Landscape Scale Measures of Steelhead (*Oncorhynchus mykiss*) Bioenergetic Growth Rate Potential in Lake Michigan and Comparison with Angler Catch Rates

Tomas O. Höök[1],*, Edward S. Rutherford[1], Shannon J. Brines[1], Christine A. Geddes[1], Doran M. Mason[2], David J. Schwab[2], and Guy W. Fleischer[3],†

[1]*University of Michigan*
School of Natural Resources and Environment
Institute for Fisheries Research
Ann Arbor, Michigan 48109-1084

[2]*NOAA, Great Lakes Environmental Research Laboratory*
Ann Arbor, Michigan 48105-1593

[3]*USGS-BRD*
Great Lakes Science Center
Ann Arbor, Michigan 48105

ABSTRACT. *The relative quality of a habitat can influence fish consumption, growth, mortality, and production. In order to quantify habitat quality, several authors have combined bioenergetic and foraging models to generate spatially explicit estimates of fish growth rate potential (GRP). However, the capacity of GRP to reflect the spatial distributions of fishes over large areas has not been fully evaluated. We generated landscape scale estimates of steelhead (*Oncorhynchus mykiss*) GRP throughout Lake Michigan for 1994-1996, and used these estimates to test the hypotheses that GRP is a good predictor of spatial patterns of steelhead catch rates. We used surface temperatures (measured with AVHRR satellite imagery) and acoustically measured steelhead prey densities (alewife, *Alosa pseudoharengus*) as inputs for the GRP model. Our analyses demonstrate that potential steelhead growth rates in Lake Michigan are highly variable in both space and time. Steelhead GRP tended to increase with latitude, and mean GRP was much higher during September 1995, compared to 1994 and 1996. In addition, our study suggests that landscape scale measures of GRP are not good predictors of steelhead catch rates throughout Lake Michigan, but may provide an index of interannual variation in system-wide habitat quality.*

INDEX WORDS: Steelhead, Lake Michigan, bioenergetics, spatial model, habitat, AVHRR.

INTRODUCTION

Several recent studies demonstrate that different regions of Lake Michigan have distinct physical and chemical attributes (Schwab *et al.* 1999), and densities of both lower (Sprules *et al.* 1991, Nalepa *et al.* 2000) and upper (Brandt *et al.* 1991; Höök *et al.* 2003, 2004) trophic level organisms vary spatially. Since the physical, chemical, and biological characteristics of an environment in large part control fish consumption, growth, mortality, and production, it follows that these vital rates will also vary among regions of Lake Michigan. Quantifying and understanding such spatial variation in vital rates could greatly aid in the management of Lake Michigan's fish stocks. Unfortunately, the cost and effort necessary to estimate spatially-explicit vital rates throughout Lake Michigan using traditional methods renders such an undertaking impractical, and if individual fish move extensively among regions, then it may in fact be impossible to estimate region-specific vital rates.

To overcome such obstacles and quantify local habitat quality, Brandt *et al.* (1992) introduced an approach by which spatially explicit measures of

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*Corresponding author. E-mail: thook@umich.edu
†Present address: NMFS, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, WA 98112

water temperature and prey densities are integrated to generate a grid of spatially explicit estimates of fish growth rate potential (GRP). Under this approach, potential consumption within a particular volume of water (i.e., grid cell) is estimated with a foraging sub-model (as a function of temperature and prey density) and GRP within the same volume of water is estimated with a bioenergetics sub-model (as a function of potential consumption and temperature). Thus, the degree of spatial overlap between suitable temperatures and prey densities is the key determinant of GRP. Several authors have now used this approach to measure the quality of particular habitats by estimating potential growth (Brandt *et al.* 1992, Brandt and Kirsch 1993, Mason *et al.* 1995, Nislow *et al.* 2000), consumption (Walline *et al.* 2000), production (Höök *et al.* 2003), and carrying capacity (Luo *et al.* 2001).

Mason and Brandt (1996) demonstrated that the spatial scale at which GRP is estimated can dramatically influence mean GRP values within particular areas, and the degree of heterogeneity perceived within such areas. Most prior efforts to quantify GRP have involved modeling a particular plane of water at a relatively fine spatial scale (but see Luo *et al.* 2001, Höök *et al.* 2003). For instance, Goyke and Brandt (1993) estimated GRP for chinook salmon (*Oncorhynchus tshawytscha*) and lake trout (*Salvelinus namaycush*) within 78 m² cells (1 m deep by 78 m wide) in Lake Ontario. As Wiens and Milne (1989) point out, one should choose a spatial scale of analysis based upon the particular organism and question of interest. The relatively fine spatial scale employed by Goyke and Brandt (1993) and others is likely appropriate for considering the behavior of individual fish foraging in a limited area. This scale is particularly appropriate if the area of interest has a vertical dimension, because physical and biological features in marine and lacustrine systems can vary dramatically over short distances along the vertical axis. However, a coarser scale of analysis that allows for some integration across space is more appropriate when considering horizontal, regional differences throughout large systems. For instance, in developing a three-dimensional model for Atlantic menhaden (*Brevoortia tyrannus*) GRP throughout Chesapeake Bay, Luo *et al.* (2001) divided their environment into 4,000 cells, each approximately 5 × 10 km along the horizontal plane, but only 2 m deep.

