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Spatial Modeling of Aquatic Habitat From a Fish's Perspective

Patchy distributions of organisms and environmental conditions are characteristic traits of aquatic environments. Yet biological and physical measurements are often averaged over large spatial scales when used in environmental models. From a fish's perspective, local rather than spatially averaged conditions determine available habitat. We found that a horizontal cell size of 40 m preserved environmental heterogeneity in habitat quality analyses. Habitat quality was quantified using prey density, prey size, and water temperature data in bioenergetic models to estimate the potential growth of adult walleye (*Stizostedion vitreum vitreum*) in Lake Erie. Maps of potential growth rates showed that walleye growth is more sensitive to changes in water temperature than to changes in prey density. Addition of a programming language or increasing the flexibility of data formats would increase the use of commercial GIS systems in environmental modeling.

INTRODUCTION

Heterogeneity in spatial distributions of organisms is a near universal trait of aquatic environments (Hensen 1911, Hardy 1935, Hardy 1936). Efforts to explain biological patchiness have traditionally correlated organism counts with measures of physical conditions (Denman and Powell 1984, Legendre and Demers 1984, Mackas et al. 1985). From a fish's perspective, simple descriptions of physical or biological structure may not adequately characterize fish habitat. Fish growth and foraging are two examples of biological processes that are influenced by local water mass properties (e.g. temperature), prey densities, and prey sizes. The resulting distributions and growth of fish are functional responses to local habitat conditions. One way to quantify habitat quality of fish is to integrate water temperature and prey distributions in bioenergetic models of fish growth. Bioenergetic models use a mass balance approach where energy gained by consumption is partitioned into growth, metabolism, and waste (Winberg 1956, Kitchell et al. 1974, 1977). Bioenergetic models can be parameterized for any species of interest and used to map habitat quality.

Traditional bioenergetic models of fish growth depict all habitat as a homogeneous volume. Water temperatures and prey densities are arbitrarily set to average values from a large environment such as a lake. This eliminates spatial heterogeneity in model calculations and implicitly sets the spatial resolution or grain of the model equal to the range or extent of the environment being modeled. An often stated criticism of this approach is that model results do not accurately reflect biological and physical heterogeneity present in the environment (Stephens and Krebs 1986). As a supporting example, Lasker (1978) showed that survival of larval anchovy (*Engraulis mordax* Girard) depends on ephemeral patches of high prey density. A steady diet of average prey densities leads to starvation.

As an alternative to using mean prey densities and temperatures, spatially-explicit bioenergetic models incorporate heterogeneous prey distributions and physiologically-important, environmental conditions in model calculations (Brandt et al. 1992). High-resolution, continuous data from surveyed transects are placed in two-dimensional matrices. Matrix elements represent cells with sizes small enough to assume homogeneous conditions within each cell. The use of small cell sizes increases the spatial resolution of model calculations greater than the spatial range of the modeled environment. The potential growth of a specified predator is estimated in each cell using measured water temperatures, prey biomass densities, and prey sizes. This approach has been used to examine spatial patterns of planktivory in Chesapeake Bay (Luo and Brandt 1993), to map seasonal growth potentials of fish in Chesapeake Bay (Brandt and Kirsch 1993), to examine predator-prey overlap as a function of water temperature in the Great Lakes (Goyke and Brandt 1993), and to define habitat quality based on predator physiology (Mason et al. 1995).

This study uses spatial variance in fish densities to set cell size in spatially-explicit bioenergetic models of walleye growth in Lake Erie. Setting cell size in any spatial model is a trade-off between maintaining heterogeneity of the environment in model calculations, and reducing data resolution to accommodate logistic constraints imposed by sampling or data processing. When using underwater acoustics to sample fish densities, each cell of the data matrix must contain a sufficient number of isolated individuals to accurately estimate the average size of fish in each cell. Cell sizes in spatially-explicit bioenergetic models have been as small as 25 m horizontal by 0.5 m vertical (e.g. Luo and Brandt 1993, Brandt and Mason 1994). The corresponding variance in fish lengths or fish densities have not been quantified as a function of cell size. We use potential growth rate to quantify habitat quality. Variance patterns in the distribution of habitat quality are then compared to patterns of spatial variance in fish density.

METHODS

Data Acquisition

As part of a Canadian-American research program, continuous measures of fish size, fish density, and water temperature were recorded at night along transects in the three basins of Lake Erie during September, 1994. Lengths of the three transects used in this study

were 27.5 km in the western basin, 42 km in the central basin, and 35.5 km in the eastern basin.

