The schooling and foraging ecology of lake herring (*Coregonus artedi*) in Lake Opeongo, Ontario, Canada

S.W. Milne, B.J. Shuter, and W.G. Sprules

Abstract: We used a combination of suspended gill nets and hydroacoustics to investigate the schooling behaviour of lake herring (*Coregonus artedi*) in Lake Opeongo, Ontario, Canada. Lake herring form schools during the day but are dispersed at night and this change occurs at a light threshold of roughly 0.04 lx. Schools range in maximum linear dimension from 100 to 2300 cm with the majority under 1000 cm. The light threshold for school formation is well below that at which their principal predator, lake trout (*Salvelinus namaycush*), are able to detect prey. This suggests that schooling may provide advantages in addition to predator avoidance. We observed that lake herring stomachs were fuller during the day than at night, indicating that schooling herring forage more efficiently during the day than individual herring do at night. Furthermore, herring stomach fullness increased with school size, suggesting that schooling enhances foraging opportunities for individual members. We speculate that this is due either to social facilitation of feeding when herring are in the presence of conspecifics, or to corporate vigilance, or "many eyes", which allows individual fish to spend less time being alert to predators and more time feeding.

Résumé : Nous avons utilisé une combinaison de filets maillants suspendus et de techniques hydroacoustiques pour étudier le comportement de formation de bancs chez le cisco de lac (*Coregonus artedi*) au lac Opeongo, Ontario, Canada. Les ciscos forment des bancs durant la journée et se dispersent durant la nuit; le changement se produit à un seuil de lumière d'approximativement 0,04 lx. Les bancs varient en taille linéaire maximale de 100 cm à 2300 cm, la plupart atteignant moins de 1000 cm. Le seuil lumineux pour la formation des bancs est bien inférieur à celui auquel leur prédateur principal, le touladi (*Salvelinus namaycush*), est capable de détecter ses proies. Cela laisse croire que la formation de bancs peut procurer des avantages autres que l'évitement des prédateurs. Nous avons observé que les estomacs de ciscos de lacs sont plus remplis durant le jour que la nuit, ce qui indique que les ciscos en bancs s'alimentent plus efficacement le jour que les ciscos solitaires la nuit. De plus, les estomacs sont d'autant plus remplis que les bancs sont de grande taille, ce qui indique que la formation de bancs multiplie les occasions de s'alimenter pour les membres du banc. Nous pensons que cela est dû ou bien à une facilitation sociale de l'alimentation lorsque les ciscos sont en présence de poissons de même espèce, ou alors à la vigilance collective par des « yeux multiples » qui permet à chaque poisson de passer moins de temps en alerte vis à vis de ses prédateurs et plus de temps à s'alimenter.

[Traduit par la Rédaction]

Introduction

Traditional models of fish production incorporate system-wide averages of predator and prey abundances and assume that spatial arrangements of organisms are homogeneous within a constant environment (Brandt et al. 1992). They also assume that foraging is a stochastic process, with predators randomly encountering prey that are randomly distributed in the water. In fact, prey fish distributions are often patchy in space and time, and in particular, schooling is so prevalent in fish that there must be clear adaptive advantages to such spatial behaviour (Biette and Geen 1980; Huth and Wissel 1992). Fish aggregated in schools experience lower rates of encounter with predators and are less likely to be consumed if attacked because predators quickly become satiated and remaining prey can escape (Pitcher 1986). "Many eyes" within a school increase the chance of detecting predators (Turner and Pitcher 1986) as well as locating food (Pitcher 1986; Peuhkuri et al. 1995). On the other hand, there are costs to schooling, such as increased visibility to

Received 25 November 2004. Accepted 10 January 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 4 June 2005.
J18425

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Can. J. Fish. Aquat. Sci. **62**: 1210–1218 (2005) doi: 10.1139/F05-030

predators (Pitcher 1986; Litvak 1993) and increased intraspecific competition.

The lake herring (*Coregonus artedi*; hereinafter referred to as herring) is a schooling planktivore common in colder lakes throughout Canada and the northern United States (Scott and Crossman 1973). It was introduced into Lake Opeongo, Ontario, in 1948 to improve the quality of sport fishing for lake trout (*Salvelinus namaycush*) (Matuszek et al. 1990) and quickly established as the primary prey species for lake trout. Herring continue to act as an important link between lake trout and the zooplankton community within the system (Matuszek et al. 1990).

The purpose of our investigation was to identify the mechanisms responsible for the schooling behaviour of herring in Lake Opeongo. Do they school solely as a function of predator avoidance or are there other benefits to the behaviour? In particular, we will test the hypotheses that (*i*) schooling increases with light intensity in the water column, (*ii*) schools disperse when light levels are too low for lake trout to detect herring, (*iii*) herring feed more at night, when the threat of predation is minimized, and (*iv*) food consumption increases with school size.

Methods

Study lake

Lake Opeongo is the largest lake in Algonquin Provincial Park, Ontario, with an area of approximately 5500 ha and over 115 km of shoreline. It is an oligotrophic lake with a maximum depth of 53 m and a mean depth of 14.8 m. The lake comprises three major basins that are similar in area and joined by small channels. The fish community in the lake is quite diverse, but our study focuses on the lake herring and its principal predator, the lake trout. Our work was concentrated within a 800 m × 800 m site in the northern section of the south basin, where water depth was approximately 20 m.

