Spatially Explicit Measures of Production of Young Alewives in Lake Michigan: Linkage Between Essential Fish Habitat and Recruitment[1]

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ABSTRACT: The identification and protection of essential habitats for early life stages of fishes are necessary to sustain
fish stocks. Essential fish habitat for early life stages may be defined as areas where fish densities, growth, survival, or
production rates are relatively high. To identify critical habitats for young-of-year (YOY) alewives (*Alosa pseudoharengus*)
in Lake Michigan, we integrated bioenergetics models with GIS (Geographic Information Systems) to generate spatially
explicit estimates of potential population production (an index of habitat quality). These estimates were based upon
YOY alewife bioenergetic growth rate potential and their salmonine predators' consumptive demand. We compared
estimates of potential population production to YOY alewife yield (an index of habitat importance). Our analysis sug-
gested that during 1994–1995, YOY alewife habitat quality and yield varied widely throughout Lake Michigan. Spatial
patterns of alewife yield were not significantly correlated to habitat quality. Various mechanisms (e.g., predator migra-
tions, lake circulation patterns, alternative strategies) may preclude YOY alewives from concentrating in areas of high
habitat quality in Lake Michigan.

Introduction

The identification and protection of critical hab-
itats for early life stages of fishes is essential for
sustainable fisheries management. The Sustainable
Fisheries Act requires managers "to promote and
protect essential fish habitat" (EFH), and defines
EFH as "those waters and substrates necessary to
fish for spawning, breeding, feeding or growth to
maturity." The identification of EFH can be com-
plicated by a lack of data. Several authors have in-
ferred the quality of a specific habitat (we define
habitat as an area characterized by both abiotic
and biotic factors) for the early life stages of a fish
species from the presence or density of an early
life stage. If growth or mortality rates vary among
habitats, then the presence or relative abundance
of an early life stage may reveal little regarding the
ultimate yield of fish biomass or number of recruits
from a habitat.

The relative merit of a habitat for juvenile ani-
mals is a function of habitat-specific growth and
mortality rates (Werner and Gilliam 1984). Houde
(1997) related this idea to fish recruitment and
suggested that the ratio of instantaneous mortality
rate (M) to instantaneous growth rate (G) provides
an index of recruitment potential. This index is
synonymous with instantaneous population pro-
duction. If $M/G < 1$, the population production
is positive (i.e., the biomass of a fish population
within a habitat is increasing), and conversely if
$M/G > 1$, the population production is negative.
The utility of this index for assessing the quality or
importance of habitat is limited for two reasons.
The density of a species in a habitat may directly
and indirectly influence its own growth and mor-
tality rates. We suggest that the quality of a habitat
should be judged by the characteristics of that hab-

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itat, independent of species density. The M/G index is also expressed on a per unit basis, and the yield of recruits from a habitat is ultimately a function of M, G, and the number of young fish in the habitat. It is therefore necessary to differentiate between habitat quality and habitat importance for a fish population. The importance of a habitat should be judged by the actual contribution of recruits from the habitat (i.e., both densities and vital rates should be considered).

In practice, quantifying habitat quality and importance is quite difficult, particularly in large ecosystems. Although densities of young fish in particular areas can be readily measured, growth and particularly mortality rates associated with these areas are far more complicated to estimate. Traditional methods of estimating growth and mortality rates require repeated population sampling (i.e., high effort), and if there is a high degree of movement between habitats, it may not be possible to estimate habitat-specific vital rates. To overcome these sampling obstacles, Brandt et al. (1992) developed a spatially-explicit approach that considers heterogeneity in the spatial distributions of prey and temperatures to map growth rate potential. Several authors have now used similar approaches to estimate potential growth of fish in particular habitats (Brandt et al. 1992; Brandt and Kirsch 1993; Mason et al. 1995; Nislow et al. 2000).

We present an analysis that builds upon ideas developed by Brandt et al. (1992) to generate spatially explicit estimates of potential growth, mortality, and production. Several authors have used bioenergetics models to estimate system-wide consumptive demand of predators and mortality rates of prey (Hewett and Stewart 1989; Brandt et al. 1991; Hartman and Margraf 1993). Walline et al. (2000) used a bioenergetics approach to generate spatially-explicit estimates of lavnun (*Acanthobrama terraesanctae*) consumption, and Luo et al. (2001) used the spatially-explicit approach to quantify the carrying capacity of the Chesapeake Bay for Atlantic menhaden (*Brevoortia tyrannus*). We are unaware of any previous studies that have used this approach to generate spatially explicit estimates of potential production within a system.