The Lake Michigan steelhead (*Oncoryhnchus mykiss*) population constitutes an economically and ecologically important fishery. A recent analysis by Höök *et al.* (2004) revealed that catch rates of Lake Michigan steelhead by sport anglers are temporally and spatially variable. In addition, this analysis suggested a relationship between catch rates and surface temperatures (Höök *et al.* 2004). We hypothesize that a spatio-temporal integration of temperatures and prey densities (i.e., GRP) can also account for variation in catch rates. Fitness of individual steelhead in Lake Michigan should theoretically be growth-dependent, and thus GRP may be a useful proxy for habitat quality. Habitat quality for populations consisting of small and/or young fish is a function of both growth and mortality rates (Werner and Gilliam 1984). Similarly, habitat quality for mature fish searching for appropriate spawning habitats is at least in part a function of factors other than their own growth rate.

Past attempts to link GRP with fish growth rates and distributions have been equivocal. Tyler and Brandt (2001) used individual-based simulations to evaluate the effectiveness of GRP as a measure of habitat quality for alewives (*Alosa pseudoharengus*). Within their simulated environments, average GRP was strongly correlated with (but did not quantitatively match) individual growth rates (Tyler and Brandt 2001). Similarly, Luecke *et al.* (1999) found a significant relationship between mean lake trout (*Salvelinus namaycush*) condition and the proportion of modeled habitat cells with positive GRP. Others have attempted to correlate growth rate potential with the spatial distribution of organisms. Tyler and Brandt (2001) compared the spatial distributions of simulated alewives and GRP, and found a relatively poor correlation between fish density and GRP. This latter finding is similar to that of Wildhaber and Crowder (1990), who found that a bioenergetic integration of food and temperature was a relatively poor predictor of bluegill (*Lepomis macrochirus*) habitat choice. On the other hand, Nislow *et al.* (2000) observed that age-0 Atlantic salmon (*Salmo salar*) tended to occupy stream sites with positive GRP, rather than sites with negative GRP.

In this paper, we adapt the approach presented by Brandt *et al.* (1992) to generate landscape-scale measures of GRP for steelhead throughout Lake Michigan during September 1994-1996. Our intent is to consider horizontal, regional differences in steelhead GRP. Thus, we choose a relatively coarse spatial scale relevant to both the Lake Michigan steelhead population and the anglers that exploit it. In addition, we test the hypothesis that GRP is a useful predictor of spatial variation in steelhead catch rates.

METHODS

Based upon the approach presented by Brandt *et al.* (1992), we developed an integrated foraging-bioenergetics model to generate landscape-scale, spatially-explicit estimates of steelhead GRP in Lake Michigan as a function of water temperature and alewife abundance. To facilitate our analysis, we divided the surface of Lake Michigan into a grid of 273 10 × 10 minute grid cells (individual cells ~13 km × ~18 km; Fig. 1). We limited our analysis to the upper (0–25 m) portion of the water column (i.e., the well mixed layer during late summer), because steelhead (both in the Pacific Ocean and the Great Lakes) primarily inhabit surface waters (Ruggerone *et al.* 1990, Burgner *et al.* 1992, Aultman and Haynes 1993). In addition, based upon data availability we restricted our analysis to the month of September for the years 1994–1996. For each year, we estimated average steelhead GRP within individual 10-minute grid-cells. We then calculated lake-wide mean GRP by averaging our estimates of GRP within individual 10-minute grid-cells.

MODEL STRUCTURE

We used a bioenergetics model for Great Lakes steelhead as parameterized by Rand *et al.* (1993) to model GRP of a 3.5-kg steelhead (the approximate mean size of harvested steelhead, Michigan Department of Natural Resources, Fisheries Division, unpublished data). This model takes the form of classic bioenergetics models (e.g., Kitchell *et al.* 1977) in which weight-specific growth (G) is estimated on a daily basis,

$$G = C - (R + SDA + F + U) \qquad (1)$$

where C is weight-specific consumption, R is weight-specific respiration, SDA is weight-specific specific dynamic action, F is weight-specific egestion, and U is weight-specific excretion. For our analysis, we set GRP equal to G in equation 1. We assumed that adult steelhead had an energy density of 9,210 J g^{-1} (Rand *et al.* 1993), and that during September their alewife prey had an energy density of 8,000 J g^{-1} (Stewart and Binkowski 1986, from Flath and Diana 1985).

The functional response relating alewife density to steelhead consumption in Lake Michigan is unknown. Thus, we used a relatively simple foraging submodel,

