

## Overwinter Survival of Juvenile Lake Herring in Relation to Body Size, Physiological Condition, Energy Stores, and Food Ration

KEVIN L. PANGLE<sup>1</sup> AND TRENT M. SUTTON\*

Purdue University, Department of Forestry and Natural Resources,  
195 Marsteller Street, West Lafayette, Indiana 47907-1159, USA

RONALD E. KINNUNEN

Michigan Sea Grant, Michigan State University, 710 Chippewa Square, Suite 202,  
Marquette, Michigan 49855, USA

MICHAEL H. HOFF<sup>2</sup>

U.S. Geological Survey, Great Lakes Science Center, Lake Superior Biological Station,  
2800 Lakeshore Drive East, Ashland, Wisconsin 54806, USA

**Abstract.**—Populations of lake herring *Coregonus artedii* in Lake Superior have exhibited high recruitment variability over the past three decades. To improve our understanding of the mechanisms which influence year-class strength, we conducted a 225-d laboratory experiment to evaluate the effects of body size, physiological condition, energy stores, and food ration on the winter survival of age-0 lake herring. Small (total length [TL] range = 60–85 mm) and large (TL range = 86–110 mm) fish were maintained under thermal and photoperiod regimes that mimicked those in Lake Superior from October through May. Fish in each size-class were maintained at two feeding treatments: brine shrimp *Artemia* spp. ad libitum and no food. The mortality of large lake herring (fed, 3.8%; starved, 20.1%) was significantly less than that of small fish (fed, 11.7%; starved, 32.0%). Body condition and crude lipid content declined for all fish over the experiment; however, these variables were significantly greater for large fed (0.68% and 9.8%) and small fed (0.65% and 7.3%) fish than large starved (0.49% and 5.7%) and small starved (0.45% and 4.8%) individuals. Final crude protein and gross energy contents were also significantly greater in large fed lake herring (17.6% and 1,966 cal/g), followed by small fed (17.1% and 1,497 cal/g), large starved (15.4% and 1,125 cal/g), and small starved (13.2% and 799 cal/g) fish. Lake herring that died during the experiment had significantly lower body condition and energy stores relative to those of the surviving fish. These results suggest that the depletion of energy stores contributes to greater winter mortality of small lake herring with limited energy uptake and may partially explain the variability in recruitment observed in Lake Superior.

Lake herring *Coregonus artedii* were once the primary species harvested from Lake Superior, comprising 74% of the total U.S. commercial yield for the lake (Anderson and Smith 1971; Baldwin et al. 1979). Populations collapsed lakewide during the late 1960s as a result of overexploitation, and stocks have failed to recover to historical levels (Selgeby 1982; Hoff 2004). Since 1970, the year-class strength of lake herring in Lake Superior

has been highly variable, fluctuating by a factor of nearly 4,000 (Hoff 2004). Although the mechanisms which regulate the recruitment variability of lake herring remain unknown, Selgeby (1982) indicated that some form of density-independent mortality regulates year-class strength and has limited recovery of depressed stocks.

The year-class strength of most fish populations is determined during the first year of life (Craig 1980; Henderson et al. 1988). One factor that is known to influence recruitment is body size, particularly during the first winter of life (Toneys and Coble 1979; Post and Prankevicus 1987; Post and Evans 1989; Smith and Griffith 1994; Meyer and Griffith 1997; Gotceitas et al. 1999; Sutton and Ney 2001). Over the course of the winter at temperate latitudes, the physiological condition of fishes can decline as energy stores become depleted (Pierce et al. 1980; Toneys and Coble 1979;

\* Corresponding author: tsutton@purdue.edu

<sup>1</sup> Present address: Michigan State University, Department of Fisheries and Wildlife, 13 Natural Resources Building, East Lansing, Michigan 48824, USA.

<sup>2</sup> Present address: U.S. Fish and Wildlife Service, Fisheries Division, Bishop Henry Whipple Federal Building, 1 Federal Drive, Ft. Snelling, Minnesota 55111-4056, USA.

Received July 23, 2003; accepted April 14, 2004

Cunjak 1988; Cargnelli and Gross 1997; Hurst et al. 2000). The capacity for energy storage is directly dependent on fish body size, where lipid and protein content comprise a greater portion of total body mass in larger individuals (Wicker and Johnson 1987; Thompson et al. 1991; Miranda and Hubbard 1994). Weight-specific basal metabolism is also size dependent, creating a greater relative energy demand for smaller fish (Shuter and Post 1990). As a result, smaller individuals may completely exhaust their energy reserves before winter ends and die at a disproportionately greater rate than larger fish of the same cohort due to starvation, disease, predation, or immunosuppression (Henderson et al. 1988; Johnson and Evans 1991; Miranda and Hubbard 1994; Hurst et al. 2000; Sutton and Ney 2001).

Variability in age-0 lake herring body size at the onset of winter could similarly influence recruitment and contribute to the variability in year-class strength that has been observed in Lake Superior. The growth of age-0 lake herring in the Laurentian Great Lakes is confined to the ice-free period, with maximum growth occurring from June through August (Smith 1956; Dryer and Beil 1964; Edsall and DeSorcie 1999). The body size of lake herring immediately prior to the onset of winter is primarily dependent upon the length of the growing period, water temperature, and prey availability (Hile 1936; Carlander 1945; Anderson and Smith 1971; McCormick et al. 1971; Selgeby et al. 1978; Kinnunen 1997). Kinnunen (1997) reported that a 4.2°C increase in water temperature allowed the 1987 cohort in Lake Superior to grow 32% longer than the 1986 year-class. In addition, the northern shoreline along Minnesota was consistently the coolest among all areas of Lake Superior, while the southern shoreline along Wisconsin was consistently the warmest, resulting in a 25–29-mm length difference for fish exposed to warmer waters (Kinnunen 1997). In addition, Minnesota waters supported the lowest biomass (kg/ha) of lake herring, while Wisconsin waters experienced an 11-fold increase in biomass between 1978 and 1995 (Hoff, unpublished data). Therefore, annual and regional differences in growth and year-class strength among lake herring stocks in Lake Superior appear to provide conditions which may facilitate size-dependent winter survival.