The specific objective of our study is to evaluate both the quality and importance of various habitats (i.e., areas) in Lake Michigan for young-of-year (YOY) alewives (*Alosa pseudoharengus*). Several mechanisms have been hypothesized to affect alewife population size in Lake Michigan, including temperature and salmonine consumption (Heufelder et al. 1982; Stewart and Ibarra 1991; Jones et al. 1993). Whatever the causes, it is apparent that alewife recruitment and production vary temporally in Lake Michigan. We hypothesize that re-

cruitment and production also vary spatially (i.e., across habitats). Different regions in Lake Michigan have distinct physical and chemical attributes (Beletsky et al. 1999; Hayes 1999; Schwab et al. 1999), and densities of both lower (Sprules et al. 1991; Nalepa et al. 2000) and upper (Brandt et al. 1991) trophic levels vary spatially, suggesting that the capacity for alewife production differs among regions. Understanding how habitat quality and importance vary spatially in Lake Michigan should aid in predicting population abundance and recruitment potential of alewives and lead to more effective management of the species.

Methods

We used spatially explicit data on surface temperatures and salmonine, zooplankton and alewife densities to estimate habitat quality and importance for YOY alewives in nearshore areas in southern and central Lake Michigan. Although we focused upon a limited area of Lake Michigan, to facilitate our analysis, we divided the entire lake into 26 separate zones. Most of these zones were approximately 30 × 30 minutes (i.e., 39 × 54 km), but due to a lack of data in some regions and a desire to separate embayments from the lake proper, the areas of some zones were dramatically different (Fig. 1).

We limited our analysis to August and September 1994 and 1995, as dictated by the availability of hydroacoustic estimates of alewife abundance and zooplankton biomass densities. These months are likely critical for alewife recruitment in Lake Michigan. Several authors (Brown 1972; Flath and Diana 1985; O'Gorman and Schneider 1986; Bergstedt and O'Gorman 1989) have suggested that YOY alewives in Lake Michigan must attain a minimum size by late fall to survive the winter. Yearling alewife growth and consumption are clearly highest in August and September (Flath and Diana 1985; Stewart and Binkowski 1986; Hewett and Stewart 1989), and YOY alewife growth and consumption are likely also highest during these months (Hewett and Stewart 1989). By August YOY alewives have reached a size at which they are vulnerable to predation by salmonines.

HABITAT QUALITY

We believe that the quality of a habitat should be measured as a function of habitat-specific growth and mortality rates, independent of species density. In order to model YOY alewife habitat quality throughout Lake Michigan, we assumed uniform alewife densities (10,000 g ha^{-1}), and we independently modeled potential instantaneous YOY alewife growth (G) and mortality (M).
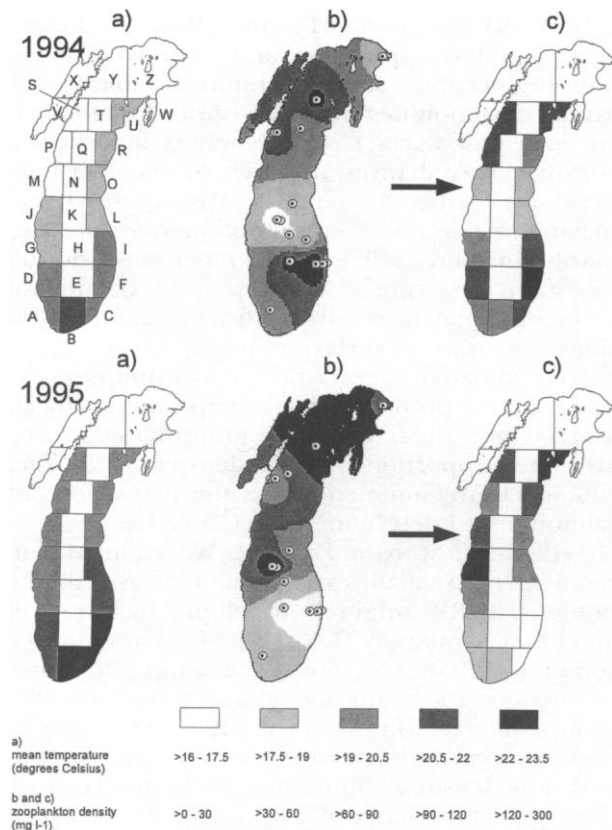
Fig. 1. Lake Michigan, 1994 and 1995. a) Mean surface temperatures (measured via AVHRR satellite imagery) in 30-minute study zones during August–September. Shaded zones are those included in the analysis. The single letter adjacent to or within a zone indicates the zone name. b) Zooplankton biomass densities (mg l^{-1}) interpolated using inverse distance weighted procedures. Locations of U.S. Environmental Protection Agency zooplankton stations sampled during August are indicated by circles. c) Interpolated zooplankton biomass densities summarized by 30-minute zones.

