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ON THE APPLICATION OF HYDROACOUSTIC METHODS TO ANALYSES OF THE DISTRIBUTION AND ABUNDANCE OF PELAGIC FISHES: BEHAVIORAL AND STATISTICAL CONSIDERATIONS.

by

Alfred R. Appenzeller

A thesis presented to the Faculty of Graduate Studies and Research of McGill University in partial fulfilment of the requirements for the Degree of Doctor of Philosophy.

Department of Biology,
McGill University,
Montreal, Quebec, Canada

August 1992

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McGill University
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Memorandum

TO: Shelley
Thesis office

DATE: February 19, 1993

FROM: Susan Gregus
Graduate Studies Coordinator
#6403 (Room W4/1)

SUBJECT: Alfred Appenzeller

As requested, a shorter version of Alfred Appenzeller's thesis title.

Application of hydroacoustics to analyses of distribution and abundance of fishes.

Iron will's demanded of
The student of the Way-
It's always on the mind.
Forget all - good, bad.
Suddenly it's yours.

-Rijunkyoku, 11 c

ABSTRACT

This thesis explored the influence of fish behavior and distribution on the accuracy and precision of quantitative estimates of fish biomass and abundance as assessed by hydroacoustic techniques. Rainbow smelt (Osmerus mordax), a pelagic fish known to undertake diel vertical migrations and to exhibit changes in aggregation intensity associated with these movements was used as the model species for this study. The diel vertical migrations of smelt resulted in their potential inaccessibility to the acoustic gear. To obviate this problem a model of the diel migration of smelt based on observations of their behavioral responses to ambient light and water temperatures, was developed and used to time acoustic estimates of fish biomass and abundance to periods when they were unbiased by inaccessibility. Acoustic surveys were then conducted to evaluate the direct influence of fish aggregation on estimates of fish abundance, and to examine the effect of changes in fish distributions on the statistical validity of acoustic analyses. Comparative acoustic surveys, conducted when fish were schooled and dispersed, showed abundance was underestimated by up to 50 % when schooling prevailed. The influence of changes in the level of fish patchiness, induced by diel schooling, on the statistical precision of acoustic estimates of abundance and biomass was found to be insignificant. Cluster sampling, a robust approach to the inherent problems of transect sampling created by autocorrelated data series was applied to acoustic data for the first time and its effectiveness was assessed. Cluster sampling yielded estimates of biomass and of abundance that were more precise than were estimates based on the traditional approach of analyzing complete transects.

RÉSUMÉ

L'emphase du présent travail porte sur l'étude de l'influence du comportement des poissons et de leur distribution sur la précision d'estimés quantitatifs de biomasse et d'abondance effectués à l'aide de relevés hydroacoustiques. L'espèce choisie pour cet étude, l'éperlan arc-en-ciel (Osmerus mordax), est reconnue pour ses migrations verticales diurnes, qui affectent en même temps le taux d'aggrégation des individus. Ces migrations verticales ont été observées dans le milieu et induisaient un biais des estimés dû au fait que certains spécimens se trouvaient hors de portée du faisceau acoustique. Pour contourner ce problème, un modèle mathématique décrivant le comportement migratoire de l'éperlan a été mis au point. En utilisant ce modèle, la distribution verticale des poissons devenait corrélée avec l'intensité de la lumière ambiante, de même qu'avec la température de l'eau. Des estimés hydroacoustiques de biomasse et d'abondance ont par la suite été effectués, en tenant compte du patron de migration vertical décrit, pour

étudier l'effet de l'aggrégation des poissons sur la précision des estimés obtenus. La robustesse statistique des estimés a également été évaluée en fonction de divers patrons de distribution. Des relevés effectués lorsque les individus étaient dispersés par rapport aux moments ou il y avait aggrégation à l'intérieur de bancs, ont démontrés une sous-estimation de l'abondance de l'ordre de 50 % lorsqu'un comportement grégaire prévalait. Par contre, un changement dans le taux d'aggrégation des individus ne semblait pas influencer de façon significative la précision des estimés. La technique d'échantil-lonnage par groupements (cluster sampling) a été utilisée pour permettre de résoudre les problèmes d'auto-corrélation inhérent à l'échantillonnage de type continu effectué le long de radiales. Cette approche, utilisée pour la première fois sur des données hydroacoustiques, s'est révélée être plus performante pour augmenter la précision des estimés que les méthodes utilisées traditionnellement.

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CONTRIBUTIONS TO ORIGINAL KNOWLEDGE

1) I have provided empirical evidence to reject the null hypothesis that the vertical distribution of smelt is not influenced by light. I found that the diel migration patterns of this species covaried strongly and predictably with ambient illumination levels. The analysis of fish distribution developed, which uses statistical moments to characterize the dispersion and the preferred depth of fish in the water column, provided a new means of quantitatively assessing the proximate mechanisms influencing vertical migration. Differences in the predictability of vertical boundaries and strong asymmetry in the vertical distributions of smelt suggest that avoidance of high light levels is an important proximate factor regulating the observed diel vertical migrations of these fishes.

2) My thesis provides the first substantial empirical evidence that hydroacoustic fish population estimates are biased negatively when fish are aggregated in dense schools. These results demonstrate that the assumption of linearity between echo strength and fish abundance under all natural fish densities cannot be sustained, and that estimates of acoustic fish biomass and abundance must be corrected to account for effects of fish aggregation. Consequently, alternative methods of acoustic data calibration and/or

improvements in acoustic ensonification models of fish schools must be developed and applied.

3) I have demonstrated, for the first time, that cluster sampling when applied to acoustic transect sampling design results, on average, in higher sample precision than does sampling and analysis of whole transects. This appears to result from a more effective utilization of the information contained in such sample data. I conclude that it is desirable to incorporate within-transect data analysis into survey designs and statistical analysis by applying cluster analysis techniques.

I also demonstrated that spatial correlations in the distribution of fishes <u>in situ</u> may lead to biases in the calculation of sample errors when improper assumptions are made regarding the independence of consecutive within-transect samples. Failure to validate the assumption of independence and to apply appropriate modifications to survey design and for statistical analyses lead to considerable overestimation of sample precision.

4) I demonstrate, for the first time, that fish patchiness induced by diel schooling behavior, does not influence the sample precision of hydroacoustic transect sampling when compared with surveys where fish are dispersed. This demonstrates that changes in the small-scale patchiness

(within transects) does not impact on the estimation of sample errors when using transect sampling. The major influence on sample precision is therefore large-scale patchiness resulting in differences of fish abundance within the total survey area.

ACKNOWLEDGEMENTS

I thank Jim McKinney and Khelef Hamadou for assistance in the field. David Levy and George Rose introduced me to the hydroacoustic world. Bob Johnson (Canadian Biosonics) provided technical support and advice. Joe Rasmussen collaborated in quantitative in situ fish sampling using vertical nets.

Francois Gerlotto (Centre ORSTOM laboratoire d'hydobiologie-oceanoghraphie, Montpellier), Yvan Simard (Fisheries and Oceans Canada, Mont-Jolie) and Egil Ona (Institute of Marine Research, Bergen, Norway) provided valuable criticm of my hydroacoustic work.

Chris Chambers and Tom Miller gave valuable advice and criticism. I thank my committee members, Drs. J. Rasmussen and D. Kramer for their guidance and support and for playing a vital role in the direction that this research took. Finally, I am indebted to my supervisor, Dr. W.C. Leggett, whose confidence in me kept this work flowing.

I also wish to thank the people of Canada and The Federal Republic of Germany, who have enabled me to do this work by promoting international student exchange programs. Personal funding was provided by a scholarship from the Canadian Government Award.

In addition, travel subsidies provided by the Department of Biology (Mc Gill) and the Clemens Travel Fund enabled me to

present much of this work at national and international meetings.

GENERAL INTRODUCTION

The knowledge of the nature and causes of variability in the abundances of fishes in time, and in space, continue to be among the major unanswered questions in fisheries science. There is a great need for improved sampling methods with which to research these questions (Shepherd 1988; Peterman 1990). Hydroacoustic methods are increasingly used to quantify the distribution and abundance of fishes and invertebrates (Johannesson and Mitson 1983; MacLennan and Simmonds 1992). In the aquatic environment, where visibility is generally low (Blaxter 1980; Kirk 1983), acoustic methods offer several new possibilities for the exploration and sampling of aquatic organisms:
1) Acoustic surveys can be extended beyond the typical scale of conventional sampling techniques, since much larger areas can be searched rapidly (Johannesson and Robles 1977; Bailey and Simmonds 1990). 2) Acoustic sampling yields real time information on the vertical and horizontal distributions of organisms. Such information is very difficult to obtain from conventional catch based methods. 3) Acoustic sampling is non-destructive. This facilitates the replication of surveys.

There is substantial evidence that fish behavior influences the catchability of fish when conventional sampling methods are used (Blaxter and Parrish 1965; Leggett and Jones 1971; Peterman and Steer 1981; Morse 1989). There is also increasing evidence that such behavior may play a role in the ability to reliably assess fish abundance with hydroacoustic methods (Olsen et al. 1983a). Many observations on possible biases in the acoustic quantification of fish biomass and abundance, possibly related to fish behavior, have been obtained from comparisons of day and night survey data. However, to date these studies have often yielded contradictory results. A variety of hypotheses have been advanced to explain these differences (Croker and Mathisen 1972; Aglen 1983a; Soria and Freon 1991). It is clear that there is a need to quantify the influence of fish behavior, and especially diel changes in fish behavior and distribution, on the nature and quality of acoustic data.

My global objective in this thesis was to assess the influence of changes in the patterns of distribution and aggregation of fishes on the accuracy and precision of hydroacoustic estimates of fish abundance and biomass. One distributional characteristic, known to cause bias in hydroacoustic sampling, is changes in the vertical distribution of fish in the water column on a diel or longer time scale (Shotton and Bazigos 1984). Thus changes may cause fish to be partially, if not completely, inaccessible to the acoustic beam when they are located close to the bottom or in near-surface waters. Fish and invertebrates that migrate vertically in the water column therefore constitute a specific problem when designing acoustic surveys, especially when the extent of these movements cannot be assessed and/or major quantitative inaccuracies resulting from these movements are unnoticed (Thorne 1977).

A second component of fish behavior believed to be important to the assessment of abundance by both conventional and acoustic sampling techniques is changes in fish aggregation and schooling behavior (Croker and Mathison 1972; Aglen 1983a). The echointegration technique has become a standard method with which to quantify fish abundance and biomass (Johanneson and Mitson 1983; MacLennan 1990). An important assumption in these assessments is the existence of a linear relationship between hydroacoustic echo intensity and fish abundance at all fish densities (Foote 1983). This assumption has, however, been shown to be inadequate in situations in which fish aggregations are very dense and/or spatially large (Roettingen 1976; Burczinsky et al. 1990; Toresen 1991). An important question is therefore whether, in the daily routine of acoustic surveys corrections for these effects must be incorporated into the analysis of acoustically derived estimates of fish abundance and biomass.

Several attempts have been made to address this question via experiments conducted on caged fish, and to apply such results to natural schools and acoustic field surveys (Roettingen 1976). However, important differences in the behavior of fish in captivity, in the dimensions of fish schools in cages and in the wild, and other problems associated with extending the results of such approaches to field situations have caused the validity of such approaches to be questioned (Roettingen 1976; Johanneson and Losse 1977; Toresen 1991). On the other hand, data obtained from field based hydroacoustic studies may be influenced by uncontrolled sources of variability that may lead to problems in identifying the likely causes of observed differences from field observations (Soria and Freon 1991: Appenzeller and Leggett in press).

I therefore sought a natural system in which these problems could be minimized, and in which the basic problems created by changes in diel vertical migration and aggregation could be systematically investigated.

I also sought a system in which to assess the effects of changes in the spatial structure of target organisms on the statistical efficiency of surveys designed to quantify animal abundance. It is generally accepted that increases in the patchiness and heterogeneity of the distributions of animals result in a decrease in survey precision and efficiency (Downing 1979; Gerlotto and Stequart 1983; Krebs 1989). Patchiness may also produce failures to detect temporal trends in animal abundance when using survey data, since sample variances may increase with the degree of patchiness. Hence, the power to test hypotheses concerning changes in population size are lowered (Peterman 1990).

The question of patchiness has implications for survey designs and the analysis of acoustic data. Hydroacoustic methods yield sequential data collected along transect lines traversed by the survey vessel (Johanneson and Mitson 1983). Controversy and uncertainty abounds concerning the appropriate survey designs and the statistical analysis of such data (Shotton and Bazigos 1984; Jolly and Hampton 1990b). Eberhardt (1978) and Jolly and Hampton (1990a+b) have advocated random sampling of an array of possible transects, Nickerson and Dowd (1977) and Kimura and Lemberg (1981) have recommended continuous zig-zag patterns which cover the survey area most efficiently. Williamson (1982), on the other hand, found that when serial correlation of within-transect data is prevalent, sample errors could be seriously underestimated. There is, therefore, a need for a greater knowledge of appropriate survey designs and for statistical analyses which do not require the making of assumptions about <u>in situ</u> fish distributions when such knowledge is not available a priori.

My approach was to investigate these questions by studying a fish species with known patterns of diel distribution. I chose Lake Memphremagog, located on the Quebec-Vermont border, as the study site. The pelagic fish community of this lake is dominated by landlocked rainbow smelt (Osmerus mordax), a species described as light sensitive, that is known to exhibit diel changes in its vertical distribution (Ferguson 1965; Dembinski 1971; Heist and Swenson 1983). Acoustic quantification of the smelt population was greatly facilitated by the fact that adult smelt are restricted to the deeper sub-thermocline waters of the central basin of the lake during the summer months. Hence, they could be effectively acoustically surveyed during both day and night within a relatively short time period, and the surveys could be readily repeated throughout the season. Moreover, fish abundances within the survey area increased predictably during the season as individuals retreated from the warmer shallow basins of the lake during the summer. Thus hypotheses could be tested under varying levels of overall abundance in the survey area.

The following specific questions were addressed in my thesis:

A) What are the implications of diel vertical migrations for the acoustic assessment of fish populations?

B) Is vertical migration of fish regulated by environmental factors? There is evidence that environmental variables such as temperature (Sameoto 1984; Levy 1987; Rudstam and Magnuson 1985; Rose 1988) and light (Boden and Kampa 1967; Bary 1967; Melnikov et al. 1981; Levy 1990b) have a potential as predictors of fish distributions. Hence, I sought to test the null hypothesis that vertical distribution is not influenced by light and temperature.

C) Is it possible to model diel vertical migration, and to determine from such models a temporal window for acoustic fish surveys unbiased by differences in vertical fish distribution?

D) Does fish schooling impact the accuracy of survey results in light of potential systematic biases in acoustic abundance measurements?

E) Does fish schooling impact on the statistical precision of survey results in light of differences in fish patchiness?

F) Does serial correlation of acoustic data impose a problem to conventional survey design, and how can such problems with statistical assumptions and analysis of transect data be avoided?

I report my results in 4 chapters, each written in the form of an original manuscript for submission to a scholarly journal. The thesis is in accordance with The Guidelines Concerning Thesis Preparation, Faculty of Graduate Studies and Research, McGill University, which states:

"The candidate has the option, subject to the approval of the Department, of including as part of the thesis the text, or duplicated published text, of an original paper or papers. Manuscript-style theses must still conform to all other requirements explained in the Guidelines Concerning Thesis Preparation. Additional material (procedural and design data as well as descriptions of equipment) must be provided in sufficient detail (e. g. in appendices) to allow clear and precise judgement to be made of the importance and originality of the research reported. The thesis should be more than a mere collection of manuscripts published or to be published. It must include a general abstract, a full introduction and literature review and a final overall conclusion. Connecting texts which provide logical bridges between different manuscripts are usually desirable in the interest of cohesion. It is acceptable for theses to include, as chapters, authentic copies of papers already published, provided these are duplicated clearly and bound as an integral part of the thesis. In such instances, connecting texts are mandatory and supplementary explanatory material is

always necessary. Photographs or other materials which do not duplicate well must be included in their original form. While the inclusion of manuscripts co-authored by the candidate and others is acceptable, the candidate is required to make an explicit statement in the thesis of who contributed to such work and to what extent, and supervisors must attest to the accuracy of such claims at the Ph. D. Oral Defense. Since the task of the Examiners is made more difficult in these cases, it is in the candidate's interest to make the responsibilities of authors perfectly clear.

The complete text of the above must be cited in full in the introductory sections of any theses to which it applies."

All aspects of the research reported here, theoretical, practical, and field data collection, were conducted solely by myself. My supervisor, W.C. Leggett, who is co-author of the publications and of the presentations referred to below, assisted as advisor, co-worker, and editor. He also provided funds for research and conferences.

Chapter 2 which deals with the accuracy of acoustic estimates, has been accepted for publication:

Appenzeller A.R. and Leggett W.C. 1992 (in press). Bias in hydroacoustic estimates of fish abundance due to acoustic shadowing: Evidence from day-night surveys of vertically migrating fish." Can. J. Fish. Aquat. Sci. 00: 000-000.

The other 3 chapters are to be submitted to Can. J. Fish. Aquat. Sci. co-authored by my thesis supervisor W.C. Leggett.

Several aspects of my thesis research have been presented at national and international meetings:

Appenzeller A.R. and W.C. Leggett 1991. The role of sample scale and fish distribution for the assessment of sample error by hydroacoustic transect sampling. Canadian Conference For Fisheries Research, Guelph, Ont., January 1991.

Appenzeller A.R. and W.C. Leggett 1991. The influence of fish schooling on precision of hydroacoustic estimates of fish abundance. American Society for Limnology and Oceanography, Conference, Halifax N S., June 1991.

Appenzeller A.R. and W.C. Leggett 1991. Spatial distribution of pelagic fish (Osmerus mordax). The influence of light and temperature on diurnal and seasonal patterns. NATO Advanced Study Institute on Rhythms in Fish, Lennoxville Quebec, August 1991.

Appenzeller A.R. and W.C. Leggett 1992. Does fish schooling result in lower estimates of fish abundance as assessed by hydroacoustic methods? Canadian Conference For Fisheries Research, Halifax N.S., January 1992.

Appenzeller A.R. and W.C. Leggett 1992. The influence of fish schooling on accuracy and precision of hydroacoustic fish estimates. ICES Symposium on Fish Behavior in Relation to Fishing Operations, Bergen, Norway, June 11-13, 1992.

I also presented the following invited lectures during the course of my thesis :

Appenzeller A.R. 1991. Einfluß des Fischschwarmverhaltens auf Echolottechnische Fischbestandsaufnahmen. Fischerei Institut des Landes Baden-Württemberg, Langenargen, Germany, July 1991.

Appenzeller A.R. 1991. Einfluß des Fischschwarmverhaltens auf Echolottechnische Fischbestandsaufnahmen. EAWAG Institut für Seen- und Fischereiwissenschaften, Kastanienbaum, Switzerland, July 1991.

Appenzeller A.R. 1991. The influence of fish schooling on accuracy and precision of hydroacoustic fish estimates. Maurice Lamontagne Institute, Fisheries and Oceans Canada, Mt. Jolie, PQ, November 1991.

CHAPTER 1

DIEL VERTICAL DISTRIBUTION OF RAINBOW SMELT (**Osmerus mordax, Osmeridae**): EVALUATION OF MODELS OF FISH VERTICAL MIGRATION

ABSTRACT

This chapter examines diel changes in the vertical distribution patterns of rainbow smelt, Osmerus mordax, in Lake Memphremagog. I tested the null hypothesis that diel vertical movements of fish are not related to illumination levels. Fish depth distribution was measured using hydroacoustic techniques. Spatial patterns of fish were monitored from June to October (1988 & 1990) to account for seasonal changes. I rejected the null hypothesis. A strong relationship ($r^2 = 0.83$) relating light and fish depth was obtained for the upper boundary of the fish vertical distribution, as measured by the 95th percentile of fish depth. However, only a weak relationship ($r^2 = 0.14$) was observed for the lower 95th percentile fish depth. Fish depth was also related to the thermocline depth during the night and when water temperatures were >18 °C. The results suggest that models relating light and fish depth are applicable, with some limitations, to rainbow smelt. The vertical migrations of smelt were characterized as reflecting a strong avoidance of high light levels ($>0.1\ \mu W/cm^2$) with considerable variation in light levels (3-4 orders of magnitude) experienced by the whole fish population. Smelt appear to avoid environmental thresholds of temperature and light by aggregating at the upper boundary of their vertical distribution during day and night. A model of fish diel vertical migration based on these findings is presented.

INTRODUCTION

The occurrence of diel vertical migrations has been reported for a wide range of zooplankton and fish taxa (Woodhead 1966; Blaxter 1975; Lampert 1989). While no unifying theory explaining such behavior exists, a number of hypotheses have been advanced which relate to both its ultimate and proximate causes. The bioenergetic hypothesis proposes that diel vertical migrations are strategies for exploiting thermal gradients in the watercolumn thereby optimizing the energetic balance or growth of migrators (McLaren 1963; Brett 1971; Geller 1986; Wurtsbaugh and Neverman 1988). The predator avoidance hypothesis, in contrast, suggests that the avoidance of light related mortality is the ultimate cause of such behavior (Eggers 1978; Stich and Lampert 1981; Gliwicz 1986; Gabriel and Thomas 1988; Clark and Levy 1988). It has also been hypothesized that diel vertical migrations of fishes serve as a strategy for enhancing foraging success, and may also be directly related to the behavior of prey (Dembinski 1971; Turuk 1973; Begg 1976; Blaxter 1980; Janssen and Brandt 1980; Wurtsbaugh and Li 1985).

A common characteristic of many vertical migrations is that they exhibit a regular cyclicity, possibly driven by endogenous rhythms (Enright and Hamner 1967; Neilson and Perry 1990). Moreover, these cycles appear to match changes in ambient light levels. In fish that migrate vertically, these movements have been observed to correspond to the depth of equal light intensities (isolumes) during the dawn and dusk periods (Clarke and Backus 1964; Boden and Kampa 1967; Blaxter 1975). The daylight depth of occurrence of several fish species has been linked to water transparency thereby supporting the hypothesis that light is an important regulator of the depth of fish in the water column (Woodhead 1966; Dickson 1972; Isaacs et al. 1974; Kampa 1976; Levy 1990b). Additional evidence for light-mediated changes in the vertical distribution of fishes has been provided by the observation that fish move to shallower waters during solar eclipses. This observation also suggests that vertical migration is not a circadian process (Schüler 1954; Backus et al 1965; Kampa 1976).

Two main hypotheses have been advanced to account for the proximate causes of light as a regulator of diel migrations in fishes and invertebrates (Forward et al. 1984). The light-preference (LP) hypothesis suggests that the observed patterns of diel vertical migration in fish and invertebrates is an adaptation to specific low light levels (Laßleben 1952, Boden and Kampa 1967; Bohl 1980; Levy 1987). Using this hypothesis, Melnikow et al. (1981) proposed that if the light preference of the animal in question were known, their depth distribution could be predicted from a knowledge of factors determining illumination levels. The second hypothesis proposes that the behavior is a response to the rate of change in illumination (Ringelberg 1964; Bary 1967). This hypothesis, termed the RIC hypothesis, invokes conditioning of animals to the illumination level to which they were exposed during the previous period (Ringelberg 1964). The RIC hypothesis overcomes two problems associated with a light-adaptation mechanism. First the ability of animals to measure and track absolute light levels is not required; second, a basis is provided for both negative (morning) and positive (evening) phototactic behaviors during the diel movement patterns.

Despite ample evidence for light mediated vertical migrations of fishes, it is clear that the specific patterns exhibited can be highly variable relative to ambient light levels, can change over the season and may also reverse their pattern with respect to light (Brawn 1960; Woodhead 1966; Turuk 1973; Blaxter and Parish 1965; Levy 1990a). Several authors (Blaxter 1975; Heath et al 1988; Neilson and Perry 1990) commenting on this variety of behaviors, particularly as they relate to light-mediated responses, have observed that most reports of diel vertical migrations in fishes are circumstantial, and that the proposed light-regulating mechanisms have not been substantiated with rigorous tests involving in situ measurements of the variables in question.

The fundamental question to be answered is whether it is possible to develop empirical models that reliably predict the depth distribution of fish on a diel and/or seasonal basis.

Beyond the interest in the basic biology and mechanisms of diel migrations, the practical importance of a more complete knowledge of the pattern and basis of diel vertical migrations in fishes has recently developed rapidly as a consequence of the implications of such behavior for the application of hydroacoustic methods to the assessment of fish distribution, abundance, and biomass (Thorne 1977; Shotton and Bazigos 1984; Appenzeller and Leggett (in press)).

My objectives in this study were to 1) quantitatively assess the pattern of vertical migration in a species known to be light sensitive; 2) evaluate the _in situ_ changes in light levels with depth associated with theses movements and 3) evaluate the null hypothesis that the patterns of vertical movements in these fish and ambient light were unrelated.

METHODS

STUDY SITE AND HYDROACOUSTIC METHODS

I chose Rainbow smelt, (Osmerus mordax), as my model species. Smelt have frequently been described as light-sensitive (Ferguson 1965), and are known to exhibit diel vertical migrations moving to deeper waters during the day and to shallower waters at night (Dembinski 1971; Argyle 1982; Heist and Swenson 1983; Burczinsky et al 1987). I conducted my study in the central basin of Lake Memphremagog (Quebec - Vermont). Smelt dominate the pelagic fish community of this basin. Lake Memphremagog has a total surface area of 83 km2 and contains three distinct basins which differ in mean depth. (south basin 6.9 m, central basin 50.9m, north basin 13.5m). Its maximum depth 105 m, occurs in the central basin. This basin is an elongated (15 km x 2 km), deep trench with very steep shorelines. Waters of depths <30m comprise less than 10% of the total basin surface area. The depth and the shoreline steepness of this basin provide almost unlimited and continuous access to smelt via hydroacoustic sampling.

The vertical distribution of smelt was assessed with hydroacoustic methods. A 2-km transect oriented perpendicular to the shore was sampled 228 times during 1988 (n= 161) and 1990 (n= 67). In 1988 the period of sampling extended from

June to October and data were recorded on 29 different calendar days; in 1990 sampling occurred during July and August (5 calendar days). The majority of the vertical distribution data was collected during 10 sunset and 8 sunrise periods on different days during the field seasons.

I employed a 120 kHz Biosonics Model 105 dual beam echosounder (beam widths 11 and 25 degrees) to quantify the numerical abundance and biomass of smelt in the study area. The system was mounted in a 5 m outboard powered boat. The transducer, which was mounted in a V-fin towing body, was suspended by elastic cords from a davit. This mounting effectively dampened wave induced motion of the transducer, which was towed at a depth of 1 m. Electrical power was supplied from a gasoline powered AC generator. Boat speed during all surveys was maintained at 8.5 km/h. All lights were extinguished during night sampling to avoid attraction or disturbance of the fish being surveyed.

Fish biomass and average fish size were quantified by 20-log R (echointegration) and 40-log R (dual beam) amplification of echosignals, respectively. Fish abundance was estimated by dividing the total biomass by the average fish size. During most surveys I employed 20 log R and 40 log R amplifications on alternate pings. Ping rate was 5/sec and pulse length was 0.4 and 0.8 ms. All acoustic signals were recorded for subsequent analysis using a Biosonics recorder interface coupled to a video recorder. Data analysis was performed on these recorded data. Depth related noise peaks at 100 m depth were generally < 50 mV at 20log R amplification, and ranged from 100 to 200 mV at 40 log R amplification. During daylight hours, when the fish were schooling, the maximum voltages recorded were < 8 volts.

The vertical distribution of fishes was averaged over the full transect for each depth zone studied. Echo integrated estimates of fish abundance (no./m^3) were subdivided into 1 m depth windows from depths 2 - 60 m. For depths between 60 - 105 m I integrated over 5 m depth intervals. I found fish abundance to be very low at depths > 60m. I therefore restricted my analyses of fish distribution to the depth range 2 - 60 m.

I conducted a series of trials to calibrate and identify echo signals. I ensonified targets at a fixed location in the lake, then sampled immediately with a 9 m^2 vertical haul net. Only smelt were caught (dominant length class of 12 cm (SD 1.8)). A less abundant size class averaging 5 cm standard length was also caught. Acoustic biomass estimates for each trial were compared with the actual fish biomass caught in the net hauls. When compared by regression analysis, these estimates resulted in a significant positive relationship p <0.01: $r^2 = 0.70$; $n = 12$) relating acoustic estimate and catch (in g/m^2):

$$\text{fish catch} = -0.08 + 0.92*\text{acoustic estimate} \quad (1)$$

The slope did not differ significantly from 1 ($p > 0.25$), and the intercept was not significantly different from 0 ($p=0.96$).

From July through August 1990 I restricted my analyses to the depth range 10 - 60 m, because waters < 10 m were inhabited by large numbers of smaller non-migrating larval and juvenile fishes which made assessment of vertical movements into and out of this layer unreliable.

ENVIRONMENTAL VARIABLES

Time of day

The time of the beginning and end of each transect was recorded in Eastern Standard Time (average transect duration was 25 min). Time measures were transformed to local time by calibrating to the time of the sun's zenith at Lake Memphremagog (local noon). I determined the difference between Eastern Standard Time and local time (average: + 45 min.) from observations of the timing of sunset and sunrise conducted repeatedly during the season. This local time correction was used to obtain symmetry in the time-depth data about noon. I further converted local time to hours from midnight (+/-) for use in regression analysis.

Light

Light intensity measurements where made with an underwater irradiameter (Kahl Scientific Instrument Corp., model 268 wa 310). The instrument had a measurement range of 0.1 to 10000 μW per cm^2 (sensitivity was scale related). The unit allowed me to measure ambient light on board the survey vessel and light levels at depth to a depth of 30 m. Ambient light readings were recorded every 5 min and were averaged over the entire transect for statistical analyses. To derive illumination levels at the depths where fish occurred I empirically modeled the reduction of ambient light levels as a function of 1) light transmission through the water surface and 2) light attenuation in the water column with depth.

Light transmission was assessed empirically, and was used to calculate the percentage of ambient light energy that entered the water column. Concurrent measurements of ambient and immediate sub-surface light levels yielded the following relationship:

$$\text{Transmission (\%)} = 0.3 + 0.09 * \log(\text{ambient Light}) \qquad (2)$$

($r^2 = 0.41$; $p= < 0.01$; $n= 82$).

