

Do spatial models of growth rate potential reflect fish growth in a heterogeneous environment? A comparison of model results

Tyler JA, Brandt SB. Do spatial models of growth rate potential reflect fish growth in a heterogeneous environment? A comparison of model results.

Ecology of Freshwater Fish 2001: 10: 43–56. © Munksgaard, 2001

Abstract – Spatial models of fish growth rate potential have been used to characterize a variety of environments including estuaries, the North American Great Lakes, small lakes and rivers. Growth rate potential models capture a snapshot of the environment but do not include the effects of habitat selection or competition for food in their measures of environment quality. Here, we test the ability of spatial models of fish growth rate potential to describe the quality of an environment for a fish population in which individual fish may select habitats and local competition may affect per capita intake. We compare growth rate potential measurements to simulated fish growth and distributions of model fish from a spatially explicit individual-based model of fish foraging in the same model environment. We base the model environment on data from Lake Ontario and base the model fish population on alewife in the lake. The results from a simulation experiment show that changes in the model environment that caused changes in the average growth rate potential correlated extremely highly ($r^2 \geq 0.97$) with changes in simulated fish growth. Unfortunately, growth rate potential was not a reliable quantitative predictor of simulated fish growth nor of the fish spatial distribution. The inability of the growth rate potential model to quantitatively predict simulated fish growth and fish distributions results from the fact that growth rate potential does not consider the effects of habitat selection or of competition on fish growth or distribution, processes that operate in our individual-based model and presumably also operate in nature. The results, however, do support the use of growth rate potential models to describe the relative quality of habitats and environments for fish populations.

J. A. Tyler¹, S. B. Brandt²

¹Worcester Polytechnic Institute, Department of Biology and Biotechnology, Worcester, Massachusetts, ²NOAA Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan, USA

Key words: growth rate potential; fish bioenergetics; individual-based model; habitat selection; habitat quality; fish growth; density dependence

Jeffrey A. Tyler, Worcester Polytechnic Institute, Department of Biology and Biotechnology, 100 Institute Rd., Worcester, MA 01609, USA; e-mail: tylerj@wpi.edu

Accepted for publication September 5, 2000

Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Advances in remote sensing technology and an increased appreciation of the importance spatial heterogeneity in the environment have led to the development of spatially explicit techniques to model the environment for fishes (Tyler & Rose 1994; Giske et al. 1998). By combining spatially explicit data with behavioral, physiological or life history models, researchers have made significant strides in modeling spatial heterogeneity of pelagic

environments in fitness-related currencies (Fiksen et al. 1995; Hinckley et al. 1996; Perry et al. 1996). These types of models have been used to investigate the effect of environmental change, either natural or anthropogenic, on a number of different fish populations.

Growth is a commonly used fitness currency for describing the quality of pelagic environments for fish (Brandt et al. 1992; Rand et al. 1997). Fish growth rate potential is the rate of growth predicted for a specific species and life-stage of fish in

the absence of competition. The growth rate potential of an environment may be modeled with data on water temperature and food density that are used as inputs to foraging and bioenergetic models of fish growth (Brandt & Kirsch 1993; Mason et al. 1995; Tyler 1998). Spatial models of fish growth rate potential show how the spatial variation in food and temperature affect fish habitat quality for a number of species in a variety of environments including striped bass (*Morone saxatilis*) in Chesapeake Bay (Brandt et al. 1992; Brandt & Kirsch 1993), lake trout (*Salvelinus namaycush*) and chinook salmon (*Oncorhynchus tshawytscha*) in Lake Ontario (Goyke & Brandt 1993), and in Lake Michigan (Mason et al. 1995), walleye (*Stizostedion vitreum*) in Lake Erie (Horne et al. 1996) and lake trout in Flaming Gorge reservoir, Wyoming (Luecke et al. 1999).

Spatial models of fish growth rate potential represent an important advance in the use of bioenergetic models to understand how environmental heterogeneity might affect fish habitat. Earlier applications of bioenergetic models showed how water temperature and food availability affect fish growth and production and the non-linear effects of temperature and food on growth (Kitchell et al. 1977; Peterman 1981; Stewart & Ibarra 1991; Sprules & Goyke 1994). Also, bioenergetic models have increased our understanding of the species- and life stage-specific nature of fish growth (Kitchell et al. 1977; Hewett & Johnson 1992; Hartman & Brandt 1993). The majority of applications of bioenergetic models, however, used average conditions to describe the environment and assumed the environment to be homogeneous (Stewart et al. 1981, 1983; Madenjian 1991; Rand et al. 1995). Spatial models show wide variation in fish growth rate potential across the spatial extent of an environment. Assuming a homogeneous environment with average conditions can have an important effect on the assessment of a habitat's quality (Mason & Brandt 1996; Hondorp 1998). Spatial models of fish growth rate potential have shown how the joint distribution of water temperatures and food densities affect fish habitat quality. These models have been used to examine 1) the quality of an environment for different fish species (Goyke & Brandt 1993), 2) seasonal changes in fish habitat quality (Brandt & Kirsch 1993) and 3) the suitability of an environment for an introduced fish species (Demers et al. in press).

The density of competitors can have a large effect on habitat or environment quality (Fretwell & Lucas 1970; Milinski & Parker 1991). However, spatial models of fish growth rate potential have described the environment in terms of growth for a specific fish species, independent of the abun-

dance or distribution of the fish population (Brandt et al. 1992). Fish foraging and growth, key factors of habitat quality, may be affected by fish number (Boisclair & Leggett 1989; Fox & Flowers 1990) and distribution (Godin & Keenleyside 1984; Power 1984; Tyler & Gilliam 1995). Individual-based models of fish populations have shown that the abundance and distribution of fish can effect their survival and growth rates in a density-dependent manner (DeAngelis et al. 1991, 1994; Rose & Cowan 1993; Tyler & Rose 1997; Giske et al. 1998). These kinds of models are particularly well suited tools for exploring the effect of population abundance and distribution on the quality of habitats and of environments for individuals (DeAngelis & Gross 1992; Tyler & Rose 1994).

In this study we examine the effectiveness of spatial models of fish growth rate potential to describe the quality of a pelagic habitat for a fish population that may vary in the number of individuals and in which individuals select habitats with a growth maximization rule. We compare the environment's growth rate potential to the simulated growth of fish in an individual-based population model (hereafter: simulated fish growth). We base the model environment on data from the pelagic zone of Lake Ontario's western basin and the simulated fish on alewife (*Alosa pseudoharegus*), one of the two dominant planktivores of Lake Ontario (O'Gorman et al. 1987). We compute the growth rate potential for fish in this environment with the same techniques as those used in previous studies of spatial heterogeneity in growth rate potential (Brandt et al. 1992; Tyler 1998). We compute simulated fish growth with a spatially explicit individual-based model that describes a simulated alewife population in which consumption of zooplankton by individual alewife may be affected by local fish density, and individual alewife select habitats based on a growth maximization rule. We compare growth rate potential with simulated fish growth so that we may assess the correspondence of growth rate potential values to the growth that fish may achieve when competition and habitat selection can affect fish growth, and thereby the value of growth rate potential as a measure of fish habitat quality.

Model description

Environment

We use the same model environment, based on the pelagic zone of the western basin of Lake Ontario, to calculate fish growth rate potential in the spatial model of the environment and simulated fish growth in the spatially explicit individual-based model. The environment is a grid of 100×100 cells.