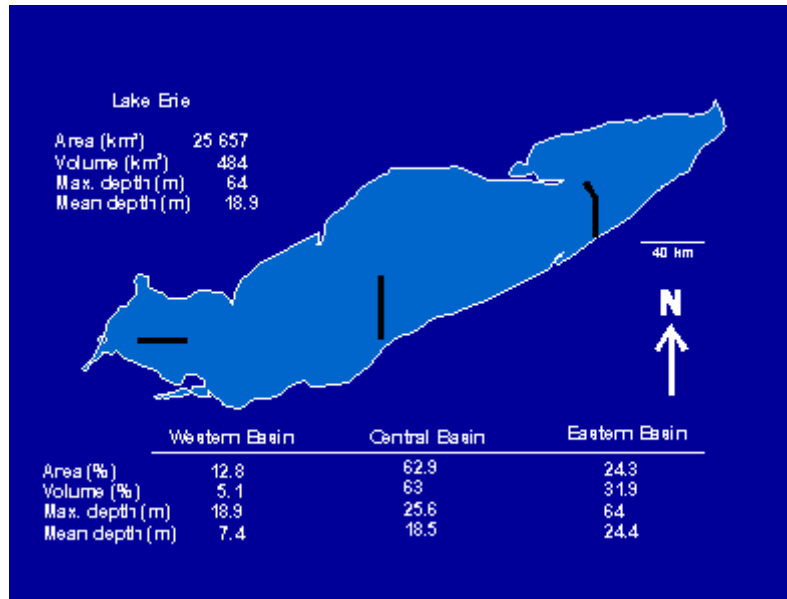


Fig. 1. Map of Lake Erie showing transects in the western (27.5 km), central (42 km), and eastern (35.5 km) basins.

Fish densities and sizes were measured using a 120 kHz scientific acoustic sonar (BioSonics Model 102, 10° and 25° dual beam). Sonars sample the water column by sending short, repetitive, pulses of high frequency sound in a directed beam downward as the survey vessel moves across the surface of the water. Since sound travels through freshwater at approximately 1500 meters per second ($m s^{-1}$), the entire water column can be quickly sampled. The sampling rate was set at one sample per second. The transducer was towed near the water surface at an average speed of $2.0 m s^{-1}$. Full details of the acoustic equipment can be found in Brandt et al. (1991) and Mason et al. (1995). Water temperatures were simultaneously sampled at 2 Hz using a conductivity-temperature-depth (CTD) recorder attached to a hydrodynamic V-fin that was raised and lowered at approximately $1 m s^{-1}$ as the boat steamed along transects (cf. Stockwell and Sprules 1995). This 'tow-yow' sample design was converted to a two-dimensional profile of the water column by linearly interpolating temperature values in cells not sampled by the CTD. A mean value was calculated for cells with multiple measures. Cell size in the temperature data was matched to the resolution of the acoustic data.

Echo-squared integration (cf. Dragesund and Olsen 1965, Clay and Medwin 1977, MacLennan and Simmonds 1992) was used to determine the relative density of fish prey in each cell. In an initial analysis to determine the appropriate cell size for bioenergetic models, fish densities were averaged in 4 meter horizontal by 0.5 meter vertical cells. To exclude surface noise or bottom echoes, the top 2.5 m and bottom 1.0 m of the water column were not included in integration analyses. Target strengths of individual fish that were detected in each cell were estimated using a BioSonics Model 281 dual-beam signal

processor (Traynor and Ehrenberg 1979, Burczynski and Johnson 1986). Target strengths of individual fish are later converted to fish lengths using an empirical target strength-length relationship (see reviews by Cushing 1973, Midttun 1984, Foote 1991). To increase accuracy of target strength estimates, only fish within a maximum of 4° from the transducer acoustic axis were used in dual-beam analyses (Burczynski and Johnson 1986, Burczynski et al. 1987).

The univariate spectral analysis program BMDP1T (Dixon 1983) was used to quantify the variance in fish densities as a function of horizontal spatial scale (Jenkins and Watts 1969, Koopmans 1974, Chatfield 1984). This technique simultaneously estimates the variance of a continuously recorded variable over a range of wave numbers or frequencies. The inverse of a wave number or frequency is equivalent to the spatial scale. The range of scales examined in any analysis extends from twice the sample resolution to half the length of the data series. Two-dimensional fish density and walleye potential growth rate data were vertically-integrated over the entire water column to produce a one-dimensional data series for spectral analyses. This summation is analogous to examining fish distribution in a transparent water column from a vantage point above the water surface. The resulting spectral density estimates, a measure of variance in the frequency domain, were plotted as a function of frequency. The total variance in any data series is approximated by the area under the spectral density curve (Denman 1975). An averaging window of 0.01 cycles m^{-1} was used to compute final spectral density estimates. To permit direct comparison of spatial variance among the three transects, all spectral density estimates were centered (i.e. subtract the mean) and standardized (i.e. divide by the variance of the original series) (Denman 1975).

