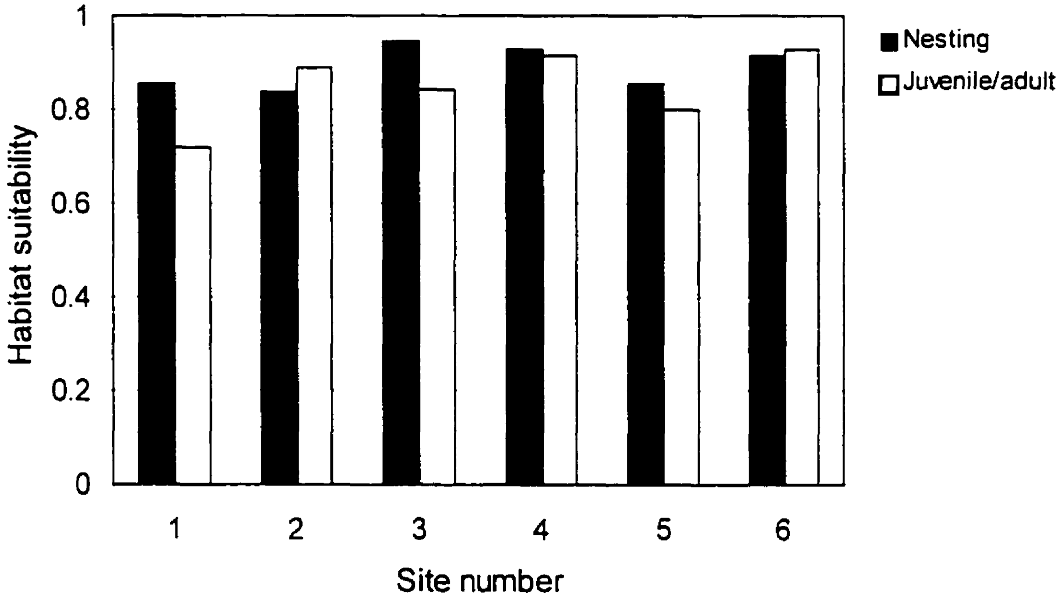


Figure 2.13: Habitat suitability for nesting and juveniles/adults in six sites of the control lake.

Control population

Smallmouth bass numerical density in North America ranges from 0.74 to 164 adults (age 3+)/ha with biomass densities of 0.52 to 82.90 kg/ha (Carlander 1977). Smallmouth bass numerical density in the control lake was 8.89 adults/ha with a biomass density of 4.86 kg (adults)/ha.

Habitat available:required represents the percentage of optimal habitat available. The optimal habitat is defined as the habitat required by either the YOY or juveniles/adults if each individual occupied non-overlapping home ranges. If the optimal habitat were available this ratio would be one. YOY habitat available:required is calculated when the YOY disperse from the nest site. For the control lake, this ratio was 0.07. The ratio of habitat available:required for the juveniles and adults was 0.03, indicating that there was substantial crowding at equilibrium in both the YOY and juvenile/adult habitats.

Mean length at age was slightly larger than the North American average (Figure 2.14). However the growth computed by the model is within the range seen in North America.

Mean annual air temperature

Numerical and biomass densities of the smallmouth bass in the control lake were positively correlated with mean annual air temperature (Figure 2.15). At temperatures of 1.8 °C, the population became extinct within 25 years.

Substrate

Changing the substrate composition of the control lake through the 10th -90th percentile range had no substantial effect on the overall suitability of the sites for nesting or for juveniles/adults (Figure 2.16). Accordingly, the substrate changes produced very little change in density or growth rates of the smallmouth bass (Figure 2.17).

Total dissolved solids concentration

Smallmouth bass densities increased with higher [TDS] (Figure 2.18). Juveniles and adults were larger at [TDS] of 21 mg/L than juveniles and adults at [TDS] of 38 mg/L and 150 mg/L, at maximum this difference was 9.8mm (Figure 2.18c), a substantially smaller effect than that generated by temperature changes.

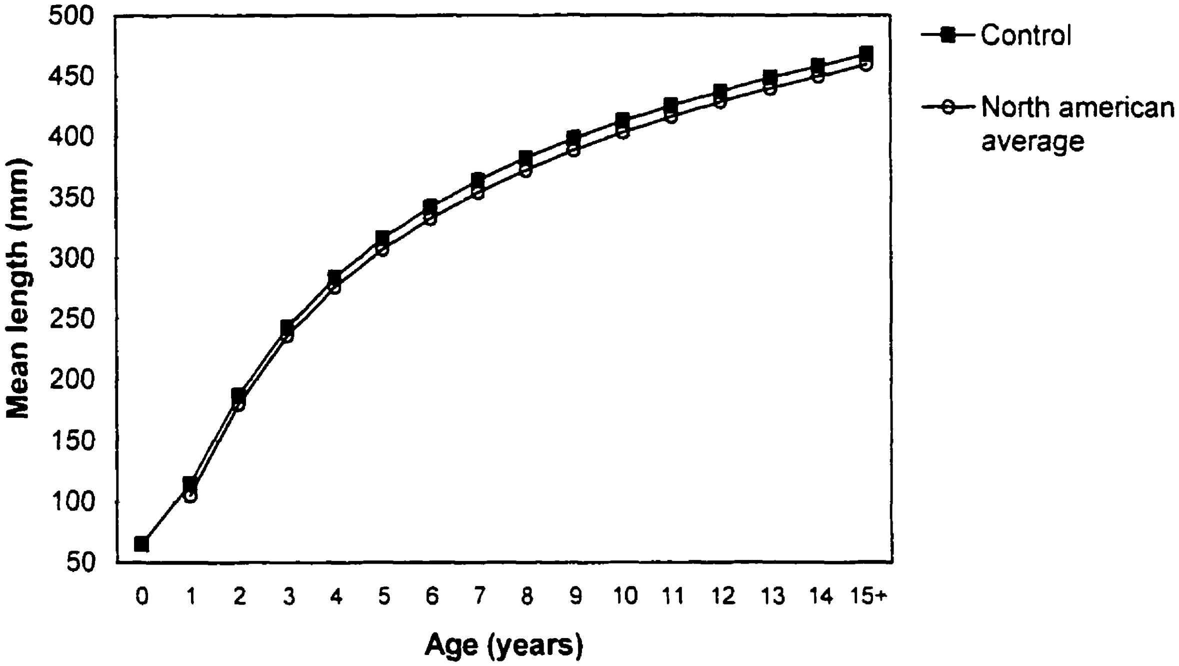


Figure 2.14: Mean length at age (mm) for control population and average smallmouth bass growth in eastern North America (Carlander, 1977).

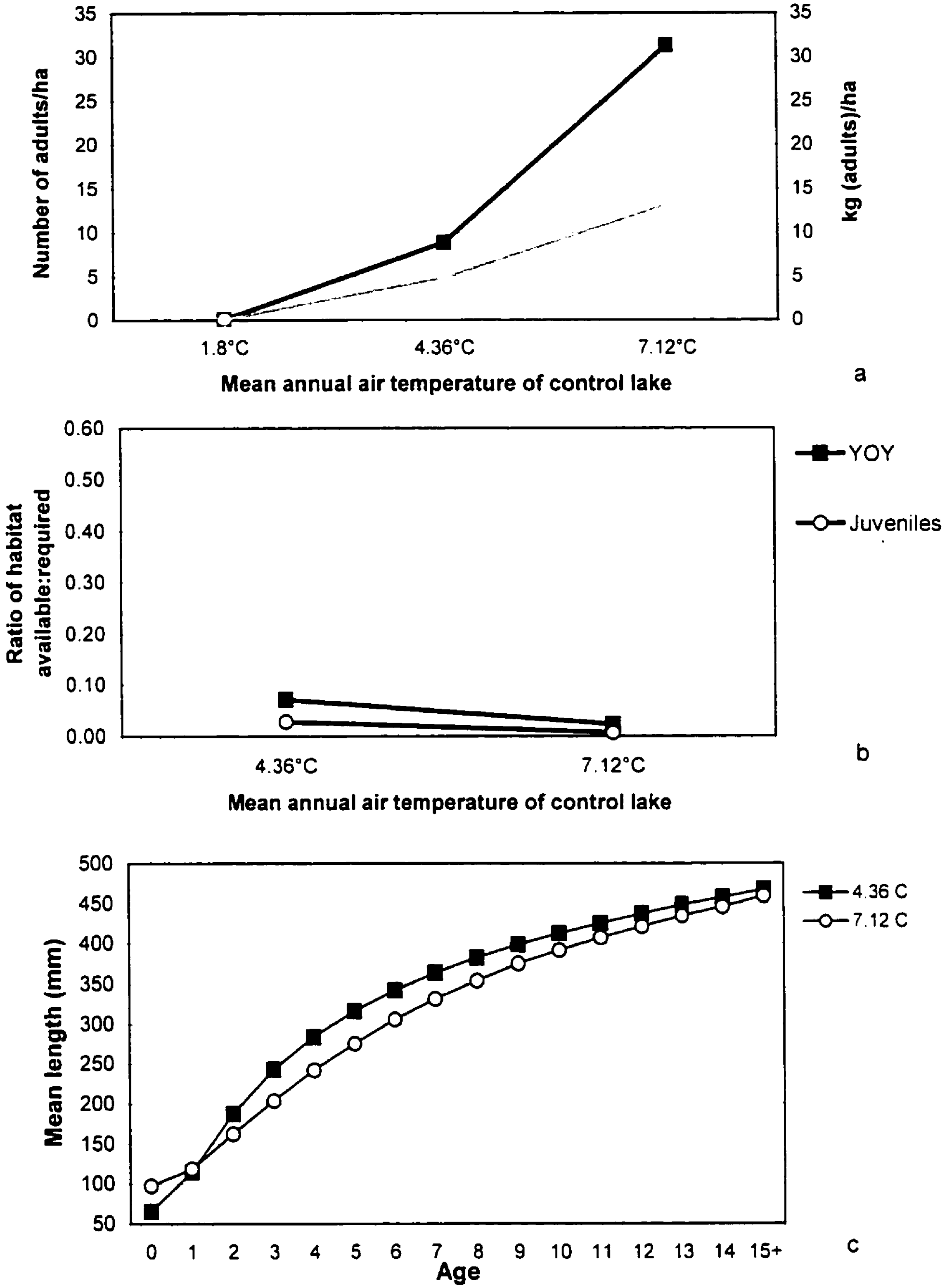


Figure 2.15: Temperature effects on smallmouth bass density (squares) and biomass (circles) (a), YOY and, juvenile and adult habitat available:required (b) and mean length at age (c).

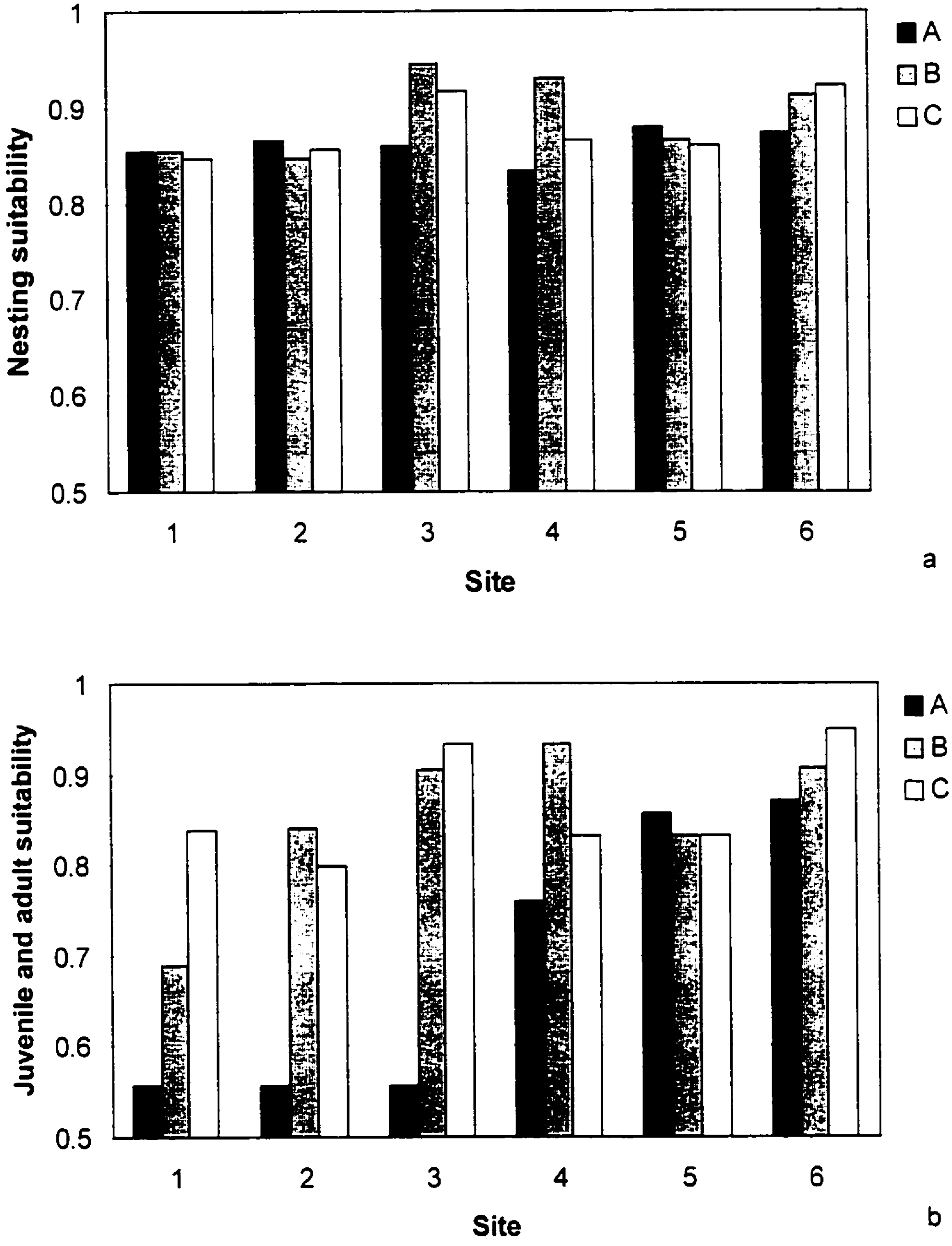


Figure 2.16: Suitability of six different sites in control lake for nesting (a) and, juvenile and adults (b) at three different substrate compositions. A represents substrate composed of 42% sand, 52% weed and 6% litter. B represents substrates composed of 8% sand, 13% sand and rocks, 2% gravel, 44% rock, 15% weed and 18% litter. Substrate C is comprised of 51% sand, 12% gravel, 27% rock, 5% weed and 4% litter.

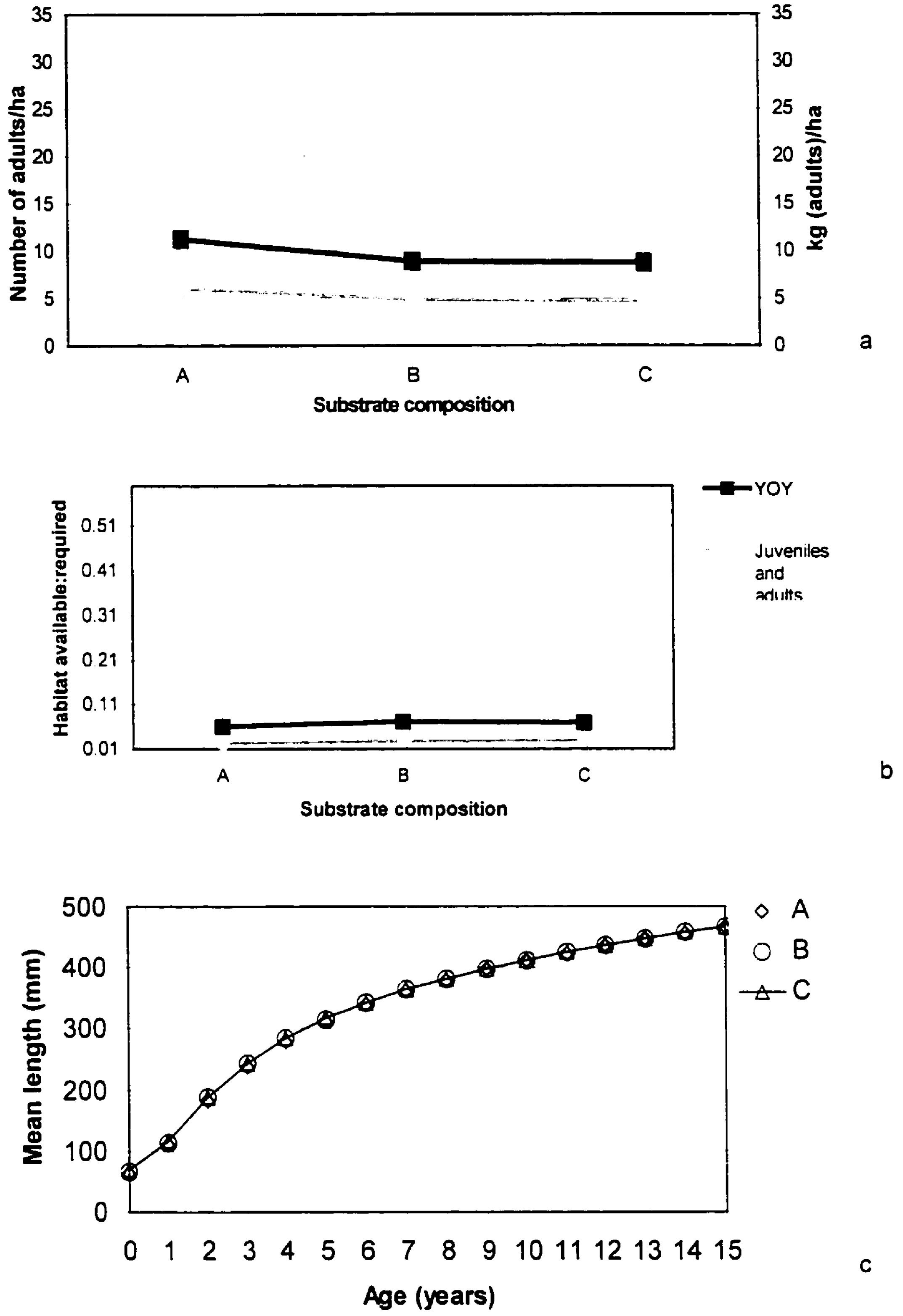


Figure 2.17: Effects of substrate composition on smallmouth bass density (squares) and biomass (circles) (a), YOY and, juvenile and adult habitat available:required (b) and mean length at age (c).

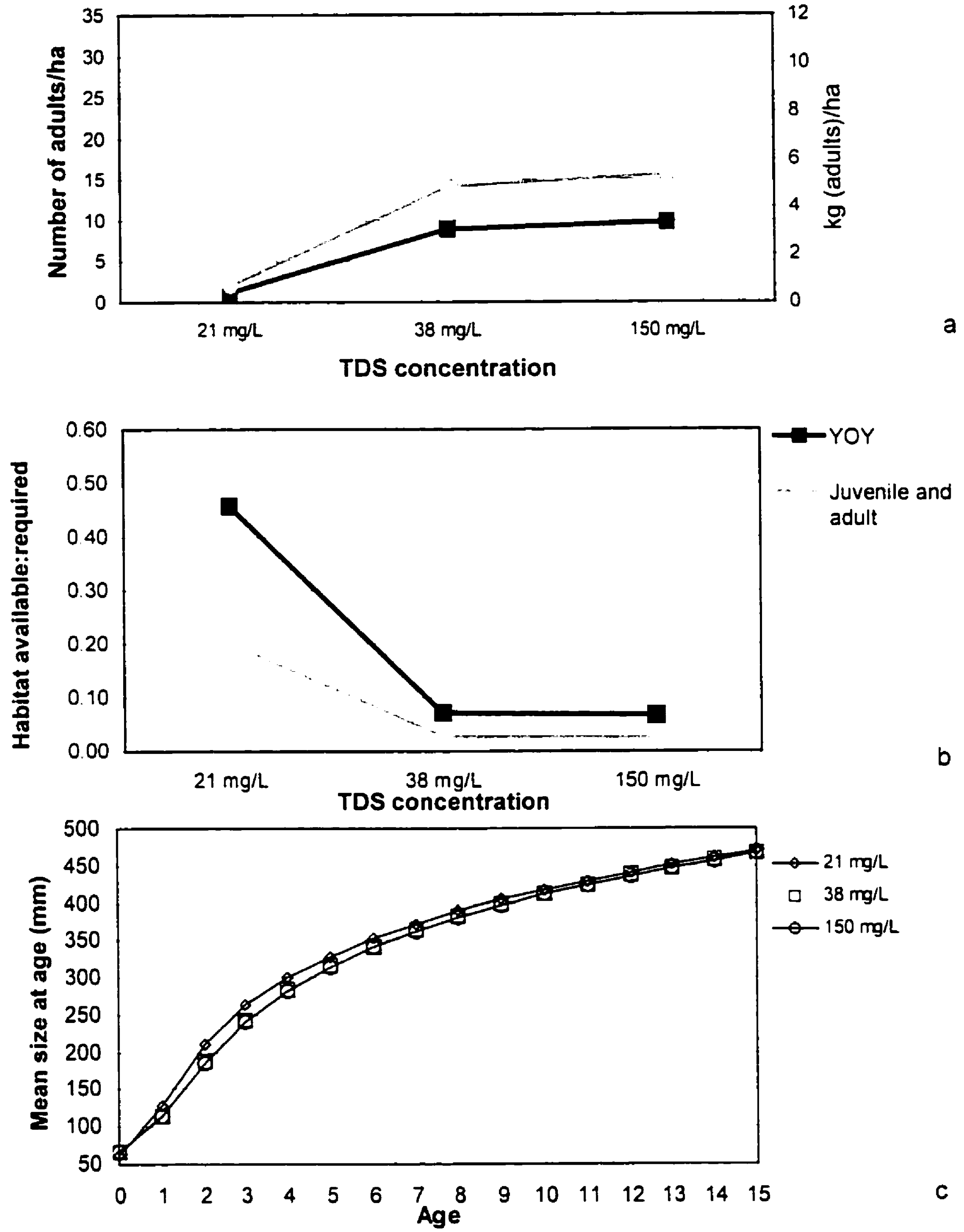


Figure 2.18: Effects of different total dissolved solids concentrations [TDS] on smallmouth bass density (squares) and biomass (circles) (a), YOY and, juvenile and adult

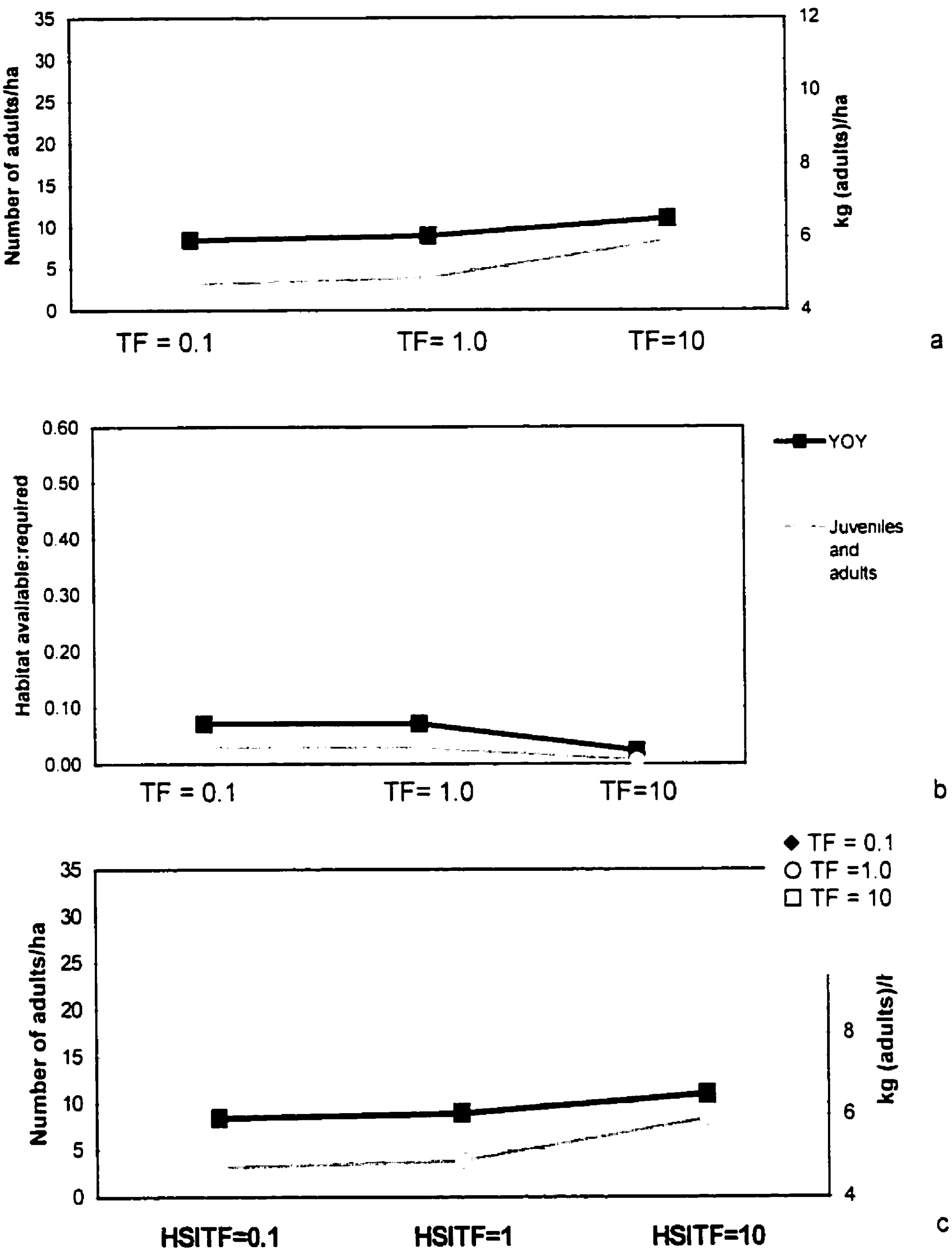


Figure 2.19: Effects of different TF values on smallmouth bass density (squares) and biomass (circles) (a), YOY and, juvenile and adult habitat available:required (b) and mean length at age (mm) (c).