The objective of this study was to evaluate the effects of body size, physiological condition, energy stores, and food resource availability on the winter survival of juvenile lake herring over a 225-d laboratory experiment at conditions that mim-

icked an average Lake Superior winter. The anticipated results of this study were that (1) the physiological condition and proximate composition of lake herring during the first year of life would be directly proportional to fish body length and feeding level; (2) the utilization of stored body energy and loss of body mass over the winter would be greater for smaller lake herring within the age-0 cohort; and (3) age-0 lake herring in large body size and fed treatments would experience lower winter mortality than small and starved groups. Based on these study results, we will gain a better understanding of the role of biotic and abiotic factors that influence recruitment variability of lake herring in Lake Superior.

### Methods

Juvenile lake herring were cultured from eggs obtained from spawning adults collected in commercial gill nets from Keweenaw Bay, Lake Superior, in December 2001. Fertilized eggs were incubated at the Red Cliff Tribal Hatchery (Bayfield, Wisconsin) in 6-L MacDonald jars at 8°C until they reached the eyed stage. Eggs were then transported to the Purdue University Aquaculture Research Laboratory (West Lafayette, Indiana) and incubated at similar conditions until hatching. Following hatching, larvae were reared in four, 650-L flow-through aquaria and fed a combination of live brine shrimp *Artemia* spp. nauplii (Summit Artemia, Instar Technologies, Hyrum, Utah) and a moist formulated feed (Bio-Grower feed, Bio-Oregon, Inc., Warrenton, Oregon) ad libitum. Water quality in the rearing aquaria was maintained at the following conditions: temperature, 13.0 ± 1.0°C; dissolved oxygen, greater than 8.5 mg/L; and flow rate, 6 L/min. Lake herring were reared under these conditions for 180 d until they reached 50–129 mm total length (TL) in late August 2002.

The laboratory experiment was conducted in a recirculating culture system containing twenty-four 110-L aquaria. Water outflow in each aquarium was controlled using a 26-mm-diameter standpipe enclosed by a 78-mm-diameter Venturi tube and drained into three, 800-L settling chambers which contained biomedial and air stones to provide supplemental aeration. Water was passed through two 50-µm and one 100-µm mechanical particle filters, and an eight-bulb ultraviolet sterilizer using a 1.5-horse power (1 horse power = 746 W) electric pump before returning to experimental aquaria. Water flow to each aquarium was maintained at 3.8 L/min, and temperature was controlled using three submersible chiller units (Frigid Units, Inc., Toledo,

Ohio). Photoperiod was controlled using the computer program ModScan32 to correspond with the light regime at 46.5°N latitude (WinTECH Software Design, Lewisburg, West Virginia). Total ammonia nitrogen and nitrite-nitrogen concentrations were monitored weekly using the Hach DR2000 spectrophotometer (Hach Company, Loveland, Colorado), while temperature and dissolved oxygen levels were monitored using a YSI 6-Series sonde (Yellow Springs Instruments, Yellow Springs, Ohio). Water quality parameters were maintained at acceptable levels over the duration of the experiment (dissolved oxygen [range = 8.52–9.55 mg/L]; total ammonia-nitrogen [range = 0.02–0.06 mg/L]; and nitrite-nitrogen [range = 0.004–0.008 mg/L]), no significant differences being detected among experimental aquaria (one-way analysis of variance [ANOVA], all  $P > 0.11$ ).

Prior to the start of the experiment, juvenile lake herring were separated into either a small (range = 50–85 mm TL) and large (range = 85–129 mm TL) size-class. These size-classes were the lower and upper halves of the range of lengths that would be expected for age-0 lake herring in Lake Superior immediately prior to the onset of winter (Kinnunen 1997). Thirty small or 15 large fish were randomly allocated to each aquarium (eight aquaria per size-class), with the biomass being similar among aquaria ( $0.92 \pm 0.02$  g/L), regardless of treatment ( $F_{3,15} = 3.01$ ,  $P = 0.08$ ). Sixty small and 30 large individuals not used in the experiment were measured for TL to the nearest 1 mm, weighed to the nearest 0.01 g wet weight, and frozen at  $-80^{\circ}\text{C}$  for subsequent proximate-composition analyses. Two feeding regimes were also used during the experiment: an ad libitum ration of *Artemia* nauplii twice each day (0800 and 1600 hours) and starvation. This broad range in feeding ration treatments was chosen because it is not known whether juvenile lake herring feed during winter months. Each feeding regime was randomly assigned to four aquaria within each size-class. Thus, a  $2 \times 2$  (body size  $\times$  feeding ration) block design was conducted, with each treatment having four replicates.

Following a 14-d acclimation period, lake herring were subjected to environmental conditions that they would be expected to encounter in Lake Superior from October through April. Over a 52-d period, water temperature was decreased from  $10\text{--}2^{\circ}\text{C}$  at a rate of  $0.15^{\circ}\text{C}/\text{d}$ , and remained static at  $2^{\circ}\text{C}$  for 130 d. Water temperature was then increased over a 43-d period to  $10^{\circ}\text{C}$  at a rate of  $0.19^{\circ}\text{C}/\text{d}$ . During the experimental period, uneaten food and fecal material

were removed by siphon on a daily basis, and dead fish were removed from each aquarium and frozen for subsequent proximate-composition analyses. On days 75 and 150 of the experiment, 25% of the surviving fish in each tank were randomly collected and removed, measured for TL and wet weight to the nearest 1 mm and 0.01 g, respectively, and frozen at  $-80^{\circ}\text{C}$  for subsequent proximate-composition analyses. All fish remaining at the end of the experiment (day 225) were sacrificed, measured for TL and wet weight as described previously, and frozen prior to proximate-composition analyses. Percent mortality ( $A$ ) for each treatment that occurred between each sampling period was calculated as

$$A = (1 - [N_s / (N_0 - X)]) \times 100,$$

where  $N_s$  is the number of surviving individuals per treatment of sample  $s$ ,  $N_0$  is the initial number of fish per treatment, and  $X$  is the total number of fish removed from mortality or sampling prior to the sample period. Total length and wet weight of individual fish sampled during the experiment were used to calculate Fulton condition factor ( $[\text{wet weight}/\text{TL}^3] \times 10^5$ ; Anderson and Neumann 1996).

*Proximate-composition analyses.*—Crude lipid, crude protein, and gross energy content were analyzed from lake herring sampled on days 0, 75, 150, and 225 of the experiment and from those fish that had died during the experimental period. All fish were dried at  $100^{\circ}\text{C}$  for 24 h to determine whole-body moisture content (Helrich 1990). For each sampling date, fish samples were homogenized and pooled with other individuals of the same replicate tank, resulting in four subsamples per treatment for each date. Fish that died during the experiment were pooled separately. Dried tissue (1 g) of each replicate was placed in a Soxhlet apparatus using a 2:1 mixture of chloroform and methanol for 24 h to extract lipids (Folch et al. 1957), and whole-body crude lipid content was calculated as  $\{[(\text{initial weight} - \text{extracted weight}) \times 100] / \text{initial weight}\}$ , where all weights are in milligrams.