Model Inputs

Surface Temperatures. During September, YOY alewives in Lake Michigan primarily occupy the upper mixed layer of the water column (Brandt 1980; Argyle et al. 1998). We assumed the surface temperature in an area to be indicative of the ambient temperature of water occupied by YOY alewives. We measured surface temperatures through satellite AVHRR (Advanced Very High Resolution Radiometry) imagery from National Oceanic and Atmospheric Administration's CoastWatch program (Schwab et al. 1999). This program records surface temperatures at a resolution of approximately 2.6 km, up to four times each day. We calculated the average surface temperature within a study zone for a particular day as the mean of all AVHRR measurements taken within the study zone during the day of interest. We then used these data to deter-

mine the average daily surface temperature within each of our study zones during August–September (Fig. 1a). We used these average values as inputs for our model.

Zooplankton Biomass and Distribution. We used zooplankton biomass densities measured by U.S. Environmental Protection Agency to index spatial variation in alewife prey (Bertram unpublished data). Zooplankton samples were collected during August 1994 and 1995 at different stations (1994, 16 stations; 1995, 15 stations) throughout Lake Michigan (Fig. 1b). To our knowledge, these data are the most spatially-complete measures of zooplankton biomass density available for Lake Michigan.

Additional information regarding zooplankton sampling is presented elsewhere (e.g., Makarewicz et al. 1995). Vertical samples were taken of the top 20-m of the water column with a metered, 64-μm mesh, 0.5-m diameter conical zooplankton net. Immediately after completing a tow, samples were preserved by adding soda water followed by a sugar-formalin solution. In the laboratory, sub-samples were counted to estimate taxa-specific zooplankton densities. Total zooplankton biomass density (mg l^{-1}) was estimated for each station by multiplying taxa-specific densities by taxa-specific mean weights.

To interpolate zooplankton biomass throughout Lake Michigan, we used an inverse distance weighting approach. Under this approach, we created a grid of 2,000 × 2,000 m cells, with each cell having an interpolated zooplankton biomass density (Fig. 1b). We averaged cell biomass densities within our study zones to generate zone-specific estimates of zooplankton biomass (Fig. 1c).

Salmonine Abundance and Distribution. We estimated the density of salmonine predators within each study zone based upon recreational catch data and estimates of lake-wide population abundances. Charter boat angler creel data were collected lake-wide by Illinois, Michigan, and Wisconsin Departments of Natural Resources during our study period. These data included number of fish caught during a fishing trip, as well as location, number of anglers, and time spent fishing. Since different fishing trips targeted different species (i.e., some targeted non-salmonines such as yellow perch, *Perca flavescens*), we only considered trips when at least one salmonine was captured. Each year we calculated catch-per-unit-effort (CPUE) for five species of salmonines (coho salmon *Oncorhynchus kisutch,* steelhead *O. mykiss,* chinook salmon *O. tshawytscha,* brown trout *Salmo trutta,* and lake trout *Salvelinus namaycush*) within each zone, as number of fish caught divided by angler hours during August–September.

TABLE 1. Inputs for bioenergetics models to estimate salmonine consumption of YOY alewives.