TF value

Nest densities were 0.09-0.25, 0.37-0.41 and 0.42-0.43 nests/100m^2 in the six sites at TF values of 10, 1 and 0.1 respectively. Changes in the density of nests in response to HSI (Figure 2.8) had a small effect on the numerical and biomass densities. The size at age decreased at the highest TF value (Figure 2.19).

Lake size

Nonmontonic changes in numerical density with lake size warranted extra simulations using the 30th and 70th percentile (54 and 253 ha) lake sizes in Ontario. Using all five lake sizes, smallmouth bass density was consistent until somewhere in the interval of 253 and 990.5 ha (Figure 2.20). Further analysis revealed that the number of adults/km of shoreline and kg (adults)/km of shoreline was positively and linearly related to lake size (Figure 2.21). Smallmouth bass were smaller in the largest lakes (Figure 2.21).

Mean depth and mean monthly windspeed

At mean depths of 2.1 m, 5.7 m (control) and 13.1 m, the thermocline depth was 5.2 m, 6.3 m and 7.6 m respectively. Changing the mean depth had little effect on the numerical or biomass density and growth (Figure 2.22). Windspeed at the range of lake sizes used in the simulation (16 ha –990.5 ha) also had little effect on any of the model outputs (Figure 2.23).

P value

Changing the P-value had no effect on the numerical density but the biomass density increased 2.3 times with a 4 times increase in P (Figure 2.24a). P value also had a strong positive relationship with size at age. P-values of 0.25 versus 1.0 produced a length difference of almost 10 cm in the older age class (Figure 2.24).

Increasing nesting versus juvenile/adult habitat supply

Adult numerical and biomass densities increased several-fold as nesting habitat increased from 25% to 150% of the control but niether density was affected by changes in the supply of juvenile/adult habitat (Figure 2.25).

YOY crowding stayed constant as the supply of both the nesting and juvenile/adult habitat changed. (Figure 2.26a and b). Juvenile/adult crowding increased 4.8-fold as nesting habitat area increased 6 times (Figure 2.26a). Increasing the juvenile/adult by six

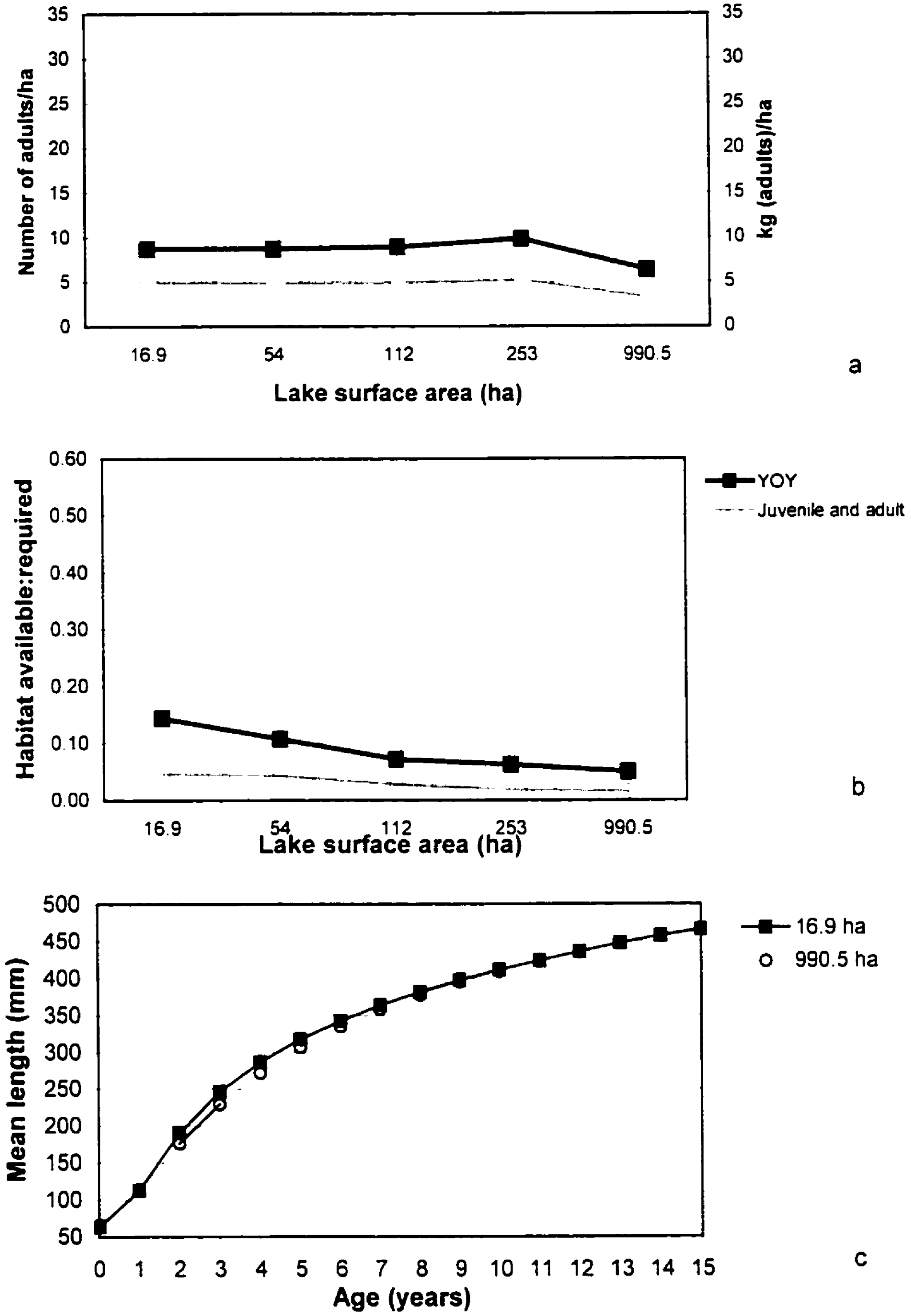


Figure 2.20: Effects of lake size on smallmouth bass density (squares) and biomass (circles) (a), YOY and, juvenile and adult habitat available:required (b) and mean length at age (mm) (c).

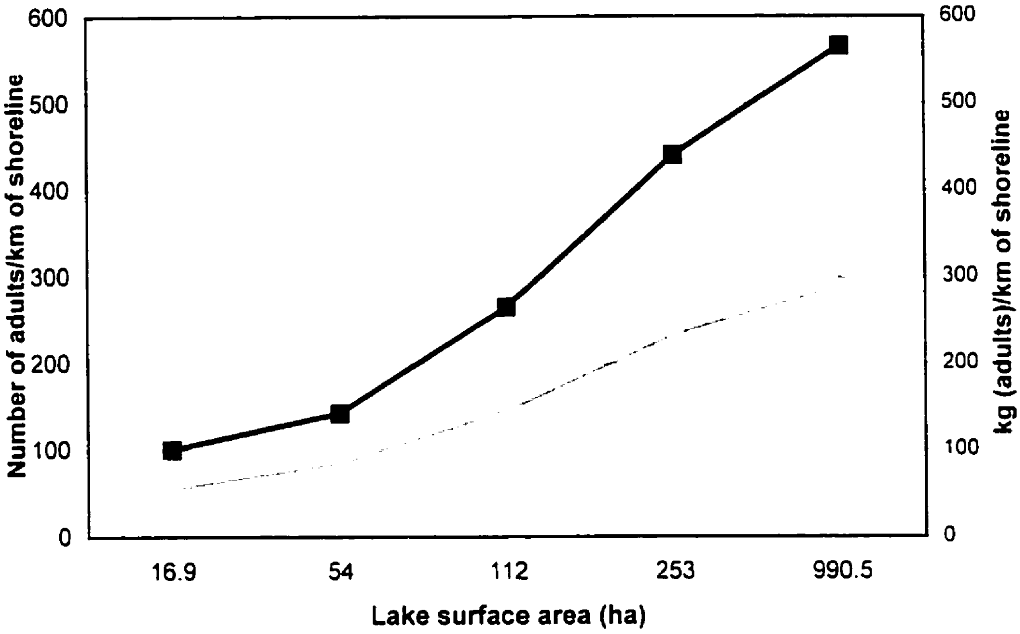


Figure 2.21: Effects of lake size on the number of adults/km (squares) and biomass (circles) of shoreline.

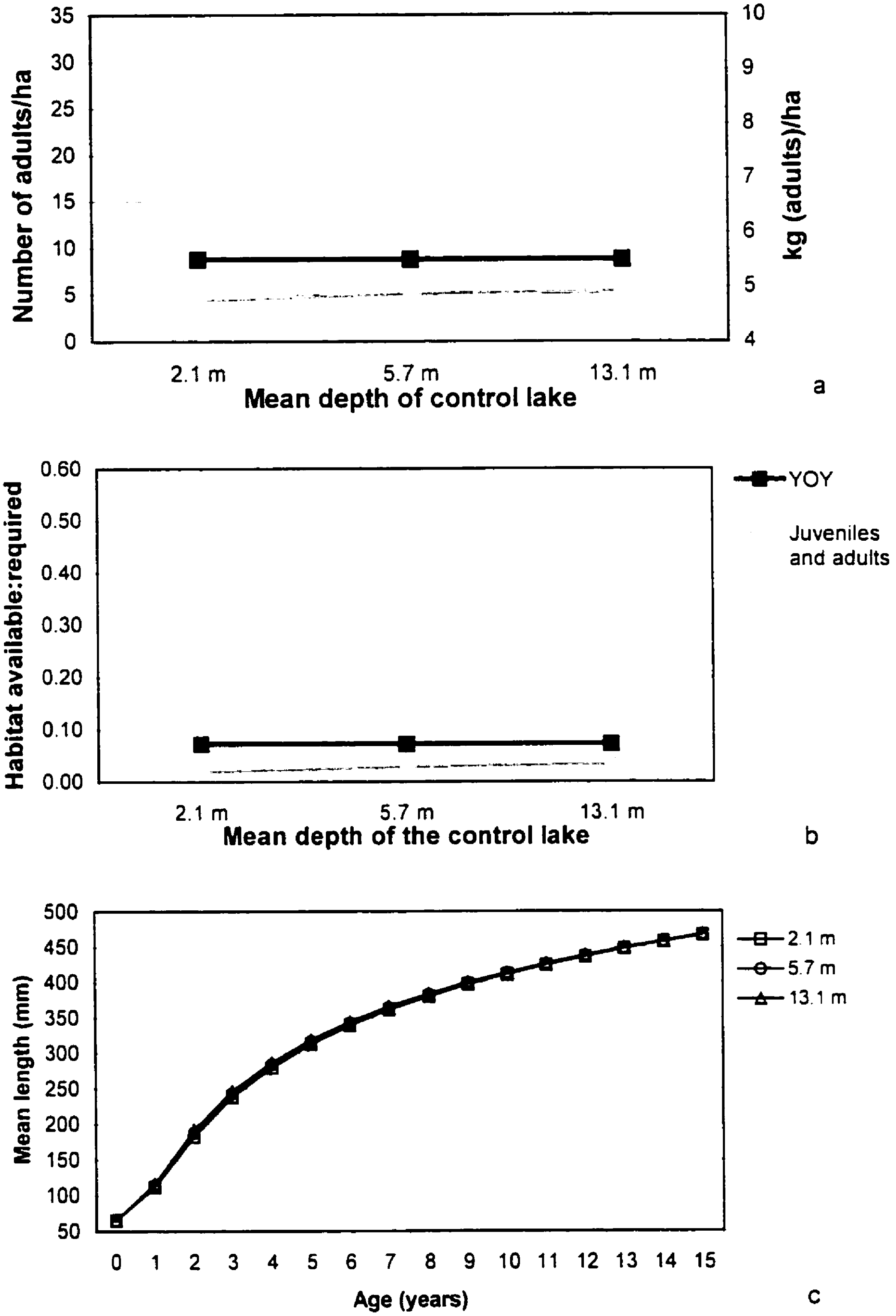


Figure 2.22: Effects of changes in mean depth on smallmouth bass density (squares) and biomass (circles) (a), YOY and, juvenile and adult habitat available:required (b) and, mean length at age (mm) (c).

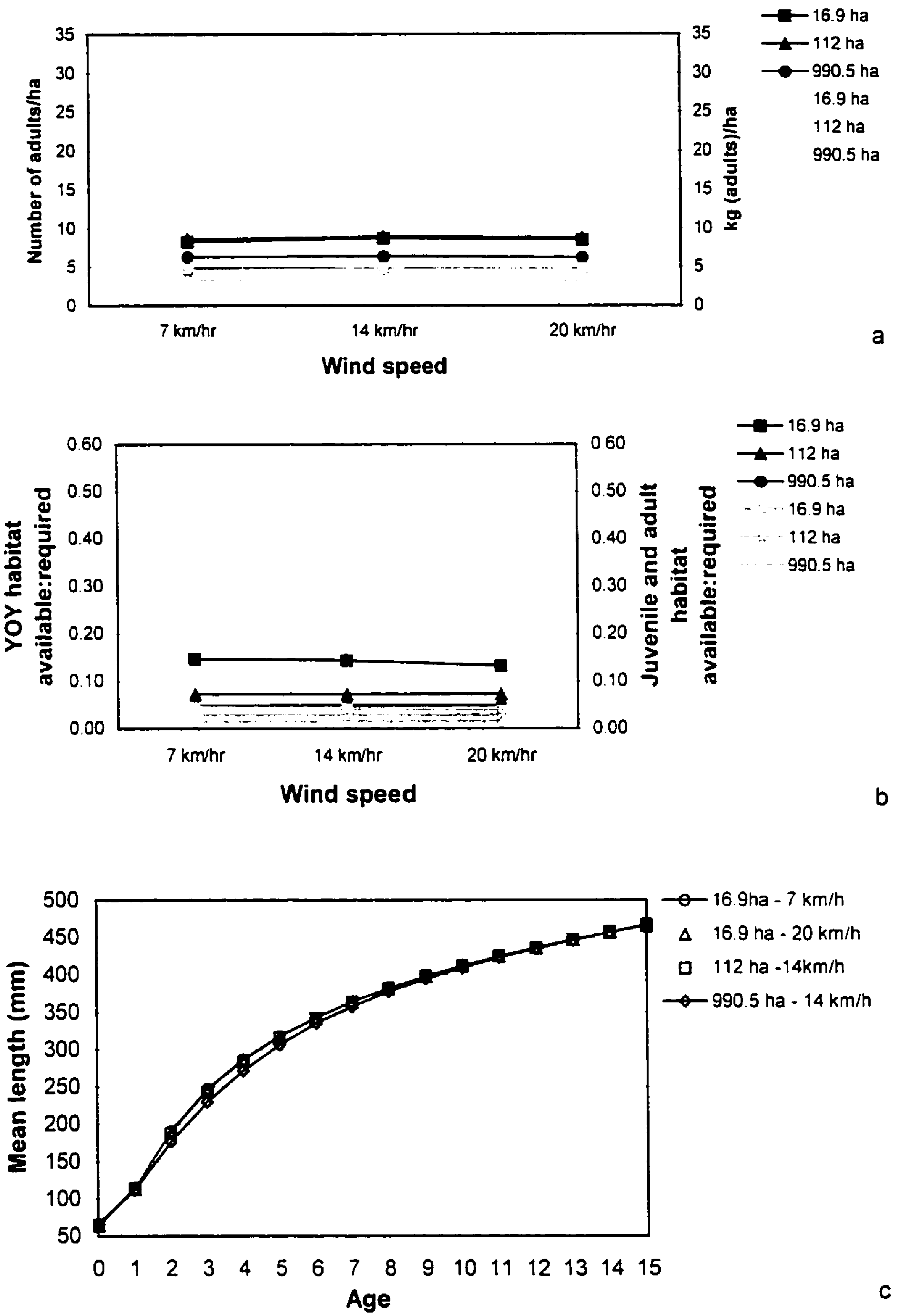


Figure 2.23: Effects of mean monthly windspeed (km/h) on smallmouth bass density (filled-in) and biomass (open) (a), YOY (black) and, juvenile/adult habitat (grey) available:required (b) and, mean length at age (mm) (c).

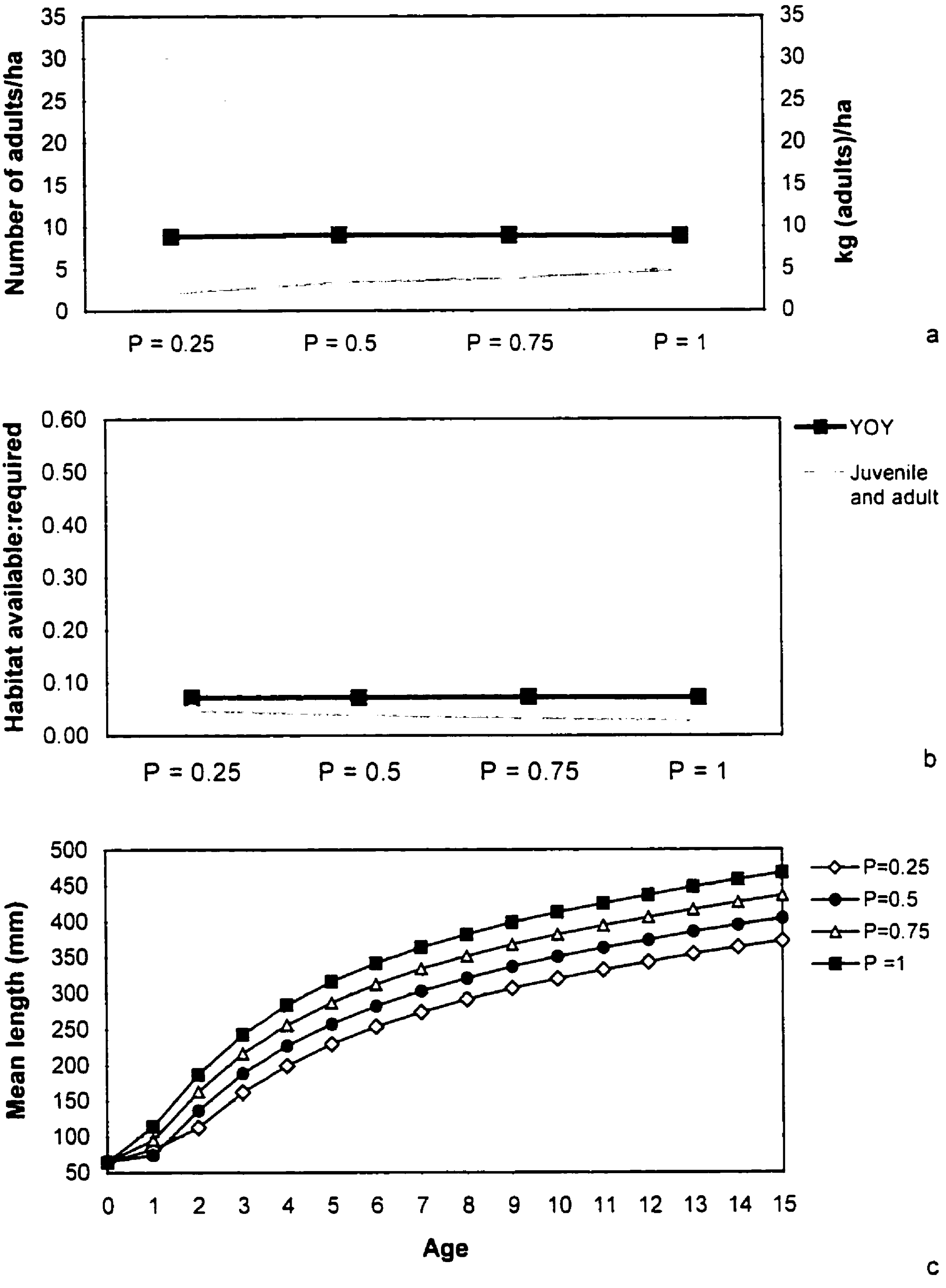


Figure 2.24: Effects of different P values on smallmouth bass density (squares) and biomass (circles) (a), YOY and, juvenile/adult habitat available:required (b) and, mean length at age (mm) (c).