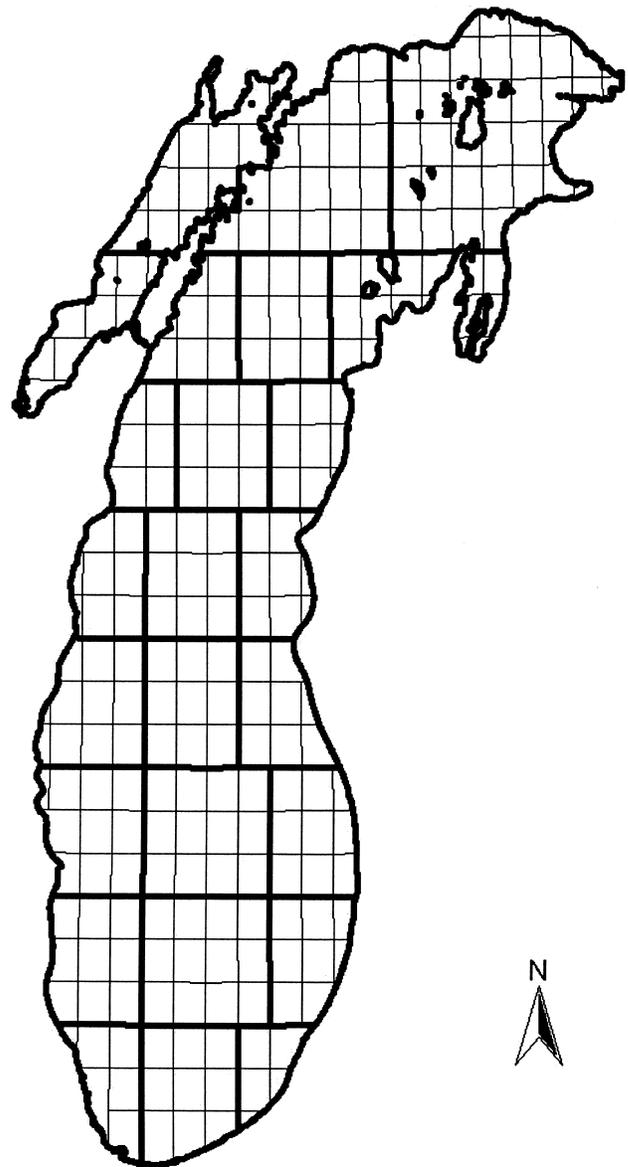$$C = p(N) \times C_{max} \qquad (2)$$

FIG. 1. *Lake Michigan divided into 273, 10-minute by 10-minute grid cells (thin lines) and 26, approximately 30-minute by 30-minute grid cells (bold lines).*

where C_{max} is the maximum daily consumption (g g^{-1} d^{-1}) of steelhead at a particular ambient temperature, and p is a function of alewife density (N) and is defined as the proportion of C_{max} obtained. We allowed p to vary linearly with alewife density up to p = 1, with p = 0 when alewife density equals 0, p = 0.38 at the average alewife density from 1994–1996 (i.e., 17.7 kg ha^{-1}) and p = 1 at and above some critical alewife density (i.e., 46.6 kg

ha^{-1}). This type of functional response is comparable to that suggested for lake trout in Lake Michigan (Eby *et al.* 1995).

We estimated the proportion of maximum consumption at the average alewife density (p = 0.38) by simulating annual growth of an average harvested steelhead with Fish Bioenergetics 3.0 (Hanson *et al.* 1997). In so doing, we assumed that an average harvested steelhead grows from 2.5-kg to 3.8-kg during a year (J. Bence and E. Smith, Dept. of Fisheries and Wildlife, Michigan State University, East Lansing, MI, 48824, personal communication). We also assumed that the ambient temperature occupied by a steelhead during a day is equal to whichever is warmer, 1) the lake-wide average surface temperature (from Advanced Very High Resolution Radiometry, AVHRR, measurements; averaged over 1994–1996) or 2) 4°C. Finally, we assumed that a steelhead's diet consists of 50% invertebrates (3,500 J g^{-1}) and 50% alewives during January through June, and 100% alewives during the remainder of the year (Robert Elliot, USFWS, personal communication), and that alewife energy densities change seasonally from a minimum of 4,800 J g^{-1} to a maximum of 9,000 J g^{-1} (Flath and Diana 1985, Stewart and Binkowski 1986). With these diet and temperature inputs, we calculated the proportion of maximum consumption necessary to achieve the observed annual growth (i.e., p = 0.38).

DATA LAYERS

Surface Temperatures

We obtained surface water temperatures through satellite AVHRR imagery available through NOAA's CoastWatch program (Schwab *et al.* 1999). We assumed that surface temperatures reflected temperatures from depths of 0 to 25 m. NOAA's CoastWatch program records surface temperatures for the Great Lakes at approximately 2.6 km resolution, up to four times a day. We averaged all surface temperatures recorded within a cell on a given day to calculate the daily mean temperature within a cell, and averaged these daily mean temperatures to calculate a cell's monthly mean temperature.

Prey Densities

We used estimates of alewife densities to index variation in steelhead prey. During September, steelhead in Lake Michigan feed almost exclusively on alewives (Robert Elliot, USFWS, personal communication). We used hydroacoustic-based estimates of

alewife abundance collected by the USGS Great Lakes Science Center to quantify the spatial distributions of alewives in the epilimnion (0–25 m; see Argyle *et al.* 1998 for details). Total fish biomass was measured acoustically along individual line transects. Total biomass was then partitioned among species, based upon fish species composition in simultaneously deployed midwater trawls. Sampling was undertaken during September and early October (8 September to 11 October in 1994; 14 September to 18 September in 1995; 15 September to 13 October in 1996), and an average of 16 acoustic transects were completed each year (Fig. 1).