	Foraging Temperature (°C)	Proportion of YOY Alewives in Diet*	Daily Consumption (Proportion of Maximum)
Coho salmon	12	0.25	0.52
Steelhead	15	0.36	0.30
Chinook salmon	11	0.22	0.68
Lake trout	10	0.12	0.52
Brown trout	15	0.36	0.32

* From Madenjian et al. (2002) and Elliot personal communication.

Estimates of the total number and biomass of salmonines in Lake Michigan from 1965–present were taken from Madenjian et al. (2002). The annual variation for these estimates between 1994–1995 was minimal. We used these estimates to approximate the average number of adult salmonines in Lake Michigan during 1994–1996 (coho salmon—1,800,000; steelhead—3,500,000; chinook salmon—12,000,000; brown trout—2,400,000; lake trout—8,000,000). We used catch rates and the size of zones to partition the salmonine populations amongst individual zones, ultimately estimating number of salmonines per hectare within each 30 × 30 minute zone. We assumed a linear relationship between catch rates and fish densities. Given that catch rates were likely indicative of both feeding activity levels and densities, and that our fundamental objective was to index predation by salmonines (not actual densities), we feel this approach was justified.

Model Structure

Salmonine Consumptive Demand. We indexed the predation pressure exerted upon YOY alewives by estimating the daily salmonine consumptive demand (CD) per hectare within each of our study zones. We combined estimates of salmonine density with estimates of individual consumptive demand. We began by estimating consumption by an average size individual of each species (from Madenjian et al. 2002, coho salmon—1.25 kg; steelhead—2.5 kg; chinook salmon—3.5 kg; brown trout—2 kg; lake trout—2 kg) within each zone, using previously estimated bioenergetics parameters (Stewart et al. 1983; Stewart and Ibarra 1991; Rand et al. 1993). Because we are unaware of any bioenergetics model developed for brown trout in the Great Lakes, we estimated consumption by individual brown trout by applying Rand et al.'s (1993) model for steelhead. We used mass-at-age information (Madenjian et al. 2002) and Fish Bioenergetics 3.0 (Hanson et al. 1997) to estimate the proportion of maximum consumption for each salmonine species (Table 1). We followed Stewart et

al.'s (1983), Stewart and Ibarra's (1991), and Rand et al.'s (1993) approaches and assumed that salmonines occupied set temperatures (Table 1). We assumed salmonines undertake brief foraging excursions into warmer surface waters in order to consume YOY alewives, then return to cooler temperatures to digest their prey. We supposed that maximum salmonine consumption rates are primarily functions of ambient temperatures during digestion (i.e., cooler set temperatures) and not ambient temperatures during brief foraging excursions (i.e., warmer surface waters).

We estimated species-specific consumptive demand as the product of daily consumption by an average individual, number of individuals per hectare, and proportion of YOY alewives in the diet (Table 1). We summed across the five species of salmonines to determine total CD (g ha^{-1} d^{-1}).

YOY Alewife Growth Potential. We adopted and modified the spatially explicit model of growth rate potential (GRP) originally developed by Brandt et al. (1992) to quantify YOY alewife habitat (e.g., Mason et al. 1995). The model is a composite of two submodels: a foraging model and a bioenergetics growth model (Hanson et al. 1997). The model requires spatial information for water temperature and prey density as input and can be used to produce spatial estimates of GRP (g g^{-1} d^{-1}).

We used the bioenergetics model for alewife as parameterized by Stewart and Binkowski (1986) to model the growth of a 6-g YOY alewife and used AVHRR measured surface temperatures as inputs for this sub-model. We estimated consumption using a linear functional response with a threshold (i.e., asymptote). We assumed that at average zooplankton density, YOY alewife would forage at a rate of about 47% of their maximum consumption, the average consumption rate estimated by Stewart and Binkowski (1986) for Lake Michigan YOY alewife. We allowed the proportion of maximum consumption (p value) to vary linearly with zooplankton density up to p = 1, with p = 0 when zooplankton biomass equals 0, p = 0.47 at the average zooplankton biomass density (i.e., 81 mg l^{-1}) and p = 1 at and above some critical zooplankton biomass density (i.e., 172 mg l^{-1}). As an aside, age-specific size and condition of Lake Michigan alewives have not changed dramatically since the 1970s (Madenjian et al. 2002), suggesting that age-specific consumption rates have also not changed dramatically over this time period. We therefore feel justified in using an estimated average p value of 0.47, even though this estimate was derived from pre-1986 measures.

