

Annual variation in habitat-specific recruitment success: implications from an individual-based model of Lake Michigan alewife (*Alosa pseudoharengus*)

Tomas O. Höök, Edward S. Rutherford, Thomas E. Croley II, Doran M. Mason, and Charles P. Madenjian

Abstract: The identification of important spawning and nursery habitats for fish stocks can aid fisheries management, but is complicated by various factors, including annual variation in recruitment success. The alewife (*Alosa pseudoharengus*) is an ecologically important species in Lake Michigan that utilizes a variety of habitats for spawning and early life growth. While productive, warm tributary mouths (connected to Lake Michigan) may contribute disproportionately more recruits (relative to their habitat volume) to the adult alewife population than cooler, less productive nearshore habitats, the extent of interannual variation in the relative contributions of recruits from these two habitat types remains unknown. We used an individual-based bioenergetics simulation model and input data on daily temperatures to estimate alewife recruitment to the adult population by these different habitat types. Simulations suggest that nearshore lake habitats typically produce the vast majority of young alewife recruits. However, tributary habitats may contribute the majority of alewife recruits during years of low recruitment. We suggest that high interannual variation in the relative importance of habitats for recruitment is a common phenomenon, which should be considered when developing habitat management plans for fish populations.

Résumé : L'identification des habitats importants de frayère et de nurserie pour les stocks de poissons peut améliorer la gestion des pêches, mais elle est compliquée par divers facteurs, dont la variation annuelle du succès du recrutement. Le gaspureau (*Alosa pseudoharengus*) est une espèce d'importance écologique au lac Michigan qui fraye et se développe dans des habitats multiples. Les embouchures productives de tributaires plus chauds (reliés au lac Michigan) peuvent fournir une quantité disproportionnée de recrues (par rapport au volume représenté par ces habitats) à la population adulte de gaspareaux par comparaison aux habitats plus frais et moins productifs près des berges; cependant, l'importance de la variation interannuelle des contributions relatives de ces deux types d'habitat reste inconnue. Dans un modèle de simulation bioénergétique basé sur l'individu, nous utilisons les températures journalières comme données d'entrée pour estimer le recrutement de gaspareaux vers la population adulte à partir de ces différents types d'habitat. Les simulations laissent croire que les habitats le long des berges fournissent généralement la très grande majorité des recrues de gaspareaux. Cependant, les années de faible recrutement, il se peut que les tributaires produisent la majorité des recrues. Nous croyons que la forte variation interannuelle de l'importance relative des habitats pour le recrutement est un phénomène commun dont on doit tenir compte lors de l'établissement de plans de gestion pour les populations de poissons.

[Traduit par la Rédaction]

Introduction

The identification and subsequent protection of habitats that support production of early life stages is critical for the

effective management of fish populations. Several initiatives (e.g., the Sustainable Fisheries Act) directly or indirectly address the need for classification of habitats that contribute disproportionate numbers of individuals to adult fish popula-

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tions, either on an areal basis (i.e., nursery habitats; Beck et al. 2001, 2003) or in total (i.e., effective juvenile habitats; Dahlgren et al. 2006). While a focus on spatial differences is appropriate when discriminating among habitats, recruitment dynamics and early life processes of fish also are characterized by high temporal variation (e.g., Hjort 1914; Cowan and Shaw 2002). As such, habitat-specific production rates of juvenile fish are likely to vary over time (e.g., Hilborn et al. 2003; Berkeley et al. 2004; Schindler et al. 2006). Therefore, even the most productive habitats will experience periods of low recruitment (e.g., Peterman et al. 2003).

There is a growing recognition of the biocomplexity of fish populations (Hilborn et al. 2003; Ruzzante et al. 2006). Many fish stocks are characterized by spatially and temporally distinct substocks, which contribute differentially to adult populations and fisheries (Iles and Sinclair 1982; Ruzzante et al. 2000; Andrews et al. 2006). In fact, studies suggest that relative habitat-specific recruitment can vary at annual (e.g., Berkeley et al. 2004) and even decadal (e.g., Hilborn et al. 2003) time scales. Such phenomena imply that management plans that prioritize conservation of the seemingly fittest substocks and most productive habitats are inadequate, and instead, for many systems fish populations and habitats should be managed to maximize genetic (e.g., Ryman et al. 1995) and environmental diversity, respectively.

While it is apparent that the relative contributions of specific habitats to system-wide fish recruitment can vary inter-annually, mechanistic understanding of such phenomena is lacking. Herein, we present a mechanistic, individual-based model (IBM) to explore interannual variation of both nursery and effective juvenile habitats. An IBM framework is appropriate for depicting annual variation in habitat-specific recruitment because (i) it accounts for individual phenotypic variation and allows for movement among habitats; (ii) it can bridge the gap between temporally dynamic models of fish populations and static analyses of fish–habitat linkages (Minns et al. 1996); and (iii) it can provide mechanistic-derived estimates of habitat-specific recruitment when empirical relationships between habitat-specific recruitment and annual measures of physical and biological factors are unavailable.

Our model is based upon the Lake Michigan alewife (*Alosa pseudoharengus*) population. While alewives are exotic in Lake Michigan, they constitute the forage base for economically important salmon and trout. Further, the Lake Michigan alewife population is a useful model in that the stock biology (Norden 1967; Brown 1972) and habitat utilization (Goodyear et al. 1982; Höök et al. 2007) of this clupeid are similar to many exploited populations throughout the world. Alewife year-class strength in the Great Lakes is positively correlated to summer temperatures (O’Gorman et al. 2004; Madenjian et al. 2005). This temporal association suggests that recruitment success also may vary among habitats, with warmer habitats yielding more young-of-year (YOY) alewives. In fact, field studies

during 2001 and 2002 indicate that (i) densities of young alewife are greater in drowned river mouth lakes, which are smaller, warmer, and more productive than cooler, near-shore areas of Lake Michigan (Höök 2005) and (ii) because of a better growth environment, earlier hatching dates, and size-dependent over-winter mortality, tributary habitats likely yield more young alewife (on a volumetric basis; Höök et al. 2007). Nonetheless, the volume of water contained in nearshore areas of Lake Michigan is at least two orders of magnitude greater than all tributary habitats combined (Höök 2005), and chemical analyses of otolith cores suggest that the majority of alewife recruits in 2002 (age-1 fish in spring) actually inhabited nearshore Lake Michigan during early life (Dufour et al. 2005). However, the 2002 growing season was relatively warm, so habitat-specific contributions estimated for this year may not be indicative of cooler years.

Materials and methods

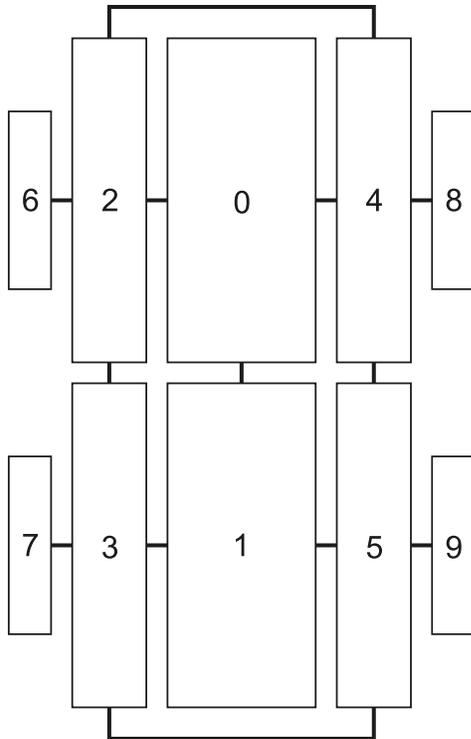
Model description

Here, we present an overview of the model (details of the model are presented in the Supplemental Materials³). The model simulates YOY alewife emergence, growth, survival, and movement throughout Lake Michigan and tributary habitats over a 180-day period (1 May to 27 October). Although the model describes individual-level dynamics of YOY alewives, the model actually tracks 20 000 “super-individuals”, with each super-individual potentially representing a multitude of individual fish (e.g., Scheffer et al. 1995). In addition to the number of individual fish represented by a super-individual, other individual-level variables include length (mm), weight (g), percentage of weight composed of storage tissue, percentage of weight composed of structural tissue, and location. The model progresses at daily time steps, and individual level variables are updated each day. The model represents a simplified version of Lake Michigan and surrounding tributary habitats as 10 discrete compartments: two offshore compartments (0–1), four nearshore compartments (2–5), and four tributary compartments (6–9; Fig. 1). Each compartment represents a well-mixed epilimnion (top 10 m of water column) of the corresponding habitat, with homogeneous temperatures, water clarities, and prey densities.

