

THE SELECTIVE ADVANTAGE OF DIEL VERTICAL MIGRATION BEHAVIOR
IN JUVENILE SOCKEYE SALMON AND KOKANEE (*Oncorhynchus nerka*)

By

DAVID ALAN LEVY

B.Sc., McGill University, 1975
M.Sc., The University of British Columbia, 1977

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES
(Department of Zoology)

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

March, 1989

©David Alan Levy, 1989

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Zoology

The University of British Columbia
Vancouver, Canada

Date March 23, 1989

Abstract

The widespread occurrence of diel vertical migration behavior in pelagic aquatic organisms suggests that there is a selective advantage of the behavior compared to a static vertical depth distribution in the water column. Juvenile sockeye salmon (*Oncorhynchus nerka*) are active diel vertical migrators within pelagic lacustrine habitats, usually migrating over vertical distances covering tens of meters. The migrations are timed such that the animals occupy shallow depths during crepuscular and nocturnal periods, and spend daytime periods relatively deep in the water column.

Hydroacoustic surveys were undertaken in fifteen British Columbia sockeye and kokanee lakes in order to compare predictions from selective advantage theories with the performance of the animals under field conditions. Juvenile sockeye undertook diel vertical migrations in all systems studied with the exception of Nimpkish Lake, where the migrations were periodically reversed, and Chilko Lake, where the migrations were periodically relaxed. None of the single factor theories correctly predicted all of the features of juvenile sockeye diel vertical migration. A multifactor theory, which interpreted the migration as a three-way compromise between foraging, predator avoidance, and the optimization of nocturnal metabolic efficiency, provided the most realistic explanation for the selective advantage of the behavior. The field observations also supported a hypothesized sensory mechanism for the behavior involving light and temperature controlling the day and night depth positions respectively.

Two distinct kokanee diel migratory patterns were observed within Okanagan Lake. One group of animals migrated in a similar fashion as juvenile sockeye, while the second group undertook a reversed diel vertical migration. Target strength estimates from a high frequency echosounder suggested that small juveniles comprised the first group, while larger sub-adults comprised the second. The field observations are consistent with an ontogenetic shift in kokanee diel vertical migratory behavior within Okanagan Lake.

Crustacean zooplankton prey organisms of juvenile sockeye maintained static diel vertical distributions within three Fraser River system sockeye lakes. Within Babine Lake, the cladoceran *Bosmina coregoni* undertook reversed diel vertical migrations probably in response to the vertical migrations undertaken by the predatory copepod *Heterocope septentrionalis*. Within Nimpkish Lake, where juvenile sockeye undertook reversed diel vertical migrations, *B. coregoni* as well as other planktonic crustacea undertook diel vertical migrations. The correspondance between vertical migratory patterns in zooplankton and planktivores suggests a tight coupling in the diel migratory behavior of adjacent trophic levels with potentially important consequences for pelagic aquatic community structure.

Table of Contents

Abstract	ii
List of Tables	v
List of Figures	vi
Acknowledgements	x
I. Introduction	1
II. Theories of Diel Vertical Migration	6
Sensory mechanisms for migration	7
Adaptive significance of migration	9
1) Foraging hypothesis	9
2) Bioenergetic hypothesis	10
3) Predator avoidance hypothesis	11
Multifactor hypotheses	13
4) Foraging and predator avoidance combined: the "antipredation window"	13
5) Foraging and bioenergetics combined	16
6) Bioenergetics and predator avoidance combined	17
7) Antipredation window and bioenergetics combined	17
III. Research Strategy	20
Schedule and location of lake visits	24
IV. Methods	27
Hydroacoustic methods	27
Field data collection procedures	28
Echo signal processing	33
1) Echo integration	33
2) Target strength	38
3) Echo counting	39
Limnological methods	39
Zooplankton sampling methods	41
V. Test of the Sensory Mechanism	43
Influence of light on vertical migration	43
Influence of temperature on vertical migration	50
Discussion	62
VI. Tests of Selective Advantage Theories	64
1) Foraging hypothesis	64
2) Bioenergetic hypothesis	67
3) Predator avoidance hypothesis	71
4) Multifactor hypotheses	78
Discussion	82

Table of Contents (continued)

VII. Ontogenetic Shifts in Diel Vertical Migration Behavior	84
Diel vertical migrations by kokanee	85
Discussion	90
VIII. Coevolution of Vertical Migratory Behavior in <i>O. nerka</i> and Zooplankton Prey .	96
Juvenile sockeye and kokanee feeding behavior	96
Diel vertical movements of zooplankton in sockeye and kokanee lakes	100
Discussion	105
IX. Summary: The Selective Advantage of Diel Vertical Migratory Behavior in <i>O. nerka</i>	108
X. References	112
Appendix 1. Timing of Lake Visits	124
Appendix 2. Location of Sampling Sites	125
Appendix 3. 1986 Diel Echogram Sequences from Babine Lake	140
Appendix 4. Temperature at Maximum Nocturnal Echo Integrator Voltage	144

List of Tables

Table 3-1. Predictions of juvenile sockeye diel vertical migration hypotheses	21
Table 3-2. Geographical and limnological characteristics of study lakes	26
Table 8-1. Occurrence of prey in the stomach contents of juvenile sockeye and kokanee within northwest Pacific lakes	97