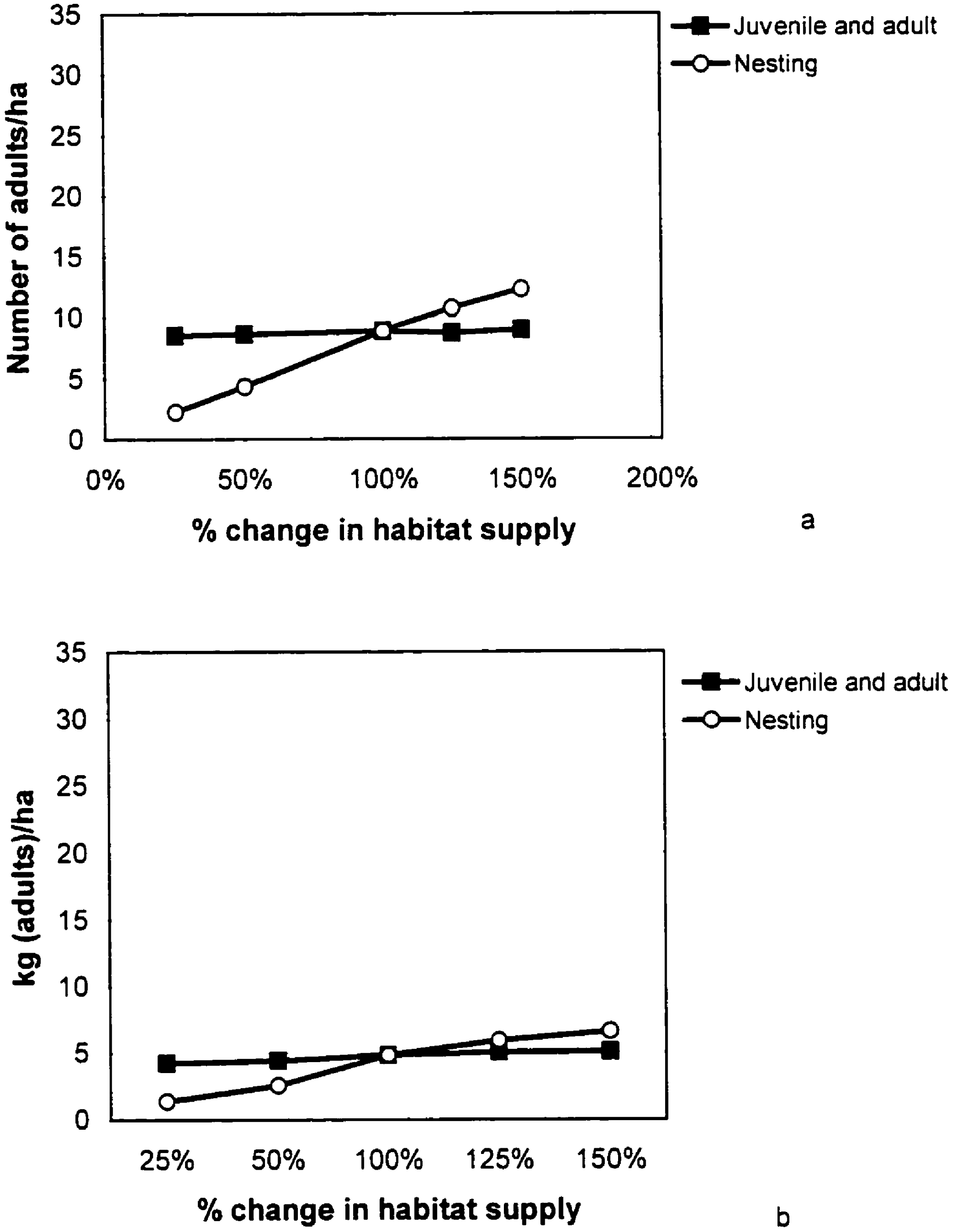


Figure 2.25: Effects of changing the habitat supply on the density (a) and biomass (b) of smallmouth bass populations in the control lake.

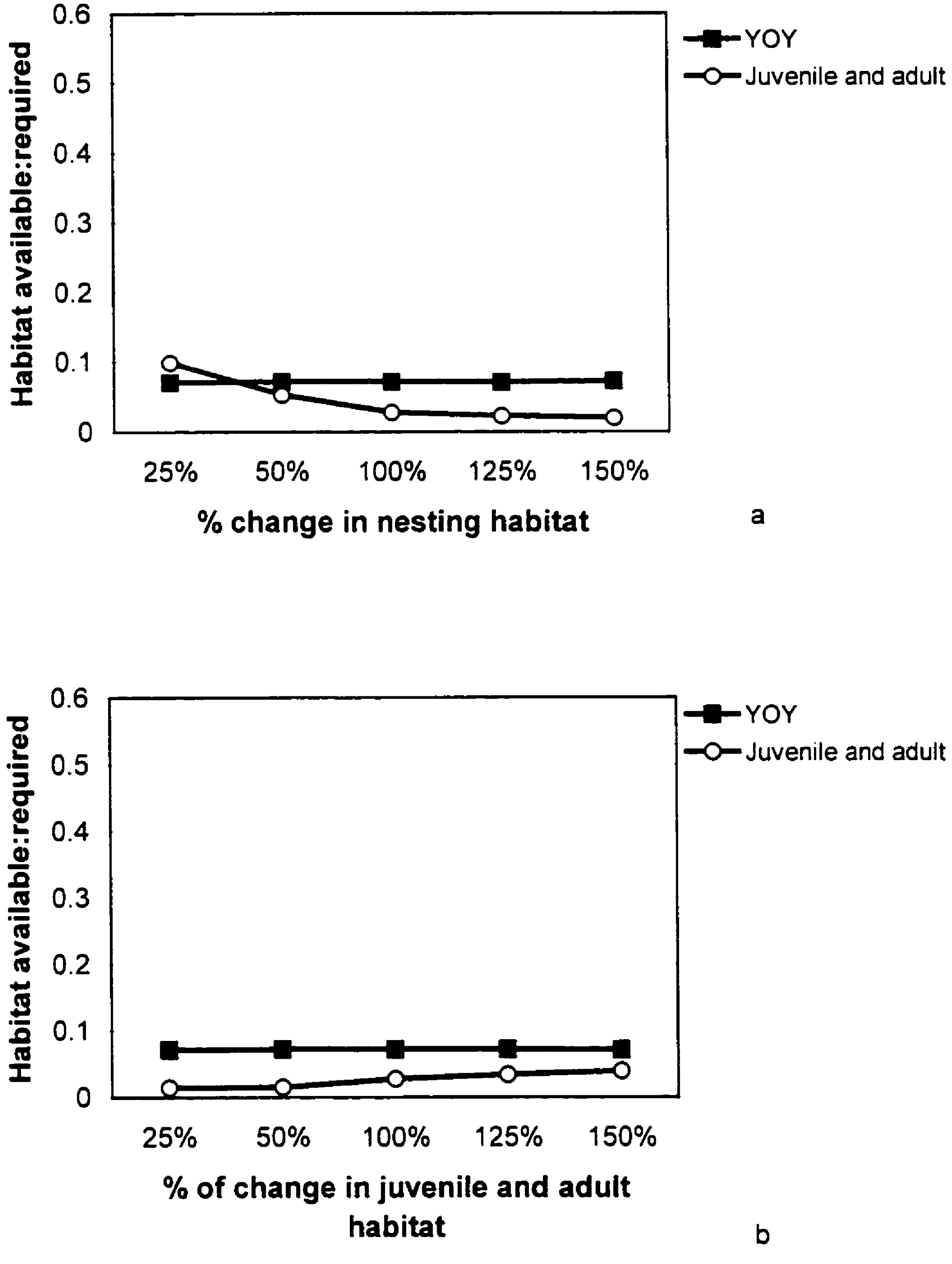


Figure 2.26: Effects of changing the nesting habitat supply (a) and, the juvenile/adult habitat supply (b) on the YOY and juvenile/adult habitat available:required.

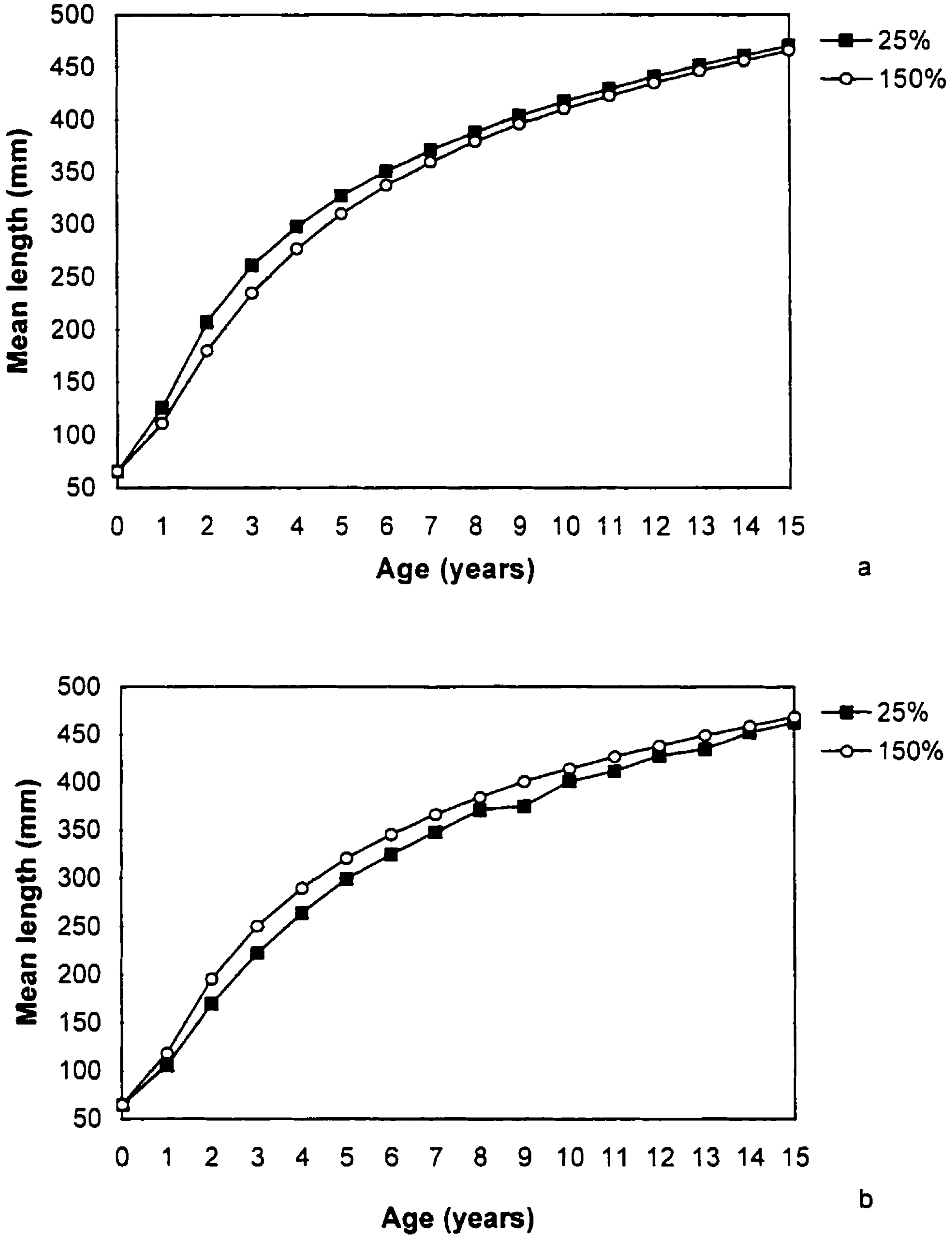


Figure 2.27: Effects of changing the nesting habitat supply (a) and the juvenile and adult habitat supply (b) on mean length at age. For easier interpretation, only the mean lengths at age for the 25% and 150% habitat supplies are provided.

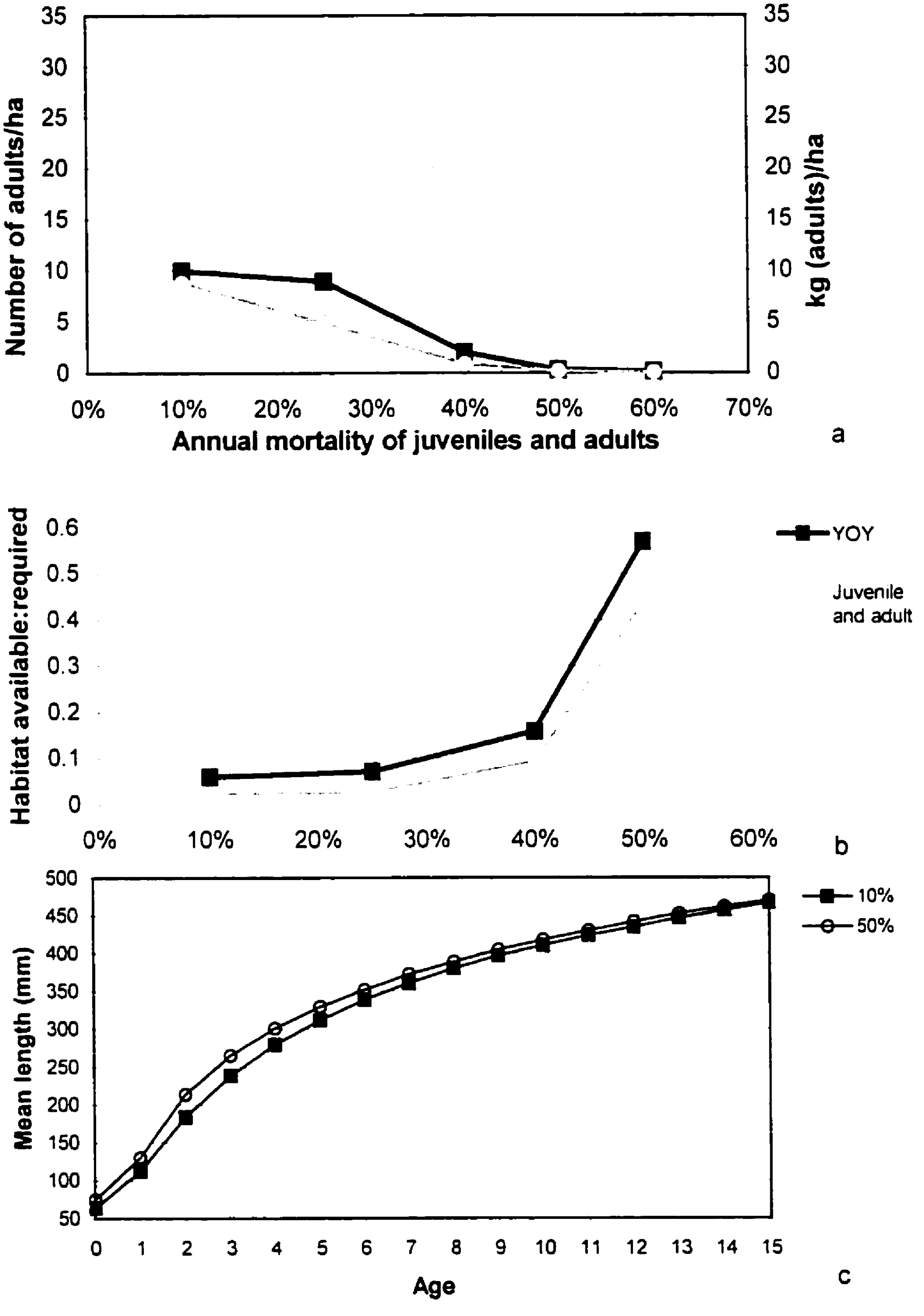


Figure 2.28: Effects of changing annual mortality on smallmouth bass density (squares) and biomass (circles) (a), YOY and juvenile/adult habitat available:required (b) and, mean length at age (mm) (c). For easier interpretation only the mean lengths of the 10% and 50% are shown.

times habitats decreased the juvenile/adult crowding by 2.6 times. As nesting habitat increased mean length decreased for all ages. In contrast, length at age increased as the supply of adult habitat increased (Figure 2.27).

Annual mortality

Changes in annual mortality had dramatic effects on densities (Figure 2.28). At mortality levels of 60% the smallmouth bass populations went extinct. As mortality increased, mean length at age decreased as a result of reduced density.
This is more evident throughout the earlier ages (Figure 2.28c).

2.5.5. Discussion of sensitivity analyses

Control population

Results of the control simulation validate the accuracy of the model outputs. Nest densities calculated by the model (0.37 - 0.41 nests/100m^2) fell within the range of nest densities in Ontario, 0.01 – 0.43 nests/100m^2 (Witzel unpublished data 1988; Harker 1982). Numerical and biomass densities (8.89 adults/ha and 4.86 kg/ha, respectively) were also within the range of densities seen in wild smallmouth bass populations in eastern North America, 0.74 -164adults/ha and 0.52-82.90 kg/ha (Carlander 1977). North American data were used for these comparisons since they are readily available in the primary literature while data from only a few lakes in Ontario are available. Mean length at age was slightly higher than the North American average (Figure 2.14). However the growth computed by the model is within the growth range seen in natural populations.

The ratios of habitat available:required for both the YOY and, juveniles and adults were less than 0.10. This indicates that smallmouth bass populations can sustain a substantial degree of overlap in their home ranges. Using the habitat characteristics of the control lake, maximum growth can be calculated for each age when juveniles and adults occupy non-overlapping home ranges. Comparing this growth curve to the actual growth curve of the control population, we can see the negative effects of density on smallmouth bass growth (Figure 2.29). The upper limit of numerical density in North America (164 bass/ha) suggests that wild populations do support considerable crowding in their home ranges.

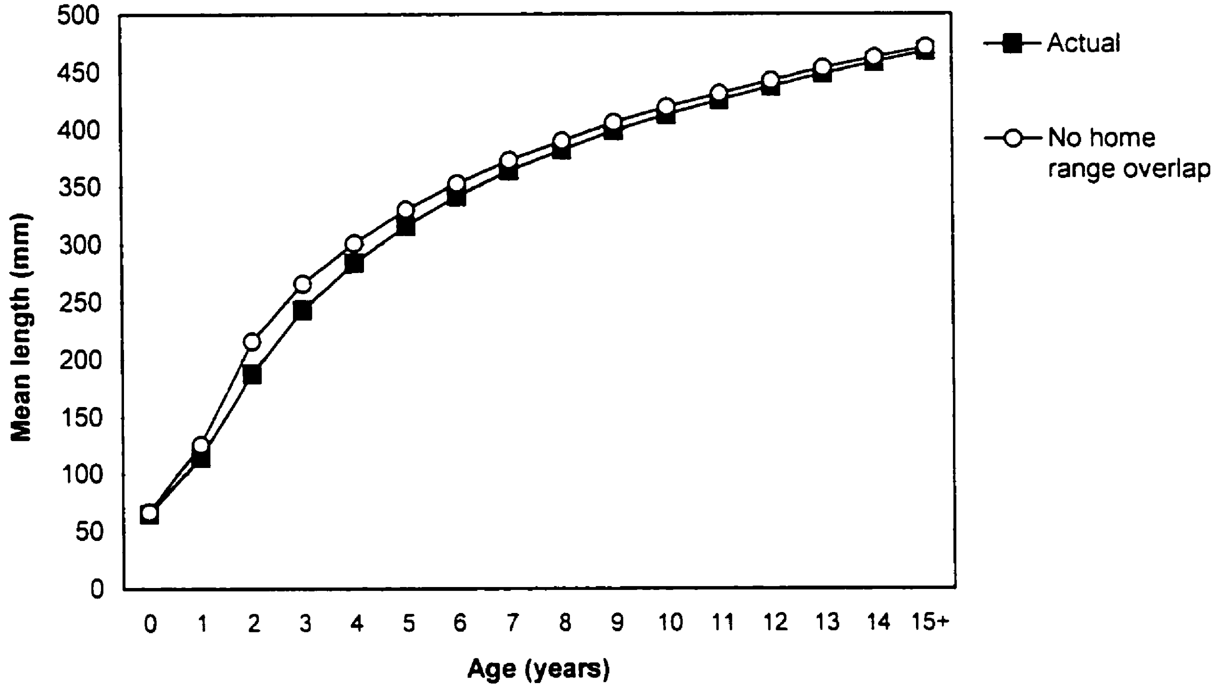


Figure 2.29: Smallmouth bass growth in control lake with (actual) and without (no home range overlap) density-dependent effects.

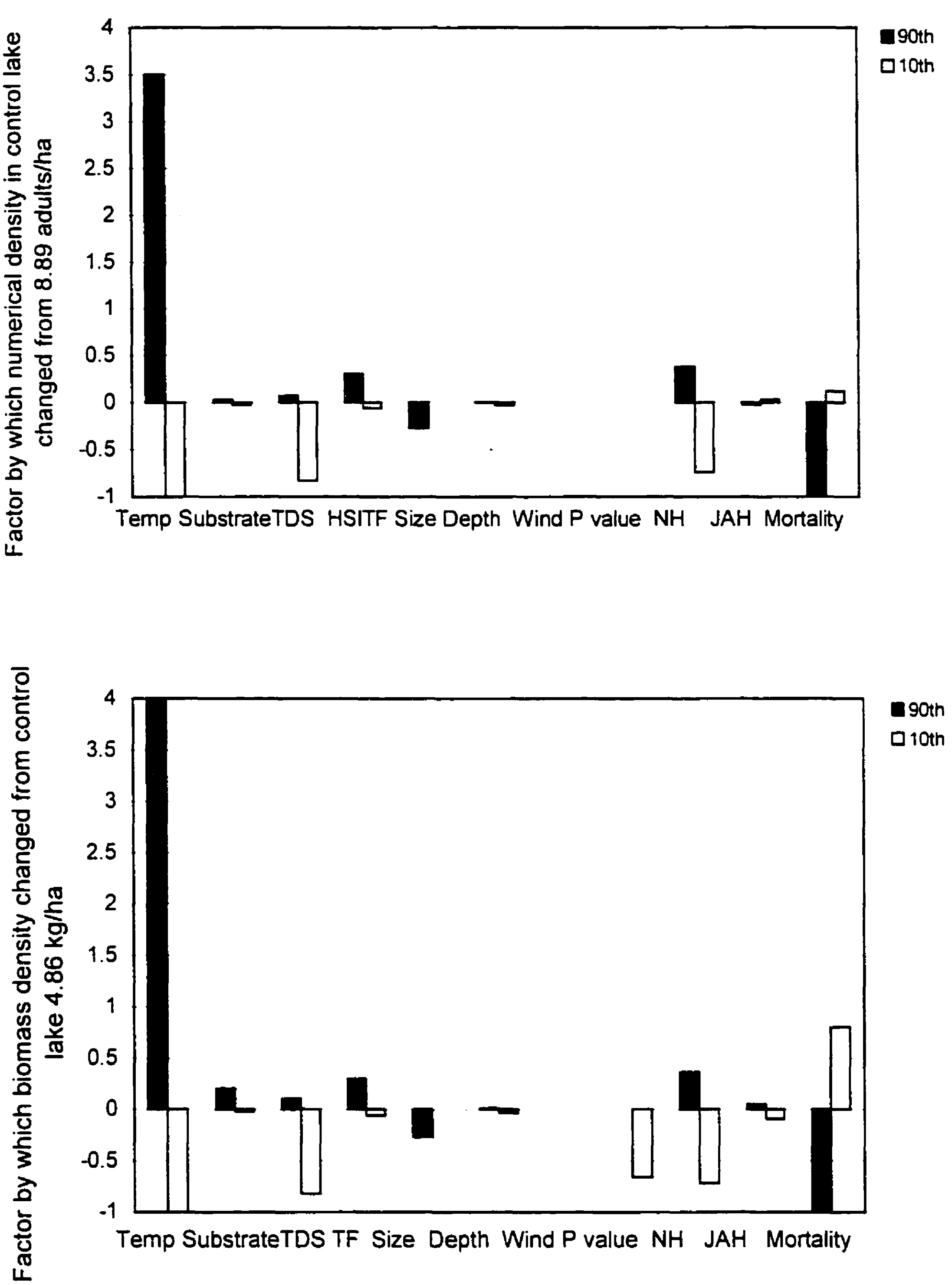


Figure 2.30: Sensitivity of model to habitat variable inputs. Zero represents the control numerical and biomass densities. Inputs having a negative effect are shown as <0, to calculate the actual value of these variables use control*(1- graph value). Temp= mean annual air temperature, Size= lake size, Depth= mean depth of control lake, Wind= mean monthly windspeed, NH=nesting habitat supply, JAH= juvenile/adult habitat supply. For substrate 10th and 90th=substrate composition A and C. For nesting and juvenile/ adult habitat supply, 10th and 90th=25 and 150%. For P value 10th=0.25 and 90th=control and for mortality 10th=60% and 90th=10%.