The primary inputs for the IBM are year-specific estimates of daily Lake Michigan water temperatures from a physical model (Croley 1989, 1992; Croley and Assel 1994; Fig. 2). Croley and Assel’s (1994) temperature model predicted lake-wide average daily water temperatures at the surface and multiple depths based on observed measures of cloud cover, humidity, wind velocity, and air temperature at various locations. Model predictions closely match observed Lake Michigan surface temperatures (Croley 1992), and the model has been used to model environmental effects on alewife dynamics (Madenjian et al. 2005). Based on a plethora of measured temperatures (Schwab et al. 1999; Höök et al. 2004, 2007), we developed equations to relate daily mean surface temperature

³Supplementary data for this article are available on the journal Web site (cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3766. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Fig. 1. Diagram of the spatial distribution of habitat compartments represented within the individual-based model. Compartments 0–1 represent offshore Lake Michigan habitats; 2–5 represent nearshore Lake Michigan habitats; and 6–9 represent tributary habitats. Thick connecting lines demonstrate how individual alewives can move between habitat compartments.

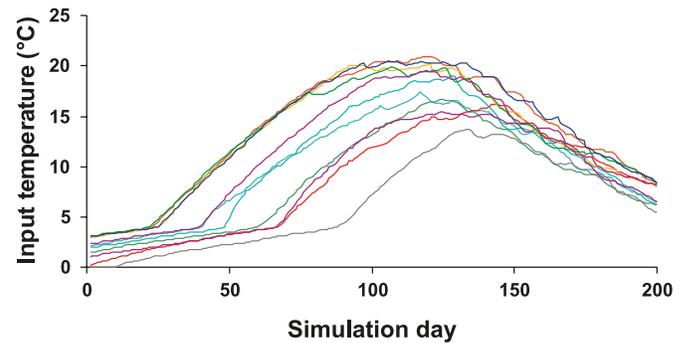


in Lake Michigan to daily, habitat-specific, mean epilimnetic temperature in each of the 10 model compartments (see Supplemental Materials³).

In addition to temperature, water clarity and prey densities also vary among habitat compartments. Based on field observations, water clarity in tributary mouths is generally much lower than that in Lake Michigan. Further, as YOY alewives primarily feed on zooplankton, the model depicts three microzooplankton types (copepod nauplii, rotifers, and *Dreissena* spp. veligers) and four macrozooplankton size categories. Prey categories vary in length (and hence vulnerability to gape-limited predators), mass, energy content, and seasonal density (see Supplemental Materials³).

In Lake Michigan, adult alewives spawn and larvae subsequently emerge over an extended time period (late May to early August; Jude et al. 1981a, 1981b; Höök et al. 2007) and in a variety of habitats (Wagner 1972; Goodyear et al. 1982; Mansfield 1984). In each nearshore and tributary habitat compartment (2–5 and 6–9, respectively; see Fig. 1), 2500 super-individuals emerge over a 41-day period. The actual number of super-individuals emerging each day was determined from a parametric distribution function, with a mean at the midpoint of the 41-day emergence period (the day of peak emergence). Each year the same total number of individuals emerged in each habitat compartment, but time of emergence varied among years. Peak emergence dates in each compartment are determined each year as a function of habitat-specific temperatures and time of year.

Fig. 2. Daily temperature inputs from Croley's (1989 and 1992) temperature model for 1992–2002. Each line represents a specific year.



Although the same number of super-individuals emerges in each habitat compartment, super-individuals emerging in different compartments initially represent different numbers of individual alewives (based on field observations of larval alewife densities and the volume of water represented by each habitat compartment). Therefore, super-individuals emerging in nearshore habitats initially represent substantially more individual alewives than super-individuals emerging in tributary habitats.

Model alewives emerge at 4 mm total length (Auer 1982) and 137 μg (6.3% storage tissue and 93.7% structural tissue). Subsequently, individual size and energy composition (Flath and Diana 1985; Stewart and Binkowski 1986; Hewett and Stewart 1989) are updated daily using a bioenergetics framework (Hanson et al. 1997). The model includes a foraging submodel similar to a model presented by Letcher et al. (1996), which tracks alewife encounter rates with their zooplankton prey and uses an optimal foraging approach to model which prey types are included in individuals' diets.

The encounter rate of an individual YOY alewife with a particular zooplankton prey type is a function of the individual fish's total length and swimming speed (a function of size and temperature; Stewart and Binkowski 1986; Klumb et al. 2003), water clarity in the habitat, and density and individual length of the prey type. Time spent attacking and handling prey reduces the time an individual fish can search, attack, and handle other prey; thus, individual alewives only include prey items that should maximize their net daily energy intake (Charnov 1976; Stephens and Krebs 1986). Prey-specific capture success and handling time are dependent on individual fish length, and consumption is limited by gape diameter. After determining which prey to include in an individual's diet (based upon optimal foraging criteria), the number of prey items consumed by an individual fish is randomly selected (from a binomial distribution). However, daily consumption is constrained to not exceed the physiological maximum daily consumption rate (Stewart and Binkowski 1986; Letcher et al. 1996, 1997). Individual alewives lose energy through respiration, egestion, excretion, and specific dynamic action (Stewart and Binkowski 1986; Klumb et al. 2003), and daily energy gain (and tissue growth) is calculated as the difference between daily energy consumed and energy lost.

Mortality occurs through predation and starvation and is

evaluated daily. Predation mortality declines with increasing size (Mansfield and Jude 1986) and is higher in tributary habitats than in other compartments (based on unpublished trawling and acoustics surveys; T. Höök, D. Mason, and D. Krueger, University of Michigan and NOAA's Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan). Starvation mortality only occurs if the percentage of body mass composed of storage tissue declines below a size-specific threshold.

Each day, individual alewives potentially move (passively or actively) to adjacent habitat compartments (Fig. 1). Potential movements are evaluated in two stages: (i) individuals are randomly assigned to either move or remain in their current habitat box as a function of length (i.e., smaller individuals were more likely to move; Höök et al. 2006), and (ii) if individuals move, then the direction of movement (i.e., new habitat compartment) is randomly assigned. The model assumes that individuals moving within Lake Michigan are most likely to move in the direction of prevailing cyclonic water currents (i.e., counterclockwise in the Northern Hemisphere; Beletsky et al. 1999).

Model simulations

We simulated YOY alewife dynamics in Lake Michigan habitats for 11 years (1992–2002). The model was initiated each year with daily temperature inputs from the physical model (Fig. 2; Croley 1989, 1992; Croley and Assel 1994), which were used to assign habitat-specific daily temperatures to each of the habitat compartments. Primary model outputs were lengths, weights, and energy densities of individuals alive on simulation day 180 (27 October), as well as individuals' birth dates and natal and current habitats.

We evaluated habitat-specific recruitment as the number of individual alewives ≥ 60 mm at the end of simulations (27 October). In general, smaller fish tend to have lower energy stores and higher weight-specific respiration rates and are therefore less likely to survive extended periods of limited feeding. Alewives in the Great Lakes likely feed little during winter, as evidenced by large decreases in somatic tissue energy densities from late fall to spring (Flath and Diana 1985). For this reason, several authors have suggested that YOY alewives in the Great Lakes must reach some minimum size to survive winter (Brown 1972; O'Gorman and Schneider 1986; Bergstedt and O'Gorman 1989). Collections of yearling alewives suggest that the minimum length of yearling alewives in spring is 65 mm (Höök et al. 2007). Thus, allowing for the possibility of limited over-winter growth, we assumed that YOY alewives must reach a minimum length of 60 mm by the end of the simulation to survive winter.