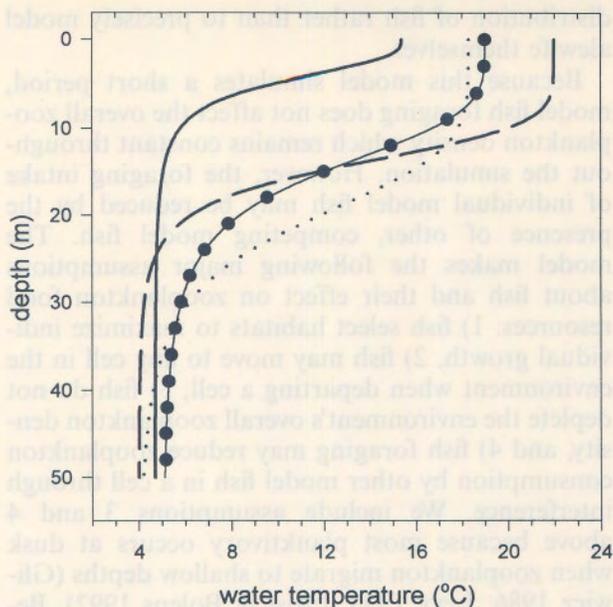


Fig. 1. Water temperature profiles used to create temperature fields in the model. Temperature profiles were collected in Lake Ontario (—) on June 6, 1996 in the western basin (D. W. Hondorp, J. K. Horne & J. A. Tyler, unpublished data), (---) on July 11, 1995 in the central basin, (.....) and on July 17, 1995 (W. G. Sprules, unpublished data) in the western basin. These represent temperature profiles with a shallow, medium and deep thermocline in Lake Ontario. An averaged water temperature profile (—•—) was used to create the water temperature field for model corroboration simulations.

Each cell has a volume (V) of 10 m^3 and an assigned water temperature and zooplankton density.

We use a suite of model environments that differ in water temperature field and zooplankton density. Temperature fields are taken from data collected in Lake Ontario in the summer of 1995 and 1996 (Fig. 1). We distinguish between temperature fields based on the depth of the thermocline that occurs at 4–8 m, (“shallow”), 12–17 m (“medium”) and 12–25 m (“deep”). Average temperatures differ between the three temperature fields with values of: 6.1°C (shallow), 10.1°C (medium) and 11.1°C (deep). In all model environments zooplankton are distributed according to a normal, random distribution with variance equal to the mean. Average densities of zooplankton are set at one of three levels: 25, 50, and $100 \text{ zooplankton} \cdot \text{l}^{-1}$ and represent low, medium and high densities of zooplankton found in Lake Ontario (W. G. Sprules, University of Toronto, personal communication). Individual zooplankton are assigned a size of 0.4 mm and $25 \mu\text{g}$ wet weight.

Growth rate potential

Spatial models of fish growth rate potential describe the environment in the currency of the ex-

pected growth ($\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$) a fish may achieve given the available food and water temperatures (Brandt et al. 1992). These models explicitly consider spatial heterogeneity in habitat quality as measured by growth rate potential for a specified size and species of fish. Growth rate potential is affected by the abundance and distribution of food, water temperatures and the physiology of the fish being modeled (Goyke & Brandt 1993; Horne et al. 1996; Hondorp 1998). A complete description of spatial modeling fish growth rate potential may be found in Tyler (1998).

The bioenergetics model for fish growth used in the spatial model of growth rate potential and in the spatially explicit individual-based model is based on the well-established “Wisconsin” model (Hewett & Johnson 1992; Hansen 1997). The model uses a mass-balance approach to find fish growth in which growth (G) is computed as food consumption (C) minus the energetic costs of respiration (R), egestion (F), excretion (U) and specific dynamic action (S):

$$G = C - (R + F + U + S) \quad (1)$$

All components of the bioenergetics model are species-, size- and temperature-dependent. We use the parameters developed for growth of alewife (Stewart & Binkowski 1986). We assign the fish a length of 150 mm and weight of 24.4 g (wet weight), which approximates a 2-year-old alewife (O’Gorman et al. 1987; Rand et al. 1994).

To compute consumption of zooplankton by model fish, we use the foraging model of Gerritsen & Strickler (1977). The foraging model computes consumption of zooplankton (CZ) as the multiple of zooplankton density (ZD , $\text{number} \cdot \text{l}^{-1}$), the volume searched (VS) by the model fish, and capture probability (P_{capture}):

$$CZ = ZD VS P_{\text{capture}} \quad (2)$$

The volume searched by a model fish (VS) is that of a cylinder with radius slightly greater (25%) than the fish’s gape area (GA) and length equal to the distance swum by the fish (DS).

$$VS = \frac{\Pi(1.25GA)^2 DS}{10^6} \quad (3)$$

$$GA = 0.02586 L^{1.7967} \quad (4)$$

L = length of model fish, distance swum by a fish is $DS = (SS \cdot L \cdot TF)$, SS = swimming speed in body lengths/s and is set to 2.0, $TF = 3600$ which is the number of seconds in the 1-h foraging period. Equation 4 for GA (mm^2) as a function of fish length comes from data collected on menhaden (*Brevoortia tyrannus*) (Kyle J. Hartman, University of West Virginia, personal communication). VS is

in mm^3 , so dividing by 10^6 converts VS to units of liters.

The ratio of energy density in predator and prey strongly affect growth computations made by bioenergetic models (Hartman & Brandt 1995a). In alewife, energy density changes seasonally (Stewart & Binkowski 1986). Here we use an energy density for model alewife of $1900 \text{ cal} \cdot \text{g}^{-1}$ wet weight (Stewart & Binkowski 1986) and an energy density for zooplankton of $450 \text{ cal} \cdot \text{g}^{-1}$ wet weight (Snow 1972; Hewett & Johnson 1992) in our calculation of growth rate potential.

Simulated fish growth

We use a spatially explicit individual-based model to determine the distribution of model fish and to calculate simulated fish growth. Simulated fish growth is the growth achieved by model fish in a simulation of the spatially explicit individual-based model and includes any effects of competition and habitat selection that may affect zooplankton consumption by model fish. Simulated fish growth calculations in the spatially explicit individual-based model use the same bioenergetics model as that used in the spatial model of fish growth rate potential (equations 1, 2 and 4). Simulated fish growth and growth rate potential differ in that zooplankton consumption by model fish may be reduced through the foraging of competing model fish in the individual-based model, but there is no such competition in the spatial model of growth rate potential. The mechanism for modeling zooplankton consumption in the individual-based model is described in detail below (see section on search and consumption).

The individual-based model allows individual model fish to move about the model environment using a growth maximization habitat selection rule. As in the spatial model of fish growth rate potential, the model fish have a length of 150 mm and wet weight of 24.4 g. The model simulates fish foraging during a 1-h foraging period. Fish feed only on the zooplankton in the cell, or patch, that they inhabit. At the end of the foraging period model fish either depart to a new cell or remain in their current cell based on the growth maximization habitat selection rule. The behavioral rules used in the model, particularly the habitat selection rule, may not truly be appropriate for alewife. Specifically, the model allows individuals to move independently and there is no aggregation or schooling behavior incorporated into the habitat selection rule. We take this liberty in modeling alewife because we aim to assess the ability of growth rate potential models to describe habitat quality when competition and habitat selection affect the

distribution of fish rather than to precisely model alewife themselves.

Because this model simulates a short period, model fish foraging does not affect the overall zooplankton density which remains constant throughout the simulation. However, the foraging intake of individual model fish may be reduced by the presence of other, competing model fish. The model makes the following major assumptions about fish and their effect on zooplankton food resources: 1) fish select habitats to maximize individual growth, 2) fish may move to any cell in the environment when departing a cell, 3) fish do not deplete the environment's overall zooplankton density, and 4) fish foraging may reduce zooplankton consumption by other model fish in a cell through interference. We include assumptions 3 and 4 above because most planktivory occurs at dusk when zooplankton migrate to shallow depths (Gliwicz 1986; Levy 1990; Frost & Bolens 1992). Because zooplankton migrate to the surface and have high population numbers, we assume that their populations cannot be depleted in a short period and if local foraging does cause a short-term reduction in zooplankton density, then zooplankton migration will renew the food resource.

Search and consumption

Alewife are filter-feeding planktivores and in the spatially explicit individual-based model, the foraging of model fish begins with the same common depiction of a planktivore intake that is used to compute zooplankton consumption (CZ) for the spatial model of fish growth rate potential (equations 2, 3 and 4) (Gerritsen & Strickler 1977; Aksness & Giske 1993; Rose & Cowan 1993). Therefore, in the absence of other model fish, consumption of zooplankton by individual model fish in the individual-based model is no different than in the spatial model of fish growth rate potential.