Light levels in the water column were highly correlated with depth ($n = 28$; $r^2= 0.99$) according to the general equation:

$$\ln I(d) = \ln I(s) - \epsilon * D \qquad (3)$$

whereby $I(d)$ is the light intensity at a given depth d in m; and $I(s)$ is the light intensity directly below the water surface; ϵ is the attenuation coefficient and D is depth in m. Attenuation coefficients derived empirically for the top 30 m were also used to calculate light illumination levels at greater depths. I assumed that the optical properties of the water column did not change with depth (Kirk 1983). Weekly, direct measurements of light levels ($\mu W/cm^2$) to depths of 30m indicated that light attenuation exhibited very little change over the course of my investigation. I therefore used an average attenuation value (0.40 SD 0.04; natural logarithmic scale) in all calculations of light levels at depth.

These combined attenuation and transmission values were used to calculate light levels at depth from my near-continuous ambient light readings. For comparison with illumination levels given in the literature which were reported in units other than $\mu W/cm^2$ I used conversion factors given in Brock (1981).

Temperature

Temperature profiles were conducted weekly. These were repeated on both the east and west ends of the transect to account for possible differences in the vertical profile caused by internal waves which are known to occur in Lake Memphremagog. Temperature was recorded at 1-m intervals to a depth of 40 m.

QUANTIFICATION OF VERTICAL FISH DISTRIBUTION

The depth of ensonified fish was generally quantified over an entire transect. Therefore acoustic fish density estimates were averaged into consecutive 1-m depth intervals from 2 - 60 m. These measurements resulted in typical frequency distributions of the average fish density for each depth interval. Targets were not uniformly distributed with depth. Rather, they occurred within a limited depth range and exhibited a clear peak which varied in depth with time (Fig. 1). From these depth distributions meaningful statistics had to be derived in order to analyze changes in the vertical fish depth over time and in relation to environmental variables. Since the higher statistical moments (variance, skewness) could not be generated from these data, I calculated the following statistics in order to characterize the observed fish depth distributions: 1) the upper 95 th percentile, 2) the mode, and 3) the lower 95 th percentile (Fig. 2).

These parameters were considered useful and biologically meaningful since they characterize 1) the depth at which the maximum fish density occurred (the mode) which I assumed to be an indicator of the preferred depth; 2) the approximate range of vertical dispersion (given by the upper and lower 95th percentiles). I chose the 95th percentiles since they constitute a robust measure of fish range and dispersion, and are relatively unaffected by outliers which were frequently observed. At the same time, they describe the behavior of the majority of the fish population (90%) which was contained within these moments.

FIGURE 1

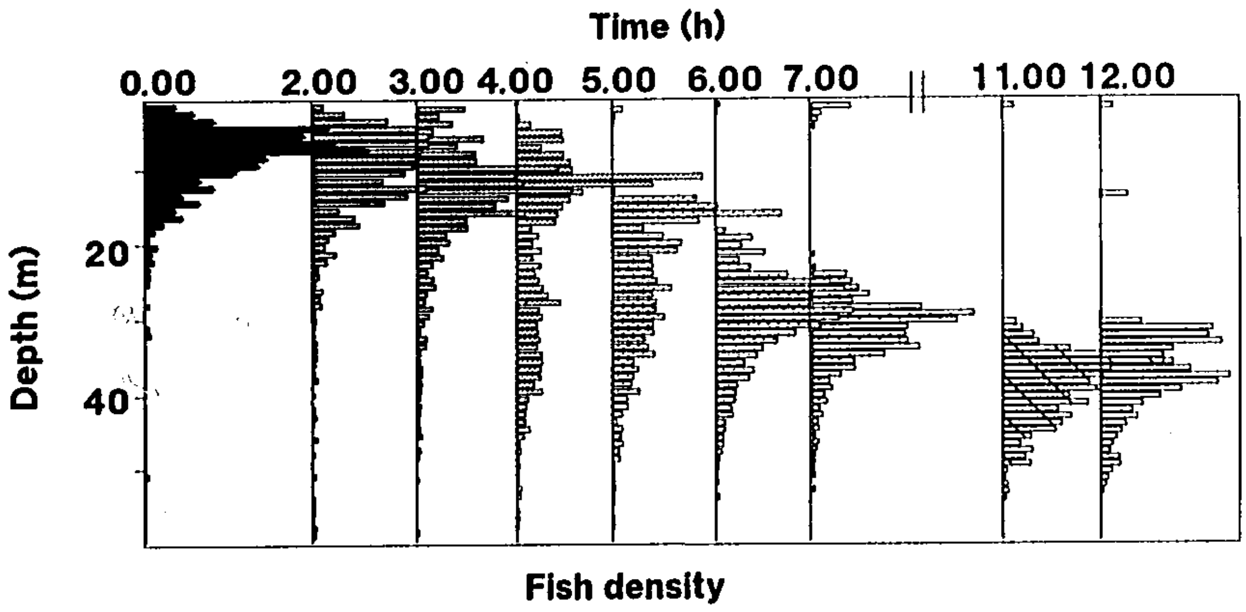
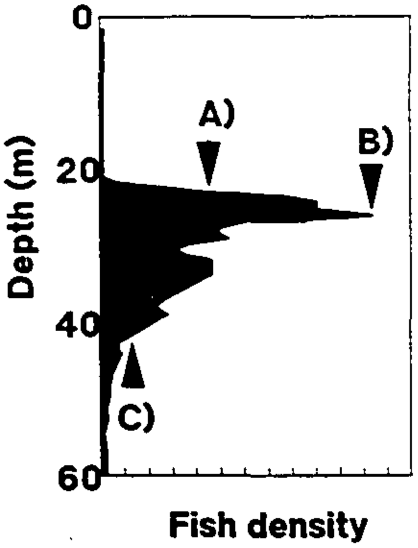

Time (h)
0.00
2.00
3.00
4.00
5.00
6.00
7.00
11.00
12.00
Depth (m)
20
40
Fish density

Fig. 1. The vertical migration pattern of smelt in the Central Basin of Lake Memphremagog as observed by hydroacoustic methods on an arbitrary day (8/6/88). Each panel records fish density measurements from an entire transect across the lake subdivided into 60 1-m depth intervals. Fish densities were highest in the upper water column at night-time (0.00 - 3.00-hr), and shifted subsequently into deeper water layers between 4.00 - 7.00-hr. At 11.00 and 12.00 highest fish densities were found in the deep water between 30 - 40m.

FIGURE 2



	Depth of fish (m)	
A) Upper	23	95th percentile
B) Maximum fish density	26	Mode
C) Lower	42	95th percentile

Fig. 2. Statistical moments used to characterize depth/density distributions of smelt in Lake Memphremagog. An example from a typical hydroacoustic record based on an entire transect is given. Arrows indicate the depth measures used, these were: 1) the upper 95th percentile (a robust measure of the upper boundary); 2) the mode = maximum fish density (a measure of the preferred depth interval); 3) the lower 95th percentile (a measure of the lower boundary of fish distribution).

RESULTS

Smelt exhibited a strong vertical migration. They were typically concentrated in the upper 10 - 15 m during nighttime hours, and migrated to deeper waters during daylight. Typically, peaks in daytime distributions occurred at 30 - 40 m. Aggregation patterns also varied between day and night. Smelt were dispersed during the night and formed dense schools during daylight hours. This change in aggregation pattern was coincident with their vertical displacement.

The pattern of vertical migration was modified by water temperature. When epilimnetic temperatures exceeded 18 °C, smelt aggregated just below the thermocline depth during nighttime hours.

Time of day

To describe the diel vertical displacement of smelt I fitted a sigmoid function to the depth distribution data, using hours from midnight (+ or -) as the independent variable (Fig. 3). A good fit to the data was obtained for the upper 95th percentile depth ($r^2 = 0.73$; $p < 0.01$) and for the depth of maximum fish density (modal depth) ($r^2 = 0.71$; $p < 0.01$). However, the fit to the lower 95th percentile depth was poor ($r^2 = 0.24$; $p < 0.01$; Table 1). Fish depths cycled on a diel basis between two depth states expressed by the model asymptotes. These asymptotic depth distributions occurred between 00.00 to 03.00 h (darkness) and 08:00 - 12.00 h (daylight). Vertical movements occurred during the intervals between these times of "stable" depth (Fig. 3).

FIGURE 3

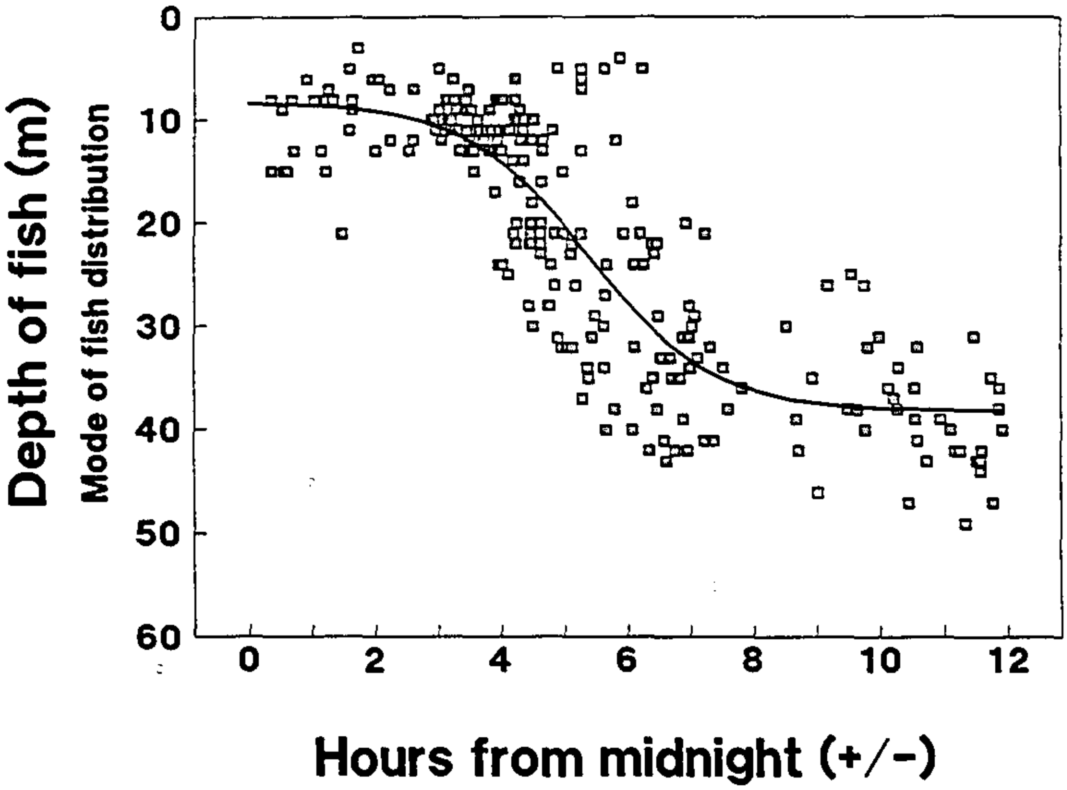

Depth of fish (m)
Mode of fish distribution
0
10
20
30
40
50
60
0
2
4
6
8
10
12
Hours from midnight (+/-)

Fig. 3. Relationship between the mode (maximum fish density) of vertical smelt distributions and time of day. The time variable is expressed as hours from midnight (+/-). Each point represents data from an entire transect (n=228).

Table 1. Results of nonlinear regression analysis (sigmoid model) of characteristics of smelt depth distributions as a function of time. Data for transects are combined for the analysis (n = 228). The time variable is given in hours from midnight (+/-). The dependent variable, depth of fish in m, is measured by three moments of the depth frequency distribution as noted.
Model: Depth = A + B / [1 + exp(C - D * Time)]

Dependent variable	Coefficients					
	A	B	C	D	r^2	p
upper 95th percentile	4.73	27.7	5.35	0.94	0.73	<0.01
Modal fish density	8.25	29.9	5.53	1.02	0.71	<0.01
lower 95th percentile	40.54	11.9	3.72	0.63	0.24	<0.01

Fish depth distributions were asymmetric. There was a marked trend for fish to be aggregated nearer the upper boundary of their vertical range during both the day, and at night. This was indicated by the modal fish density being closer to the upper, than to the lower 95 th percentile fish depth (Table 1). Additionally, the vertical range at which 90 % of the fish biomass occurred (the range between the upper and lower 95 th percentiles), changed with time of day. Smelt were contained within a much narrower depth band during the day than at night.

Ambient light

Fish depth during daylight hours was linearly related to the log of ambient light. These relationships were highly significant for the upper 95th percentile depth ($r^2 = 0.83$), and the modal depth ($r^2 = 0.78$); but the relationship with the lower 95th percentile was weak ($r^2 = 0.14$; Table 2; Fig. 4). Residuals from the linear model relating the upper 95th percentile depth to the log of light were nonlinear. I obtained an improved fit to this data by applying a linear model with two lines intersecting at a light level of 10 $\mu W/cm^2$ and at a depth of 9 m ($r^2 = 0.87$; $p < 0.01$; Table 2; Fig. 4). This illumination level was typical for the dusk and dawn period. This model suggests that the strong linear relation of ambient light on the upper 95th percentile depth of fish was dampened in the upper water layers < 9 m when fish were close to the surface of the lake.

FIGURE 4

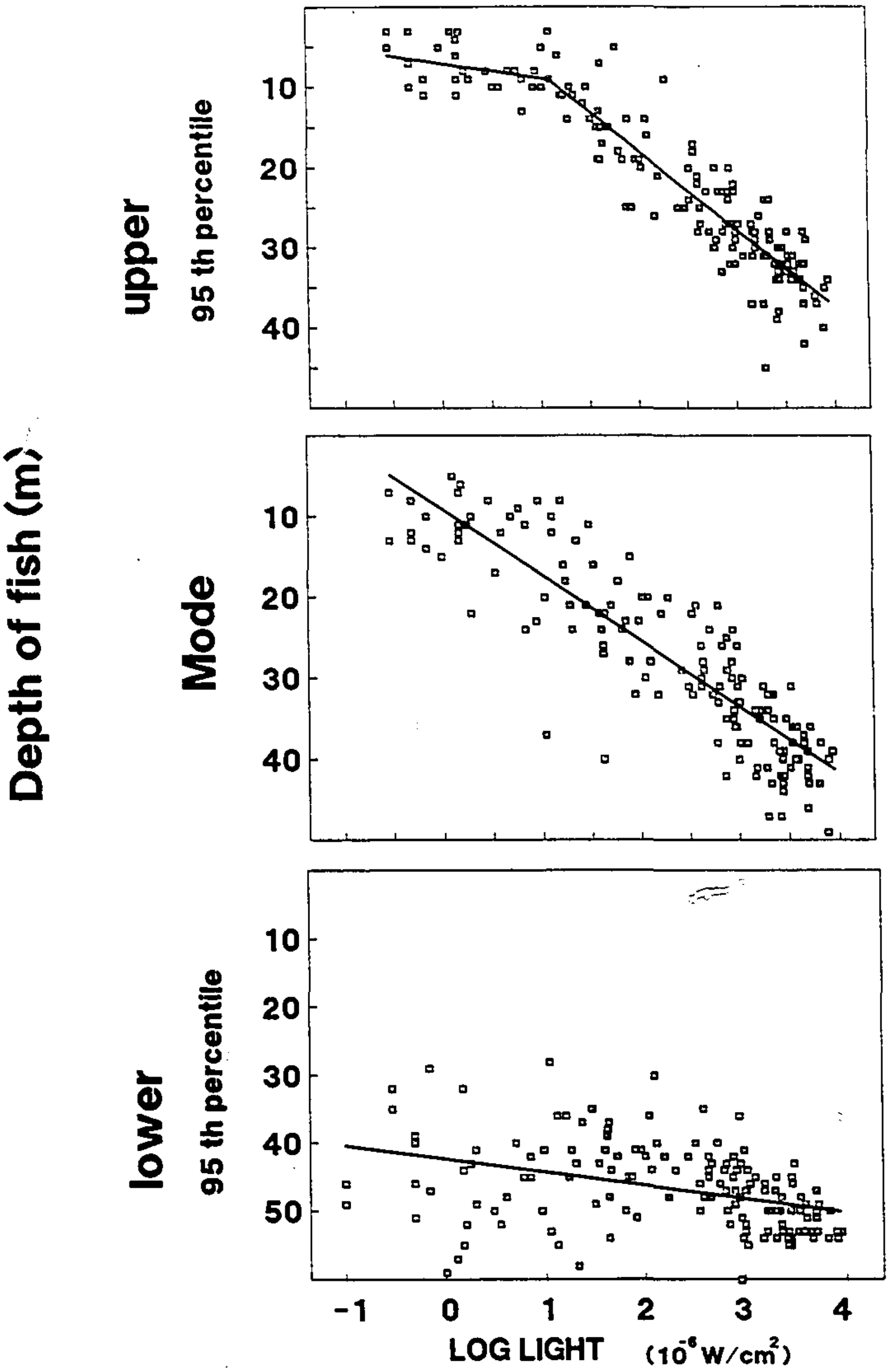

Depth of fish (m)
upper
95 th percentile
Mode
lower
95 th percentile
10
20
30
40
10
20
30
40
10
20
30
40
50
-1
0
1
2
3
4
LOG LIGHT (10^{-6} W/cm^2)

Fig. 4. The relationship between fish depth and light. Linear regression models were fitted for the mode and lower 95th percentile. For the upper 95th percentile depth a model with two intersecting lines was applied. Data are based on 148 fish depth distributions.

Table 2. Results of regression analyses of three characteristics of smelt depth distributions relative to in situ light ($n = 148$). Depth in m; light in $\mu W/cm^2$. Model 1 is a linear model; Model 2 consists of two intersecting lines applied to the upper 95th percentile of smelt depth. Std. errors are given in parenthesis.

Model 1: $Depth = A + B * \log(Light)$

Dependent variable	Coefficient		r^2	p-value
Depth of fish	A	B		
upper 95th percentile	3.95 (0.75)	7.79 (0.29)	0.83	< 0.001
Modal fish density	9.29 (0.93)	8.09 (0.36)	0.78	< 0.001
lower 95th percentile	42.27 (1.03)	1.94 (0.40)	0.14	< 0.001

Model 2: $Depth = A + B*(X - C) + D*\sqrt{[(X - C)^2 + E^2]}$

	Coefficients						
Dependent variable	A	B	C	D	E	r^2	p
upper 95th percentile	9.04	5.8	1.11	3.95	$5*10^{-6}$	0.87	<0.01

Light at fish depth

Measures of ambient above-surface light together with empirical models of light transmission and attenuation in the water column, were used to calculate illumination levels at fish depth. These illumination levels averaged 0.11 μW/cm^2 (SD 0.42) at the depth of the upper 95th percentile, and 0.012 μW/cm^2 (SD 0.03) at the modal depth. At the lower 95 percentile of the fish depth distribution illumination levels were very low, averaging $9*10^{-6}$ μW/cm^2 (SD $4*10^{-5}$).

To investigate whether these illumination levels exhibited any relationship with time of day, I examined diel trends in the predicted light level for each of the selected moments of the fish distribution: There was a significant ($p = < 0.001$) but weak ($r^2 = 0.13$) negative relationship between the upper 95th percentile depth and hours from midnight. A similar pattern was observed for the modal depth ($p <0.001$; $r^2 = 0.10$). In contrast, I found a significant ($p <0.001$; $r^2 = 0.10$), but weak, positive trend with hours since midnight for the lower 95th percentile fish depth (Table 3; Fig.5). The slopes of these relationships were significantly different from 0. These results indicate 1) a weak change in the light levels associated with the vertical change of fish during the daylight period with higher illumination levels prevailing during the crepuscular hours, and lower levels during the daytime when fish are typically schooling in deeper water (negative relationship with time of the upper 95th percentile and the depth of maximum fish density); and 2) the range of illumination levels to which 90 % of the fish population (between the upper and lower 95th percentiles) were exposed to was not constant over the time of day. Rather, a greater range occurred during the crepuscular hours (Fig. 5).

FIGURE 5

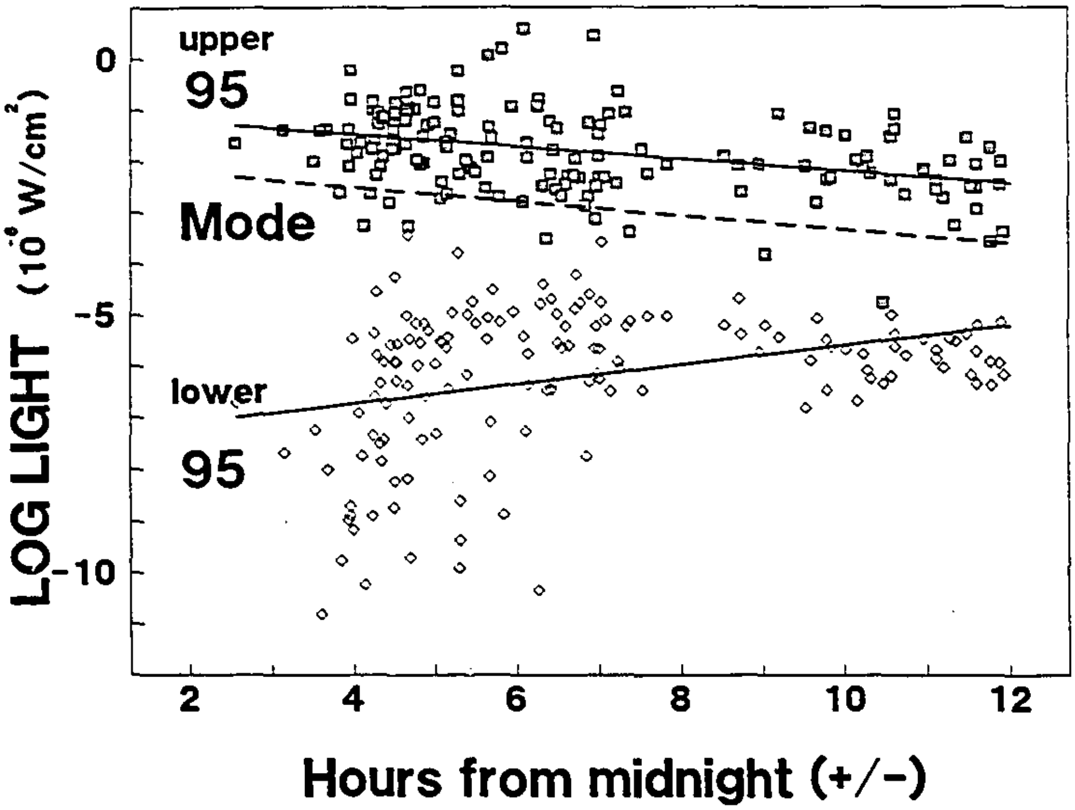

upper
95
Mode
lower
95
LOG LIGHT (10^{-6} W/cm^2)
0
-5
-10
2
4
6
8
10
12
Hours from midnight (+/-)

Fig. 5. The relationship between the predicted light (log $\mu W/cm^2$) at selected moments of the fish depth distribution and time of day. Squares indicate the upper 95th percentile depth, diamonds the lower 95th percentile of fish depth. The predicted lines for the upper 95th percentile, the mode (maximum fish density; dashed line), and 95th percentile depth are indicated.

Table 3. Relationships between calculated light levels at the depth of smelt (for three characteristics of the depth distribution: upper, lower 95 percentiles and mode) as a function of time of day. Light in $\mu W/cm^2$; time is measured as hours from midnight (+/-); (n = 148). Standard error in parenthesis.

Model: $\log(\text{Light}) = A + B * (\text{Time})$

Dependent variable (Illumination)	Coefficient		r^2	p-value
	A	B		
at upper 95th percentile	-1.02 (0.18)	-0.12 (0.025)	0.13	< 0.001
at modal fish density	-1.95 (0.23)	-0.14 (0.032)	0.11	< 0.001
at lower 95th percentile	-7.45 (0.32)	0.18 (0.045)	0.10	< 0.001

Temperature

Epilimnion temperatures increased from 11 to 25 °C between early June and mid August, and declined thereafter to a minimum of 10 °C in early October. The depth of the thermocline (mixed layer depth) increased during the season. There was no evidence of an influence of seasonal changes in temperature on the vertical distributions of smelt (upper 95 percentile depth, and modal depth), when the complete day-night data set ($n = 228$) was analyzed ($p = 0.87$; $p = 0.27$). However a weak, but significant ($p < 0.001$) relationship between thermocline depth and the depth of the lower 95 percentile of the distribution was observed ($r^2 = 0.23$).

The effect of thermocline depth on fish depth was stronger when the night distributions were analyzed independently. When epilimnetic waters exceeded 18 °C the upper limit of the distribution remained below the thermocline (Fig. 6). In early spring and late fall, when smelt were not constrained by epilimnetic temperatures > 18 °C, they entered the near-surface waters where they were less vulnerable to the hydroacoustic gear. Decreases in echo-integration values were observed at night during these times. Smelt were readily observed at the surface at night at these times.

I excluded data on fish distributions collected when surface temperatures were < 18 °C, and observed a significant ($p < 0.001$) relationship between thermocline depth and fish depth (Table 4). The upper 95th percentile of fish depth at night was most strongly related to the depth of the thermocline ($n = 69$; $p = <0.001$; $r^2 = 0.53$). The relationship between modal and lower 95 percentile fish depths and thermocline depth were also significant ($p < 0.001$) but were weaker ($r^2 = 0.17$ and 0.21 respectively; Table 4).

FIGURE 6

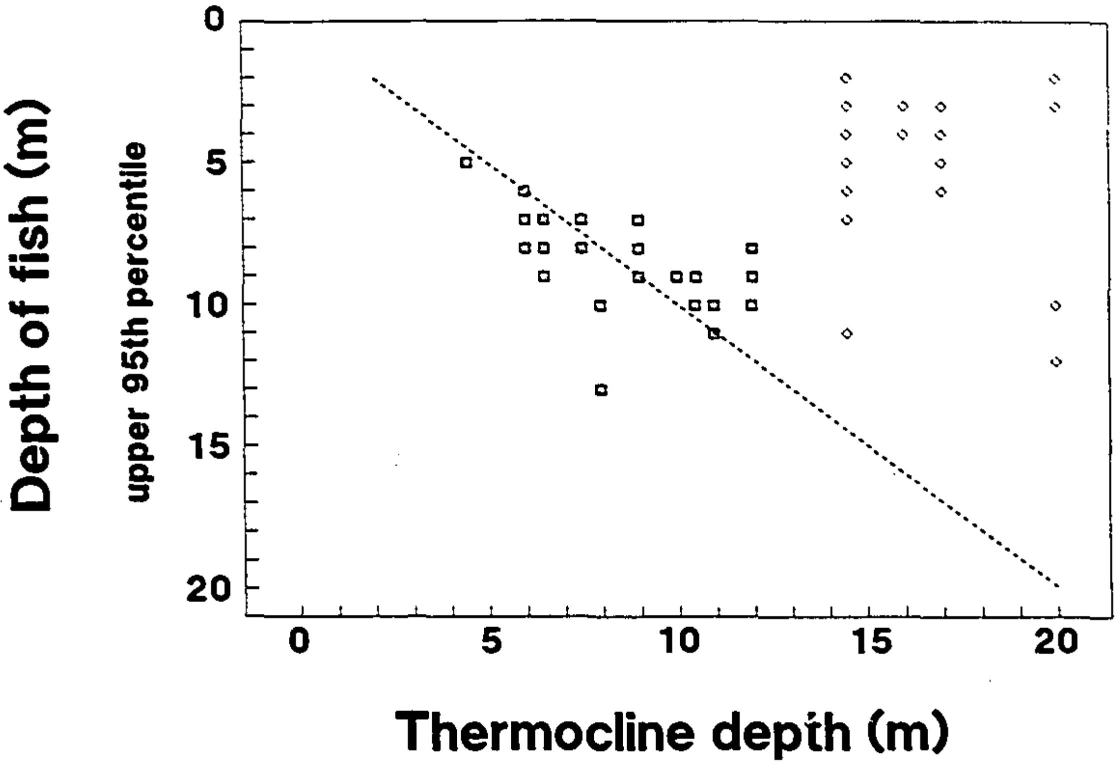

Depth of fish (m)
upper 95th percentile
0
5
10
15
20
0
5
10
15
20
Thermocline depth (m)

Fig. 6. Influence of the depth of the thermocline on the upper 95th percentile fish depth. Squares indicate surface temperatures > 18 °C, diamonds show data for surface temperatures < 18 °C. The broken line indicates equal depths of thermocline and the 95th percentile. Data above this line indicate a distribution for which the upper 95th percentile is within the eplilimnion, data below the line are cases for which the upper 95th percentile is below the thermocline.

Table 4. Relationship between three characteristics of the vertical depth distribution of smelt and thermocline depth. Depth of fish and thermocline depth are given in m. For these analyses only transect data from night surveys and epilimnetic water temperatures >18 °C were used (n = 69). Standard error in parenthesis.
Model: Depth of fish = A + B * (Thermocline depth)

Dependent variable Depth of fish	Coefficient		r^2	p-value
	A	B		
upper 95th percentile	4.11 (0.52)	0.49 (0.057)	0.53	< 0.001
Modal fish density	5.42 (1.58)	0.64 (0.173)	0.17	< 0.001
lower 95th percentile	32 (2.45)	1.13 (0.268)	0.21	< 0.001

DISCUSSION

Evidence for light avoidance in smelt

My results are consistent with previous observations (Ferguson 1965) that smelt are "light sensitive" and avoid waters having high light levels. Daytime illumination levels in surface waters may exceed several thousand $\mu W/cm^2$. However, the average illumination level at the upper boundary of smelt distributions in Lake Memphremagog was 0.12 $\mu W/cm^2$ (SD 0.42), and the light level associated with the modal depth was 0.012 $\mu W/cm^2$ (SD 0.03). By way of comparison Heist and Swenson (1983) reported maximum smelt densities at illumination levels of < 0.001 $\mu W/cm^2$ in Lake Superior, and Dembinski (1971) reported that smelt schools in Polish lakes occurred at light levels ranging from 0.004 to 20 $\mu W/cm^2$. These data suggest a strong and persistent tendency of smelt to avoid light levels > 20 $\mu W/cm^2$. The variation in the light levels associated with smelt distributions in these studies could result from differences in the calibration and sensitivity of the light sensors used.