List of Figures

Figure 1-1. Diel variation in mid-summer juvenile sockeye depth distribution in Babine Lake, Lake Washington, and Great Central Lake. Data from Narver (1970), Woodey (1972), and Barraclough and Robinson (1972) respectively. Shaded area indicates depth range occupied by juvenile sockeye	3
Figure 2-1. Feeding and mortality rates of an idealized planktivore, as functions of predator visual range (vertical scales are arbitrary); redrawn from Clark and Levy (1988,fig.3)	15
Figure 2-2. Body weight and probability of survival of simulated crepuscular- and daylight-feeding planktivores; redrawn from Clark and Levy (1988,fig.5)	15
Figure 2-3. Frequency distribution of temperatures at which maximum nocturnal trawl catches of juvenile sockeye were made during the period of thermal stratification of Lake Washington in 1970; redrawn from Woodey (1972,fig.12)	23
Figure 3-1. Temperature profiles from Owikeno Lake obtained during September of 1952. Data from Foskett (1958)	25
Figure 3-2. Location of study lakes within the province of British Columbia	25
Figure 4-1. Block diagram showing analysis sequence during A) data collection and B) echo signal processing	29
Figure 4-2. Diel sequence of echograms showing migration of juvenile sockeye salmon within A) upper 80m of Shuswap Lake, July 18-19, 1987, and B) upper 30m of Fraser Lake on Aug.21-22, 1986. Numbers shown above echograms indicate time of sampling (PDST)	31
Figure 4-3. Diel sequence of echograms showing migration of juvenile sockeye salmon within upper 40 m of Babine Lake on Aug. 19-20, 1986. Numbers above echograms indicate time of sampling (PDST)	32
Figure 4-4. A) Diel echogram sequence from Quesnel Lake on Aug. 23-24,'86, indicating daytime disappearance of fish targets from field of 15 degree transducer, and B) daytime echogram with 6 degree transducer showing juvenile sockeye fish targets between 60-90 m	34
Figure 4-5. Comparison of echograms from Shuswap Lake on A) July 3'87 and B) July 18'87, and C) Chilko Lake on July 15'87, showing effect of vessel noise on juvenile sockeye nocturnal vertical distribution	35
Figure 4-6. Comparison of a nocturnal echogram from Kennedy Lake on Sep.3, 1986, with echo integrator results	37
Figure 4-7. Echo integrator <i>B</i> values used for conversion of 40 Log R-amplified echo data to 20 Log R-amplified equivalents	37
Figure 4-8. Echograms showing echo returns produced by ping pong balls suspended at different depth levels within Shuswap Lake, Sept.29, 1987	40
Figure 4-9. Mean and standard deviation (bars) for target strengths (measured in decibels) estimated for ping pong balls suspended in Shuswap Lake, Sept.29, 1987	40
Figure 5-1. Mean daytime depth of fish targets plotted against the light extinction coefficient, <i>K</i> , in Babine, Owikeno, Quesnel, Shuswap and Okanagan lakes. Okanagan data for the lowermost mode of a bi-modally depth-distributed population (see Fig. 7-1)	44

Figure 5-2. Diel sequence of echograms from Basin 2 of Owikeno Lake obtained on Oct. 1-2'85 with a 70kHz Simrad EY-M. Elongated vertical traces on echograms produced by gas bubbles within the water column	46
Figure 5-3. Daytime echograms obtained from the four different basins of Owikeno Lake on Oct. 2'85	47
Figure 5-4. Light and temperature profiles for 2 different basins of Owikeno Lake on Oct. 1-2'85, shown in relation to the depth distribution of acoustic targets	48
Figure 5-5. Sequential light extinction profiles during 2 crepuscular periods: A) dusk at Cultus Lake on Apr. 15'86, and B) dawn at Great Central Lake on May 27'86. Time of sampling shown adjacent to the curves	49
Figure 5-6. Diel patterns of juvenile sockeye depth distribution within Babine Lake during 1986. Diagrams based on diel echogram sequences shown in Appendix 3	51
Figure 5-7. Effect of moonrise on juvenile sockeye depth distribution within Babine Lake on June 26'86	52
Figure 5-8. Echogram from nocturnal transect across Shuswap Lake on a calm, moon-lit night (Nov. 5'87)	53
Figure 5-9. Temperature at the depth of maximum echo integrator voltage. Lake sampling dates and locations listed in Appendix 4	53
Figure 5-10. Day and night echograms obtained from Babine Lake, 1986, shown in relation to the temperature profiles	55
Figure 5-11. Day and night echograms obtained from Shuswap Lake, 1987, shown in relation to the temperature profiles	56
Figure 5-12. A) Juvenile sockeye nocturnal echogram from a transect across the main axis of Quesnel Lake on Sep. 22'86, and B) mean depth of acoustic targets as computed from 6 distinct echo integrator sequences	57
Figure 5-13. Establishment of a Kelvin wave in a temperate lake as a result of Coriolis force operating on a wind-driven seiche. Redrawn from Goldman and Horne (1983,fig.5-20)	59
Figure 5-14. A) Juvenile sockeye nocturnal echograms, and B) echo integrator results across the main axis of Quesnel Lake on Aug. 12'87	60
Figure 5-15. Alteration in Quesnel Lake temperature profiles over a 25.5 hour period on Aug. 11-12'87	61
Figure 5-16. Quesnel Lake temperature profiles at 3 measuring points across Transect 6 on Aug.12'87 at T=04:30-05:00 (PDST)	61
Figure 6-1. Day and night vertical depth profiles of the predominant zooplanktonic organisms within Babine Lake on Aug. 5-6, 1967, as indicated by averaging depth-stratified Miller samplers from 8 discrete depths; redrawn from Narver (1970,fig.11)	65
Figure 6-2. Day and night vertical depth profiles of the predominant crustacean zooplankton species captured in plankton pump samples from Babine Lake on 2 dates during 1986. Kites depict relative abundance of organisms at 5 particular depths throughout the upper 30 m of the water column	66

Figure 6-3. Day and night vertical depth profiles of the predominant crustacean zooplankton species captured in plankton pump samples from Cultus, Quesnel and Shuswap Lakes	68
Figure 6-4. Diel vertical migration of juvenile sockeye in Cultus Lake on Sep. 29-30, '86 ..	69
Figure 6-5. Distribution of temperatures experienced by migrating juvenile sockeye within B.C. sockeye lakes during A) nocturnal, and B) daytime periods. Diel temperature difference experienced by migrants indicated on distribution C	70
Figure 6-6. Diel vertical migration of echo targets under isothermal conditions within Lakelse Lake on June 21-22'86. Upper echograms show diel change in fish depth distribution, while lower graph shows the temperature for the upper 25 m of the water column	72
Figure 6-7. Frequency distribution of calculated light intensities at the daytime depth of maximum fish biomass (shown on Fig. 5-1)	74
Figure 6-8. Effect of the quantity of irradiance on the mean reaction distance of cutthroat trout and Dolly Varden to artificial and natural prey; redrawn from Henderson and Northcote (1985,fig.2)	74
Figure 6-9. Diel echogram sequences from Chilko Lake obtained on A) July 15-16'87, and B) Aug. 14-15'87	75
Figure 6-10. Diel echogram sequence from Little Shuswap Lake on July 19-20'87. Echograms obtained by drifting at slow velocity	77
Figure 6-11. Comparison of target strengths of fish distributed in both shallow (0-20 m) and deep (40-60 m) water within Little Shuswap Lake at T=21:30 (PDST) on July 19, 1987 ...	77
Figure 6-12. Diel echogram sequences from Nimpkish Lake on A) June 17-18'86, B) Sept. 8-9'86, and C) Sept. 16-17'86. Echogram marks between 20-40 m on June 17-18'86 caused by electrical noise	80
Figure 6-13. Day and night echograms and echo integrator depth profiles from Nimpkish Lake for 3 sampling dates in 1986	81
Figure 7-1. Diel echogram sequences from Okanagan Lake on A) July 21-22'87, and B) Sept.30-Oct.1'87. Dispersed marking on echograms due to returns from <i>Mysis relicta</i>	86
Figure 7-2. Results of counting echotargets in 5m depth intervals within Okanagan Lake on 4 sampling dates of 1987. Count data are scaled by the effective sampling volume within each depth interval, and expressed as a proportion of the total target density within the pelagic water column. Note logarithmic scale. Temperature profile shown on the right	87
Figure 7-3. Target strength distribution within the water column of Okangan Lake during 1987 day and night hydroacoustic transects	89
Figure 7-4. Diel echogram sequences and scaled echocount data for Kootenay Lake hydroacoustic transects on Sept. 25-26'87	91
Figure 7-5. Target strength distribution within the water column of Kootenay Lake during day and night transects undertaken Sept. 25-26'87	92
Figure 7-6. Diel echogram sequences and scaled echo count data for Skaha Lake hydroacoustic transects on July 23-24'87	93
Figure 7-7. Target strength distribution within the water column of Skaha Lake during day and night transects undertaken July 23-24'87	94