Crude protein content was determined using a nitrogen analyzer (Perkin-Elmer 2410 Series II, Norwalk, Connecticut) following procedures outlined by Helrich (1990). Samples (0.2 g per replicate) were combusted to estimate total nitrogen content, which was converted to crude protein using the following relationship: percent nitrogen  $\times 6.25$ . Gross energy content (cal/g ash-free dry weight) was determined using a Parr oxygen com-

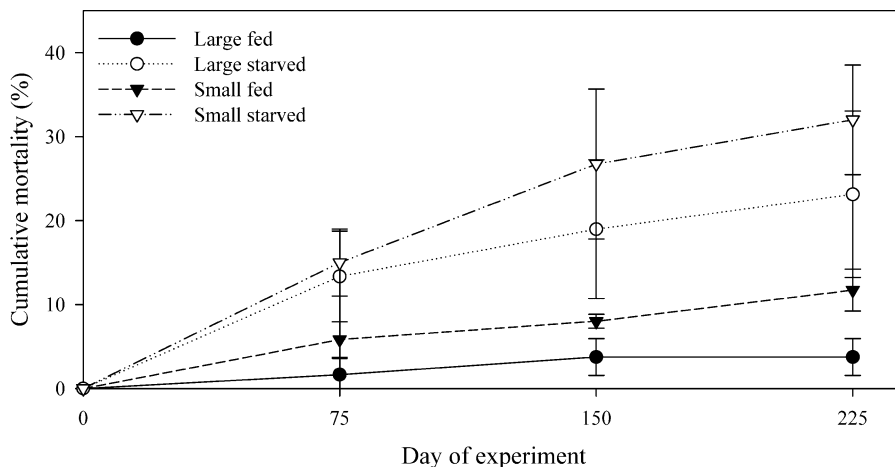


FIGURE 1.—Cumulative mortality of large and small lake herring subjected to fed and starved feeding treatments (see text) over the 225-d laboratory experiment. Values are means  $\pm$  SEs of four replicates per treatment group.

bustion bomb calorimeter (Parr Instruments, Moline, Illinois) following procedures described by Pierce et al. (1980).

**Data analysis.**—To detect differences in body size, Fulton condition factor, and proximate-composition parameters among treatments, data were analyzed by means of a factorial repeated-measures ANOVA following general linear model (GLM) procedures of the Statistical Analysis System (Zar 1999). A factorial ANOVA following GLM procedures was used to compare final mean percent mortality among treatments. An interaction term between body size and food ration treatments was included in both factorial analyses. A one-way blocked ANOVA following GLM procedures was used to detect overall differences in experimental parameters between lake herring that survived the experiment and those that died blocked by treatment group (i.e., small fed, small starved, large fed, and large starved treatments). All percentage data were arcsine-transformed prior to statistical analysis (Zar 1999). Median, range, skewness, and kurtosis were also calculated to better describe changes to the length- and weight-frequency distributions from the beginning to the end of the simulated winter period.

## Results

### Mortality

Lake herring mortality was strongly influenced by body size and feeding ration treatment over the experimental period (Figure 1). On day 75, the mean mortality of large and small starved lake herring was 13.4% and 15.0%, respectively, while

that of large and small fed fish remained low (1.7% and 5.8%, respectively). The difference in mean mortality continued to increase over the experimental period, with a final cumulative mean mortality on day 225 of 20.1% and 32.0%, respectively, for large and small starved lake herring and 3.8% and 11.7%, respectively, for large and small fed fish. Over the duration of the experiment, mortality was significantly greater in small body size and starved treatments ( $F_{1,15} = 5.80$ ,  $P = 0.05$ ;  $F_{1,15} = 11.65$ ,  $P < 0.01$ , respectively). No significant interaction term was identified among body size and food ration treatments for lake herring mortality during the experiment ( $F_{3,15} = 0.14$ ,  $P = 0.72$ ).

### Body Size

Changes in lake herring body length during the experimental period varied among size and feeding ration treatments (Figure 2a). At the onset of the experiment, the mean TL of large lake herring (97.5 mm) was significantly greater ( $F_{1,15} = 38.95$ ,  $P < 0.01$ ) than that of small individuals (76.2 mm), regardless of feeding treatment. The final mean TL of lake herring was 120.3 and 104.2 mm, respectively, in large fed and starved treatments and 95.4 and 85.5 mm, respectively, in small fed and starved treatments. Over the duration of the experiment, the starved treatment had a significant negative affect on mean TL ( $F_{1,15} = 24.81$ ,  $P < 0.01$ ). However, no significant interaction term was identified among the body size and food ration treatments of lake herring for TL ( $F_{1,15} = 0.27$ ,  $P = 0.61$ ). During this period, the length-frequency

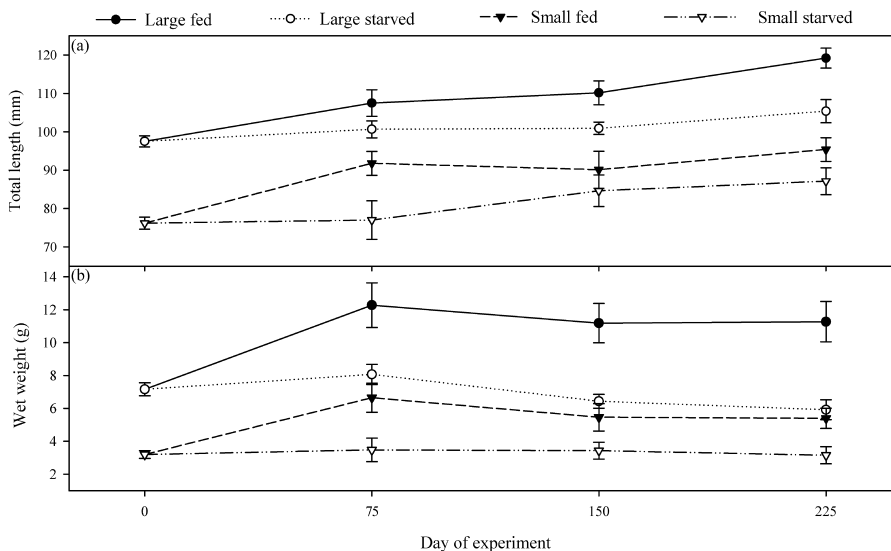


FIGURE 2.—(a) Total length and (b) wet weight of large and small lake herring subjected to fed or starved feeding treatments over the 225-d laboratory experiment. Values are means  $\pm$  SEs of four replicates per treatment group.

distributions for large and small lake herring became narrower in range (Table 1). Further, the length-frequency distribution of large fed and starved fish became more bimodal, with negative changes in skewness and kurtosis. In contrast, the final length-frequency distribution of small fed and starved fish became more positively skewed, unimodal, and positively kurtotic.