Summary of sensitivity analysis

Increasing the mean annual air temperature, [TDS], area available for nesting and decreasing mortality all increased the numerical and biomass densities of smallmouth bass in the control lake (Figure 2.30). Temperature had the greatest effect on numerical density. Warmer temperatures increased the density of smallmouth bass in the control lake while cold temperatures led to extinction in the control lake. An annual mortality of 60% for the juveniles and adults also led to population extinction. Mean depth and windspeed had no effect on numerical density in the control lake. However, greater mean depths did increase the size of the smallmouth bass in the control lake. A lower P value decreased the biomass density in the control lake but had no effect on numerical density (Figure 2.30).

Temperature

Temperature had the greatest effect of any model parameter on smallmouth bass population dynamics (Figure 2.30). The numerical and biomass densities were both positively correlated with temperature (Figure 2.15). However, higher temperatures affected the YOY and juveniles/adults differently. Mean YOY length at the end of the growing season increased from 65 mm to 97 mm with the increase in temperature whereas juvenile/adult growth was negatively related to temperature. Increasing the mean annual air temperature lengthens the ice-free season and produces warmer water temperatures. For the YOY, this leads to shorter development times and a longer summer growth period resulting in larger individuals at the end of the season. Since mortality is calculated daily while on the nest and, as a function of size after dispersal (See 2.4.3. Nesting mortality), shorter development times and faster growth also result in higher survival throughout the summer and first winter. Therefore more individuals are recruited to the juvenile/adult population. As the density increases the aforementioned density-dependent effects reduce the growth rates for the juveniles and adults.

However, in nature, southern populations are larger than their northern counterparts (Figure 2.31). This suggests that the model is overestimating the density-dependent effects on growth at higher temperatures and equation 18 should be modified to improve the model's performance. A preliminary investigation of this revealed that modifying the density-dependent equation from:

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

to:

$$G_{ACT} = G_{MAX}(AA^{0.5}) / (AA^{0.5} + 0.0101(THR^{0.5}) \qquad (25)$$

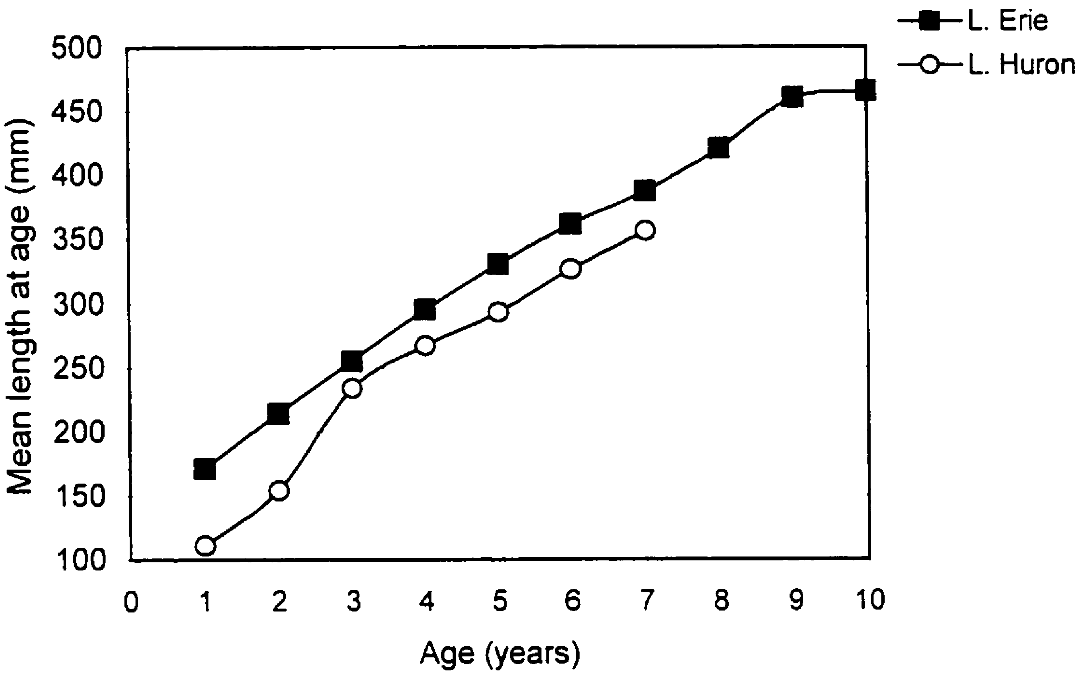


Figure 2.31: Mean length at age (mm) of a southern population (L. Erie) and a northern population (L. Huron) of smallmouth bass demonstrating the effects of different thermal environments on smallmouth bass growth (Carlander 1977).

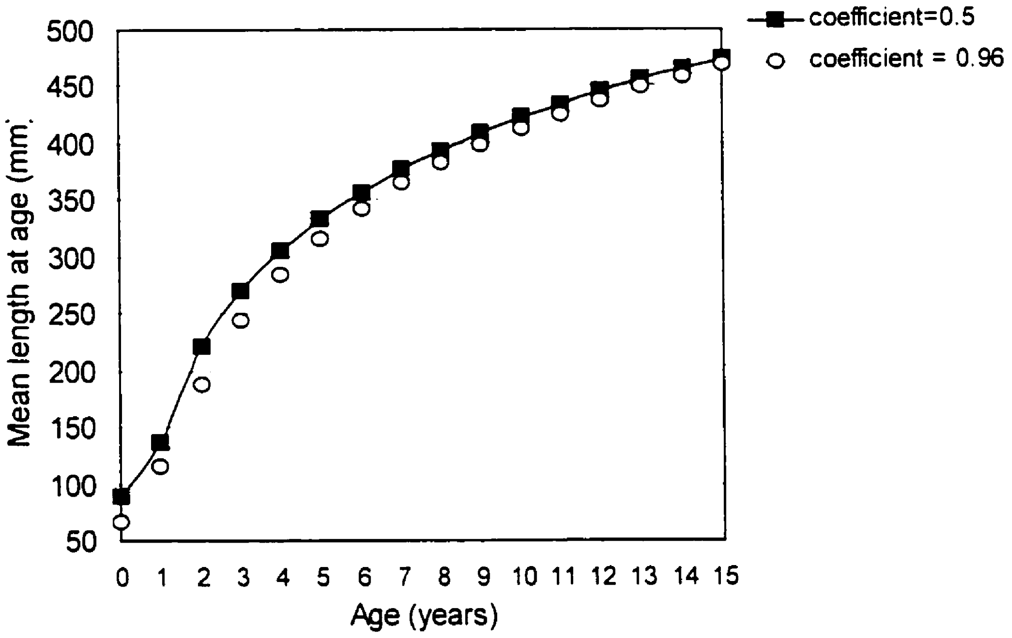


Figure 2.32: Mean length at age (mm) when a density coefficient of equation 18 is altered to reflect the observed growth of natural populations at high mean annual air temperatures (7.12 °C).

produces mean lengths at age that resemble the temperature effects observed in natural populations (Figure 2.32).

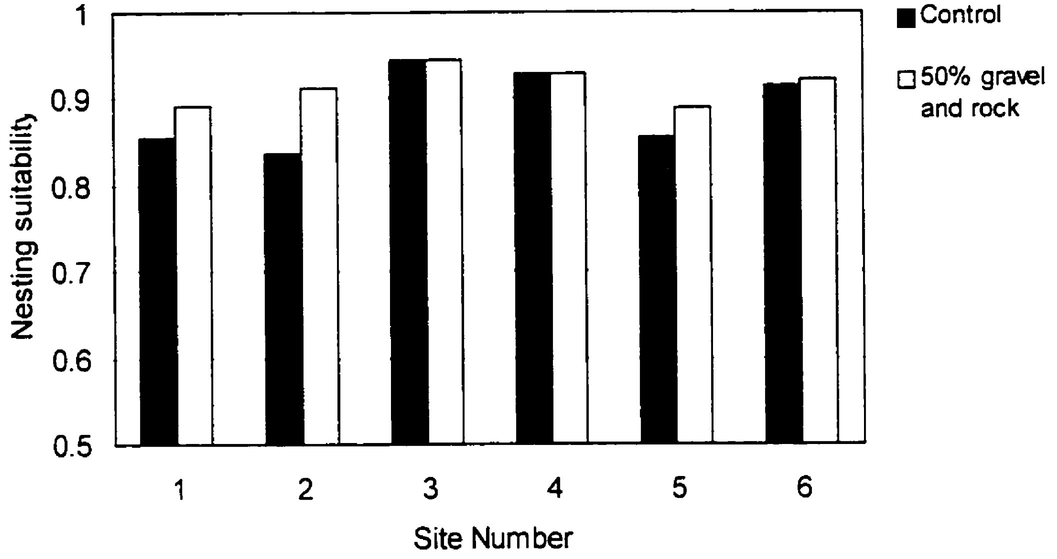
Substrate composition

Smallmouth bass are known to spawn on sand, gravel and rock substrates (Coble 1975; Wiegmann et al. 1992). In recognizing the importance of these substrates to smallmouth bass and other freshwater species, many habitat rehabilitation projects involve depositing gravel and rock substrates in littoral areas (Environment Canada 2000). However, our results suggest that introducing these substrates may have no positive effect on the suitability of these areas for smallmouth bass nor do they increase the long-term numerical and biomass densities of smallmouth bass in the lake (Figure 2.17).

The fact that densities and growth were not affected by modelled changes in substrate composition suggests that the range of substrate compositions in our sample of Ontario lakes are not varied enough to affect smallmouth bass population dynamics. Perhaps more extreme changes in substrate such as those seen in habitat rehabilitation projects where gravel and rock are introduced to entire shorelines will yield a different result. To investigate this, a simulation was performed in which 50% of the non-gravel and rock substrates in each site were removed and replaced with 25% gravel and 25% rock. This simulation yielded higher nesting and juvenile/adult suitabilities for each of the sites (Figure 2.33) but did not affect the long term numerical and biomass density in the control lake. This suggests that although substrate is important in determining the spatial distribution of nests and juveniles/adults, its effects are overwhelmed by the effects of temperature and density on growth and survival.

Total dissolved solids

Lower [TDS] decreased the numerical and biomass density in the control lake (Figure 2.18). [TDS] is a measure of food availability and is used to calculate P for the YOY (See Productivity and prey abundance). The nonlinearity of the numerical and biomass densities (Figure 2.18) reflects the pattern of the [TDS] versus observed/expected growth used to relate [TDS] to YOY growth (See 2.2.7. Productivity and prey abundance; Figure 2.7). As more YOY survive at higher [TDS] due to improved growth, recruitment into the population increases and the density-dependent effects on growth can be seen in the smaller size of the juveniles and adults. Friesen (1998) found that smallmouth bass YOY fed twice as much food as their counterparts, grew at a rate of 1.85 mm/day versus 1.66



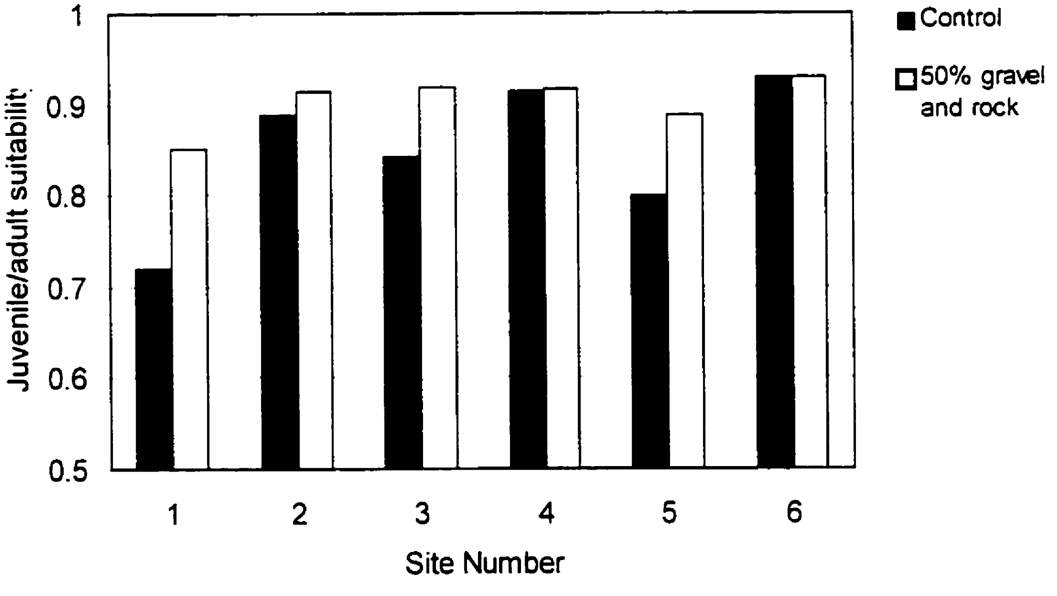


Figure 2.33: Substrate suitability for nesting and juveniles/adults in six sites of the control lake after 50% of non-gravel and rock substrates are replaced with 25% gravel and 25% rock. This simulation was performed to investigate if restoration projects that introduce gravel and rock to stretches of lake shorelines actually improve smallmouth bass stocks.

mm/day for the controls.

TF value

Numerical and biomass densities were positively related to the TF value (Figure 2.19). This can be attributed to the higher survival of the YOY at lower nest densities. Having fewer nests results in fewer YOY competing for resources within a site, therefore increasing nest densities and subsequently YOY densities in the control lake will result in fewer YOY recruited to age 1. YOY data from three studies were used to determine if this pattern also exists in nature (Neves 1975; Serns 1984; Friesen 1998). In all studies egg or YOY abundance were negatively related to percent survival (Figure 2.34). Although these studies were not a direct measure of density effects on YOY to age 1 they do indicate that the model is correctly relating YOY survival to YOY density.

Lake size

A lake size decrease to 16.9 ha had little effect on the density of smallmouth bass in the control lake however an increase to 990.5 ha from 253 ha decreased the density of smalllmouth bass in the control lake (Figure 2.20). Adults/ha decreased at a lake size of 990.5 ha because the usable habitat represented a smaller portion, 20%, of the total surface area of the lake compared with 40 - 88% of the total surface area in the smaller lakes. Therefore although the smallmouth bass abundance increased in the large lake, the density decreased because an increasing proportion of the total lake area was uninhabited.

Concomitant with lake size increases was an increase in the numerical (adults/km of shoreline) and biomass (kg (adult)/km of shoreline) densities (Figure 2.21). The effects of lake size are different using adults/km of shoreline because the area of the juvenile/adult habitat does not increase in proportion to the increase in the lake perimeter. This is due to the thermocline depth decreasing nonlinearly with increased lake size (See 2.2.4. Depth).

Mean depth

Increasing mean depth had no effect on smallmouth bass numerical density but did increase the biomass density (Figure 2.22). Increasing the mean depth lowered the thermocline depth thus expanding the juvenile/adult habitat area (See 2.2.4. Depth suitability for juveniles and adults). This increased the foraging area and decreased the density within the juvenile/adult habitat so fish grew larger and thus, biomass density increased.

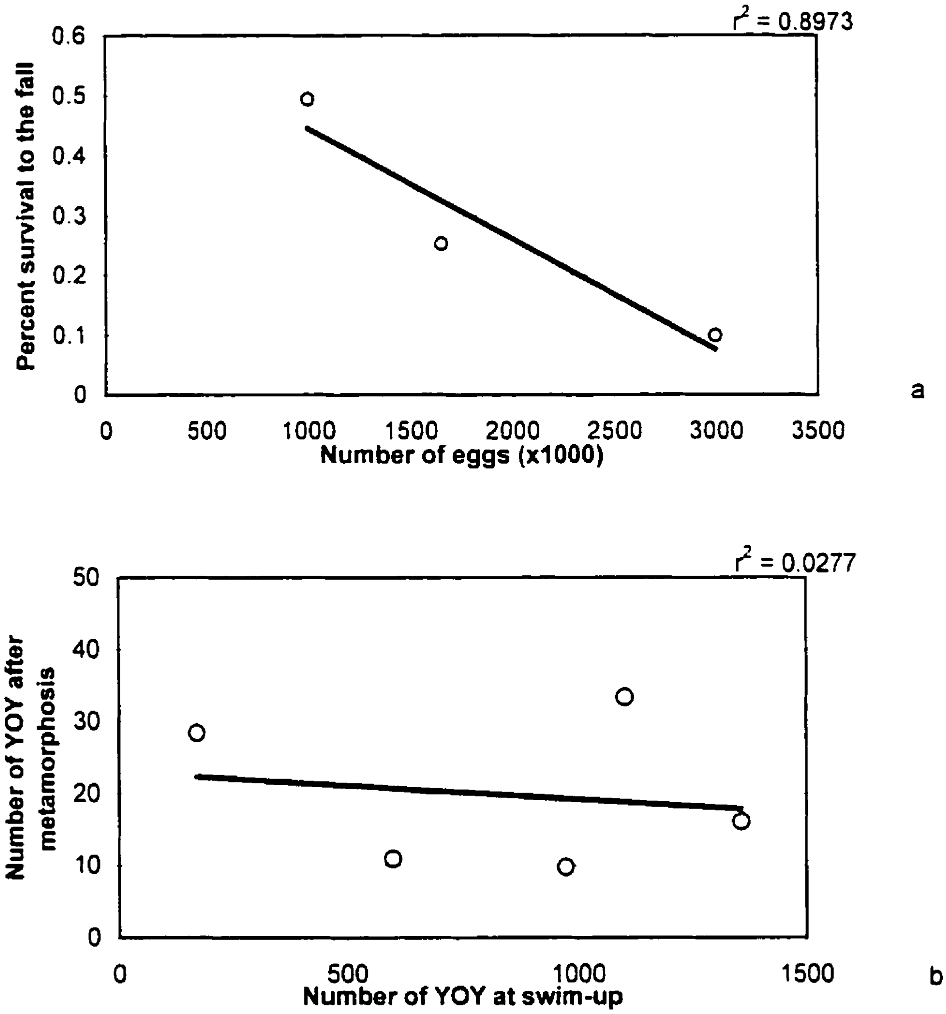


Figure 2.34: Results of three studies indicating the negative effect egg or YOY density has on YOY survival. a) Total number of eggs deposited in Nebish Lake in 1979-1981 versus number of YOY surviving to the fall (Sems 1984). b) Number of YOY present at first feeding in Jones Bay, Lake Opeongo versus number of YOY surviving after metamorphosis (Friesen 1998).

Mean monthly windspeed

Increasing the mean monthly windspeed in the different sized lakes did not affect the numerical and biomass density of smallmouth bass (Figure 2.23). In the model, windspeed influences the suitability of the sites for nesting (See 2.3.5. Wave action). For all three lake sizes, windspeeds were not powerful enough to negatively affect nesting suitability. In larger lakes, the negative effects of wave action on nesting suitablity become apparent (See Chapter Three*)*.

P value

As with mean depth, changing the P value altered the size and biomass density of the control population. At lower P values biomass density decreased but numerical density did not change (Figure 2.24). In natural populations P may decrease due to an increase in adult density or a shortage in the food available. These can both lower consumption and as consumption decreases, growth decreases.

Amount of nesting versus juvenile/adult habitat area

Increasing the nesting versus juvenile/adult habitat area had opposite effects on smallmouth bass numerical and biomass densities and size (Figure 2.25). Increasing the juvenile/adult habitat supply had no effect on density whereas increases in the nesting habitat available increased density. This indicates that changes in the abundance of nesting habitat can have a severe impact on smallmouth bass populations. In terms of conservation or restoration, increasing the area available for nesting that is, the area between 0.5 m and 2.5 m deep in a lake will increase population densities provided juvenile and adult mortality does not change.

The results of this and some of the other simulations suggest that a larval bottleneck exists in smallmouth bass populations. With a YOY bottleneck resources at a single point in time influence a cohort's abundance for the rest of its life (Shuter 1990). In this simulation increasing the area for nesting and YOY growth increased population densities. A YOY bottleneck is also demonstrated in the [TDS] simulation where higher productivity in the YOY habitat enhanced YOY growth and subsequent survival. This led to a 20% increase in population density (Figure 2.18). In the temperature simulation, increased YOY survival led to a 350% increase in numerical density (Figure 2.15). Temperature during the first year of life has been widely accepted as one of the most important variables affecting abundance of a cohort at adulthood (Shuter et al. 1980; MacLean et al. 1981; Rejwan et al.1999). These findings suggest that smallmouth bass conservation or restoration should focus on the nesting habitat and/or habitat features that improve YOY survival.

Mortality

Total mortality in the Great Lakes and smaller lakes in Ontario averages approximately 57% per year (Coble 1975). With this level of mortality, our model predicts population sizes that are much lower than those actually observed in nature (Figure 2.28) (Shuter et al. 1987; Ryan et al 1999). This discrepancy may be due to the structure of the mortality component of the model.

The model assumes a constant mortality rate once fish reach age 1. Coble's (1975) estimate refers to a combination of natural and harvest mortality. Data from Lake Erie indicate that harvested fish are on average age 3 and older (MacGregor and Witzel 1984). In Lake Opeongo harvested fish are on average ≥ age 5 (Shuter et al. 1987). These examples imply that the 60% mortality for all fish ≥ age 1 (in the model) is underestimating survival in the earlier years of life because it incorrectly assumes the fish age 1 and 2 are subject to fishing mortality. The mortality model should consider the age of recruitment into the fishery and modify the mortality rate accordingly. Therefore in Lake Erie for example, mortality for age 1 and 2 should be 25% while fish ≥ age 3 have mortality set to 57%. This would produce higher estimates of population size and explains why populations can sustain such high levels of mortality.

2.6. IMPLICATIONS FOR SMALLMOUTH BASS POPULATIONS AND CONSERVATION

Habitat alterations that led to higher YOY survival (increased temperature, [TDS] and absolute nesting area) increased smallmouth bass densities, hence adult abundance is largely determined by survival of the YOY.

Our findings are consistent with Minns et al. (1991); habitat restoration projects must take into account the habitat supply and demand being placed by the fish population. Our substrate composition findings particularly highlight a potential problem with some conservation efforts today. The addition of gravel and rocks to areas in a lake may improve the short term habitat quality in some areas of the lake but may have little effect on the long-term numerical and biomass density of smallmouth bass in that lake.

Habitat alterations that improved the survival of the YOY for example, increased temperature, [TDS] and nesting area substantially increased population densities. This suggests that conservation or restoration efforts should focus on improving the nesting habitat. This can involve introducing shelters to areas impacted by detrmental wave action such as those seen in Outer Bay of Long Point Bay (Chapter Three). Introducing fill to areas of a lake can increase the amount of available habitat for nesting by increasing the area between 0.5 and 2.5 m deep. To increase the smallmouth bass density without altering habitat, annual mortality should be regulated by setting catch limits, size limits or enforcing catch and release practices.

Chapter Three
Validation of the smallmouth bass habitat model

Abstract

A technical error occurring in the implementation of the ideal free distribution of the nesting males and juveniles/adults is first discussed. Preliminary analysis showed that this error does not affect the predicted population density of smallmouth bass in a lake but does lead to an incorrect distribution of nests and juveniles/adults. Consequently, comparisons of predicted versus observed nest and juvenile/adult densities in different sites of Lake Opeongo and Long Point Bay, Lake Erie were not performed in the model validation.

The smallmouth bass habitat model was validated using nest density, catch and creel data from Lake Opeongo, Ontario and Long Point Bay, Lake Erie. Simulations were performed using the habitat characteristics that describe these systems. These simulations showed that the calculated nesting and juvenile/adult suitabilites are positively related to observed nest densities and CUE data, respectively, but the relationships were not strong in either lake. Mean lengths at age were within those normally seen in the smallmouth bass populations of both lakes.