Fish sampling

One of the principal objectives of our study was to obtain information on the size and spatial distribution of herring schools in the wild. Such observations are difficult to make because the size and spatial position of fish schools can change on a continuous basis and over relatively large spatial scales. One option is the use of suspended gill nets that provide a "snapshot" of the spatial pattern of fish at the time of capture as well as a sample of fish for species identification and relevant individual measurements. On the other hand, such invasive techniques could affect apparent school size and shape, and gillnet dimensions would have to match the typical size and spatial patterning of schools for accurate assessments to be made. Hydroacoustic techniques provide better spatial coverage, but calibration of the signal to the size and species of fish encountered is challenging, and determination of school dimensions depends on the nature of edge-detection algorithms used in analysis of the acoustic data. In this study we chose to use simultaneous gillnetting and hydroacoustics to acquire information on herring schools, and to seek concordance in the results from these approaches for making the most rigorous estimates of school metrics.

Gillnetting

Gillnetting was done during 1999 in spring (10–23 May), when thermal stratification was weak, in summer (1–17 July), when thermal stratification was strong, and in fall (8–18 October), immediately before overturn. Monofilament gill nets 45 m long and 2.2 m high and of 25-mm stretched mesh were used to capture herring. Nets were deployed at chosen depths by using a combination of float and anchor lines. The site was sampled twice during each sampling day — in midafternoon (from 1201 to 1745) and at night (from 2300 to 0422 of the same or following day). These sampling periods were chosen to obtain the greatest contrast in schooling behaviour and to avoid the crepuscular period of transition. During each sampling period, nets were set at three sampling depths: 4 and 16 m plus the depth of the 12 °C isotherm, the preferred temperature for lake herring (Rudstam and Magnuson 1985). The depth of the 12 °C isotherm ranged from 1 to 11 m through the study period. Nets were set 150 m apart parallel to one another and perpendicular to the maximum fetch in the basin. Nets were set for short periods — a mean of 34 min during the day and 21 min during the night — to minimize deterioration of herring stomach contents and minimize the number of schools caught at any one time. Over the study period, a total of 120 nets were set (6–8 per depth × 3 depths × 2 periods (day and night) × 3 seasons).

Immediately after the nets were retrieved, the individual fish were removed and their position in the net was marked with a unique identification number. Stomachs were removed and preserved in 10% formalin. The body was kept for later sex determination and measurement of fork length, total length, and mass without the stomach.

Hydroacoustic analysis of herring spatial patterns

A hydroacoustic survey of the northern section of the South Arm of Lake Opeongo was completed during the day and night in May, July, and October. Survey transects were designed to overlap the suspended gill nets both spatially and temporally. A split-beam Simrad EY500 120-kHz hydroacoustic system with an ES120-7° transducer was used to record the spatial distribution and behavioural changes of individual herring as well as herring schools. All acoustic data were analyzed using EchoView® version 1.51.20 (Sonardata Tasmania Pty Ltd. 1999*a*) and schools were detected and measured using the School Detection Module within EchoView® (Sonardata Tasmania Pty Ltd. 1999*b*). Schools were detected by the downward-looking acoustic transducer as the survey vessel proceeded along a sampling track. The School Detection Module defines a school by including only pixels that are (*i*) contiguous and (*ii*) have an echo strength that exceeds a minimum (we used –55 dB). The software computes the height of a school at the random point of encounter by subtracting the depth of the shallowest pixel in the defined region from the depth of the deepest one. The length of the school is computed by using the Pythagorean theorem to subtract the global positioning system (GPS) coordinates of the first pixel encountered in the defined region from the last one encountered. EchoView® can correct for errors in these dimensions caused by school depth and position relative to the acoustic beam, but we did not do this because Lake Opeongo is shallow enough that beam angles are narrow and pulse lengths are short and errors are consequently small.

There are two common fish species in Lake Opeongo that form schools — lake herring and yellow perch (*Perca flavescens*). However, yellow perch are not known to occupy the cool-water pelagic regions that we sampled in this study, and none was captured in the gill nets. We thus assumed that any acoustically detected schools were of herring. Only those single targets with strengths between –47 and –37 dB were included in the nighttime analyses because Love's (1977) general equation predicts that fish in the size range of Lake Opeongo herring (minimum, mean, and maximum total length = 99, 144.5, and 175 mm, respectively) have target strengths in this range.