Lake herring in the fed treatments increased in mean wet weight over the experimental period, while starved fish declined in mean wet weight (Figure 2b). The final mean wet weight of large fed and starved fish was 11.9 and 5.6 g, respectively, while small fed and starved fish weighed 5.7 and 2.9 g, respectively. Over the experiment, fish in the starved treatment had a significant neg-

ative affect on mean wet weight ( $F_{1,15} = 49.86, P < 0.01$ ). No significant interaction term was exhibited among body size and food ration treatments for wet weight ( $F_{3,15} = 0.27, P = 0.61$ ). Over the experimental period, the weight-frequency distributions for large and small lake herring became more broad in range (Table 1). Similar to length-frequency distributions, the weight-frequency distribution of the small size-class of fish became more positively skewed and kurtotic, while the large size-class became more negatively skewed and kurtotic over the experiment.

*Fulton Condition Factor*

The condition of all lake herring treatment groups decreased over of the experiment, the de-

TABLE 1.—Descriptive statistics of lake herring length- and weight-frequency distributions for large and small size-classes sampled on experimental days 0 and 225.

Size-class	Day of experiment	Median	Range	Skewness	Kurtosis
<b>Total length (mm)</b>					
Large	0	95.0	87–120	1.01	0.87
	225	110.0	97–125	0.11	-1.11
Small	0	76.0	55–84	-0.18	-1.02
	225	91.0	76–103	-0.09	-0.72
<b>Wet weight (g)</b>					
Large	0	6.8	4.1–13.2	0.93	0.81
	225	7.2	4.9–15.5	0.79	-0.60
Small	0	2.9	1.9–4.7	0.36	-1.27
	225	4.3	1.7–8.0	0.39	-0.47

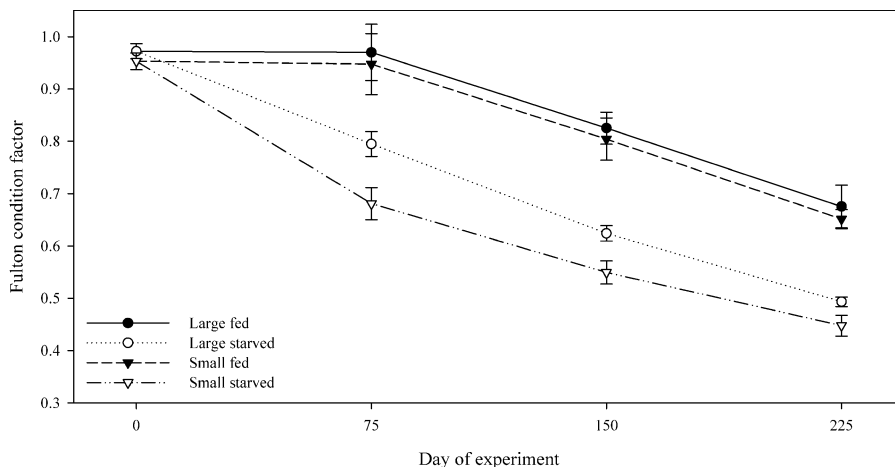


FIGURE 3.—Fulton condition factor of large and small lake herring subjected to fed and starved feeding treatments over the 225-d laboratory experiment. Values are means  $\pm$  SEs of four replicates per treatment group.

clines being strongly influenced by body size and feeding ration (Figure 3). Although the initial mean Fulton condition factor did not differ significantly among treatments ( $F_{3,15} = 2.69$ ,  $P = 0.09$ ), condition declined for large and small starved fish (0.80 and 0.68, respectively) after d 75. Between days 75 and 150, mean Fulton condition factor began to decline for fish in both fed treatments, regardless of body size. Final mean Fulton condition factor was greater for large and small fed lake herring (0.68 and 0.65, respectively) than large and small starved fish (0.49 and 0.45, respectively). Large body size and fed treatments had a significantly greater condition factor over the duration of the experiment ( $F_{1,15} = 4.59$ ,  $P = 0.05$ ;  $F_{1,15} = 79.01$ ,  $P < 0.01$ , respectively). No significant interaction term was identified among body size and food ration treatments for Fulton condition factor over the experiment ( $F_{3,15} = 1.36$ ,  $P = 0.27$ ).

#### Proximate Composition

Declines in the crude lipid content of lake herring varied among the experimental treatments (Figure 4a). At the onset of the experiment, the mean crude lipid content of large lake herring (12.9%) was significantly greater ( $F_{3,15} = 32.43$ ,  $P < 0.01$ ) than that of small lake herring (9.5%). By day 75, mean crude lipid content declined in large starved fish (10.9%) but remained relatively constant in all other groups. The mean crude lipid content of small starved individuals (6.0%) also declined by day 150. The final mean crude lipid content was greater in large and small fed treat-

ments (9.8% and 7.3%, respectively) than that for large and small starved fish (5.7% and 5.8%, respectively). Over the experiment, large body size and fed treatments had a significantly greater crude lipid content than small body size and starved treatments ( $F_{1,15} = 26.81$ ,  $P < 0.01$ ;  $F_{1,15} = 77.05$ ,  $P < 0.01$ , respectively). No significant interaction term was identified among body size and food ration treatments for crude lipid content during the experiment ( $F_{3,15} = 3.91$ ,  $P = 0.07$ ).

Crude protein content differed among body size and feeding ration treatments over the experiment (Figure 4b). There were no large differences in crude protein content among groups on days 0 and 75 of the experiment; however, on day 150, an increase in crude protein content was observed for large and small fed lake herring (17.2% and 16.4%, respectively). This contrast increased by the final sampling period, where the mean crude protein content of large and small fed treatments (17.7% and 17.1%, respectively) was greater than that of large and small starved fish (15.4% and 13.2%, respectively). Over the experiment, fish in large body size and fed treatments had a significantly greater crude protein content than small body size and starved treatments ( $F_{1,15} = 10.36$ ,  $P < 0.01$ ;  $F_{1,15} = 99.79$ ,  $P < 0.01$ , respectively). No significant interaction term was identified among body size and food ration treatments for crude protein content ( $F_{3,15} = 3.99$ ;  $P = 0.06$ ).