The model overestimated the nest densities in both systems. This may be attributed to the model incorrectly describing the effects of density on nesting and overestimating the potential number of males available for nesting. The model uses descriptions of density effects from a pike habitat model since the exact pattern of density effects on smallmouth bass is unknown due to a lack of information. The results of these simulations provide an estimate of the direction of error and indicate how the model can be improved. The simulations demonstrate how the model can be applied to different lake systems. The results and discussion indicate how components of the model can be improved to better describe habitat effects on smallmouth bass populations.

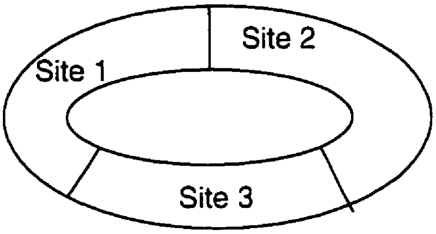
3.1. ERROR IN IDEAL FREE DISTRIBUTION

Sensitivity analysis of the TF component of the nesting sub-model (Chapter Two) indicated that an error was occurring in the implementation of the ideal free distribution of nesting males and the juveniles/adults. To explain the error, a diagrammatic representation is provided using a lake that has only three sites each having the same area available for nesting, that is, 2000 m^2 (Figure 3.1). Site 1, 2 and 3 have suitabilities of 0.92, 0.91 and 0.84, respectively. As the number of nesters in site 1 increases, the suitability of that site for future nesting decreases to the point where the next male in the population chooses site 2. At this time the program enters a recalculated suitability value for site 1 for example, 0.905 since it is less suitable than site 2 (0.91). The model then starts assigning males to site 2 and recalculates the suitability of site 2 each time a male is assigned. The error occurs at this point; instead of comparing the suitability of site 2 to the next most suitable (site 1 (0.905)), it compares site 2 to site 3, which has a suitability of 0.85. This results in several males being incorrectly assigned to site 2 since the model does not recognize that the next most suitable site is actually site 1. When one views the Access table in which the new suitability calculations for each site are stored, it reads that the model should be comparing site 2's suitability to that of site 1, but this is not happening (Figure 3.1). This anomaly suggests that a temporary file is being stored in Visual Basic that instead compares the suitability of a site to the next numerical site (compares site 2 to site 3). This error may be responsible for the poor relationships between predicted and observed nest densities in both lakes. Similar programming was used to calculate the distribution of the juveniles and adults. Therefore, habitat choices for that stage are also in error. Future work is required to determine how to correct for this error in the implementation of the ideal free distribution.

Preliminary analysis showed that this error does not affect the density of smallmouth bass in the lake but does lead to an incorrect distribution of nests and juveniles/adults throughout the lake. Therefore the model validation in this chapter was restricted to comparisons of the predicted suitabilities of the sites for nesting and juveniles/adults versus observed nest densities and juvenile/adult catch data.

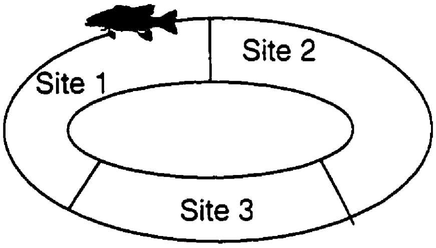
3.2. LAKES USED FOR MODEL VALIDATION

The smallmouth bass habitat model was validated using data on smallmouth bass populations in Lake Opeongo, Ontario and Long Point Bay, Lake Erie. These water bodies are very different in size, seasonal timing of spawning and quality of nesting habitat. In Lake



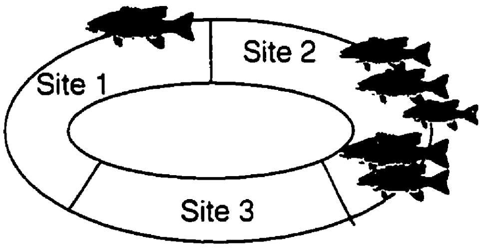
Site	Area	Nesting suitability
1	2000	0.92
2	2000	0.90
3	2000	0.84

FIRST LOOP OF IDEAL FREE DISTRIBUTION CODE: first male from the largest and oldest age class is assigned to site 1



Site	Area	Nesting suitability	Recalculated suitability
1	2000	0.92	0.899
2	2000	0.90	
3	2000	0.84	

SECOND MALE : the suitability of the first site is now 0.899 which is <0.90 in site 2 therefore the second male is assigned to site 2



Site	Area	Nesting suitability	Recalculated suitability
1	2000	0.92	0.899
2	2000	0.90	0.888
3	2000	0.84	

ERROR: Instead of now taking the third male and comparing the suitability of site 2 to site 1 (0.888 versus 0.899) the model compares site 2 to site 3 therefore males are assigned to site 2 until the suitability of site 2 is less than site 3 only then does the model assign males to site 1

Figure 3.1: Diagrammatic representation of error occuring during ideal free distribution of nesting males. Future work is required to fix this error.

Opeongo, nesting begins in late-May to early-June and occurs on rock, gravel and sand substrates. In Long Point Bay, nesting begins in mid-May and the prime nesting habitat is composed of sand and macrophytes. To validate, the model simulations were performed using the habitat characteristics that described these two systems. The results were compared to the nesting, creel and catch data available for these lakes. Nesting suitability and predicted nest densities were compared to observed nest densities in each lake. In Lake Opeongo, juvenile/adult suitability and predicted densities (adults/ha) were compared to catch data (fish/trapnet). In Long Point Bay, juvenile/adult suitability and predicted densities were compared to catch per unit effort data (CUE) (no./rod-h).

Lake Opeongo

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. The lake is oligotrophic and consists of four basins joined by narrow channels (Figure 3.2).

Smallmouth bass were introduced into Lake Opeongo in the late 1920's (Martin and Fry 1973) and a long-term creel survey has been in effect since 1936 (Shuter et al. 1987). Along with creel data there are trap net and mark-recapture data for the juvenile and adult Opeongo population.

Long term nest maps are also available for Lake Opeongo, specifically four years of whole lake nest distributions and 20+ years of nesting in Jones Bay, the primary nesting area (Ridgway unpublished data). Nesting occurs in late-May – early-June and lasts for three to four weeks (Ridgway et al. 1989). Males nest at depths ranging from 0.25 – 2.5 m and from 1 to 50 m from the shoreline (Rejwan et al. 1996). Water temperature, shoreline reticulation and wind exposure are related to the distribution of smallmouth bass nests in Lake Opeongo (Rejwan et al. 1999).

Long Point Bay, Lake Erie

Long Point Bay (42° 37N, 80° 10' W) is located along the north shore of Lake Erie. The bay is divided into two distinct regions, Inner and Outer Bay, due to a submerged sand bar that extends from Turkey to Pottohawk Point (Figure 3.3). 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 1984). Outer bay is approximately 27,500 ha and is deeper than Inner bay with a mean depth of approximately 15 m (Witzel 1989).

Smallmouth bass are the single most sought after species for the summer sport

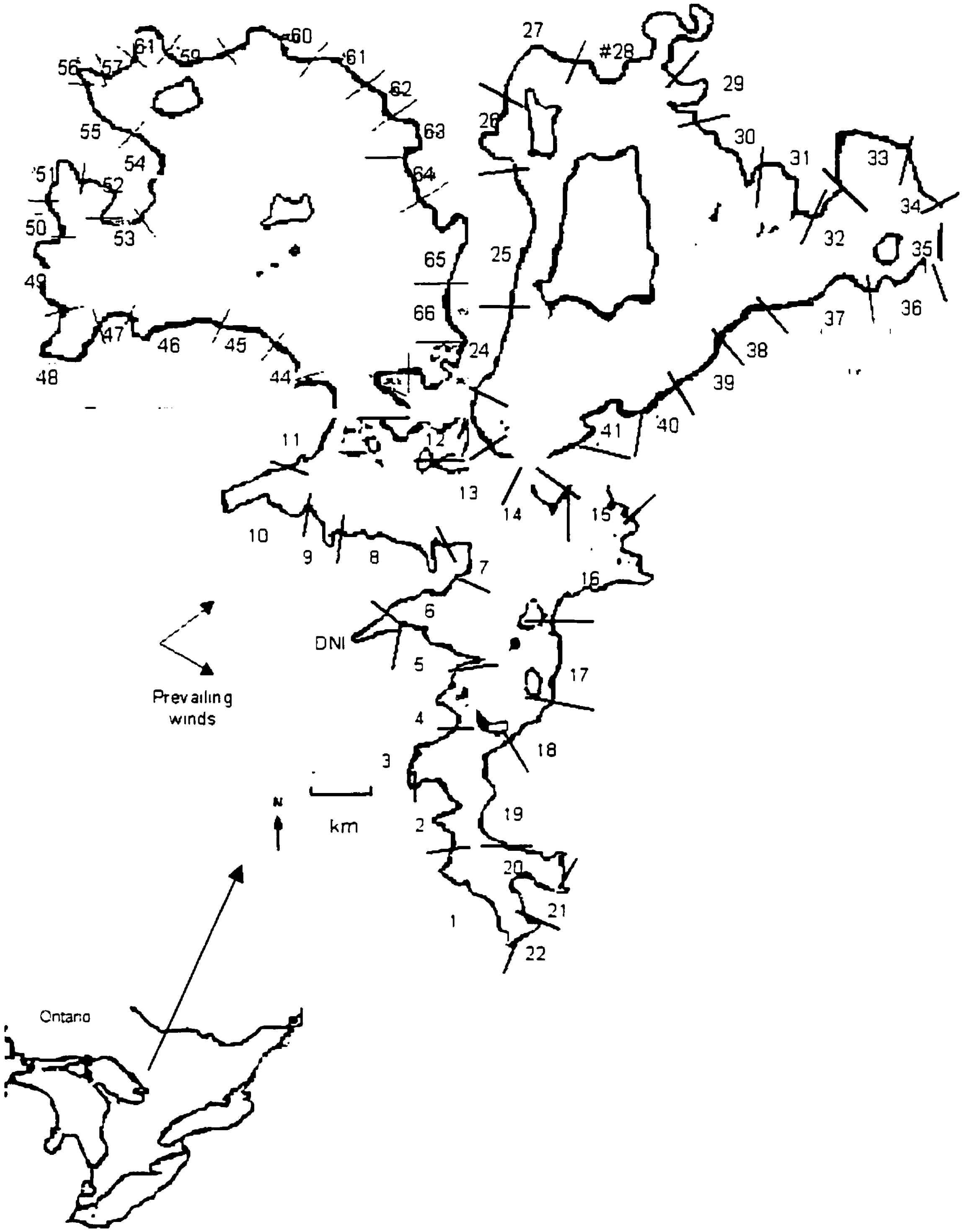


Figure 3.2: Map of Southern Ontario indicating location of Lake Opeongo (a) and, map of Lake Opeongo.

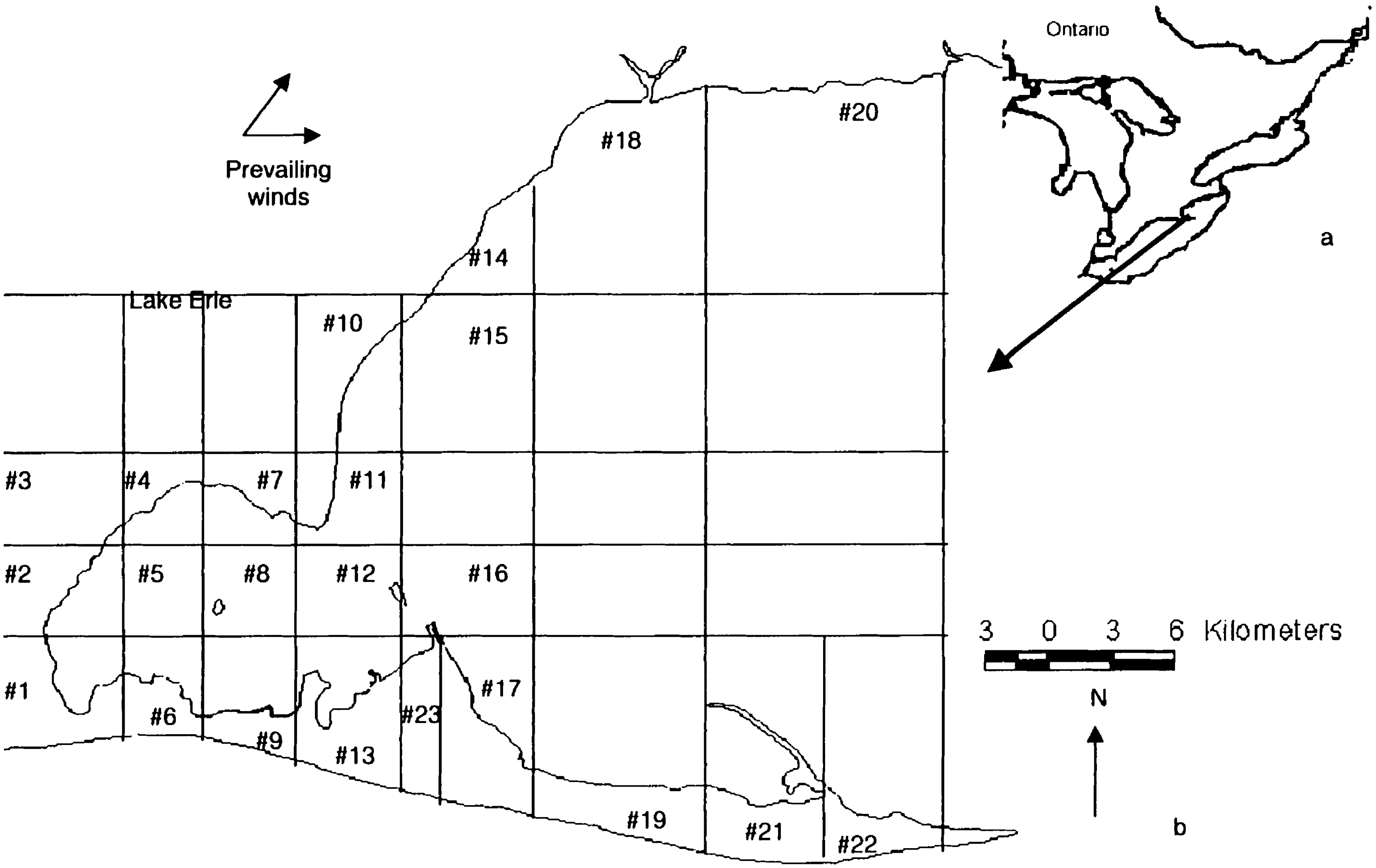


Figure 3.3: Map of Southern Ontario a) and Great Lakes indicating location of Long Point Bay, Lake Erie b).

fishery of Long Point Bay (Witzel 1989). This population has been studied using index netting, creel surveys and trawling data.

Nesting primarily occurs in Inner Bay where the shallow, warm waters provide excellent habitat for spawning (Goff 1986). Adults immigrate from Outer Bay to Inner Bay to spawn in May (Witzel 1989). Wind has been identified as the most influential factor affecting the locations of nests in Long Point Bay (Goff 1986).

3.2. LAKE OPEONGO AND LONG POINT BAY SIMULATION SCENARIOS

Each lake shoreline was divided arbitrarily into a number of subsections (sites) to be modelled individually. Lake Opeongo was divided into 68 sites and Long Point Bay was divided into 23 sites. Summaries of the habitat variable values for each lake are provided in Tables 3.1 and 3.2. Mean annual air temperature for each lake was estimated using the 60 year mean annual air temperature for each region (Environment Canada 2000). In Lake Erie this equalled 8 °C and in Lake Opeongo it was 4.75 °C. The substrate compositions of the different sites in each lake were determined from substrate maps (Ridgway unpublished data; Bakelaar unpublished data).

A mean depth of 14.8 m in Lake Opeongo produced a thermocline depth of 11.3 m (See Chapter Two, equation 5). For each site, the area available for nesting (0.5 - 2.5 m) and for juveniles/adults (0 - 11.3 m) were calculated from digitized maps using Scion Image software (Scion Corporation, Beta 3b).

Less than one percent of the area in Inner Bay is deeper (3.05 m) than the suitable nesting depths for smallmouth bass, therefore the whole area was considered available for both nesting and juvenile/adult habitat. In Outer Bay the area between 0.5 and 16.7 m (the bottom of the epilimnion) was used for the juvenile/adult habitat.

Mean monthly wind speeds for each lake were taken from the nearest weather station to the lake site (Environment Canada 2000). The effective fetch of each site was calculated using the method described in Appendix A. Directional wind data for Lake Opeongo came from a study conducted in 1970 -1974 (Finlay, *In review*). Directional wind data for Long Point Bay were not readily available, but the prevailing direction is known. Winds are predominantly from the west and southwest therefore these two directions together represent the wind direction for at least 50% of the time. These directions were assigned frequencies of 25% and each of the other directions, N, NW, S, SE, E and NE were assumed to occur 8.3% of the time.

TDS in Lake Opeongo was 29 mg/L while TDS in Lake Erie was 172.5 mg/L

Table 3.1: Habitat characteristics for Lake Opeongo, Ontario.

Site	Area of shoreline (m^2)	Sand (%)	Sand and rock	Gravel	Rock	Weed	Litter	Effective fetch (m)	Sand (JA)	Gravel (JA)	Rock (JA)	Weed (JA)	Litter (JA)	Area available for juveniles and adults (m^2)
1	22000	0.00	0.50	0.25	0.00	0.25	0.00	96.29663	0.00	0.75	0.00	0.25	0.00	530000
2	10000	0.25	0.00	0.50	0.00	0.25	0.00	202.033	0.25	0.50	0.00	0.25	0.00	110000
3	22000	0.00	0.00	0.20	0.00	0.20	0.60	521.0174	0.00	0.20	0.00	0.20	0.60	150000
4	60000	0.00	0.00	0.80	0.00	0.20	0.00	336.7731	0.00	0.80	0.00	0.20	0.00	680000
5	105000	0.00	1.00	0.00	0.00	0.00	0.00	345.1112	0.00	1.00	0.00	0.00	0.00	360000
6	39000	0.00	0.00	1.00	0.00	0.00	0.00	746.4015	0.00	1.00	0.00	0.00	0.00	580000
7	98000	0.00	0.00	0.00	1.00	0.00	0.00	524.1452	0.00	0.00	1.00	0.00	0.00	110000
8	86000	0.00	0.00	0.90	0.00	0.10	0.00	610.6549	0.00	0.90	0.00	0.10	0.00	280000
9	241000	0.00	0.00	1.00	0.00	0.00	0.00	197.1328	0.00	1.00	0.00	0.00	0.00	150000
10	270000	0.00	0.00	0.60	0.00	0.40	0.00	301.6508	0.00	0.60	0.00	0.40	0.00	580000
11	31000	0.00	0.00	1.00	0.00	0.00	0.00	475.623	0.00	1.00	0.00	0.00	0.00	680000
12	24000	0.00	0.50	0.00	0.50	0.00	0.00	415.18	0.00	0.50	0.50	0.00	0.00	280000
13	170000	0.00	1.00	0.00	0.00	0.00	0.00	1629.936	0.00	1.00	0.00	0.00	0.00	780000
14	39000	0.00	0.20	0.70	0.00	0.00	0.00	1292.389	0.00	0.90	0.00	0.00	0.00	780000
15	520000	0.10	0.00	0.80	0.10	0.00	0.00	1499.723	0.10	0.80	0.10	0.00	0.00	1280000
16	510000	0.00	0.10	0.75	0.15	0.00	0.00	1137.669	0.00	0.75	0.25	0.00	0.00	880000
17	460000	0.10	0.00	0.70	0.00	0.20	0.00	675.6297	0.10	0.70	0.00	0.20	0.00	810000
18	420000	0.00	0.00	1.00	0.00	0.00	0.00	891.0691	0.00	1.00	0.00	0.00	0.00	820000
19	310000	0.00	0.25	0.25	0.00	0.00	0.00	703.1119	0.00	0.50	0.00	0.00	0.00	880000
20	180000	0.00	0.00	0.00	0.20	0.00	0.00	681.3407	0.00	0.00	0.20	0.00	0.00	290000
21	450000	0.00	0.25	0.25	0.00	0.50	0.00	235.9154	0.00	0.50	0.00	0.50	0.00	780000
22	210000	0.50	0.00	0.00	0.50	0.00	0.00	394.3771	0.50	0.00	0.50	0.00	0.00	166000
23	282000	0.87	0.00	0.00	0.13	0.00	0.00	130.5862	0.87	0.00	0.13	0.00	0.00	540000
24	117000	0.00	0.00	1.00	0.00	0.00	0.00	325.2308	0.00	1.00	0.00	0.00	0.00	227200
25	155000	0.25	0.00	0.25	0.25	0.00	0.00	213.7098	0.25	0.25	0.25	0.00	0.00	388700
26	48000	0.00	0.00	0.00	1.00	0.00	0.00	134.1285	0.00	0.00	1.00	0.00	0.00	114600
27	53000	0.60	0.00	0.00	0.00	0.00	0.00	71.14274	0.60	0.00	0.00	0.00	0.00	414000
28	116000	0.00	1.00	0.00	0.00	0.00	0.00	295.2399	0.00	1.00	0.00	0.00	0.00	470000
29	365000	0.00	0.00	0.75	0.25	0.00	0.00	305.7639	0.00	0.75	0.25	0.00	0.00	824000

Table 3.1 continued

30	203000	0.00	0.00	0.50	0.00	0.50	0.00	246.9945	0.00	0.50	0.00	0.50	0.00	534000
31	331000	0.00	0.00	1.00	0.00	0.00	0.00	924.4171	0.00	1.00	0.00	0.00	0.00	695000
32	65000	0.00	0.00	1.00	0.00	0.00	0.00	325.2308	0.00	1.00	0.00	0.00	0.00	233200
33	59000	0.00	0.00	0.50	0.50	0.00	0.00	281.6932	0.00	0.50	0.50	0.00	0.00	160000
34	205000	0.00	0.00	1.00	0.00	0.00	0.00	307.5421	0.00	1.00	0.00	0.00	0.00	460000
35	97000	0.00	1.00	0.00	0.00	0.00	0.00	440.3512	0.00	1.00	0.00	0.00	0.00	290000
36	139000	0.75	0.00	0.25	0.00	0.00	0.00	255.8637	0.75	0.25	0.00	0.00	0.00	417000
37	84000	0.50	0.00	0.00	0.00	0.00	0.50	54.00304	0.50	0.00	0.00	0.00	0.50	108000
38	95000	0.00	0.00	1.00	0.00	0.00	0.00	687.817	0.00	1.00	0.00	0.00	0.00	252000
39	37800	0.00	0.00	1.00	0.00	0.00	0.00	504.5915	0.00	1.00	0.00	0.00	0.00	166000
40	153000	0.33	0.00	0.00	0.33	0.00	0.00	525.8941	0.33	0.00	0.33	0.00	0.00	345500
41	204000	0.00	0.00	0.50	0.00	0.00	0.00	399.6415	0.00	0.50	0.00	0.00	0.00	324000
42	34000	0.00	1.00	0.00	0.00	0.00	0.00	569.4308	0.00	1.00	0.00	0.00	0.00	149000
43	202000	0.00	0.00	0.75	0.25	0.00	0.00	354.9347	0.00	0.75	0.25	0.00	0.00	427000
44	45000	0.00	0.00	0.00	0.50	0.00	0.00	599.6778	0.00	0.00	0.50	0.00	0.00	105000
45	30000	0.00	0.00	1.00	0.00	0.00	0.00	344.511	0.00	0.00	0.00	0.00	0.00	85000
46	90000	0.00	0.00	1.00	0.00	0.00	0.00	1564.669	0.00	1.00	0.00	0.00	0.00	370000
47	60000	0.25	0.00	0.00	0.50	0.00	0.25	467.2308	0.25	0.00	0.50	0.00	0.25	55000
48	50000	0.10	0.45	0.45	0.00	0.00	0.00	337.8542	0.10	0.90	0.00	0.00	0.00	80000
49	80000	0.25	0.00	0.50	0.00	0.25	0.00	537.6894	0.25	0.50	0.00	0.25	0.00	105000
50	40000	0.00	0.50	0.00	0.50	0.00	0.00	220.3402	0.00	0.50	0.50	0.00	0.00	40000
51	27000	0.00	0.25	0.00	0.00	0.75	0.00	227.8019	0.00	0.25	0.00	0.75	0.00	225000
52	31000	0.00	0.00	0.50	0.50	0.00	0.00	744.2729	0.00	0.50	0.50	0.00	0.00	130000
53	6500	0.00	0.00	0.00	1.00	0.00	0.00	430.388	0.00	0.00	1.00	0.00	0.00	255000
54	13500	1.00	0.00	0.00	0.00	0.00	0.00	453.7975	1.00	0.00	0.00	0.00	0.00	145000
55	62500	0.00	0.00	0.60	0.40	0.00	0.00	294.14	0.00	0.60	0.40	0.00	0.00	140000
56	140500	0.00	0.00	0.00	0.00	0.70	0.30	185.7037	0.00	0.00	0.00	0.70	0.30	440000
57	4300	0.00	0.00	1.00	0.00	0.00	0.00	557.9367	0.00	1.00	0.00	0.00	0.00	185000
58	4150	0.00	0.00	1.00	0.00	0.00	0.00	287.807	0.00	1.00	0.00	0.00	0.00	85000
59	13500	0.00	0.00	1.00	0.00	0.00	0.00	752.6055	0.00	1.00	0.00	0.00	0.00	180000
60	12000	0.80	0.00	0.20	0.00	0.00	0.00	440.1638	0.80	0.20	0.00	0.00	0.00	280000
61	18000	1.00	0.00	0.00	0.00	0.00	0.00	1533.839	1.00	0.00	0.00	0.00	0.00	460000

Table 3.1 continued

62	40000	1.00	0.00	0.00	0.00	0.00	0.00	1368.67	1.00	1.00	0.00	0.00	0.00	585000
63	22000	1.00	0.00	0.00	0.00	0.00	0.00	1656.389	1.00	0.00	0.00	0.00	0.00	375000
64	12500	0.00	0.00	1.00	0.00	0.00	0.00	779.3459	0.00	1.00	0.00	0.00	0.00	735000
65	22000	0.00	0.45	0.45	0.00	0.10	0.00	1383.989	0.00	0.90	0.00	0.10	0.00	430000
66	32500	0.00	0.00	1.00	0.00	0.00	0.00	1894.96	0.00	1.00	0.00	0.00	0.00	105000
67	80000	0.00	0.50	0.00	0.00	0.00	0.00	476.6653	0.00	0.50	0.00	0.00	0.00	210000
68	30000	0.00	1.00	0.00	0.00	0.00	0.00	1151.559	0.00	1.00	0.00	0.00	0.00	285000

JA = juveniles and adults

Table 3.2: Habitat characteristics of Long Point Bay, Lake Erie.