Model Structure

Spatially-explicit bioenergetic models of fish growth rate potential are fully described in Brandt et al. (1992). In brief, the first step in this process combines echo integration with target-strength analyses to form two-dimensional matrices of fish size and density. Echo integration analysis provides measures of relative fish densities. Absolute density is estimated by dividing relative fish density by the average target strength in each cell. Cells that lack target strength measures were assigned an average target strength randomly chosen from a Gaussian probability distribution of target strengths based on the mean and standard deviation from the entire transect. Target strengths were converted to fish lengths using Foote's (1987) empirical regression equation for clupeid fish. Prey fish lengths were converted to biomass using length-weight equations derived from samples collected in Lake Erie during September 1994 by the Ohio Department of Natural Resources.

Foraging by the predator was based on the encounter-rate model of Gerritsen and Strickler (1977). Prey density and size was used to estimate prey availability in each cell. Encounter of predators with prey was modeled as a function of reactive distance (i.e. maximum distance where predators react to prey), the ratio of predator to prey swimming speeds, and prey densities (Gerritsen and Strickler 1977, Gibson and Ezzi 1990, Persson and Greenberg 1990). Reactive distance of predators to prey was assumed equal to

predator body length. Predator swimming speed was modeled as a function of predator weight (Ware 1978). Prey swimming speed was assumed negligible relative to that of the predator. Consumption of prey in each cell was estimated as the predator-prey encounter rate discounted by an assumed probability of consumption. The foraging efficiency of walleye was assumed to be 0.001. This figure represents a 10% efficiency in prey detection, a 10% predator attack rate, and a 10% rate of prey capture and ingestion. The number of prey consumed was converted to biomass consumed in each cell using length-weight relationships for each prey species. Consumption by a predator is limited by the amount of prey that can be consumed, assimilated, and evacuated over a specified time period. Temperature- and weight-dependent functions are used to limit species-specific daily consumption. Final output of the bioenergetic model is potential growth rate ($\text{g g}^{-1} \text{day}^{-1}$) of a specified type and size of predator in each cell.

The bioenergetic model used in this study was parameterized for a 450 mm, 990 g walleye. Predator weight was estimated using a length-weight regression based on samples of walleye taken in the western basin of Lake Erie during September 1988 (Hartman 1989). Predators were assigned an energy density of 5.0208 kJ g^{-1} wet weight (Hewett and Johnson 1992). Variable and parameter values used in consumption, respiration, specific dynamic action (i.e. basal metabolism), egestion, and excretion equations matched those used for walleye by Kitchell et al. (1977).

Walleye eat a diverse set of prey whose proportion in the diet depends on prey availability and location (Bur and Witzel 1995). Walleye primarily eat age-0 fish (Chevalier, Forney 1974, Knight et al. 1984) and select for soft-rayed prey (Forney 1974, Knight et al. 1984). In Lake Erie, gizzard shad (*Dorosoma cepedianum*) and rainbow smelt (*Osmerus mordax*) are two dominant components of walleye diet (Bur and Witzel 1995). Based on data from stomach samples, a 450 mm walleye consumes prey ranging from 40 mm to 135 mm in length (cf. Fig. 6, Knight et al. 1984). When calculating the consumption of prey biomass, all fish within this length range were assumed to be shad in the western basin, an equal mixture of shad and smelt in the central basin, and smelt in the eastern basin (cf. Bur and Witzel 1995). Gizzard shad and rainbow smelt were assigned energy densities of 4.1236 kJ g^{-1} (Pierce et al. 1980) and 5.4392 kJ g^{-1} (Foltz and Norden 1977) wet weight, respectively. The smelt energy density value used in this study was not significantly different from the one derived by Rand et al. (1994) for smelt sampled during September in Lake Ontario.

RESULTS

Patterns of spatial variance in fish densities were consistent among the three Lake Erie transects (Fig. 2). Maximum spatial variance of relative fish density occurred at the largest scale (360 m) that significantly contributed to the spatial variance in each transect. Spatial variance in fish density decreased from large to intermediate spatial scales, plateaued at intermediate scales (approximately 180 m), and then decreased at varying rates to the smallest scale analyzed (8 m). The rate of decrease in spatial variance from intermediate to small scales was greatest in the western basin.