The gross energy content of lake herring in starved treatments declined over the duration of the experiment, while the that of fed fish remained

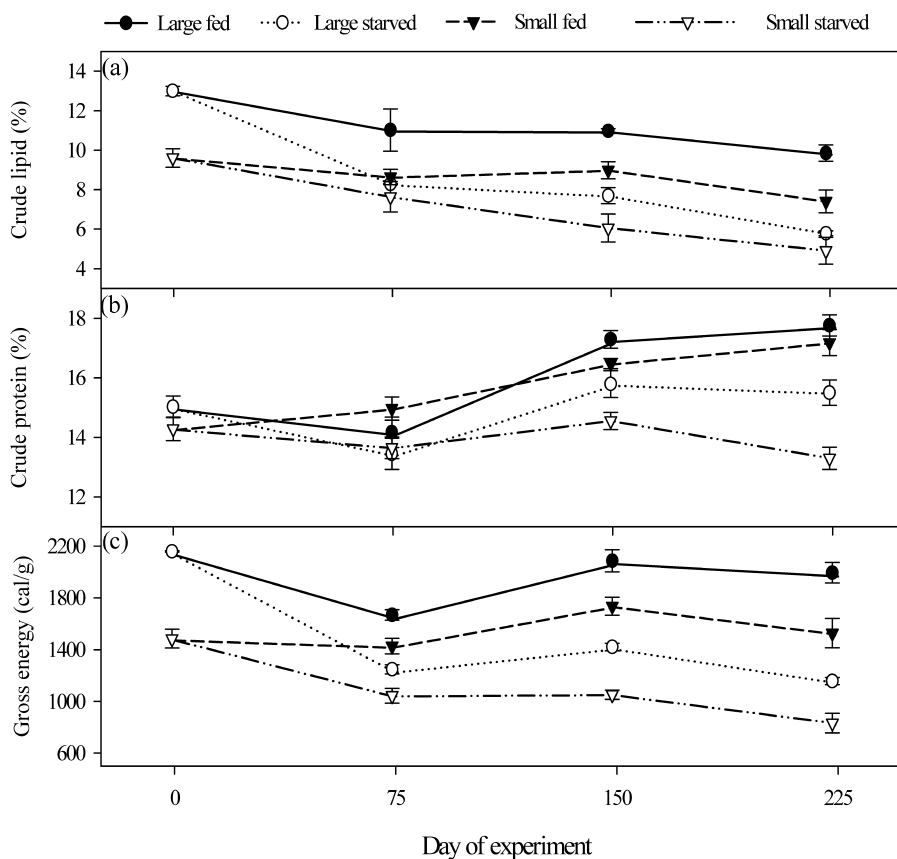


FIGURE 4.—Proximate-composition variables of large and small lake herring subjected to fed and starved feeding treatments over the duration of the 225-d experiment: (a) crude lipid content, (b) crude protein content, and (c) gross energy content. Variables are reported as a percent of wet weight except for gross energy content, which is reported as cal/g of wet weight. Values are means  $\pm$  SEs of four replicates per treatment group.

relatively constant (Figure 4c). Initial gross energy content was significantly greater ( $F_{3,15} = 38.93$ ,  $P < 0.01$ ) in large (2,132 cal/g) than in small fish treatments (1,454 cal/g). After day 75, small fed lake herring (1,395 cal/g) had a greater mean gross energy content than large starved fish (1,216 cal/g). By day 150, the mean gross energy content of fish in large and small fed treatments (2,058 and 1,706 cal/g, respectively) was greater than that of large and small starved fish (1,390 and 1,018 cal/g, respectively). Gross energy content remained relatively constant over the remainder of the experiment between feeding ration treatments, regardless of body size. Over the experimental period, large body size and fed treatments had significantly greater effects on mean gross energy content than small body-size and starved treatments ( $F_{1,15} = 74.00$ ,  $P < 0.01$ ;  $F_{1,15} = 249.93$ ,  $P < 0.01$ , respectively). No significant interaction term was

identified among body size and food ration treatments for gross energy content ( $F_{3,15} = 0.79$ ,  $P < 0.40$ ).

#### Comparison of Surviving versus Dead Fish

The experimental parameters for lake herring that survived the 225-d study were significantly different than those of fish that died (Table 2). Surviving lake herring were larger in body size, the mean TL of survivors being significantly greater than that of dead fish ( $F_{1,3} = 107.5$ ,  $P < 0.01$ ). In addition, the wet weight of surviving lake herring was also significantly greater than the wet weight of fish that died ( $F_{1,3} = 5.87$ ,  $P = 0.05$ ). In contrast, mean condition factor did not differ significantly between surviving and dead lake herring ( $F_{1,3} = 0.52$ ,  $P = 0.50$ ). Mean crude lipid content was significantly greater for surviving lake herring than for those that died ( $F_{1,3} = 15.93$ ,  $P$

TABLE 2.—Body size, physiological condition, and energy stores of large and small lake herring subjected to fed and starved feeding treatments grouped according to whether fish survived and died over the 225-d experimental period. Values are the means and ranges of four replicates per treatment group. See text for an explanation of the treatments.

Variable	Fate of fish	Large fed	Large starved	Small fed	Small starved
Total length (mm)	Survived	120.3 (117–125)	104.2 (101–107)	95.4 (91–103)	85.5 (79–93)
	Died	97.4 (89–102)	90.0 (87–92)	72.7 (63–80)	66.2 (62.3–74.0)
Wet weight (g)	Survived	11.9 (10.1–15.5)	5.6 (5.0–6.5)	5.7 (4.6–7.3)	2.9 (2.0–4.0)
	Died	7.2 (5.3–9.8)	4.9 (3.7–6.5)	3.2 (2.5–4.9)	2.4 (1.7–4.0)
Fulton condition factor	Survived	0.67 (0.61–0.79)	0.49 (.48–0.52)	0.65 (0.60–0.67)	0.45 (0.41–0.50)
	Died	0.61 (0.76–0.50)	0.55 (0.40–0.64)	0.60 (0.44–0.78)	0.40 (0.37–0.49)
Crude lipid (%)	Survived	9.7 (8.7–10.8)	5.6 (5.4–5.9)	7.4 (7.0–8.7)	4.8 (3.5–6.6)
	Died	7.9 (5.6–10.0)	4.0 (3.4–4.5)	6.3 (5.7–7.4)	3.3 (2.9–4.2)
Crude protein (%)	Survived	17.7 (17.0–18.4)	15.4 (14.6–16.4)	17.1 (16.5–18.4)	13.2 (12.2–13.9)
	Died	14.1 (13.1–15.2)	13.2 (12.7–14.4)	14.8 (12.7–16.0)	13.4 (12.9–14.2)
Gross energy (cal/g)	Survived	1,966 (1,856–2,200)	1,124 (1,069–1,177)	1,497 (1,241–1,705)	799 (607–933)
	Died	1,339 (1,244–1,421)	816 (626–898)	1,280 (1,072–1,408)	658 (505–810)