Figure 8-1. Three possible diel migratory patterns of zooplankton in relation to the diel movements of a predominant planktivore 101

Figure 8-2. Day and night vertical depth profiles of the predominant zooplankton species captured in plankton pump samples from Nimpkish Lake on 2 dates during 1986 103

Figure 8-3. A) Diel vertical migration of *Mysis relicta* within Okanagan Lake on Sept. 30 - Oct. 1, 1987, and B) nocturnal mysid distribution in relation to the temperature profile 104

Acknowledgements

I am indebted to my wife and dearest companion Karen for personal support and continual willingness to accept collect phone calls from all parts of the province. The research was ably supervised by Dr. T.G. Northcote and a supervisory committee of Drs. K. Hyatt, J.D. MacPhail, W. Neill, and C. Walters. Dr. C. Clark of the Institute of Applied Mathematics (UBC) provided invaluable input and stimulation early during the study. R. Johnson of Canadian BioSonics Ltd. introduced me to fisheries hydroacoustics, supplied the necessary training and equipment to carry out the study, and enthusiastically supported the project. BioSonics Inc. (Seattle) provided access to echo signal processing equipment. Westwater Research Centre (UBC) made their Boston Whaler and van available for my use.

Numerous federal and provincial biologists supported the research and provided expertise and/or assistance with field logistics, including U. Orr and D. Peacock (DFO, Prince Rupert), I. Williams (DFO, Nanaimo), H. Enzenhofer, J. Hume, and K. Morton (DFO, Cultus Lake), and E. Parkinson and C. Bull (B.C. Fish and Wildlife Branch). L. Sennewald undertook microscopic counting of zooplankton. N. Butler kindly assisted with zooplankton identification, and also provided useful comments on a preliminary thesis draft.

Research funding was provided by two Fisheries and Oceans Subvention Awards to Dr. T.G. Northcote, as well as an NSERC postgraduate scholarship.

This research was stimulated by Dr. J.R. Brett's classical (1971) paper on juvenile sockeye environmental physiology and a 30 sec conversation with Dr. M. Swift in 1985.

Acknowledgements are extended to the following for permission to reprint previously published Figures:

Page 15, Figure 2-1. The University of Chicago Press.

Page 15, Figure 2-2. The University of Chicago Press.

Page 19, Figure 2-3. Dr. J. Woodey.

Page 59, Figure 5-13. Goldman and Horne, *Limnology*, Copyright ©1983 by McGraw-Hill, Inc.

Page 65, Figure 6-1. The Journal of the Fisheries Research Board of Canada.

Page 74, Figure 6-8. The Canadian Journal of Fisheries and Aquatic Sciences.

I. Introduction

"There are many unsolved problems of pelagic natural history, but one seems more baffling than any other: that of vertical migration."

Sir Alister Hardy (1958, p. 199)

The diel vertical migrations undertaken by aquatic organisms comprise one of the most common forms of co-ordinated mass movement within the biosphere. As the sun sets over the world's oceans and lakes, massive numbers of animals actively ascend from deeper dark waters into shallow surface layers. At dawn, after passing the night in shallow water, the organisms descend to a characteristic daytime depth level. The behavior is widespread and has evolved independently in many thousands of species from all major animal phyla, as well as in dinoflagellates. Observations of diel vertical migration behavior date back to those made by Cuvier on *Daphnia* in the early 1800's (Cushing 1951) as well as those made on board the first oceanographic vessels. In the Challenger Expedition Report, Sir John Murray (1885; cited by Cushing 1951, p. 159) wrote: *"The great majority of plankton organisms live at various depths down to and even deeper than 100 fathoms during the day and only come to the surface at night."*

Diel vertical migration is defined here as a synchronized movement by aquatic organisms in the vertical plane, with a periodicity of 24 h. The migration involves a regular alternation between spatially separated day and night depth strata. The widespread occurrence of the behavior suggests that there is a strong selective advantage of diel vertical migration compared to a static vertical distribution (the maintenance of a fixed depth in the water column). The nature of the selective advantage is not immediately apparent, and a large number of hypotheses have been put forward.

Among fish, diel vertical migrations are undertaken by both pelagic and demersal species. Demersal fishes are usually associated with a bottom substrate by day and tend to move off bottom and into the water column at night (Beamish 1966; Bowman and Bowman 1980). In contrast,

pelagic species often complete their diel vertical migrations in a water column devoid of solid structure which might serve as a vertical reference.

There are similarities in the diel vertical migrations of unrelated pelagic species. For example, herring (*Clupea harengus*) in the ocean undertake a diel pattern of vertical migration (Blaxter 1985) which resembles the behavior of many freshwater planktivores, including juvenile sockeye salmon (*Oncorhynchus nerka*) in British Columbia lakes. Both species feed on planktonic crustacea and there are marked similarities in the vertical distance traveled, as well as in the number, timing, and duration of surface ascents. The parallel vertical migratory behavior in these two unrelated species suggests that similar selective pressures have operated on both species during the course of evolution.

Diel horizontal migration, between littoral and pelagic areas, is another form of diel habitat shift that occurs in certain freshwater planktivores (e.g. Hall et al. 1979; Wurtsbaugh and Li 1985). Both vertical and horizontal migrants alternate between spatially separated day and night sub-habitats in a precisely-timed and regular fashion. Such habitat shifts usually coincide with diel shifts in schooling behavior (aggregated during the day, dispersed during the night). Both types of migration can be considered as a form of specialized diel time budgeting between alternate habitats.