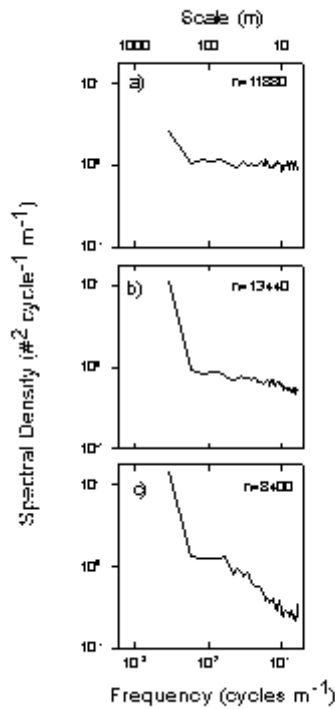


Fig. 2. Spectral density estimates of relative fish densities in a) western, b) central, and c) eastern basins of Lake Erie plotted as a function of frequency (bandwidth 0.01, centered, normalized). Periods (m) are shown on upper X axis.

Concentrations of spatial variance, characterized by distinct peaks in spectral density plots, were not observed in any of the three transects. Peaks in spatial variance are biologically interpreted as characteristic patch sizes. The rapid drop in spatial variance over a short range of scales indicates that fish densities were most heterogeneous at the largest scales sampled. In the eastern and central basins, spatial variance in the horizontal distribution of relative fish density did not dramatically decrease at scales smaller than 120 m. Variability in fish densities monotonically decreased at scales smaller than 120 m in the western basin. A cell size of 40 m horizontal by 0.5 m vertical was chosen to calculate average temperature, absolute prey size and density, and predator potential growth rates. Increasing the horizontal resolution above 40 m (i.e. smaller cell sizes) would not significantly increase the amount of spatial heterogeneity included in bioenergetic calculations. A cell size of 40 m horizontal also increases the probability that several individual targets would be present in each cell for the conversion of target strength to fish lengths.

In general, the thermal structure of the Lake Erie water column typified a two-layer, stratified lake. A warm upper layer ($\sim 20^{\circ}\text{C}$) overlaid a cooler layer when the water column was deeper than the thermocline (approximately 25 m). Maximum depths in the western and central basin transects did not exceed thermocline depth (Fig. 3). Minimum temperature of the cool layer in the eastern basin transect was 4.9°C .

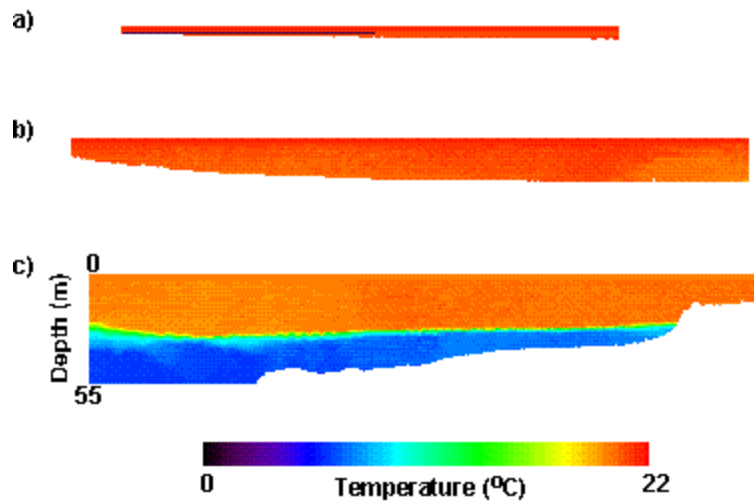


Fig. 3. Average temperature ($^{\circ}\text{C}$) of transects sampled in the a) western, b) central, and c) eastern basins of Lake Erie. Cell size is 40 m horizontal by 0.5 m vertical.

The spatial distribution of fish sizes, identified from single acoustic targets, differed among the three transects (Fig. 4). In the western basin, aggregations of larger fish were located at the inshore and offshore ends of the transect. In the central basin, larger fish were located along bottom and in two near-surface groups. These near-surface groups of large fish coincided with two aggregations of intermediate sized fish mid-way, and at the offshore end of the transect. Along the eastern basin transect, larger fish were distributed throughout the water column offshore and were concentrated near the thermocline at the nearshore end of the transect. Intermediate sized fish were aggregated just above the thermocline along the length of the eastern basin transect.