We stratified the acoustic estimates of alewife abundance along individual transects by 10-m bathymetric depths. This procedure transformed continuous transects into a series of discrete data points, with each data point falling midway between adjacent 10-m isobaths. We then used a kriging approach to interpolate point-measures of alewife densities lake-wide. This approach involves two general steps: quantifying the spatial structure of the data and making predictions accordingly. These predictions are based upon the nearness and direction of neighbors. However, natural barriers are not considered. We therefore concluded that Green Bay and Traverse Bay estimations were suspect and excluded these embayments from our analyses. We fitted a model for each year's data, creating grids of 865 m^2 cells for both estimates of alewife density and standard errors. We then summarized these model predictions by 10-minute grid cells, allowing us to readily link this spatial data layer with others. All kriging was done in the ArcGIS Geostatistical Analyst module using the ordinary kriging algorithm (ESRI 2002). Results of the kriging models were comparable to results from other geostatistical methods we used to interpolate alewife densities, including Triangular Irregular Networks and inverse distance weighting (DeMers 1999).

Steelhead Harvest

We calculated charter boat angler catch rates based on creel data collected by the Illinois, Michigan, and Wisconsin Departments of Natural Resources (DNR) from 1994 to 1996. Charter boat captains recorded data from each fishing trip, including; date, location (i.e., 10-minute grid-cell), number of anglers, hours spent fishing, and number and species of fish caught. Some fishing trips appeared to target non-salmonines (e.g., yellow perch, *Perca flavescens*). Since such fishing trips could bias our

estimates of steelhead catch-per-unit-effort (CPUE), we excluded all fishing trips when > 0 yellow perch were caught. Out of 7,159 fishing trips during September 1994–1996, we only excluded 117 trips (1994 = 71; 1995 = 33; 1996 = 13). We calculated the CPUE of steelhead for each trip as the total number of steelhead caught divided by the total number of angler hours. We calculated the average lake-wide, monthly CPUE as the mean CPUE of individual trips (1994, n = 2,380; 1995, n = 2,184; 1996, n = 2,478). We calculated average CPUE for an individual 10-minute grid-cell as the mean CPUE of individual trips within the corresponding grid-cell.

DATA ANALYSIS

We compared estimates of GRP with mean monthly steelhead CPUE in the corresponding 10-minute grid-cells, by 1) calculating Spearman rank-correlation coefficients and 2) using independent t-tests to compare mean steelhead CPUE in cells with positive versus negative GRP ($\alpha = 0.05$). In so doing, we were forced to account for the fact that data violated the standard statistical assumption of independence. The data layers used in our analyses (surface temperatures, alewife densities, and steelhead CPUE) were significantly, positively autocorrelated (based upon calculated Moran's I and Gerry's C statistics), and thus measurements in adjacent cells were not independent of each other (Legendre 1993). Also, because alewife densities were interpolated throughout Lake Michigan, estimates of alewife densities in one cell were obviously dependent upon measurements in other cells. In order to overcome these violations of independence, we opted to limit our analyses to those 10-minute grid-cells which were intersected by alewife acoustic transects (Fig. 2). Model inputs (i.e., mean temperatures and alewife kriging estimates) and mean catch rates within these subsets of cells were no longer significantly, positively autocorrelated.

Measures of GRP are dependent upon the spatial scale of analysis (Mason and Brandt 1996). To evaluate whether measures of GRP and associations between GRP and steelhead CPUE were robust to variation in scale, we also conducted the analyses at a coarser spatial scale, 30 × 30-minute grid-cells (Fig. 1). We estimated mean monthly surface temperatures and alewife densities within 30-minute grid-cells, and then used these data as inputs to estimate GRP. We then compared these estimates with steelhead CPUE in corresponding 30-minute grid-cells.

Measures of GRP are also dependent upon the temporal scale of analysis. At fixed consumption rates, bioenergetics models predict non-linear changes in growth with changes in temperature. Thus, our use of mean monthly surface temperatures as inputs to estimate monthly GRP within 10-minute grid-cells is not equivalent to estimating daily GRP within 10-minute grid-cells and then averaging over a month. In order to evaluate the effects of this disparity, we estimated daily GRP within individual 10-minute grid-cells (as a function of daily mean temperatures and interpolated alewife densities) and then averaged these daily estimates over a month to determine mean monthly GRP. We then compared these new estimates of mean monthly GRP with average monthly CPUE of steelhead in corresponding 10-minute grid-cells.

RESULTS

Lake-wide mean GRP varied among years, and was positive in 1995 and negative in 1994 and 1996 (Table 1). The proportion of 10-minute grid cells with positive GRP also was greater in 1995 (0.80) relative to 1996 (0.35) and 1994 (0.02). This is consistent with interannual variation in mean temperatures and alewife densities (Table 1).

During September of 1994–1996, Lake Michigan surface temperatures varied spatially (Fig. 2). Not surprisingly, temperatures tended to decrease with increasing latitude. In addition, temperatures were on average warmer in the eastern region, relative to the western region of the lake (this tendency did not hold for 1996). Alewife densities also varied spatially, and during 1995 and 1996, alewife densities increased with latitude. During 1994 however, we observed the opposite trend; alewife densities tended to decrease with latitude (Fig. 2). Steelhead GRP tracked variation in both temperature and alewife densities. On average, steelhead GRP tended to increase with latitude. During the three years we examined, we calculated the overall highest GRP values for west central Lake Michigan during 1995. However, this region did not contain the highest GRP values during our two other study years (Fig. 3).