My data clearly show that the moments of the vertical distributions of smelt were related strongly and significantly to ambient light levels. I therefore reject the null hypothesis that diel vertical migration in smelt is not influenced by light. The changes in fish depth in relation to light levels I observed could be interpreted as "fish following optimal light levels" as has been hypothesized by the LP hypothesis (Boden and Kampa 1967; Blaxter 1975; Melnikov et al 1981). In general, this hypothesis was supported by my data since the modal depth varied predictably with light levels, indicating a persistent preference of fish for a fixed illumination level throughout the day.

However, my analysis of the range of the fish depth distribution, measured by the upper and lower 95th percentiles of fish depth, yield strong indications that the behavior of these fishes was guided by negative phototactic behavior. This is suggested by: 1) The shape of the smelt depth distributions which exhibited a strong asymmetry, the mode of the distribution being closest to the upper 95th percentile depth. This skewness was repeatedly observed in data from single transects. The analysis of distributional moments for the entire data series also revealed this skewness. 2) The ranges of the fish depth distribution, measured by the upper and lower 95th percentiles, differed considerably in their predictability during the investigation. The lower 95th percentile of the smelt depth distribution was highly variable in relation to time of day, and was only weakly related to ambient light levels. In contrast, the upper 95th percentile was very strongly related to light levels and to the time of day.

These results suggest that the vertical depth distribution of fishes cannot be predicted consistently from a knowledge of the upper and lower boundaries of fish light preferences as suggested by Melnikov et al. (1981). Rather, the observed variability in patterns reflects considerable deviation from fixed light levels for the lower boundary of the fish population. This suggests that the major impact of light on the vertical distribution of smelt may be a compression of the available space in the vertical dimension. Consequently, fish aggregated at the upper boundary of their depth distribution at a fixed light level, and responded strongly to changes in the depth of this illumination threshold. This view is also supported by the fact that the upper 95th percentile depth showed the strongest relationship to changes in ambient light.

I conclude that the avoidance of high illumination levels rather than the seeking of a light optima is the dominant proximate cause for the vertical distribution patterns I observed. Heath et al. (1988) studied the vertical distribution of larval herring, Clupea harengus, and found two patterns of diel behavior; the distribution of deeper fish was more strongly related to ambient light than was the distribution of fish in the near surface waters where light levels were highest. They interpreted this pattern to reflect positive phototactic behavior by herring larvae leading to aggregation in the upper water layers during the day. In comparison, my data, which exhibit the opposite trend in fish depth distributions relative to light, suggest a negative phototactic behavior was prevalent.

While the upper water layers were generally avoided by the smelt, and they tended to aggregate below a fixed illumination level, considerable variations in light levels prevailed within the depth range of the population over the time course of our investigation. The sources of these variations could not be assessed with my data. One possible explanation is that feeding behavior was variable over the season. Such variability in fish diel vertical behaviors, directly related to variations in the depth distribution of their prey, have been observed for alewife (Alosa pseudoharengus) by Janssen and Brandt (1980). They found that vertical movements of alewives were influenced by vertically migrating prey organisms. While such coordinated movement patterns of fish and prey have been observed on several occasions (Begg 1976; Janssen and Brandt 1980), they do not appear to be general (Levy 1987). It is also possible that a size or age related change occurs in the diel behavior of smelt. Such changes have been proposed for coregonid species (Laßleben 1952; Hamrin 1986).

Temperature

In addition to the effects of light, I also found that temperature had an important effect on the vertical distribution of smelt at night when epilimnetic temperatures were > 18 °C. At these times fish aggregated near the base of the thermocline. This suggests a change in the dominant limiting factor with high light levels prevailing during the daylight hours, forcing the fish into deeper waters, and high surface temperatures prevailing at night when the light barrier was absent. This change in limiting factors revealed itself in the two intersecting lines in the relationship between ambient light and the upper 95th percentile fish depth. These lines intersected at an illumination level of 10 $\mu W/cm^2$, a typical dawn or dusk illumination level, and at a depth of 9 m. The model suggests that once the fish were above this depth, the influence of light on the upper 95th percentile depth diminished.

The influence of water temperature on smelt distribution is well documented. Evans and Loftus (1987) described landlocked rainbow smelt as a species with an eurythermal habit with young-of-the-year occurring in warm waters and larger fish occurring in cooler water habitats. Their review of adult smelt temperature preferences observed in the field suggested an upper limit of 16 to 18 °C. Burczinsky et al (1987) also reported that the upper boundary of the vertical distribution of smelt was associated with the thermocline when summer epilimnion temperatures exceeded 18 °C.

Patterns of fish vertical distribution involving aggregation in the metalimnetic waters close to the thermocline have also been reported for other vertically migrating fish species (Narver 1970; Wurtsbaugh and Neverman 1988; Levy 1990b). Levy (1987) suggested that such distributional patterns are common at night when temperature acts as a major sensory mechanism for fish. My results, together with those of Levy (1990b), suggest that the diel vertical migration patterns of smelt and other fish species are guided primarily by accommodations to the light and temperature environment. If such governing mechanisms are general, it should be possible to derive models of vertical distributions.

A model of diel vertical migration

Melnikov et al (1981) provided a mathematical equation relating the depth of fish to illumination levels. In their model fish depth was considered to be a function of variables known to influence light levels in the water column. A prerequisite for the application of this model is a detailed knowledge of illumination levels and of the light ranges preferred by the species in question. However, my results suggest that the ranges of illumination associated with a given fish population may change during the day, with a broader range during the crepuscular hours and a more narrow range during daylight. Moreover, my data show that the application of such a model, using the ranges of distribution, may be difficult to apply, since great differences in predictability were observed for the upper and lower boundaries of the population and strong asymmetry prevailed in the fish depth distribution.

Given this variability, how should we approach the development of models that predict the vertical distribution of light sensitive aquatic animals through time? When relating fish depth to time of day, diel vertical movements have frequently been assumed to be sinusoidal and to track ambient light changes (Neilson and Perry 1990). The sigmoid model I derived for smelt suggests that the vertical migration of animals in the water column is, however, characterized by a two stage positioning of the fish in the upper and lower water layers during darkness and bright daylight, and a rapid transition between these stages during the crepuscular hours. My data also suggest that the maximum rate of change in vertical depth occurs at the time of sunrise (ascending) and sunset (descending). This typical timing pattern was also reported for marine vertical migrations by Bary (1967). My data indicate that this timing is related to the very high changes in illumination (over 3 - 4 orders of magnitude) during crepuscular hours, while these levels range only over 1 - 2 orders of magnitude during daylight hours (Fig. 7).

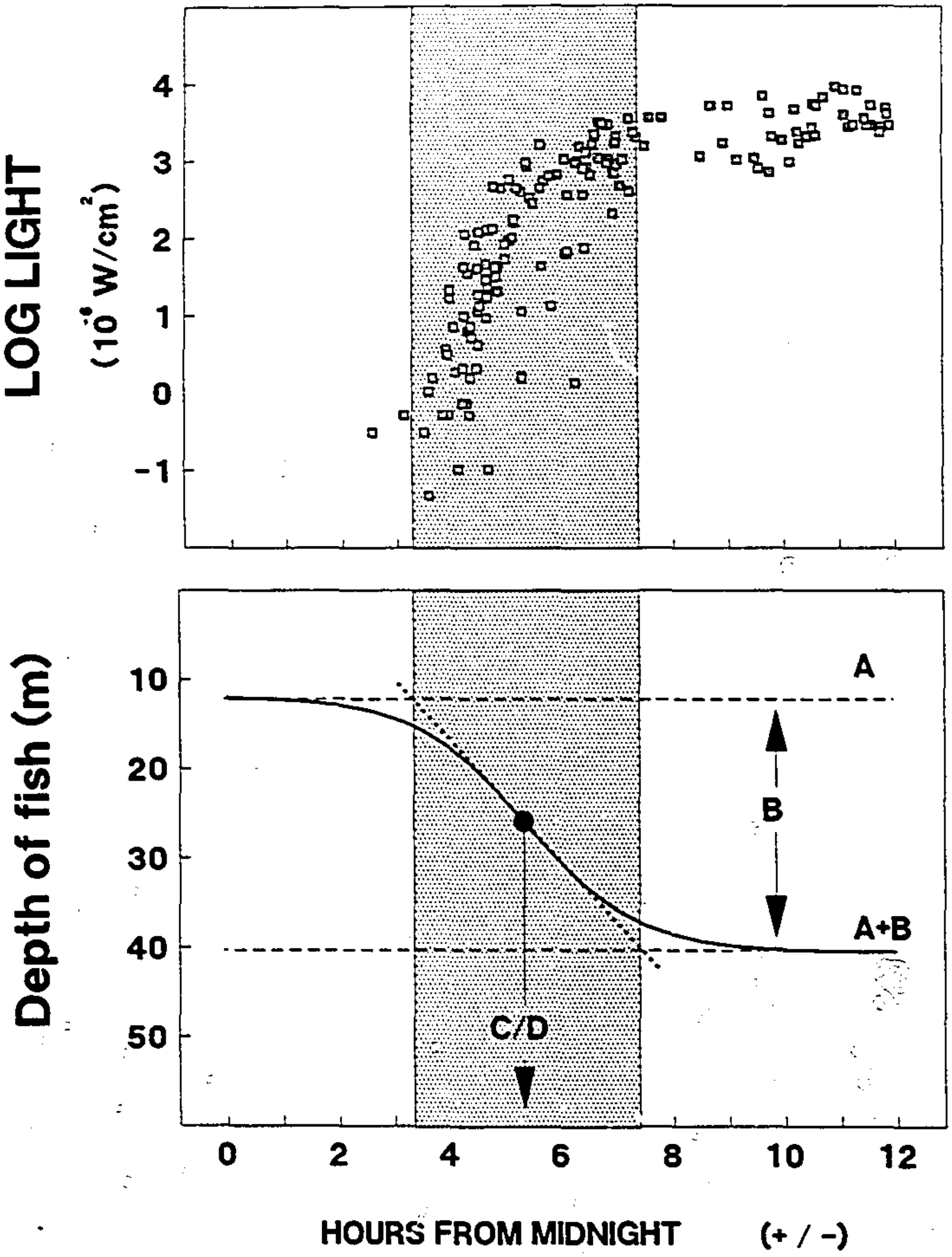
I found fish depth to be linearly related to the log of ambient light as light energy is attenuated logarithmically with depth (Kirk 1983; Parson et al. 1977). I conclude that the nature of the depth-log(light) relationship, together with the diel pattern in illumination levels, is responsible for the timing of vertical migration of animals that track fixed illumination levels.

The logistic model I employed to describe diel changes in the vertical distribution of smelt facilitates a quantitative description of several characteristics of vertical migration behavior. The general form of this model is:

$$\text{Depth} = A + B / [1 + \exp(C - D * \text{Time})] \quad (3)$$

where fish depth is measured in meters and time is measured as hours from midnight (+/-). In this model the average diel range of migration is represented in the coefficient B; the upper (A) and lower (A+B) stages are characterized by the asymptotes of the model; the migration speed between states is expressed by the slope of the curve at the inflection point. This point has the coordinates [2A+B]/2 and (C/D) (Fig. 7).

FIGURE 7



LOG LIGHT
(10^{-6} W/cm^2)
4
3
2
1
0
-1
Depth of fish (m)
10
20
30
40
50
A
B
A+B
C/D
0
2
4
6
8
10
12
HOURS FROM MIDNIGHT (+ / -)

Fig. 7. Model of diel vertical migration of smelt in relation to time (hours since midnight). The parameters of the sigmoidal model fitted to the data are indicated. Depth of fish (mode of the distribution) can be predicted from time of day. In the upper panel the diel pattern in change of ambient light (log scale) observed during this investigation is indicated. The shaded area indicates the hours during which the major vertical displacement of fish was observed, and during which the log of light changes over 3 to 4 orders of magnitude.

This model was found to fit the observed modal and upper 95 percentile data with high accuracy. These moments indicate the preferred and the upper threshold depth layers of the population. An additional advantage of this model is that it facilitates calculation of the speeds of vertical migrations, and it can serve as a guide for estimating the times of stable positioning of modal depth layers. Such information is valuable when estimating fish biomass with acoustic methods. The model can also be used to predict how changes in environmental factors affect night fish distributions. For example, in my study the upper asymptote (A) was set by the depth of an uninhabitable warm water layer near the surface. An increase in water turbidity should lead to a decrease in B, the range of the vertical migration, and also to a decrease in the slope at the inflection point reflecting a reduced speed of vertical migration. Additionally species adapted to lower illumination levels should exhibit increased ranges (B) of their vertical migrations.

Practical applications of vertical migration models

A knowledge of the patterns of vertical migration of fish can have considerable practical application in hydroacoustic fish surveys (Shotton and Bazigos 1984). My results suggest that during times of the year when surface temperatures are cold, (in this case < 18 °C) the upper boundary of smelt distributions approach the surface where fish become inaccessible to the acoustic beam. Hence, a considerable bias could occur if hydracoustic surveys were conducted at night when such conditions prevail. In my study, estimates of fish abundance declined by up to 50 % at such times.

In shallow lakes, or coastal oceans, where light illumination near the bottom approaches or exceeds levels typically avoided by the species in question, fish may be located very close to the bottom during the day. Under such conditions quantification by acoustic methods may be impossible during daylight hours because fish and bottom signals cannot be reliably separated. Under such situations, only night surveys conducted subsequent to the development of a well-defined thermocline and unsuitable epilimnetic temperatures would yield reliable estimates of fish biomass. In short, the seasonal and diel time window during which accurate hydroacoustic biomass or abundance estimates can be made may be short, and optimal, or at least acceptable, time for such surveys may be species and/or site-specific.

Ultimate causes of vertical migration and their relation to light

While the objective of my study was not to evaluate hypotheses related to ultimate causes of vertical migration, my data do shed some light on these questions. Several reviews of the vertical distribution patterns of pelagic species (both marine and freshwater) indicate a considerable similarity in diel vertical migrations (Woodhead 1966; Bary 1967; Blaxter 1975; Levy 1987; Levy 1990b). The question arises whether these similarities in behavior might be grounded in similar selection pressures as proposed by Levy (1990b).

One hypothesis for the evolution of vertical migration frequently put forward is that the behavior evolved as a consequence of light related mortality, and that it has an antipredation function (Iwasa 1982; Gliwitz 1986; Gabriel and Thomas 1988; Lampert 1989). This hypothesis is based on the assumption that predation and the reactive distances of visually searching predators increase with light intensity (Vinyard and O'Brien 1976; Jacobs 1978; Iwasa 1982; Clark and Levy 1988). Recent work by Clark and Levy (1988) suggest that vertically migrating juvenile fish might optimize the trade-offs between fast growth and high mortality by feeding during the twilight, when predation risk is reduced relative to that during daylight. This model, developed primarily for juvenile sockeye salmon, could be applicable to other juvenile or adult fish. The patterns described by Narver (1970) and Levy (1987 and 1990b) are very similar to those I observed for smelt. For example the illumination levels at which sockeye juveniles were observed during daylight was 0.1 μW/cm² (1 - 10^{-4} μW/cm²). These light levels are very similar to those observed for smelt in my study. Smelt predators (large lake trout, Salvelinus namaycush) are common in Lake Memphremagog, and the diel patterns of smelt distribution I observed are consistent with light avoidance behavior. Direct proof for such an effect of predators on the vertical distribution of fish has not yet been provided, although it has been documented for zooplankton (Luecke 1986; Bollens and Frost 1989). A simple yet valuable test would consist determining whether fish diel vertical migration patterns occur in the absence of predators.

In contrast to this view, Pitcher and Turner (1986) provided support for the hypothesis that the twilight period may be a dangerous time for plankivorous fish since predators could approach them easily during low illumination levels. This view is derived from the "twilight hypothesis" advanced by McFarland and Munz (1974), who argued that predators are very successful during the twilight period because their prey are maladapted in an environment with changing illumination levels. Fish predators in reef systems have been found to be most successful during the twilight (Hobson 1972).

The time required for a change from light to dark adaptation in the vertebrate eye can be up to an hour (Nicol 1989) and depends upon the light intensity during the previous light period (strong illumination being responsible for a delay; Nicol 1989). However, it might also be hypothesized that vertically migrating fish can maintain appropriate visual adaptation by remaining in low illumination layers, thereby maximizing their feeding and predator avoidance. Blaxter (1980) and Nicol (1989) reported that, in teleost fish, the threshold for changes in light-dark adaptation of the eye occurs between 1 and $5*10^{-4}$ $\mu W/cm^2$ with an average of 0.4 $\mu W/cm^2$ (Blaxter 1980). It is not possible to determine from my data whether the eyes of rainbow smelt remain light adapted throughout the day or if, and at what times, changes to dark adaptation might occur. However, my study does provide evidence that these fish may maintain themselves at depths and at light levels at which light-adapted vision prevails. This would be important for both feeding and predator avoidance since only light-adapted eyes provide colour vision and high visual acuity, a precondition for successful feeding in visual predators (Blaxter 1980).

Maintenance of a stable photoenvironment which allows continuous adaptation to low illumination levels might therefore yield preadaptation of the eye to twilight feeding conditions. Vertically migrating fish might therefore maintain a considerable advantage over non-migrating predators or prey during crepuscular feeding periods since their eyes need not to adapt to changing illumination levels. The coincidence of low illumination levels observed for vertical migrating smelt and other fish species (Boden and Kampa 1967; Blaxter 1975; Levy 1990b) with those light levels at which retinomotor movements and changes in dark-light adaptation prevail, could also serve as an explanation for how fish measure absolute illumination levels and maintain themselves within an isolume layer. Such a mechanism might be provided by changes in vision from color to black and white during retinomotor movements.

CHAPTER 2

BIAS IN HYDROACOUSTIC ESTIMATES RELATED TO FISH SCHOOLING BEHAVIOR: EVIDENCE FROM DAY-NIGHT SURVEYS OF VERTICALLY MIGRATING FISH.

ABSTRACT

I investigated the hypothesis that fish schooling behavior leads to underestimation of fish abundance when assessed by acoustic methods. Current methods for acoustic quantification of fish abundance rely on the assumption that fish biomass and numerical fish abundance are linearly related to acoustic scattering under all natural fish densities. However, cage experiments as well as field observations have indicated that acoustic shadowing effects occur at very dense and large aggregations of fish. Acoustic surveys of the pelagic fish community of Lake Memphremagog, Quebec, were conducted when fish were aggregated and dispersed. These differences in aggregation were related to diel responses to light levels. I found that estimates of fish abundance, as measured by echo integration, were consistently and significantly lower when fish were aggregated in dense schools. This bias was not due to diel changes in average echo level per fish, which exhibited no relationship to diel changes in vertical and horizontal distributions. I conclude that the reduced abundance estimates obtained when fish were aggregated resulted from acoustic shadowing. My data suggest this bias may be as large as 50%.

INTRODUCTION

Hydroacoustic methods are being used increasingly in freshwater and marine systems to quantify fish abundance and biomass. The accuracy of acoustically derived abundance data depends largely on established empirical relationships between echo strength and units of fish size or fish biomass (Love 1971; Love 1977; Foote 1987). The echo integration approach to abundance assessment has been proposed as the standard method (Johanneson and Mitson 1983; MacLennan 1990), because it can be applied in situations where echoes from single fish, or from aggregations, are measured. An important unresolved question, however, is whether the relationship between fish abundance and echo signal, quantified as integrated echo values, is independent of the nature and intensity of fish aggregation in typical field survey situations, or whether echo measurements must be adjusted for bias related to fish aggregation (Foote 1983; Toresen 1991). Current calibration methods assume that fish aggregation has no influence on the integrated echo (Johannesson and Losse 1977; Foote 1983; Bayona 1984).

In an attempt to answer this question, Roettingen (1976) and Foote (1983) conducted experimental studies on caged fish. Their investigations led to conflicting conclusions. Foote (1983) reported a linear relationship between echo intensity and fish biomass under all fish densities measured.

In contrast, Roettingen (1976) found echo intensity to be linearly related to fish abundance only at lower fish densities. At high fish densities a "shadowing effect" was observed, which resulted in underestimation of fish biomass (Fig. 1). Field investigations into the nature of this relationship have also produced conflicting results. Aglen (1983a) reported that fish biomass estimates were generally lower when fish were dispersed during nighttime surveys. He concluded that these differences were related to the different echo thresholds he applied. However, Bazigos (1975), Gerlotto (1989) and Soria and Freon (1991) have all reported that acoustic estimates of biomass were more frequently higher when fish were dispersed at night, relative to when they were aggregated during the day. Bazigos (1975) and Soria and Freon (1991), hypothesized that vessel avoidance by schooling fish during daylight hours (as observed by Olsen et al 1983a), combined with acoustic shadowing effects (Gerlotto 1989) may have produced these results. Toresen (1991) quantified the absorption of acoustic energy in relation to fish density in herring schools, and observed that increasing fish density was associated with a loss in bottom signal intensity, thereby providing direct evidence of shadowing at high fish densities. The resolution of these conflicting results lies in acoustic surveys where the effects of fish avoidance and the effects of acoustic shadowing can be separated.

In addition to possible problems associated with shadowing in dense schools, the question arises whether the average target strength (TS) of fish remains constant when fish change their depth during diel vertical movements, a behavior commonly associated with changes in aggregation (Dembinski 1971; Blaxter 1975; Woodhead 1966). Such depth-related effects, together with changes in the tilt angles of fishes at day and night (Buerkle 1983; Blaxter and Batty 1990), could explain the observed variability in day-night acoustic estimates of fish numerical abundance and biomass (Foote 1983).

Major uncertainties regarding the accuracy of acoustic estimates of fish numbers and biomass may also occur if the vertical distribution of fishes and the diel changes in their distribution are not known prior to sampling (Shotton and Bazigos 1984). This occurs because some fish in the targeted population could be inaccessible to the acoustic beam either by being at the surface (Thorne 1977) or near the bottom (Burczinsky et al. 1987) where acoustic signals are unreliable.

In the in situ study reported here I sought to evaluate the direction and magnitude of biases in hydroacoustic estimates of fish numerical abundance and biomass resulting from changes in fish aggregation. Specifically I sought to rigorously evaluate Roettingen's hypothesis that fish aggregation leads to underestimation of fish biomass when assessed by hydroacoustic methods.

FIGURE 1

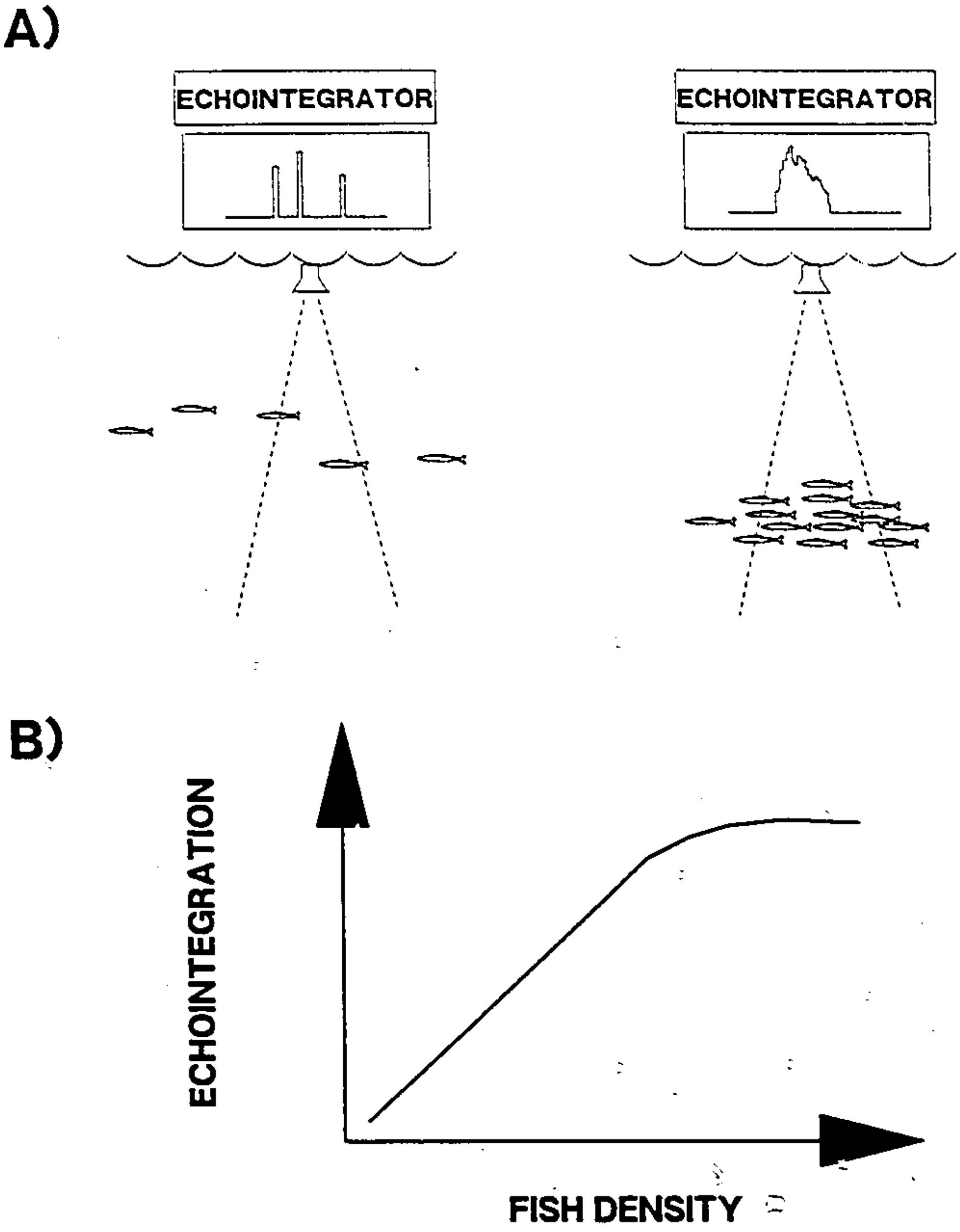

A)
ECHOINTEGRATOR
ECHOINTEGRATOR
B)
ECHOINTEGRATION
FISH DENSITY

Fig. 1. A) Ensonification of fish that are dispersed (left) and schooled (right), and resulting echo signals. When fish are dispersed, echo signals are separated and appear as single spikes (one for every fish). When fish are schooling, a multiple echo is received (from many fish ensonified together).

B) A generalization of Roettingen's (1976) study that suggested a linear relationship between true fish density (# of fish in the experimental cage) and echo-integrated estimates of density made at low fish densities. At high fish densities the echo-integrated values reached a plateau.

NATURAL FISH DENSITIES AND ACOUSTIC SHADOWING EFFECTS REPORTED IN THE LITERATURE

I first addressed the question, "Are natural densities of schooling fish within the range of fish densities in those experimental studies in which acoustic shadowing effects were observed?" Resolution of this question is important, because shadowing effects have been observed only under very high fish densities, below which a linear relationship between echo scatter and fish abundance seems to occur (Roettingen 1976). Additionally, experimental comparisons of small (12 cm) and large (35 cm) fish have revealed that shadowing effects occur at the much higher densities characteristic of smaller fishes (Roettingen 1976).

To assess this question, I used Pitcher and Partridge's (1979) empirical model, which relates schooling fish densities to fish body size. This model is based on comparisons of observed nearest neighbour distances between schooling fishes and the corresponding volume inhabited by a single fish within the school. I calculated the water volumes occupied by individual fish within a school by applying two factors, one for dense schools (factor 0.6) and one for looser aggregations (factor 1) (see: Pitcher and Partridge 1979) (Fig. 2). Using this approach I compared the fish sizes and densities used by Roettingen (1976) and Foote (1983) in their experimental studies with the fish densities predicted for equivalent sizes using the Pitcher and Partridge model

(1979) (Table 1; Fig. 2).

This comparison indicates that Roettingen's (1976) experiments were conducted at fish densities that included the range of densities predicted by the Pitcher and Partridge model. However, his maximum densities where shadowing effects occurred, greatly exceeded the maximum predicted by the model using a factor of 0.6. Foote's (1983) experiments, in contrast, were clearly conducted at fish densities that matched only the lower limits of the natural fish densities predicted from the model. This suggests that Foote's conclusion that echo scatter is a strictly linear function of the <u>in situ</u> fish biomass may have resulted from his failure to investigate a sufficiently wide range of fish densities.

Toresen's (1991) study, however, supports the conclusion that acoustic shadowing effects may exist in situations where aggregations are very large. His data show that bottom echo strength was a negative function of the vertical extension of the fish layer above. This finding strongly supports Roettingen's (1976) conclusion that acoustic shadowing is related not only to density effects, but also to the total number of fish within the acoustic beam. Given that natural schools may occupy volumes many meters to perhaps hundreds of meters in vertical and horizontal extent, a large number of fish can be ensonified simultaneously by a single echo wave (Toresen 1991). The echo return from such a wave might be considerably altered in strength and time delay, as a consequence of the development of variable acoustic wave paths within the fish school due to multiple reflectance of the sound energy.