While the general pattern of planktivore diel vertical migration usually involves a dusk ascent and a dawn descent, details of vertical migration vary greatly among geographical localities. For example, differences occur in the vertical amplitude, as well as the frequency of surface ascents by juvenile sockeye salmon in Babine, Washington, and Great Central Lakes (Fig. 1-1). As well, there is at least one population of juvenile sockeye (Lake Tustumena on the Kenai Peninsula, Alaska) where diel vertical migration behavior is reversed (Thorne 1983B). Any theory to explain juvenile sockeye vertical migration should account for such between-lake differences in vertical migratory activity.

Most sockeye salmon spend their first year of life in the pelagic zone of a freshwater nursery lake where they undertake characteristic diel vertical migrations. There are major differences in the morphometry, biological community composition, and limnological characteristics of sockeye

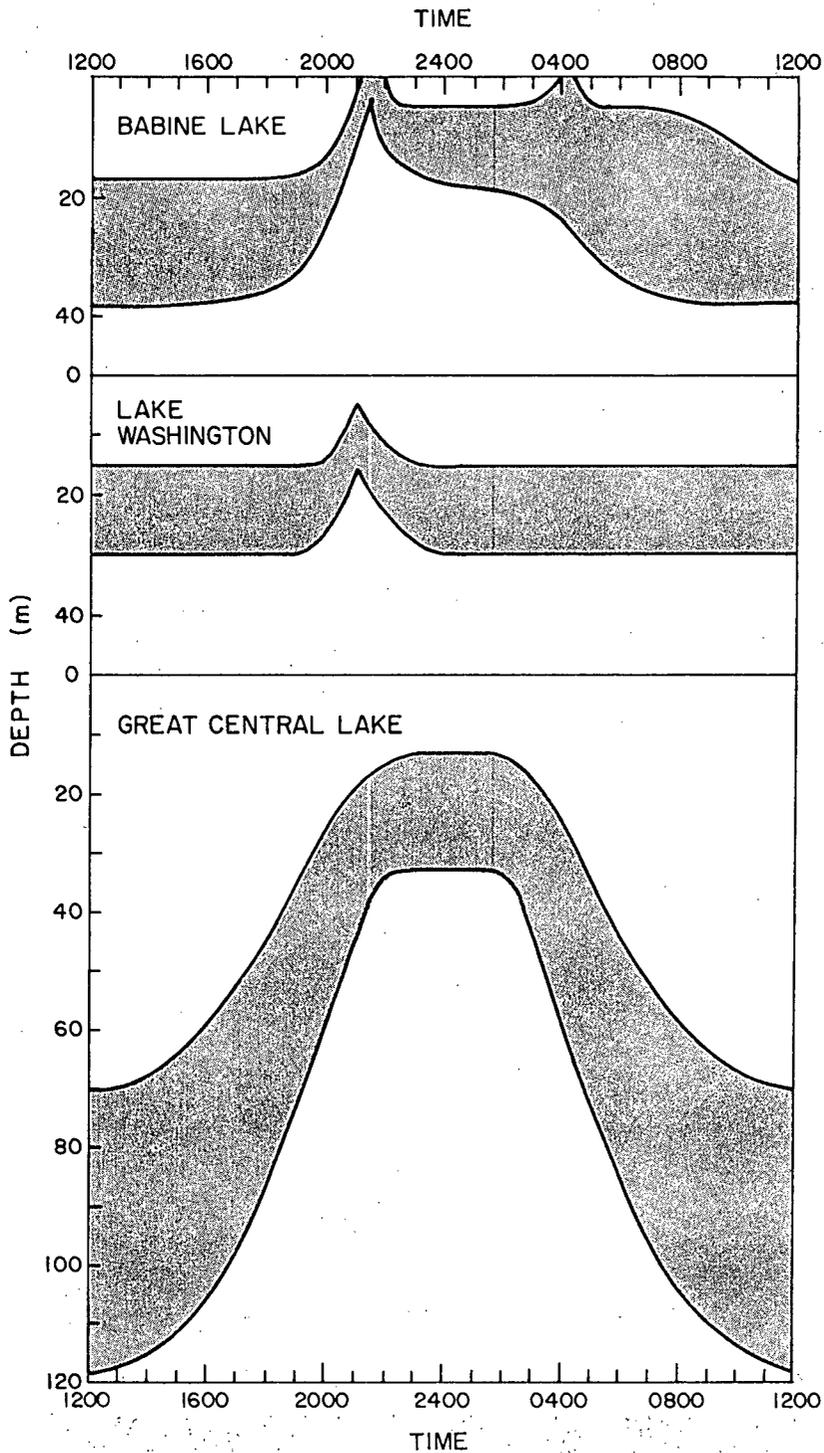


Figure 1-1. Diel variation in mid-summer juvenile sockeye depth distribution in Babine Lake, Lake Washington, and Great Central Lake. Data from Narver (1970), Woodey (1972), and Barracough and Robinson (1972), respectively. Shaded area indicates depth range occupied by juvenile sockeye.

lakes (Foerster 1968), as well as substantial seasonal changes. These environmental and biological differences should affect the diel migratory behavior of the fish in predictable ways. By comparing the vertical migrations of the animals under diverse conditions, observed differences in behavior may indicate how the animals have adapted to different variables.

Recent theory correctly predicts the timing of bluegill sunfish ontogenetic habitat shifts between littoral and pelagic regions (Gilliam 1982; Werner and Gilliam 1984). The Gilliam-Werner theory is based on an optimal control model of the trade-off between food consumption and the risk of predation in different habitats. While diel migrations occur over comparatively short time scales, the general principle of optimizing the trade-off between growth (via feeding) and predation risk can also be applied to diel habitat shifts, such as diel vertical migration.

Kokanee, the non-anadromous form of sockeye, complete most of their life cycle within the pelagic zone of a lake. Several investigators have documented reversed diel vertical migrations of sub-adult kokanee (Northcote et al. 1964; Rieman and Bowler 1980), suggesting the possibility of an ontogenetic shift in kokanee diel migratory behavior. It is important to determine whether such a shift occurs, and whether it can be predicted on the basis of current theory.

Diel vertical migrations are undertaken by numerous zooplanktonic animals, and recent findings suggest that such migrations confer a survival advantage on certain freshwater species (Zaret and Suffern 1976; Stich and Lampert 1981; Gliwicz 1986A). Reduced mortality through vertical migration can only be achieved, however, if the zooplankters minimize spatial contact with their planktivorous predators. Since juvenile sockeye are active vertical migrators, this potentially precludes a survival advantage of diel vertical migration (with the same diel timing as sockeye) by zooplanktonic prey species.