= 0.01). Although mean crude protein content was not significantly different between lake herring that survived than those that died ( $F_{1,3} = 2.67$ ,  $P = 0.15$ ), the fish that survived the experiment had significantly greater mean gross energy content than those that died ( $F_{1,3} = 28.46$ ,  $P < 0.01$ ).

### Discussion

Our results indicated that the overwinter mortality of juvenile lake herring was strongly influenced by body size and the availability of food resources. During the winter period, fish in large and fed treatment groups experienced less mortality than small and starved individuals, and the mean body size of fish that survived the experiment period was greater than those that died. In addition, the final length-frequency distributions of the small fed and starved fish became more positively skewed and unimodal as a result of the mortality of the smallest individuals. This pattern of size-dependent mortality has also been observed in other fishes. Meyer and Griffith (1997) found that large body size had a positive effect on the winter survival of age-0 rainbow trout *Oncorhynchus mykiss* and brook trout *Salvelinus fontinalis*. Sutton and Ney (2001) reported that the length-frequency distribution of age-0 striped bass *Morone saxatilis* shifted from bimodal to unimodal over the winter because small fish were lost from the age-0 cohort. Similar findings have also been reported for field studies which evaluated the size distributions of age-0 fishes before and after winter (Toneys and Coble 1979; Henderson et al. 1988; Post and Evans 1989).

Based on the differences between lake herring that survived and those that died over the exper-

iment, winter mortality appeared to have resulted from the depletion of energy stores. The cause of mortality was likely due to the fish's inability to maintain basal activities, such as ionoregulation (Savitz 1971). Further, the proximate composition of lake herring suggests that smaller individuals were more susceptible to this form of mortality. At the onset of winter, Fulton condition factor and the crude lipid, crude protein, and gross energy contents of large fish (regardless of feeding ration treatment) were greater than for small individuals. In contrast, small fish have been shown to devote greater energy to somatic growth than to the elaboration of lipid reserves (Henderson et al. 1988). During our study, this difference increased as winter progressed, with the greatest declines in physiological condition and energy stores occurring for small and starved lake herring. Because of the allometric relationship associated with body size and basal metabolism (Pierce et al. 1980; Toneys and Coble 1979; Cunjak 1988; Cargnelli and Gross 1997; Hurst et al. 2000), small lake herring exhibited greater depletions in energy reserves over the winter period than larger conspecifics.

The differential changes in lake herring proximate-composition parameters provided further evidence of a size-dependent utilization of energy stores and winter mortality. The crude lipid content of lake herring declined in all experimental treatments during the initial 75 d of the study, while differences in crude protein content among large and small lake herring did not occur until day 150. Because of their high specific energy value (8,000 cal/g) and digestibility, lipids are the primary energy store used by fish and thus are the first energy source to be metabolized (Halver 1976; Pierce et

al. 1980; Post and Evans 1989). The utilization of proteins, which do not offer high energy content (5,700 cal/g), indicates the loss of lipid reserves (Savitz 1971; Kirjasniemi and Valtonen 1997). Because proteins cannot endogenously sustain the metabolic demand of fish for long periods of time (Brody 1945; Chang and Idler 1960; Jobling 1980), fish must maintain a baseline level of lipid stores to survive periods of low energy intake (Hoar 1983). As a result, lake herring in small body size and starved treatments were more likely to exhaust their lipid reserves prior to the end of winter and suffer mortality during this time period.

Our study results are similar to the extent of winter mortality observed for other age-0 fishes. Oliver et al. (1979) indicated that smaller age-0 smallmouth bass *Micropterus dolomieu* were more likely to deplete energy reserves below a critical level during winter, resulting in the mortality of these fish. Similarly, Hunt (1969) and Smith and Griffith (1994) found that small age-0 brook trout and rainbow trout exhibited greater winter mortality than larger conspecifics. Johnson and Evans (1991) examined the effects of ad libitum feeding and starvation on the winter survival of age-0 white perch *Morone americana* and found that starved fish of the smallest size-class exhibited the highest mortality. However, no mortality occurred for fish maintained at the ad libitum feeding treatment. These studies illustrate the importance of body size and food ration to winter survival and support the findings of our experiment.

Although the winter mortality of small juvenile lake herring was significantly greater than that of large individuals, other studies have reported higher mortality rates than we observed in our study. Henderson et al. (1988) determined that, on average, the smallest component of the age-0 sand smelt *Atherina boyeri* cohort was lost over a 240-d winter period. Similarly, Thompson et al. (1991) observed that small starved age-0 Colorado pikeminnow *Ptychocheilus lucius* experienced 100% overwinter mortality over a 210-d winter period. During the winter in Lake Superior, age-0 lake herring may exhibit greater mortality than we observed in our laboratory study. Long-term exhaustion of energy stores in small starved lake herring led to a large decline in wet weight and body condition and an overall emaciated appearance. Further, these fish were lethargic and unresponsive to daily tank maintenance. Chick and Van Den Avyle (2000) found that age-0 striped bass at a similar physiological state were less responsive to simulated predator attacks. Reduced respon-

siveness has also been reported for age-0 capelin *Mallotus villosus* (Elliott and Leggett 1998). Low body condition can also lead to a compromised immune system, resulting in the inability of weakened individuals to resist pathogens and parasites (Lemly and Esch 1984; Hockett and Munduhl 1988; Tort et al. 1998). Because small lake herring in our study exhibited low condition by the end of the experiment, these fish may be more susceptible to predation and disease in a natural environment. In addition, recruitment models of Lake Superior lake herring populations have indicated that extended winter periods negatively affect recruitment (Hoff 2004). As a result, the mortality rates observed in our laboratory study may underestimate those actually experienced in wild populations.