M/G. In order to use Houde's (1997) index of recruitment potential (M/G) as a measure of habitat quality, we transformed salmonine CD and YOY

alewife GRP to potential daily instantaneous mortality (M) and growth (G), respectively.

$$M = \ln\left(\frac{10,000 \text{ g ha}^{-1}}{10,000 \text{ g ha}^{-1} - \text{salmonine CD}}\right)$$

$$G = \ln(1 \text{ g} + \text{GRP})$$

HABITAT IMPORTANCE

We used acoustic-based estimates of YOY alewife abundance collected by the U.S. Geological Survey Great Lakes Science Center to estimate the spatial distribution of habitat importance (see Argyle et al. 1998 for details). Total fish biomass along an individual line transect was measured acoustically, and YOY alewife biomass was determined by partitioning total fish biomass among species and life stages based upon species compositions in simultaneously deployed midwater trawls. Sampling was undertaken during September and early October (September 8 to October 11, 1994; September 14 to 18, 1995), and an average of 18.5 acoustic transects were completed each year (16 in 1994, 21 in 1995).

We stratified the acoustic abundance estimates along individual transects by 10-m bathymetric depths. We 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 TIN (Triangular Irregular Network) model to interpolate YOY alewife densities lake-wide, creating a grid of 2,000 × 2,000 m cells (DeMers 1999). If the majority of cells in a zone overlapped with our TIN model, we averaged these data within a zone to estimate the average YOY alewife biomass per unit area. We compared results of our TIN model to results from other methods to interpolate YOY alewife densities, including kriging and inverse distance weighting, and the resulting spatial patterns in YOY alewife densities were very similar for the different methods.

ANALYSIS

Annual and Regional Differences

To consider regional differences for habitat characteristics (temperature, zooplankton biomass densities, GRP, and salmonine CD), quality and importance, we grouped zones into seven regions: south (zones A, B, and C), southeast (zones F and I), central-east (zones L and O), northeast (zones R and U), southwest (zones D and G), central-west (zones J and M), and northwest (zones P and S). We analyzed annual, regional, and interaction effects with two-way analysis of variance (ANOVA), treating all factors as fixed and independent. We

viewed annual observations within zones as replicates. For most metrics each region had four replicates (two for each year). Effects were considered significant at $\alpha = 0.05$.

Habitat Quality Versus Importance

To determine if the yield of YOY alewives (i.e., habitat importance) was greater in areas of high habitat quality, we correlated observed YOY alewife density in a zone with our measure of M/G. To explore if other factors influence YOY alewife density, we also correlated YOY alewife density to mean temperature, zooplankton biomass density, M, and G. Spearman rank correlation coefficients were considered significant at $\alpha = 0.05$.

Results

Conditions in Lake Michigan were dramatically different between our two study years. Mean ($\pm$ SE) August–September surface temperatures were significantly greater during 1995 (20.7 $\pm$ 0.3°C) as compared to 1994 (18.4 $\pm$ 0.3°C; Table 2). Mean alewife yield was significantly greater during 1995 (26.2 $\pm$ 5.0 kg ha^{-1}) as compared to 1994 (2.8 $\pm$ 0.9 kg ha^{-1}; Table 2). Despite these clear annual differences, mean zooplankton biomass densities (1994, 92.6 $\pm$ 6.8 mg l^{-1}; 1995, 77.0 $\pm$ 13.5 mg l^{-1}) and several model outputs were essentially similar for the two years. Neither mean salmonine CD (1994, 189 $\pm$ 117 g ha^{-1} d^{-1}; 1995, 181 $\pm$ 79 g ha^{-1} d^{-1}), alewife GRP (1994, 0.041 $\pm$ 0.006 g g^{-1} d^{-1}; 1995, 0.038 $\pm$ 0.007 g g^{-1} d^{-1}), daily M (1994, 0.019 $\pm$ 0.003; 1995, 0.018 $\pm$ 0.002), daily G (1994, 0.040 $\pm$ 0.004; 1995, 0.037 $\pm$ 0.006), or M/G (1994, 0.65 $\pm$ 0.15; 1995, 0.73 $\pm$ 0.06) were significantly different between 1994 and 1995 (Table 2).