Site	Area of shoreline (m^2)	Sand (%)	Sand and rock	Gravel	Rock	Weed	Litter	Effective fetch (m)	Sand (JA)	Gravel (JA)	Rock (JA)	Weed (JA)	Litter(JA)	Area available for juveniles and adults (m^2)
1	5620000	0.10	0.00	0.00	0.00	0.90	0.00	1838.4	0.10	0.00	0.00	0.90	0.00	5620000
2	6877650	0.10	0.00	0.00	0.00	0.80	0.00	6103.2	0.10	0.00	0.00	0.80	0.00	6877650
3	2895075	0.00	0.00	0.00	0.00	1.00	0.00	5991.6	0.00	0.00	0.00	1.00	0.00	2895075
4	6935425	0.30	0.00	0.00	0.00	0.30	0.00	7531.8	0.30	0.00	0.00	0.30	0.00	6935425
5	8413375	0.50	0.00	0.00	0.00	0.00	0.00	7343.4	0.50	0.00	0.00	0.00	0.00	8413375
6	3208950	0.30	0.00	0.00	0.00	0.40	0.00	2493	0.30	0.00	0.00	0.40	0.00	3208950
7	9045756	0.70	0.00	0.00	0.00	0.10	0.00	3633	0.70	0.00	0.00	0.10	0.00	9045756
8	12579641	0.85	0.00	0.00	0.00	0.00	0.00	7347.6	0.85	0.00	0.00	0.00	0.00	12579641
9	7252106	0.40	0.00	0.50	0.00	0.10	0.00	6233.4	0.85	0.00	0.00	0.10	0.00	7252106
10	5643129	0.45	0.00	0.00	0.00	0.50	0.00	6146.4	0.45	0.00	0.00	0.50	0.00	5643129
11	10238074	0.70	0.00	0.00	0.00	0.10	0.00	10036.2	0.70	0.00	0.00	0.10	0.00	10238074
12	8299758	0.70	0.00	0.00	0.00	0.00	0.00	8795.4	0.70	0.00	0.00	0.00	0.00	10354690
13	5870639	0.25	0.00	0.00	0.00	0.70	0.00	2799	0.25	0.00	0.00	0.70	0.00	11878960
14	6623996	0.10	0.00	0.50	0.00	0.40	0.00	7084.8	0.10	0.50	0.00	0.40	0.00	15693410
15	4469186	1.00	0.00	0.00	0.00	0.00	0.00	9691.8	1.00	0.00	0.00	0.00	0.00	10591683
16	9394004	0.40	0.00	0.00	0.00	0.10	0.00	9969	0.40	0.00	0.00	0.10	0.00	22253164
17	5127220	0.15	0.00	0.00	0.00	0.85	0.00	6321.6	0.15	0.00	0.00	0.85	0.00	17123164
18	9067584	0.10	0.00	0.20	0.20	0.40	0.00	10796.4	0.10	0.20	0.20	0.40	0.00	21508627
19	7888136	0.60	0.00	0.00	0.00	0.20	0.00	2533.8	0.60	0.00	0.00	0.20	0.00	19683892
20	8038406	0.10	0.00	0.10	0.25	0.50	0.00	18376.8	0.10	0.10	0.25	0.50	0.00	19041679
21	8520000	0.60	0.00	0.00	0.00	0.20	0.00	3175.2	0.60	0.00	0.00	0.20	0.00	8522647
22	8350000	0.80	0.00	0.00	0.00	0.20	0.00	9536.4	0.80	0.00	0.00	0.20	0.00	16422314
23	2127220	0.20	0.00	0.00	0.00	0.80	0.00	3126	0.87	0.00	0.13	0.00	0.00	2127220

(Ontario Ministry of Natural Resources, ARU1 database; Berst and McCrimmon 1966). pH and dissolved oxygen were set to 7 and 10 respectively in both lakes.

Mortality

Since extensive mortality data are available for the two populations, more detailed annual mortality estimates could be entered into the model. Default annual mortality for the juvenile/adult sub-model is 25%. In Lake Opeongo, annual mortality for age 5 and up is 53% (Coble 1975; Shuter et al. 1987). Therefore the smallmouth bass habitat model code was modified accordingly. For age 1 to 4 mortality was set to 25% annually.

Annual mortality estimates in Lakes Huron and Michigan range from 51 - 58% from both angling and natural sources (Coble 1975). The mean mortality in these lakes (55%) was used for the Lake Erie simulation. The average age of harvest in Long Point Bay was 3-4 years (MacGregor and Witzel 1984). This was incorporated into the Long Point Bay simulation by setting the survival level of age 3 and up to 45%; age 2 and younger were exposed to natural mortalities of 25%.

3.3. RESULTS

Lake Opeongo

Nesting maps were used to calculate the observed nest densities in Lake Opeongo (Ridgway unpublished data). Nesting suitabilities ranged from 0.60-0.99 (Figure 3.4). Calculated nesting suitability was positively but poorly related to observed nest densities ($r^2 = 0.04$).

The poor relationship between nesting suitability and observed nest densities in Lake Opeongo suggests that another habitat factor(s) important to nesting in Lake Opeongo has(ve) been overlooked in developing this model. For example, Rejwan (1996) found that temperature and shoreline complexity explained 75 % of the variation in nest densities in sites at the 1 km scale in Lake Opeongo. Tree regression analysis also revealed that shoreline complexity was positively related to nest density in warm sites (Rejwan et al. 1999).

Trap net catch data were used as indicators of juvenile/adult distribution throughout Lake Opeongo (Lester unpublished data). Unfortunately 20 of the modelled sites were not sampled during the trap net study therefore no juvenile/adult estimates were available for those sites. Juvenile/adult habitat suitability did not fare much better than the nesting habitat suitability when compared to trap net catch data for Lake Opeongo ($r^2 = 0.02$, Figure 3.5). As with the nesting model, the weak relationship between juvenile/adult suitability and CUE may be attributed to real substrate preferences being different in Lake Opeongo than those specified in the model. Future research will be required to determine the substrate preferences of juveniles and adults in Lake Opeongo.

Although the model poorly predicted the suitability of sites for nesting and the juveniles/adults, the predicted numerical density of smallmouth bass ≥ age 5 was within 2% of the observed (Shuter et al. 1987). At equilibrium, model estimates are 0.842 compared to the observed 0.853 smallmouth bass/ha (Table 3.3). Although nest densities were grossly overestimated (Table 3.3), density-dependent effects on growth and subsequent size-dependent mortality of the YOY in the model reduce juvenile/adult population levels to those seen in nature.

Estimates of the mean lengths at age were slightly larger than the lengths observed in Lake Opeongo but within the range typically recorded for the lake (Figure 3.6). Since the model predicted water temperatures well in Lake Opeongo (Appendix A), these growth differences cannot be attributed to temperature differences. Instead our estimates of food availability (P) may be responsible for this difference. In the Opeongo simulation P was set to 1; however in the YOY component of the model, P was calculated to be 0.93 at a [TDS] of 29 mg/L (Equation 9, Chapter Two, Productivity and prey abundance). This suggests that food may also be limited in the later years of life. Unfortunately no empirical estimate of P is available for Lake Opeongo. Therefore values of 0.95 – 0.80 at increments of 0.05 were entered into another simulation. A P value of 0.85 most accurately described the growth observed in Lake Opeongo (Figure 3.7).

Long Point Bay, Lake Erie

Nesting suitabilities in Long Point Bay ranged from 0-0.88 with all sites along the north shore (site #10, 14, 18, 20) having suitabilities of zero (Figure 3.3). Due to the large size of Long Point Bay, nesting surveys are limited to dive locations throughout Inner bay. Nesting data were available for 10 of the 23 sites used in the simulation. Observed nest density data were not available for Outer Bay although nesting rarely (reported in one of five nesting surveys conducted in Long Point Bay) occurs in sites #10, #17 and #19-21. Nesting has never been recorded in sites #14 and 18 (Witzel 1997; Savoie et al. 1982). Of the sites sampled, nesting suitability was positively related to observed nest densities ($r^2 = 0.42$, Figure 3.8)

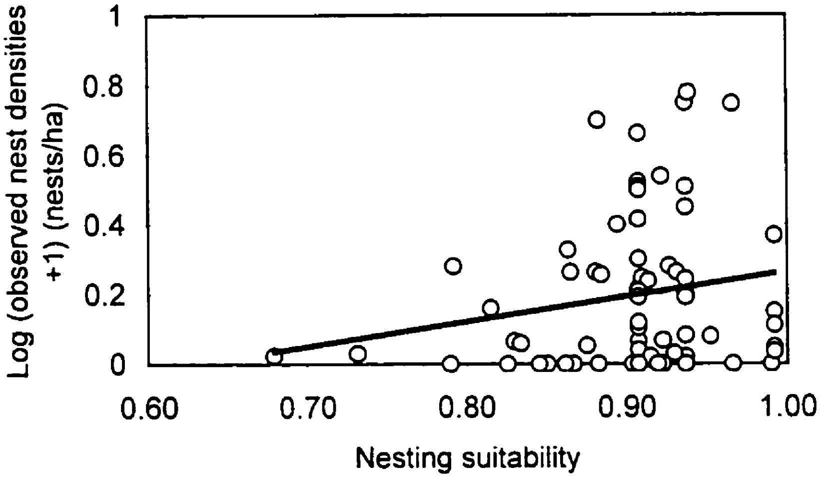


Figure 3.4: Nesting suitability (r^2=0.04, n=68, p=0.21), predicted nest densities versus log (observed nest densities) for 68 sites in Lake Opeongo. Solid line is linear regression.

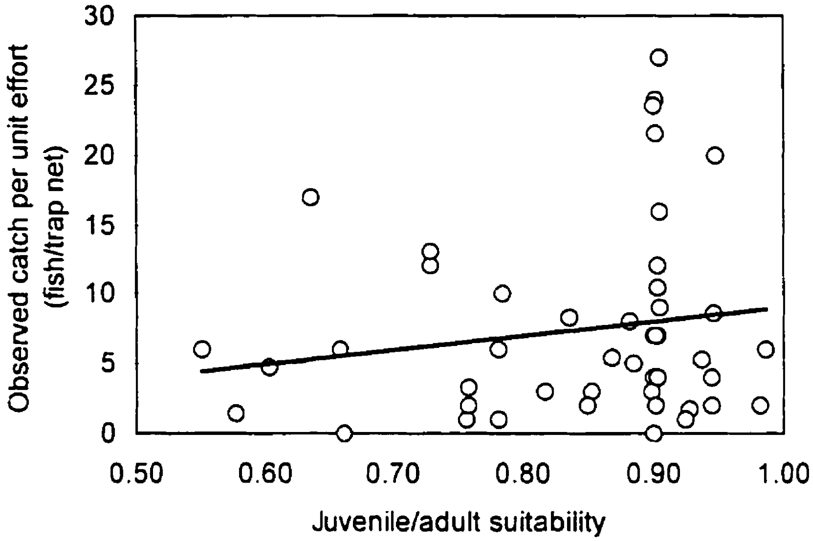


Figure 3.5: Juvenile/adult suitability (r^2=0.04, n=48, p=0.17) versus CUE (fish/ trap net) for 48 sites in Lake Opeongo sampled during a 1994 trap net study (Lester unpublished data). Solid line represents linear regression.

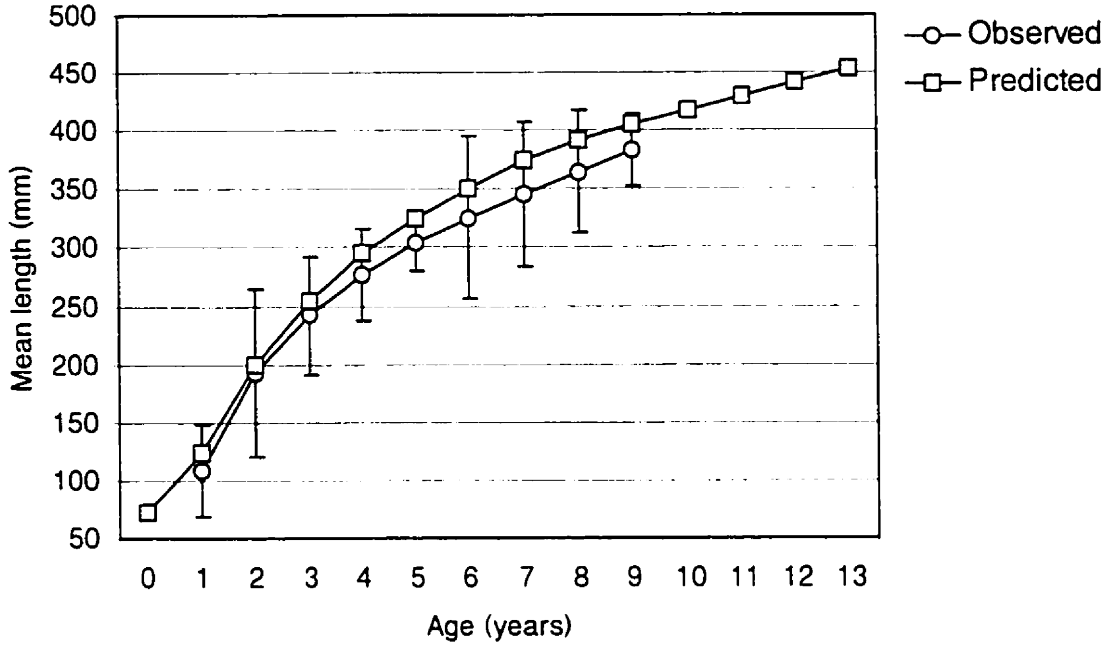


Figure 3.6: Observed and predicted mean length at age for the smallmouth bass population in Lake Opeongo. Bars represent the range of observed values for the Opeongo population in 1987. 1987 represents a typical distribution of mean lengths at age for the Opeongo population.

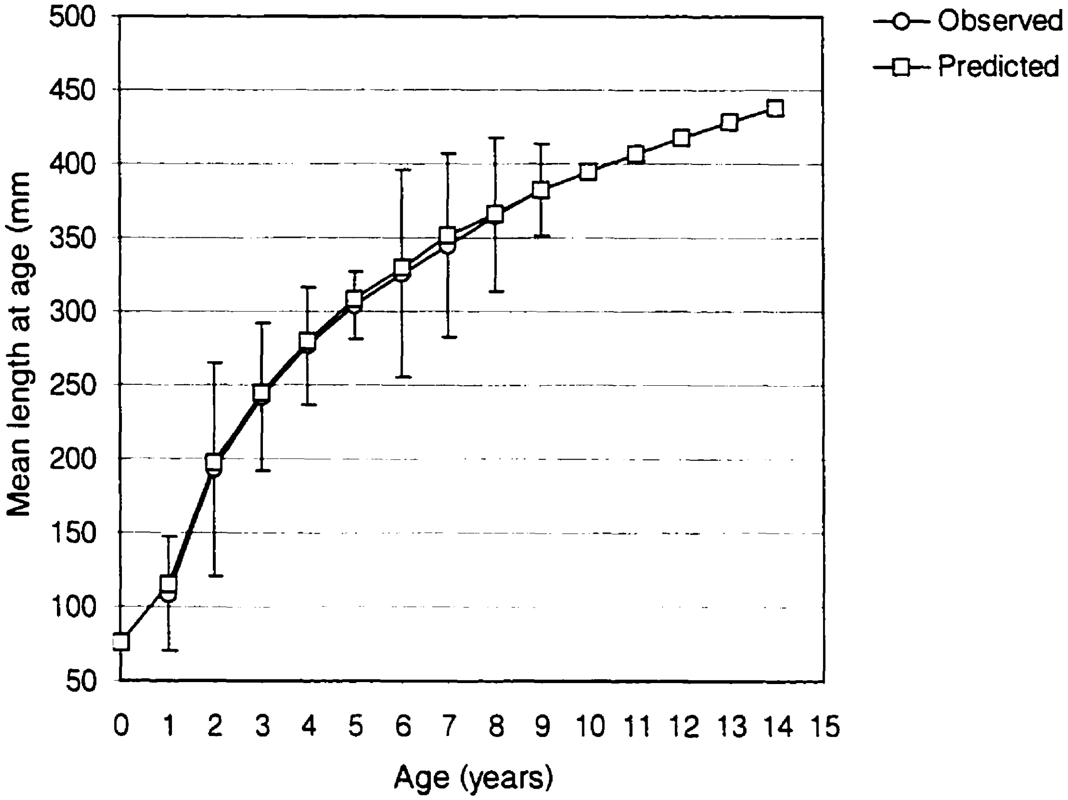


Figure 3.7: Observed versus predicted mean length at age in Lake Opeongo with P set to 0.85.

The model results indicate that little spawning occurs in Outer Bay despite an abundance of suitable substrates. The apparent avoidance of these sites has commonly been attributed to the slow warming rate and temperature fluctuations in Outer Bay (Witzel 1989). However, our model highlights another potential reason why these sites go unused. Suitabilities in the Outer Bay sites, especially along the north shore were zero due to wave action. The large effective fetches of these sites (>6000 m) coupled with mean wind speeds of 12 km/h during the months of spawning limits nesting in these areas. Goff (1986) also found that accumulated hours of strong winds (>28 km/h) negatively influences offspring survival in Long Point Bay. This suggests that the nesting habitat in Outer Bay may be improved by providing shelter from wave action.

Juvenile/adult suitabilities in Long Point Bay ranged from 0-0.77 (Figure 3.9). CUE (no./rod-h) data from creel surveys were used to compare model predictions to the relative densities of juvenile/adult smallmouth bass in Long Point Bay. Unfortunately site-specific CUE estimates are not available and the data represent mean estimates for three different regions of Long Point Bay: Inner Bay (sites #1-13), Outer Bay (sites #14-19, 21) and the Nanticoke area (site #20). A Student's T-test showed sites with higher CUE's (1.141 bass/rod-h) had higher juvenile/adult suitabilities than sites #1-13 that had lower CUE's ($T_{0.05,(1),20} = -1.601$, $p = 0.06$, Figure 3.9).

According to Witzel (1989), the Long Point Bay population density is between 11.93 and 12.33 fish ≥ 2 years of age/ha. At equilibrium the model estimates a population of approximately 24.63 fish ≥ 2 years of age/ha.

Empirical mean lengths at the end of the growing season were not available for the YOY, however length estimates were available for the end of August. These were compared to model estimates of YOY (Age 0) growth (Figure 3.10). Mean lengths at age were within the range observed in Long Point Bay (1981-1983) but fish ≥ age 3 were consistently smaller than the mean (Figure 3.10). This may be attributed to the model's overpredicted density of juveniles and adults, since growth is negatively related to density.

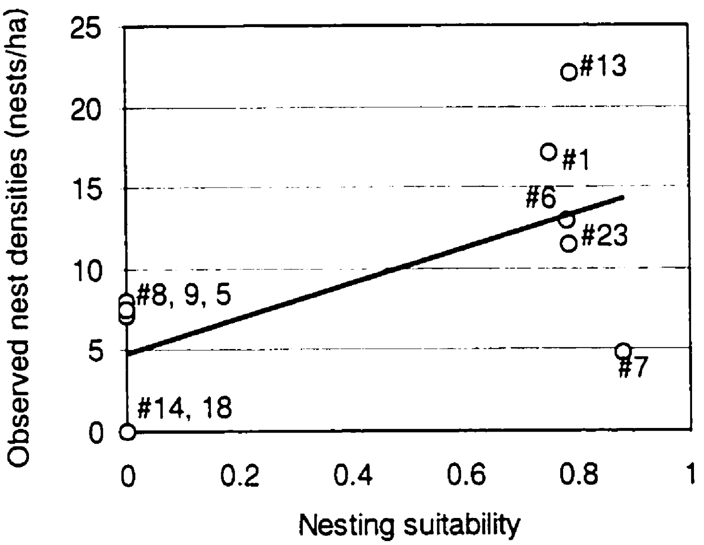


Figure 3.8: Nesting suitability (r^2=0.42, n=10, p=0.04), predicted nest densities (r^2=0.28, n=10, p=0.12) versus log (observed nest densities) for 10 of the 23 sites sampled in Long Point Bay, Lake Erie during a 1988 nesting survey (Witzel unpublished data). Nest density estmates were not available for the remaining 13 sites. Numbers represent site numbers. Dashed line represents 1:1 relationship. Observed nest density data were not available for sites 2-4, 10-12, 17, 19-21.