One caveat of our experimental design was the diet used in the study for feeding juvenile lake herring. We used *Artemia* nauplii instead of a food source native to Lake Superior because culturing large quantities of natural food types would not have been logistically possible. *Artemia* nauplii have a comparable body size to the zooplankton prey of lake herring during winter (Link et al. 1995), and can be intensively cultured in a laboratory environment (Bengtson et al. 1991). Although *Artemia* nauplii are not an optimal diet for juvenile lake herring (Pangle et al. 2003), all fish in the laboratory experiment were fed the same, so the observed trends should reflect those of lake herring populations in Lake Superior. However, the realized level of mortality and mortality rate may be higher or lower than we observed in our study. Further, the gross energy content observed in wild Lake Superior lake herring was similar to those found in our experimental fish (Vondracek et al. 1996), indicating that *Artemia* nauplii were similar to natural zooplankton prey as an energy source. Therefore, we do not believe that the use of *Artemia* nauplii significantly influenced the results of this laboratory experiment.

The results of this study suggest that winter mortality may influence recruitment variability in Lake Superior lake herring populations. Knowledge of this mechanism can be used to enhance the accuracy of population dynamics models in forecasting annual and regional recruitment variability in lake herring stocks. However, additional research is required to fully understand the causes of winter losses for this species, particularly focusing on the potential impact of predation and disease that may result from poor physiological condition and low energy stores. This information

would shed further light on the importance of winter survival as a mechanism that may regulate year-class strength and limit the recovery of depressed lake herring stocks in Lake Superior.

### Acknowledgments

We thank W. Mattes and G. Fischer for assistance in the collection and incubation, respectively, of the lake herring eggs used in this study. We would also like to acknowledge the efforts of L. Jefferson, J. Bobb, W. Shull, and the personnel at the Purdue University Aquaculture Research Laboratory in fish rearing and maintenance. Constructive comments on earlier drafts by J. DeWoody, P. Brown, D. Hayes, and three anonymous reviewers improved this manuscript. The experimental procedures used in this research were approved by the Purdue University Animal Care and Use Committee as protocol 01-023. This publication is a result of work sponsored by the Michigan Sea Grant College Program. The project number is M/PD-6, under federal grant NA76RGO133 from the National Sea Grant, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and from the State of Michigan. The U.S. Government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation appearing hereon. This research was approved for publication as manuscript 17623 by the Purdue University Agricultural Research Program.

### References

- Anderson, E. D., and L. L. Smith. 1971. Factors affecting abundance of lake herring (*Coregonus artedii* Lesueur) in western Lake Superior. *Transactions of the American Fisheries Society* 100:691-706.
- Anderson, R. O., and R. M. Neumann. 1996. Length, weight, and associated structural indices. Pages 447-482 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Baldwin, N. S., R. W. Saalfeld, M. A. Ross, and H. J. Buettner. 1979. Commercial fish production in the Great Lakes 1867-1977. Great Lakes Fishery Commission Technical Report No. 3, Ann Arbor, Michigan.
- Bengtson, D. A., P. Léger, and P. Sorgeloos. 1991. Use of *Artemia* as a food source for aquaculture. Pages 225-285 in R. A. Browne, P. Sorgeloos, and C. N. A. Trotman, editors. *Artemia* biology. CRC Press, Boca Raton, Florida.
- Brody, S. 1945. *Bioenergetics and growth*. Reinhold, New York.
- Cargnelli, L. M., and M. R. Gross. 1997. Fish energetics: larger individuals emerge from winter in better condition. *Transactions of the American Fisheries Society* 126:153-156.
- Carlander, K. D. 1945. Growth, length-weight relationship and population fluctuations of the tullibee *Leucichthys artedii tullibee* (Richardson), with reference to the commercial fisheries, Lake of the Woods, Minnesota. *Transactions of the American Fisheries Society* 73:125-136.
- Chang, V. M., and D. R. Idler. 1960. Biochemical studies of sockeye salmon during spawning migration. XII. liver glycogen. *Canadian Journal of Biochemistry and Physiology* 38:553-558.
- Chick, J. H., and M. J. Van Den Avyle. 2000. Effects of feeding ration on larval swimming speed and responsiveness to predator attacks: implications for cohort survival. *Canadian Journal of Fisheries and Aquatic Sciences* 57:106-115.
- Craig, J. F. 1980. Growth and production of the 1955 to 1972 cohorts of perch, *Perca fluviatilis* L., in Windermere. *Journal of Animal Ecology* 49:291-315.
- Cunjak, R. A. 1988. Physiological consequences of overwintering in streams: the cost of acclimatization. *Canadian Journal of Fisheries and Aquatic Sciences* 29:279-288.
- Dryer, W. R., and J. Beil. 1964. Life history of lake herring in Lake Superior. *Fisheries Bulletin* 63:493-530.
- Edsall, T. A., and T. J. DeSorcie. 1999. The growth-temperature relation and preferred temperatures of juvenile lake herring. *Archive of Hydrobiology, Special Issues: Advances in Limnology* 57:335-342.
- Elliott, J. K., and W. C. Leggett. 1998. Larval condition and vulnerability to predation: an analysis based on mixed-prey experiments. *Canadian Journal of Fisheries and Aquatic Sciences* 55:626-630.
- Folch, J., M. Lees, and G. H. S. Stanley. 1957. A simple method for the isolation and purification of total lipids from animal tissues. *Journal of Biological Chemistry* 226:497-509.
- Gotceitas, V., D. A. Methven, S. Foster, and J. A. Brown. 1999. Effects of body size and food ration on overwinter survival and growth of age-0 Atlantic cod, *Gadus morhua*. *Environmental Biology of Fishes* 54:413-420.
- Halver, J. E. 1976. Formulating practical diets for fish. *Journal of the Fisheries Research Board of Canada* 33:1032-1039.
- Helrich, K., editor. 1990. *Official methods of analysis of the Association of Official Analytical Chemists*, 15th edition. Association of Official Analytical Chemists, Inc., Arlington, Virginia.
- Henderson, P. A., R. H. Holmes, and R. N. Bamber. 1988. Size-selective overwintering mortality in the sand smelt, *Atherina boyeri* Risso, and its role in population regulation. *Journal of Fish Biology* 33:221-233.
- Hile, R. 1936. Age and growth of the cisco, *Leucichthys artedii* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. U. S. Bureau of Fisheries 48, *Bulletin* 19:211-317.