In the presence of other model fish, zooplankton consumption may be reduced through competition for the common resource. Individual fish may consume $1/n$ of the zooplankton encountered simultaneously (ZES) by n model fish. ZES is a multiple of the volume simultaneously searched by n fish and the zooplankton density in that volume. Actual zooplankton consumption (C_{act}) is calculated as:

$$C_{act} = ZD (VS - VSS_{total}) P_{capture} + C_{vss} \quad (5)$$

Where VSS_{total} = the total volume simultaneously searched by more than a single model fish, and C_{vss} = consumption of zooplankton found in the volume simultaneously searched by more than one model fish. C_{vss} is found via:

$$C_{vss} = ZES_i P_{capture} \quad (6)$$

Where ZES_i =zooplankton encountered simultaneously by i model fish. Of the zooplankton encountered simultaneously, each model fish may capture $1/n$, which is included in the computation of ZES below.

The total volume simultaneously searched by model fish that encounter each other (VSS_{total}) is found by taking the multiple of the number of encounters between i model fish in a cell with n fish ($E_{i,n}$), the volume simultaneously searched in each encounter (VSS_i) and summing across all n fish in the cell.

$$VSS_{total} = \sum_{i=2}^n E_{i,n} VSS_i \quad (7)$$

The number of encounters between i model fish in a cell with n model fish ($E_{i,n}$) is computed as the number of ways that i model fish may be selected in a group of n , times the encounter rate (ER), times the time spent foraging (TF):

$$E_{i,n} = \binom{n}{i} (ER)^{i-1} TF \quad (8)$$

Assuming that model fish move randomly in a cell, the encounter rate between two competitors (ER , encounters $\cdot s^{-1}$) is computed as (Gerritsen & Strickler 1977; Bailey & Batty 1984):

$$ER = \frac{\Pi \left(\frac{2L}{\Pi^2} + GA \right)^2 \left(\frac{4SS}{3L} \right)}{V} \quad (9)$$

In computing the number of encounters between model fish ($E_{i,n}$), we use encounter rate as the mean probability of encountering a competitor per second. The actual number of encounters experienced by each individual model fish is a determined via a normal, random deviate with a mean of $E_{i,n}$ ($\bar{x} = \sigma^2$).

Each model fish may capture $1/n$ of the zooplankton encountered in the volume VSS_{total} . Computing the zooplankton encountered simultaneously (ZES) relies on calculating the volume simultaneously searched with i fish (VSS_i) in a cell with n fish. VSS_i is then multiplied by zooplankton density divided by i (ZD/i) to account for the fact that each model fish may capture only $1/i$ of the zooplankton in that volume. When two model fish encounter each other, each receive half of the zooplankton in the volume simultaneously encountered. When more than two model fish encounter each other simultaneously ($i > 2$), the volume searched simultaneously is that searched by all i model fish and that searched by fewer than i model

fish. Therefore, VSS_i is the sum of volume searched simultaneously by j model fish, $i \geq j > 1$:

$$VSS_i = \sum_{j=2}^i \frac{u_{j,i}}{10^6} \quad (10)$$

$U_{i,j}$ =the volume searched simultaneously by j model fish when i model fish are encountered. Dividing $U_{i,j}$ by 10^6 converts the units from mm^3 to liters. Calculating ZES requires calculating $U_{i,j}$ but also includes zooplankton density.

$$ZES_i = \sum_{j=2}^i \frac{u_{j,i}}{10^6} \frac{ZD}{j} \quad (11)$$

We use equations 10 and 11 to calculate VSS_i and ZES_i for $2 \geq i \geq 4$. We treat cases in which $i \geq 5$ as a special case for which the calculations of VSS_i and ZES_i take a form described later.

The volume searched simultaneously by an encounter between model fish is determined by the angle (α) at which the model fish encounter each other. When two individuals encounter each other, $i = 2$, we assume that on average $\alpha = 45^\circ$ (Fig. 2). Over a large number of encounters assuming that $\alpha = 45^\circ$ is valid because for $i = 2$, α may range 0-90. In this case, α may range from 0 to 90 because for

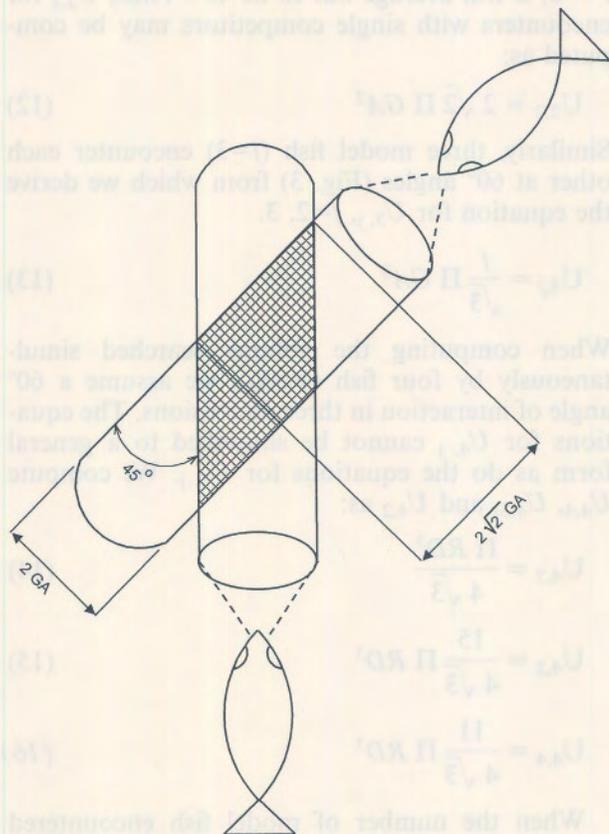


Fig. 2. Volume searched simultaneously (VSS) by two foraging fish (shaded area)

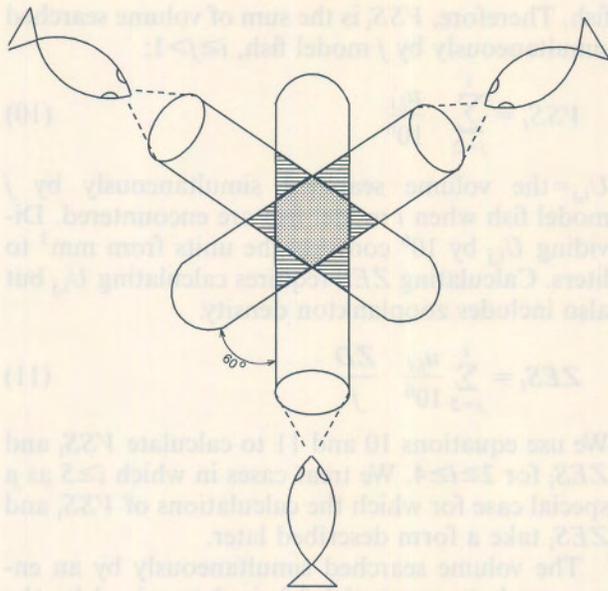


Fig. 3. Volume searched simultaneously (VSS) by three foraging fish. Stippled area is shared by all three, dashed area is shared by only two.

all values of α , $90 > \alpha \geq 180$ VSS_2 is identical to the value computed for the angle α' where $\alpha' = 180 - \alpha$. For a sufficiently large number of encounters with $i = 2$, α will average out to be 45° . Thus, $U_{2,2}$ for encounters with single competitors may be computed as:

$$U_{2,2} = 2 \sqrt{2} \Pi GA^3 \quad (12)$$

Similarly, three model fish ($i=3$) encounter each other at 60° angles (Fig. 3) from which we derive the equation for $U_{3,j}$, $j=2, 3$.

$$U_{3,j} = \frac{j}{\sqrt{3}} \Pi GA^3 \quad (13)$$

When computing the volume searched simultaneously by four fish (VSS_4), we assume a 60° angle of interaction in three dimensions. The equations for $U_{4,j}$ cannot be simplified to a general form as do the equations for $U_{3,j}$. We compute $U_{4,4}$, $U_{4,3}$, and $U_{4,2}$ as:

$$U_{4,3} = \frac{\Pi RD^3}{4 \sqrt{3}} \quad (14)$$

$$U_{4,2} = \frac{15}{4 \sqrt{3}} \Pi RD^3 \quad (15)$$

$$U_{4,4} = \frac{11}{4 \sqrt{3}} \Pi RD^3 \quad (16)$$

When the number of model fish encountered simultaneously equals or exceeds five ($i \geq 5$), we simplify our characterization of the volume search-

ed simultaneously (VSS_i) and zooplankton encountered simultaneously (ZES_i). We continue to assume that the average angle of encounter is 60° . The volume encountered simultaneously by all fish is a sphere with a radius = GA . As i increases, the volume simultaneously searched by j individuals, $i > j > 2$, becomes negligible and we do not include it in the calculation of VSS_i or ZES_i . The remaining volume searched simultaneously is shared between two model fish only. The search volume shared by two model fish is approximated as a cylinder with a cone removed on each end and the sphere shared by all i model fish removed from the middle (Fig. 4). When $i \geq 5$, VSS_i is approximated as:

$$VSS_{i \geq 5} = 1.623 \Pi GA^3 \quad (17)$$

To compute ZES_i for $i \geq 5$, zooplankton density and the amounts shared by 2 and by i model fish must be included:

$$ZES_{i \geq 5} = \Pi GA^3 ZD \left(0.873 + \frac{4}{3(i-1)} \right) \quad (18)$$