Model analysis

To explore the effects of stochastic components of the simulation model on annual size distributions and habitat-specific contributions, we executed the model multiple (at least five) times for selected years. In addition, to consider how model assumptions regarding temporal and spatial patterns of zooplankton densities influenced final size distributions and habitat-specific contributions, we ran model simulations assuming that zooplankton densities were uniform over time and across habitat compartments. Two zoo-

plankton densities were used: (i) zooplankton densities set at 1.5 times minimum levels (see Supplemental Materials B, Table SB2³) and (ii) zooplankton densities set at three times minimum levels. Finally, we executed additional simulations to consider how certain model assumptions (i.e., predation mortality, habitat-specific temperatures, movement, hatching dates, and size threshold to survive winter) influenced final size distributions of simulated alewives and habitat-specific contributions of alewife recruits (see Supplemental Materials³).

To analyze our model outputs, we discriminated among three classes of individual alewives: (i) Lake Michigan residents, (ii) migrants (i.e., alewives born in tributaries that subsequently moved into Lake Michigan), and (iii) tributary residents (i.e., alewives born in tributary compartments that remained in natal habitat compartments throughout the simulation). Further, to consider model dynamics, we focused on three representative years: 1995 (an average thermal year), 1996 (the coldest year), and 1998 (the warmest year). To facilitate comparisons across years and habitats, we also evaluated early-life vital rates (daily instantaneous growth (G) and mortality (Z)) for individuals who emerged in different habitat compartments during 1995, 1996, and 1998. For each super-individual, we calculated growth and mortality rates from the day of emergence until 35 days after emergence. We chose this time period because it roughly corresponds to recent field-derived estimates of alewife growth and mortality rates (see Höök 2005).

Model corroboration

We used a pattern-matching approach (Grimm et al. 2005) to corroborate model outputs. First, we compared size distributions of simulated alewives at the end of the 2002 model run with size distributions of YOY alewives captured in nearshore Lake Michigan and Muskegon Lake (a drowned river mouth lake) during October and November 2002; we also compared vital rates of simulated alewives with vital rates estimated for larval alewives captured during summer 2001 and 2002 in nearshore Lake Michigan and Muskegon Lake (see Höök 2005). Second, we compared model predictions of alewife recruitment (number of individuals reaching >60 mm total length during year t) with observed recruitment success (from US Geological Survey, Great Lakes Science Center's fall bottom trawl surveys). We calculated observed recruitment success as recruitment per unit of spawner biomass; recruitment is defined as biomass of age-3 alewives during year $t + 3$, and spawner biomass is estimated as adult biomass during year t (see Madenjian et al. 2005). Finally, we compared simulated habitat-specific contributions of surviving alewives during 2002 with estimates of habitat-specific contributions derived from isotopic signatures in age-1 alewife otolith cores (Dufour et al. 2005).

Results

In general, IBM simulations suggested that during 1992–2002, the majority of alewives recruiting to the adult Lake Michigan population (YOY longer than 60 mm on simulation day 180) emerged in Lake Michigan proper (Fig. 3). On average, 5.1×10^8 alewives per year were large enough

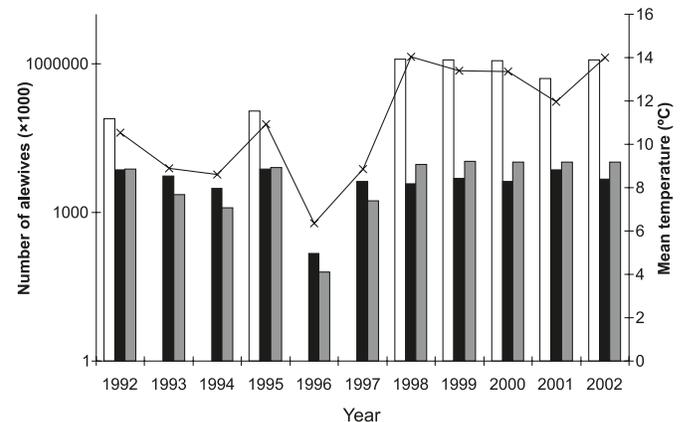
Table 1. Mean lengths (mm) and dates of birth of three classes of young-of-year (YOY) alewives (*Alosa pseudoharengus*) alive on simulation day 180 (27 October), with mean daily temperature inputs for 1992–2002.

| Year | Mean temp. (°C) | Mean length (mm) | | | Mean birth day | | |
|------|-----------------|-------------------------|------------------------------------|---------------------|-------------------------|------------------------------------|---------------------|
| | | Lake Michigan residents | Tributary – Lake Michigan migrants | Tributary residents | Lake Michigan residents | Tributary – Lake Michigan migrants | Tributary residents |
| 1992 | 10.55 | 42.8 | 73.8 | 85.1 | 72 | 55 | 55 |
| 1993 | 8.89 | 23.8 | 57.9 | 76.0 | 96 | 62 | 62 |
| 1994 | 8.59 | 20.6 | 49.9 | 66.5 | 100 | 65 | 64 |
| 1995 | 10.92 | 44.1 | 75.3 | 84.6 | 75 | 57 | 58 |
| 1996 | 6.37 | 16.5 | 32.4 | 43.9 | 101 | 71 | 67 |
| 1997 | 8.87 | 22.1 | 53.6 | 71.4 | 99 | 65 | 64 |
| 1998 | 14.05 | 82.9 | 97.6 | 87.3 | 57 | 47 | 48 |
| 1999 | 13.40 | 80.5 | 94.0 | 85.9 | 58 | 48 | 48 |
| 2000 | 13.34 | 80.8 | 94.4 | 86.7 | 57 | 47 | 47 |
| 2001 | 11.96 | 59.2 | 85.1 | 86.8 | 69 | 54 | 55 |
| 2002 | 13.99 | 80.3 | 95.1 | 86.2 | 59 | 48 | 48 |

to survive the winter, out of which 5.0×10^8 emerged in Lake Michigan habitat compartments. However, given that the volume of water contained in nearshore Lake Michigan is more than two orders of magnitude greater than that in all tributary mouths combined (Höök 2005), on a volumetric basis, tributary mouths were roughly twice as productive as nearshore habitats. Further, during relatively cold years, alewife recruitment was much lower, and relative contributions of tributary habitat compartments increased greatly. In fact, although 98% of survivors (from 1992–2002) emerged in Lake Michigan, the annual percent contribution of survivors from Lake Michigan ranged from 0% to 99% (mean = 60%; Fig. 3). Of those fish alive on simulation day 180, migrants and tributary residents tended to have emerged earlier than Lake Michigan fish (Table 1). In addition, migrants and tributary residents tended to be larger than fish that spent their whole life in Lake Michigan (Table 1; Fig. 4).

Survival rates and relative contributions of recruits varied across habitat types (Lake Michigan versus tributaries) and specific habitat compartments (Table 2). On average, individuals emerging in tributaries were more likely to recruit to the adult population. However, during warm years (e.g., 1998), survival rates (individual probability of recruitment) were actually higher for individuals emerging in Lake Michigan (Table 2 and Fig. 5). Not surprisingly, individuals born early tended to grow to larger sizes by the end of simulations (Fig. 5). In turn, during cold years, such early-emerging individuals were most likely to survive the growing season and subsequently recruit to the population (i.e., reach 60 mm by the end of the simulation). However, during warm years of fast growth, late-emerging individuals risked mortality for a relatively short time period and simultaneously were able to obtain a sufficient size by the end of the simulation. As a consequence, during warm years, recruitment success was actually greatest for late-emerging individuals (Fig. 5).