Spatial analysis of herring captured in gill nets

All captured fish were wedged in the meshes of the gill net and hence the direction of travel prior to capture could be ascertained. Most fish aggregations were composed of fish travelling in a uniform direction, but in some instances aggregations included individuals oriented in both directions. In all such cases the majority of fish were oriented in one direction and the few fish directed the opposite way strongly overlapped the main aggregation. We interpreted these aggregations to represent single schools of fish that encountered the net from one direction but with a few stray individuals reversing direction, perhaps in the confusion of the encounter with the gill net. We thus combined fish travelling in both directions in the calculation of an index of aggregation (IA). We used nearest neighbour (NN) analysis (Clark and Evans 1954) to assess the spatial aggregation of herring captured in the gill nets. The IA was computed as R_A/R_E, where R_A is the observed median NN distance and R_E is the median NN distance expected for a random set of locations within the net. A random set of point locations within an unbounded two-dimensional area has an expected IA of 1.0, a uniform set has an expected IA greater than 1.0 (maximum 2.16), and a clumped set has an expected IA less than 1.0 (minimum approaches 0). We constructed the following procedure to identify observed IAs that differed statistically from that expected for a random set of fish locations. First, we determined the distribution of R_E, the expected distance for random observations, for each possible sample size (total number of fish captured in a net) by randomly and independently placing a number of points equal to the sample size in a simulated 4500 cm × 220 cm rectangle (the dimensions of gill nets), computing the median NN distance and repeating this procedure 10 000 times. Then, for each observed NN value we estimated the probability that it came from a random spatial distribution as the proportion of R_E values in the simulated distribution (for the appropriate sample size) that exceeded the observed NN value. This probability was then assigned to the IA value calculated from the observed NN value. Observed values based on fewer than six fish were not included in this analysis because we found the simulated R_E distributions to be unstable for samples sizes less than six, even after 10 000 iterations. We did not need to make additional corrections for edge effects in these analyses (Boots and Getis 1988) because our numerically derived estimates of R_E already included the edge effects associated with a bounded area equal in size to that of our gill nets.

Given the wide variety of spatial patterns of herring in the gill nets, we decided to calculate the maximum linear dimensions of captured herring schools using the following algorithm. For each gill net we computed the median Euclidean distance between each fish and all others in the net. We then removed from the analysis those fish for which the median distance was in the upper 10% of the set of distances (to avoid situations such as a single fish distant from an aggregation inflating school size). The maximum median distance for the remaining fish was then computed as the length of the school in the net. This calculation will overestimate school size if there is more than one clump of fish in a net and will underestimate school size if there is a single, well-prescribed clump of fish (because outliers are removed).

Lake trout tracking

Eight adult lake trout were implanted with ultrasonic tags (CTT-83-2, Sonotronics, Tuscon, Arizona, USA) and released back into the South Arm of Lake Opeongo during the spring of 2000. During August 2000, each tagged trout was followed over a 12- to 20-h period, with geographic position and time recorded every 10–12 min. Light intensity was continuously measured at the surface using HOBO® HLI light loggers (Onset Computer Corporation, Bourne, Massachusetts, USA). Movement ($m \cdot min^{-1}$) of lake trout was determined by measuring the Euclidean distance and time elapsed between sequential coordinate locations. Observations were classified into nighttime (surface light intensity <0.04 lx) and daytime (>320 lx), the mean speed was computed for each day and night observation period, and a Kruskal–Wallis test was used to test the hypothesis that mean speed was the same for daytime and nighttime. All lake trout tracking data were provided from unpublished data by L. Flavelle (Department of Biology, University of Waterloo, Waterloo, ON N2L 3G1) and T. Janoscik (Department of Biology, University of Toronto at Mississauga, Mississauga, ON L5L 1C6).

Physical and zooplankton sampling

A light meter (Hobo® HLI) was used to continuously measure surface light intensity at a stationary point in the sampling site every minute during the sampling period. Three additional light meters were submerged at approximately the same depths as the gill nets. This information, in addition to estimates of the light-absorption coefficient taken from vertical profiles with a light meter (LI-192SB quantum sensor, LI-COR Inc., Lincoln, Neb., USA) every 2 weeks, was used to estimate the light intensity at depth over the time the nets were set. Temperature and dissolved-oxygen profiles were measured at 1-m intervals at the site (Model 58 oxygen/temperature meter, Yellow Springs Instruments Inc., Yellow Springs, Ohio, USA). These temperature data were used to establish the depth of the 12 °C isotherm.

Zooplankton samples were pumped from the water column at each of the three netting depths during both daytime and nighttime sets. Forty litres of water were pumped through a 110 μm mesh sieve, the sieve was rinsed into a jar, and the sample was preserved in a 2%–4% sugar-buffered formalin solution.

Processing of fish stomachs and zooplankton

We randomly selected a minimum of 10 herring stomachs (or all stomachs if fewer fish were captured) from each of the gillnet samples used in the aggregation analysis. The contents of each stomach were placed in a 53 μm mesh filter, rinsed to remove residual preservative, and added to a "plankton shaker" (after Alden et al. 1982) for gentle filtering through four sequential Nitex sieves of 500, 400, 202, and 53 μm mesh. After the shaking was completed, the filters were removed and the contents rinsed into preweighed aluminium drying pans. After filtering, the contents of the 53 and 202 μm mesh filters were rinsed into separate drying pans and the contents of the 500 and 400 μm mesh filters were pooled into a third pan. Samples were dried at 60 °C for 20–28 h, removed, and weighed on a Sartorius 1207 MPZ digital balance. Total dry mass of the herring stomach contents was calculated by summing the masses of individual fractions.