- Hoar, W. S. 1983. General and comparative physiology, 3rd edition. Prentice-Hall, Englewood Cliffs, New Jersey.
- Hockett, C. T., and N. D. Munduhl. 1988. Effects of black spot disease on thermal tolerance and condition factor of three cyprinid fishes. *Journal of Freshwater Ecology* 5:67–72.
- Hoff, M. H. 2004. Biotic and abiotic factors related to lake herring recruitment in the Wisconsin waters of Lake Superior, 1984–1998. *Journal of Great Lakes Research* (In press.).
- Hunt, R. L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. *Journal of Fisheries Research Board of Canada* 26:1473–1483.
- Hurst, T. P., E. T. Schultz, and D. O. Conover. 2000. Seasonal energy dynamics of young-of-the-year Hudson River striped bass. *Transactions of the American Fisheries Society* 129:145–157.
- Jobling, M. 1980. Effects of starvation on proximate chemical composition and energy utilization of plaice, *Pleuronectes platessa* L. *Journal of Fish Biology* 17:325–334.
- Johnson, T. B., and D. O. Evans. 1991. Behavior, energetics, and associated mortality of young-of-the-year white perch (*Morone americana*) and yellow perch (*Perca flavescens*) under simulated winter conditions. *Canadian Journal of Fisheries and Aquatic Sciences* 48:672–680.
- Kinnunen, R. E. 1997. The effect of Lake Superior surface water temperature on lake herring (*Coregonus artedii*) length and year-class strength. Doctoral dissertation. Michigan Technological University, Houghton.
- Kirjasniemi, M., and T. Valtonen. 1997. Size-dependent over-winter mortality of young-of-the-year roach, *Rutilus rutilus*. *Environmental Biology of Fishes* 50: 451–456.
- Lemly, A. D., and G. W. Esch. 1984. Effects of the trematode *Uvulifer ambloplites* on juvenile bluegill, *Lepomis macrochirus*: ecological implications. *Journal of Parasitology* 70:475–492.
- Link, J., J. H. Selgeby, M. H. Hoff, and C. Haskell. 1995. Winter diet of lake herring (*Coregonus artedii*) in western Lake Superior. *Journal of Great Lakes Research* 21:395–399.
- McCormick, J. H., B. R. Jones, and R. F. Syrett. 1971. Temperature requirements for growth and survival of larval ciscos (*Coregonus artedii*). *Journal of Fisheries Research Board of Canada* 28:924–927.
- Meyer, K. A., and J. S. Griffith. 1997. First-winter survival of rainbow trout and brook trout in the Henrys Fork of the Snake River, Idaho. *Canadian Journal of Zoology* 75:59–63.
- Miranda, L. E., and W. D. Hubbard. 1994. Length-dependent winter survival and lipid composition of age-0 largemouth bass in Bay Springs Reservoir, Mississippi. *Transactions of the American Fisheries Society* 123:80–87.
- Oliver, J. D., G. F. Holetton, and K. E. Chua. 1979. Over-winter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperatures. *Transactions of the American Fisheries Society* 108:130–136.
- Pangle, K. L., T. M. Sutton, and P. B. Brown. 2003. Evaluation of practical and natural diets for juvenile lake herring. *North American Journal of Aquaculture* 65:91–98.
- Pierce, R. J., T. E. Wissing, J. G. Jaworski, R. N. Givens, and B. A. Megrey. 1980. Energy storage and utilization patterns of gizzard shad in Acton Lake, Ohio. *Transactions of the American Fisheries Society* 109:611–616.
- Post, J. R., and D. O. Evans. 1989. Size-dependent mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1958–1968.
- Post, J. R., and B. Prankevicius. 1987. Size-selective mortality in young-of-the-year yellow perch (*Perca flavescens*): evidence from otolith microstructure. *Canadian Journal of Fisheries and Aquatic Sciences* 44:1840–1847.
- Savitz, J. 1971. Effects of starvation on body protein utilization of bluegill sunfish (*Lepomis macrochirus* Rafinesque), with a calculation of caloric requirements. *Transactions of the American Fisheries Society* 100:18–21.
- Selgeby, J. H. 1982. Decline of lake herring (*Coregonus artedii*) in Lake Superior: an analysis of the Wisconsin herring fishery, 1936–78. *Canadian Journal of Fisheries and Aquatic Sciences* 39:554–563.
- Selgeby, J. H., W. R. MacCallum, and D. V. Swedberg. 1978. Predation by rainbow smelt (*Osmerus mordax*) on lake herring (*Coregonus artedii*) in western Lake Superior. *Journal of the Fisheries Research Board of Canada* 35:1457–1463.
- Shuter, B. J., and J. R. Post. 1990. Climate, population viability, and zoogeography of temperate fishes. *Transactions of the American Fisheries Society* 119: 314–336.
- Smith, R. W., and J. S. Griffith. 1994. Survival of rainbow trout during their first winter in the Henrys Fork of the Snake River. *Transactions of the American Fisheries Society* 123:747–756.
- Smith, S. H. 1956. Life history of lake herring of Green Bay, Lake Michigan. U.S. Fish and Wildlife Service, Fishery Bulletin 109(57):87–138.
- Sutton, T. M., and J. J. Ney. 2001. Size-dependent mechanisms influencing first-year growth and winter survival of stocked striped bass in a Virginia main-stream reservoir. *Transactions of the American Fisheries Society* 130:1–17.
- Thompson, J. M., E. P. Bergersen, C. A. Carlson, and L. R. Kaeding. 1991. Role of size, condition, and lipid content in the overwinter survival of age-0 Colorado squawfish. *Transactions of the American Fisheries Society* 120:346–353.
- Toneys, M. L., and D. W. Coble. 1979. Size-related, first winter mortality of freshwater fishes. *Transactions of the American Fisheries Society* 108:415–419.
- Tort, L., F. Padros, J. Rotllant, and S. Crespo. 1998. Winter syndrome in gilthead sea bream *Sparus au-*

- rata*—immunological and histopathological features. *Fish and Shellfish Immunology* 8:37–47.
- Vondracek, B., B. D. Giese, and M. G. Henry. 1996. Energy density of three fishes from Minnesota waters of Lake Superior. *Journal of Great Lakes Research* 22:757–764.
- Wicker, A. M., and W. E. Johnson. 1987. Relationship among fat content, condition factor, and first-year survival of Florida largemouth bass. *Transactions of the American Fisheries Society* 116:264–271.
- Zar, J. H. 1999. *Biostatistical analysis*, 4th edition. Prentice-Hall, Upper Saddle River, New Jersey.