There was no apparent spatial relationship between steelhead GRP and CPUE (Fig. 3), and Spearman rank correlation tests indicated no significant associations between these two variables (1994, $\rho = -0.03$, n = 29; 1995, $\rho = 0.03$, n = 41; 1996, $\rho = 0.11$, n = 17). Similarly, there was no significant difference between mean steelhead CPUE in 10-minute grid-cells with positive GRP and cells with
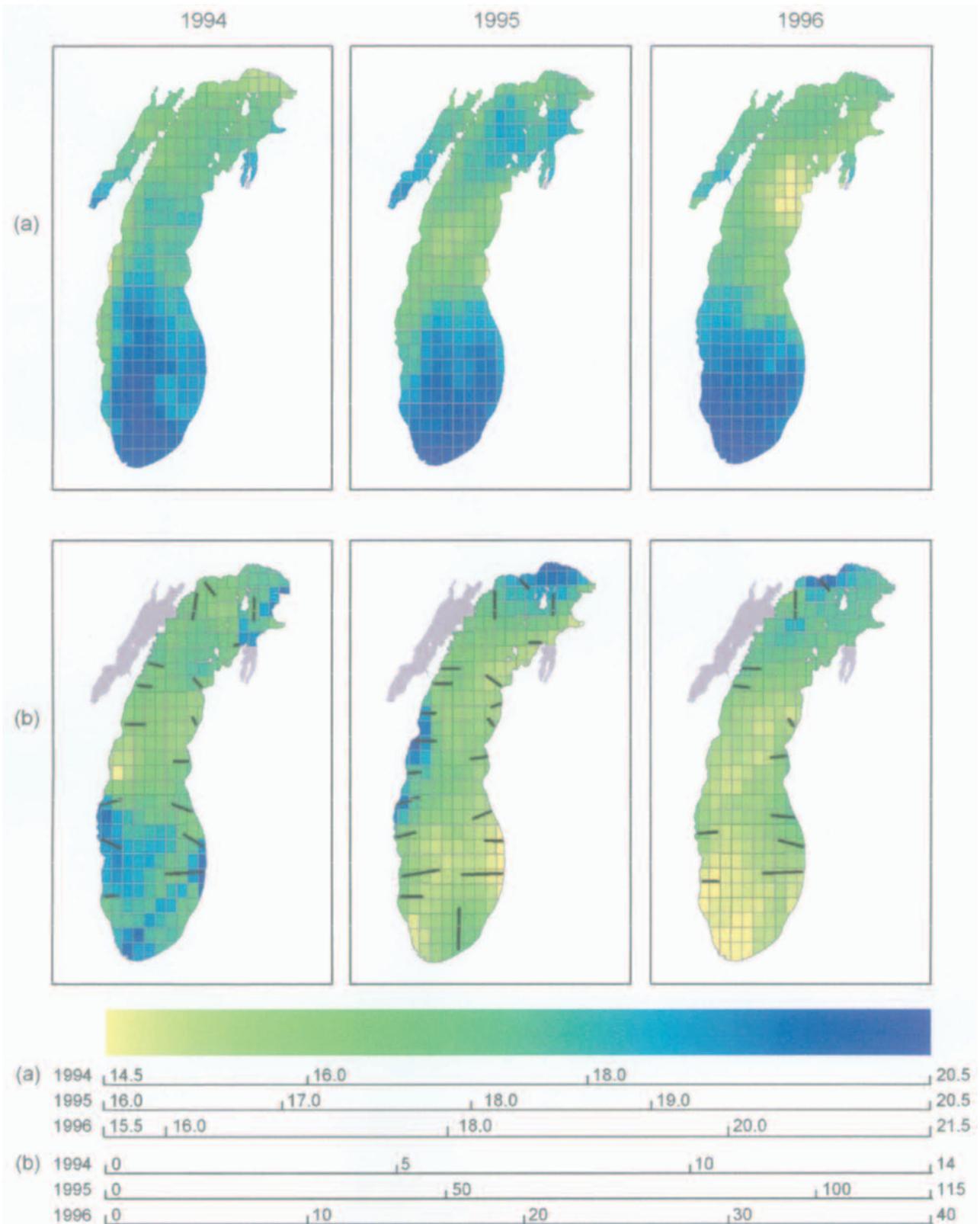
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FIG. 2. *Lake Michigan September 1994–1996: a) Mean satellite-measured surface temperatures (°C) and b) USGS-GLSC acoustic transects (black points) and interpolated alewife densities summarized by 10-minute grid cells (kg ha^{-1}). Note that scales differ among years.*

TABLE 1. *Lake Michigan, September 1994–1996: Mean temperature ±SE (°Celsius; measured via AVHRR satelite imagery), alewife density ±SE (kg ha⁻¹: measured acousticaly), steelhead growth rate potential ±SE (GRP; g g⁻¹ d⁻¹), and steelhead cpue.*

	Mean temperature °Celsius	Mean alewife density kg ha^{-1}	Mean GRP g g^{-1} d^{-1}	Mean steelhead cpue fish hr^{-1}
1994	18.0 ± 0.1	6.5 ± 0.2	-0.0049 ± 0.0001	0.064 ± 0.002
1995	18.6 ± 0.1	36.3 ± 1.5	0.0090 ± 0.0005	0.068 ± 0.003
1996	18.7 ± 0.1	11.0 ± 0.5	-0.0030 ± 0.0004	0.104 ± 0.004

negative GRP (1994, no cells with positive GRP, n = 29; 1995, t = 0.21, n = 41; 1996, t = 0.09, n = 17).