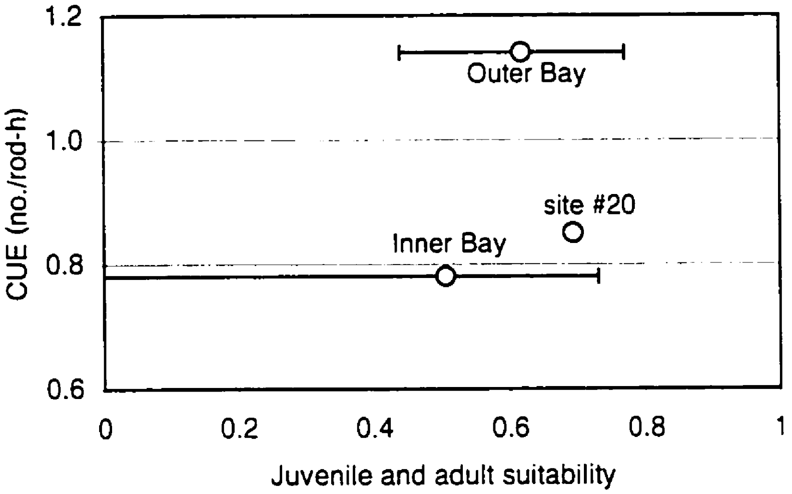


Figure 3.9: Juvenile/adult suitability ($T_{0.05,(1),20}$=-1.60, p=0.06) versus CUE (no./rod-h) for all sites Long Point Bay, Lake Erie. Bars represent range of suitabilities and densities at each CUE.

3.4. COMPARISON OF LAKE OPEONGO AND LONG POINT BAY, LAKE ERIE

The model described nesting habitat better in Lake Erie than in Lake Opeongo. In Long Point Bay, wave action limited nesting in Outer Bay while in Lake Opeongo wave action had no detrimental effect on nesting. This demonstrates that the habitat features limiting nesting may differ in lakes of different sizes.

Nesting suitability was positively related to observed nest densities in both lakes but in neither lake was the relationship strong. This suggests that a component important to smallmouth bass nesting has been neglected. As aforementioned, shoreline complexity has been strongly related to nest densities in Lake Opeongo. Another possible factor that is important to consider for the nesting sub-model is the importance of temperature to YOY. In the nesting sub-model temperature influences nesting suitability in terms of whether the site will warm up to 16 °C before the mean temperature of the lake reaches 24 °C that is, the end of the spawning season. No variable has been included that explicitly links temperature to the suitability of a site for the YOY. To incorporate this into the program another temperature variable should be included in the suitability equation that accounts for temperature suitability for the YOY. For example, as with the juvenile/adult model, sites with the highest maximum temperature can be given a higher suitability than the other sites.

Predicted nest densities were overestimated in both lakes (Table 3.3). This may be attributed to two components of the nesting sub-model, the assignment of males to nests and the potential number of reproductive males in the population.

In the model the potential number of nests in a site is determined by the habitat of that site (See Chapter Two, Nest distribution) however, the actual number of nests in each site is determined using the ideal free distribution theory. Basically, as the number of nesters in a site increases, the suitability of that site decreases and nesters are then assigned to nests in the next most suitable site of the lake. The effects of density on the suitability of a site is programmed using this equation (Figure 3.11):

$$HSI_{NACT} = HSI_N(AA^{0.96})/(AA^{0.96} + 0.0101(TNA^{0.96})) \qquad (26)$$

HSI_{NACT}= actual suitability (recalculated suitability after nester density increases)
HSI_N = maximum suitability (suitability calculated by model)
AA = nesting area available (area between 0.5 and 2.5 m deep)
TNA = total nest area required (230 m^2 (minimum nest area) multiplied by the number of nesters)
0.96=coefficient which results in $HSI_{NACT}=0.5(HSI_N)$
0.0101=scale coefficient which ensures that $HSI_{NACT}=0.99(HSI_N)$ when AA = TNA

The overestimated nest densities suggest that the model is underestimating the effects of density on nesting, , negative density dependent effects are only evident at extremely high densities, and therefore too many nests are assigned to each site(Figure 3.11). To improve this component of the model, the equation needs to be modified to increase the density effects on nesting. The new equation can be (Figure 3.11):

$$HSI_{NACT} = HSI_N(AA^5)/(AA^5 + 0.0101(TNA^5))$$

Another component of the nesting sub-model that can be changed to correct the overestimated nest densities concerns the potential number of nesters. In the model, all males ≥ age 3 are capable of nesting; however this may be overestimating the potential number of nesters. For example, in Lake Opeongo only fish 4 and older nest (Post 1982; Dunlop Department of Zoology, University of Toronto, pers. comm.) therefore allowing males age 3 to nest is overestimating the nesting population.. To improve this component of the model the number of potential nesters should be limited to age 4 and older. No estimate of the age of nesters is available for Long Point Bay.

Observed nest densities and juvenile/adult densities were approximately 10 and 14 times (respectively) greater in Long Point Bay than Lake Opeongo (Table 3.3). This can be attributed to the greater supply of nesting area (area between 0.5 and 2.5 m deep) in Long Point Bay. As the nesting habitat supply simulation (Chapter Two) showed increasing the nesting area affords more nests and more YOY produced to be recruited into the population.

These simulations demonstrate how the model can be applied to different lake systems. The results indicate how components of the model can be improved to better describe habitat effects on smallmouth bass populations.

3.5. RUN-TIME REQUIREMENTS

Run-time requirement is the time required for the model to complete one 40-year simulation. It is a function of the size of the population being modelled as well as the capacity of the computer being used. The performance estimates presented are for a Pentium II, 350 MHz computer with 128 MB RAM. For the control simulations, the model required from 2 to 4 hours to complete with a population of approximately 12,000 individuals and used 100 MB of virtual memory during the simulation. The Opeongo simulation required 24 hours and 800 MB of memory for a total population of 47,000 age 1+ individuals. Due to the size of the Long Point Bay population, 548,000 age 1+ individuals, the program required an enormous amount of virtual memory. When the memory requirements approached 1GB computations ceased (due to lack of available memory).

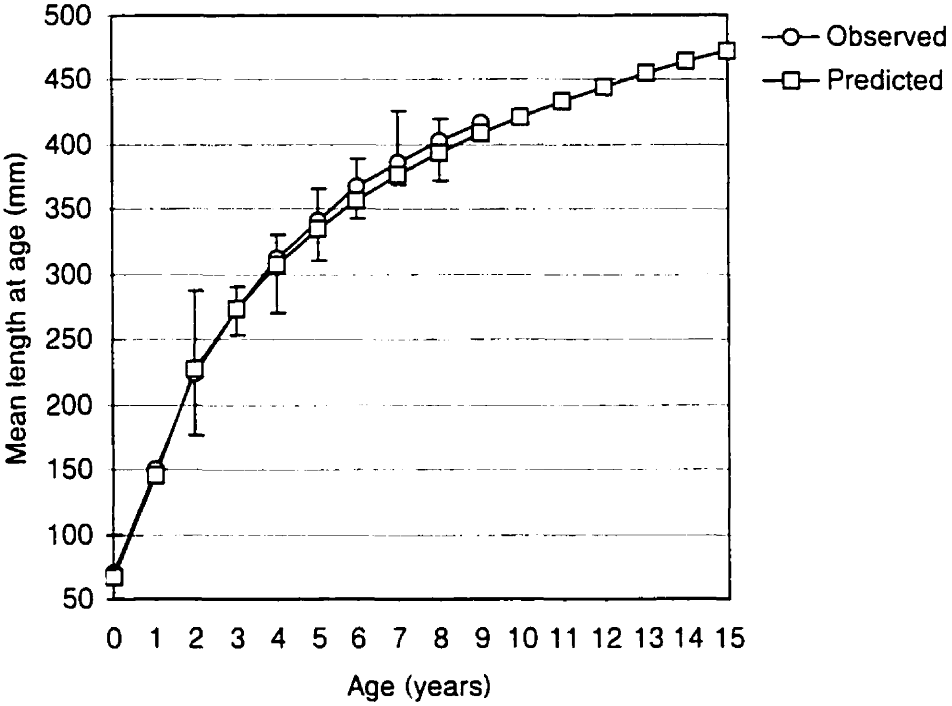


Figure 3.10: Observed and predicted mean length at age for the smallmouth bass population in Long Point Bay, Lake Erie. Bars represent range of lengths recorded for different ages during 1981-1983 studies (MacGregor and Witzel 1984). Age 0 represents mean lengths at the end of August (Witzel unpublished data).

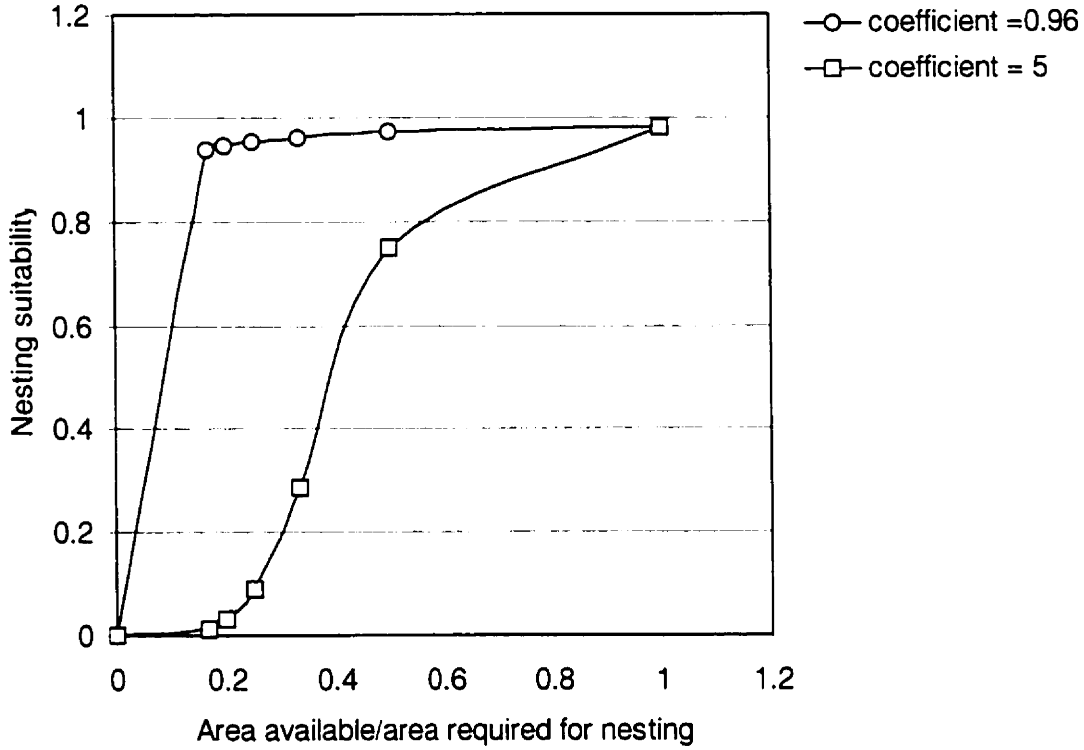


Figure 3.11: Change in density-dependent effects on nesting suitability when the scaling coefficient of equation 26 is changed from 0.96 to 5 to demonstrate how model can be improved to better describe nest densities in lakes.

Therefore to complete the Long Point Bay simulation, four runs were performed with each looping for ten years (duration 2 days). The last calculated population of the previous ten years was used as the starting point for the next ten year run.

The time and memory-consuming step of the model involves the calculation of the ideal free distribution of the juveniles and adults. The model generates a table in MSAccess that lists each individual and the site they will occupy. With populations of 548,000 individuals this requires large amounts of time and memory. Most lakes in Ontario are much smaller than Long Point Bay and Lake Opeongo and, have fewer individuals therefore improving the model performance is not a pressing concern at this time.

Table 3.3: Summary of Lake Opeongo and Long Point Bay, Lake Erie simulations.

Lake	Observed nest densities (nests/ha)	First simulation Predicted nest densities (nests/ha)	Observed juvenile/ adult density (no./ha)	First simulation Predicted juvenile/ adult density (no./ha)
Opeongo	0.87	9.94	0.85	0.84
Long Point Bay	9.10	22.55	11.91	37.81

General Conclusions

A smallmouth bass habitat model was developed to estimate how changes in habitat may affect smallmouth bass populations. This involved the ammalgamation of data from the primary literature, University of Toronto and Ontario Ministry of Natural Resources. The habitat characteristics that have been incorporated into the model include mean annual air temperature, substrate composition, mean monthly windspeed, effective fetch, [TDS], pH, dissolved oxygen and depth. A sub-model was developed to predict littoral water temperatures from mean annual air temperature and effective fetch. A wave action sub-model was developed to predict wave heights throughout the month of nesting from mean monthly windspeed and effective fetch.

Using the habitat data, the model first maps the suitability of different sites in a water body for nesting and the juveniles/adults. Nest and population distributions are then computed using the ideal free distribution theory to provide nest and juvenile/adult density estimates in each site. Growth is then calculated as a function of density and habitat. Mortality is size-dependent for the YOY and set at s constant rate for older fish. The model was programmed using Microsoft® Visual Basic® 6.0 and is an interactive application allowing the user to input habitat data and make decisions about the type of output the model will produce.

Sensitivity analysis was performed using a control lake that represented the median habitat characteristics of 1646 smallmouth bass lakes throughout Ontario. These analyses revealed that increasing the mean annual air temperature, [TDS] and nesting area available (area between 0.5 m – 2.5 m depth contours) improved the survival of the YOY and had the greatest positive influences on smallmouth bass numerical density (Figure 2.29). Mean depth and windspeed had no effect on numerical density in the control lake. However, greater mean depths did increase the size of the smallmouth bass in the control lake. A lower P value decreased the biomass density in the control lake but had no effect on numerical density (Figure 2.29). Annual mortality levels of 60% led to extinction of the control population.

The results of these simulations suggest that a YOY bottleneck exists in smallmouth bass populations. With a YOY bottleneck resources at a single point in time influence a cohort's abundance for the rest of its life (Shuter 1990). Habitat alterations that improved the survival of the YOY for example, increased temperature, [TDS] and nesting area substantially increased population densities. This suggests that conservation or restoration efforts should focus on improving the nesting habitat. This can involve introducing shelters to areas impacted by detrmental wave action such as those seen in Outer Bay of Long Point Bay. Introducing fill to areas of a lake can increase the amount of available habitat for nesting by increasing the area between 0.5 and 2.5 m deep. To increase the smallmouth bass density without altering habitat, annual mortality should be regulated by setting catch limits, size limits or enforcing catch and release practices.

Closer inspection of the program code after the TF sensitivity analysis revealed that the ideal free distribution of the nesting males and juveniles/adults was erroneous. Future work is required to improve this component of the program but preliminary analysis showed that this error does not affect the predicted population density of smallmouth bass in a lake. It did however identify that the error can lead to the incorrect distribution of nests and juveniles/adults. Consequently, comparisons of predicted versus observed nest and juvenile/adult densities in different sites of Lake Opeongo and Long Point Bay, Lake Erie were not performed in the model validation.

The smallmouth bass habitat model was validated using nest density, catch and creel data from Lake Opeongo, Ontario and Long Point Bay, Lake Erie. Simulations were performed using the habitat characteristics that describe these sytems. These simulations showed that the calculated nesting and juvenile/adult suitabilites are positively related to observed nest densities and CUE data, respectively, but the relationships were not strong in either lake. Mean lengths at age were within those normally seen in the smallmouth bass populations of both lakes.

The model overestimated the nest densities in both systems. This may be attributed to the model incorrectly describing the effects of density on nesting and overestimating the potential number of males available for nesting. Improvements that can be made to these components of the model are discussed.

The model validation demonstrates how the model can be applied to different lake systems. The results indicate how components of the model can be improved to better describe habitat effects on smallmouth bass populations. The results of the sensitivity analysis and model validation indicate that the program can be used to determine the effects of habitat changes on smallmouth bass population densities but further modification is required to successfully determine site-specific habitat suitabilities for smallmouth bass. Improvements to the ideal free distribution programming of the model should enhance the ability of the model to predict the spatial distribution of nests and juveniles/adults in a water body.

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APPENDIX A

Predicting Littoral Temperatures in Lakes

Littoral water temperature is one of the most important factors driving the reproduction and growth of smallmouth bass however, littoral temperature data are rarely available. To solve this problem, we developed an empirical model to predict littoral temperatures in different areas of a lake using data from Lake Opeongo (Finlay et al. *In review*). A littoral water temperature model has been developed by Shuter and Matuszek (1996) but it does not incorporate the influence of wind on littoral temperatures. Wind events can tilt the thermocline of a lake resulting in warm waters downwind and cool hypolimnetic waters in upwind areas (Spigel and Imberger 1980).

Stowaway temperature loggers were used to record temperatures every 15 minutes throughout the littoral zone of Lake Opeongo from twenty days after ice-out till the end of October 1998. They were placed at depths ranging from 1 - 2.5 m. The effective fetch of each thermistor location was calculated by measuring the distance across the water to the furthest point of land along the prevailing wind direction(s) (Scheffer et al. 1992). The equation used was:

$$F=\Sigma(\cos(a)*L(a))/(\Sigma\cos(a))$$

F = effective fetch (m)
a = the angle of measurement (-45°, 0° and +45°) where 0° represents the direction of the prevailing winds
L = the distance (m)

The effective fetches in eight directions (N, NE, E, SE, S, SW, W, NW) were calculated for each thermistor location. Weather data from Lake Opeongo provided estimates of the proportional occurence of each wind direction (Finlay et al. *In review*). The effective fetches in each direction were then weighted using these proportions and summed to produce the effective fetch of each thermistor site.

Once retrieved and calibrated, the average daily water temperature was computed for each of the loggers. The average daily temperatures of all loggers together represented the mean daily littoral temperatures for the whole lake. The daily deviations from the mean littoral temperatures were then calculated for each logger. These daily deviations were then averaged for each season (spring, summer and fall). Spring, summer and fall were defined by day, June 21 was the onset of summer and September 21 represented fall. Logger sites which were consistently warmer or cooler than the mean temperatures throughout the ice-free season were then choosen to analyze the influence of wind (effective fetch) on littoral water temperatures.

These thermistors had effective fetches ranging from 184 – 960 m. Deviations from the spring littoral temperatures ranged from -0.66 °C to 0.67 °C. Summer deviations ranged from -0.5 °C to 0.54 °C and in the fall from -0.97 °C to 0.54 °C. Regression analyses were performed to model the relationships between effective fetch and the deviations from the mean littoral temperatures in each season (Figure A.1).

THE MODEL

The model developed by Shuter et al. 1983 (Shuter et al. model) to predict surface water temperature cycles was modified to represent littoral temperatures. This model was derived from temperature measurements taken offshore over the deepest part of the lake at a nominal depth of 1 m. It uses mean annual air temperature, mean depth and ice-free day to produce a symmetrical sine wave representing surface temperatures during the ice-free season.

The first component of the Shuter et al. model to be modified was mean depth. After inputting depths of 1-5 m into the Shuter et al. model, it was apparent that a depth of 2m most closely fit the observed mean littoral temperatures in Lake Opeongo. Therefore the mean depth value of the Shuter et al. model was converted to a littoral depth value of 2 m.

Secondly, the Shuter et al. model predicts surface temperatures therefore some coefficient that represents the seasonal difference between littoral (2 m deep) and surface (0 m) temperatures had to be included. For example, at the beginning of the ice-free season littoral depth (2 m) temperatures would be close to 4°C while the surface is frozen. Plotting the difference between temperatures at littoral depth (2m) and the surface throughout the ice-free season produced the following polynomial (Figure A.2):

$$y=0.0004d^2-0.0859d+4$$

y = the difference between temperatures at surface and at 2 m
d = the day in the ice-free season

The effective fetch findings were then added to the Shuter et al. model to produce the following seasonal models for littoral water temperatures:

Spring: $T(A,Z,d,c) = (0.48*\ln(c)-2.96)+[(Tmax(A,Z)-T0)*\sin(\pi*d/D(A,Z)+T0)-1]+(0.0004*d^2-0.0859d+4)$

Summer: $T(A,Z,d,c) = (0.311*\ln(c)-1.97)+[(Tmax(A,Z)-T0)*\sin(\pi*d/D(A,Z)+T0)-1]+(0.0004*d^2-0.0859d+4)$

Fall: $$T(A,Z,d,c) = (0.417{*}\ln(c)-2.71)+[(Tmax(A,Z)-T0){*}\sin(\pi{*}d/D(A,Z)+T0)-1]+(0.0004{*}d^2-0.0859d+4)$$

T= temperature (°C)
A = mean annual air temperature
d = day in the ice-free season
Tmax = maximum temperature calculated as function of A and littoral depth (2 m)
c = effective fetch (m)
D= duration of ice free season

MODEL VALIDATION AND DISCUSSION

Five sites in Lake Opeongo that were not used to construct the model were used to validate it. Effective fetches in these sites ranged from 538 to 1481m. Six sites in Long Point Bay, Lake Erie were also used to validate the model (Doka unpublished data). The effective fetches in these sites ranged from 2686 to 14856m. Predicted temperatures were calculated at ten day intervals throughout the ice-free season and plotted against the observed temperatures on those days. Observed temperatures were not available for the entire ice-free season in Lake Erie so comparisons were made when possible.
Predicted temperatures were similar to the observed in the five sites of Lake Opeongo (r^2=0.80 - 0.85, Figure A.3). The slopes of predicted to observed temperatures in all sites were less than one (Table A.1). This suggests that the model is underestimating the cooler littoral temperatures seen during spring and fall while overestimating temperatures in the summer. Since thermistors were removed three to four weeks after the onset of fall (September 21), observed temperatures in the fall occupy only two or three points on each graph (Figure A.3). Fall predictions were also within two degrees of the observed temperatures therefore we can assume that most of the cooler observed temperatures are from the spring. The discrepancy between the model predictions and observed temperatures in the spring can be explained upon closer investigation of the observed temperatures. 1998 was an El Niño year and air temperatures in Central Ontario were much warmer than normal from October to May. For example temperatures were 6°C above normal in February (Environment Canada 2000). Using the average air temperature typically seen in Central Ontario underestimated the mean annual air temperature during 1998.

In Long Point Bay, the slopes of the Lake Erie regressions are closer to one than in Lake Opeongo (Figure A.4 and A.5). A linear regression of the data from all sites revealed that the model generally predicted 1 °C lower than the observed temperature (r^2=0.91, Table

A.2). This suggests that the model calculates littoral water temperatures in Lake Erie even more accurately than in Lake Opeongo.

Overall the model validation demonstrated that the littoral water temperature model developed here can successfully be used to estimate average littoral temperatures throughout different littoral areas of a lake.