The approach taken in this study was to seek evidence for relevant theories of juvenile sockeye diel vertical migration by selectively comparing fish migratory behavior in a diverse set of lakes within British Columbia. Diel movements were compared to concurrent limnological measurements and plankton distributions in order to test sensory mechanism and selective advantage theories, which are reviewed in Section II. Sections III and IV describe the field design and methods respectively. Sections V and VI compare the observed patterns of migration and predictions from

theory. Ontogenetic shifts in diel migratory behavior in kokanee are described in Section VII. Diel vertical movements of zooplankton are compared to those of their major predators in Section VIII. Finally, a revised interpretation for the selective advantage of the behavior, in light of the recent field observations, is presented in Section IX.

II. Theories of Diel Vertical Migration

Diel vertical migrations are undertaken by planktonic invertebrates and are also well known among fish on the basis of observed day-night differences in catches by commercial fishermen (e.g. Woodhead 1966). There is a large body of theory within the ecological literature (see reviews by Cushing 1951; McLaren 1963; Hutchinson 1967; Longhurst 1976; Dingle 1980; Kerfoot 1985; and Bayly 1986) concerning the diel vertical migrations of aquatic organisms. Within this section, I review theories which pertain to the behavior in juvenile sockeye salmon and kokanee.

In animal behavior, it is important to distinguish between proximate and ultimate causation (Krebs and Davies 1981). A proximate cause is usually a sensory mechanism that explains how the animals accomplish their migration. An ultimate cause is an evolutionary explanation which interprets the behavior in terms of its survival value. The importance of addressing both the proximate as well as the ultimate explanation is that the sensory mechanism must be compatible with the evolutionary explanation (and vice versa). It may be possible to eliminate certain ultimate explanations if behavioral mechanisms are incapable of providing a means for achieving a supposed selective advantage. *"More and more biologists have learned that functional and evolutionary biology are not an 'either-or' situation, but that no biological problem is solved until both proximate and ultimate (=evolutionary) causations are determined"* (Mayr 1982, p. 131).

At the ultimate level, the challenge is to understand the selective advantage associated with diel vertical migration and the adaptive significance of the behavior. Historically, the concept of adaptation has created confusion (Dobzhansky 1956; Williams 1966; Curio 1973; Brandon 1984) because of its tautological connotations and its synonymous interpretation as fitness. Yet it is one of the most important concepts in ecology and Cowles (1904; cited by Colwell 1985, p. 771) has stated: *"If ecology has a place in modern biology, surely one of its great tasks is to unravel the mysteries of adaptation"*. The definition of adaptation used in the present context is that of a

relative measure (Brandon 1984): Animal *a* is better adapted than animal *b* in environment *E* if and only if *a* is better able to survive and reproduce in *E* than is *b*.

Currently, the usefulness of the adaptation concept in behavioral ecology is a subject of debate. At one extreme are biologists (e.g. Mayr 1974) who argue that the adaptive significance of a behavior can be studied scientifically, while at the other are those (e.g. Gould and Lewontin 1979) who focus on constraints to the process of adaptation in a changing environment. One healthy repercussion of the debate is a requirement for more stringent standards of evidence: "*The burden of proof has been firmly shifted to the proponent of adaptive explanations for the features of organisms, populations, communities, or ecosystems*" (Colwell 1985, p. 774).

Below, I consider possible sensory mechanisms involved in juvenile sockeye diel vertical migration, and then describe hypotheses which account for the adaptive significance of the behavior.

Sensory mechanisms for migration

Diel vertical movements of aquatic organisms are often crepuscular, suggesting that changing light intensity might serve as a primary sensory stimulus for movement. Deep scattering layers in the ocean, composed partially of myctophid fishes (Backus et al. 1968; Barham 1966) undertake diel vertical migrations that are associated with changes in light intensity (e.g. Boden and Kampa 1967). The role of light in vertical migrations of fish has been reviewed by Woodhead (1966) and Blaxter (1974) who observed that some vertical migrants such as herring follow the vertical movement of particular isolumens. At high latitudes, both in the Arctic and Antarctic Oceans, diel vertical migration of fish is absent (Blaxter 1974). Deep scattering layers of marine organisms respond to solar eclipses by ascending and descending as light intensities decrease and increase (Backus et al. 1965), and can be displaced with artificial lights. On one occasion near the Canary Islands, a deep scattering layer was experimentally displaced downwards from 60 to 300 m (Blaxter and Currie 1967).

The crepuscular timing of diel vertical migration (Narver 1970; Barraclough and Robinson 1972; Eggers 1978) suggests that juvenile sockeye respond to a light stimulus. Water clarity characteristics may affect the amplitude of juvenile sockeye vertical migration. Their relatively deep daytime distribution in Great Central Lake (70-120 m) and the large amplitude of vertical movement there (Barraclough and Robinson 1972) is probably related to the deep light penetration into this lake. Narver (1970) reports a September Secchi depth of 14 m for Great Central Lake compared with 4 m for Babine Lake. At Lake Tustumena on the Kenai Peninsula (Alaska) during June of 1981 when there was virtually no dark period due to its high latitude, juvenile sockeye did not migrate vertically (Thorne 1983B).

Fish are highly temperature-sensitive and possess sophisticated thermoregulatory behaviors (Rozin and Mayer 1961; Neill et al. 1972). The sensory system responsive to temperature is the general cutaneous segmental innervation (Sullivan 1954; Murray 1971). During conditioned response experiments (reviewed by Murray 1971) a majority of fish tested were sensitive to temperature changes between $0.05 - 0.1^{\circ}\text{C}$. Smith (1985) has suggested that predictable thermal gradients might be used as orienting stimuli in fish migrations and there are numerous examples (reviewed by Reynolds 1977) of temperature serving as a proximate stimulus affecting movements and hence distribution of fish populations.

The nocturnal distribution of juvenile sockeye in lakes suggests that the fish might be responding to a temperature stimulus. At night juvenile sockeye commonly stay in the vicinity of the thermocline (Narver 1970; McDonald 1973). During the period of thermal stratification of Lake Washington, fish were distributed in a narrow range of temperatures between $7.6 - 11.0^{\circ}\text{C}$ (Woodey 1972), about 4°C lower than the preferred $12 - 15^{\circ}\text{C}$ in laboratory-induced vertical temperature gradients (Brett 1952).

These observations suggest a sensory mechanism which involves both light and temperature cues: Day-time depth distribution and the timing of vertical movement may result from the fish following a particular light intensity level. Night-time depth distribution may be due to thermoselection behavior.