Habitat selection and movement

Fish move about the environment with a growth maximization habitat selection rule similar to the marginal value theorem (Charnov 1976). Individual fish remain in a cell until their growth rate in

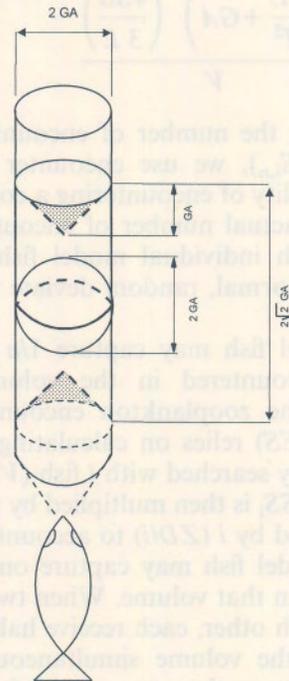


Fig. 4. Volume searched simultaneously (VSS) by five or more foraging fish. Sphere in the middle is shared by all fish. The remainder of the affected cylinder is shared by only two fish. See text for more detail.

that cell drops below a continually updated expectation of the average growth they would find in the environment. This rule causes simulated fish to remain in cells where their growth rate exceeds their average previous growth rate, but to leave cells in which their growth is lower than their average previous growth rate. When leaving a cell, fish move to any cell in the 100×100 cell environment selected at random.

Individual fish maintain an independent estimate of the average growth rate that they receive in the environment (γ). All fish are assigned an initial estimate of expected growth (γ_{prior}) which affects their cell departure early in the simulation (Bernstein et al. 1988). Fish are assigned $\gamma_{\text{prior}} = 2.0 \cdot GRP_{\text{max}}$ (GRP_{max} = maximum growth rate potential in the environment). We assign γ_{prior} this value to force fish to move about the environment frequently at the start of the simulation and gain values of γ appropriate for the environment. Lower values of γ_{prior} cause model fish to settle into areas with low growth rate potential values and bias the final fish distribution. (See Bernstein et al. 1988 for a more complete discussion of the effect of changing values of γ_{prior} on forager distribution.) Estimated growth (γ) is updated each step of the model (γ), as foragers gain experience. New γ values are a weighted mean of previous value and of the actual growth (g) received in the current model step.

$$\gamma_{s+1} = \gamma_s \delta + g_s (1 - \delta) \quad (19)$$

where δ is the weighing or "memory" factor ($\delta = 0.9$) and determines the effect of previous experience on the current value of γ (McNamara & Houston 1987; Bernstein et al. 1988). $\delta = 0.9$ causes distributions of foragers to reliably reflect tradeoffs in resources and competition when individual movement is not spatially constrained (Bernstein et al. 1988, 1991; Tyler & Hargrove 1997).

Model simulations

Simulations begin with model fish randomly distributed across the environment, which has a normal, random zooplankton distribution with variance equal to the mean and temperature field taken from one of the profiles in Fig. 1. Because the distribution of a population of foragers is commonly dynamic rather than static, even once an equilibrium has been reached (Milinski 1979, 1988; Power 1984; Tyler 1991) we determined that the equilibrium distribution of model fish is reached when the number of fish moving between cells each step of the model is within 5% of the average number moving for the last 30 model steps. We used this criterion because when met, the correlation between distributions of fish at successive model

steps was typically high ($r \geq 0.82$) and the overall distribution of the model fish population was constant.

Model fish move frequently at the beginning of simulations and by the end, move much less frequently. Because of the high value of γ_{prior} and of the memory factor, δ , assigned to the fish, 100% of the population typically moved for each of the first 15 model steps. Equilibrium distribution criteria were commonly met at between 60 and 90 steps.

Calibration and corroboration

We used simulated fish growth of the model fish population to calibrate the individual-based model and corroborate that its predictions of fish growth and population distribution are consistent with existing data and accepted theory. Our selection of predator and prey energy density values and of capture probability for fish foraging on zooplankton are based on previous studies. The final adjustments made to capture probability produced reasonable growth rates. Daily growth rates of age-2 alewife fall in the range of 0.25% to 0.5% per day (O'Gorman et al. 1987) which, for our model fish (150 mm, 24.4 g) translates to a range of daily growth rates of 0.061–0.122 $\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$. Energy densities of alewife (Stewart & Binkowski 1986) and of zooplankton (Snow, 1972) change seasonally. The values chosen for this model (fish: 1900, zooplankton: 450 $\text{cal} \cdot \text{g}^{-1}$) fall within the reported ranges.

We ran simulations with no effect of competition for zooplankton on the foraging of model fish ($VSS_{\text{total}} = 0$) to calibrate the model. The water temperature field used was based on an average of the Lake Ontario water temperature profiles (Fig. 1), and zooplankton density was 50 l^{-1} . We adjusted capture probability (P_{capture}) so that both simulated fish growth and growth rate potential fell into the range of growth rates previously observed for Lake Ontario alewife (0.061–0.122 $\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$). Capture probability used for all

Table 1. Simulated fish growth and growth rate potential from corroboration simulations. Means computed from three simulation runs per treatment. Growth rate potential means are computed for all simulations, but differ only with zooplankton number.

Zooplankton $\cdot \text{l}^{-1}$	Simulated fish growth fish (number $\cdot \text{m}^{-3}$)			Growth rate potential
	0.4	3.2	25.6	
25	0.045	0.045	0.045	0.037
50	0.086	0.086	0.086	0.074
100	0.158	0.158	0.158	0.137

Table 2. Correlation (r) between growth rate potential and number of model fish per cell in corroboration simulations and maximum number of fish in a cell (fish_{max}). In all cases, the minimum number of fish in a cell was 0. Reported values are the mean from three simulations per treatment.

Zooplankton $\cdot \text{l}^{-1}$	Fish (number $\cdot \text{m}^{-3}$)					
	0.4		3.2		25.6	
	r	fish_{max}	r	fish_{max}	r	fish_{max}
25	0.515	5.00	0.724	28.33	0.768	195.33
50	0.494	6.33	0.722	27.00	0.763	186.67
100	0.517	6.67	0.704	41.00	0.745	315.67

simulations was $P_{\text{capture}}=0.90$. In these simulations simulated fish growth was approximately $0.086 \text{ g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ and growth rate potential was approximately $0.075 \text{ g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$.

We conducted a set of 27 simulations to confirm that patterns of growth and habitat selection of model fish are consistent with accepted theory. In corroboration simulations there was no effect of competition on zooplankton consumption by model fish, the environment was limited to a 25×25 cell grid, and the temperature field was an average of those taken from Lake Ontario (Fig. 1). We ran three simulations at each of three different zooplankton densities (25, 50, 100 zooplankton $\cdot \text{l}^{-1}$), and three different model fish densities (0.4, 3.2 and $25.6 \text{ fish} \cdot \text{m}^{-3}$). We had the following three expectations concerning fish growth: 1) growth would increase as zooplankton density increased, 2) because there was no effect of competition on model fish consumption, growth would be unaffected by model fish density, and 3) because model fish select habitats to maximize growth, mean simulated fish growth of the model fish population would exceed mean growth rate potential in the model environment. All three expectations were borne out in the corroboration simulations (Table 1).