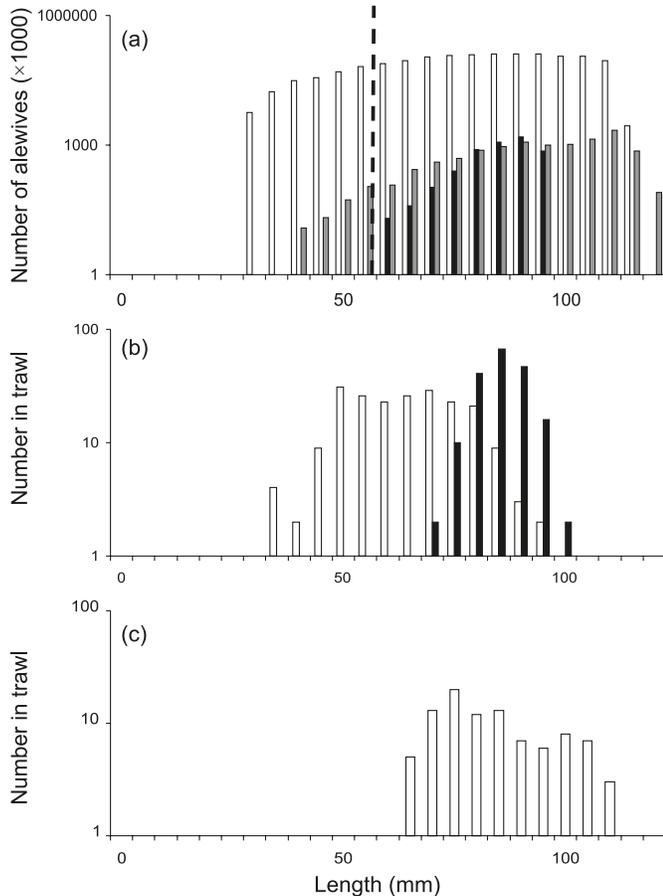
During 1995 and 1996, early-life growth was highest for individuals emerging in tributary habitats, but during warm years, average growth rates were higher in Lake Michigan compartments (Table 3 and Fig. 6). Relationships between time of emergence and early-life growth were also apparent, and during 1995 and 1996, individuals emerging later grew slower (Fig. 6). Differences in early-life mortality rates

Fig. 3. Numbers of young-of-year (YOY) alewives (*Alosa pseudoharengus*) >60 mm on simulation day 180 (27 October), with mean daily temperature inputs (lines) for 1992–2002 (open bars, Lake Michigan; solid bars, tributary residents; gray bars, tributary – Lake Michigan migrants). Note logarithmic scale for left-hand y axis.

among habitat compartments were less dramatic. Nonetheless, in 1996, early-life mortality rates were noticeably higher in Lake Michigan habitat compartments (Fig. 6). During warm years, such as 1998, there was no apparent temporal relationship between day of emergence and early-life survival. However, during cooler years, mortality rates tended to be higher for late-emerging individuals (Fig. 6). For individuals emerging at the same time, growth and mortality rates were more variable in tributaries than in Lake Michigan; thus early-life *G/Z* values also tended to be more variable in tributary habitats (Fig. 6).

Repeated simulations suggested that stochastic components of the model have only minor influences on model outputs. Assumptions regarding zooplankton densities clearly influenced final length distributions and habitat-specific contributions (Table 4). However, qualitative differences among habitats in growth and recruitment success were maintained when zooplankton densities were set at uniformly low or high values (Table 4). Similarly, while relaxation of certain model assumptions (relating to predation mortality, habitat-specific temperatures, movement, hatching dates, and the

Fig. 4. Alewife (*Alosa pseudoharengus*) length distributions. (a) Lengths of three classes of individual alewives (open bars, Lake Michigan; solid bars, tributary residents; gray bars, tributary – Lake Michigan migrants) alive on day 180 during a 2002 model simulation. The broken line represents the 60 mm length threshold that individuals must reach to survive winter. (b–c) Comparison between length distributions of young-of-year (YOY, age-0; panel b) and yearling (age-1; panel c) alewives caught by bottom and mid-water trawls in nearshore Lake Michigan (open bars) and Muskegon Lake (solid bars) during October–November 2002 and April–June 2003, respectively (data from Höök et al. 2007). Note logarithmic scale for y axes.



size threshold to survive winter) influenced quantitative model predictions, qualitative conclusions of our model simulations (i.e., high interannual variation in habitat-specific recruitment) were robust to these individual assumptions (see Supplemental Materials³).

Model outputs are consistent with empirical field observations. Lengths of simulated alewives at the end of the 2002 model run were more variable and on average greater than lengths of alewives captured in nearshore Lake Michigan and Muskegon Lake during October and November 2002. However, model- and field-derived length distributions largely overlapped (Fig. 4). In comparing model predictions of alewife year-class strength with recruitment success indexed by US Geological Survey – Great Lakes Science Center’s fall bottom trawl surveys, we were only able to compare nine pairs of data (no data for 1995 and 1997).

Table 2. Survival rates of alewives (*Alosa pseudoharengus*) to the end of the simulation and over winter. Mean survival rates are presented for individuals emerging in eight habitat compartments during three representative simulation years.

| Natal habitat compartment | Simulation timeframe* | Simulation year | | |
|---|-----------------------|-----------------|-------|-------|
| | | 1995 | 1996 | 1998 |
| Nearshore Lake Michigan habitats | | | | |
| 2 | End | 0.005 | 0.000 | 0.025 |
| | Over winter | 0.000 | 0.000 | 0.016 |
| 3 | End | 0.013 | 0.000 | 0.029 |
| | Over winter | 0.001 | 0.000 | 0.027 |
| 4 | End | 0.016 | 0.000 | 0.032 |
| | Over winter | 0.002 | 0.000 | 0.029 |
| 5 | End | 0.018 | 0.000 | 0.029 |
| | Over winter | 0.006 | 0.000 | 0.028 |
| Tributary habitats | | | | |
| 6 | End | 0.014 | 0.000 | 0.018 |
| | Over winter | 0.008 | 0.000 | 0.017 |
| 7 | End | 0.018 | 0.003 | 0.015 |
| | Over winter | 0.015 | 0.000 | 0.015 |
| 8 | End | 0.019 | 0.002 | 0.017 |
| | Over winter | 0.017 | 0.000 | 0.017 |
| 9 | End | 0.018 | 0.004 | 0.007 |
| | Over winter | 0.017 | 0.001 | 0.007 |

*End, the proportion of individuals alive on simulation day 180, 27 October; Over winter, the proportion of individuals alive and >60 mm on simulation day 180, 27 October.

Nonetheless, for these 9 years, model predictions of recruitment success were significantly and positively correlated with empirical measures of year-class strength ($r = 0.58$). Finally, our model estimates of habitat-specific contributions to the 2002 year class were similar to estimates based on isotopic analysis of otolith cores from age-1 alewives captured during 2003. Chemical analyses of otoliths by Dufour et al. (2005) suggested that out of 41 yearling alewives, only one showed an isotopic signature somewhat consistent with early life in a drowned river mouth lake. Thus, otolith analyses suggested that 0%–2.4% of alewife survivors spent early life in a drowned river mouth lake (Dufour et al. 2005). This range is consistent with our model estimate that 1.3% of alewife survivors during 2002 emerged in drowned river mouth lakes.

Discussion

With a rather straightforward model and a single annual input variable (i.e., temperature), model simulations predicted high interannual variation in estimates of relative habitat-specific recruitment success of alewife in Lake Michigan. Similar phenomena occur in nature and are potentially common (e.g., Hilborn et al. 2003; Berkeley et al. 2004). We suggest that high interannual variation in relative habitat-specific recruitment success may particularly be common for stocks at the latitudinal extremes of a species’ geographical range and for fish populations inhabiting large, heterogeneous systems (e.g., alewives in Lake Michigan). Myers (1998) proposed that year-class strength of Northern Hemisphere fish stocks near the northern edge of their geo-

Fig. 5. Day of emergence (x axis) plotted versus (a) total length (mm) at the end of simulations (day 180), (b) proportional survival to the end of simulations, and (c) over-winter survival for super-individual alewives (*Alosa pseudoharengus*) emerging in Lake Michigan (compartments 2–5; black points) and tributary (compartments 6–9; gray points) habitats during three representative simulation years (1995, 1996, and 1998).