Analyses at a coarser spatial scale (30-minute grid-cells) did not qualitatively change the results. Mean GRP was still greater during 1995 (0.0085 ± 0.0016 g g^{-1} d^{-1}) relative to 1996 (-0.0046 ± 0.0011 g g^{-1} d^{-1}) and 1994 (-0.0051 ± 0.0002 g g^{-1} d^{-1}), and the proportion of cells with positive GRP was greater during 1995 (0.83) compared to 1996 (0.22) and 1994 (0). In addition, there was no significant relationship between GRP and steelhead CPUE based on Spearman rank correlation coefficients (1994, $\rho = -0.15$, n = 21; 1995, $\rho = -0.15$, n = 22; 1996, $\rho = -0.01$, n = 22), and there were no significant differences between mean steelhead CPUE in 30-minute grid-cells with positive GRP and cells with negative GRP (1994, no cells with positive GRP, n = 21; 1995, t = 1.61, n = 22; 1996, t = 1.31, n = 22).

Calculating mean September GRP as the average of daily estimates of GRP also did not qualitatively change the results. Mean GRP was still greater during 1995 (0.0072 ± 0.0005 g g^{-1} d^{-1}) relative to 1996 (-0.0047 ± 0.0004 g g^{-1} d^{-1}) and 1994 (-0.0050 ± 0.0001 g g^{-1} d^{-1}), and the proportion of 10-minute grid cells with positive GRP remained greater in 1995 (0.75) relative to 1996 (0.29) and 1994 (0.01). Further, there was no significant relationship between GRP and steelhead CPUE. Spearman rank correlation coefficients were not significant (1994, $\rho = -0.03$, n = 29; 1995, $\rho = 0.04$, n = 41; 1996, $\rho = 0.11$, n = 17), and mean steelhead CPUE in 10-minute grid-cells with positive GRP versus negative GRP were not significantly different (1994, no cells with positive GRP, n = 29; 1995, t = 0.33, n = 41; 1996, t = 0.78, n = 17).

DISCUSSION

Our analyses suggest that potential steelhead growth rates in Lake Michigan are highly variable in both space and time. Such variation in GRP is perhaps not surprising given that the two inputs used to estimate GRP (mean temperature and alewife densities) vary annually (Madenjian *et al.* 2002) and spatially (Höök *et al.* 2003). During our study period (September 1994–1996), we estimated the over-all greatest steelhead GRP in west central Lake Michigan during 1995. This region is highly productive, with frequent upwelling events and high densities of both benthic invertebrates and zooplankton (Sprules *et al.* 1991, Nalepa *et al.* 2000, Höök *et al.* 2004). During 2 of the years examined (1995 and 1996), we also estimated high GRP in far northern Lake Michigan. This region is not very well studied, but its bathymetry is characterized by a high degree of vertical relief, suggesting frequent upwellings and high potential productivity. In short, some of the spatial trends we found in steelhead GRP were consistent with underlying spatial variation in physical and biological factors.

At the spatial and temporal scales of our analyses, steelhead CPUE did not match spatial variation in GRP. The inability of GRP to predict CPUE throughout Lake Michigan does not necessarily indicate that the model is flawed. It is possible that at a finer spatial scale CPUE would match GRP (however, the data available to us preclude analyses at finer spatial scales). In addition, the ultimate purpose of GRP models is not to predict catch rates, but rather to index habitat quality within a region or entire system. There are several potential reasons why our estimates of GRP do not spatially match CPUE; 1) our model may not adequately depict steelhead growth potential, 2) CPUE may be a poor index of steelhead density, and 3) the maximization of growth potential may not be the primary basis for habitat choice by Lake Michigan steelhead.