Alternative sensory mechanisms theoretically capable of predicting sockeye diel depth distributions include 1) a diel shift in temperature preference, and 2) a diel shift in pressure sensitivity. Both of these mechanisms need to be coupled with light in order to account for the diel timing of migration. Some fish species have diel thermoregulatory rhythms (Reynolds and Casterlin 1979). Most diel changes in temperature preference, however, are only a few °C. Juvenile sockeye encounter temperature differences as much as 12°C in Babine Lake (Narver 1970; McDonald 1973) and there is currently no evidence of diel shifts in temperature preference of the required magnitude to account for fish diel vertical migration. Fish with swimbladders are sensitive to pressure differences (Blaxter 1979) because of pressure-operated stretch receptors on the wall of the swimbladder (Qutob 1962). One prediction of a pressure-mediated sensory mechanism is a constancy of sockeye depth distribution pattern (seasonally) within a lake.

Adaptive significance of migration

1) Foraging hypothesis

Juvenile sockeye are largely planktivorous during their period of lake residence (Table 8-1) so necessarily must overlap with zooplankton populations in time and space. Most juvenile sockeye feeding occurs during crepuscular periods in relatively shallow water (Narver 1970; Barraclough and Robinson 1972; McDonald 1973; Doble and Eggers 1978). Occasionally, juvenile sockeye feed during other portions of the diel cycle, including the middle of the day in relatively deep water and also at night under conditions of calm water and bright moonlight (Narver 1970).

The foraging hypothesis contends that diel vertical movements result from the fish pursuing and following concentrations of vertically migrating prey organisms so as to maximize capture rates and minimize search time. At least some planktivores including alewives in Lake Michigan (Janssen and Brandt 1980) and freshwater sardines in Lake Kariba (Begg 1976) track the diel vertical movements of their zooplankton prey. There are other potential foraging benefits of vertical migration to planktivores besides maximizing contact with prey. A vertically ascending planktivore has the advantage of an illuminated background to provide visual contrast with its zooplankton

prey (Zaret and Suffern 1976), an important factor in fish vision. As well, a vertical migrant might be able to "census" its prey organisms (Woodhead 1965) especially if horizontal currents operate in different depth strata. Diel vertical migration would reduce the probability of re-encountering plankton patches that had been locally depleted due to previous foraging activity.

The foraging hypothesis requires that (1) zooplanktonic prey organisms migrate vertically, and (2) there be a close correspondence in the diel distribution patterns of planktivore and prey. The timing of planktivore vertical movements should coincide closely with those of the zooplankton.

2) Bioenergetic hypothesis

McLaren (1963) was the first to suggest that bioenergetic benefits might be realized by diel vertical migrants. The McLaren hypothesis maintains that vertically migrating zooplankton in thermally stratified waters would achieve an energetic advantage (over non-migrants) if they reduced their daytime metabolic costs by temporary residence in cold hypolimnetic water. Brett (1971) extended this concept to vertically migrating juvenile sockeye. Metabolic rate calculations suggested a possibility for metabolic cost reductions while the fish occupied the hypolimnion and Brett concluded that "*...sockeye have evolved a pattern of thermoregulation peculiarly adapted to maximizing growth, through the selective pressure of bioenergetic efficiency*" (Brett 1971, p. 112).

A bioenergetic hypothesis requires that juvenile sockeye are food-limited and grow at rates less than the physiological maximum. There exists good empirical evidence that juveniles of some sockeye populations are food-limited during their lake residency: when such sockeye lakes are artificially fertilized, smolt sizes increase and marine survival rates are enhanced (Hyatt and Stockner 1985). The density-dependent growth rates that have been observed in Babine (Johnson 1961), Owikeno (Ruggles 1966) and Frazer (Kyle et al. 1988) lakes further indicate that juvenile sockeye often grow at less than maximum rates. Brett (1983) estimated that a 5g, one-year-old sockeye smolt has achieved only one third of its potential size during its residence in the nursery lake.

Laboratory evidence suggests that diel vertical migration by juvenile sockeye has energetic consequences. Biette and Geen (1980) reared sockeye under controlled constant and cyclic temperatures (fluctuating on a diel time scale) and found that when food rations were low, highest

growth rates occurred in fish exposed to cyclic temperatures. Similar experimental results have been obtained for rainbow trout where diel temperature fluctuations were shown to be beneficial to growth (Hokanson et al. 1977). While diel temperature fluctuations evidently promote faster fish growth, it may be misleading to accept this as evidence confirming the bioenergetic hypothesis. Vertically migrating fish, especially those with swimbladders, incur significant energy costs in order to compensate for the accompanying hydrostatic changes (Alexander 1971, 1972). These costs were not considered by Biette and Geen (1980) and would effectively diminish a growth advantage due to diel temperature fluctuations. Calculations by Alexander (1972) suggest that the energetic cost to a vertical migrant with a swimbladder, of hydrostatic compensation at its daytime depth, is on the order of $25 \text{ cm}^3 \text{ oxygen} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$. However, these hydrostatic compensation costs may be relatively small in comparison to the differences in metabolic costs between active metabolism at high temperature, and *standard* metabolism at low temperature. Measurements by Brett (1964) indicate that for yearling sockeye, the difference in active metabolism at 15°C , and standard metabolism at 5°C , is on the order of $850 \text{ mg oxygen} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$. ($1 \text{ mg } \text{O}_2/\text{l} = 0.70 \text{ cm}^3 \text{ O}_2/\text{l}$).

Perhaps the most serious criticism of the bioenergetic hypothesis concerns the timing of vertical movements. For a visual feeding planktivore, daytime occurrence in the illuminated zone where prey concentrate would seem to be advantageous over a daytime distribution at depth where light levels are low and prey are sparse or absent. A reversed vertical migration by juvenile sockeye, whereby the fish occupied surface waters by day, and deep water at night, would result in a cyclic thermal regime similar to that experienced by "normal" vertical migrants (but out of phase by 12 h). The increased foraging opportunities provided to such migrants would presumably result in higher growth rates because of the freshwater growth limitation experienced by many sockeye populations. Whereas bioenergetic considerations could be important in affecting nocturnal distribution and movements (at light levels below the visual feeding threshold), the bioenergetic hypothesis in its current form seems inadequate to explain the full cycle of juvenile sockeye vertical migration.

3) Predator avoidance hypothesis

Among certain freshwater zooplankton, diel vertical migration is evidently caused by intensive predation pressure from visual feeding planktivores (Zaret and Suffern 1976; Stich and Lambert

1981; Gliwicz 1986A). Eggers (1978) hypothesized that juvenile sockeye in Lake Washington keep to regions of the water column where light intensity is low and limit their foraging time so as to minimize the possibility of being detected by squawfish, a visual-feeding piscivore.