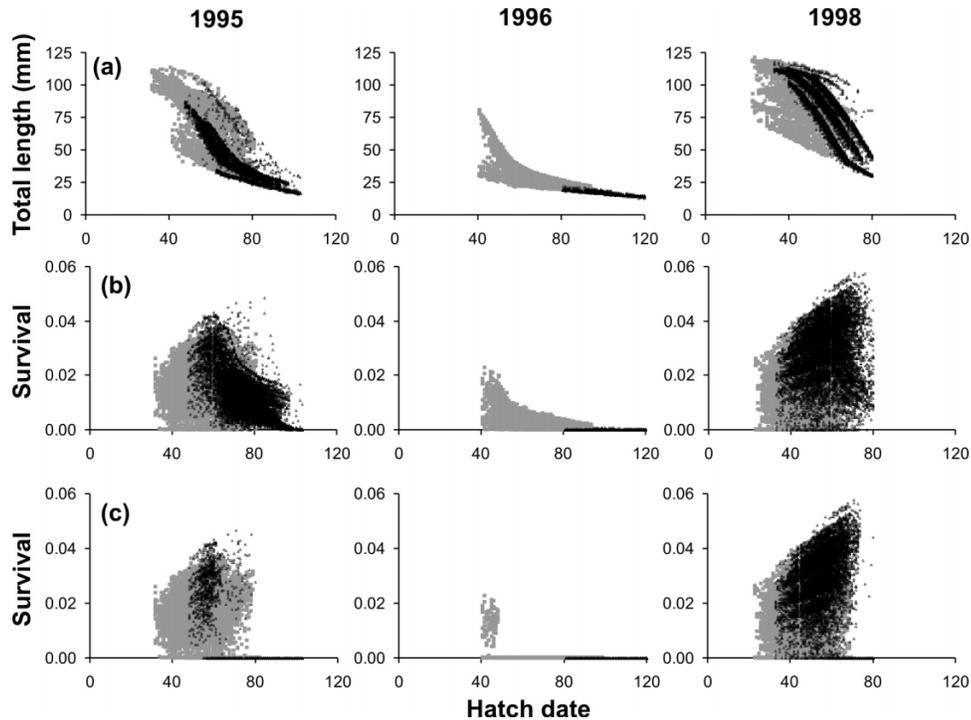


Table 3. Early-life growth rates ($\text{mm}\cdot\text{day}^{-1}$; mean \pm standard deviation) of simulated super-individuals emerging in eight habitat compartments during three representative simulation years.

| Habitat compartment | Simulation years | | |
|---|------------------|-----------------|-----------------|
| | 1995 | 1996 | 1998 |
| Nearshore Lake Michigan habitats | | | |
| 2 | 0.45 \pm 0.15 | 0.19 \pm 0.01 | 0.92 \pm 0.07 |
| 3 | 0.74 \pm 0.12 | 0.18 \pm 0.01 | 0.97 \pm 0.03 |
| 4 | 0.76 \pm 0.10 | 0.18 \pm 0.01 | 0.97 \pm 0.03 |
| 5 | 0.83 \pm 0.10 | 0.18 \pm 0.01 | 0.96 \pm 0.03 |
| Tributary habitats | | | |
| 6 | 0.90 \pm 0.12 | 0.28 \pm 0.09 | 0.93 \pm 0.04 |
| 7 | 0.96 \pm 0.05 | 0.54 \pm 0.17 | 0.84 \pm 0.09 |
| 8 | 0.96 \pm 0.05 | 0.48 \pm 0.14 | 0.88 \pm 0.07 |
| 9 | 0.95 \pm 0.03 | 0.65 \pm 0.17 | 0.69 \pm 0.19 |

graphic range should be positively related to annual measures of temperature. Shuter and Post (1990) demonstrated that growing season temperatures can influence autumn sizes of YOY fish; thus, summer temperatures largely control the extent of over-winter mortality. Whether or not these processes also translate to annual variation in habitat-specific recruitment success within a system likely depends on the diversity of thermal habitats available. For instance, individuals composing a fish population in a small, isolated lake should experience fairly similar thermal environments during their first year of life; thus, habitat-specific contribu-

tions within such a small, homogeneous system will likely vary little. On the other hand, habitat-specific contributions across larger heterogeneous systems, such as a large lake with embayments and tributaries or a river system within a diverse geological landscape, can potentially vary dramatically from year to year (e.g., Hilborn et al. 2003; Berkeley et al. 2004).

While fisheries managers often use quantitative models for short-term (within 1–2 years) predictive purposes, individual-(agent-) based models lend themselves to more exploratory analyses (Bankes 1993, 2002; Jones et al. 2006). Thereby, we view our analysis as a heuristic exercise, and we focus upon qualitative outcomes. Nonetheless, we followed Grimm et al.'s (2005) approach and found that various hierarchical patterns within our individual-based simulations matched empirical observations. Thus, simulation results are likely informative for understanding the ecology of Lake Michigan alewife.

Model simulations indicate that the contributions of specific habitats to overall alewife recruitment vary annually. During cold years of low recruitment, tributary habitats appear to contribute relatively high numbers of young alewives. These predicted annual differences in habitat importance resulted from different temperature inputs (i.e., temperatures are the only annual inputs, and general simulation conclusions were maintained with fixed, uniform zooplankton densities) and size-dependent over-winter mortality. Several authors suggest that YOY alewife must reach some minimum size to survive winter (O'Gorman and Schneider 1986; Bergstedt and O'Gorman 1989; Höök et al. 2007). Ultimately, over-winter survival is likely a function

Fig. 6. Day of emergence (x axis) plotted versus early-life (a) instantaneous daily growth (G), (b) instantaneous daily mortality (Z), and (c) G/Z for super-individual alewives (*Alosa pseudoharengus*) emerging in Lake Michigan (compartments 2–5; black points) and tributary (compartments 6–9; gray points) habitats during three representative simulation years (1995, 1996, and 1998).

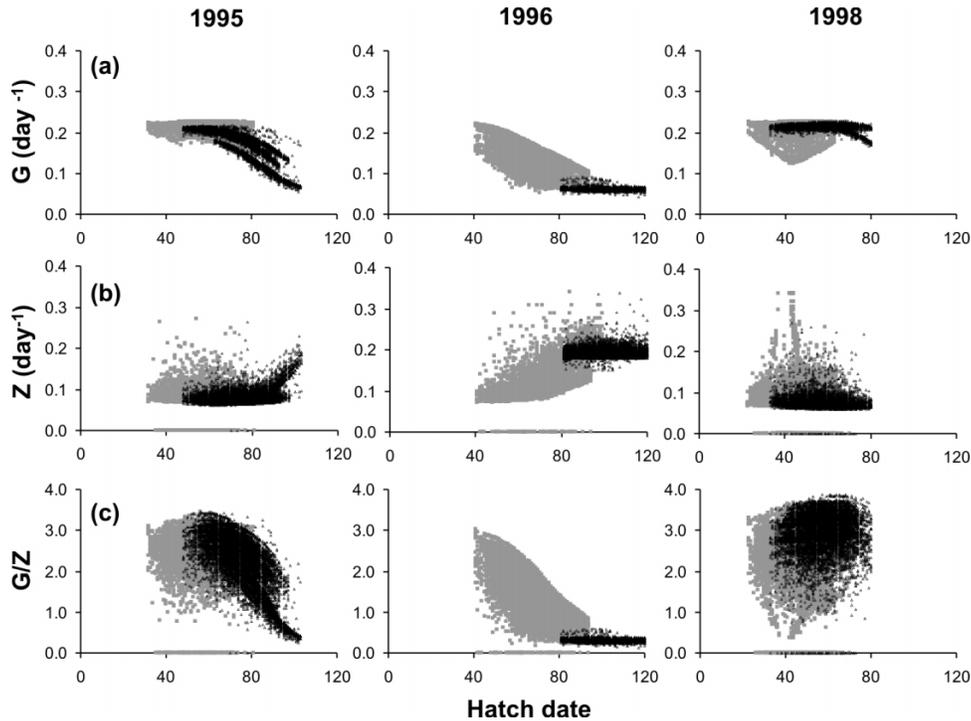


Table 4. Number of survivors (i.e., ≥ 60 mm) and mean lengths (mm) of three classes of young-of-year (YOY) alewives (*Alosa pseudoharengus*) alive on simulation day 180 (27 October) during a cold (1996), average (1995), and warm (1998) year, with different assumed zooplankton densities.