Entire zooplankton samples pumped from the water column were rinsed through a 53 μm mesh sieve, dried, and weighed as above.

Statistical analysis of prey consumed

There was no evidence of a relationship between fish size and mass of stomach contents (separate analyses of covariance (ANCOVA) of stomach contents among gill nets with fish length as the covariate for each of the six season / time of day combinations), probably because the size range of herring in Lake Opeongo is quite narrow (111–150 mm for fish used in this ANCOVA). Hence, we ignored fish size in all subsequent analyses.

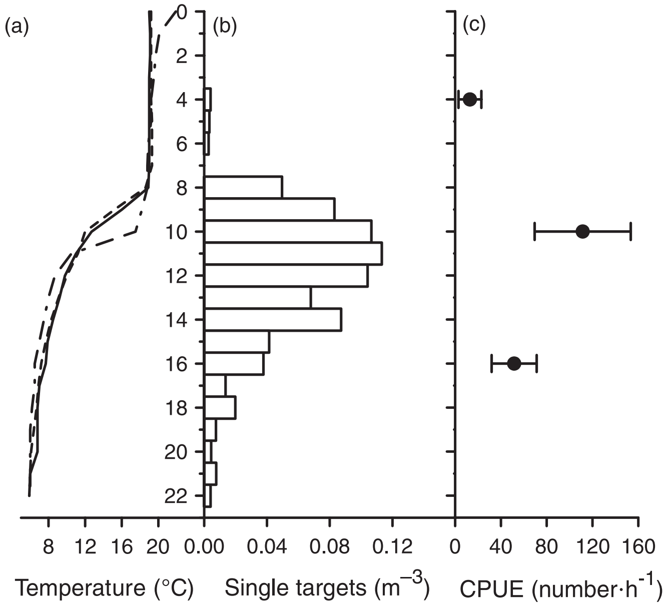
To test whether the mass of prey consumed by herring differed between daytime and nighttime, we conducted a separate single-factor analysis of variance for each season. We used the median stomach contents from each gill net that caught at least six fish as an independent replicate and time (day versus night) as the treatment. Parametric assumptions were confirmed by a Bartlett's homogeneity of variance test and a normal plot of residuals (Zar 1999).

If the herring respond to prey concentrations in their habitat, we predict that there will be an association between the mass of food in the stomachs and the concentration of zooplankton in the water column. We conducted separate ANCOVAs for the daytime and nighttime data. For each ANCOVA, the dependent variable was the median stomach contents in a gill net, the treatment was the period (May, July, October), and the covariate was the zooplankton concentration in the water column adjacent to the gill nets.

Prey consumption by herring in relation to school size

We assumed that there was a direct relation between the size of a herring school and the number of fish captured when the school encountered a gill net. For this assumption to be reasonable, schools must fit within the area of the gill nets used, and the length:height ratio of schools must be fixed (otherwise schools with the same number of fish could intersect nets differently). We confirmed these assertions by regressing school height on length using the 136 daytime herring schools identified by the School Detection Module in the EchoView® software, and compared school dimensions with gillnet dimensions (see Results). To quantify the relation between school size and mass of prey consumed, we regressed the median stomach contents of 10 fish randomly selected from a gill net (or all fish if there were fewer than 10) against the number of fish in a gill net. Using all fish in the nets avoids the need to make subjective decisions about the boundaries of individual schools, given the range of spatial patterns found in the nets, thus making ours a conservative test.

Fig. 1. Comparison of acoustic and gillnet estimates of lake herring (*Coregonus artedi*) abundance in relation to water temperature during nighttime sampling in July. The acoustic data (*b*) are single-target counts of herring-sized objects at various depths over an 891-m long transect through the gillnet sampling area from 2225 to 2247 on 11 July 1999. The gillnet data (*c*) are given as catch per unit effort (CPUE); mean ± standard error) for herring caught in all nets set during the nights of 11–13 July 1999 and temperature profiles (*a*) were taken during the day or night on the same dates.

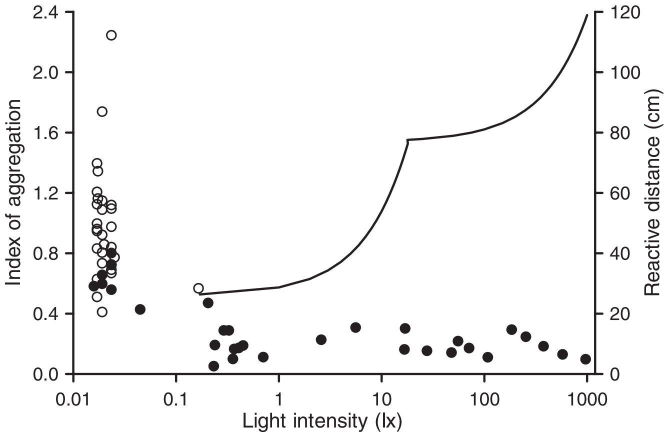


Results

Schooling behaviour of herring

There is good agreement between hydroacoustic and gillnet estimates of herring abundance in the water column (Fig. 1). Acoustic data are most accurate below approximately 5 m and the data indicate a continuous range of single acoustic targets in the herring target strength range. The only fish caught by the corresponding gill net were herring, and the catches per hour at 10 and 16 m are in roughly the same ratio as the abundances of acoustic targets at these depths (Fig. 1). In a similar October comparison, acoustic and gillnet estimates both indicate that fish are abundant at 16 m, but other net sets were at depths too shallow for reliable comparison with acoustic data. In May the gillnet estimates indicated that all fish were in shallow water and none were at 16 m, and although the acoustic estimates are not reliable at the shallow depths, they do indicate no fish at 16 m. As in July, the only fish caught by gill nets in May and October were herring. We take these observations to be a strong