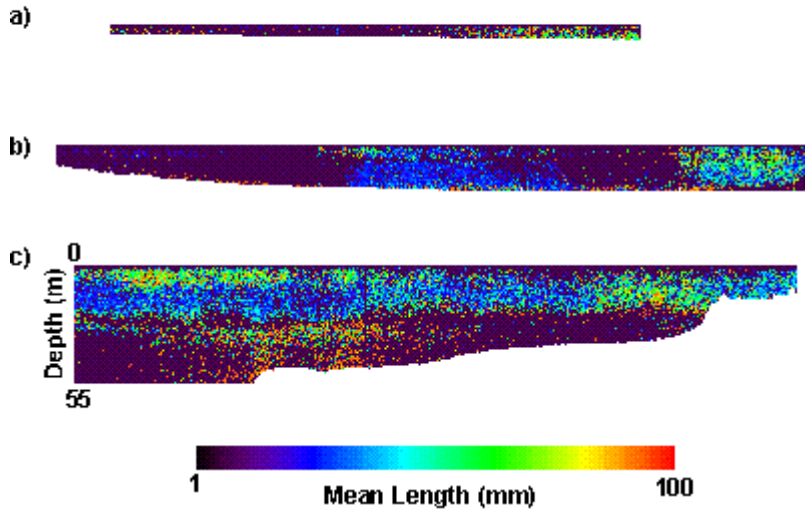


Fig. 4. Mean lengths (mm) of individual acoustic targets in the a) western, b) central, and c) eastern basins of Lake Erie. Target strengths were converted to fish lengths using Foote's (1987) equation for clupeid fish.

Patterns of variance in fish lengths (Fig. 5) closely matched patterns of average fish length along each transect (Fig. 4). High variance in fish length indicates a mixture of fish sizes within a cell. In the western basin, fish lengths varied most in the offshore third of the transect. Variance in fish lengths was highest along the bottom of the central basin transect with two vertical bands of variance in the middle and at the offshore end of the transect. In the eastern basin, fish lengths varied throughout the upper layer of the transect.

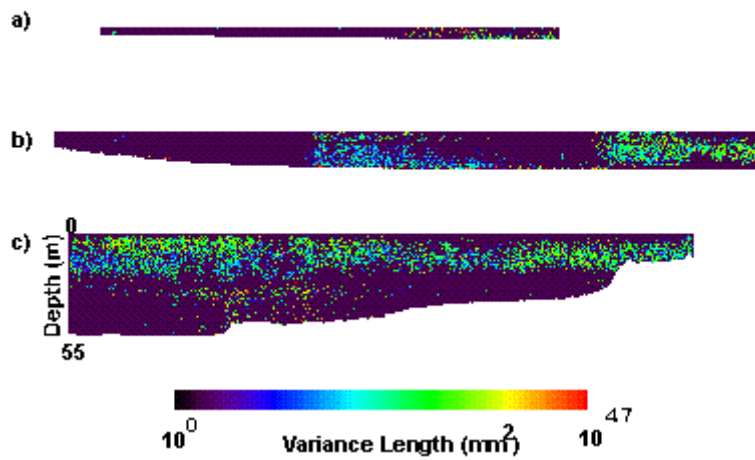


Fig. 5. Variance (mm^2) of fish lengths within cells from transects sampled in the a) western, b) central, and c) eastern basins of Lake Erie.

Densities of fish in each cell were calculated by dividing acoustic measures of relative density by the average target strength in that cell. No discernable spatial patterns of fish density were evident in the western basin transect (Fig. 6). Fish density was highly variable throughout the water column. In contrast, the central basin transect was divided into three sections by two vertical bands of dense fish concentrations. Fish densities were highest at the surface and along bottom. In the eastern basin, high densities of fish were located near-surface and along the length of the thermocline.

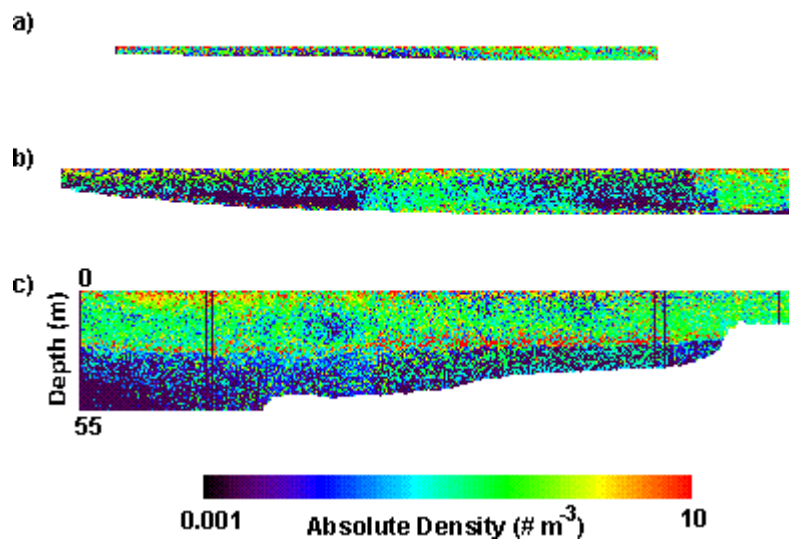


Fig. 6. Numeric density of fish ($\# \text{m}^{-3}$) from transects sampled in the a) western, b) central, and c) eastern basins of Lake Erie.