| Year | Prey density | No. of survivors | | | Mean length (mm) | | |
|------|---------------|-------------------------|------------------------------------|---------------------|-------------------------|------------------------------------|---------------------|
| | | Lake Michigan residents | Tributary – Lake Michigan migrants | Tributary residents | Lake Michigan residents | Tributary – Lake Michigan migrants | Tributary residents |
| 1995 | Variable | 1.09×10^8 | 8.00×10^6 | 7.48×10^6 | 44.1 | 75.3 | 84.6 |
| | Uniform, low | 1.24×10^8 | 2.16×10^6 | 1.36×10^6 | 44.6 | 68.6 | 62.2 |
| | Uniform, high | 1.93×10^8 | 7.32×10^6 | 6.52×10^6 | 45.8 | 74.0 | 80.0 |
| 1996 | Variable | 0 | 6.23×10^4 | 1.49×10^5 | 16.5 | 32.4 | 43.9 |
| | Uniform, low | 0 | 2.03×10^4 | 4.51×10^4 | 16.5 | 31.4 | 42.7 |
| | Uniform, high | 0 | 4.74×10^4 | 1.18×10^5 | 16.6 | 32.2 | 43.3 |
| 1998 | Variable | 1.24×10^9 | 9.38×10^6 | 3.75×10^6 | 82.9 | 97.6 | 87.3 |
| | Uniform, low | 1.46×10^9 | 2.64×10^6 | 5.23×10^5 | 84.1 | 94.9 | 60.5 |
| | Uniform, high | 1.95×10^9 | 8.82×10^6 | 3.23×10^6 | 85.7 | 97.8 | 81.5 |

of both an individual’s size (which influences mass-specific metabolic rate and thus over-winter energy utilization) and energy density (which determines the amount of stored energy that can be utilized over winter). However, bioenergetics models are generally not well suited to depict energy utilization during a period of resource scarcity; thus, using a bioenergetics approach to model over-winter energy utilization as a function of size and energy density is problematic. Therefore, it was appropriate for us to model over-winter mortality as a function of size, because (i) past studies have suggested a relationship between YOY alewife size and over-winter survival, (ii) biases likely arise when using a bioenergetics approach to simulate over-winter energy utilization, and (iii) simulated alewives maintained a fairly tight

relationship between length and energy density (i.e., for predictive purposes, length and energy density were essentially interchangeable). While several studies suggest that the critical size threshold that alewives must reach to survive winter is approximately 60 mm, it is possible that during some years smaller individuals also survive. For instance, Madenjian (unpublished data) found that during May 1994–1995, lake trout (*Salvelinus namaycush*) in Lake Michigan consumed a very small number of alewives between 45 and 60 mm (described in Madenjian et al. 1998). If such small individuals subsequently survive the spring and recruit to the adult population, then a size threshold less than 60 mm would be appropriate. Obviously, a shorter size threshold would alter model predictions of annual habitat-specific re-

cruitment. However, the general qualitative conclusions of our model simulations (i.e., high interannual variation in habitat-specific recruitment) are robust to the assumption of a much shorter size threshold (e.g., 45 mm).

Some authors suggest that winter severity also may be an important determinant of alewife year-class strength (Brown 1972; Flath and Diana 1985; O’Gorman et al. 2004). However, based on statistical analysis of long-term data sets, Madenjian et al. (2005) demonstrate that although high winter severity had an insignificant negative effect on year-class strength, the influence of this environmental feature on recruitment success of Lake Michigan alewives is far less than growing season temperatures and salmonine predation. Nonetheless, it is possible that annual variation in winter severity could adjust model predictions of relative habitat contributions. Specifically, it is likely that cooler winters would favor over-winter survival of even larger alewives (>60 mm) and thereby inflate interannual variation in relative habitat-specific recruitment success.

Relative recruitment success of alewife varied among years depending on hatch date. Simulated individuals benefited by emerging as late as possible and growing quickly to obtain the ultimate size threshold to survive winter. In other words, late-emerging individuals risk mortality over a shorter time period than early-emerging individuals. During cold years, late-emerging individuals did not recruit, and even though early-emerging alewives may have been susceptible to potential mortality over an extended period, these initial cohorts were able to grow to 60 mm. Such interannual variation in hatch dates of successful recruits is consistent with the notion that interannual variation in population-level recruitment can be minimized by maintaining a population that spawns over an extended time period (e.g., Garvey et al. 2002). Further, as timing of spawning is partially a genetically determined trait, it follows that maintenance of intra-specific genetic diversity should promote sustainability and resilience of fish populations (Ryman et al. 1995; Policansky and Magnusson 1998; Berkeley et al. 2004).

We modeled zooplankton densities deterministically and ran two types of simulations: (i) spatially and temporally variable zooplankton densities and (ii) uniform zooplankton densities. In simulations with variable zooplankton densities, we relied on density estimates from 2001 and 2002 to depict temporal variation in habitat-specific zooplankton densities. Thus, we did not explicitly model prey depletion and potential density-dependent effects on alewife food availability. Instead, zooplankton density values implicitly incorporated top-down, density-dependent controls, in that density values were derived from natural systems in which fish predation influences temporal patterns of zooplankton densities. This approach for modeling prey densities was appropriate because we only represented young alewife foragers. Other types of fish that compete with young alewives also influence zooplankton community composition and densities. Explicitly accounting for density-dependent prey depletion without tracking the multitude of competitive foragers could lead to inaccurate depictions of zooplankton dynamics. Nonetheless, it is evident from simulations with uniform zooplankton densities that zooplankton densities can influence individual recruitment success. To evaluate the potential impact of model alewife consumption on zooplankton densities, we calculated

the total daily consumption of zooplankton prey types in each habitat compartment during 1998 (the warmest year of highest recruitment and presumably the greatest consumption of zooplankton by young alewives). We then compared total consumption with total biomass of available zooplankton. In so doing, we found that model YOY alewives tended to consume a very small proportion of available zooplankton. The greatest percent consumption of zooplankton ($\sim 0.13\%$ of available biomass) occurred for large-bodied zooplankton on simulation day 110 in habitat compartment 7. In addition, simulations with spatially and temporally uniform zooplankton densities suggest that temperature (and not zooplankton densities) is the primary determinant of recruitment success.

In conclusion, interannual variation in recruitment success among habitats should be considered when formulating habitat management plans. At the population level, annual recruitment can vary tremendously, confound stock management, and affect long-term population viability. Our analyses suggest that management that increases diversity of habitats may lessen interannual variation in system-wide recruitment success. It would be useful to extend this type of model to follow cohorts for numerous years and thereby better understand the long-term implications of habitat diversity for population sustainability. Further, the use of higher resolution spatial data could facilitate model application at hierarchical habitat scales and thereby improve model predictions. Ultimately, a diversity of habitats may not be critical for maintaining the Lake Michigan alewife population. Our simulations suggest that if growing season temperatures were low for several successive years, then this population would consist almost exclusively of individuals who emerged in drowned river mouth lakes. However, alewives in Lake Michigan are iteroparous, typically mature at age-2, and older individuals (up to age-8) are fairly common in lake-wide collections (Brown 1972; Madenjian et al. 2003). In fact, bottom trawl surveys suggested that the 1998 year class (a very abundant cohort) was still a major contributor to spawning stock in 2004. Thus, more than six consecutive cold years may be necessary for Lake Michigan’s alewife population to be dominated by tributary fish, and such a sequence of cold conditions is unlikely in the future. On the other hand, if semelparous or short-lived fish species experience high interannual variation in relative habitat-specific contributions of young fish, then a plethora of habitat types may be necessary to sustain such fish stocks. Thus, for a variety of fish stocks, interannual variation in system-wide recruitment success can likely be minimized by maintaining (or perhaps enhancing) habitat diversity.