Fig. 2. Indices of aggregation (IA) for lake herring in the gill nets in relation to light intensity. Each point represents a single net catch of at least seven fish. Solid circles represent gill nets in which the IA was statistically different from random and open circles represent gill nets in which the aggregation was random. The reactive distances for lake trout (*Salvelinus namaycush*) from Vogel and Beauchamp (1999) are also plotted.



indication that hydroacoustic and gillnet estimates of fish abundance show good agreement and that our single target strength criterion of –47 to –37 dB corresponds to herring.

Spatial analyses of gillnet catches indicated that fish were typically spread out from one another during the night but formed schools during the day (Fig. 2). At light levels above 0.04 lx, the IA was statistically different ($p < 0.05$) from random in all instances and indicated that fish were aggregated at the scale of the gill net. At light levels below 0.04 lx, 82% of the IAs were statistically indistinguishable from random. These observations suggest that herring schools form or break up at a threshold light intensity, and this is confirmed by repeated acoustic observations of school dissipation indicating that this phenomenon occurs predictably at dusk and that it happens quite quickly (S.W. Milne, unpublished data). Our data suggest that this light threshold is at or near 0.04 lx, which is much greater than for other similar-sized species — 0.000 03 lx for *Engraulis mordax* (Hunter and Nicholl 1985) and 0.000 011 lx for *Trachurus symmetricus* (Hunter 1968). A model of lake trout reactive distance (Vogel and Beauchamp 1999) dependent on light intensity and turbidity (average turbidity for Lake Opeongo is 1.17 nephelometric turbidity units; A. Skinner, Ontario Ministry of Natural Resources, 300 Water Street, Peterborough, ON K9J 8M5, personal communication) indicates that the visual acuity of lake trout, which feed intensively on herring, does increase rapidly as light intensity goes up. However, this increase does not begin until around 4 lx (Fig. 2), two orders of magnitude higher than the threshold intensity for herring schooling (approximately 0.04 lx; Fig. 2). Furthermore, during the day (surface light intensity >319 lx), when herring form schools, lake trout swim faster than they do at night (<0.4 lx; Kruskal–Wallis test, χ^2 = 64.2, p < 0.0001), but this increase in swimming speed does not occur until light intensities are much higher than those that evoke schooling (Fig. 3) and intensities are similar to those that permit a rapid increase in reactive distance according to the Vogel–Beauchamp model (Fig. 2).

Fig. 3. Displacement rates of adult lake trout fitted with ultrasonic tags in relation to light intensity at the lake surface. Each point on the graph is the average displacement rate for all individual fish detected during a tracking session. The plotted line is a transformed linear regression fitted to displacement rate versus log light intensity.