Our GRP model estimates could be deficient either because the constituent models (bioenergetics and foraging) are flawed or because model inputs (alewife densities and surface temperatures) are in-
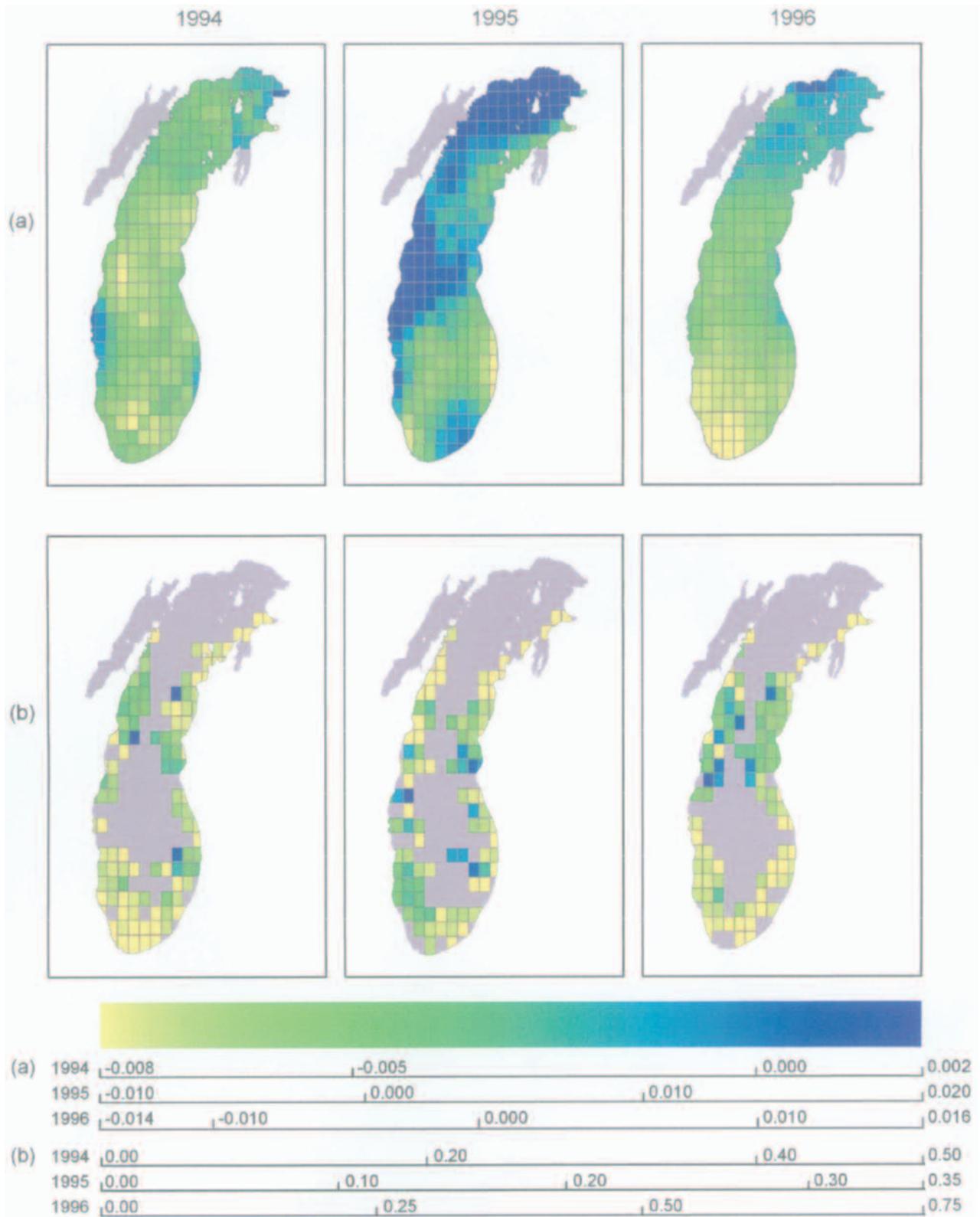
FIG. 3.   a) Growth rate potential (GRP; g g^{-1} d^{-1}) of a 3.5-kg steelhead and b) Average catch per unit effort (CPUE; number caught per angler hour) within Lake Michigan, 10-minute grid cells during September 1994–1996. Note that scales differ among years.

adequate. Bioenergetics models are used extensively within fisheries management and are generally assumed to provide adequate estimates of fish growth and consumption. However, some studies (e.g., Hartman and Brandt 1993, Munch and Conover 2002, Trudel *et al.* 2004, Slaughter *et al.* 2004) point to potential biases associated with bioenergetics models. The functional response relating alewife density to steelhead consumption in Lake Michigan is unknown. Thus, we used a simple type I model with a threshold at a critical prey density. A non-linear function relating alewife density and steelhead consumption would obviously have affected our measures of GRP, but we have no basis for using such a function. Based on past studies and available data, we assumed that during September, steelhead feed exclusively on alewives. However, consumption of alternative prey could transform areas with apparently low GRP into areas supporting high steelhead growth rates. Past studies suggest that steelhead primarily inhabit surface waters (Ruggerone *et al.* 1990, Burgner *et al.* 1992, Aultman and Haynes 1993) and we therefore assumed that surface water temperatures are indicative of the ambient thermal conditions experienced by steelhead. However, if steelhead undertake excursions into deeper waters, or if surface temperatures are merely indicative of the top layer (< 1m) of the water column (i.e. during extremely calm and sunny days), then steelhead would experience cooler ambient thermal conditions. Such biases could lead us to either over- or under-estimate GRP.

Our estimates of steelhead CPUE are likely imperfect indices of steelhead abundance. Abundance and CPUE are not likely linearly related (e.g., Peterman and Steer 1981, Bannerot and Austin 1983, Post *et al.* 2002), and catch rates are undoubtedly influenced by ambient conditions (i.e., temperature, water clarity, and food availability) and angler skill and preference. Even so, CPUE is used extensively to index temporal variation in fish abundance and should at least coarsely reflect spatial variation in abundance. Ideally, local steelhead CPUE should be compared with fishery-independent estimates of abundance. Unfortunately, such data for steelhead are not available. However, the data set utilized in this analysis also includes information on catches of other salmonines, and spatio-temporal comparisons between angler catch rates of chinook salmon and fishery-independent estimates of chinook salmon abundances agree fairly well (Edward Rutherford, University of Michigan, unpublished data). Finally, the relative fit and shape of the relationship between

CPUE and fish abundance should depend on how effort is measured. Angler hours have been used in past studies of Lake Michigan salmonines (Schmalz *et al.* 2002, Höök *et al.* 2003); nonetheless another measure of effort may be less biased. To explore this possibility, we calculated CPUE within 10-minute grid-cells (September 1994–1996) as steelhead caught per angler hour, trip hour, and trip. These three measures of CPUE were all highly spatially, positively correlated with each other, and no measure of CPUE was significantly correlated with GRP.