There was also a high degree of spatial variation among habitat variables (Table 2). However, only surface temperature, salmonine CD, and alewife daily M appeared to maintain consistent spatial patterns across years (Table 2, Figs. 1a and 2a). Although region had a significant effect on these three variables, the interaction term between year and region was not significant. Region also had a significant effect for zooplankton biomass density, alewife GRP, daily G, and alewife. The interaction term was also significant for these latter variables, suggesting that their spatial patterns were not consistent across years (Table 2, Figs. 1b and 2b). Region did not have a significant effect on alewife production, but the interaction term for M/G was significant, suggesting high within-region variability in alewife production (Fig. 3a).

The yield of YOY alewives appeared to be only loosely related to habitat quality (Fig. 3). YOY alewife density in individual zones was negatively cor-

TABLE 2. Two-way ANOVA diagnostics. ANOVA's analyzed the main effects of year and region and the interaction between these two main effects (year × region). CD = consumptive demand, GRP = growth rate potential, M = mortality rate, and G = growth rate.

	MS	F	df	p
Mean temperature				
Year	32	143.3	1	<0.05
Region	3.9	17.6	6	<0.05
Year × region	9.2×10^{-2}	0.4	5	0.83
Zooplankton density				
Year	5.1×10^2	0.7	1	0.42
Region	3.1×10^3	4.2	6	<0.05
Year × region	4.4×10^3	6.0	5	<0.05
Salmonine CD				
Year	8.8×10^2	0.3	1	0.60
Region	3.1×10^4	10.4	6	<0.05
Year × region	3.7×10^3	1.2	5	0.35
YOY alewife GRP				
Year	1.1×10^{-4}	0.8	1	0.40
Region	7.6×10^{-4}	5.2	6	<0.05
Year × region	1.3×10^{-3}	9.0	5	<0.05
Daily M				
Year	9.9×10^{-6}	0.3	1	0.59
Region	3.3×10^{-4}	10.3	6	<0.05
Year × region	4.0×10^{-5}	1.3	5	0.34
Daily G				
Year	9.6×10^{-6}	0.7	1	0.41
Region	7.0×10^{-4}	5.3	6	<0.05
Year × region	1.2×10^{-3}	9.3	5	<0.05
M/G				
Year	0.17	0.49	1	0.49
Region	0.61	1.8	6	0.17
Year × region	1.90	5.6	5	<0.05
Alewife yield				
Year	3.2×10^3	104.7	1	<0.05
Region	3.1×10^2	10.1	6	<0.05
Year × region	3.5×10^2	11.4	5	<0.05

Fig. 2. Lake Michigan, August–September 1994 and 1995. a) Model-derived measures of salmonine consumptive demand (g d^{-1} ha^{-1}) for individual 30-minute zones. Salmonine consumptive demand within individual zones was calculated as a function of salmonine density (see text). b) Model-derived measures of YOY alewife growth rate potential (GRP; g g^{-1} d^{-1}) for individual zones. YOY alewife GRP within individual zones was calculated as a function of surface temperature and zooplankton biomass density (see text).

related with M/G during both 1994 and 1995, but these correlations were not significant (Table 3). YOY alewife yield also was not significantly correlated to daily mortality, growth, or density of food (zooplankton biomass density). During 1994 YOY alewife yield was significantly, and positively correlated with surface temperature, although the correlation between alewife yield and surface temperature during 1995 was insignificant and negative (Table 3). The coolest mean temperatures during 1995 were roughly equivalent to the warmest mean temperatures during 1994 (Fig. 1a). This annual difference in mean temperature may account for the different directions of the temperature-alewife correlations during the two years.