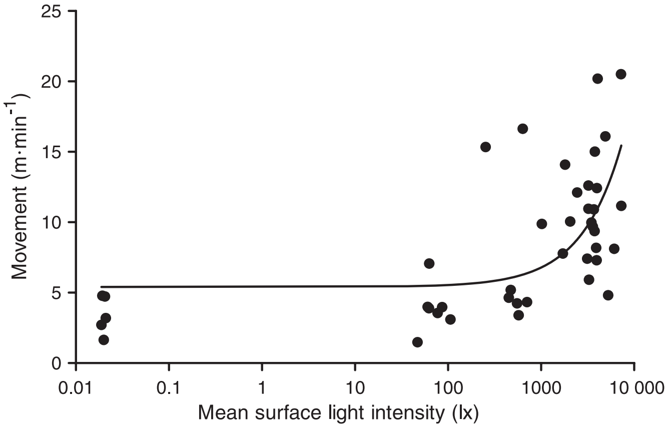
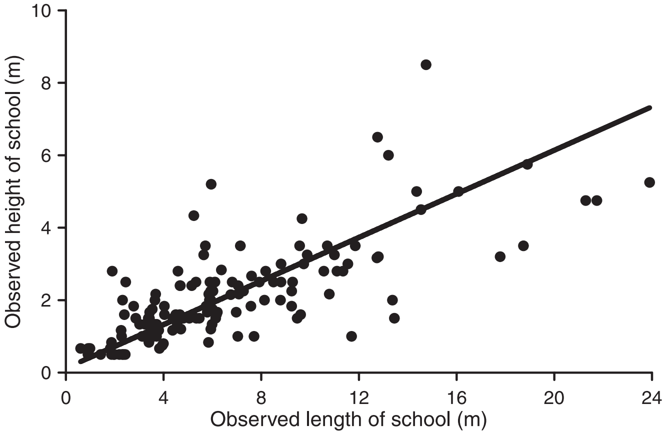
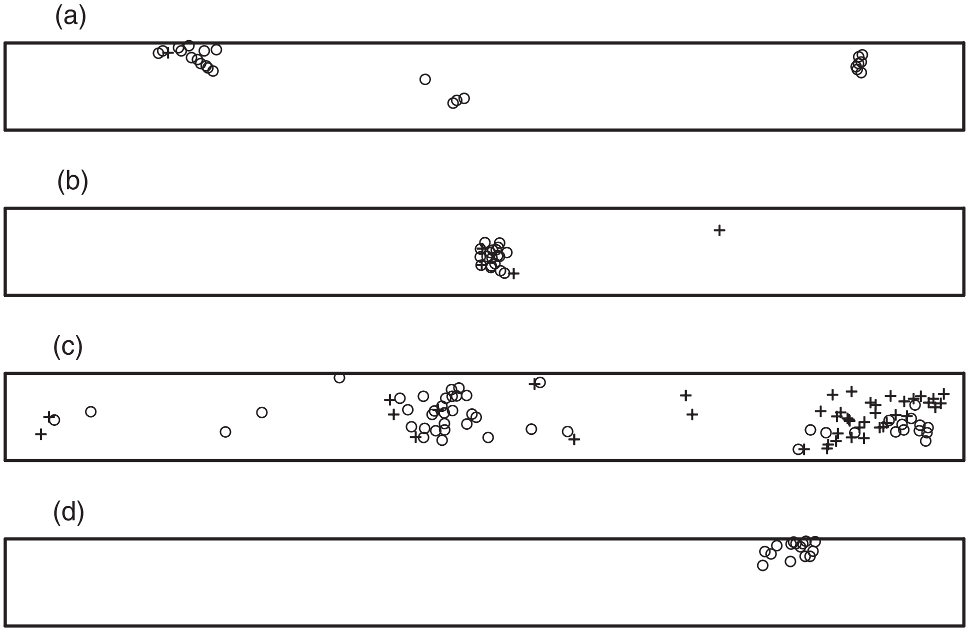


Fig. 4. The sizes of lake herring schools determined from EchoView® School Detection Module analyses of daytime acoustic data from all sampling seasons. Median length and height of the schools are 5.8 and 1.8 m, respectively. The slope of the geometric mean regression (plotted line) is 0.30 with an intercept of 0.12.



Acoustic measurements of herring school size across all sampling seasons indicate that school height increases with length (Fig. 4). A geometric mean regression (Sokal and Rohlf 1995) fitted to these data passes very close to the origin (intercept = 0.12) indicating a fixed height:length ratio for all schools regardless of size (slope = 0.30). This indicates that schools are roughly circular disks and we assume that they are elliptical in cross section. Noting that median school length and height are 5.8 and 1.8 m, respectively, the cross-sectional area of the median size of a school that encounters a gill net would be 8.2 m^2. Gillnet sets were 45 m long and 2.2 m high so that the median-sized herring school would occupy 8.3% of a gill net. The majority of schools (81%) were less than 10 m long and would individually occupy less than 24% of the net area, assuming the elliptical model with an aspect ratio of 0.3. These observations indi-

Fig. 5. Patterns of lake herring distributions from selected daytime gillnet sets. The rectangles represent the 45 m × 2.2 m dimensions of the gillnet sets (not to scale). Each symbol represents a single fish, and + and ○ indicate opposite directions of travel upon encounter with the net; *a* and *b* show data from individual net sets from May, *c* shows data from July, and *d* shows data from October.

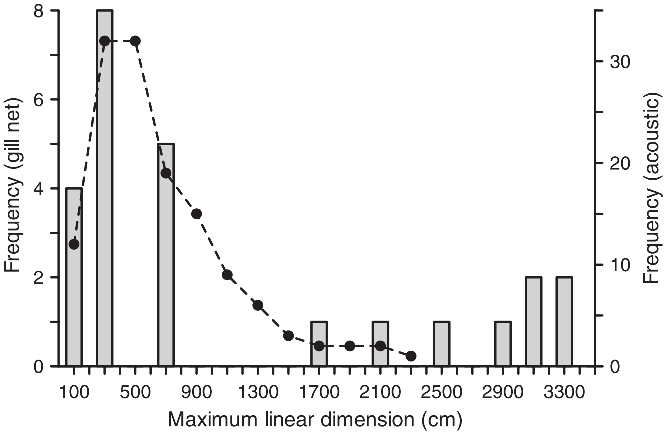


cate that the majority of herring schools would be entirely captured within the gill nets we used.

We observed a wide variety of patchy distributions of herring in daytime gillnet sets (Fig. 5). Multiple schools varying in size were caught in some nets (Fig. 5*a*), while in others it appeared as if a single school was captured entirely within the net (Fig. 5*b*). School boundaries were more difficult to define in some instances (Fig. 5*c*), whereas in others only a part of a school may have been captured (Fig. 5*d*). Some schools consisted entirely of fish travelling in the same direction at the time of capture (Fig. 5*d*), whereas others contained fish travelling in opposite directions (Fig. 5*c*). As described in Methods, we consider any distinct aggregation of fish, regardless of travel direction, to be a single school. Our net sets were of short duration (mean of 31 min) and a high proportion of the 63 daytime sets caught fewer than seven or no fish (38 sets, or 60% of the total), This indicates low herring concentrations relative to the sampling area of the nets and hence a very small chance that two schools coming from opposite directions would encounter the net at the same place.