FIGURE 2

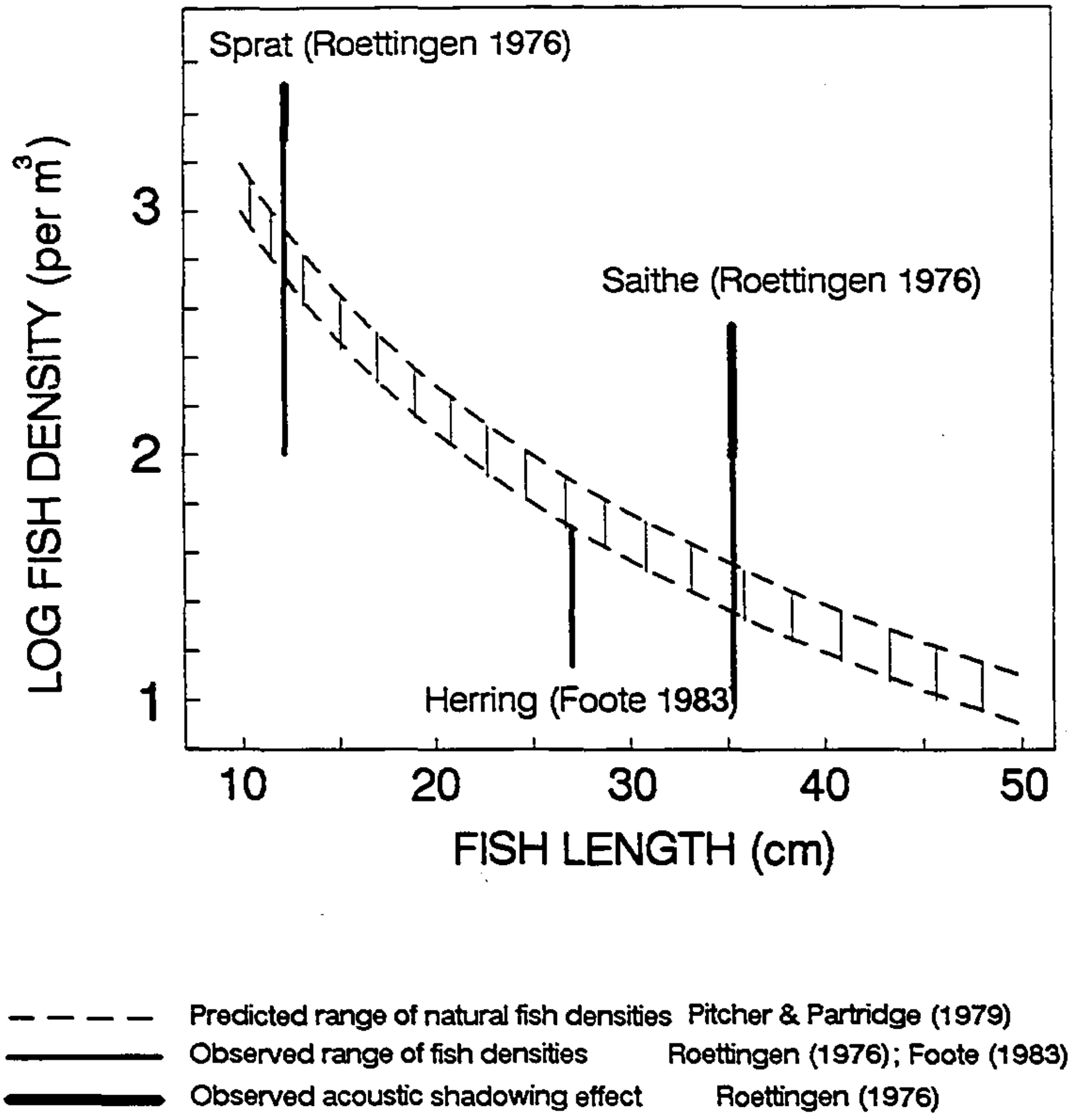

Sprat (Roettingen 1976)
Saithe (Roettingen 1976)
Herring (Foote 1983)
LOG FISH DENSITY (per m^3)
3
2
1
10
20
30
40
50
FISH LENGTH (cm)
Predicted range of natural fish densities Pitcher & Partridge (1979)
Observed range of fish densities Roettingen (1976); Foote (1983)
Observed acoustic shadowing effect Roettingen (1976)

Fig. 2. A graphic representation of Pitcher and Partridge's (1979) model relating fish size (X-axis; length in cm) to fish density (Y-axis; fish/m^3, logarithmic scale). The model densities are indicated by broken lines, the lower line indicating low levels of fish aggregation (factor 0.6), the upper line indicating high density polarized schools (factor 1). Superimposed are experimental ranges of caged fish densities used by Roettingen (1976) and Foote (1983) to assess whether changes in fish densities result in deviations from a linear relationship between echo density and integration estimates of density (medium sized line). The heavy line depicts the range of fish densities at which Roettingen (1976) observed shadowing effects.

Table 1. Fish species, sizes and densities employed in cage experiments by Roettingen (1976) and Foote (1983) in order to test whether acoustic shadowing effects occur. In comparison fish densities derived from Pitcher and Partridge's school model (1979) are given for equivalent sizes of caged fish.

	Roettingen 1976		Foote 1983
A) Fish species	Sprat	Saithe	Herring
B) Observed mean Fish length (cm)	12.1	35.1	27.1
C) Observed Range of fish densities (fish per m^3)	100-3500	10-350	14-57
D) Observed Acoustic Shadowing effects (fish per m^3)	1800-2600	100-130	none
E) Predicted Range (model) of fish densities (fish per m^3)	560-880	23-36	50-80

IN SITU STUDIES

STUDY AREA

I selected the central basin of Lake Memphremagog, Quebec-Vermont as my study site for the in situ trials. Lake Memphremagog has a total surface area of 83 km², is long (40 km in south - north direction) and narrow (average width 2.4 km) and contains three distinct basins that differ in mean depth. (south basin 6.9 m, central basin 50.9m, north basin 13.5m; Fig. 3). The central basin is the deepest part of the lake and approximates 110m. This basin has a surface area of 20.5 km², and accounts for almost two-thirds of the total lake volume. The basin is an elongated (15 km x 2 km), deep trench with very steep shorelines. Waters of depths < 30m represent less than 10% of the total basin surface area (Fig. 4). The depth and the shoreline steepness of this basin provided almost unlimited acoustic access to its pelagic fish population, which is dominated by rainbow smelt (Osmerus mordax), which as a species are known to school by day, and disperse at night (Dembinski 1971; Argyle 1982; Heist and Swenson 1983; Burczinsky et al 1987).

I used vertical net hauls operated from deep water (60 - 80 m) to the surface (net opening area 9m²) to identify and to calibrate acoustic signals. This method worked well at night, but did not yield fish catches during the day when fish distributions were highly patchy. Only rainbow smelt were caught. The dominant length class captured was 12 cm T.L.(std. dev. 1.8). A smaller but less abundant size class averaging 5 cm T.L. also observed in these catches.

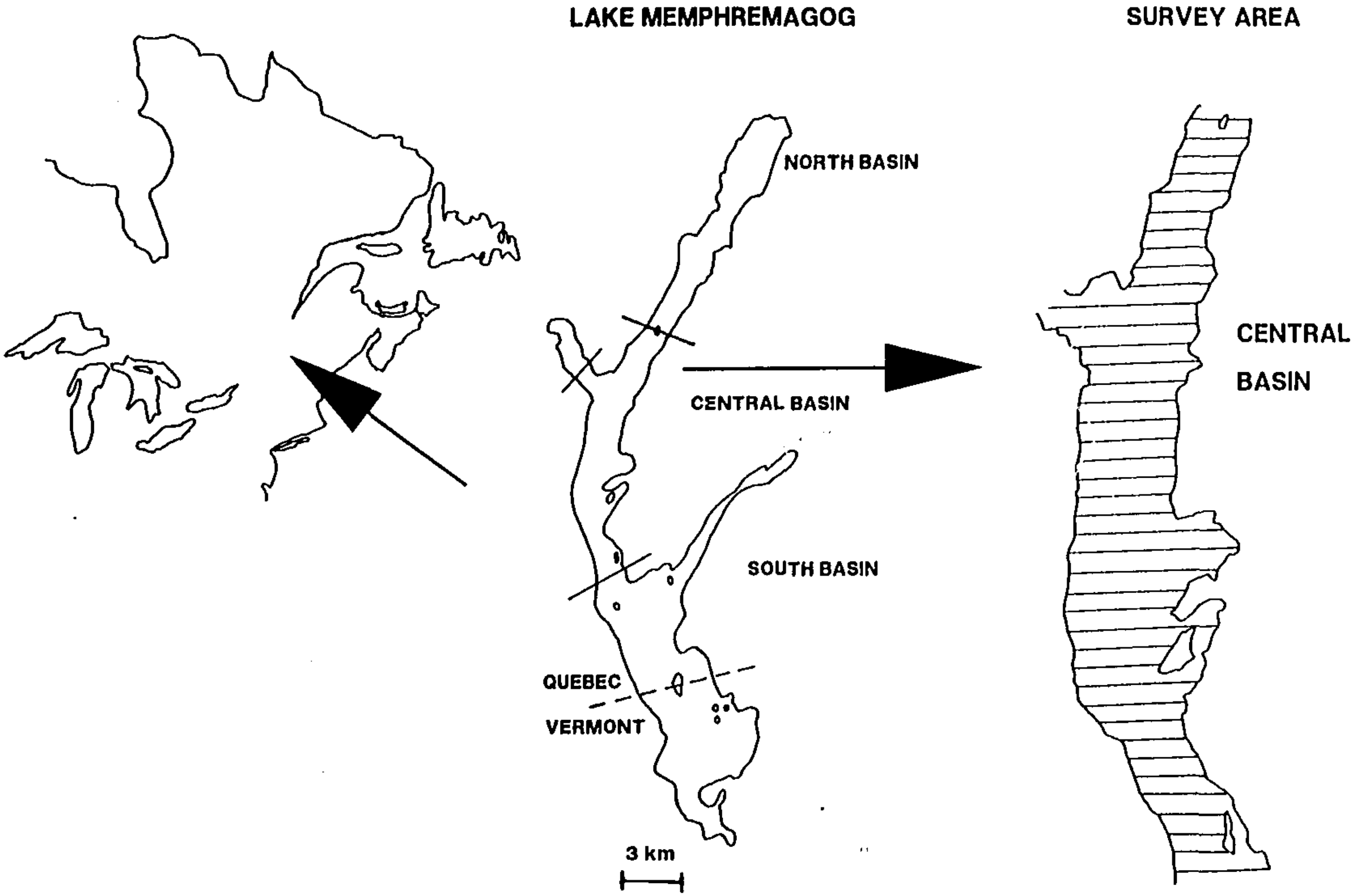
During early summer I observed larval and young-of-the-year juvenile smelt (avg. length 2 - 3 cm) were observed and caught in the upper water layers (max. 10 m depth). Young-of-the-year smelt were captured with a 1 m^2 net with 2 mm mesh size. In these trials I used only vertical hauls made during darkness. Echosounder records showed that these young-of-the-year smelt did not perform diel vertical migrations. Rather they remained in the epilimnion during both day and night. They were therefore separated vertically from the larger fish. The abundance and dominant size categories of smelt captured in nets were consistent with size and abundance estimates obtained acoustically immediately prior to net sampling.

In addition to these catch based identifications I was able to visually identify adult smelt which were attracted to the surface in large numbers by strong flashlights shone at the water surface at night during spring time.

The transparency of the water in the study area was measured by secchi disk and an underwater light meter. Over the course of the investigation (July to September 1988 and 1990) secchi depths were 4 - 8m. Direct measurements of light levels ($\mu W/cm^2$) to depths of 30 m indicated that the depth at which

1 % of the underwater surface light remained (lower limit of the phototrophic zone) varied between 9 - 13 m over the course of this study. Light levels at other depths were calculated using water column extinction coefficients and surface light intensities (see chapter 1).

FIGURE 3



LAKE MEMPHREMAGOG

SURVEY AREA

Fig. 3. Lake Memphremagog, Quebec-Vermont. The study area used to estimate acoustic fish abundance is shown on the right. This area was subdivided into 40 parallel transects from which 12 were selected at random for each complete survey (for detailed description of the procedure see text: survey design).

FIGURE 4

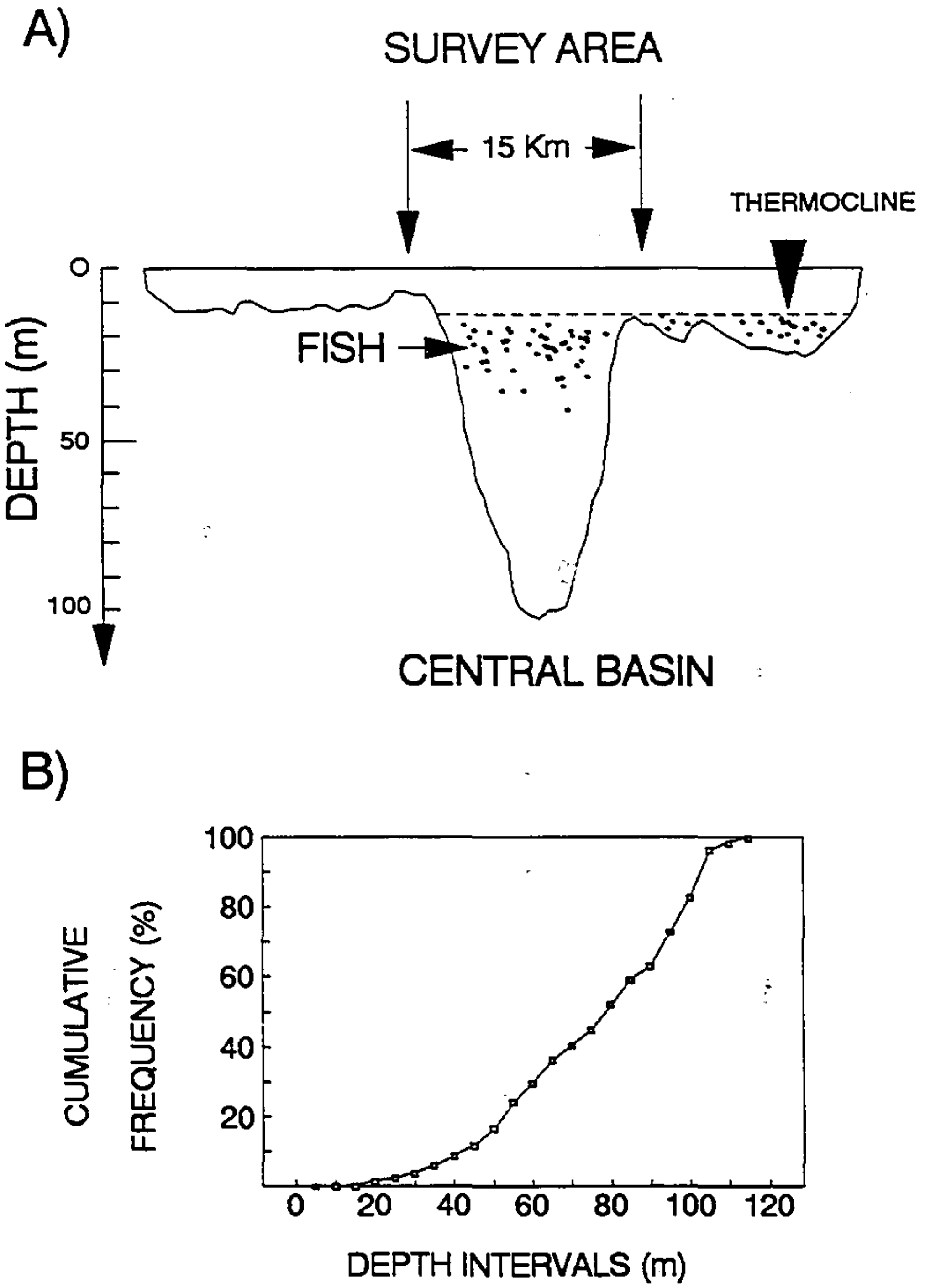

A)
SURVEY AREA
15 Km
THERMOCLINE
0
50
100
DEPTH (m)
FISH
CENTRAL BASIN
B)
100
80
60
40
20
CUMULATIVE FREQUENCY (%)
0
20
40
60
80
100
120
DEPTH INTERVALS (m)

Fig. 4. A) Morphology across Lake Memphremagog. A typical summer fish distribution (dots) below the thermocline (broken line) is indicated. B) Cumulative depth distribution in the Central Basin survey area as derived from acoustic depth records of 12 transects (n = 4000 soundings).

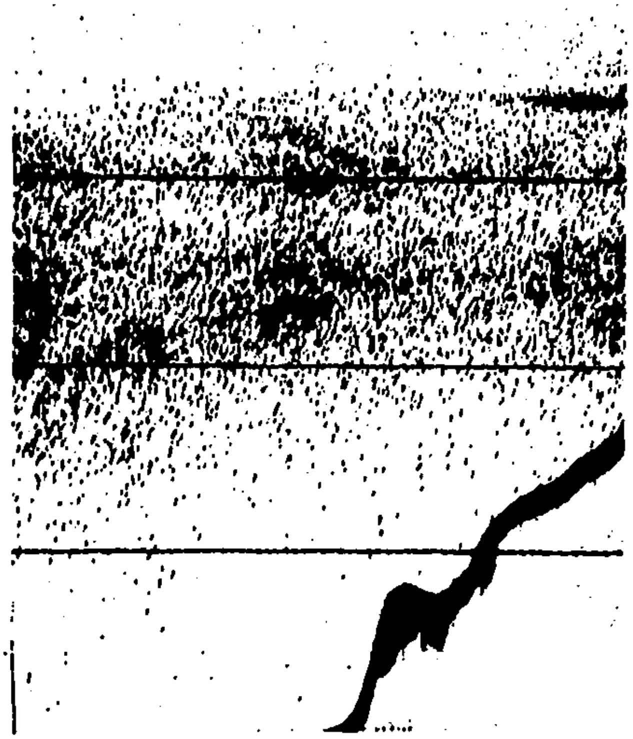
ACOUSTIC TECHNIQUES

I used a 120-kHz Biosonics Model 105 dual beam echosounder (beam width 11 and 25 degrees) to quantify the numerical abundance and biomass of pelagic fishes. The system was mounted in a 5m outboard powered boat. The transducer, which was mounted in a V-fin towing body, was suspended by elastic cords from a davit. This mounting effectively dampened wave induced motion of the transducer, which was towed at a depth of 1 meter. Power was supplied from a gasoline powered electric generator. Boat speed during all surveys was maintained at 8.5 km/h. During night sampling all lights were extinguished to avoid attraction or disturbance of the fish. I obtained an estimate of total fish biomass of the pelagic fish population through echo integration of 20 log R amplified signals. I also quantified the average size of the targets by analysis of 40 log R dual beam signals. During all surveys I used 20 log R and 40 log R amplifications on alternate pings. The ping rate was 5 per second and the pulse length was 0.4 and 0.8 ms. All acoustic signals were recorded for subsequent analysis using a Biosonics recorder interface coupled to a VCR. All data analysis was performed on these recorded data. Depth-related noise peaks at 100 m depth were generally < 50 mV at 20log R amplification, and ranged from 100 to 200 mV at 40 log R amplification. I used the same receiver gain factor at +6 dB for both day and night surveys. The maximum voltages recorded from dense schools were < 8 volts. Echo integrated data were processed at 50 pings per sample interval. This equates to a linear scale of 45 - 50 m. Relative fish densities were expressed as V^2/m^2 of lake surface area. Fish density figures presented in this paper are either averages obtained from spatial intervals of 50 m or averages based on complete transects of length 1 - 2 km. I excluded signals from the top 10 meters from the analysis, because we found these waters to be inhabited principally by smaller non-migrating larval and juvenile fish. In order to quantify diel vertical distribution patterns of fish, the echo-integration processor was subdivided into 1 m depth windows, and density values were averaged across a complete transect.

SURVEY DESIGN

a) Continuous sampling of a single transect

I used two different survey designs. First, I adopted an approach in which a single transect was ensonified repeatedly over 12 or 24 hours. This provided continuous information on diel changes in fish distributions. It also yielded comparative estimates of fish abundance obtained at a single transect location when smelt were alternately aggregated and dispersed (day and night). The data used in these investigations were collected during July - September of 1988 and 1990. During these periods the surface waters of the lake exceeded 18° C and a strong thermocline was established at depths ranging from 5 (early July) to 15 m (mid September). The thermocline blocked the vertically migrating smelt from entering the warm surface layer at night. In late summer with depths of the thermocline exceeding 10 m it also prevented movement of smelt into the shallow South basin of Lake Memphremagog (Fig. 4 A). During the day smelt schools were located in deeper water but remained well above the lake bottom (Fig .5). They were, therefore, continuously accessible to the acoustic beam.



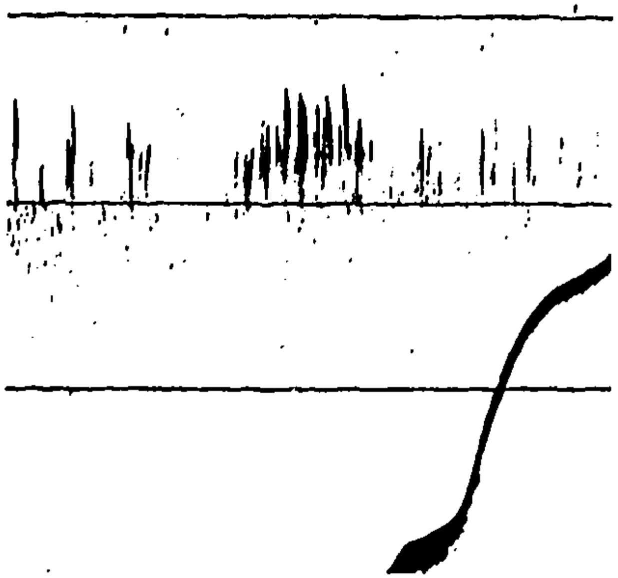


Fig. 5. Echo-chart of an identical transect across Lake Memphemagog during the night (left) and during the day (right). Fish are dispersed in the water column at night (single signals) and are aggregated in schools during the day. The dark band on the right lower corner is the lake bottom signal. The vertical scale is indicated by 20 m depth lines. The horizontal scale is highly compressed with a total length of ca. 2 km.

b) Whole lake estimates

I next conducted surveys designed to yield estimates of the total number of pelagic fish in the Central Basin. These investigations were conducted from mid July to early September of 1990. I conducted biweekly day and night surveys, in total 9 during the day and 7 at night. A particular day survey was followed within 24-h by a night survey or vice versa. To estimate the number of fish in the Central basin, I selected 12 parallel, east-west transects at random from a total of 40 predetermined, equally-spaced lake segments that covered the entire Central basin (Fig. 3). I ensonified these 12 transects within an interval of 4-5 hours. To avoid damage to the boat and the transducer I avoided water depths < 5 m near the shore. Generally, the 5 m depth contour was located within 20 m of the beach. Throughout our investigations the thermocline was located between 8 and 10 m depth. I estimated fish biomass by echo integration. These acoustic data were averaged over 50-m spatial intervals. The total survey consisted of 360 to 400 of 50-m averages located along the 12 transects. The average transect length was 1400 m. Estimates of fish biomass were calculated using only full transect data (n=12 per survey) and were computed from the average acoustic level per survey. For these analysis I used 20 log R amplified echo signals, which were processed by a digital echo integrator. All individual transect means were weighted by the corresponding transect length, because transects varied in length.

I calculated the average acoustic size of individual fish by processing 40 log R amplified echoes and computing the average TS for all fish ensonified on each survey using standard Biosonics processing. This method is based on echo signals obtained from two channels (dual beam echosounding) using only targets selected as single fish echoes. For additional information on this technique see Trayner and Ehrenberg (1979), Ehrenberg (1984) and Burczinsky and Johnson (1986). To transform acoustic sizes (target strength) into units of fish length, I used the general relationship for target strength and fish length established by Love (1977):

$$TS = 18.4 \log (l) - 1.6 \log (f) - 61.6 \qquad (1)$$

where: TS = target strength in decibels
l = length of fish in cm;
f = frequency in kilohertz

I used this equation, despite the evidence (Rose and Leggett 1988), that the relationship for target strength and fish length can be highly variable among species, because in our study the exact relationship for smelt was not known. This possible inaccuracy, however, does not influence my results which are entirely based on relative changes in acoustic fish sizes during day and night.

To convert echo integration estimates into estimates of fish biomass, I derived scaling factors based on the average TS of the fish surveyed. This approach is described in detail in Burczinsky and Johnson (1986). I determined mean TS for each survey. The average calibration factor (16 surveys) to convert the integrated echo data from units of V^2/m^2 to fish/m^2 was 0.6.

RESULTS

DIEL PATTERNS OF SPATIAL DISTRIBUTION

Repeated continuous acoustic sampling along a 2-km transect provided information on diel changes in fish distribution and acoustic estimates of fish abundance. As previously noted, the pelagic fish population of Lake Memphremagog's Central basin is dominated by rainbow smelt (Osmerus mordax). Consistent with earlier observations (Dembinski 1971; Argyle 1982; Heist and Swenson 1983; Burczinsky et al 1987) these smelt exhibited distinct diel patterns of schooling and vertical displacement which are related to the light levels and the thermal structure of the water column (Evans and Loftus 1987; chapter 1). The first component of this diel pattern, vertical displacement of the fish, resulted in the following day-night patterns: fish were located in mid water (30-50 m) during the day, well off the bottom, and moved up to depths adjacent to the thermocline (10-20 m) at night. The second component of the day-night pattern consisted of a change in aggregative behavior: during daylight hours smelt aggregated in dense schools. During the night smelt were more dispersed into regular scattering layers (Fig. 5 and 6). The transition between these distinct day and night patterns occurred at twilight.

FIGURE 6

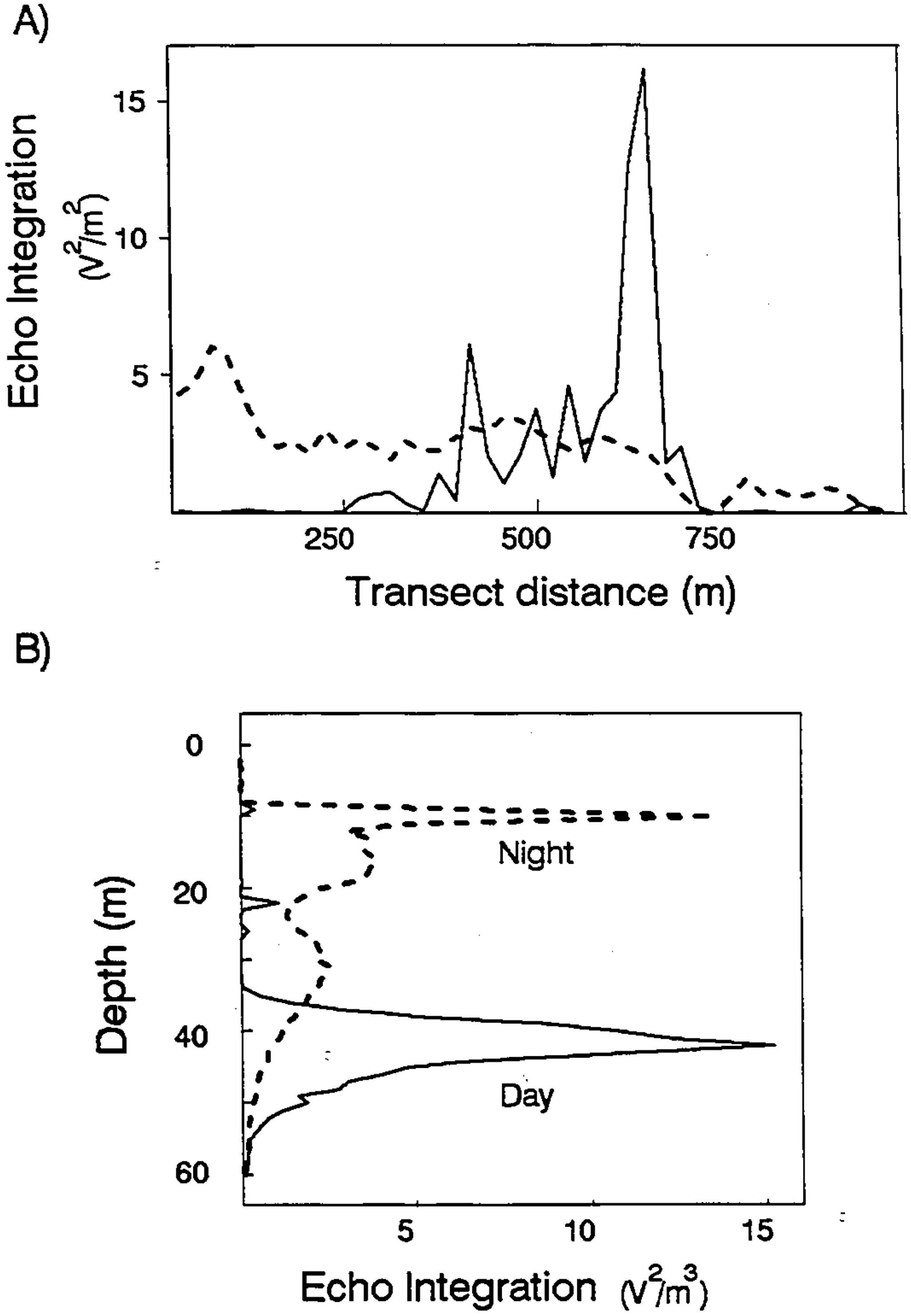

A)
Echo Integration
(V^2/m^2)
15
10
5
250
500
750
Transect distance (m)
B)
Depth (m)
0
20
40
60
Night
Day
5
10
15
Echo Integration (V^2/m^3)

Fig. 6. A) Typical day-night changes of horizontal distribution of fish derived from echo signal of a transect sequence (values averaged over 50 m and over all depths). During the day (continuous line) high variability of acoustic values derived from schools were prevalent. During the night (broken line) less variable data due to dispersion of fish were observed. B) Diel vertical distribution patterns of fish in Lake Memphremagog averaged across a transect (22/8/88). Echo-integration values are separated into 1 m depth intervals (day = continuous line; night = broken line).

Measurements of surface ambient light energy during daytime, together with measurements of light absorption in the water column as a function of depth (chapter 1), were used to calculate light levels at the depths where fish schools were located during acoustic surveying. Schooling smelt were typically observed at depths with light levels $< 0.01\ \mu W/cm^2$ during day surveys. These values refer to the maximum of the fish biomass distribution with depth and are calculated on the basis of complete transects.

DAY - NIGHT REPLICATES

Measurements of echo scatter (quantified by echo integration) yielded estimates of fish abundance that increased at sunset, peaked at night, decreased near sunrise and were at their lowest during daylight hours (Fig. 7). To statistically evaluate these trends I compared echo integration abundance estimates derived from replicated transects surveyed within a single 24-hour period. Fourteen of 17 such day-night comparisons had higher echo scatter (higher estimated abundance) during the night (Table 2). The mean echo scatter and calculated fish density during night surveys was significantly greater than that of day surveys (paired t-test; t= 2.89; df: 16; p= 0.011). A regression model using estimates of fish density during daylight hours as the dependent variable and estimates of fish density during darkness as the independent variable, revealed a significant ($p = 0.001$; $r^2 = 0.53$; $n = 17$) positive relationship (Table 3; Fig. 8). Although the intercept was not significantly different from zero, the slope of this regression (0.53) was significantly ($p < 0.01$) different from 1.