We also expected that once the model fish distri-

bution became stable the correlation between spatial distributions of growth rate potential and of model fish would be reasonably high. This was true for simulations with the two highest number of model fish ($25.6 \cdot \text{m}^{-3}$, 16,000 total and $3.2 \cdot \text{m}^{-3}$, 2000 total), but not for the lowest number of model fish ($0.4 \cdot \text{m}^{-3}$, 250 total) (Table 2). The finding that correlations between growth rate potential and model fish were high only when numbers of model fish were high is somewhat expected. Small numbers of model fish lead to a low range in the number of fish per cell while large numbers lead to a wide range in fish per cell (Table 2). In simulations with low model fish numbers, the variation possible in a cell's growth rate potential is much greater than the variation possible in the number of fish per cell. This alone can account for the difference in correlation between growth rate potential and fish numbers found in the corroboration simulations. In sum, we take the results of the corroboration simulations to indicate that the model produces reasonable growth rates and distributions of model fish.

Design of simulation experiment

We conducted a three-way factorial simulation experiment to investigate the effect of changing en-

Table 3. Analysis of variance of the effect of zooplankton density (Z), fish number (F) and water temperature field (T) on average simulated fish growth and the environmental average growth rate potential in the factorial simulation experiment. As a part of the analysis of variance, we report mean squared error (MS), % mean squared error (%MS) and variance estimates (VE) for each factor.

Source	DF	Simulated fish growth			Growth rate potential		
		MS	%MS	Ve	MS	%MS	VE
Zooplankton $\cdot \text{l}^{-1}$ (Z)	2	0.0594	67.85	1.57×10^{-3}	0.0568	96.75	1.55×10^{-3}
Fish number (F)	3	0.0251	28.67	8.39×10^{-4}	1.09×10^{-33}	0.00	0.00
Temperature field (T)	2	3.02×10^{-4}	0.34	6.57×10^{-7}	9.79×10^{-4}	1.67	1.45×10^{-6}
Z \times F	6	0.0024	2.78	2.68×10^{-4}	1.23×10^{-34}	0.00	0.00
Z \times T	4	2.78×10^{-4}	0.32	2.14×10^{-5}	9.27×10^{-4}	1.58	7.73×10^{-5}
F \times T	6	2.16×10^{-5}	0.02	1.75×10^{-8}	3.59×10^{-35}	0.00	0.00
Z \times F \times T	12	2.14×10^{-5}	0.02	7.13×10^{-6}	3.24×10^{-36}	0.00	3.09×10^{-10}
Error	72	5.46×10^{-8}	0.00	5.46×10^{-6}	9.26×10^{-9}	0.00	9.26×10^{-9}
Total	107	0.0875	100.0		0.0587	100.0	

environmental conditions and fish population number on simulated fish growth and on environment-wide growth rate potential. To change environmental conditions we manipulated zooplankton density and water temperature field. Three levels of zooplankton density (25, 50 and 100 zooplankton \cdot l $^{-1}$) and three water temperature fields (shallow, medium and deep thermoclines; Fig. 1) were used in the experiment. Four levels of model fish number were used (total numbers: 4000, 16,000, 64,000, 256,000; number \cdot m $^{-3}$: 0.04, 0.16, 0.64, 2.56). We performed three simulations of each treatment, for a total of 108 simulations. For comparison, we also conducted an identical simulation experiment in which the presence of competing model fish in a cell did not affect per capita zooplankton consumption ($VSS_{total}=0$).

We used analysis of variance (ANOVA) to partition variation in simulated fish growth and the environment's mean growth rate potential among main effects in the simulation experiment. We do not report *P*-values for the ANOVA as determinants of significance because degrees of freedom may be made arbitrarily large by simply executing more replicate simulations. Instead we report the percentage of the total mean square (%MS = $100 \cdot MS_{factor} / \sum MS_{factor}$) and variance estimates (VE) attributed to each main effect and interac-

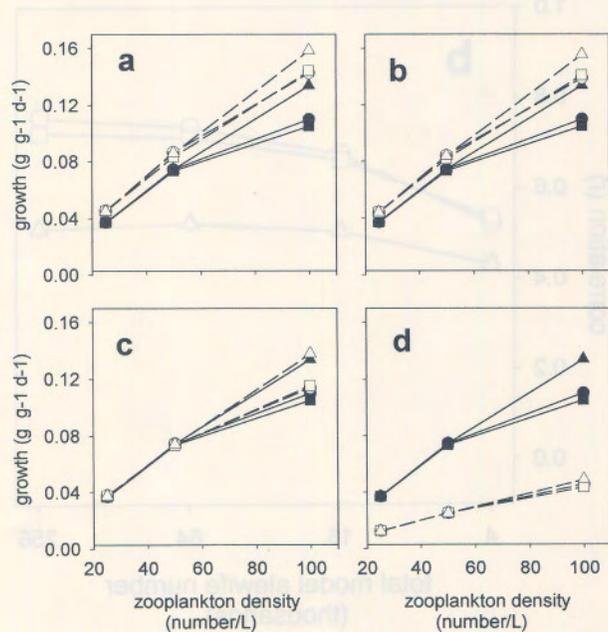


Fig. 5. Changes in environment-wide mean growth rate potential and mean simulated fish growth as zooplankton density and water temperatures change in the simulation experiment. Results are shown for the four population sizes: 4000 (a), 16,000 (b) 64,000 (c) and 256,000 (d) model fish. Temperature fields are (○) shallow June 6, 1996, (□) medium, July 11, 1995, and (△) deep, July 17, 1995. Closed symbols are the growth rate potential, open symbols are simulated fish growth.

Fish growth in heterogeneous environments

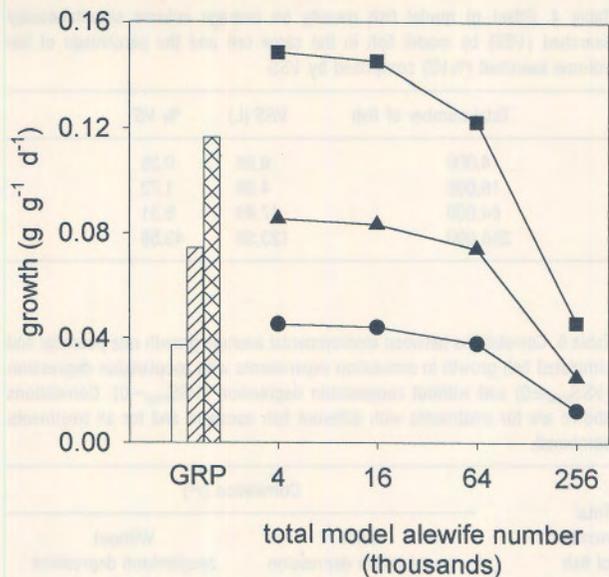


Fig. 6. Effect of changes in fish number on simulated fish growth and comparison to environmental average growth rate potential. Data shown are at three different zooplankton densities. Simulated fish growth are line plots; bar graphs are average growth rate potential (●, open bar) 25 \cdot l $^{-1}$, (▲, single hatched bar) 50 \cdot l $^{-1}$ and (■, double hatched bar) 100 \cdot l $^{-1}$. Data are averaged among simulations with different temperature fields and random number sequences.

tion. Main effects and interactions that account for more than 5% of the total mean square may be considered important. %MS is unaffected by degrees of freedom and thus better identifies important effects in simulation experiments such as these than do *P*-values (Tyler & Rose 1997; Tyler & Hargrove 1997). Variance estimates allow us to rank the factors in order of the observed variance attributed to each.

Results

ANOVA of variance (AOV) of the three-way factorial experiment showed that both the average simulated fish growth and the average growth rate potential were both strongly affected by changes in zooplankton density (Table 3). There was a near linear increase in both simulated fish growth and growth rate potential as zooplankton density increased (Fig. 5). Differences in the water temperature field had a small, but detectable, effect on growth rate potential and simulated fish growth. However, water temperature field only affected simulated fish growth and growth rate potential at the highest zooplankton density (100 zooplankton l $^{-1}$) (Fig. 5). At lower zooplankton densities, the water temperature field did not affect simulated fish growth or growth rate potential. Water temperature accounted for a small amount

Table 4. Effect of model fish density on average volume simultaneously searched (VSS) by model fish in the same cell and the percentage of the volume searched (%VS) comprised by VSS.