Discussion

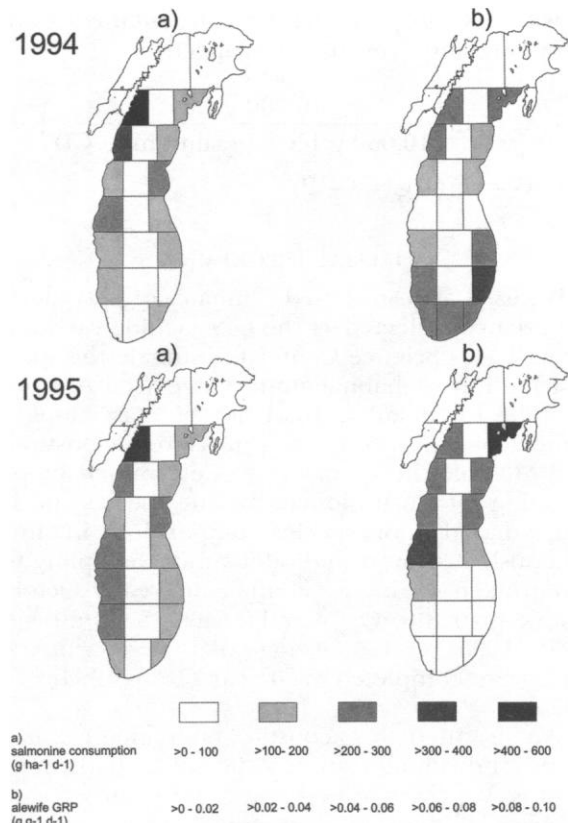Estimates of relative habitat quality and importance for YOY alewives in Lake Michigan were variable among years and regions. Spatial patterns of relative habitat quality did not closely match spatial patterns of alewife yield. The zones with highest habitat quality for YOY alewives varied between the two years and were located in the southern portion of the lake during 1994 and in the northern portion of our study area during 1995. Alewife yield, although variable, was on average highest in western Lake Michigan. The appearance of a large year class in 1995 illustrated how habitat importance may change greatly with annual variation in recruitment.

Lack of spatial overlap between habitat quality and habitat importance is likely not unique to the Lake Michigan alewife population, but may be common for many fish stocks. In such cases, a high quality habitat may yield an insignificant number of recruits, either because the density of fish in that habitat type is low or because the habitat type
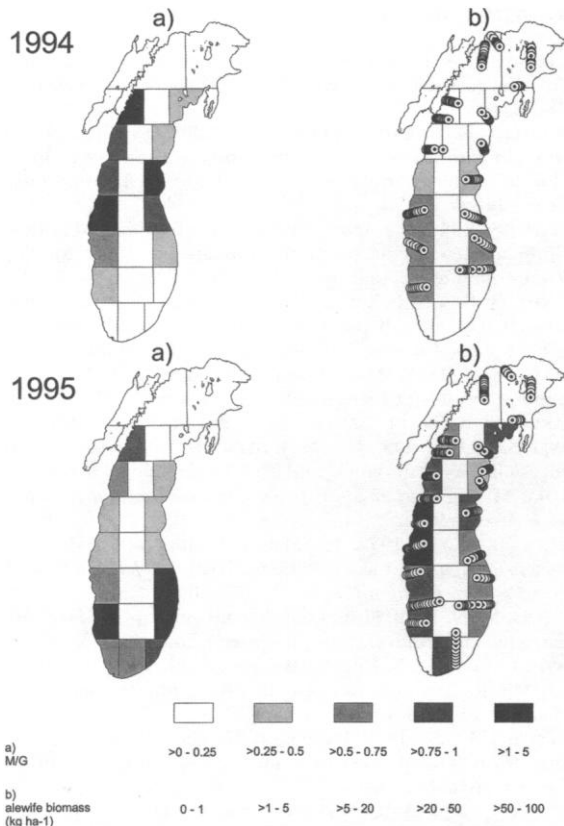
Fig. 3. Lake Michigan, 1994 and 1995. a) Model-derived measure of YOY alewife habitat quality as indexed by instantaneous daily mortality (M) and growth (G). b) YOY alewife yield (kg ha⁻¹) summarized by 30-minute zones. Circles indicate U.S. Geological Survey-Great Lakes Science Center acoustic transects. Data from these transects were interpolated using TIN (Triangular Irregular Network) models, and summarized by 30-minute zones. The TIN models did not cover four and two zones during 1994 and 1995, respectively.

TABLE 3. Spearman rank correlation coefficients, relating YOY alewife yield in 30-minute zones to habitat variables in corresponding zones (1994 n = 11; 1995 n = 13).