FIGURE 7

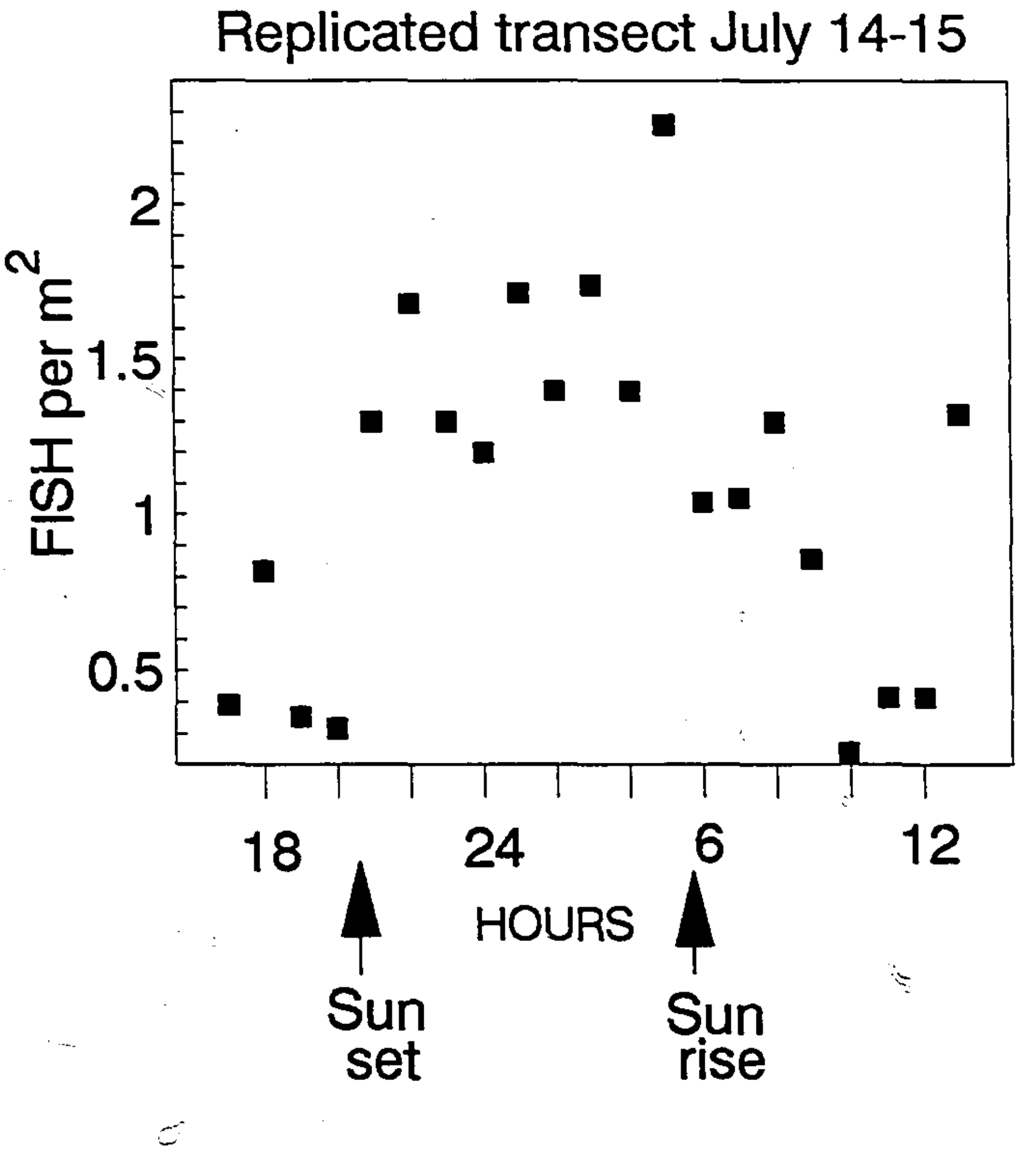

Replicated transect July 14-15
FISH per m^2
2
1.5
1
0.5
18
24
6
12
HOURS
Sun set
Sun rise

Fig. 7. Fish density as measured repeatedly along a single transect over 24 hours on July 14/15 1988. The day-night pattern is typical of that observed during 24-hour studies conducted during June - September 1988 & 1990.

Table 2. Day-night comparison of fish densities (fish/m^2) obtained from replicated acoustic transects in Lake Memphremagog. Equivalent day-night estimates were conducted within 24-h at the same transect location. The number of replicates (N) and the year of investigation are indicated.

	DAY	N	NIGHT	N	YEAR
	0.50	3	1.31	2	1988
	1.50	4	1.32	3	"
	0.60	2	1.44	5	"
	0.66	5	1.57	5	"
	0.85	3	3.03	1	"
	2.25	1	4.87	1	"
	1.58	3	2.95	2	"
	1.52	2	2.16	4	"
	2.86	9	2.21	2	"
	1.95	2	2.26	2	"
	2.34	6	2.40	2	"
	2.36	4	2.79	5	"
	0.85	5	0.73	5	1990
	0.14	3	0.26	4	"
	0.28	6	0.49	5	"
	0.29	4	0.57	4	"
	0.19	3	0.33	3	"
Mean	1.22	17	1.81	17	
S.Dev.	0.89		1.22		

FIGURE 8

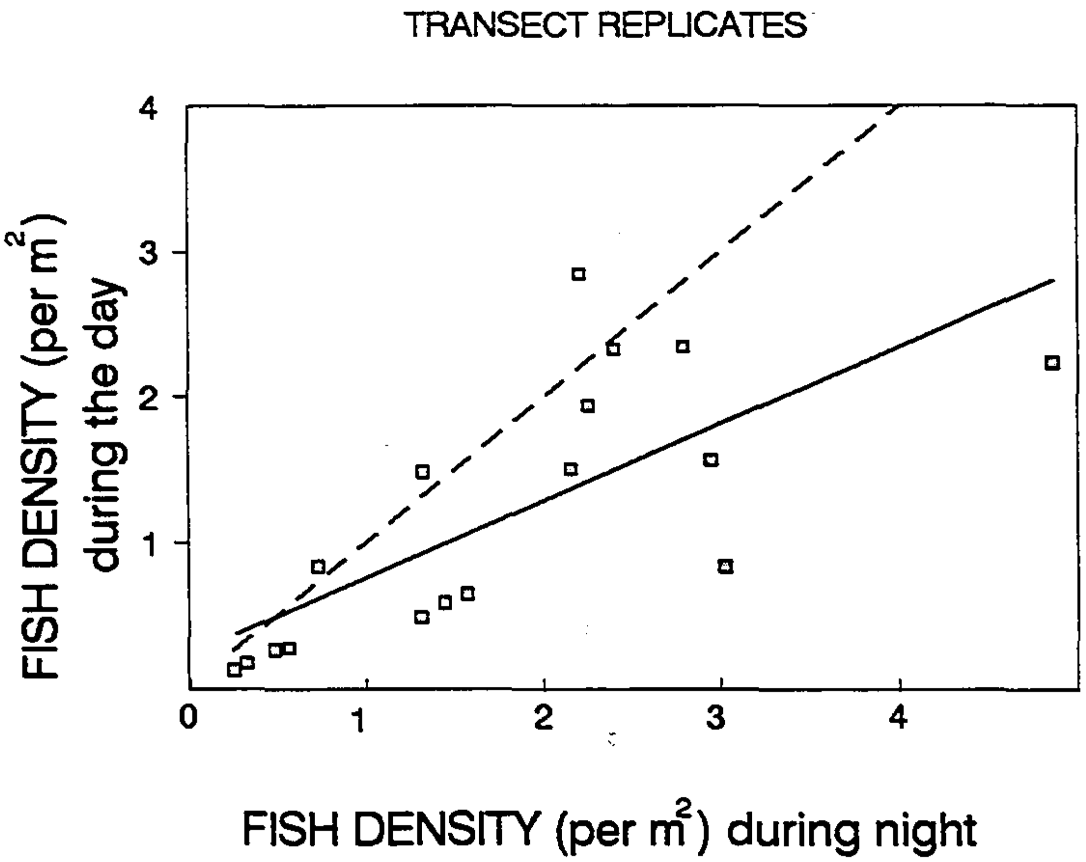

TRANSECT REPLICATES
4
3
2
1
0
1
2
3
4
FISH DENSITY (per m^2) during the day
FISH DENSITY (per m^2) during night

Fig. 8. Mean night (X axis) and day (Y axis) hydroacoustic estimates of fish density, obtained during day-night surveys, conducted over 24 hours on identical transects. Fish densities are averaged across the complete transect. (continuous line indicates calculated regression line; solid line indicates the line of equality)

Table 3. Regression analysis of day-night differences of replicated acoustic transects in Lake Memphremagog. Comparable estimates were conducted within 24-h. Estimates are given in fish/m^2.
Model: Day densities = A + B*(night densities)

Variable	Coefficient	S.E.	p
A	0.26	0.28	0.36
B	0.53	0.24	0.001
	r^2= 0.53	N = 17	

ACOUSTIC FISH SIZE MEASUREMENTS

During the summer of 1990 I conducted 16 quantitative acoustic surveys of the Central Basin. During each I estimated average fish size and fish abundance acoustically in the basin during both day and night. The selection of single echoes to determine fish size was performed using Biosonics echo shape criteria for single fish echoes. Day surveys yielded fewer single fish echoes than did night surveys because of the tendency for smelt to school during daylight. On average, I obtained 1111 (std. dev. 1122) single echoes per day survey and 2711 single echoes (std. dev. 1327) per night survey. Covariance analysis of the average strength of single echoes in relation to day, night and season was conducted. I applied a multiple regression model to the acoustic data using fish size as the dependent variable and a day-night dummy variable (day=0; night=1) as the treatment effect. The covariate was season, expressed as calendar day. The interaction between treatment (day-night) and covariate (calendar day) was not significant ($p = 0.46$)

The covariance analysis revealed (Table 4; Figure 9):

1) no significant difference in average acoustic fish length between day and night ($p = 0.57$); and,

2) no significant change in average acoustic fish length over time ($p = 0.38$).

FIGURE 9

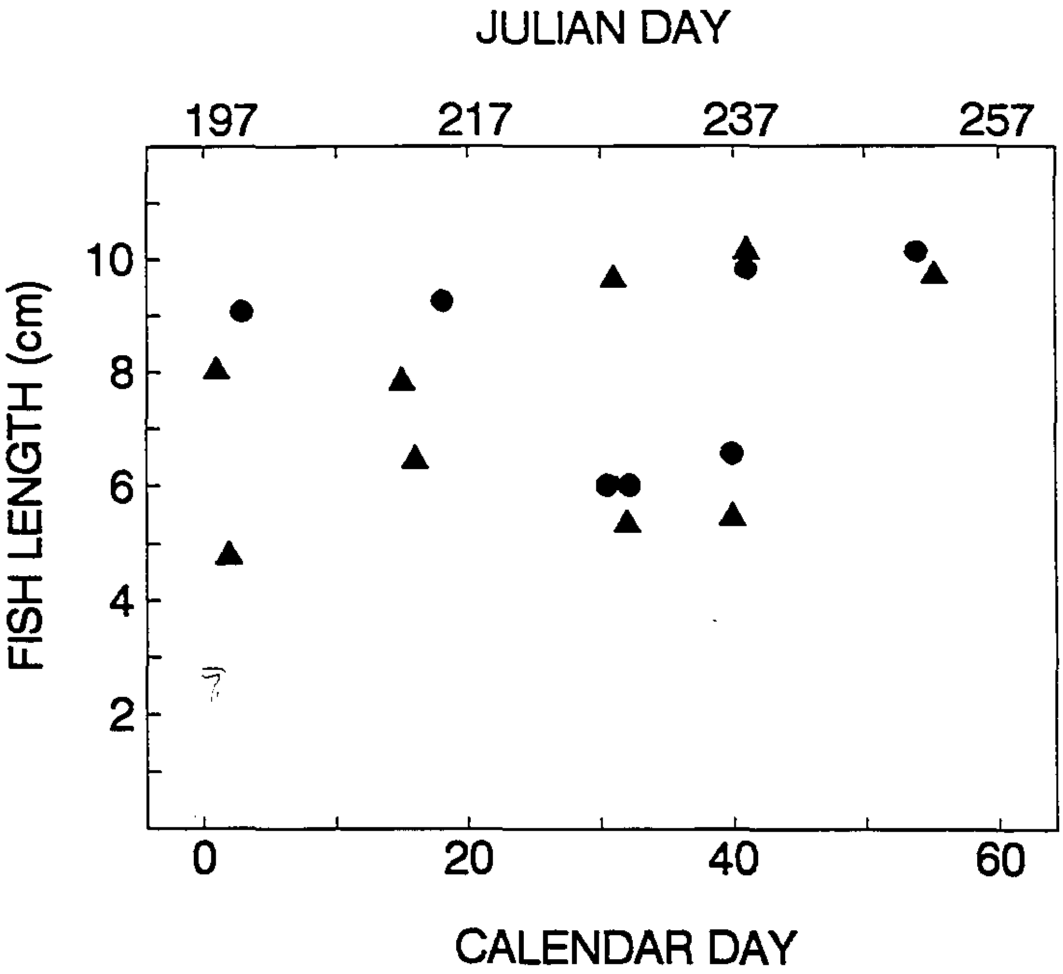

JULIAN DAY
197
217
237
257
FISH LENGTH (cm)
10
8
6
4
2
7
0
20
40
60
CALENDAR DAY

Fig. 9. Hydroacoustic estimates of mean fish length (target strength) obtained from surveys of Central Basin of Lake Memphremagog conducted throughout the summer of 1990. (circles = night; triangles = day surveys).

Table 4. Analysis of covariance for fish target strengths measured in Lake Memphremagog. Day-night (day=0; night=1) is the treatment variable; calendar day is the covariate. Both variables were insignificant.
Model: Acoustic fish size = A + B*(Day-Night) + C*(cal.day)

Variable	Coefficient	S.E.	p
A	-48.67	1.1	<0.001
B	0.63	1.095	0.57
C	0.03	0.032	0.38
	$r^2 = 0.10$	N = 16	

Anova

Source	SS	Df	MS	F	p
Regression	6.33	2	3.17	0.69	0.52
Residuals	59.79	13	4.6		

DAY-NIGHT WHOLE BASIN ESTIMATES OF FISH ABUNDANCE

My analysis of acoustic fish size led me to conclude that observed variations in average TS were not a product of day-night or seasonal influences. I therefore calibrated the acoustic fish abundance data (echointegrated values in V^2/m^2) for each survey using the average scaling factor (0.6 fish/V^2) derived from all surveys ($n = 16$). To assess the influence of day-night and seasonal changes in fish behavior and abundance on acoustic fish estimates, I conducted an analysis of covariance by applying a multiple regression model to the acoustic data. I used estimated fish abundance as the dependent variable and a day-night dummy variable (day=0; night=1) as the treatment effect. The goal of this analysis was to determine whether acoustic fish abundance changed significantly between day and night. I used calendar day as a covariate for fish abundance in order to determine seasonal changes in fish abundance. Before conducting the analysis of covariance, I tested for significant interactions between covariate and treatment by applying a multiple regression model with fish abundance as the dependent variable treatment effect (day-night), covariate (calendar day) and interaction term (day-night variable * calendar day) as independent variables. I found that the interaction term was not significant ($p = 0.39$). It was therefore dropped from further analysis. The analysis of covariance with treatment variable (day=0; night=1) and covariate (calendar day) revealed that the treatment effect and covariate were highly significant ($p < 0.001$) with an overall r^2 of 0.86. This analysis revealed the following (Table 5):

1) Fish abundance increased with time during the study ($p < 0.001$); and,

2) Estimates of numerical abundance were significantly ($p < 0.001$) lower during the day than at night (Fig. 10).

FIGURE 10

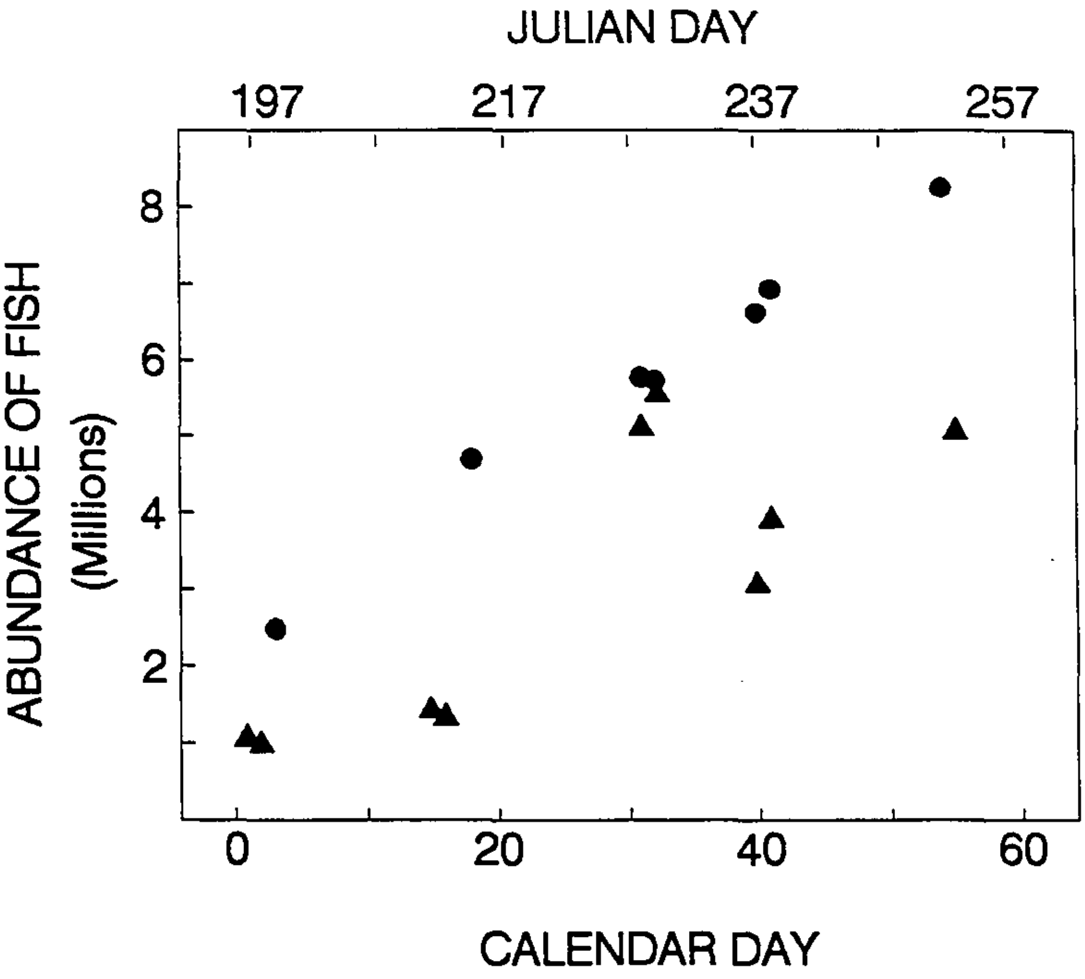

JULIAN DAY
197
217
237
257
ABUNDANCE OF FISH
(Millions)
8
6
4
2
0
20
40
60
CALENDAR DAY

Fig. 10. Hydroacoustic estimates of the number of fish for the central basin of Lake Memphremagog obtained from acoustic surveys conducted during the summer of 1990. (circles = night; triangles = day surveys)

Table 5. Analysis of covariance for fish abundance measured in Lake Memphremagog during 16 acoustic surveys. Day-night (day=0; night=1) is the treatment variable; calendar day is the covariate. Both variables are significant. Fish abundances are given in total numbers of fish; estimate for central basin only.

Model: Fish abundance = A + B*(Day-Night) + C*(cal.day)

Variable	Coefficient	S.E.	p
A	$6.4*10^5$	$4.6*10^5$	0.19
B	$2.2*10^6$	$4.6*10^5$	<0.001
C	$9.4*10^4$	$1.4*10^4$	<0.001
	$r^2 = 0.86$	N = 16	

Anova

Source	SS	Df	Ms	F	p
Regression	$0.68*10^{14}$	2	$0.34*10^{14}$	41.41	<0.001
Residuals	$0.11*10^{14}$	13	$0.82*10^{12}$		

DISCUSSION

I observed that acoustically derived estimates of fish abundance were significantly lower during the day than at night. These differences were consistent in the results of two different survey designs: 1) repeated acoustic surveying of a single transect during day and night; and 2) acoustic estimates of fish abundance in the entire basin during day and night. Spatial patterns of fish differed between day and night. Distributions were consistently highly aggregated and patchy during daylight hours and were highly dispersed at night.

The measured acoustic differences were not due to day-night differences in the availability of fish to the beam, because throughout the study the fish remained within a thermal refuge and could be targeted with the sampling gear with equal effectiveness during day and night. I also found that diel vertical displacement of the fish, which coincided with the diel change in patchiness, did not result in significant changes in the average TS for solitary fish. These data clearly indicate that the day-night differences in measured fish abundance cannot be explained by depth-related changes in behavior that result in changes in the average TS of fish. The illumination levels at the depths occupied by fish during daylight hours were very low ($<0.01\ \mu W/cm^2$; depth = 30-40 m). The observed differences in acoustic measurements, were not, therefore, a consequence of diel differences in fish avoidance of the survey vessel.

I therefore conclude that the lower estimates of fish abundance consistently obtained when surveys were conducted during daylight, were caused primarily by diel changes in fish aggregation and in particular, the dense schooling of these fish during daylight hours. In two separate analyses (24-hr surveys along single transects and day-night whole lake surveys) my data indicate that acoustic abundance estimates obtained by ensonifying fish when they were densely schooled were, on average, approximately 50% lower than estimates obtained by ensonifying fish at night.

Evidence for acoustic shadowing of fish in aggregations

These in situ observations of wild fish fully support Roettingen's hypothesis that acoustic shadowing can lead to a significant underestimation of fish abundance when the acoustic backscatter is generated by dense schools. The question arises whether day-night differences in acoustic scatter can be causally linked to this effect, and whether it will be possible to generalize these findings. The answers to these questions are critical for any attempt to model and correct biases in fish abundance estimates resulting from acoustic shadowing.

Bazigos (1975), Gerlotto (1989) and Soria and Freon

(1991) have hypothesized that day-night differences observed in their acoustic studies were mainly the result of bias introduced by fish avoidance during the day. This hypothesis is supported by the observations of Olsen et al. (1983a and b), who observed that schools of fish avoid survey vessels by swimming to greater depths. They further suggest flight reactions of fish increase with their proximity to the surface and is stronger in relation to the survey vessel speed. However, Olsen et al (1983a) also reported that "a comparison between day and night observations did not indicate any great difference in reaction patterns." It is questionable, therefore, whether observed day-night differences in acoustic estimates in general, and specifically those in my study, could be attributed to the flight reactions of fish.

In fact, contrary to expectations derived from the avoidance hypothesis, my abundance estimates were greatest during night when the fish were located near the surface (i.e. in closer proximity to the survey vessel). Flight reactions related to vessel avoidance, which typically consist of fish escaping to greater depths, should produce marked changes in average echo levels, because the tilt angle of the fish in the acoustic beam will change (Olsen et al. 1983b). While such effects may also occur when fish are very close to the surface and the survey vessel, we observed no significant changes in average TS between day and night surveys during the >3 month duration of our study in 1990. This may be because the fish studied were typically located at least 10 m below the surface at night and even deeper during the day (25-40 m) and were therefore not disturbed by the boat.

In general there are two ways in which fish can detect the presence of survey vessels: acoustic signals ("noise") and visual signals. I observed that, during darkness and during the day, the fish studied showed no obvious flight reactions to avoid boat noise (motors). This might be explained by the fact that most fish species are sensitive only to frequencies below 2000 Hz, the major exception being the cypriniform fishes (Myrberg 1978). My survey vessel was small (5m) and, both the boat and generator were powered by high frequency motors, unlike vessels used in ocean surveys (Olsen et al. 1983b). Because the fish we surveyed were closer to the surface (appr. 10 m) during the night-time surveys, and because these surveys yielded higher abundance estimates, it is unlikely that noise disturbance could be responsible for the day-night differences in fish abundances I observed.

Finally, it is very unlikely that the fish surveyed in my study were disturbed by visual signals because all light sources were extinguished during night surveys. I had, in fact, observed that smelt can be attracted by a strong flashlight, and by illuminating the water column for several minutes. It could, of course, be hypothesized that during the day fish located at depths between 30-40 m could see the survey vessel and react. This hypothesis can also be rejected because light transparencies in the study area were insufficient to allow visual detection of the boat by fish located at these depths. Secchi depth extinctions conducted during the investigation generally occurred at depths between 4 and 8 meters while the depth at which smelt schools occurred during day light hours (30-40 m) typically had light levels < 0.01 μW per cm^2. It is very unlikely that smelt could see a 5 m boat from a depth 30 m at such low illumination. Woodhead (1966) noted that "even in oceanic waters maximum sighting ranges of fish would probably be little more than 35 m, and that for most fish they will be much less than 17 m even in good conditions". Blaxter (1980) has demonstrated that sighting distances of fish are reduced dramatically under the influence of both low illumination levels and high beam attenuation in the water column related to turbidity. Using Blaxter's data I estimated the sighting distance for fish under the light intensity and turbidity conditions measured in Lake Memphremagog at the depths occupied by smelt to be < 3m (beam attenuation coef. 0.4; light intensity < 0.01 $\mu W/cm^2$). I also observed that smelt schools, when ensonified during daylight hours, exhibited flight reactions to a video camera lowered from the boat only when the camera reached a depth approximately 5 meters shallower than that of the schools.

Physiological factors have also been hypothesized to influence day-night differences in acoustic abundance estimates. Foote (1983) hypothesized that the average TS may change during diel vertical migrations. Changes in swimbladder volumes with depth could, for example, produce lower average target strengths for fish in deeper waters. However, this would also lead to negative buoyancy with a corresponding requirement for swimming or changes in the tilt angle to compensate for sinking. It is not clear whether these effects occur, and whether the combined reactions would result in lower average TS. Ona (1990) has shown that the average TS of fish may vary considerably for a species. He found that a factors such as the degree of gut filling and body fat content can lead to natural variations of acoustic target strengths. While such sources of variance in acoustic TS may occur, my data, obtained over three months of surveys, revealed no such day-night or seasonal variation.

I conclude, therefore, that the day-night differences in estimates of fish abundance observed during my surveys resulted from acoustic shadowing related to the aggregating behavior of the fishes I studied. Toresen (1991) also showed that acoustic shadowing occurs in natural aggregations of herring.

Seasonal increase in fish abundance in the central basin

My data revealed a >3-fold increase in fish abundance during the study period of summer 1990. At the same time, I found no significant seasonal changes in the average acoustic size of these fishes. These trends were consistent in both day and night survey data. The most plausible explanation for this seasonal increase in fish abundance within central basin is that smelt exhibited a seasonal intra-lacustrin migration within Lake Memphremagog during the investigation. This migration led to a large-scale aggregation of the adult stock in the deeper and colder waters of the central basin as fish left the shallower north and south basins in search of a thermal refuge during the summer months. This conclusion is consistent with the observation that adult smelt schools were frequently observed in the south and north basins in the spring when water temperatures there were < 18° C.

The intra-lacustrin migration hypothesis is also supported by observations that adult smelt surveyed in the central basin showed strong avoidance behavior to water temperatures > 18 °C (chapter 1; also see Evans and Loftus 1987), and did not enter surface waters exceeding these temperatures. The seasonal warm-up of the lake's surface waters, which ultimately reached temperatures as high as 25 °C, and the resulting gradual increase in the depth of the thermocline, results in a decrease in acceptable thermal habitat which is most pronounced in the shallower south basin of the lake. In both 1988 and 1990, during late summer water temperatures exceeded 18 °C, at all depths in this basin. In the north basin only small pockets of cooler waters, which were restricted to deeper areas, were observed. The central basin alone provided a large thermal refuge at this time. These seasonal movements to deeper hypolimnetic refuges have been previously reported for smelt (Burczinsky et al. 1987).

Consequences for calibration of acoustic data

My data strongly support the hypothesis that acoustic shadowing occurs when fish are densely aggregated. This, in turn, implies that acoustic scattering is linearly related to fish abundance only when fish are not aggregated in dense schools. The assumption of a linear relationship between fish abundance and acoustic scattering is central to current hydroacoustic assessment methods. A reassessment of methods currently employed for scaling echo integrated measurements is thus necessary. The currently used scaling methods are:
1) Single fish signals are counted from an acoustic monitor to establish a relationship between numbers of fish and echo integrated values measured coincidentally (Midtun and Nakken 1977; Bayona 1984). These derived calibration factors, which relate echo levels and real fish units, are then applied to

acoustic measurements without reference to the aggregation patterns of fish.

Since single fish cannot normally be counted from the multiple fish echo typically derived from a school, this method lacks proof of validity. For example, Johannesson and Losse (1977) found a discrepancy between calibration factors derived by counting single fish and by direct calibration of acoustic measurements conducted by net caged fish with "more relevant fish densities". They wrote that "the net cage constant was about 30 % higher than that obtained from the counting method", and concluded that "this discrepancy observed does not permit a conclusive explanation". Our findings strongly suggest that this phenomenon may have resulted from acoustic self-shadowing of fish when aggregated.

Haug and Nakken (1977) when relating trawl catches to echo integrated values observed that the results deviated in respect to fish density levels. They hypothesized that "large differences in relative units between fish catches and acoustic values are probably caused by a systematic underestimation of low fish densities when using trawls". My findings suggest the alternative hypothesis that at high fish densities the echo integrated values could be too low, thus resulting in underestimation of fish abundance.