Total number of fish	VSS (L)	% VS
4,000	0.98	0.35
16,000	4.89	1.72
64,000	17.89	6.31
256,000	123.58	43.58

Table 5. Correlations between environmental average growth rate potential and simulated fish growth in simulation experiments with zooplankton depression ($VSS_{total} \geq 0$) and without zooplankton depression ($VSS_{total} = 0$). Correlations shown are for treatments with different fish numbers and for all treatments combined.

Total number of fish	Correlation (r^2)	
	With zooplankton depression	Without zooplankton depression
4,000	0.9757	0.9766
16,000	0.9736	0.9756
64,000	0.9944	0.9757
256,000	0.9735	0.9755
All treatments	0.5617	0.9759

of the variability (%MS, and VE) in simulated fish growth and growth rate potential (Table 3).

The number of model fish in the environment had an important effect on the mean simulated fish growth (Table 3, Fig. 6). Increased model fish number caused a decrease in simulated fish growth observed in the population at all levels of zooplankton density. At low numbers of model fish (4000, 16,000), average simulated fish growth exceeded the environment's growth rate potential. At the highest number of model fish, average simulated fish growth was much lower than growth rate potential (Fig. 5, Fig. 6). The effect of model fish number on simulated fish growth resulted from localized competition for zooplankton in cells where fish numbers were high. The volume searched simultaneously by model fish increased markedly as the number of model fish increased (Table 4). At the highest number of model fish, over 40% of the total volume searched by an individual fish (283.6 liters) was searched simultaneously by other model fish, indicating high levels of competition for zooplankton in these situations.

An interaction between model fish density and zooplankton density did affect simulated fish growth (Table 3), in that it accounted for nearly 3% of mean squared error and was the only effect other than zooplankton density and model fish number with a %MS greater than 1%. Judging the magnitude of importance for this interaction is difficult. Clearly the relationship between average

simulated fish growth and number of model fish differs based on the zooplankton density (Fig. 6). However, the %MS and VE accounted for by the interaction is quite low.

Changes in the average simulated fish growth correlated highly with changes in mean growth rate potential in the environment when the number of model fish was held constant (Table 5) or when there was no competition for zooplankton by

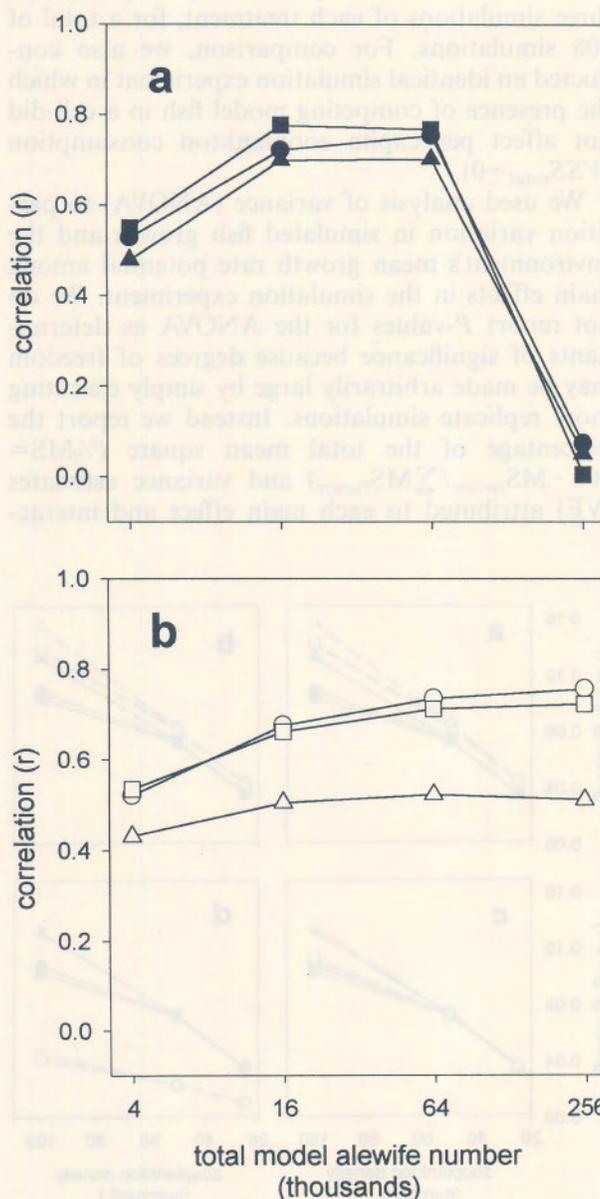


Fig. 7. Changes in the correlation between the growth rate potential and number of model fish per cell as total model fish number increases for simulations in which model fish foraging could cause zooplankton depression (a) and could not cause zooplankton depression (b). Data are averaged across simulation with different temperature fields and random number seeds. Results from simulations with three levels of zooplankton $\cdot l^{-1}$ are shown: 25 (\bullet), 50 (\blacktriangle), and 100 (\blacksquare).

model fish ($VSS_{\text{total}}=0$). When competition affected their consumption of zooplankton and all simulations were analyzed together, the environment's mean growth rate potential correlated poorly with mean simulated fish growth. The low correlation between mean simulated fish growth and mean growth rate potential when all simulations are combined results from simulations with 256,000 model fish. Excluding those simulations from the correlation analysis causes simulated fish growth and growth rate potential again to correlate very highly ($r^2=0.9490$). Simulations with the highest model fish number are also those in which competition for zooplankton was greatest (as measured by VSS_{total} , Table 4).

The correlation between the growth rate potential of a cell and the number of fish in the cell varied with the number of model fish in the simulation. The effect of model fish number on the correlation between growth rate potential and the number of fish per cell was much stronger in the simulations when model fish foraging could affect their consumption of zooplankton than in simulations when model fish foraging did not affect zooplankton consumption (Fig. 7). When fish foraging could affect consumption, there was a dramatic decline in the correlation between growth rate potential and the number of fish per cell at the highest number of model fish. The highest correlations between growth rate potential and fish per cell appeared at the two intermediate numbers of total fish (16,000, 64,000). When model fish foraging did not affect consumption, there was a consistent positive relationship between model fish number and correlation between growth rate potential and the number of fish per cell.

Discussion

The results of this model and simulation experiment indicate that changes in the average growth rate potential in the environment correlate well with changes in the average simulated fish growth (Fig. 5). The relationship between environmental growth rate potential and simulated fish growth was strong even though in the individual-based model fish select habitats according to a growth maximization rule in a heterogeneous environment, and model fish foraging could reduce the per capita consumption of zooplankton. Within each population size, the correlation between simulated fish growth and growth rate potential was extremely high (>0.9 , Table 5). The only case in which the correlation between growth rate potential and simulated fish growth was not high was when 1) fish foraging could affect per capita consumption of zooplankton, and 2) the correlation

analysis included results from simulation with 256,000 model fish and lower numbers of model fish. Growth rate potential changes did not correlate with simulated fish growth changes in this situation because at the highest number of fish, competition effects on per capita zooplankton consumption greatly reduced the model fish consumption of zooplankton and thereby simulated fish growth (Fig. 6).

The high correlation between growth rate potential and simulated fish growth in this study supports the use of growth rate potential as a measure of the environmental quality for fishes. No data currently exist that allow for a comparison between growth rate potential and observed fish growth in any specific population. In the absence of a field study, the simulation model here provides the best support to date for the use of growth rate potential analysis as a tool for measuring environmental quality. The models used in the individual-based model are among the best currently available for simulating fish foraging, growth and movement. The mechanistic detail in the individual-based model allows the response of the model fish population to environmental to conditions to be a reasonable simulation of how a real fish population might act in the field. Until a proper field study comparing growth rate potential to growth of actual fish can be conducted, this study provides the most reasonable approach to testing the value of growth rate potential as a measure of environmental quality.