There is good agreement between the length of herring schools measured acoustically and the length of those measured in the gill nets (Fig. 6). The number of schools measured in gill nets (25) was much lower than the number measured acoustically (135), but the distributions of maximum linear dimensions were very similar, with the most frequent school lengths ranging from approximately 100 to 800 cm (68% of all gillnet schools and 70% of all acoustic schools). The largest school measured acoustically was 2300 cm long, but there were six “schools” from gill nets that were longer — up to 3300 cm. However, in all six instances there was more than one clump of fish in the gill net (e.g., Figs. 5*a* and 5*c*), so these are actually overestimates of school size. Had it been objectively possible to measure these clumps individually, the right tail of the gillnet distribution would have ended up much closer to the main size mode (Fig. 6). In general, herring schools range in length from roughly 100 to 2300 cm, the majority being shorter than approximately 1000 cm (Fig. 6).

Fig. 6. Frequency distribution of lengths of lake herring schools in each of the 25 daytime gillnet sets. A distribution of the lengths of daytime schools from acoustic analysis is superimposed.



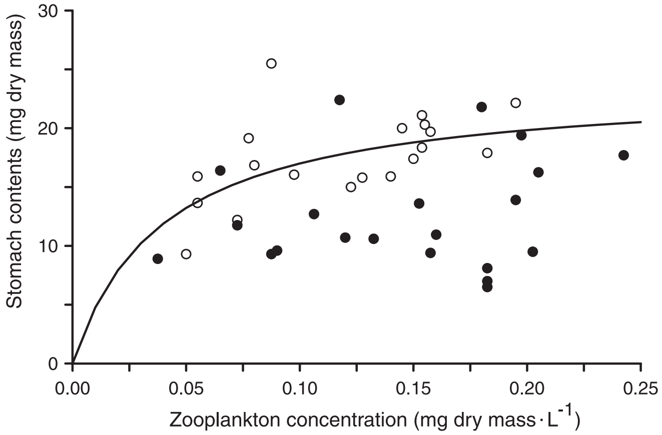
Diel patterns in herring stomach contents

Stomach contents of herring consisted primarily of zooplankton with rare occurrences of chironomid pupae in the spring night samples. Results indicate that the stomachs of herring captured during the day contained more prey than those captured at night during the May (analysis of variance, $F_{[1,16]} = 28.96$, $p < 0.001$) sampling period. This trend also existed for July ($F_{[1,8]} = 0.91$, $p = 0.37$) and October ($F_{[1,10]} = 1.13$, $p = 0.31$) but was not statistically significant. A meta-analysis based on combining the probabilities from

Fig. 7. Relationship between median stomach contents and the zooplankton concentration in the water column for day (○) and night (●). For the daytime data the statistically significant association between variables is summarized using a simple saturation curve forced through the origin:

$$Y = \frac{23.8(3.3)\,X}{0.04(0.02) + X}, \quad r^2 = 0.67$$

where Y is median stomach contents, X is zooplankton concentration, and r^2 is explained variation, and mean coefficients (with standard errors) are shown. No statistical relationship exists for the nighttime data.



these three independent tests (Sokal and Rohlf 1995) supports the overall conclusion that herring consume more food during the day than at night ($p = 0.0006$). Stomach-clearance simulations based on evacuation-rate models for other cold-water species such as sockeye salmon (*Oncorhynchus nerka*), coho salmon (*Oncorhynchus kisutch*), and rainbow trout (*Oncorhynchus mykiss*; He and Wurtsbaugh 1993) are consistent with the hypothesis that nighttime feeding is minimal and that nighttime stomach contents consist of remains of prey consumed during the day.

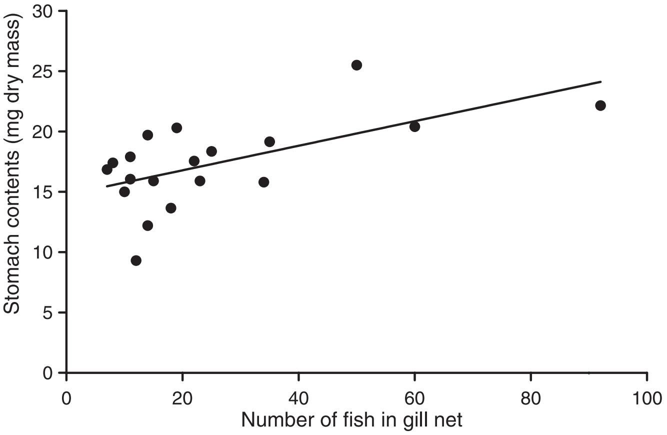
Stomach contents in relation to available prey

Analyses of daytime patterns in median stomach contents among sampling periods using zooplankton concentration in the water column as a covariate indicated a strong effect of zooplankton concentration (ANCOVA, $F_{[1,15]} = 9.7$, $p = 0.007$) that is similar across sampling periods ($F_{[2,15]} = 1.4$, $p = 0.28$). Slopes of the stomach contents – zooplankton concentration regressions were homogeneous across sampling periods (ANCOVA, $F_{[2,13]} = 0.19$, $p = 0.83$). A parallel analysis of the nighttime data indicated no effect of zooplankton concentration (ANCOVA, $F_{[1,17]} = 3.1$, $p = 0.1$). Combining data across all periods (Fig. 7) indicates a relationship between our index of daytime herring consumption and zooplankton concentration, while at night no such relationship is evident.