The fact that sockeye school by day suggests an influence of predators since schooling can function as a predator avoidance mechanism (Pitcher 1986). Mortality of juvenile sockeye can surpass 90 % in some lakes (Foerster 1938; Brett and McConnell 1950; Robinson and Barraclough 1978) primarily from predation by piscivores (Ricker 1941). In both Cultus and Great Central Lakes, most adult sockeye are lake spawners and produce fry which recruit directly into pelagic habitats with no period of littoral occupancy. Thus in such lake systems, predator-induced mortality is largely confined to the pelagic zone. In Cultus Lake juvenile sockeye are exposed to intense predation pressure from squawfish, Dolly Varden, cutthroat trout, and juvenile coho (Ricker 1941) and a threefold increase in lake survival rates followed a predator control program (Foerster and Ricker 1941). A more recent study within Cultus Lake (Steigenberger 1972) has shown that levels of squawfish abundance are similar to those encountered by Foerster and Ricker (1941).

Two critical assumptions of the predator avoidance hypothesis are first, that the piscivores which feed on sockeye themselves utilize vision as a primary method of prey detection, and second, that predation risk is positively related to light intensity. Two important predators of juvenile sockeye, cutthroat trout and Dolly Varden, are visual feeders whose reactive distances to prey are proportional, albeit differently, to light intensity (Henderson and Northcote 1985). Predation studies with juvenile sockeye (Ginetz and Larkin 1976), cyprinids (Cerri 1983) and bluegill sunfish (Howick and O'Brien 1983) as prey suggest that prey risk varies inversely with light intensity. These studies, which confined predators and prey in experimental arenas, demonstrated well developed predator avoidance behaviors that are most effective under relatively intense light conditions. The results do not necessarily contradict the predator avoidance hypothesis since the visibility of objects underwater, and hence the detectability of prey to a visual searching predator, is determined primarily by luminance contrast (Hemmings 1966; Hester 1968; Ware 1971; Lythgoe 1979). In the open pelagic waters of a lake, searching ability and detection of juvenile sockeye by visual feeding piscivores would be greatest in the illuminated surface waters when juvenile sockeye are contrasted by the lighted background of the surface. In the deeper parts of the water column, light intensities

are reduced and the light is homogeneous due to scattering and refraction (Blaxter 1970). These conditions would minimize the visual contrast between juvenile sockeye and their background.

The predator avoidance hypothesis is attractive as a simple way to account for the diel timing of vertical migration by juvenile sockeye. A difficulty arises, however, since sockeye themselves require light to search for zooplankton. Hence the rate of food intake and the risk of predation in surface waters vary over the diel cycle in a similar way. A sockeye juvenile which spent the entire diel cycle within a hypolimnetic refuge would minimize its risk to piscivores, but would inevitably face starvation within a period of several weeks (Bilton and Robins 1973). By itself, the predator avoidance hypothesis fails to account for the diel vertical migrations of juvenile sockeye. A more realistic hypothesis would explicitly consider the trade-off between zooplankton food intake and predation risk within the euphotic zone.

Multifactor hypotheses

The three single factor hypotheses can also be combined as multifactor hypotheses. Eggers (1978) was the first investigator to consider the possibility of interactions between hypotheses when he stated (p. 1123): “(Brett’s hypothesis) *is not inconsistent with the hypothesis developed here, (predator avoidance) because any energy bonus resulting from minimizing respiration costs at low temperature serves to reduce energy requirements, hence reduces the foraging time needed to ingest the needed energy, and thus decreases vulnerability to predators.*” Below, I consider the four multifactor combinations that can be derived from three single factor hypotheses (three two-factor combinations and one three-factor combination).

4) Foraging and predator avoidance combined: the “antipredation window”

Gilliam (1982) and Werner and Gilliam (1984) developed an optimal-control model of the trade-off between growth rate and predation risk. This model predicted the timing of bluegill sunfish ontogenetic shifts in habitat preference. For pre-reproductive juveniles, the model predicted that individuals should choose the habitat which minimizes the ratio of μ/g , where μ and g are the mortality and growth rates associated with a particular habitat. This model has now been extended

to account for amphibian metamorphosis patterns (Werner 1986), and in modified form (minimize the ratio of μ/f , where f is the foraging rate), the model correctly predicts habitat choices of juvenile creek chubs (*Semotilus atromaculatus*) in experimental stream enclosures (Gilliam and Fraser 1987).

A similar model was developed by Clark and Levy (1988) to account for the diel vertical migrations of juvenile sockeye. This model views the pelagic lake environment as consisting of two habitats: H_1 , a productive but risky surface habitat, and H_2 , an unproductive but safe deep-water refuge. The model assumes that zooplankton prey and piscivores are confined to the surface habitat. Dynamic optimization methods were employed to calculate the optimal crepuscular feeding interval, Δ , within H_1 such that the ratio μ/ϕ was minimized, where μ is the predator-induced mortality rate, and ϕ is the feeding rate.

The underlying predation model assumes a sigmoid-shaped functional relationship between feeding rate and visual sighting range underwater. When applied to the different trophic levels (Fig. 2-1), the model predicts a horizontal separation between the sockeye feeding rate curve (sockeye feeding on zooplankton) and mortality rate curve (piscivores feeding on sockeye). The existence of this "antipredation window" should provide a strong selective pressure for sockeye to migrate into surface waters for brief crepuscular periods. The model is capable, at least in principle, of quantitative predictions of the timing of vertical migration, although this would require several difficult parameter estimations. A trade-off was evident between the growth and survival rates of simulated crepuscular and daylight feeders (Fig. 2-2). It thus appears that diel vertical migration in juvenile sockeye could serve to promote within-lake survival at the expense of growth rate.

The antipredation window model provides a novel explanation for the adaptive significance of vertical migration in planktivores which hunt by sight and are in turn preyed upon by piscivores that also search visually. The window is a consequence of the effects of diel variations in light intensity on the differential trade-off between food intake and the risk of predation. The model assumes that variations in light intensity are directly instrumental in determining the ultimate cause of juvenile sockeye diel vertical migrations, rather than being merely an incidental cue for the achievement of bioenergetic or other objectives.