In the simulation experiment, average simulated fish growth consistently differed from the average growth rate potential. The differences between average simulated fish growth and the environment's growth rate potential were most notable at high model fish densities. The difference between simulated fish growth and growth rate potential results from the habitat selection rule that model fish used and from competition for zooplankton. Habitat selection allowed model fish to avoid areas of low growth rate potential and preferentially use areas of high growth rate potential. Thus, in simulations where model fish foraging did not reduce per capita zooplankton consumption (either number of model fish $<64,000$ or $VSS_{\text{total}}=0$), average simulated fish growth exceeded average growth rate potential. At high total model fish numbers (256,000), reduced zooplankton consumption from competition between model fish caused average simulated fish growth to fall below average growth rate potential (Fig. 6). Habitat selection by individual fish also contributed to local competition effects. Average fish density across the whole environment was not particularly high in these simulations (2.5 fish/m^3), but habitat selection caused

local densities to range much higher (6.0 fish/m³) leading to localized reductions in the per capita consumption of zooplankton by model fish and reduced simulated fish growth. These reasons explain not only why growth rate potential and simulated fish growth differed in the simulation experiment but also why growth rate potential should be expected to be a reasonable predictor of relative habitat quality but not a good predictor of observed fish growth rates in the field.

The correlation between the number of model fish in a cell and the cell's growth rate potential varied considerably with the number of model fish in the simulation. The growth rate potential of a cell and the number of fish per cell correlated well at intermediate total model fish numbers ($r \approx 0.75$) but was low for the highest and lowest total model fish numbers (Fig. 7). The low correlation between GRP and fish per cell at low model fish numbers should be expected. As mentioned earlier regarding the corroboration simulations, a fish population with low numbers cannot show the same range of variation as growth rate potential (Table 2). When a simulation includes a large number of model fish (e.g. 256,000), the number of fish per cell may vary with the same kind of magnitude as growth rate potential, but fish habitat selection combined with localized reduction of per capita zooplankton consumption cause the low correlation between growth rate potential and the number of fish per cell. Cells with high growth rate potential experienced the greatest reduction in per capita zooplankton consumption, which in turn lead to reduced numbers of model fish selecting those cells and a low correlation between growth rate potential and the number of fish per cell.

Growth rate potential was not a dependable predictor of model fish distribution at the high resolution used in the individual-based model as indicated by the low correlation between growth rate potential and fish per cell. This result, however, should be expected and should not be seen as detracting from the use of growth rate potential as an overall measure of environment quality. Fish growth does not change linearly with changes in fish density in a cell, and food consumption may be reduced by the effects of other fish on food resources, yet energetic costs do not change because of competitors. In such situations, a measure of the environment such as growth rate potential that does not include effects of competitors on resource availability often may not be a good predictor of animal distributions (Tyler & Gilliam 1995). Even when distribution predictions include competition effects, the movement ability of the animals and the scale of measure may affect the ability to predict distributions (Tyler & Hargrove 1997). Spatial

models of growth rate potential will likely not be good predictors of fish distribution at a small scale like that used in this model. However, at coarser scales, spatial models of growth rate potential may be reasonable predictors of fish distributions.

The results here partly fill the need to validate growth rate potential analysis for measuring environmental quality for fishes, which is great because of the wide and growing use of the technique. Variation in habitat quality of a number of environments has been examined with spatial models of growth rate potential. Growth rate potential models have shown seasonal (Brandt et al. 1992; Brandt & Kirsch 1993; Horne et al. 1996) and annual variation in growth rate potential (Luecke et al. 1999), differences in an environment's growth rate potential for fish of different species (Goyke & Brandt 1993; Mason et al. 1995; Hartman & Brandt 1995b) and differences in the growth rate potential for the same species foraging in different environments (Mason et al. 1995). The results of this research support the contention that the growth rate potential differences seen in the studies listed above very likely result in differences in the growth of fish in these populations.

Resumen

1. Modelos espaciales de tasas de crecimiento potencial en peces (GRP) han sido utilizados para caracterizar una variedad de ambientes que incluyen estuarios, grandes lagos y ríos. Estos modelos GRP toman puntos claves del ambiente pero no incluyen los efectos de la selección de habitat o de la competencia alimenticia en las medidas de la calidad ambiental. En este trabajo, exploramos la habilidad de modelos espaciales GRP en peces para describir la calidad de un ambiente para una población en la que los individuos puede seleccionar habitats y la competencia local puede afectar la alimentación per capita.
2. Comparamos medidas (GRP) para simular el crecimiento de los peces (SFG) y distribuciones de un modelo explícito espacialmente, basado en individuos (IBM) para peces que foragean en el mismo ambiente modelo. Basamos el ambiente modelo en datos del Lago Ontario y la población modelo, en la población de *Alosa pseudoharengus* del mismo lago.
3. Los resultados del experimento de simulación mostraron que cambios en el ambiente modelo que causan cambios en el GRP medio están altamente correlacionados ($r^2 \geq 0.97$) con cambios en SFG. Desafortunadamente, GRP no es un buen predictor cuantitativo de SFG, ni de la distribución espacial de los peces. La incapacidad del modelo GRP para predecir cuantitativamente SFG y la distribución espacial de los peces se debe a que GRP no considera los efectos de la selección de habitats o de la competición sobre el crecimiento o la distribución de los peces, procesos que operan en nuestro IBM, y presumiblemente, también en la naturaleza. Sin embargo, los resultados sí soportan el uso de modelos GRP para describir la calidad relativa de los habitats y ambientes para las poblaciones de peces.

Acknowledgments

We would like to thank a number of individuals who helped with the model and manuscript preparation. D.W. Hondorp helped supply information needed to calibrate the fish growth

and foraging parts of the model. W.G. Sprules helped supply information on the zooplankton population and water temperatures of Lake Ontario used to describe the model environment. Additional water temperature data were collected with the assistance of J.K. Horne and J. Freidhoff. E. Demers provided comments on an earlier draft of the manuscript and P. Robakiewicz helped with statistical analysis. J.A. Tyler was supported in part by NSF grant OEC9417540 to S.B. Brandt, NSF Land Margin Ecosystem Research Program DEB-9412113 and NOAA Coastal Ocean Program. Publication 1179 of the Great Lakes Environmental Research Lab.