2) The average TS is estimated by dual beam or split beam acoustic devices and is used to scale the integrated echo

values (Bayona 1984; Burczinsky and Johnson 1986). Here, too, the assumption is that the total echo signal strength measured from a school equals the sum of the signals from the individual fish being ensonified. My results clearly indicate that this approach is invalid when fish are schooled at high densities. The calibration factors I derived from TS measurements failed to yield identical estimates of fish biomass and numerical abundance of fish in a day-night comparison. Day time estimates of fish abundance, which were derived from aggregated fish, were consistently and significantly lower.

These findings lead me to conclude that acoustic estimates of fish abundance derived from ensonification of fishes that are densely schooled, such as polarized schools, are likely to be regularly biased downward due to acoustic shadowing. Several potential solutions to this problem exist. One solution would be to survey only at times when fish are dispersed, or occur in loose schools. This solution is likely to be unobtainable for some species, but in many survey situations such as the one I describe, it may be feasible to exploit day-night differences in schooling patterns to sample fish populations more accurately. Failing this, it may be necessary to consistently calibrate acoustic data derived from schooling fish by quantitative sampling. This may, however, be difficult tc achieve since many fish species are known to be difficult to sample quantitatively during daylight hours and when schooling (Woodhead 1966; Blaxter and Parrish 1965; Dembinski 1971; Leggett and Jones 1971; Northcote and Rundberg 1971; Morse 1989).

In some situations the biasing effects of fish aggregation on acoustic measurements can be established by employing the theoretical models developed by Lytle and Maxwell (1983). These theoretical models were developed to account for sound attenuation and interactions of echoes when fish occur in high densities, and when multiple layers of fish are present in the acoustic wave. Burczinsky et al (1990), in an attempt to apply this model to acoustic data obtained from dense aggregations of fish contained in enclosures, found that while the model corrected fish estimates in the right direction, it failed to yield results consistent with the known fish density, the estimates being much too low when fish were ensonified with a downward oriented transducer. This method can be tested and applied relatively easily in survey situations where a homogeneous aggregation of fish with constant acoustic signal is prevalent. However, difficulties arise when fish schools are patchy in their vertical or horizontal distribution and the survey vessel is moving along transects, as was the case in my daytime surveys and is typical of most acoustic surveys. Under these conditions the acoustic signal strength varies greatly, ranging from very high values when a school is encountered to zero values when no schools are present. When calculating in situ fish densities from echo-integration data, the echoes are typically averaged over large horizontal spatial intervals (Johanneson and Mitson 1983; Burczinsky and Johnson 1986). In my case I used 50-m intervals. However, in order to apply the Lytle and Maxwell (1983) model to correct acoustic densities obtained from in situ schools, echo integration data must be recorded from single schools which have been subdivided into thin depth layers. This greatly restricts the model's utility in large scale surveys.

It is possible, however to compute ratios of acoustic estimates obtained from comparative surveys conducted at times when fish are dispersed and again when they are aggregated in schools. Such ratios can then be applied as an "aggregation factor" in concert with the usual "scaling factor" in order to calibrate acoustic estimates of schooling fish. In my study the average "aggregation factor" required to compensate for the bias induced by day-night differences was 2.1 (std. dev. 0.66; n = 9). Clearly, it would be desirable to derive more general empirical models having reliable measures of fish aggregation and school size with which to predict effects on echo signal strength. Toresen (1991) approached this problem for dense herring aggregations by calculating the acoustic absorption in herring schools from observed losses in the bottom signal strength. For the three schools he observed, the "aggregation factor" ranged from 10 % to 41% of the observed value. These values are lower but not inconsistent with my estimate of 50 %. Soria and Freon (1991) reported that acoustic estimates of fish abundance obtained at night from tropical oceanic regions were approximately twice those obtained during day light hours. It is interesting that these diel differences are equal in direction and magnitude to those I observed, although, the possibility that the differences Soria and Freon observed might be related to fish avoidance of the survey vessel during daylight cannot be dismissed (Soria and Freon 1991).

Clearly many more such comparative studies of schooled and dispersed fishes will be required to effectively model the influence of fish aggregation and its associated acoustic shadowing on estimates of fish abundance. For the moment, however, it appears safe to conclude that estimates of fish abundance based on acoustic surveys conducted on schooling fishes should be considered regularly and significantly biased. The data available (Toresen 1991; Soria and Freon 1991; this study) indicate that the magnitude of this bias could be as high as 50%. Moreover, the results of my studies, together with those of Soria and Freon (1991) suggest that this bias may be avoided in cases where it is possible to exploit the natural behavior of fishes which alternate between aggregated and dispersed distributions and by timing the acoustic surveys to coincide with the interval during which they are dispersed.

CHAPTER 3

SERIAL CORRELATION IN TRANSECT SURVEY DATA AND THE APPLICATION OF CLUSTER SAMPLING TO HYDROACOUSTIC FISH SURVEYING.

ABSTRACT

Fish abundance data obtained by hydroacoustic surveys along fixed transects possess several inherent problems of statistical analysis which render the calculation of sample errors difficult and questionable. Three different approaches to the calculation of sample errors were compared: 1) simple random sampling of complete transects, 2) sequential data sampling from within transects, and 3) cluster-sampling with correction for spatial correlation of within-transect units. Sequential data sampling without correction for autocorrelation overestimated survey precision. The magnitude of the bias in such sample errors was closely related to the spatial correlation of the data within transects, as assessed by the intra-cluster correlation coefficient. The direction and magnitude of this bias was judged by comparing these sample errors with those obtained using cluster-sampling analysis, and those calculated from complete-transect data. I found that, on average, cluster estimates of sample precision were more precise than were estimates derived from data based on complete-transect sample units. The following conclusions emerge from these results: First, sequential data sampling within transects should be employed only in conjunction with correction of the sample variance by cluster-sampling analysis or other appropriate statistical approaches. Second, such within transect sampling designs

when properly applied are more efficient than simple random sampling of complete transects.

INTRODUCTION

Hydroacoustic sampling of aquatic organisms commonly utilizes the line transect approach, in which counts of organisms encountered while moving along lines that cross the area of interest are recorded at regular spatial intervals (Caughley 1977; Eberhardt 1978; Johanneson and Mitson 1983). According to Eberhardt (1978), transect sampling theory is based on the assumption that samples are drawn at random from the total population. However, when applied to marine fish surveys, rigid adherence to the randomness requirement results in high travel costs. This reality commonly dictates that researchers employing acoustic methods ignore the requirement for the random selection of samples (Johanneson and Mitson 1983), so that survey transect patterns are often regular, with samples drawn from consecutive sequences along a line transect. These consecutive sample sequences are commonly referred to as elementary distance sampling units, termed the EDSU (Johanneson and Mitson 1983). Central to an assessment of the statistical precision of this approach is a knowledge of the appropriate scales of sampling (Caugley 1977; Smith 1978).

Within the field of hydroacoustics, and its application to the assessment of fish biomass and abundance, a major debate is focused on the spatial autocorrelation in consecutive data series (Johanneson and Mitson 1983; Shotton and Bazigos 1984; MacLennan and MacKenzie 1988; Simard et al 1992). For example, Williamson (1982) used simulated data to demonstrate that confidence limits calculated from within transect units with high autocorrelation are statistically unreliable. His analyses revealed that spatial patterns in the distribution of animals within transects are important contributors to bias in estimates of sample error of surveys which employ within-transect data units. It is clear, therefore, that both the patterns of animal aggregation in space, the sampling designs used to assess their abundance and biomass, and the spatial scale of the sampling are central to the precision of acoustic transect sampling (Caughley 1977; Williamson 1982; Jolly and Hampton 1990a).

The objectives of this study were to explore the magnitude of the problem associated with the calculation of sample errors when fish are spatially correlated within transects and the sampling designs employed ignore key statistical requirements. A second objective was to explore an alternative survey design and statistical analysis, called cluster sampling, which might avoid or minimize the bias associated with traditional techniques. Williamson (1982) recommended cluster sampling, a hierarchical sampling method (Cochran 1977) for the application in acoustic transect sampling to alleviate inherent problems in the data analysis. This is the first application of cluster sampling to hydroacoustics following the method proposed by Hansen et al. (1970).

METHODS

Study site

The study site was Lake Memphremagog Quebec/Vermont, which has a total surface area of 8000 ha, and is long (40km) and narrow (average width 2.4 km) containing three distinct basins which differ in mean depth: south basin 6.2m; central basin 44.3 m; and north basin 14.7m. Maximum depth, 110 m, occurs in the central basin. The central basin has a surface area of 2046 ha and consists of an elongated (15 km x 2 km), deep trench with steep shorelines. The pelagic fish community of Lake Memphremagog is dominated by rainbow smelt (Osmerus mordax). These fish undergo diel changes in spatial aggregation patterns (Dembinski 1971; Burczinsky et al 1987). The diel patterns in distribution exhibited by smelt in Lake Memphremagog are described in detail in chapters 1 and 2. To summarize, during darkness, smelt dispersed into more homogeneous fish layers located at or near the thermocline. No schooling was observed during darkness. During the day individuals moved to greater depths and formed dense schools.

Acoustic devices and data processing

I employed a 120-kHz Biosonic Model 105 dual beam echosounder to quantify the abundance of pelagic fishes in the lake. Beam angles were 11 and 25 degrees. Fish density measurements were conducted only on the narrow beam. The system was mounted in a 5-m outboard powered boat. The transducer, which was mounted in a V-fin towing body, was suspended on elastic cord from a davit to dampened wave-induced motion. The transducer was towed at a depth of 1 m. Boat speed was between 8 and 8.5 km/h. During sampling all lights were turned off to minimize influence on the fish being ensonified.

The acoustic surveys were conducted in multiplexed mode using both 20 log R and 40 log R amplifications of the time varied gain on alternating pings. Ping rate was 5 pings per second with a pulse length of 0.4 ms. A video recorder was used to record all acoustic signals. All data processing was performed on these recorded data.

Depth related noise peaks at 100 m depth were generally < 50 mV at 20log R amplification, and ranged from 100 to 200 mV at 40 log R amplification. I used the same receiver gain factor at +6 dB for both day and night surveys. The maximum voltages from dense schools were < 8 volts.

Estimates of fish density were obtained by echo integration of 20 log R amplified echo signals. Data processing was performed on a Biosonics Model 121 Digital Echo Integrator. Relative fish densities were expressed as squared voltage per 1 m^2 of lake surface area. Echo integrated densities were subdivided into depth windows. Signals from the top 10 m were excluded from the analysis because the presence of small non-migrating fishes in the shallow, warm water layers biased data from these depths.

Sample design

I restricted my acoustic surveys to the central basin of Lake Memphremagog, where all fish in the population could be effectively ensonified. I conducted 7 night surveys and 9 day surveys of the smelt population in this basin during July - September 1990. The survey design employed was developed using the following two considerations. 1) In theory, when acoustically surveying a water body using a line transect approach, the total population of samples consists of imaginary, parallel, non overlapping acoustic transects covering the entire survey area. From this total transect population a random subset of individual transects is typically selected for analysis. 2) In my study, the total basin area was divided into 40 parallel 350-m-wide transects extending from shore to shore and oriented perpendicular to the long axis of the basin (Fig. 1). I consistently surveyed 12 transects. Using a random number table I selected 12 of 40 possible transect locations without replacement. A unique set of transects was drawn on each sampling date. The time required to complete acoustic surveying ranged between 4 - 5 hours. The hydroacoustic record collected along each transect was amplified at 20 log R and automatically subdivided into

50 m segments using a digital echo integrator. I also created larger intra transect segments of 100, 150, 200, 250 and 300 m dimension by calculating the average echo intensities recorded from each 50 m segment and combining them to create the larger sectors.

FIGURE 1

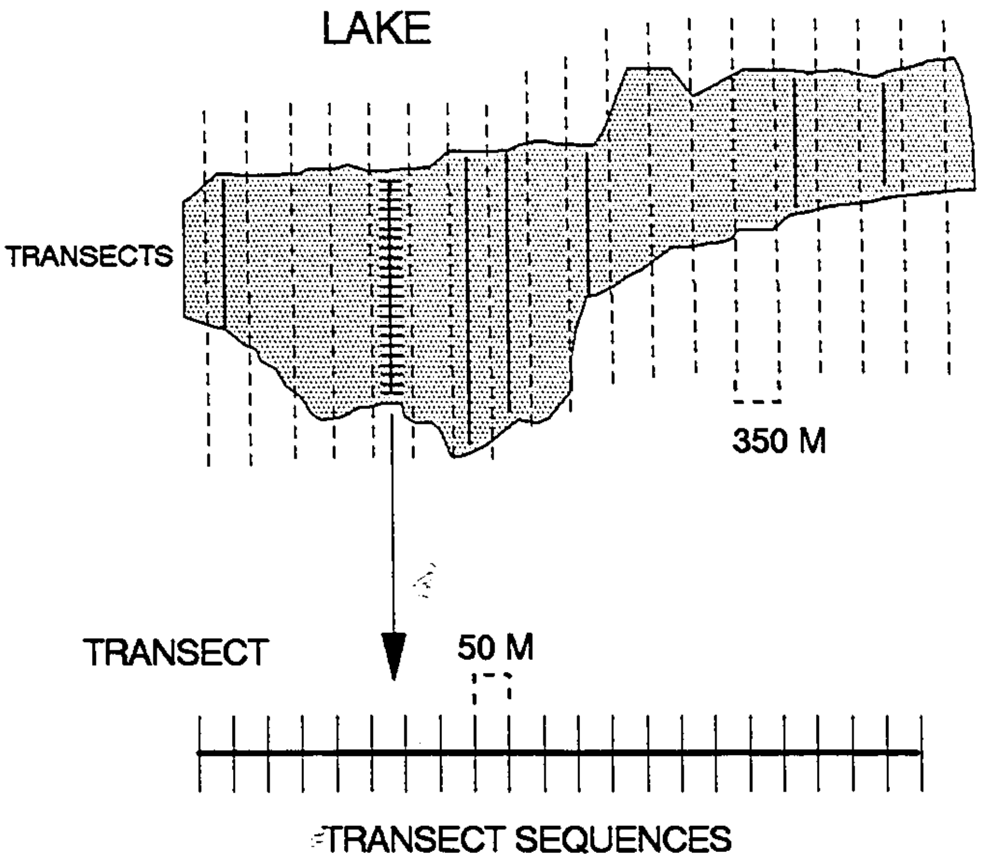


Fig. 1. Hydroacoustic sampling design and sample units as applied in this investigation. The total survey area was subdivided into parallel transect lines. For any given survey I selected 12 transects from this frame by random selection. Data was subdivided for each transect into consecutive sample units of 50 m scale.

Cluster sampling

In the treatment which follows sample precision (1/sample error) is defined as a one sided 95% confidence limit expressed as a percentage of the sample mean. Therefore, precision is high (increases), when sample error is low (decreases).

The variance of sample means was derived by two different methods:

1) No adjustment for serial correlation of data. This calculation is based on the assumption that n samples are selected independently and randomly from the sample population (Cochran 1977). The variance of the sample mean is computed using Eq. 1.

$$V(Y) = \frac{S^2}{n} \qquad (1)$$

where V(Y) = variance of the sample mean; S^2 = sample variance; and n = number of samples.

2) Adjustment for serial correlation via cluster sampling (Eq 2).

To examine the magnitude of within-transect data correlation and its influence on sample precision I employed a statistical approach known as cluster sampling (Hansen et al 1970; Konijn 1973; Cochran 1977). Cluster sampling has been proposed as an effective analytical tool in situations where random sampling is rendered inefficient due to logistic or other constraints. Cluster sampling is also particularly effective in situations in which the sample population can be subdivided into naturally occurring units and a hierarchical sampling design can be applied (Cochran 1977) such as a city subdivided into city blocks and those city blocks further subdivided into single houses (Fig. 2). In the application of cluster sampling, rather than sampling single houses based on simple random sampling designs, city blocks are selected as sample units, called clusters. All samples drawn from such clusters (i.e. individual houses within clusters) are termed within-cluster sample units. To detect possible spatial correlations between samples drawn from identical cluster units, and to adjust the estimate of variance relative to this correlation, the sample variance is subdivided into within and between cluster components. This analysis leads to a value termed the "intra-cluster correlation coefficient", or δ; a measure of the average similarity between any two samples chosen from within a single cluster (Konijn 1973). High δ values indicate that the observed variance is primarily related to between cluster differences, within cluster data being homogeneous. Low δ values are typically associated with high within cluster variance, the differences between clusters being relatively low. This difference in δ scores can therefore be used to detect spatial correlations along transects, and to correct for their effects on sample variance.

When applying cluster sampling to acoustic line transect sampling methods, the total survey area (an ocean bank, a lake etc.) is first subdivided into parallel transects (clusters). Several transects (clusters) are then selected randomly for one survey. From each transect, data are collected in a series of sequential spatial units (within cluster units = within transect sequences) (see Fig. 2).

A detailed description of the statistical theory underlying cluster sampling, and of the relevant mathematical formulations can be found in Cochran (1977), Konijn (1973) and Hansen et al (1970). The following mathematical terms and statistical definitions derived from these sources are used in this paper. The variance of the sample mean is computed following Eq. 2.

$$V(Y) = \frac{S^2(1 + \delta(m - 1))}{n} \qquad (2)$$

where m = number of within cluster units and δ = intra cluster correlation coefficient. δ is given by Eq. 3.

$$\delta = \frac{E(yij - Y)(yik - Y)}{E(yij - Y)^2} \qquad (3)$$

whereby Y = sample mean; y.. = sample values; i = transect number; and j,k = within transect sequence number. This approach assumes that in total n samples are collected in a hierarchical manner where 1) clusters are selected independently and randomly from the total population of clusters; 2) and, on average, m samples are taken from each cluster. Cluster correlation coefficients for unequal numbers of within cluster units were calculated using the mathematics given by Konijn (1973): "Statistical theory of sample survey design and analysis"; chapter 5, page 226. This extended formula was used since transect length was not constant, but varied within the survey area according to the shore to shore distance.

FIGURE 2

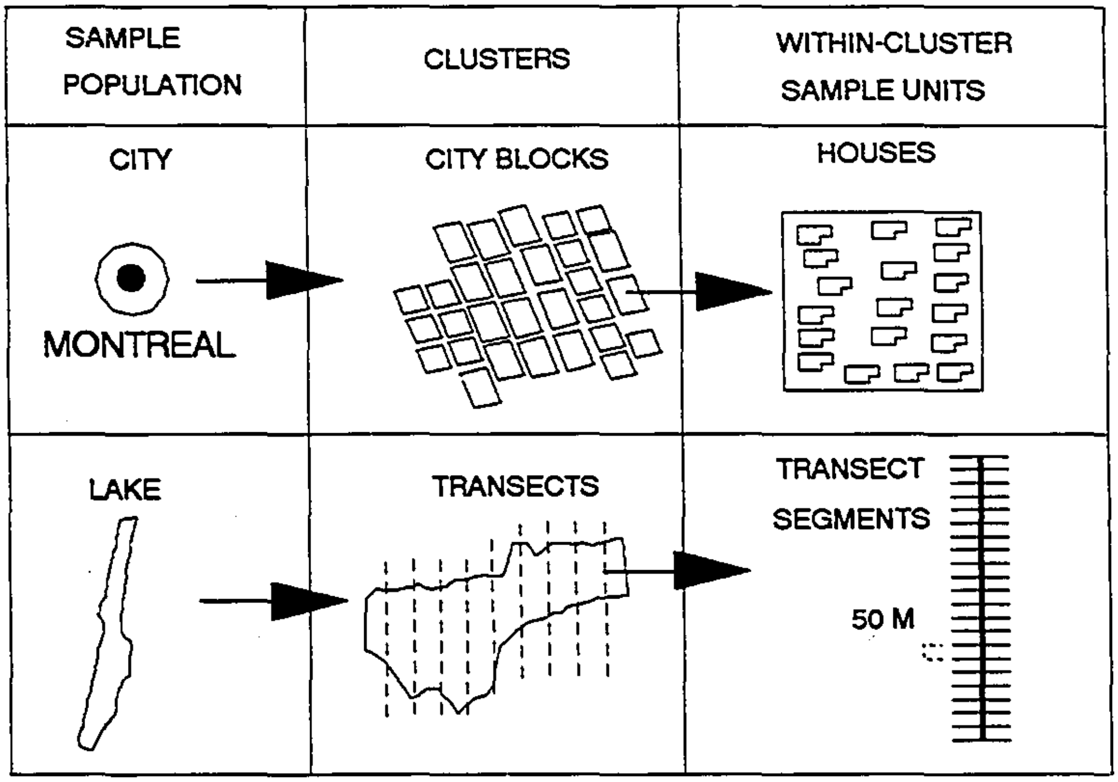

SAMPLE POPULATION
CLUSTERS
WITHIN-CLUSTER SAMPLE UNITS
CITY
CITY BLOCKS
HOUSES
MONTREAL
LAKE
TRANSECTS
TRANSECT SEGMENTS
50 M

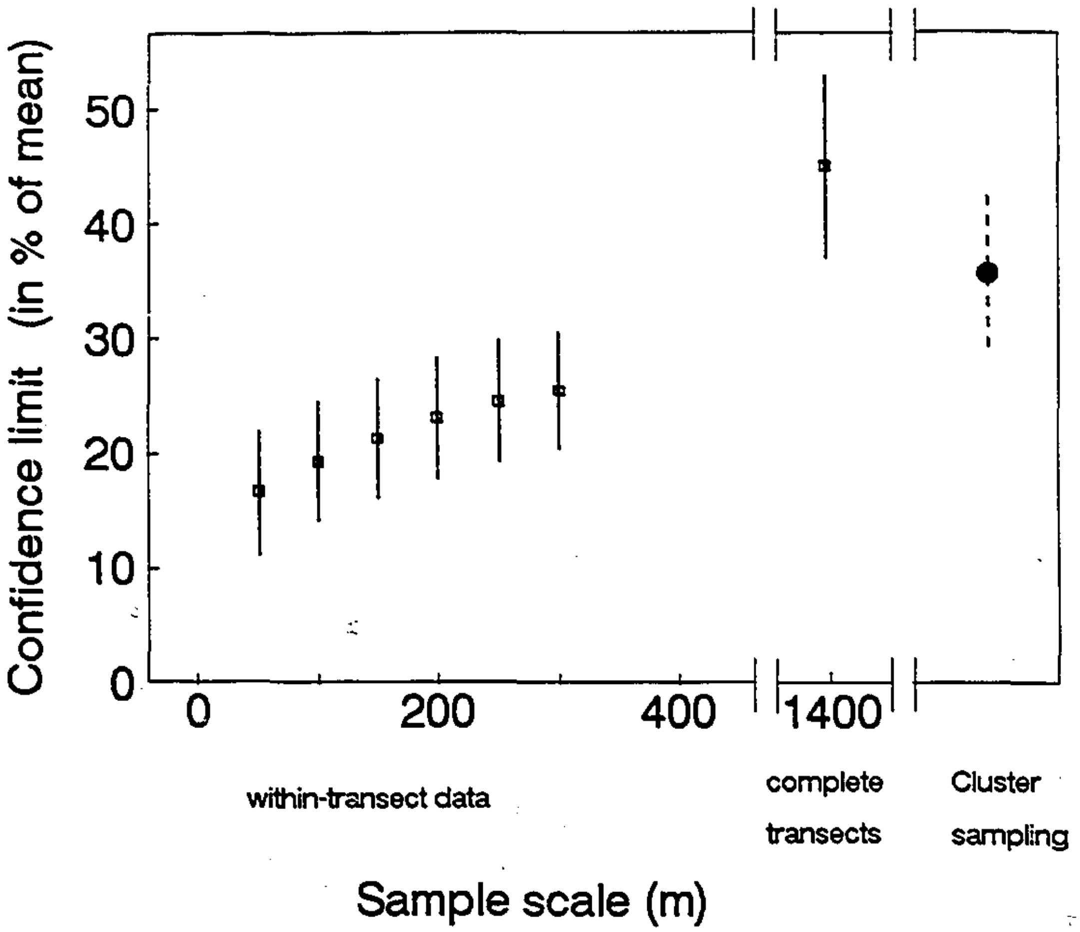
Fig. 2. Comparison of the operational units in a typical cluster sampling design. When surveying households from a city (top panel) and when surveying a lake hydroacoustically. Comparable statistical units are 1) total sample population (city households; lake) 2) cluster units (city blocks; transects) 3) within-cluster sample units (houses; within-transect sequences).

RESULTS

A. No adjustment for serial correlation

My first objective was to explore how the scale of the within-transect samples selected for analyses influenced sample error. In this analysis I ignored the potential effects of spatial correlations within transects. I used Eq. 1 to calculate the variance of the sample means. The underlying assumption in these calculations was that each transect sequence represented a valid sample unit. I calculated sample errors (95% C.L.) for all 16 surveys conducted in the central basin of Lake Memphremagog. This analysis was repeated using different sample scales ranging from 50 - 300 m at 50 m increments. I also estimated sample errors for mean fish densities based on complete transects (n=12 per survey; average transect length 1400 m). The mean sample error (16 surveys) increased with transect sequence length. The largest sampling errors being associated with analyses based on complete transects ($p< 0.001$; $r^2= 0.37$; Fig. 3; Table 1).

FIGURE 3



Confidence limit (in % of mean)
0
10
20
30
40
50
0
200
400
1400
within-transect data
complete transects
Cluster sampling
Sample scale (m)

Fig. 3. Average sample errors (+/- SD) for 16 acoustic fish surveys in Lake Memphremagog. Sample error is given as the one-sided (95%) confidence interval in % of the sample mean. Within-transect sample scales ranged from 50 to 300m. For these calculations no correction for serial correlation of within-transect data was conducted. In comparison, results from simple random sampling of complete transects and cluster sampling (50 m within-transect scales) are indicated for the same data. The average transect length was 1400m.

Table 1. Regression analysis of sample errors in relation to within-transect sampling scale for 16 acoustic surveys in Lake Memphremagog. Sample error is given in % of the sample mean; within-transect scales range from 50 to 300 m.
Model : Sample errors = A + B*(Sample scale)

Variable	Coefficient	S.E.	p
A	18.29	1.34	<0.001
B	0.019	0.002	<0.001
	$r^2 = 0.37$	N = 112	

B. Application of cluster sampling to acoustic transect data

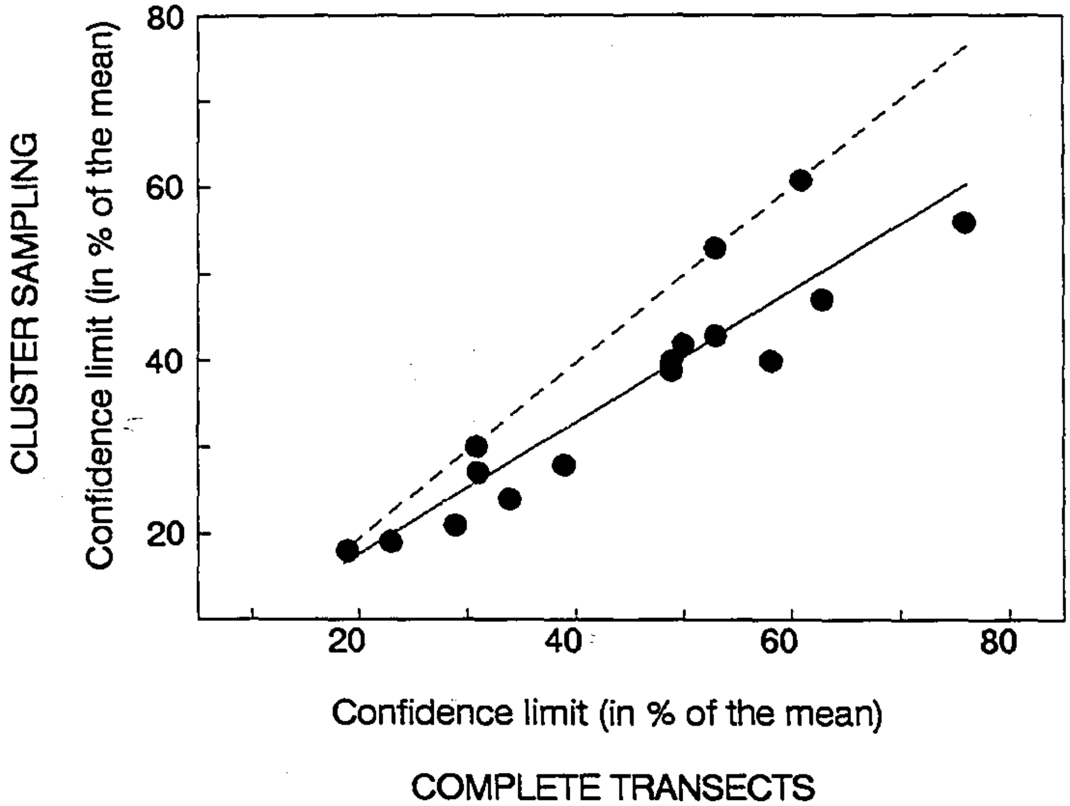
I calculated sample errors using the cluster sampling approach to data analysis. The analysis of cluster sampling was conducted on data arranged into 50 m within transect sample scales. I used Eq. 2 to calculate the variance of sample means. In general, the estimates of sample error derived from cluster sampling were similar in magnitude to those derived from data averaged over complete transects (Fig. 3).

I evaluated the influence of within sample scale dimension on sample errors calculated by cluster analysis. I found no significant difference (mean diff. = 0.25; p= 0.68; T = 0.42; n = 16) between computed sample errors based on cluster sampling analysis using data arranged in 300 m and in 50 m spatial units.