Maps of walleye potential growth rate were based on bioenergetic calculations in each cell using the average temperature and density of suitably-sized prey (between 40 mm and 135 mm in length). Maximum potential growth of walleye in the western (Fig. 7) and central basin (Fig. 8) transects coincided with dense concentrations of prey. Temperature did not strongly influence spatial patterns of walleye potential growth in these transects due to near-homogeneous temperatures throughout the water column. Water temperature did influence patterns of walleye potential growth in the deeper eastern basin transect (Fig. 9). Areas of high potential growth matched concentrations of prey along the surface and in the water layer above the thermocline. The thin band of prey below the thermocline did not result in high walleye growth rates because of cooler water temperatures. All cells with high potential growth rates were located in cells with a minimum water temperature of 19°C .

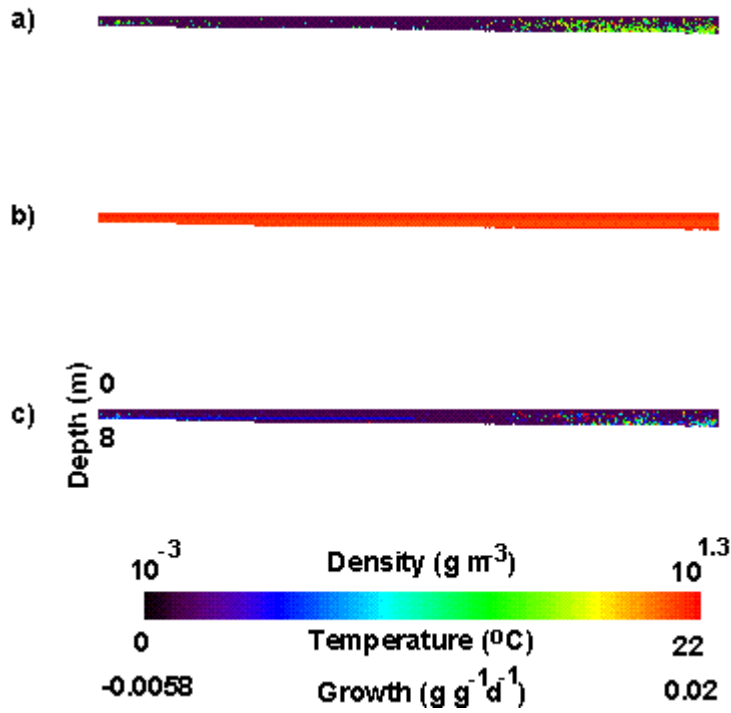


Fig. 7. a) Biomass density (g m^{-3}) of 40 to 135 mm prey fish, b) average temperature ($^{\circ}\text{C}$), and c) potential growth rate ($\text{g g}^{-1} \text{d}^{-1}$) of a 450 mm, 990 g walleye in the western basin of Lake Erie.

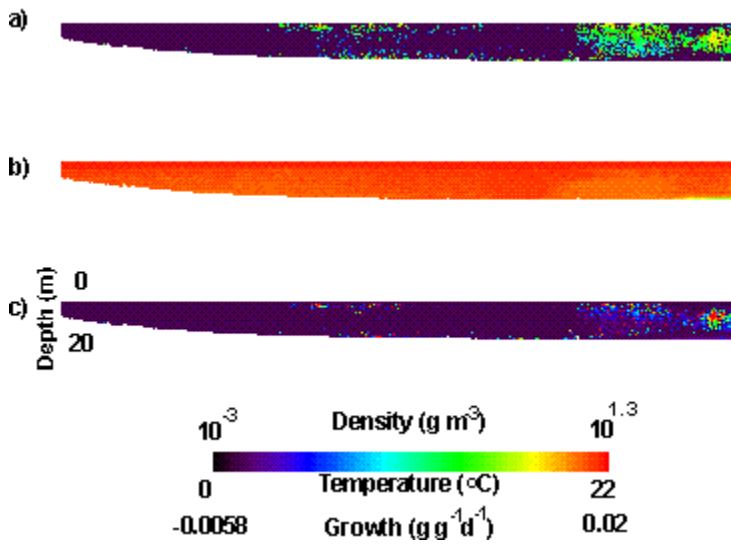


Fig. 8. a) Biomass density (g m^{-3}) of 40 to 135 mm prey fish, b) average temperature ($^{\circ}\text{C}$), and c) potential growth rate ($\text{g g}^{-1} \text{d}^{-1}$) of a 450 mm, 990 g walleye in the central basin of Lake Erie.