References

- Aksnes, D.L. & Giske, J. 1993. A theoretical model of aquatic visual feeding. *Ecological Modelling* 67: 233–250.
- Bailey, K.M. & Batty, R.S. 1984. Laboratory study of predation by *Aurelia aurita* on larvae of cod, flounder, and herring: development and vulnerability to capture. *Marine Biology* 83: 287–291.
- Bernstein, C., Kacelnik, A.C. & Krebs, J.R. 1988. Individual decisions and the distribution of predators in a patchy environment. *Journal of Animal Ecology* 57: 1007–1026.
- Bernstein, C., Kacelnik, A.C. & Krebs, J.R. 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. *Journal of Animal Ecology* 60: 205–225.
- Boisclair, D. & Leggett, W.C. 1989. Among population variability of fish growth. III. Influence of fish community. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1539–1550.
- Brandt, S.B., Mason, D.M. & Patrick, E.V. 1992. Spatially-explicit model of fish growth rate. *Fisheries* 17: 23–35.
- Brandt, S.B. & Kirsch, J. 1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. *Transactions of the American Fisheries Society* 122: 845–869.
- Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9: 129–136.
- DeAngelis, D.L., Godbout, L. & Shuter, B.J. 1991. Individual-based approach to predicting density-dependent dynamics in smallmouth bass populations. *Ecological Modelling* 57: 91–115.
- DeAngelis, D.L., Barnthouse, L.W., Van Winkle, W. & Otto, R.G. 1994. A critical appraisal of population approaches in assessing fish community health. *Journal of Great Lakes Research* 16: 576–590.
- DeAngelis, D.L. & Gross, L.J. 1992. Individual-based models and approaches in ecology: populations, communities and ecosystems. New York: Chapman and Hall.
- Demers, E., Brandt, S.B., Barry, K.L. & Jech, J.M. In press. Spatially-explicit models of growth rate potential: linking estuarine fish production to the biological physical environment. In: Hobbie, J.E., ed. *Estuarine synthesis: the next decade*. New York: Island Press.
- Fiksen, O., Giske, J. & Slagstad, D. 1995. A spatially explicit fitness-based model of capelan migrations in the Barents Sea. *Fisheries Oceanography* 4: 193–208.
- Fox, M.G. & Flowers, D.D. 1990. Effects of fish density on growth, survival, and food consumption by juvenile walleyes in rearing ponds. *Transactions of the American Fisheries Society* 119: 112–121.
- Fretwell, S.D. & Lucas, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19: 16–36.
- Frost, B.W. & Bollens, S.M. 1992. Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1137–1141.
- Gerritsen, J. & Strickler, J.R. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *Journal of the Fisheries Research Board of Canada* 34: 73–82.
- Giske, J., Huse, G. & Fiksen, O. 1998. Modeling and spatial dynamics of fish. *Reviews in fish biology and fisheries* 8: 57–91.
- Gliwicz, M.Z. 1986. Predation and the evolution of vertical migration in zooplankton. *Nature* 320: 746–748.
- Godin, J.-G. & Keenleyside, M. 1984. Foraging on patchily distributed prey by a cichlid fish (*Teleostei Cichlidae*): a test of the ideal free distribution theory. *Animal Behaviour* 32: 120–131.
- Goyke, A.P. & Brandt, S.B. 1993. Spatial models of salmonine growth rates in Lake Ontario. *Transactions of the American Fisheries Society* 122: 870–883.
- Hanson, P.C., Johnson, T.B., Schindler, D.E. & Kitchell, J.F. 1997. *Fish bioenergetics 3.0*. Madison: University of Wisconsin System Sea Grant Institute.
- Hartman, K.J. & Brandt, S.B. 1993. Systematic sources of bias in a bioenergetics model: examples for age-0 striped bass. *Transactions of the American Fisheries Society* 122: 912–926.
- Hartman, K.J. & Brandt, S.B. 1995a. Estimating energy density of fish. *Transactions of the American Fisheries Society* 124: 347–355.
- Hartman, K.J. & Brandt, S.B. 1995b. Predatory demand and impact of striped bass, bluefish and weakfish in the Chesapeake Bay: applications of bioenergetics models. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 1667–1687.
- Hewett, S.W. & Johnson, B.L. 1992. A generalized bioenergetics model of fish growth for microcomputers, version 2.0. Madison, WI: University of Wisconsin Sea Grant Institute.
- Hinckley, S., Herman, A.J. & Megrey, B.A. 1996. Development of a spatially explicit, individual-based model of marine fish life history. *Marine Ecology Progress Series* 139: 47–68.
- Hondorp, D.W. 1998. The spatial distribution of alewife (*Alosa pseudoharengus*) and rainbow smelt in western Lake Ontario: Implications for fish thermal experience, fish bioenergetics and predator-prey balance. Buffalo, NY: M.S. Thesis, Buffalo State College.
- Horne, J.K., Jech, J.M. & Brandt, S.B. 1996. Spatial modeling of aquatic habitat from a fish's perspective. In: *Proceedings of the third international conference/workshop on integrating geographic information systems and environmental modeling*. Santa Barbara, CA: National Center for Geographic Information and Analysis. WWW and CD.
- Kitchell, J.F., Stewart, D.J. & Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada* 34: 1922–1935.
- Levy, D.A. 1990. Reciprocal diel vertical migration behavior in planktivores and zooplankton in British Columbia lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 1755–1764.
- Luecke, C., Wengert, M.W. & Schneider, R.W. 1999. Comparing results of a spatially explicit growth model with changes in the length-weight relationship of lake trout (*Salvelinus namaycush*) in Flaming Gorge Reservoir. *Canadian Journal of Fisheries and Aquatic Sciences* 56 (Suppl. 1): 1–8.
- Madenjian, C.P. 1991. Limits to growth of young-of-the-year walleye (*Stizostedion vitreum vitreum*): an individual-based model perspective. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1492–1499.
- Mason, D.M., Goyke, A.P. & Brandt, S.B. 1995. A spatially-explicit bioenergetics measure of habitat quality for adult salmonines: comparison between Lakes Michigan and Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 1572–1583.
- Mason, D.M. & Brandt, S.B. 1996. Effects of spatial scale and

foraging efficiency on the predictions made by spatially-explicit models of fish growth rate potential. *Environmental Biology of Fishes* 45: 283–298.

McNamara, J.M. & Houston, A.I. 1987. Memory and the efficient use of information. *Journal of Theoretical Biology* 125: 385–395.

Milinski, M. 1979. An evolutionarily stable feeding strategy in sticklebacks. *Zeitschrift für Tierpsychologie* 51: 36–40.

Milinski, M. 1988. Games fish play: making decisions as a social forager. *Trends in Ecology and Evolution* 3: 325–330.

Milinski, M. & Parker, G.A. 1991. Competition for resources. In: Krebs, J.R. & Davies, N., ed. *Behavioural ecology: an evolutionary approach*. London: Blackwell Scientific, pp. 137–170.

O’Gorman, R., Bergsted, R.A. & Eckert, T.H. 1987. Prey fish dynamics and salmonine predator growth in Lake Ontario, 1978–1984. *Canadian Journal of Fisheries and Aquatic Sciences* 44 (suppl 2): 390–403.

Perry, R.I., Hargreaves, N.B., Waddell, B.J. & Mackas, D.L. 1996. Spatial variations in feeding and condition of juvenile pink and chum salmon off Vancouver Island, British Columbia. *Fisheries Oceanography* 5: 73–88.

Peterman, R.M. 1981. Form of random variation in salmonid smolt-to-adult relations and its influence on production estimates. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1113–1119.

Power, M.E. 1984. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. *Journal of Animal Ecology* 53: 357–374.

Rand, P.S., Lantry, B.F., O’Gorman, R., Owens, R.W. & Stewart, D.J. 1994. Energy density and size of pelagic prey fishes in Lake Ontario, 1978–1990: implications for salmon energetics. *Transactions of the American Fisheries Society* 123: 519–534.

Rand, P.S., Stewart, D.J., Lantry, B.F., Rudstam, L.G., Johannsson, O.E., Goyke, A.P., Brandt, S.B., O’Gorman, R. & Eck, G.W. 1995. Effect of lake-wide planktivory by the pelagic prey fish community in Lakes Michigan and Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 1546–1563.

Rand, P.S., Scandol, J.P. & Walter, E.E. 1997. NerkaSim: a research and educational tool to simulate the marine life history of pacific salmon in a dynamic environment. *Fisheries Research* 22: 6–13.

Rose, K.A. & Cowan, J.H. 1993. Individual-based model of young-of-the-year striped bass population dynamics. I. Model description and baseline simulations. *Transactions of the American Fisheries Society* 122: 415–439.

Snow, N. 1972. The effect of season and animal size on the caloric content of *Daphnia pulex*. *Limnology and Oceanography* 17: 909–912.

Sprules, W.G. & Goyke, A.P. 1994. Size-based structure and production in the pelagia of Lakes Erie and Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 2603–2611.

Stewart, D.J., Kitchell, J.F. & Crowder, L.B. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Transactions of the American Fisheries Society* 110: 751–763.

Stewart, D.J., Weininger, D., Rottiers, D.V. & Edsall, T.A. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 681–698.

Stewart, D.J. & Binkowski, F.P. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics modeling synthesis. *Transactions of the American Fisheries Society* 115: 643–661.

Stewart, D.J. & Ibarra, M. 1991. Predation and production by salmonine fishes in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 909–922.

Tyler, J.A. 1991. Habitat selection and foraging behavior in stream fish: ideal free models and experiments with blacknose dace, *Rhinichthys atratulus*. Albany, NY: State University of New York at Albany.

Tyler, J.A. 1998. Growth rate potential map maker: a users guide to spatial models of fish habitat combining acoustic data and bioenergetics models. Ann Arbor, MI: NOAA Great Lakes Environmental Research Laboratory Technical Report #110 (<http://www.glerl.noaa.gov/pubs/techrept/techrept.html>).

Tyler, J.A. & Gilliam, J.F. 1995. Ideal free distributions of stream fish: a model and test with minnows, *Rhinichthys atratulus*. *Ecology* 76: 580–592.

Tyler, J.A. & Rose, K.A. 1994. Individual variability and spatial heterogeneity in fish population models. *Reviews in Fish Biology and Fisheries* 4: 91–123.

Tyler, J.A. & Hargrove, W.W. 1997. Predicting spatial distributions of foragers over large resource landscapes: a modeling analysis of the ideal free distribution. *Oikos* 79: 376–386.

Tyler, J.A. & Rose, K.A. 1997. Individual-based model of fish cohort growth, movement, and survival in a spatially-explicit environment. *Journal of Animal Ecology* 66: 122–136.