C. Comparison of analytical approaches

A detailed comparison of sample errors derived from cluster sampling with those derived through simple random sampling of complete transects revealed that, on average, lower sample errors were obtained from the cluster sampling approach (on average 8.1 % of the sample error). This conclusion is supported by the fact that a regression of cluster sampling errors versus errors based on simple random sampling of complete transects (Fig. 4) yielded a slope of 0.77, significantly < 1 (p <0.01; Table 2)

FIGURE 4



CLUSTER SAMPLING
Confidence limit (in % of the mean)
80
60
40
20
20
40
60
80
Confidence limit (in % of the mean)
COMPLETE TRANSECTS

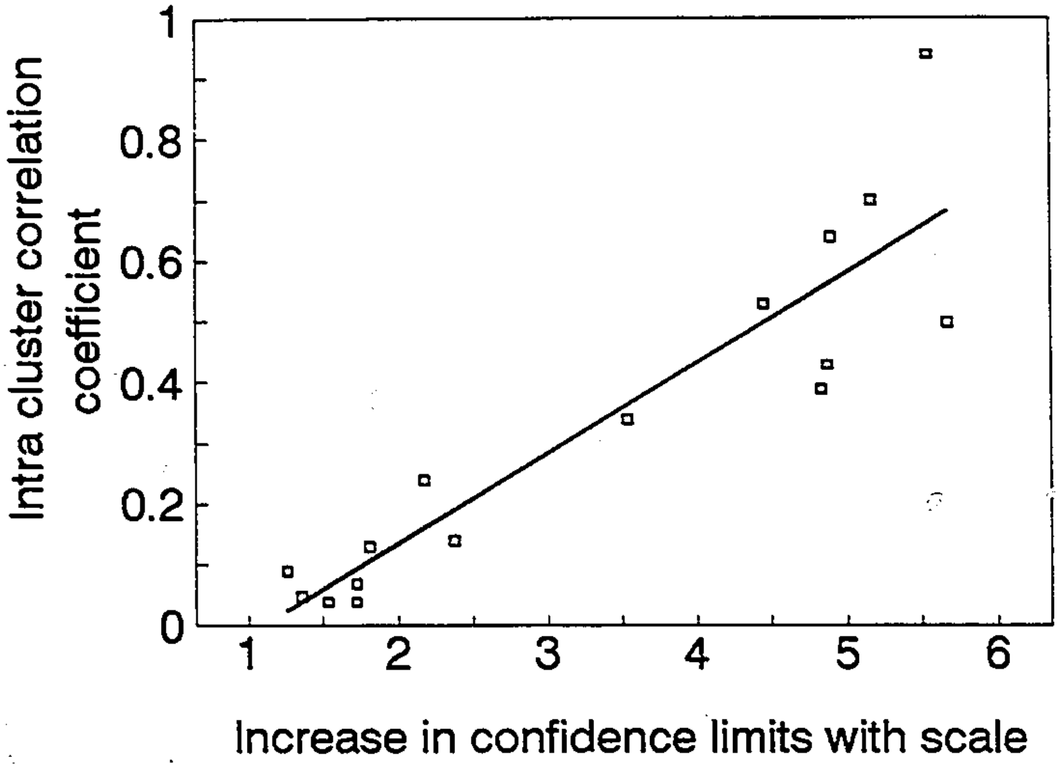
Fig. 4. Relationship between sample errors of acoustic surveys using cluster sampling analysis with sample errors calculated for the random sampling approach of complete transects. The regression analysis indicates that cluster sampling analyses result, on average, in lower sample error than analyses based on complete transect data (slope of 0.77 is significantly ($p < 0.01$) different from 1).

Table 2. Relationship between sample errors calculated by cluster sampling approach and the simple random approach, using only complete transect data as sample observations. The slope of 0.77 is significantly different from 1.
Model: cluster sampling = A + B*(simple random sampling)

Variable	Coefficient	S.E.	p
A	2.11	4.03	0.61
B	0.77	0.085	<0.001
	$r^2 = 0.86$	N = 16	

As a measure of the magnitude of the scale related instability of sample errors, I defined the ratio of the highest (1400 m complete transects) to lowest (50 m within transect) sample errors obtained for each acoustic survey. These ratios varied between 1.3 and 5.6 (Fig. 5). When regressed against the intra-cluster correlation coefficients δ for each survey, a strong positive relationship was obtained ($p < 0.001$; $r^2 = 0.84$; Table 3; Fig. 5). This result indicates that the magnitude of the bias in sampling error (as estimated from Eq. 1) related to sample scale increased with the magnitude of the within-transect data correlation. I conclude that estimates of sample error derived from within-transect data that are not corrected for within-transect data correlation are likely to be unreliable.

FIGURE 5



(50m scales : complete transect scales)

Fig. 5. Relationship between δ, the intra-cluster correlation coefficient computed for each acoustic survey, and the magnitude of scale related change in confidence limits when no correction for within-transect data correlation is made. Sample scales ranged from 50m (within-transect scales) to the scale of complete transects. This analysis shows a strong relationship ($r^2 = 0.84$) between δ values and change in confidence limits when within-transect data were uncorrected for serial correlation.

Table 3. Regression analysis of the relationship between δ, the intra cluster correlation coefficient, and the magnitude of scale related changes in confidence limits that were not adjusted for serial correlation. The change in confidence limits is given as the ratio of highest (complete transects) to lowest (50m within-transect scale) confidence limits (95%).

Model : $\delta = A + B *$ (Change in confidence limits)

Variable	Coefficient	S.E.	p
A	-0.16	0.065	0.026
B	0.15	0.018	<0.001
	$r^2 = 0.84$	N = 16	

DISCUSSION

I found that sequential analysis of conventional line transect survey data, without correction for possible autocorrelation between sequential transect elements, leads to significant underestimation of the true sample error about the mean. In addition, I observed that the magnitude of this scale related bias was directly related to the magnitude of the within transect data autocorrelation as measured by the intra cluster correlation, δ. Finally, I demonstrated that sampling designs based on cluster sampling analysis yielded lower sample errors than did simple random sampling of complete transects, presumably this difference results from a greater utilization of the available data in cluster sampling techniques. Moreover within the limits of my data, sample error, as calculated by cluster sampling analysis, was not sensitive to the scale of the sample unit.

These analyses indicate that transect-based acoustic surveys, designed to estimate the abundance or biomass of aquatic animals, may underestimate sample error if the sample scales selected for data analysis are chosen without reference to, or knowledge of, the magnitude and scale of intersample correlations in the data. These empirical results confirm Williamson's (1982) conclusion, based on simulation studies, that sample precision can be overestimated when acoustic transect data are serially autocorrelated.

Past approaches to the analysis of transect survey data may have failed to conform to the underlying assumptions of independent sample observations in the statistical analyses applied, when at the same time serial correlation between sample observations was present. As a consequence, many reported population surveys are likely to have been biased with respect to sample errors (Mathisen et al. 1977; Johanneson and Losse 1977; Heist and Swenson 1983). Burczinsky and Johnson (1986) compared several methods that either did, or did not, adjust analysis to account for correlated serial data. They found that sample errors may vary 2-3-fold depending on the analytical method used. Clearly more robust statistical designs are required for analysis of acoustic transect data.

To avoid the problems inherent in sequential sampling of transects, Eberhardt (1978) and Caughley (1977) recommended that only randomly selected complete transects be used as sample units. My analysis of cluster sampling approaches, recommended for acoustic transect sampling by Williamson (1982) and Shotton and Bazigos (1984), indicated that cluster sampling yielded significantly lower estimates of sample error than did simple random sampling of complete transects (mean difference 8%). Moreover, estimates of sample error were insensitive to scale of sampling when cluster sampling was used.

Cluster sampling is based on a well developed body of statistical theory (Hansen et al. 1970; Konijn 1973; Cochran 1977). When used in combination with the assessment of the intra cluster correlation coefficient δ a meaningful quantitative measure of the character of the spatial distribution of animals along transects can be obtained. This coefficient yields information about the components of both the within and between transect sources of variance. δ may also be used to further improve survey strategies during follow-up surveys. For example, δ values that are approximately unity are characteristic of homogeneous, within-transect data. In such situations small-scale within-transect data analysis is unlikely to improve survey efficiency, even when cluster analysis is employed. Under such conditions the only effective strategy for reducing sampling error is to sample a larger number of randomly selected complete transects. However, where δ values are $<<$ 1, cluster sampling analysis based on repeated sampling of individual transects should yield meaningful reductions in sample error.

Cluster sampling theory requires a random selection of the cluster units, within-cluster units being sampled sequentially (Cochran 1977). Therefore, when applying cluster sampling to acoustic surveys, the location of transects should ideally be chosen by random procedures. This statistical requirement for randomness in transect selection contrasts to the systematic zig-zag or rectangular survey patterns that are commonly adopted in acoustic surveys (Kimura and Lemberg 1981). This failure of survey designs to conform to assumptions of the statistical approaches employed has drawn criticism (Cochran 1977; Jolly and Hampton 1990b). The major question thereby is whether biases in estimating the sample mean may be introduced by periodic distribution patterns of the animals being surveyed (Krebs 1989).

The dangers inherent in systematic approaches are real since there is growing evidence that aquatic animal distributions frequently deviate from random, and that repetitive patterns may exist (Platt and Denman 1975; Kingsley et al 1985; Schneider and Piat 1986). For example, field studies conducted by Kingsley and Smith (1982) showed that systematic parallel transect designs which employed complete transects as sample units, lead to biased sample errors and overestimation of precision, because spatial correlations of animal abundance prevailed even between transects. In contrast, Fortin et al. (1989) showed that random and clustered sampling designs were superior to systematic designs even when the primary objective of the survey was to detect spatial structure in the distribution of organisms.

Hence, in the application of cluster sampling it would appear advisable to include in its application a method for the random, or stratified random, allocation of transect locations (this study; Jolly and Hampton 1990a). The additional travel costs imposed can be minimized by sequentially surveying preselected transect locations along the main axis of the survey area (this study).

A central question in the application of cluster sampling methods to acoustic transect designs is the optimal scale of within transect units (Cochran 1977). Within the scales employed in our study, sampling errors were independent of sample scale. However, this condition may not always prevail. The search for optimal sample scales, independent of the survey approach employed, is typically directed at increasing survey efficiency (Konijn 1973; Cochran 1977). Frequently the selection of optimum scales involves trade-offs between sample precision and costs of data collection and processing (Cochran 1977; Downing 1979; Pringle 1984; Downing and Anderson 1985; Krebs 1989). For example, Resh (1979) and Morin (1985) have shown that costs of sample handling and processing associated with an increase in sampling scale are so large that they constitute the major factor in benthic sampling schemes. However, for hydroacoustic sampling the cost differentials associated with different transect sample scales are small because echoes from fish and other organisms can be obtained at very high frequency, and the sampling rates of acoustic samplers can be increased to the scale of individual acoustic echo-waves, thereby yielding sample frequencies as high as 5/sec. Hence the costs of processing acoustic data are dependent only on the capacity of the electronic and computational equipment available. These costs have decreased dramatically with technological improvements in recent years. The important question is therefore, are there benefits to small scale sampling?

Small-scale spatial data on the distribution and abundance of organisms may have great advantages because they can reveal important details on spatio-temporal organisation of animal groups on the scale related processes that shape these distributions (Platt and Denman 1975; Greig-Smith 1979; Schneider and Piatt 1986). However, as demonstrated here, data collected on smaller scales (50 vs 300 m) do not necessarily yield greater sample precision when the primary objective is estimation of the abundance of organisms within the area of investigation.

A common perception in transect sampling is that sample scales should be increased when animals are homogenously distributed in order to avoid serial correlation of data (Caughley 1977; Smith 1978; MacLennan and MacKenzie 1988). However, as I have demonstrated in this study, cluster sampling analysis will allow data collection and analysis to be based on small within-transect sectors without significant bias regardless of spatial patterns of the animals being investigated. In my study I selected within transect sampling scales of 50 m. These units are very small relative to scales typically employed in marine acoustic surveys (Johanneson and Losse 1977; MacLennan and MacKenzie 1988), where scales of 1 nautical mile (1852 m) or more are prevalent. The differences in these scales are, of course proportional to the total scale of the areas surveyed. There would appear to be room for additional work on the optimal within-transect scales for surveys of different magnitude. An analysis of the importance of the ratio of sequence length to transect length might prove useful.

Further improvements in acoustic survey designs are possible through stratified sampling programs, whereby survey effort is allocated in relation to the abundance of fish in different subareas (Jessop and Anderson 1989; Jolly and Hampton 1990a). These, and approaches of model-based designs, such as the use of hydrographic covariates of fish abundance (Smith 1990), can, however, only effectively be applied in situations where the distribution patterns of fish within the survey area are known a priori (Jolly and Hampton 1990a).

CHAPTER 4

DO DIEL CHANGES IN PATCHINESS EXHIBITED BY SCHOOLING FISHES INFLUENCE THE PRECISION OF ESTIMATES OF FISH ABUNDANCE OBTAINED FROM HYDROACOUSTIC TRANSECT SURVEYS?

ABSTRACT

Rainbow smelt (Osmerus mordax) were studied (echo integration and dual-beam) to determine whether fish patchiness resulting from diel vertical migrations cause lowered precision in estimates of fish abundance when assessed with hydroacoustic techniques. A parallel transect design with randomly selected transect locations was used. Cluster sampling analysis was employed to solve inherent problems of small-scale transect sampling created by spatial autocorrelation of fish along transect lines. Smelt were dispersed at night and patchily distributed during the day. The observed changes in fish distribution had no influence on the precision of abundance estimates. However, when assessed seasonally, sample errors were found to decrease in association with increase in fish abundance over time.

INTRODUCTION

Estimates of the abundance of animals in a population typically rely on information obtained by sub-sampling the full population. Therefore the assessment of the magnitude of error due to sampling, the sample precision, associated with such estimates is central to sampling theory (Neter et al. 1978). Ideally, sampling schemes should minimize this sample error (Fiedler 1978). However, in some cases this is difficult to achieve due to patchiness in the distribution of organisms which may lead to high variability of sample replicates. In fisheries science, population estimates having low sample precision generally must be considered provisional, if not inadequate, as a basis for fisheries management decisions (Peterman 1990).

Currently accepted models detailing the influence of animal behavior on the precision of sampling methods contend that sample variance, and hence the sample error of estimates, increase as animal aggregation or patchiness increases (Resh 1979; Downing 1979; Gerlotto and Stequert 1983; Jessop and Anderson 1989). In theory this occurs because patchiness yields a higher variance to mean ratio (Lloyd 1967; Krebs 1989).

One important cause of patchiness in the distributions of aquatic animals, including fishes is diel vertical migration (Appenzeller and Leggett in press). In a previous paper (chapter 2), I investigated the influence of such diel changes in schooling behavior on systematic bias (accuracy) in hydroacoustic estimates of fish abundance and biomass, and found that when fish were aggregated in schools, fish abundances were underestimated considerably. In this paper I investigate whether these diel changes in fish aggregation induced by schooling behavior also affect the sample precision of these population estimates (Fig. 1). Hydroacoustic sampling, which is rapidly becoming a dominant method of assessing fish abundance, has not been adequately evaluated for such effects of fish distributions on sample precision.

Gerlotto and Steward (1983) reported that, at comparable levels of sampling effort, estimates of fish stocks obtained when the fish were heterogeneously distributed within the survey area were less precise than those obtained when fish were homogeneously distributed. This same reasoning led Thorne (1977) to conclude that fish population estimates of schooling fish derived from hydroacoustic surveys should be less precise than estimates derived from the dispersed population. He was unable to validate this concept by means of repeated surveys of fish populations which were alternately dispersed and aggregated since the diel migrations responsible for generating these patterns caused the population to be partly unavailable to the acoustic beam at night. Such day-night differences in fish aggregation are reported for many fish species (Woodhead 1966; Dembinski 1971; Blaxter 1975) and consequently such changes in spatial patterns may have a considerable effect on the sample precision of acoustic fish population estimates.

In this investigation I tested the hypothesis that patchiness, such as that exhibited by schooling fishes, results in estimates of fish abundance having lower precision, than is characteristic of estimates obtained when fish are dispersed in the water column. I also addressed the question whether seasonal changes in fish population size would lead to changes in sample precision.

FIGURE 1

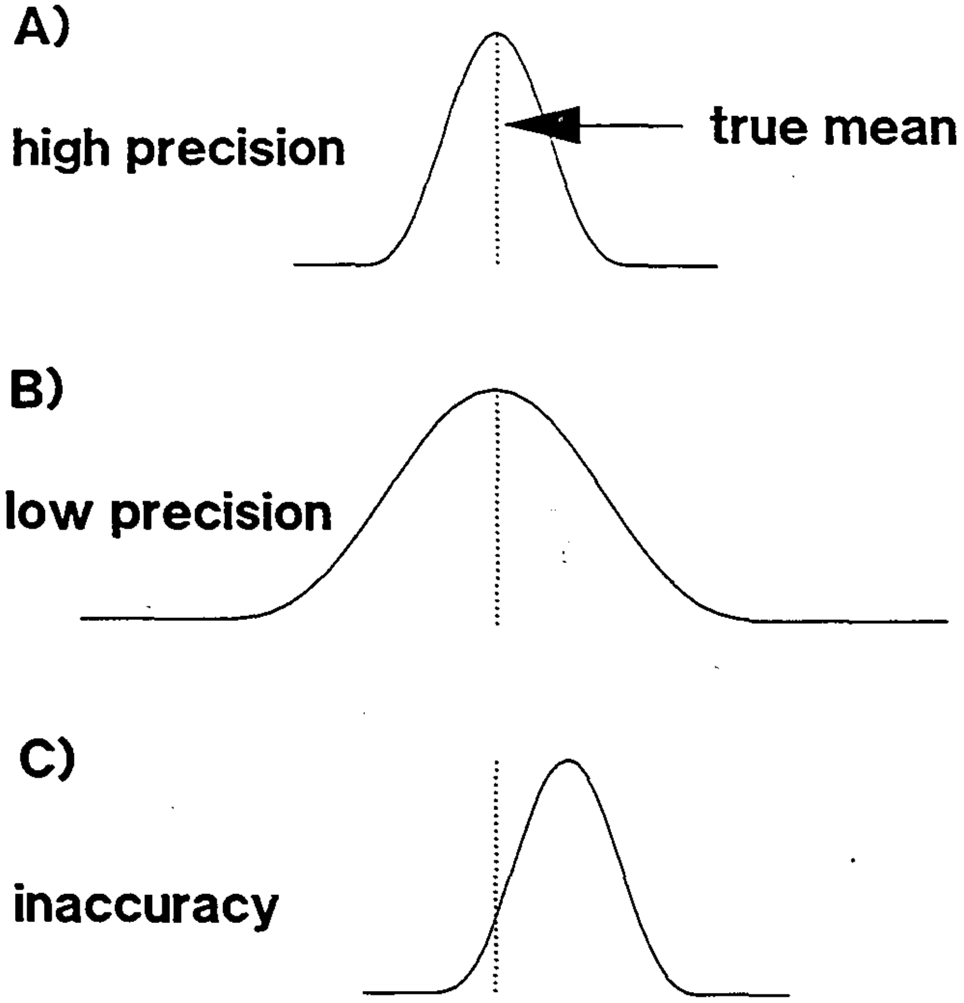


Fig. 1. Differential effects of a decrease in sample precision (A to B) and a decrease in accuracy (C) when estimating the true population mean. Decrease in precision (B) is associated with an increase of the uncertainty about the location of the sample mean (confidence limits are increased). However, a decrease in accuracy (C) leads to a systematic bias in the estimation of the true population mean. Precision can be increased by increasing sample effort, however, this is not the case with accuracy.

METHODS

RAINBOW SMELT BEHAVIOR: DIEL PATTERNS OF DISTRIBUTION

I investigated the influence of fish patchiness on the sampling precision associated with estimates of fish abundance obtained from acoustic transect surveys by studying rainbow smelt (Osmerus mordax). The study was carried out in Lake Memphremagog which is located on the Quebec-Vermont border. The lake has a total surface area of 8000 ha and is long (40km) and narrow (average width 2.4 km). It contains three distinct basins which differ in mean depth: south basin 6.2m, central basin 44.3 m, north basin 14.7m. Maximum depth, (110m) occurs in the central basin. The central basin has a surface area of 2046 ha and consists of an elongated (15 km x 2 km), deep trench with steep shoreline slopes. I restricted survey activity to the central basin, where fish could be ensonified with equal coverage during both day and night (chapter 2).

Both exploratory fishing in the open water zone of Lake Memphremagog during 1988 and 1990, and reports by sports fishermen, indicate that the pelagic fish population of Lake Memphremagog, is dominated by rainbow smelt along with lake trout (Salvelinus namaycush) and stocks of introduced Atlantic salmon (Salmo salar), the latter two species being dramatically inferior numerically to smelt. These observations, plus a quantitative comparison of fish catches in a vertical haul net, and acoustic data (chapter 1) lead me to conclude that my acoustic records were dominated by smelt echoes.

The vertical migratory behavior of smelt, and their diel patterns of aggregation and dispersion as revealed in other studies (Dembinski 1971; Argyle 1982; Heist and Swenson 1983; Burczinsky et al. 1987) were consistent with patterns revealed by my acoustic data (chapter 1 and 2). During the day adult smelt typically occurred in deeper waters (30 - 40m) where they formed dense schools. At twilight the center of mass of the fish depth distribution moved up to a position below and close to the thermocline. Few fish entered epilimnetic waters when their temperatures were > 18°C. During the night smelt dispersed into scattering layers and no schooling was observed. At dawn the fish again moved deeper and reaggregated into dense schools. This diel pattern of migration and aggregation was exploited to examine the effect of these behaviors and their resulting distributions on the precision of hydroacoustically derived estimates of abundance.

During July - September 1990 I conducted 9 day and 7 night acoustic surveys of the pelagic fish population of the central basin of Lake Memphremagog. Day-night surveys were paired within 48 hr. Sampling effort was equal in all surveys.

SAMPLE DESIGN AND DATA ANALYSIS

In a previous paper (chapter 3) I investigated the application of robust and efficient sampling designs for acoustic line transect surveys, using cluster sampling analysis (Hansen et al 1970; Konijn 1973; Cochran 1977). This approach to sampling design and statistical analysis of data was adopted here. I divided the total basin area into 40 parallel 350-m wide sectors extending from shore to shore perpendicular to the long axis of the lake, and consistently surveyed 12 transects selected randomly without replacement. A new transect set was drawn on each sampling date. Complete acoustic surveying of 12 transects was achieved in 4 to 5 hours.

The hydroacoustic record was amplified at 20 log R and was automatically subdivided into 50-m within-transect segments using a digital echo integrator. This sampling procedure yielded a hierarchical data structure of 12 large spatial units (transects: average transect length 1400 m) each consisting of sequential 50-m segments. The data were analyzed via cluster sampling analysis (chapter 3). Equation 1 was used to estimate the variance of sample means:

$$V(Y) = \frac{S^2(1 + \delta(m - 1))}{n} \qquad (1)$$

where V(Y) = variance of the sample mean; S^2 = sample variance; δ = intra cluster correlation coefficient; m = number of within transect sample units and n = total number of samples (50m -segments).

The magnitude of error due to sampling was measured by the 95% confidence interval. The lower and upper bounds of this interval were calculated as:

$$L = Y - t(1-\alpha/2)\ s(Y) \qquad (2)$$

$$U = Y + t(1-\alpha/2)\ s(Y) \qquad (3)$$

where L = lower confidence limit; U = upper confidence limit; Y = sample mean; t = probability value according to the t distribution with 0.95 confidence coefficient; s(Y) = standard error of the mean.

Precision was calculated as the one-sided confidence limit expressed as a % of the sample mean following Equation 4.

$$P = 100\ (L\ /\ Y) \qquad (4)$$

whereby P = precision; L = one sided (lower) confidence limit; Y = sample mean. The term sample error equates to the reciprocal of sample precision.

HYDROACOUSTIC METHODS

I employed a 120-kHz Biosonic Model 105 dual-beam echosounder to quantify the abundance of pelagic fishes in the study site. The system was mounted in a 5m outboard powered boat. The transducer, which was mounted in a V-fin towing body, was suspended by elastic bungy cords from a davit. This effectively dampened wave induced motion. The transducer was towed at a depth of 1 m. Boat speed was 8.5 km/h. During night sampling all lights were extinguished to minimize influence on the fish being ensonified.

The acoustic surveys were conducted in multiplexed mode using both 20 log R (echointegration) and 40 log R (dual-beam target strength) amplifications with alternating pings. Ping rate was 5/sec and pulse length was 0.4 ms. A video recorder was used to record acoustic signals. All data processing was performed on these recorded data. Data processing was performed with a Biosonics Model 121 Digital Echo Integrator. Echo integrated densities were subdivided into depth windows. Because of the presence of small non-migrating fishes observed in the shallow water layers, the signals from the top 10 m were excluded from the analysis. Additional information on acoustic devices and methods is provided in chapters 1 and 2.

RESULTS

Sample variance and serial correlation from day-night surveys

Sample variances derived when the 50-m within-transect sequences were analyzed as the primary sample units revealed marked differences between day and night surveys when fish were respectively schooled and dispersed. Typical daytime hydroacoustic data were characterized by high abundance peaks indicating the occurrence of fish schools along the transects, while night acoustic data were characterized by gradients reflecting dispersed spatial patterns of fish (Fig. 2).

These day-night differences in data structure produced different variance to mean ratios, which were employed as indicators of the spatial patchiness of the fish distributions. I computed these ratios based on 50-m sample intervals for all 16 surveys conducted. The variance to mean ratio was significantly higher in the day samples ($p = 0.007$). There was no significant seasonal change (Julian day) in the variance to mean ratios ($p = 0.1$; Table 1).

Low sample variances recorded during night surveys were related to low variance patterns observed along the transect lines. Calculated intra-cluster correlation coefficients (δ) were significantly larger in data collected at night ($p = <0.001$). There was no significant ($p= 0.78$) relationship between Julian day and δ values (Table 1). Day-night differences explained 74% of the variance in δ values. The low sample variance patterns encountered at night were primarily the result of serial correlation of data within transect units.

FIGURE 2

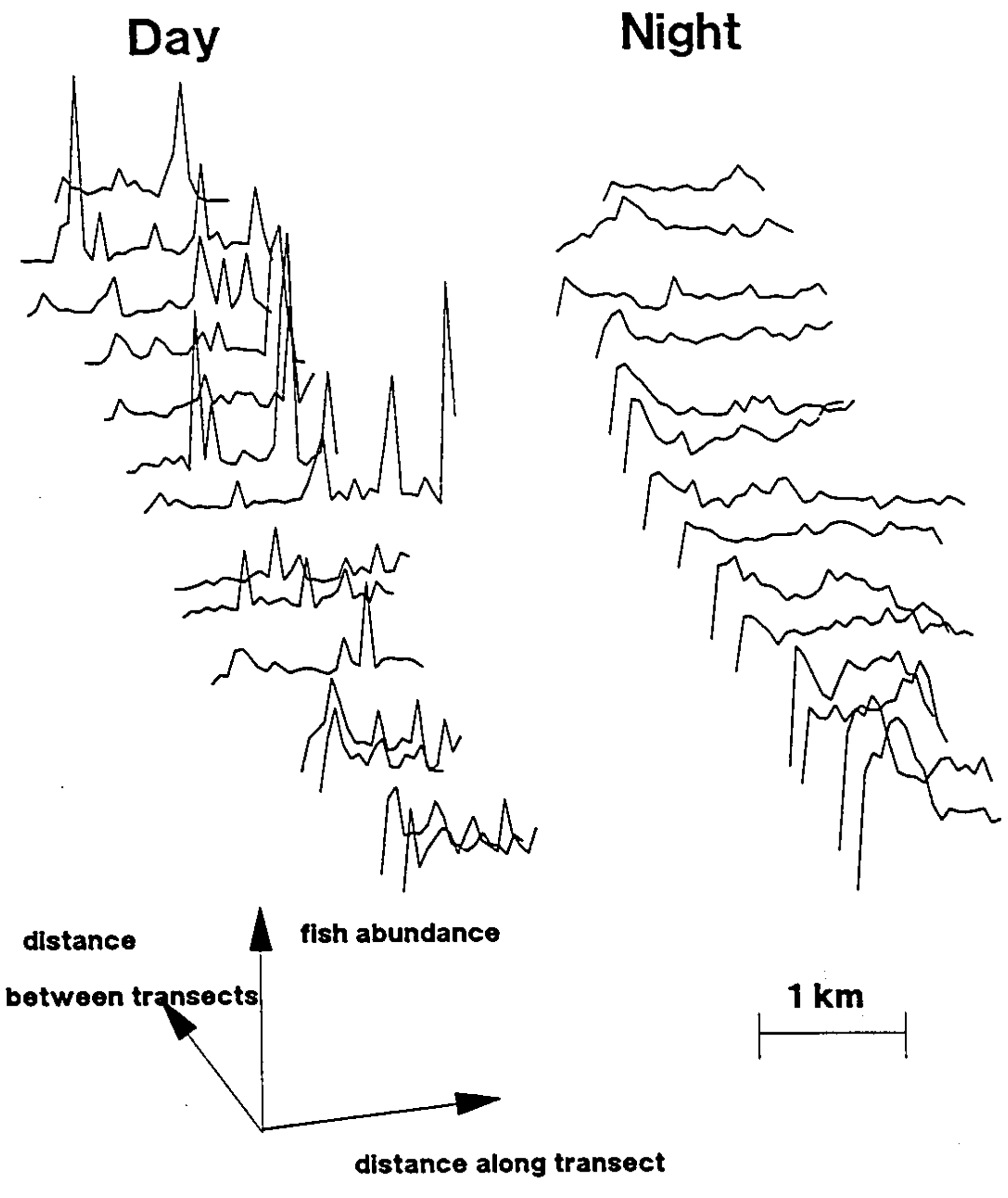
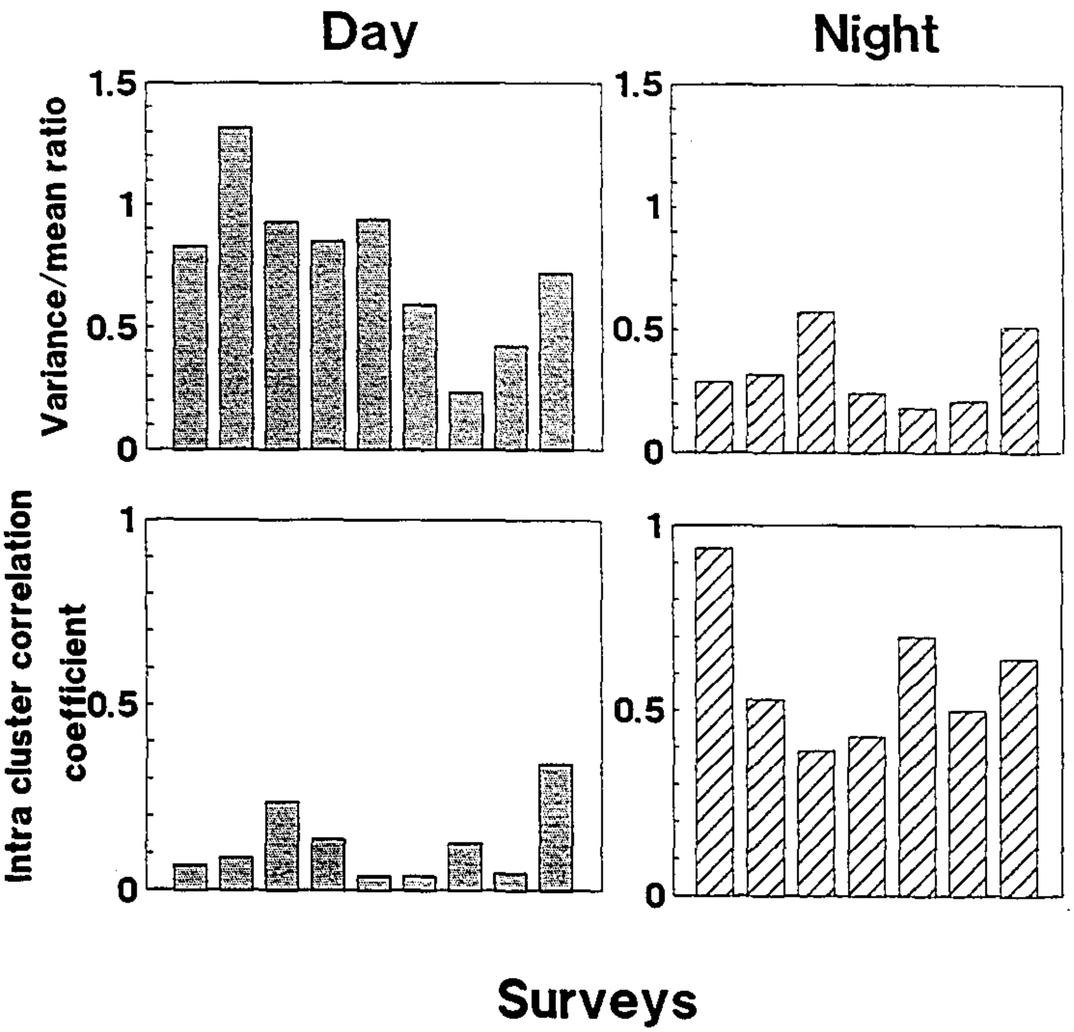

Day
Night
distance
between transects
fish abundance
distance along transect
1 km

Fig. 2. Three-dimensional representation of acoustic fish abundance for an arbitrary day and night survey (24/8/90) conducted in the central basin of Lake Memphremagog. Day survey data is characterized by high variability within transects; peaks are related to the occurrence of fish schools. In contrast, night-time data are characterized by greater data homogeneity within transects.