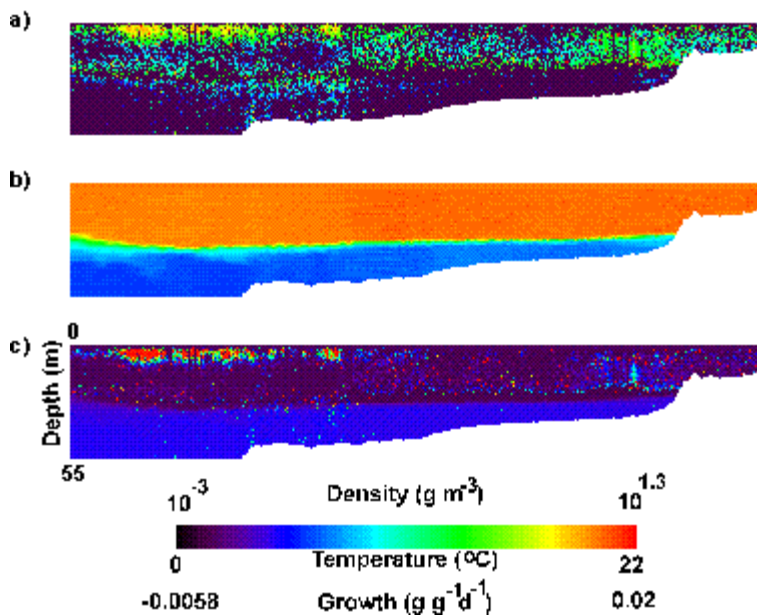


Fig. 9. a) Biomass density (g m^{-3}) of 40 to 135 mm prey fish, b) average temperature ($^{\circ}\text{C}$), and c) potential growth rate ($\text{g g}^{-1} \text{d}^{-1}$) of a 450 mm, 990 g walleye in the eastern basin of Lake Erie.

To examine scale-dependency in the spatial distribution of walleye habitat, spectral densities were computed for each transect using vertically-integrated potential growth rates (Fig. 10). Spatial variance in walleye potential growth rate was constant at spatial scales greater than 800 meters in all transects. At these large scales, spatial variance in walleye growth was an order of magnitude lower in the western basin than in the central or eastern basin. At intermediate scales (180 to 800 m), the large drop in spatial variance of potential growth rate forms a transition between two domains of spatial variance in walleye habitat quality. Slopes in transition regions matched those in spectral density plots of relative fish densities (Fig. 2).

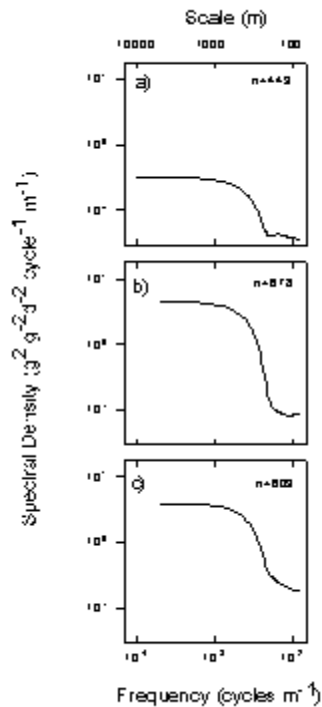


Fig. 10. Spectral density estimates of walleye potential growth rate in a) western, b) central, and c) eastern basins of Lake Erie plotted as a function of frequency (bandwidth 0.01, centered, normalized). Periods (m) are shown on upper X axis.

DISCUSSION

Growth rate potential was used to spatially index habitat quality from a fish's perspective. The technique requires high-resolution temperature and prey density data. The resulting maps of potential growth rate depict a predator's physiological response to a heterogeneous physical and biological environment. Since the entire water column is indexed, calculations are not dependent on predator distributions. Habitat quality can easily be compared among ecosystems. Summation of potential growth rates over entire water bodies can then be used as an index of fish production, to estimate fish stocking levels, to evaluate potential species introductions, and to assess the effects of environmental or anthropogenic perturbations on fish growth.

Spectral density plots were used to evaluate the distribution of spatial variance in prey densities and to choose the cell size for calculating walleye potential growth rates. Since observed patterns of spatial variance are dependent on the scale of measurement (reviewed in Horne and Schneider 1995), the choice of model resolution potentially influences interpretation of model results. If variance of a biological quantity such as density is dependent on the scale of measurement, then precision of parameter estimates also depends on measurement scale. Precision of parameter estimates can be maximized by restricting sampling and subsequent model resolution to domains of homogeneous

spatial variance (Wiens 1989). A domain of spatial variance is a range of scales with a constant or near constant slope in spectral density plots. Spatial variance domains can be demarcated using fractal geometry (Mandelbrot 1982, Sugihara and May 1990). Large changes in fractal dimension mark boundaries and indicate scales where there may be a shift in processes that generate variance in the quantity of interest (Mandelbrot 1982). The smallest homogeneous domain of spatial variance in prey distribution occurred in the western basin (40 m to 230 m, see Fig. 10). Spatial variance domains were larger in the central and eastern basins. Setting model resolution (i.e. cell size) to 40 m maintained spatial heterogeneity of prey densities observed along transects in calculations of walleye potential growth rates.