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References

- Andrews, J.M., Gurney, W.S.C., Heath, M.R., Gallego, A., O’Brien, C.M., Darby, C., and Tyldsley, G. 2006. Modelling

- the spatial demography of Atlantic cod (*Gadus morhua*) on the European continental shelf. *Can. J. Fish. Aquat. Sci.* **63**: 1027–1048. doi:10.1139/F06-006.
- Auer, N.A. (Editor). 1982. Identification of larval fishes of the Great Lakes basin with emphasis on the Lake Michigan drainage. Spec. Publ. 82-3. Great Lakes Fishery Commission, Ann Arbor, Mich.
- Bankes, S. 1993. Exploratory modeling for policy analysis. *Oper. Res.* **41**: 435–449.
- Bankes, S. 2002. Tools and techniques for developing policies for complex and uncertain systems. *Proc. Natl. Acad. Sci. U.S.A.* **99**(Suppl. 3): 7263–7266. doi:10.1073/pnas.092081399. PMID: 11997451.
- Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., and Weinstein, M.P. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience*, **51**: 633–641. doi:10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2.
- Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., and Weinstein, M.P. 2003. The role of nearshore ecosystems as fish and shellfish nurseries. *Iss. Ecol.* **11**: 1–12.
- Beletsky, D., Saylor, J.H., and Schwab, D.J. 1999. Mean circulation in the Great Lakes. *J. Great Lakes Res.* **25**: 78–93.
- Bergstedt, R.A., and O’Gorman, R. 1989. Distribution of alewives in southeastern Lake Ontario in autumn and winter: a clue to winter mortalities. *Trans. Am. Fish. Soc.* **118**: 687–692. doi:10.1577/1548-8659(1989)118<0687:DOAISL>2.3.CO;2.
- Berkeley, S.A., Hixon, M.A., Larson, R.J., and Love, M.S. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, **29**: 23–32. doi:10.1577/1548-8446(2004)29[23:FSVPOA]2.0.CO;2.
- Brown, E.H., Jr. 1972. Population biology of alewives, *Alosa pseudoharengus*, in Lake Michigan, 1949–70. *J. Fish. Res. Board Can.* **29**: 477–500.
- Charnov, E.L. 1976. Optimal foraging: attack strategy of a mantid. *Am. Nat.* **110**: 141–151. doi:10.1086/283054.
- Cowan, J.H., Jr., and Shaw, R.F. 2002. Recruitment. *In* *Fishery science: the unique contributions of early life stages*. Edited by L.A. Fuiman and R.G. Werner. Blackwell Sciences Ltd., Oxford, UK. pp. 88–111.
- Croley, T.E., II. 1989. Verifiable evaporation modeling on the Laurentian Great Lakes. *Water Resour. Res.* **25**: 781–792. doi:10.1029/WR025i005p00781.
- Croley, T.E., II. 1992. Long-term heat storage in the Great Lakes. *Water Resour. Res.* **28**: 69–81. doi:10.1029/91WR02500.
- Croley, T.E., II, and Assel, R.A. 1994. One-dimensional ice model for the Laurentian Great Lakes. *Water Resour. Res.* **30**: 625–639. doi:10.1029/93WR03415.
- Dahlgren, C.P., Kellison, G.T., Adams, A.J., Gillanders, A.J., Kendall, M.S., Layman, C.A., Ley, J.A., Nagelkerken, I., and Serafy, J.E. 2006. Marine nurseries and effective juvenile habitats: concepts and applications. *Mar. Ecol. Prog. Ser.* **312**: 291–295. doi:10.3354/meps312291.
- Dufour, E., Patterson, W., Höök, T.O., and Rutherford, E.S. 2005. Early life history of Lake Michigan alewives (*Alosa pseudoharengus*) inferred from intra-otolith stable isotope ratios. *Can. J. Fish. Aquat. Sci.* **62**: 2362–2370. doi:10.1139/f05-147.
- Flath, L.E., and Diana, J.S. 1985. Seasonal energy dynamics of the alewife in southeastern Lake Michigan. *Trans. Am. Fish. Soc.* **114**: 328–337. doi:10.1577/1548-8659(1985)114<328:SEDOTA>2.0.CO;2.
- Garvey, J.E., Herra, T.P., and Leggett, W.C. 2002. Protracted reproduction in sunfish: the temporal dimension revisited. *Ecol. Appl.* **12**: 194–205. doi:10.1890/1051-0761(2002)012[0194:PRISTT]2.0.CO;2.
- Goodyear, C.D., Edsall, T.A., Ormsby Dempsey, D.M., Moss, G.D., and Polanski, P.E. 1982. Atlas of the spawning and nursery areas of Great Lakes fishes. US Fish and Wildlife Service, Washington, D.C. FWS/OBS-82/52.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., and DeAngelis, D.L. 2005. Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science* (Washington, D.C.), **310**: 987–991. doi:10.1126/science.1116681.
- Hanson, P.C., Johnson, T.B., Schindler, D.E., and Kitchell, J.F. 1997. Fish bioenergetics 3.0. Center for Limnology, University of Wisconsin – Madison. University of Wisconsin Sea Grant Institute, Madison, Wis.
- Hewett, S.W., and Stewart, D.J. 1989. Zooplanktivory by alewives in Lake Michigan: ontogenetic, seasonal, and historical patterns. *Trans. Am. Fish. Soc.* **118**: 581–596. doi:10.1577/1548-8659(1989)118<0581:ZBAILM>2.3.CO;2.
- Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2003. Biocomplexity and fisheries sustainability. *Proc. Natl. Acad. Sci. U.S.A.* **100**: 6564–6568. doi:10.1073/pnas.1037274100. PMID:12743372.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer*, **20**: 1–228.
- Höök, T.O. 2005. Habitat-mediated production and recruitment of young alewives in Lake Michigan. Ph.D. dissertation, University of Michigan, Ann Arbor, Mich.
- Höök, T.O., Rutherford, E.S., Brines, S.J., Schwab, D.J., and McCormick, M.J. 2004. Relationship between surface water temperature and steelhead distributions in Lake Michigan. *N. Am. J. Fish. Manag.* **24**: 211–221. doi:10.1577/M02-159.
- Höök, T.O., McCormick, M.J., Rutherford, E.S., Mason, D.M., and Carter, G.S. 2006. Short-term water mass movements in Lake Michigan: implications for larval fish transport. *J. Gt. Lakes Res.* **32**: 728–737. doi:10.3394/0380-1330(2006)32[728:SWMMIL]2.0.CO;2.
- Höök, T.O., Rutherford, E.S., Mason, D.M., and Carter, G.S. 2007. Hatch dates, growth, survival and over-winter mortality of age-0 alewives (*Alosa pseudoharengus*) in Lake Michigan: implications for habitat-specific recruitment success. *Trans. Am. Fish. Soc.* **136**: 1298–1312. doi:10.1577/T06-194.1.
- Iles, T.D., and Sinclair, M. 1982. Atlantic herring: stock discreteness and abundance. *Science* (Washington, D.C.), **215**: 627–633. doi:10.1126/science.215.4533.627. PMID:17842372.
- Jones, M.L., Shuter, B.J., Zhao, Y., and Stockwell, J.D. 2006. Forecasting effects of climate change on Great Lakes fisheries: models that link habitat supply to population dynamics can help. *Can. J. Fish. Aquat. Sci.* **63**: 457–468. doi:10.1139/f05-239.
- Jude, D.J., Tin, H.T., Heufelder, G.R., Schneeberger, P.J., Madenjian, C.P., Rutecki, T.L., Mansfield, P.J., Auer, N.A., and Noguchi, G.E. 1981a. Adult, juvenile and larval fish populations in the vicinity of J.H. Campbell Power Plant, Eastern Lake Michigan, 1977–1980. University of Michigan, Great Lakes Research Division. Ann Arbor, Mich. Spec. Rep. No. 86.
- Jude, D.J., Rutecki, T.L., Madenjian, C.P., Noguchi, G.E., Schneeberger, P.J., Klinger, S.A., Godun, G.G., and Winnell, M.H. 1981b. The physical, chemical, and biological nature of Pigeon Lake, a Lake Michigan coastal lake. University of Michigan, Great Lakes Research Division, Ann Arbor, Mich. Spec. Rep. No. 78.