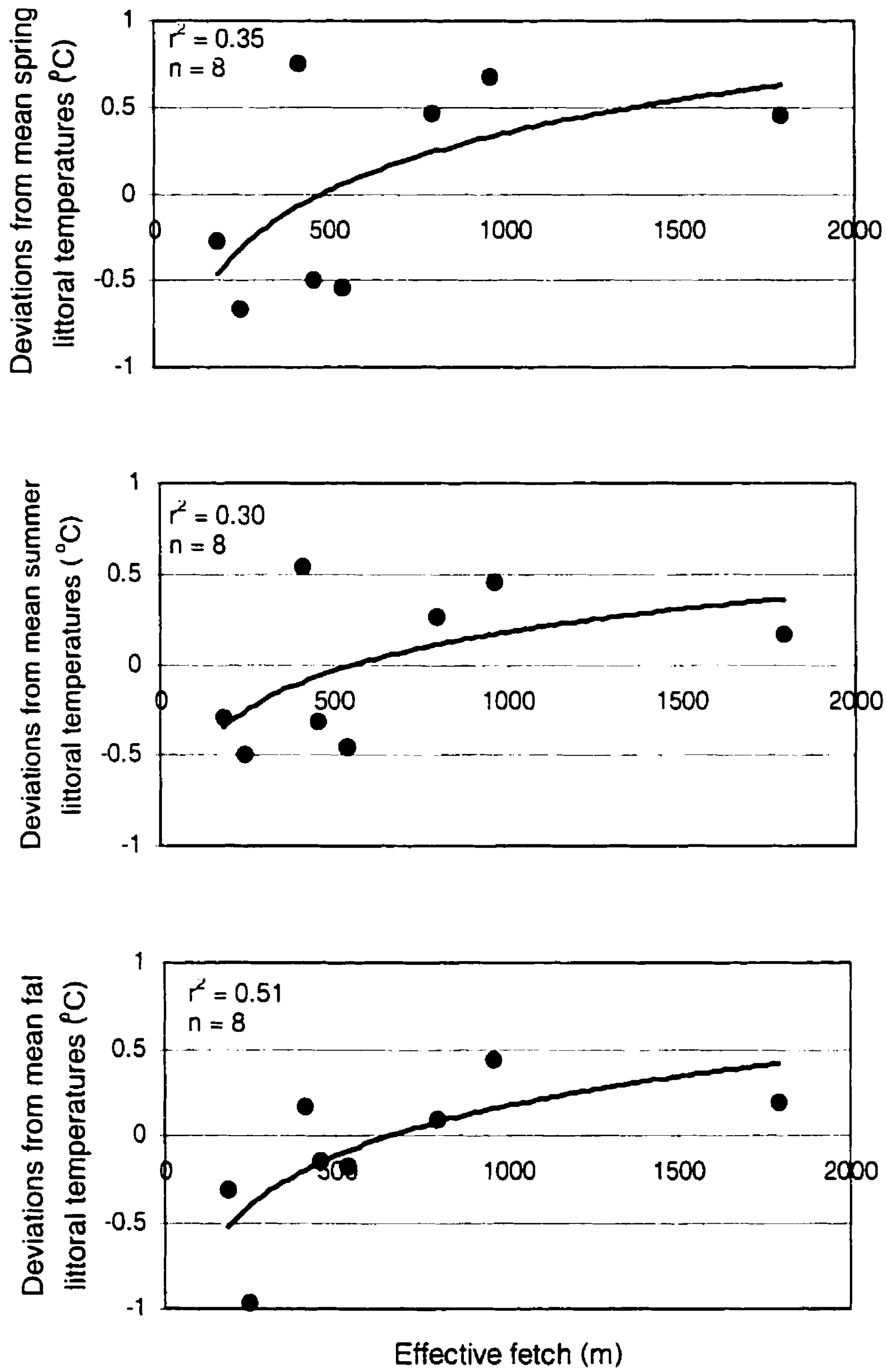

Figure A.1: Relationship between effective fetch and deviations from the mean littoral temperatures for eight sites in Lake Opeongo that were consistently warmer or cooler than the average littoral temperatures. Spring represents ice-out to June 21, summer June 21 – September 21 and fall September 21 till thermistors were retrieved.

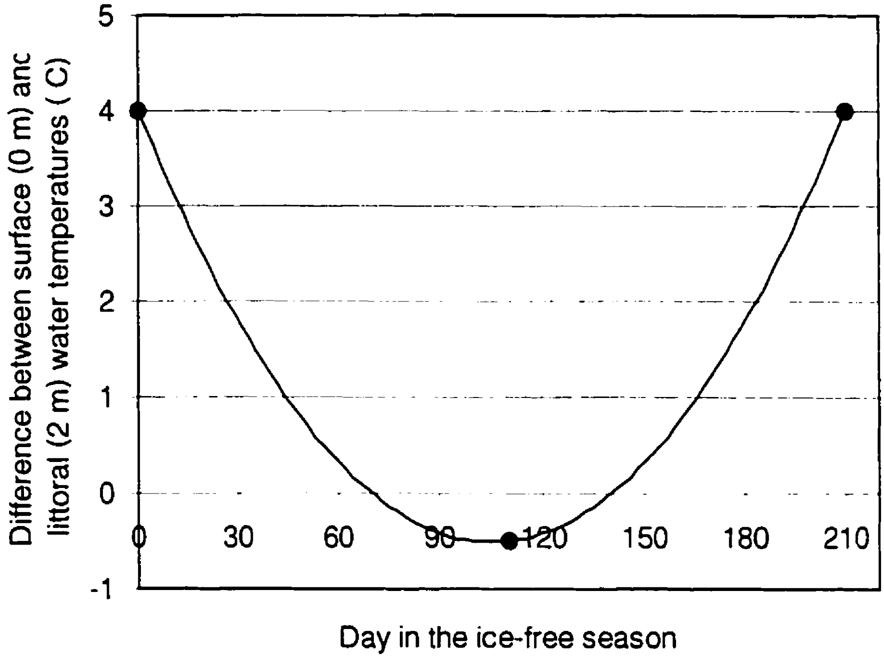

Figure A.2: A polynomial representing the difference between surface (0 m) and littoral (2 m) temperatures throughout the ice free season.

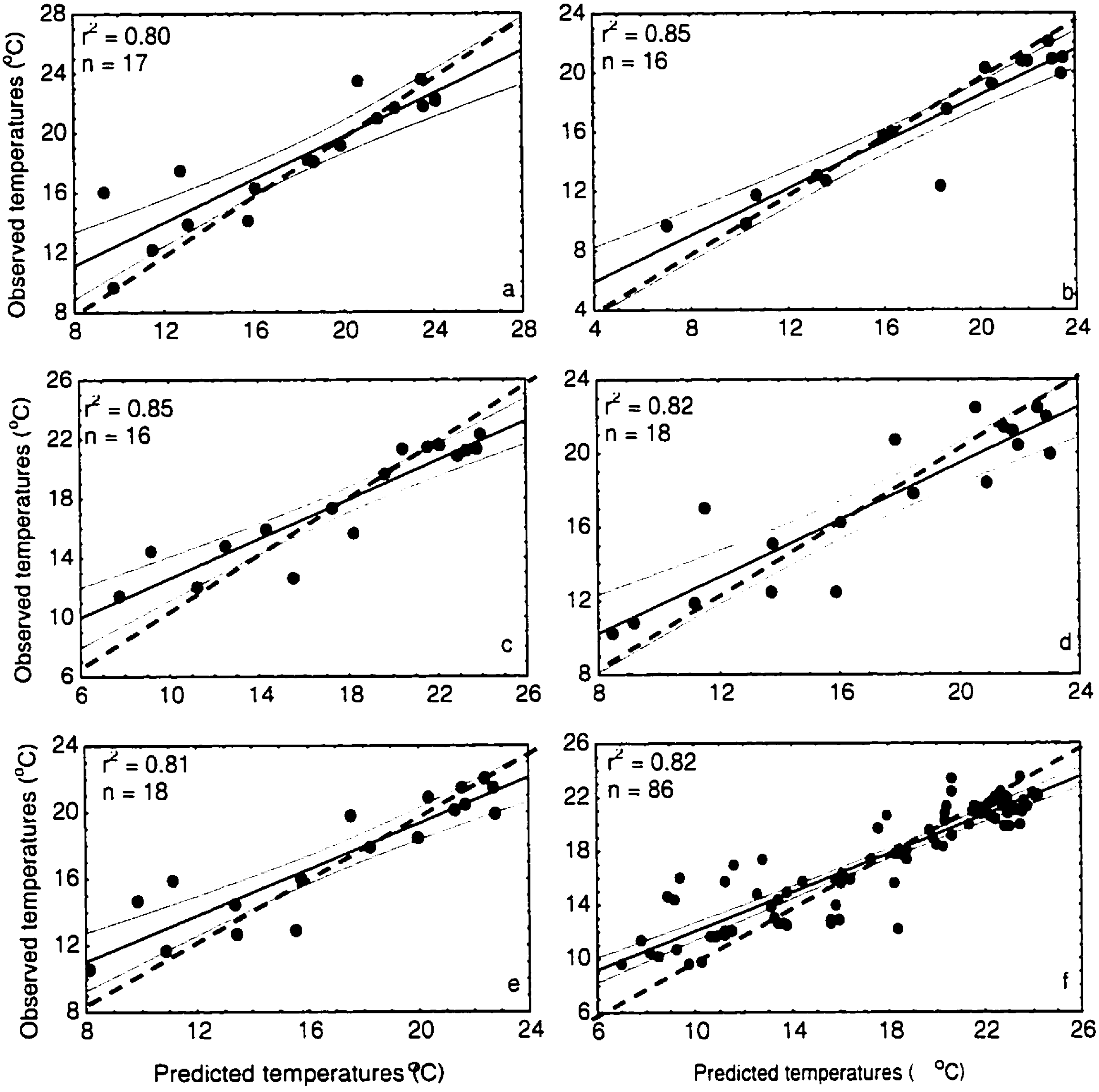

Figure A.3: Observed versus predicted temperatures for five sites in Lake Opeongo. Each point represents the predicted versus observed temperatures at ten day intervals throughout the ice-free season. Sites a to e have effective fetches of 959 m, 538 m, 1481 m, 793 m, 686 m, respectively. f) represents all data combined. The solid line represents the regression line. The dashed line represents the 1:1 relationship.

Table A.1: Slopes and y-intercepts for linear regressions of predicted versus observed temperatures in five sites in Lake Opeongo.

Site	Slope	Y-intercept
a	0.719	5.381
b	0.782	2.788
c	0.662	6.007
d	0.767	4.102
e	0.692	5.490
f (all sites)	0.719	4.863

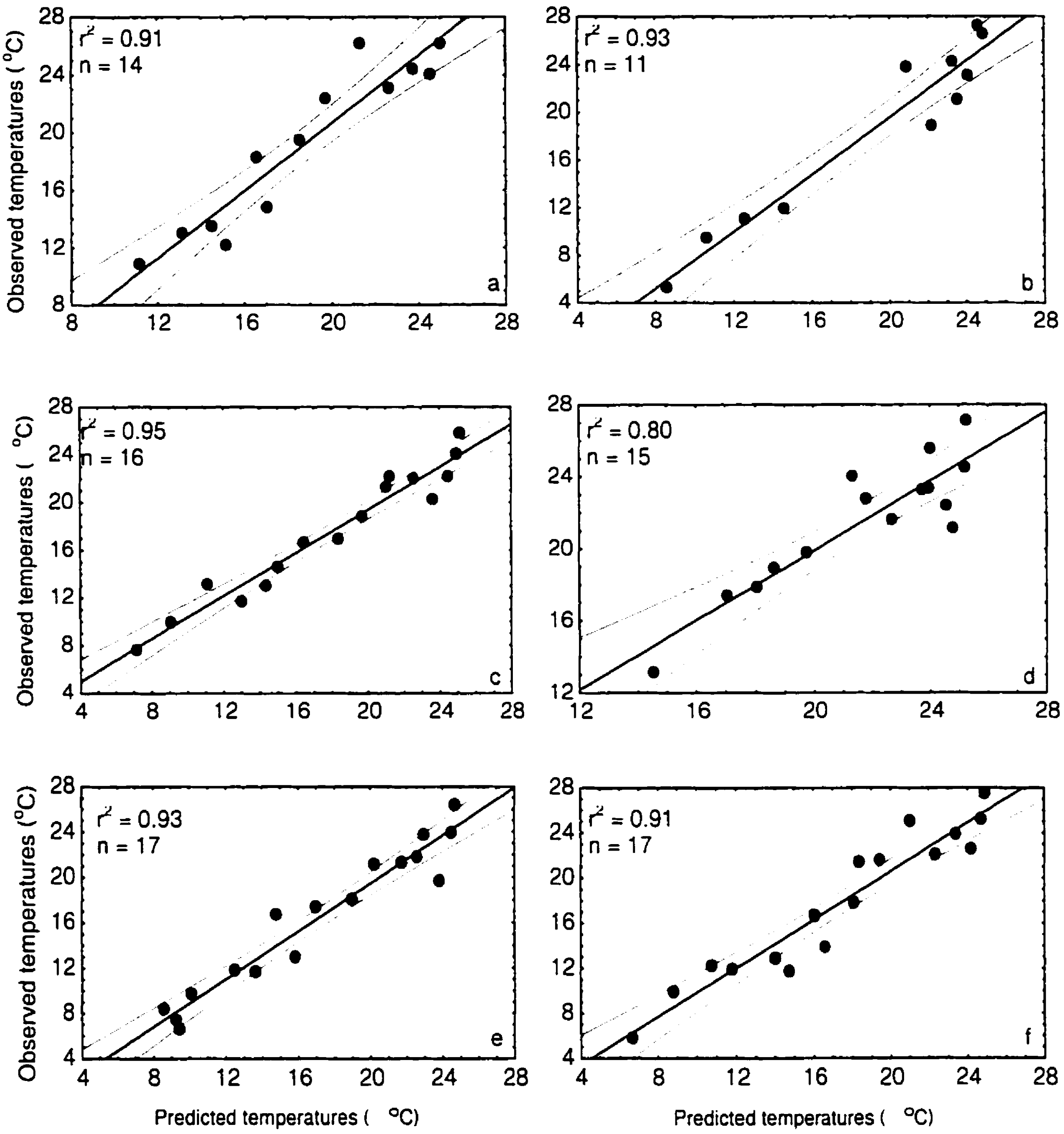

Figure A.4: Predicted versus observed temperatures for six sites in Long Point Bay, Lake Erie used to validate the water temperature model. Each point represents the predicted versus observed temperatures at ten day intervals throughout the ice-free season.

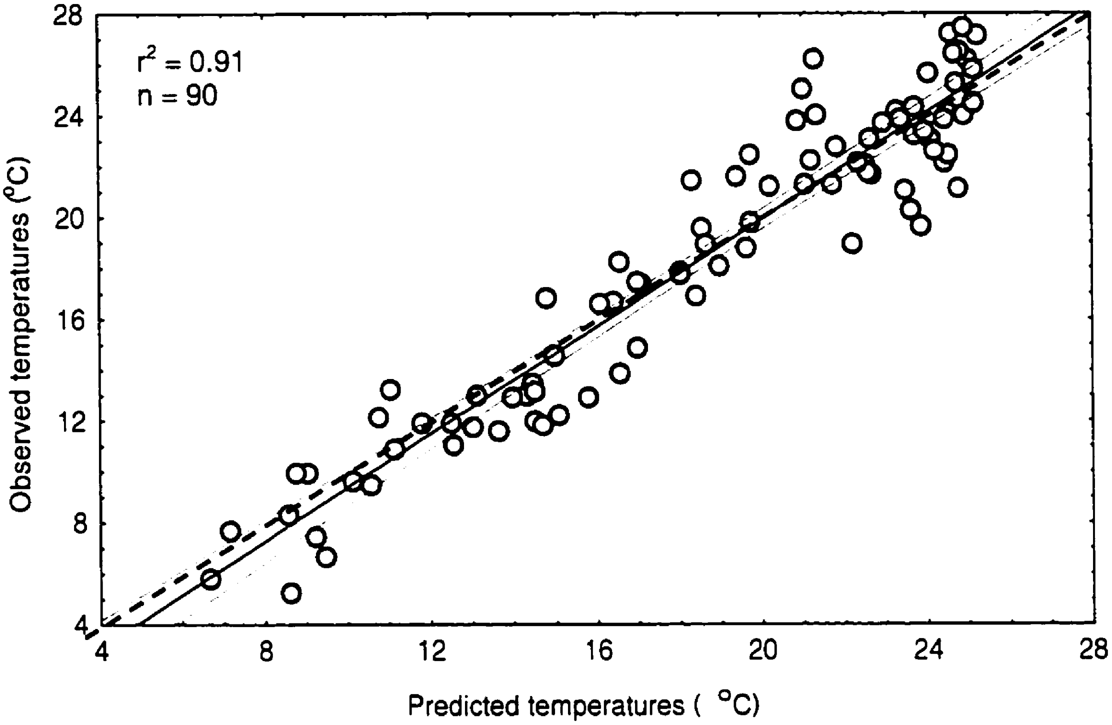

Figure A.5: Predicted versus observed temperatures throughout Long Point Bay, Lake Erie. The solid line represents the linear regression line. The dashed line represents the 1:1 relationship.

Table A.2: Slopes and y-intercepts for linear regressions of predicted versus observed temperatures in six sites in Long Point Bay, Lake Erie.

Site	Slope	Y-intercept
a	1.205	-3.288
b	1.193	-4.304
c	0.899	1.407
d	0.967	0.564
e	1.072	-0.866
f	1.054	-1.622
all sites	1.051	-1.112

APPENDIX B

Substrate suitabiliy for smallmouth bass nesting

Seven Central Ontario lakes were used to study the suitability of different substrates for smallmouth bass nesting. This included lakes, Billings (44°56', 78°22') 102 ha, Davis (44°47', 78°43') 105 ha, Four Mile (44°41', 78°45') 787 ha, Long (45°03', 78°22') 88 ha, Mountain (44°59', 78°43') 319 ha, Opeongo (45°42', 78°22') 5860 ha and Tock (45°16', 78°56') 117 ha.

Five substrate categories were defined (Harker 1982) and the shoreline length of each were mapped using whole-lake littoral surveys either by canoe or mask and snorkel.

Sand = (>80% of substrate covered by particles ≤2mm in diameter)
Sand and rock = (≥ 20% or more of substrate composed of particles >140mm and at least 50% ≤60 mm)
Gravel = (≥70% of substrate covered by particles ≤100mm and at least 10% in the 20 – 100mm range)
Rock = (≥40% or more of substrate covered by particles >140mm in diameter)
Weed = (≥40% of substrate covered by aquatic plants) and litter (≥80% of substrate covered by organic debris, logs, sticks and decaying plant material)

Active nests were distinguishable from the surrounding substrate by their depressed, saucer-like shape, the presence of eggs or fry and the presence of the guarding male. Snorkelling and canoeing were effective means of identifying smallmouth bass nests. Active nests and the substrate for each were mapped by snorkellers or canoeists during several spawning seasons in each of the study sites. Nest counts were performed during 1978 - 1980 in lakes Billings, Davis, Four Mile, Long, Mountain, and Tock. Lake Opeongo was studied in 1977-1979, 1983 -1985,1989 -1994.

Nest densities (nests/100m) in each substrate type were calculated for each year in each lake. These densities were then averaged to represent the mean density in each substrate type for each lake. The average nest density for each substrate type among all lakes was then calculated (Table A-B.1.) Substrates with higher nest densities are assumed to be more suitable for smallmouth bass nesting. The nest densities among the substrate types were then averaged to one to produce the substrate suitability equation:

$$S_N = 0.75(a) + 1(b) + 0.64(c) + 0.75(d) + 0.20(e) + 0.26(f)$$

Table A.B.1: Mean nest densities (nests/100m) in the different substrate types of seven Central Ontario Lakes (Harker 1982, Ridgway unpublished data).

Lake	**Substrate composition**					
	Sand	**Sand/rock**	**Gravel**	**Rock**	**Weed**	**Litter**
Billings	2.08		0.75	1.88	0.05	0.65
Davis	0.55		0.15	0.93	0.20	0.07
Four Mile	1.20	2.87	1.33		0.32	
Long	1.10		1.15	1.35	0.45	0.80
Mountain	0.24	0.37	0.3	0.40		0.17
Opeongo	0.23	0.30	0.34	0.27	0	0.14
Tock	0.75		1.30	0.48	0.45	0
Mean	0.88	1.18	0.76	0.88	0.24	0.30
Suitability value	0.75	1.00	0.64	0.75	0.20	0.26

APPENDIX C

Bioenergetics model used for growth component of smallmouth bass habitat model (Shuter and Post 1990).

Parameter	Parameter definition	Parameter value
CONS	consumption (g/g*d)	
CA	maximum rate for 1 g fish (g/g*d)	0.25
CB	weight component	-0.31
CQ	determines how consumption increases with temperature for temperatures below CTO	3.8
CTO	optimal temperature (°C)	29
CTM	maximum temperature (°C)	36
RESP	respiration (g/g*d)	
RA	maintenance rate for 1 g fish (g/g*d)	0.03
RB	weight exponent	-0.21
RQ	determines how respiration increases with temperature for temperatures below RTO	3.3
RTO	optimal temperature (°C)	30
RTM	maximum temperature (°C)	37
ACT	activity multiplier	2
SDA	specific dynamic action multiplier	0.16
FA	egestion multiplier, fecal waste	0.104
UA	excretion mutliplier, nitrogenous waste	0.068
P	food availability, proportion of maximum consumption	1
T	water temperature (°C)	
C_R	cost of reproduction	0.015
GROWTH(g)	growth in grams	

MODEL EQUATIONS

Functions for water temperature effects on consumption:

$$CONW := \ln(CQ)\cdot(CTM - CTO)$$

$$CONY := \ln(CQ)\cdot(CTM - CTO + 2)$$

$$CONX := \frac{CONW^{2}\cdot\left[1 + \ 1 + \frac{40}{CONY}^{\,0.5}\right]^{2}}{400}$$

$$V := \frac{CTM - T}{CTM - CTO}$$

$$CONS := CA\cdot w^{CB}\cdot p\cdot V^{CONX}\cdot \exp(CONX\cdot(1 - V))$$

Functions for water temperature effects on respiration :

$$RESPW := \ln(RQ)\cdot(RTM - RTO)$$

$$RESPY := \ln(RQ)\cdot(RTM - RTO + 2)$$

$$RESPX := RESPW^{2}\cdot\frac{\left[1 + \ 1 + \frac{40}{RESPY}^{\,.5}\right]^{2}}{400}$$

$$RV := \frac{RTM - T}{RTM - RTO}$$

$$RESP := RA\cdot w^{RB}\cdot RV^{RESPX}\cdot \exp(RESPX\cdot(1 - RV))$$

Egestion: $F := FA\cdot CONS$

Excretion: $EXC := UA\cdot(CONS - F)$

Specific dynamic action: $sda := SDA\cdot(CONS - F)$

Respiration including activity : $ARESP := ACT\cdot RESP$

GROWTH (g): $g := CONS - ACT\cdot RESP - F - sda - EXC$

Conversion from weight (g) to length (mm)

$w1 := w + w\cdot GR$ $\alpha := 4.13$ $\delta := .331$

GROWTH (mm): $GRL := 10\cdot\ \alpha\cdot w1^{\delta} - \alpha\cdot w^{\delta}$

- At maturity (age 3):
  GROWTH (g) = g – (0.015*g)

APPENDIX D

List of abbreviations for model variables

Abbreviation	Variable	Abbreviation	Variable
S_N	nesting substrate suitability	P	proportion consumed/maximum consumption
p_S	sand	[TDS]	total dissolved solids concentration
p_{SR}	sand and rock	HSI_N	habitat suitability for nesting
p_G	gravel	HSI_{JA}	habitat suitability for juveniles and adults
p_R	rock	NN	number of nests
p_W	weed	G_{ACT}	actual growth
p_L	litter	G_{MAX}	maximum growth
		THR	total home range area
S_{JA}	substrate suitability for juveniles and adults	AA	area available
g	sand	TF/HSITF	habitat suitability transformation factor
		F	fecundity
pH_S	pH suitability	H	time to hatch
		R	time to rise
dO_{2S}	dissolved oxygen suitability	L	length of fish
Z_T	thermocline depth	YOY	young-of-the-year
FT	maximum fetch	N_{YOY}	number of YOY surviving each day
Z	mean depth	A_R	energy reserves for winter
TEMP	mean annual air temperature	A_S	energy depleted to point of starvation
WH_N	wave height suitability for nesting	R	rate of depletion
g	gravitational constant	LWS	length of winter (days) used to calculate survival
EFF	effective fetch		