Scale-dependent spatial variance in the vertical distribution of prey density was not explicitly examined in this study. A one-dimensional spectral analysis was used to examine the vertically integrated distribution of spatial variance in prey densities. This implicitly assumes that a predator is not restricted from foraging at any depth along transects surveyed in Lake Erie. A two-dimensional spectral analysis was not computed because a square data matrix is used by the algorithm (Ripley 1981). The disproportionate length to depth ratio of survey transects would require a large number zeros to be added to 'square' a data matrix. The addition of zeros lowers the overall mean density and resulting growth rate. The partitioning of spatial variance by spectral analysis is sensitive to low means (Fasham 1978) and to the presence of zeros in count data (Horne 1995).

Small-scale spatial heterogeneity present in maps of walleye potential growth rate did not dominate the corresponding spectral density plots of walleye potential growth rate. Reduced spatial variance at small scales was a combined result of horizontal water temperature layers and the distribution of prey biomass concentrations. At any depth along the three Lake Erie transects, water temperatures were approximately 20 °C throughout the western, central, and in the upper layer of the eastern basin. Given the near-constant water temperatures, variance in walleye potential growth rate was proportional to variance in prey biomass density. Variance in potential growth rate was low at small spatial scales since adjacent cells are likely to have similar prey biomass concentrations and water temperatures. As the distance between high concentrations of prey biomass increased, spatial variance in walleye potential growth rates also increased.

Despite differences in depth and thermal structure, the quality of walleye habitat, as defined by potential growth rate, was similar among the three Lake Erie transects. In September the upper 25 m of the water column was close to the optimum temperature of 22 °C for walleye growth (Kelso 1972, Kitchell et al. 1977). In the western and central basin transects, prey were concentrated in the warmest water available. The highest concentrations of prey were also found in the warmest waters of the eastern basin transect. Comparison of walleye growth rate potentials in the eastern basin transect supports the proposal that growth rate potentials are more sensitive to changes in water temperature than to changes in prey density (Brandt 1993, Brandt and Kirsch 1993). In the isothermal water above the thermocline, growth rate potentials did not increase above a prey density threshold of approximately 15 g m⁻³. Small differences in prey density did

not influence growth rate potentials. When comparing potential growth rates at different temperatures, walleye growth rate potentials were higher above the thermocline than below for similar biomass densities of prey.

CONCLUSIONS

A spatially-explicit approach maintains the spatial heterogeneity of important biological and physical variables in environmental models. In aquatic ecosystems, bioenergetic models are dependent on remote sensing techniques (e.g. acoustic transects, CTD recorders) to provide high-resolution prey density and temperature data. Continuous prey distribution data that extend over three orders of spatial magnitude, were used to examine spatial variance in fish density distribution and to set cell size for the bioenergetic model. Data from discrete samples using traditional techniques (e.g. net samples, bathythermograph casts) potentially mask small-scale spatial variability in both biological and physical variables (Legendre and Demers 1984).

Data from transects surveyed in Lake Erie are two dimensional 'snapshots' of a small portion of a large aquatic environment. Prey and temperature distributions remain static during model calculations. The next step in the evaluation of habitat quality is to include temporally-indexed biological and physical data in the calculation of potential growth rates. The dynamics of fish growth may be examined by evaluating a series of spatial 'snapshots' at a specified temporal resolution (e.g. seasonally, diel, hourly). A second approach would incorporate dynamic spatial models (e.g. Sklar and Costanza 1991) in the calculation of potential growth rates. Dynamic spatial models allow conditions in each cell to vary over time as both predators and prey move among cells. Individual based models (e.g. Rose and Cowan 1993) which track the spatial and temporal trajectories of predators can then be used to examine the effect of individual differences in fish size and behavior on predator-prey interactions.

Analytic and visualization techniques used in this study are not part of a commercial geographic information system (GIS), but parallel the approach advocated by GIS developers and researchers (e.g. Goodchild et al. 1993, 1996). For this study, a GIS package could be used to manage data files and display model results. However, a programming language capable of translating acoustic data to fish densities, estimating consumption based on an encounter rate model, and using bioenergetic models to calculate walleye potential growth rate is not available within current GIS versions. The increasingly complex analytic requirements of environmental models could be accommodated within a GIS by including a programming language, or by increasing the flexibility of data formats used to import or export raw data and model results. Increasing the flexibility of data formats is preferred as this modification would not limit users to a single programming language, nor restrict the diversity of environments that may be modeled using GIS packages.

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