Prey consumed in relation to school size

On the basis of the fixed aspect ratio for herring schools (Fig. 4) and the fact that most schools fit well within the area of a gill net, we considered the number of fish found in a gill net to be directly related to the number of fish in the school that encountered the net. This measure of school size was related to the mass of prey found in the stomachs of fish within the school (Fig. 8) and indicated that fish in large schools have fuller stomachs than those in small schools.

Fig. 8. Relationship between lake herring stomach contents and the number of fish captured in a gill net. Each point is the median stomach contents of 10 randomly sampled fish (or all fish if fewer than 10 were caught) from daytime gillnet catches. The least squares linear regression is shown: $Y = 14.7 + 0.1X$, $r^2 = 0.37$, $p < 0.001$, where Y is stomach contents, X is the number of fish in the school, r^2 is the explained variance, and p is the probability associated with the statistical test of linearity.



Discussion

Our observations are consistent with the hypothesis that lake herring form schools at daybreak as light intensity increases in the water column. This overall trend is expected because vision is the primary sense used by fish to maintain schools (Whitney 1969; Bohl 1980; Partridge and Pitcher 1980), although some evidence suggests that chemical and olfactory cues may also be important (Krause 1993). Bohl (1980) suggested, specifically for herring, that light levels at night are simply too low for them to visually maintain contact with schooling neighbours.

Given that herring form schools, what are the ecological forces that make schooling behaviour advantageous? Our data suggest that schooling increases feeding efficiency for herring, an additional benefit to the increase in predator-avoidance abilities that is typically the product of schooling behaviour. If schooling were primarily a predation-defence mechanism (Magurran et al. 1985; Turner and Pitcher 1986) for herring in Lake Opeongo, we would expect their schools to disperse when light levels fall to those at which the visual acuity of lake trout, their primary predator, is reduced.

However, our data indicated that herring continue to school at light levels well below those predicted by Vogel and Beauchamp's (1999) reaction-distance model for lake trout. Our tracking data for lake trout also show that lake trout movement decreases greatly at night and that this decrease occurs at light intensities greater than those required to evoke school dispersal. These observations suggest that there must be advantages to schooling in addition to simple predator avoidance, and that herring persist in schools when predation risk is low.

What advantage is there for herring to remain in schools even when it is too dark for their predators to see them? We observed that herring stomachs are fuller during the day than at night. We also observed that the mass of prey in stomachs increases with prey abundance during the day but there is no such association at night. These observations demonstrate that schooling herring forage more efficiently during the day than individual herring feeding singly at night. They also raise the possibility that herring may even derive a feeding benefit from schooling. This is supported by our observation that individual herring from large schools had more prey in their stomachs than those from small schools. Similar observations have been made for other fish species (Pitcher and Magurran 1983; Morgan 1988; Ranta and Kaitala 1991) and it has also been noted that individual schooling fish have greater growth rates than solitary ones, possibly as a result of higher food-assimilation efficiency in the absence of isolation stress (Davis and Olla 1992; Peuhkuri et al. 1995).

Social facilitation may account for this pattern of increased per-capita foraging success in schools — the willingness of any individual to feed increases with the number of other individuals feeding (Baird et al. 1991; Ryer and Olla 1992). Alternatively, the corporate vigilance, or many-eyes, hypothesis has been proposed: as school size increases, individual fish need to spend less time being alert to predators and can thus devote more time to feeding (Bertram 1978; Morgan 1988). The many-eyes hypothesis also predicts that the effective reaction distance of a school will grow with the school diameter, hence greatly augmenting the ability of individual fish to locate patchy food resources (Pitcher et al. 1982; Baird et al. 1991; Ryer and Olla 1992). Our observation that herring schools in Lake Opeongo vary widely in length (the majority fall between approximately 300 and 1000 cm but some were as long as 2300 cm) even though large schools appear to offer a significant advantage to their members is consistent with the “optimal group size” ideas of Parrish and Edelstein-Keshet (1999). These authors point out that because many costs and benefits are associated with variation in school size (e.g., small schools offer little defence against predators, while very large schools can be easily detected by predators and individual school members may be resource-limited as a result of intraspecific competition), one would expect the optimal group size to fluctuate seasonally, daily, or hourly depending on predation pressure, food-patch size, individual hunger, and breeding stage.

Acknowledgements

We are grateful to the Harkness Laboratory for Fisheries Research for the loan of field equipment and logistic support. The Natural Sciences and Engineering Research Council of Canada and the Ontario Ministry of Natural Resources provided funding for this research.

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