GRP provides a snapshot of conditions in a heterogeneous environment, but fails to account for several important dynamic processes (e.g., prey depletion, production, competition, spawning migrations, and the cost of moving from one volume of water to another) which can influence fish location. For instance, high densities of prey may attract predators, which could subsequently deplete this high prey density. An individual predator is then faced with the option of remaining in the depleted volume or moving to another volume of water. The option it chooses should be a function of several factors, including the energetic cost of moving to a new volume and the rate at which prey biomass will increase (i.e., production rate) in its current volume. If the cost of movement and the production rate in the current volume are high, the fish may remain in its current patch, although such a volume of water has low prey densities (i.e., low GRP). Thus, prey depletion may in part explain the lack of a relationship between steelhead CPUE and GRP. Nislow *et al.* (2000), however, found a significant tendency for age-0 Atlantic salmon to occupy stream sites with positive GRP, rather than sites with negative GRP. This disparity between Nislow *et al.*'s (2000) and our results may arise from differences between the systems we studied and the spatial scales of our analyses. Nislow *et al.* (2000) modeled stream microhabitats (1 m^2), which likely experience essentially continuous, downstream drift of prey items, with the possibility of prey depletion seemingly unlikely.

Tyler and Hargrove (1997) demonstrated that even without the possibility of prey depletion, the spatial distributions of foragers in large environments will not necessarily match that of their prey, particularly if foragers are limited in their dispersal distance. This likely holds for steelhead in Lake Michigan. Although steelhead can travel up to 42 km d^{-1} (Ruggerone *et al.* 1990), they would still be limited as to the areas of Lake Michigan that they could disperse to during a single day. In addition, steelhead in Lake

Michigan do not have perfect knowledge of their environment and are unlikely to continuously be aware of optimal growth areas within the lake. Thus, because regional prey densities are dynamic, steelhead are unlikely to precisely track prey densities due in part to their limited dispersal ability and imperfect knowledge of their environment.

Even in relatively small areas (i.e., low costs of movement and more or less perfect knowledge of the environment) with no prey depletion, GRP may not match the spatial distribution of fishes. Wildhaber and Crowder (1990) evaluated how bluegills in the laboratory consider variation in temperature and prey density when choosing patches. They concluded that thermoregulation, and not the bioenergetic integration of food and temperature, was the best predictor of patch choice (Wildhaber and Crowder 1990). This may also be the case for steelhead in Lake Michigan. Höök *et al.* (2004) found consistent, significant relationships between temperature and steelhead CPUE in Lake Michigan.

In addition, inter-specific competition and staging for spawning runs may also contribute to the departure of observed steelhead distributions from GRP predictions. Steelhead share Lake Michigan with four other salmonine species (coho salmon, *Oncorhynchus kisutch*; chinook salmon; brown trout, *Salmo trutta*; and lake trout), all of which consume alewives as a primary component of their diets. There is evidence that salmonine species in the Great Lakes vertically partition the water column (Olson *et al.* 1988), and perhaps also partition their habitats horizontally (Olson *et al.* 1988; S. Brines, University of Michigan, unpublished data). Such horizontal partitioning would lead to a departure of observed steelhead distributions from GRP predictions. Lake Michigan steelhead generally enter rivers either during the late fall and early winter or during the spring (Seelbach 1993). Prior to beginning their spawning runs, steelhead aggregate at the mouths of their natal rivers or in river-mouth lakes (Seelbach 1993). The timing of such staging is unclear. However, it is possible that staging by fall and winter run steelhead initiates in late September. If staging occurs in coastal waters with relatively low GRP, this could lead to a substantial deviation in steelhead distributions from that predicted by GRP.

Our results are similar to those of Tyler and Brandt (2001), who used an individual-based model to evaluate the use of GRP as a predictor of fish growth in a heterogeneous environment. They failed to find a strong spatial relationship between GRP and fish distributions. However, they found that sim- ulated growth rates were strongly, positively correlated with mean system-wide GRP, supporting the use of GRP as a measure of relative, system-wide habitat quality (Tyler and Brandt 2001). With GRP measures from only three years, we can not explicitly evaluate if mean, lake-wide GRP is a useful indicator of interannual variation in steelhead growth and abundance (however, comparisons between annual measures of steelhead size-at-age and mean GRP tentatively suggest a positive relationship). GRP may be a useful metric with which to evaluate how habitat quality varies both among systems (e.g., Mason *et al.* 1995) and temporally within systems (e.g., Brandt *et al.* 2002). However, the static nature of this measure limits its usefulness as a predictor of fish spatial location throughout a large system. Models that incorporate important dynamic processes such as cost of movement, prey depletion, and production may be more successful at predicting fish spatial distribution.

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