FIGURE 3



Day
Night
Variance/mean ratio
1.5
1
0.5
0
1.5
1
0.5
0
Intra cluster correlation coefficient
1
0.5
0
1
0.5
0
Surveys

Fig. 3. Comparison of day-night variance to mean ratios and intra-cluster correlation coefficients, δ. Calculations were based on 50-m within transect data. Data are arranged from left to right according to season (Julian day 190 - 250 in 1990).

Table 1. Analysis of the influence of Julian day and a day-night dummy variable (day = 0; night =1) on variance to mean ratio, V/M, (model 1) and cluster correlation coefficient, δ (model 2). Variance to mean ratios, and δ were calculated using 50m within-transect data units.

Model 1: V/M = A + B*(Julian day) + C*{day(0)/night(1)}

Variable	Coefficient	S.E.	p
A	2.19	0.81	0.018
B	-0.006	0.004	0.1
C	-0.397	0.123	0.007
	$r^2 = 0.55$	N = 16	

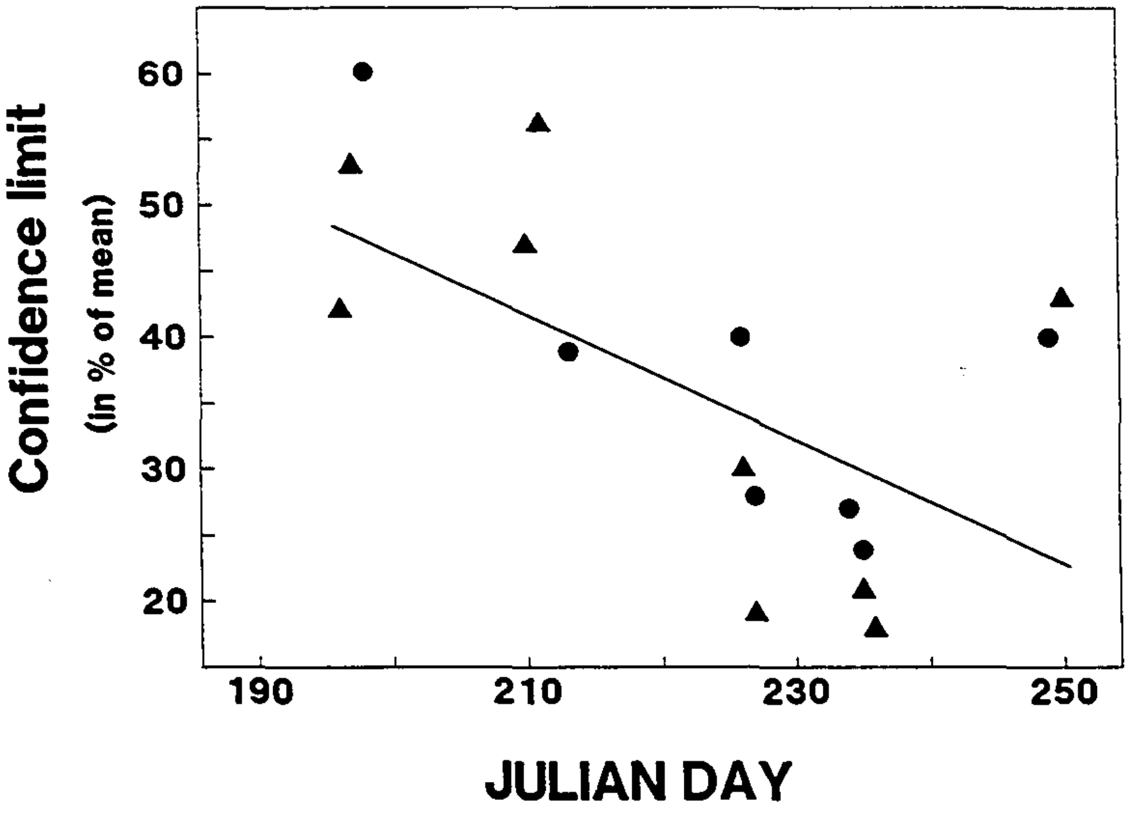
Model 2: δ = A + B*(Julian day) + C*{day(0)/night(1)}

Variable	Coefficient	S.E.	p
A	0.274	0.51	0.6
B	-0.001	0.002	0.78
C	0.467	0.077	<0.001
	$r^2 = 0.74$	N = 16	

Sample precision of day-night surveys

I employed cluster sample analysis (Eq. 1). to estimate the variance of sample means of acoustic survey data and to calculate confidence limits and sample precision (Eq. 4). I then tested the influence of day-night differences, and season (Julian day) on survey precision via a multiple regression model employing Julian day and a dummy variable representing day-night (day=0; night=1) indicators as the independent variables and sample precision as the dependent variable. There was a significant (p= 0.015) influence of season (Julian day), but no significant (p= 0.64) influence of day-night on sample precision (Fig. 4; Table 2). Differences in day-night schooling patterns did not significantly influence sample precision.

FIGURE 4



Confidence limit
(in % of mean)
60
50
40
30
20
190
210
230
250
JULIAN DAY

Fig. 4. Seasonal and diel variation in the magnitude of confidence limits (as % of the mean) of acoustic surveys calculated from cluster sampling analysis; day surveys (triangles) - and night surveys (circles) are indicated.

Table 2. Sample precision (measured as one-sided confidence limit in % of the mean) calculated by cluster sampling analysis in relation to season (Julian day) and day-night. Data were collected during 16 surveys in Lake Memphremagog. There was a significant seasonal influence on sample precision, but no significant influence of day-night patterns in fish.

Model: Precision = A + B*(Julian day) + C*{day(0)/night(1)}

Variable	Coefficient	S.E.	p
A	142.4	37.9	0.002
B	-0.48	0.17	0.015
C	2.75	5.77	0.641
	$r^2 = 0.38$	N = 16	

Influence of fish population size on sample precision

The significant seasonal increase in sample precision (Table 2) was associated with a seasonal increase in fish abundance during the study (Fig. 5). The fact that lower estimates of fish abundance were obtained during daytime is also illustrated (Fig. 5). The positive relationship between sample precision and fish population size was significant at $p = 0.03$ ($r^2 = 0.29$; Fig.6 upper panel; Table 3).

The magnitude of this relationship increased ($p = 0.004$, $r^2 = 0.47$) when day time estimates of fish abundance were corrected for systematic underestimation of fish abundance during those surveys (Fig. 6 lower panel; Table 3). To correct day estimates, I used the multiple regression model relating fish population estimates to season (Julian day) and a day-night dummy variable (see chapter 2: Table 5).

FIGURE 5

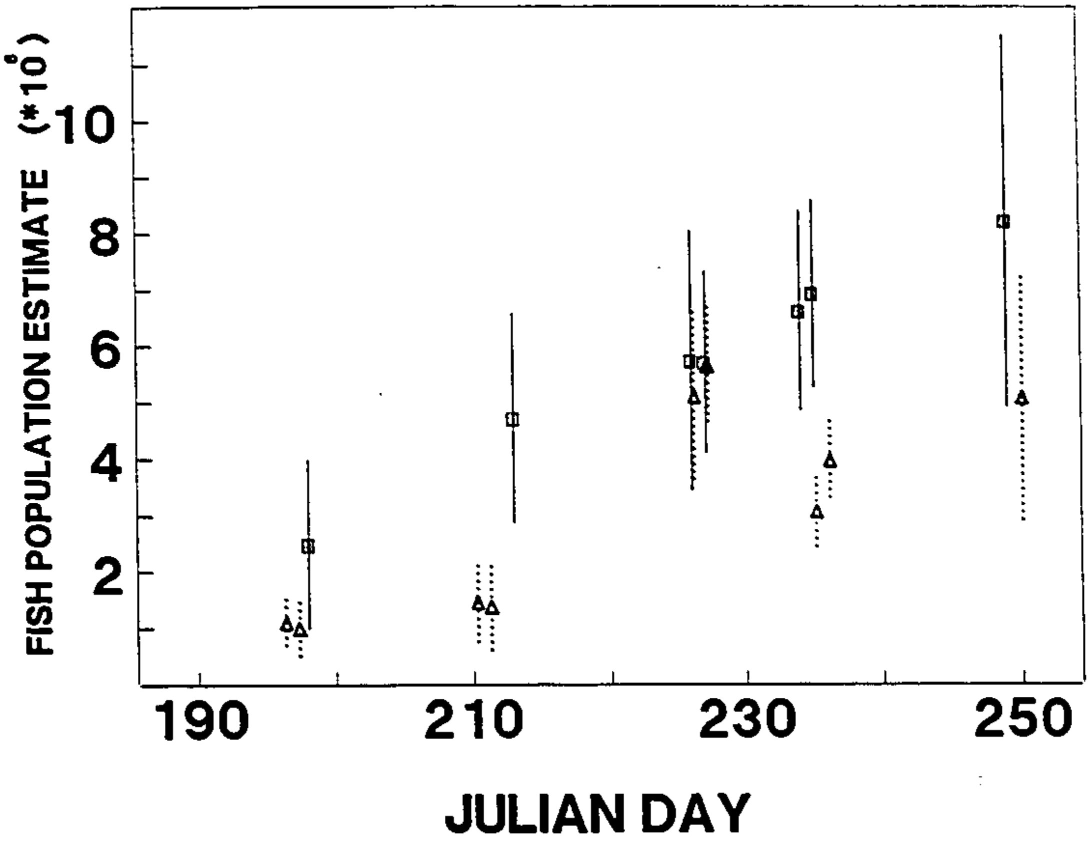

FISH POPULATION ESTIMATE (*10^6)
2
4
6
8
10
190
210
230
250
JULIAN DAY

Fig. 5. Fish population estimates (in million individuals) and confidence limits (95%) based on cluster sampling analysis. Day estimates are indicated by triangles (means) and broken lines (confidence intervals); night estimates are indicated by squares and continuous lines.

Table 3. Relationship between fish population size and sample precision for 16 surveys replicated in Lake Memphremagog during day and night. Fish population size is given in millions of fish; sample precision (95 % C.I.) in % of the sample mean. For the second model fish abundance estimates conducted during the day were corrected for systematic underestimation induced by schooling of fish.

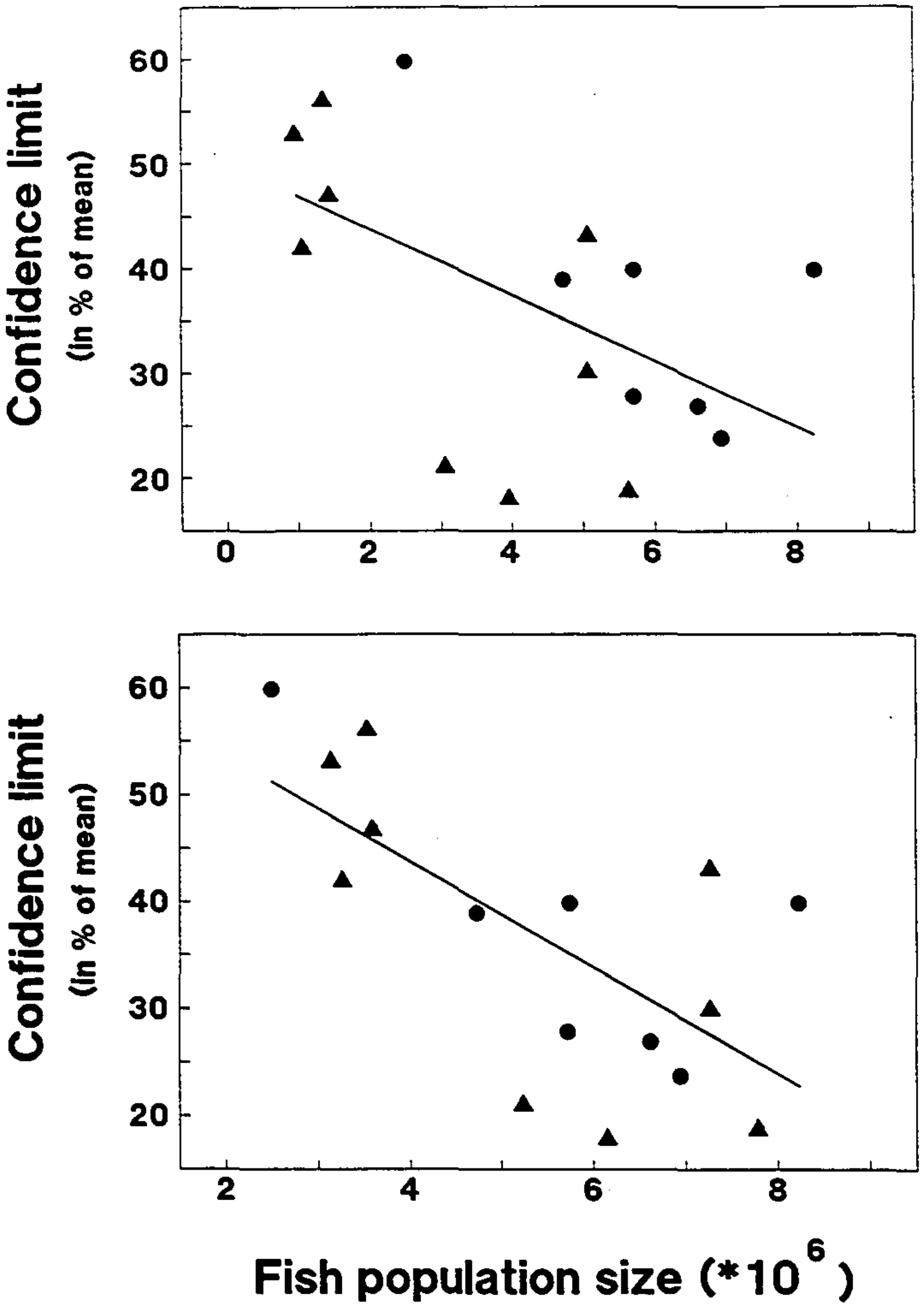
Model 1: Precision = A + B*(Population size)

Variable	Coefficient	S.E.	p
A	50.12	6.29	<0.001
B	-3.15	1.31	0.03
	$r^2 = 0.29$	N = 16	

Model 2: Precision = A + B*(Population size)

Variable	Coefficient	S.E.	p
A	63.91	8.2	<0.001
B	-4.96	1.42	0.004
	$r^2 = 0.47$	N = 16	

FIGURE 6



Confidence limit
(In % of mean)
60
50
40
30
20
0
2
4
6
8
Confidence limit
(In % of mean)
60
50
40
30
20
2
4
6
8
Fish population size (*10^6)

Fig. 6. Relationship between sample precision (one-sided confidence limits in % of the mean) and fish population size. Upper panel: Acoustic estimates of fish population size from day and night surveys in relation to sample precision. Lower panel: Relationship between fish abundance and sample precision when day estimates are corrected for systematic underestimation of fish population size due to schooling.

DISCUSSION

Patchiness and precision

I found no evidence of an influence of diel changes in aggregation on the magnitude or direction of the sample precision of estimates of smelt abundance as assessed by hydroacoustic line transects. This result is contrary to the hypothesis that surveys conducted when fish are dispersed should result in higher sample precision (Thorne 1977; Burczinsky and Johnson 1986). The rejection of this hypothesis in the case of diel changes in fish aggregation, as investigated in this study, results from statistical implications of line transect methods.

Contrary to the case of samplers of fixed scale used in random sample designs (i.e. vertical nets or benthic samplers), data obtained from acoustic transect sampling of fish populations are recorded while moving continuously along designated transect lines. Moreover, the scales of data collection can be varied by the investigator, even after the samples are collected. Under such conditions, and when detailing the influence of patchiness on sample precision, it is necessary to consider the degree of spatial correlation among consecutive within-transect samples and its effect on the independence of sequential samples (Cochran 1977; Williamson 1982; chapter 3). I previously demonstrated (chapter 3) that the magnitude of the bias in sample errors, induced by serial correlation, can be quantified with the intra-cluster correlation coefficient, δ. I also demonstrated that cluster sampling, which uses δ-values to adjust the variance of sample means, and hence, the magnitude of sample errors, provides an efficient and robust means of designing and analyzing transect samples (chapter 3).

In this study a comparison of day-night survey data revealed that when fish were dispersed at night, high intra-cluster correlation values, indicating data homogeneity of within-transect samples, were prevalent. Under such conditions variance was primarily associated with differences in fish abundances between transects. This implies that the within-transect sample units employed do not represent independent sample replicates, and that the variance of sample means must be adjusted to correct for this bias (chapter 3).

In contrast, when fish were aggregated into schools during the day, serial correlation of within-transect samples was low, hence δ-values were low. MacLennan and MacKenzie (1988) reported similar low data correlation within transect lines when schooling fish are ensonified. These low autocorrelation values result from the scattered location of the schools in space, which yields high acoustic records from sample units in which schools are ensonified, and low records from units in which schools are absent. In the surveys reported here, school diameters typically ranged between 10-

30 m. Since the data were recorded in 50 m sample intervals, high spatial resolution of school locations along the transect lines was obtained.

Hence, as a result of the diel patterns in spatial distribution, the observed changes in variance patterns were associated primarily with changes in the local data structure of within-transect sample units as indicated by the change in intra-cluster correlation coefficients. This explains the absence of significant differences in the variance of sample means, and the sample precision achieved.

This consideration of the scales of patchiness, and of the inherent problems of data analysis associated with line transect sampling, also resolves the apparent contradiction between results of this study and the general rule that an increase in patchiness of organisms is typically associated with a decrease in the sample precision of population estimates (Resh 1979; Downing 1979; Morin 1985; Vezina 1989; Krebs 1989). When comparing large-scale differences in fish distribution within the survey area, Gerlotto and Stequert (1983) and Thorne (1982) observed that homogeneous fish distributions were associated with higher sample precision than were heterogeneous distributions. My finding that comparative surveys in which fish were aggregated (day) or dispersed (night) did not yield differences in sample precision suggests that the distribution patterns of the smelt I studied, did not vary significantly between day and night on a whole basin scale.

This hypothesis is supported by observations of the diel vertical distribution patterns of smelt in Lake Memphremagog. These diel changes of aggregation and dispersion observed were strongly associated with vertical migrations which were, in turn, closely related to changes in ambient illumination (chapter 1). Therefore, during the diel changes in fish patchiness, the dominant movement of fish was in the vertical direction with a gradual clumping of fish when forming schools, or a gradual dispersion of fish when the school formations were abandoned. Lateral movements, by comparison, appear to have been small as indicated by the distribution patterns of fish within the central basin. These exhibited consistent aggregation at the southern end of the basin. This pattern was apparent during both, day and night surveys and was persistent during the study.

In summary, I conclude that the absence of changes in sample precision, when assessed on a diel basis, occurred because the large-scale (whole lake) fish distribution patterns did not change on a diel basis, changes in distribution being restricted primarily to small-scale changes in patchiness induced by schooling behaviors. This finding demonstrates that when considering patchiness and its implications for the application of line transect sampling in acoustic surveys, patchiness both at the small scale, and at the whole-survey scale must be considered. As a consequence, the general rule that organismal patchiness and sample precision are closely and negatively related is not contradicted by the results of this investigation. Rather, the importance of the scale of patchiness, relative to the sampling scale, is underscored.

Accuracy and precision of surveys

In a previous paper (chapter 2), I reported that diel changes in schooling behavior resulted in a systematic bias in estimates of fish abundance and biomass. This bias was caused by aggregated distributions which occurred during the day, leading to underestimation of fish abundance and biomass under those conditions. Incorporating the results of the present investigation, the global impact of schooling on acoustic surveys can be summarized as a potential for bias in the accuracy, but not in the precision, of estimates of fish abundance and biomass. These results are important considering the quality of acoustic data and the possibilities for their improvement.

Sample precision can generally be improved by intensifying sample effort (Neter et al 1978). For fish, this has been demonstrated by simulation models (Fiedler 1978), and by in situ comparison of hydroacoustic survey data (Aglen 1983b). These authors found that the sample precision of acoustic transect surveys was related to the degree of coverage of the survey area. Therefore, improved sample precision is directly associated with increased costs of sampling. In contrast, the bias resulting from inaccuracies induced by changes in patchiness cannot be removed by increased sampling intensity. Rather, it must be overcome by matching sampling designs to the behavior and distribution of fishes.

The effect of population size on sample precision

I observed a pronounced increase in fish abundance over the season in 1988 and 1990. Intra-lacustrin migrations of smelt provide the most plausible explanation for this seasonal increase. The likely direction of this migration was from the shallow, southern basin of the lake (where late summer surface to bottom temperatures were > 18 °C) to the deep water habitat of the central basin. This intra-lacustrin migration is consistent with known thermal requirements of adult smelt which seek cold, hypolimnetic habitats in deeper basins during the summer months (Burczinsky et al. 1987). Mathison et al. (1977) described similar seasonal changes in Pacific salmon distribution and abundance in lake Quinault.

The observed increase in fish abundance was associated with an increase in the sample precision of survey estimates. This appears to have resulted from the effect of increased abundance on the large-scale distribution of fish within the survey area. This increase produced a more homogeneous distribution, and hence, less variation in the between transect data. Thorne (1982) and Jessop and Anderson (1989) reported a similar change in sample precision in response to changes in fish abundance. Similar results have also been reported for benthos surveys, suggesting a general pattern among animal groups (Resh 1979; Downing 1979; Morin 1985).

Conclusions

Three points can be drawn from this analysis. 1) Fish schooling behavior did not affect the sample precision of acoustic surveys and as a consequence, the power to detect changes in population sizes appears to be unaffected by fish aggregation. 2) As shown in chapter 2, acoustic quantification of fishes which change their pattern of aggregation through time can lead to a change in accuracy of fish population estimates. This bias is likely to be related to an underestimation of fish abundances when ensonifying compact schools. Therefore, when the assessment of absolute fish abundance and biomass is the goal of an acoustic investigation, acoustic surveys should be performed when fish are dispersed. 3) Sample precision is higher when the fish population is maximal. Hence, knowledge of seasonal changes in fish distribution and abundance within the survey area can improve survey efficiency by facilitating the choice of optimal temporal windows for surveys.

THESIS CONCLUSIONS

This thesis provides empirical evidence of the potential for large and systematic sources of bias associated with hydroacoustic estimates of fish abundance and biomass. These biases result from failure to recognize and account for patterns of fish behavior and distribution which influence either the echo signals received (hydroacoustic shadowing) or the appropriate statistical treatment of the data (serial correlation). While the behavioral changes generating these sources of error in this study were associated with vertical migrations, any behaviors which favor patchiness or dense schooling can be expected to produce similar biases.

The approach developed to quantitatively describe the diel patterns of smelt vertical distributions in response to environmental parameters, and the use of these models to provide a basis for defining diel and seasonal temporal windows during which the fish population I studied are completely accessible to the acoustic beam is, for the moment, limited to the scales applied here. However, there is considerable evidence that similar behavioral patterns are exhibited by other fish species (Dietz 1948; Boden 1950; Blaxter and Parrish 1965; Woodhead 1966; Dembinski 1971; Thorne 1977; Hamrin 1986; Levy 1987; Dalpadado and Gjosaeter 1987, Levy 1990b). The approach developed here, therefore, has the potential to be applicable to a wider range of fish species and survey situations.

Moreover, studies of coastal migrations conducted by Rose (1988) have also demonstrated that models developed to describe enviro-regulation of fish migrations, are also applicable to large-scale movements. Hence, the potential for the application of such models to determine the optimal temporal window for acoustic surveys, mediated by a knowledge of environmental correlates of fish abundance, is high. On the other hand, my data also suggest that the seasonal and diel temporal window during which accurate hydroacoustic estimates of abundance and biomass are possible may be short and possibly also site-specific.

The results reported here clearly demonstrate that fish schooling behavior can lead to substantial (up to 50%) underestimation of the abundance and biomass of fish populations when assessed by hydroacoustic surveys. I identify acoustic shadowing effects (Roettingen 1976; Toresen 1990; Burczinsky et al 1990) as the main source of bias. This result, therefore, provides empirical evidence for the hypothesis that non-linear effects of the relationship between echointegrator output and quantity of targets (MacLennan and Simmonds 1992) can provide a serious biasing effect in the <u>in situ</u> estimation of fish abundances. It therefore appears safe to conclude that the acoustic measurement of fish abundance and biomass conducted when fish are schooling is problematical and that more accurate estimates are obtained in situations when fish are dispersed.

In addition to the problems created by acoustic shadowing, the statistical treatment applied to survey data, and the survey design can also be influenced by the behaviors exhibited by fishes. The occurrence of autocorrelated data series in fisheries surveys have been reported in the literature quite frequently (Nickerson and Dowd 1977; Burczinsky and Johnson 1986; Orlowsky 1989; Simard et al 1992). Deficiencies in addressing statistical problems created by such correlations, as demonstrated here, may cause biased estimates of sample precision when fish distributions were regular along transect lines. My results suggest that uncertainties regarding the application of statistical analysis to transect-based acoustic estimates (Kimura and Lemberg 1981; Jolly and Hampton 1990b) have led to population estimates that are biased with respect to sample errors (Thorne et al 1971; Thorne 1977; Mathison et al 1977; Johanneson and Losse 1977).

My data also indicate that the application of statistically robust techniques, such as cluster sampling, which I have explored here, can be used to improve the precision of acoustic surveys.

My comparison of sample precision derived from data obtained when fish distributions were aggregated and dispersed indicate that small-scale changes in fish patchiness produced no significant differences in the magnitude of sample precision associated with estimates of abundance. However, seasonal changes in large-scale patterns of fish abundance and distribution, which in Lake Memphremagog were produced by thermal refuging behavior, did produce systematic changes in the magnitude of the sample precision derived. It is likely, therefore, that a knowledge of the large-scale distribution patterns and seasonal migrations of fish stocks will be a key factor in achieving further improvements in the efficiency of hydroacoustic surveys.

7 Finally, the results of this thesis indicate that reliable and precise estimates of fish biomass and abundance can be obtained via hydroacoustic means provided proper attention is given to the behavior patterns of the species of interest. In the specific situation I investigated, the optimal temporal window occurred at night, in mid summer. At this time smelt were dispersed, were prevented from approaching the surface by a thermal barrier, and were concentrated due to thermal refuging. Under these conditions target strength measures are facilitated, shadowing and fish avoidance are minimized. Moreover, my studies have shown that

by exploiting diel or seasonal changes in fish behavior the potential for biases in the accuracy and precision of acoustic estimates of fish abundance and biomass can be identified, assessed and corrected. It is clear, therefore, that a greater knowledge of the diel and seasonal patterns of fish movement and aggregation, would greatly aid in the collection of high quality acoustic data that is applicable to fisheries management and other scientific purposes.

The specific conclusions of this thesis are:

1) That the null hypothesis that smelt diel vertical distributions are not influenced by light can be rejected;

2) That the vertical migratory behavior exhibited by smelt is consistent with the hypothesis of negative-phototactic behavior;

3) That changes in fish distribution and aggregation related to diel vertical migration offer seasonal time and site specific windows within which it is possible to obtain accurate quantitative assessments of fish abundance and biomass by acoustic methods;

4) That fish schooling leads to an underestimation of fish abundance by hydroacoustic methods;

5) That these reduced abundance estimates obtained when fish were aggregated resulted from acoustic shadowing;

6) That diel patterns in fish patchiness, related to diel schooling behavior and vertical migration, do not influence the precision of acoustic surveys;

7) That failure to correct for serial correlation of acoustic data may lead to overestimation of sample precision, especially when small-scale patterns in distribution are homogeneous;

8) That cluster sampling, which makes possible a more thorough utilization of transect data, yields a significant improvement in the precision of acoustic surveys and thus an overall improvement in survey efficiency.

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