Habitat Variable	1994	1995
Mean temperature	0.66	−0.50
Zooplankton density	−0.44	0.28
M	−0.30	0.27
G	−0.29	0.28
M/G	−0.17	−0.28

* Significant correlation ($p < 0.05$).

constitutes a relatively small proportion of the area in a system. For a variety of fish stocks, spatial patterns of habitat importance are likely to vary annually to a larger degree than patterns of habitat quality. Habitat importance in an area is in part a function of fish density at the beginning of some critical period and will vary greatly with year-class strength. These results imply that the identification and preservation of EFH for early life stages of fish will not likely guarantee large year classes, and the partial elimination of EFH will not likely preclude all future large year classes.

Several authors have suggested that to optimize fitness, juvenile fish should choose habitats based upon mortality and growth rates (Werner and Gilliam 1984; Gilliam and Fraser 1987; Abrahams and Dill 1989); thus densities of fish should be highest in areas where M/G is minimal (Werner and Gilliam 1984). In 1994 and 1995 YOY alewives densi-

ties did not closely match habitat quality. There are several mechanisms that could explain this apparent non-optimal behavior, including the ability of predators to closely track alewife movement, the influence of lake circulation patterns on alewife densities, and selective pressures favoring individuals that maximize present growth (and not M/G) in order to minimize future mortality.

Attempts by YOY alewives to improve the habitat quality they experience by moving from an area of high predation pressure to one of low predation pressure may be negated by salmonines responding to such migrations. Salmonines are highly mobile (Haynes et al. 1986; Haynes and Keleher 1986; Nettles et al. 1987; Ruggerone et al. 1990) and can track the movement of their prey. It might be futile for alewives to avoid high-risk areas in western Lake Michigan.

Hydrodynamic circulation patterns in Lake Michigan may cause the mismatch between observed alewife distributions and habitat quality. Alewives spawn in nearshore areas, drowned river mouths, and tributaries around Lake Michigan. Larvae are then transported into the lake proper, where they are likely at the mercy of prevailing currents. There is annual variation in prevailing currents, but the average currents produce a convergence zone in west-central Lake Michigan (Beletsky et al. 1999). The occasional high density of YOY alewives in this area may in part be due to the passive transport of larvae, rather than active selection of a risky habitat.

The spatial distribution of YOY alewives may also reflect selective processes favoring those individuals that maximize growth instead of minimizing mortality. YOY alewives must reach a minimum size in order to survive the cold Lake Michigan winter. As Werner and Gilliam (1984) suggested, minimizing M/G will maximize fitness only if vital rates do not change over time. If seasonal mortality is size selective (as may be the case for alewives during winter), fitness may be maximized by maximizing growth in the present in order to minimize mortality in the future. The west-central region of Lake Michigan (where salmonine CD is high, Fig. 2a) is highly productive. There are frequent upwelling

events and high densities of benthic invertebrates in this area (Nalepa et al. 2000; Höök unpublished data). During 1987, particularly high densities of zooplankton were observed in this region (Sprules et al. 1991). YOY alewives may occupy this relatively risky area in order to maximize growth and survive the winter.

Our study demonstrates the utility of modern sampling techniques such as acoustics and satellite imagery, and analytical tools such as geostatistics and GIS (Geographic Information Systems) for analyzing fish habitat quality and importance in large ecosystems. Several previous studies of Lake Michigan fish populations have treated the lake as a homogenous entity, and assumed that local measures reflect conditions lake wide. Physical, chemical, and biotic characteristics that structure local ecosystems vary across Lake Michigan (Brandt et al. 1991; Sprules et al. 1991; Beletsky et al. 1999; Hayes 1999; Schwab et al. 1999; Nalepa et al. 2000) leading to spatial variation in fish production. Our analysis is a first attempt to generate spatially explicit measures of fish production throughout Lake Michigan. By undertaking future sampling with this goal in mind, our techniques can be refined (i.e., more spatially explicit estimates of predator and prey densities and thus, less interpolation of data) and our analysis can become more robust. Further development and application of remote sensing technology, spatially explicit sampling techniques, and geostatistics should improve the identification of essential fish habitat.

ACKNOWLEDGMENTS

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