- Klumb, R.A., Rudstam, L.G., and Mills, E.L. 2003. Comparison of alewife young-of-the-year and adult respiration and swimming speed bioenergetics parameters: implications of extrapolation. *Trans. Am. Fish. Soc.* **132**: 1089–1103. doi:10.1577/T03-038.
- Letcher, B.H., Rice, J.A., Crowder, L.B., and Rose, K.A. 1996. Variability in survival of larval fish: disentangling components with a generalized individual-based model. *Can. J. Fish. Aquat. Sci.* **53**: 787–801. doi:10.1139/cjfas-53-4-787.
- Letcher, B.H., Rice, J.A., Crowder, L.B., and Binkowski, F.P. 1997. Size- and species-dependent variability in consumption and growth rates of larvae and juveniles of three freshwater fishes. *Can. J. Fish. Aquat. Sci.* **54**: 405–414. doi:10.1139/cjfas-54-2-405.
- Madenjian, C.P., DeSorcie, T.J., and Stedman, R.M. 1998. Ontogenetic and spatial patterns in diet and growth of Lake Trout in Lake Michigan. *Trans. Am. Fish. Soc.* **127**: 236–252. doi:10.1577/1548-8659(1998)127<0236:OASPID>2.0.CO;2.
- Madenjian, C.P., Holuszko, J., and Desorcie, T.J. 2003. Growth and condition of alewives in Lake Michigan. *Trans. Am. Fish. Soc.* **132**: 1104–1116. doi:10.1577/T02-133.
- Madenjian, C.P., Höök, T.O., Rutherford, E.S., Szalai, E., Bence, J.R., Mason, D.M., and Croley, T.E., II. 2005. Recruitment variability of alewives in Lake Michigan. *Trans. Am. Fish. Soc.* **134**: 218–230. doi:10.1577/FT03-222.1.
- Mansfield, P.J. 1984. Reproduction by Lake Michigan fishes in a tributary stream. *Trans. Am. Fish. Soc.* **113**: 231–237. doi:10.1577/1548-8659(1984)113<231:RBLMFI>2.0.CO;2.
- Mansfield, P.J., and Jude, D.J. 1986. Alewife (*Alosa pseudoharengus*) survival during the first growth season in southeastern Lake Michigan. *Can. J. Fish. Aquat. Sci.* **43**: 1318–1326. doi:10.1139/f86-165.
- Minns, C.K., Randall, R.G., Moore, J.E., and Cairns, V.W. 1996. A model simulating the impact of habitat supply limits on northern pike, *Esox lucius*, in Hamilton Harbour, Lake Ontario. *Can. J. Fish. Aquat. Sci.* **53**(Suppl. 1): 20–34. doi:10.1139/cjfas-53-S1-20.
- Myers, R.A. 1998. When do environment-correlations work? *Rev. Fish Biol. Fish.* **8**: 285–305. doi:10.1023/A:1008828730759.
- Norden, C.R. 1967. Age, growth and fecundity of the alewife, *Alosa pseudoharengus* (Wilson), in Lake Michigan. *Trans. Am. Fish. Soc.* **96**: 387–393. doi:10.1577/1548-8659(1967)96[387:AGAFOT]2.0.CO;2.
- O’Gorman, R., and Schneider, C.P. 1986. Dynamics of alewives in Lake Ontario following a mass mortality. *Trans. Am. Fish. Soc.* **115**: 1–14. doi:10.1577/1548-8659(1986)115<1:DOAILO>2.0.CO;2.
- O’Gorman, R., Lantry, B.F., and Schneider, C.P. 2004. Effect of stock size, climate, predation, and trophic status on recruitment of alewives in Lake Ontario, 1978–2000. *Trans. Am. Fish. Soc.* **133**: 855–867. doi:10.1577/T03-016.1.
- Peterman, R.M., Pyper, B.J., and MacGregor, B.W. 2003. Use of the Kalman filter to reconstruct historical trends in productivity of Bristol Bay sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* **60**: 809–824. doi:10.1139/f03-069.
- Policansky, D., and Magnusson, J.J. 1998. Genetics, metapopulations, and ecosystem management of fisheries. *Ecol. Appl.* **8**(Suppl.): S119–S123. doi:10.2307/2641369.
- Ruzzante, D.E., Taggart, C.T., Lang, S., and Cook, D. 2000. Mixed-stock analysis of Atlantic cod near the Gulf of St. Lawrence based on microsatellite DNA. *Ecol. Appl.* **10**: 1090–1109. doi:10.1890/1051-0761(2000)010[1090:MSAOAC]2.0.CO;2.
- Ruzzante, D.E., Mariani, S., Bekkevold, D., Andre, C., Mosegaard, H., Clausen, L.A.W., Dahlgren, T.G., Hutchinson, W.F., Hatfield, E.M.C., Torstensen, E., Brigham, J., Simmonds, E.J., Laikre, L., Larsson, L.C., Stet, R.J.M., Ryman, N., and Carvalho, C.R. 2006. Biocomplexity in a highly migratory pelagic marine fish, Atlantic herring. *Proc. R. Soc. Lond. B. Biol. Sci.* **273**: 1459–1464. doi:10.1098/rspb.2005.3463.
- Ryman, N., Utter, F., and Laikre, L. 1995. Protection of intraspecific biodiversity of exploited fishes. *Rev. Fish Biol. Fish.* **5**: 417–446. doi:10.1007/BF01103814.
- Scheffer, M., Baveco, M.J., DeAngelis, D.L., Rose, K.A., and Vannes, E.H. 1995. Super-individuals a simple solution for modeling large population on an individual basis. *Ecol. Model.* **80**: 161–170. doi:10.1016/0304-3800(94)00055-M.
- Schindler, D.E., Leavitt, P.R., Johnson, S.P., and Brock, C.S. 2006. A 500-year context for the recent surge in sockeye salmon (*Oncorhynchus nerka*) abundance in the Alagnak River, Alaska. *Can. J. Fish. Aquat. Sci.* **63**: 1439–1444. doi:10.1139/F06-069.
- Schwab, D.J., Leshkevich, G.A., and Muhr, G.C. 1999. Automated mapping of surface water temperature in the Great Lakes. *J. Great Lakes Res.* **25**: 468–481.
- Shuter, B.J., and Post, J.R. 1990. Climate, population viability, and the zoogeography of temperate fishes. *Trans. Am. Fish. Soc.* **119**: 314–336. doi:10.1577/1548-8659(1990)119<0314:CPVATZ>2.3.CO;2.
- Stephens, D.W., and Krebs, J.R. 1986. Foraging theory. Princeton University Press, Princeton, N.J.
- Stewart, D.J., and Binkowski, F.P. 1986. Dynamics of consumption and food conversion by the Lake Michigan alewives: an energetics-modeling synthesis. *Trans. Am. Fish. Soc.* **115**: 643–661. doi:10.1577/1548-8659(1986)115<643:DOCAFC>2.0.CO;2.
- Wagner, W.C. 1972. Utilization of alewives by inshore piscivorous fishes in Lake Michigan. *Trans. Am. Fish. Soc.* **101**: 55–63. doi:10.1577/1548-8659(1972)101<55:UOABIP>2.0.CO;2.