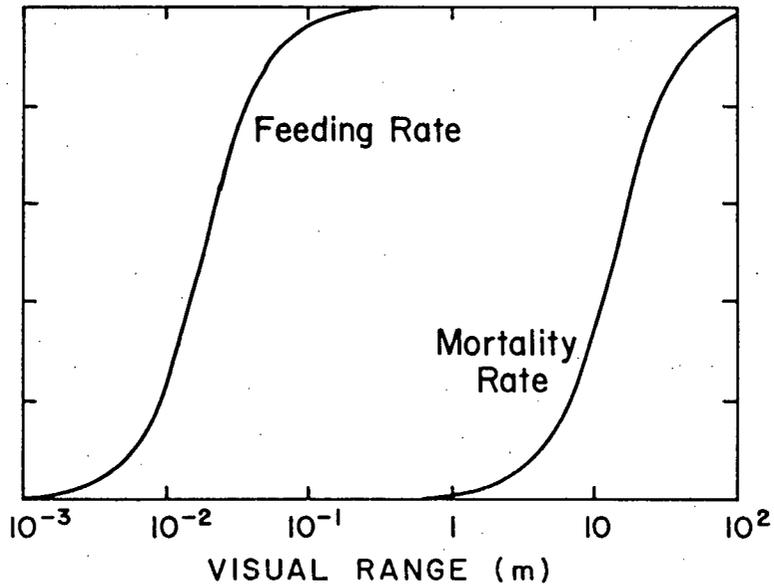


Figure 2-1. Feeding and mortality rates of an idealized planktivore, as functions of predator visual range (vertical scales are arbitrary); redrawn from Clark and Levy (1988,fig.3).

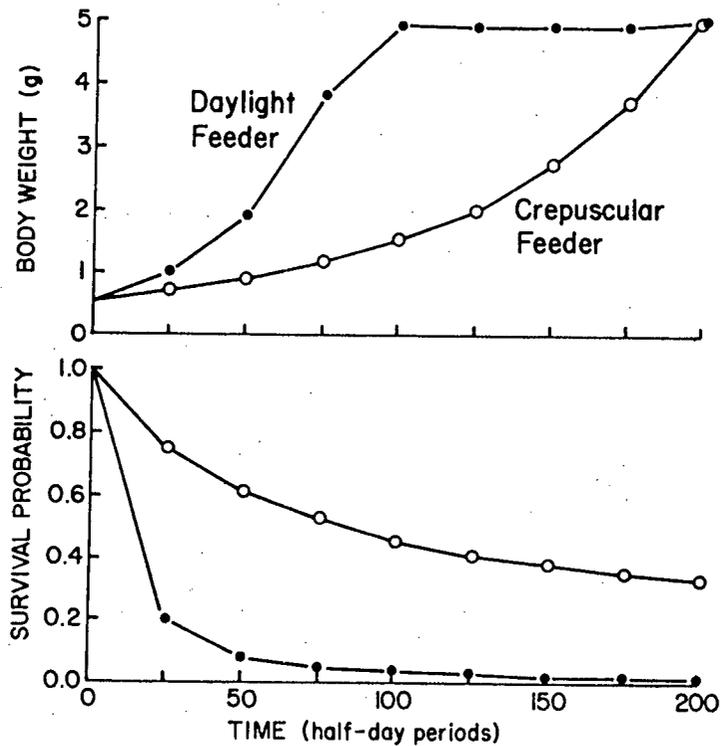


Figure 2-2. Body weight and probability of survival of simulated crepuscular- and daylight-feeding planktivores; redrawn from Clark and Levy (1988,fig.5).

5) Foraging and bioenergetics combined

This hypothesis proposes that juvenile sockeye alternate between a food-rich near-surface area and a deeper resting area where lower temperatures optimize growth rate. The relative foraging and metabolic costs and benefits would determine the amount of time spent in each sub-habitat. Because zooplankton usually concentrate in epilimnetic surface waters, and sockeye are mainly visual-feeders, this hypothesis predicts daytime occupation of surface waters, and a nocturnal descent to the thermocline.

A similar hypothesis was developed by Wurtsbaugh and Neverman (1988) to account for diel vertical migrations of juvenile sculpins (*Cottus extensus*) in Bear Lake, Utah. These fish are associated with the bottom sediments by day where they forage on benthic ostracods and cyclopoid copepods. At dusk they migrate into the water column and spend the night in shallow water at the 15°C isotherm. Wurtsbaugh and Neverman suggest that this diel vertical migration serves to increase digestion rates over those which would occur in the 5°C hypolimnion, and present data from growth experiments which supports their hypothesis. The hypothesis is similar to that proposed by McLaren (1963), only in this case, the animals ascend, rather than descend, into the water column in order to promote metabolic efficiency.

For juvenile sockeye (and probably most ectotherms) the optimal temperature for growth is dependent upon ration size. The optimal temperature for growth shifts from 15°C to 5°C as ration levels vary between > 6 % *body weight · day*⁻¹ (excess rations) to 1.5 % *body weight · day*⁻¹ (Brett et al. 1969).

Brett et al. (1969) calculated net growth efficiency values, E_n , for juvenile sockeye salmon as:

$$E_n = G/(I - M) \times 100\% \quad (2.1)$$

where G is growth, I is the food intake, and M is the fraction of the total ration that is involved in maintenance. The results suggested maximum net efficiencies, close to 40 % , at temperatures between 8 – 10°C on low ration sizes.

For juvenile sockeye, therefore, a combined foraging and bioenergetic hypothesis predicts daytime occupation of surface waters for feeding, and a nocturnal descent to the thermocline. The precise nocturnal depth distribution would depend upon ration level and the temperature structure of the water column. Under this hypothesis, sockeye would never undertake vertical excursions into the hypolimnion.

6) Bioenergetics and predator avoidance combined

During non-feeding periods of the year, the optimal bioenergetic strategy would minimize metabolic costs and growth losses by maintaining body temperatures as low as possible (Brett et al. 1969). Avoidance of visual-feeding predators could be achieved by daytime occupation of deep pelagic areas. Such areas would also provide minimum lake temperatures. Thus when sockeye do not feed, this hypothesis predicts a relaxation of diel migratory behavior and a continual occupation of deep water.

During the winter the feeding behavior of sockeye within ice-covered lakes is unknown. However, the sockeye are susceptible to piscivores at this time of the year. Foerster (1968) records predation by Dolly Varden char and cutthroat trout under the ice in mid-winter at Lakelse Lake. In southern sockeye lakes which remain ice-free through the winter, field samples suggest a low level of plankton feeding by sockeye and a high proportion of individuals (> 50 %) which do not feed (Doble and Eggers 1978).

7) Antipredation window and bioenergetics combined

The antipredation window hypothesis successfully predicts the timing and duration of juvenile sockeye vertical feeding excursions into shallow surface waters. However the model does not predict any specific nocturnal migration pattern. At light levels below the visual feeding thresholds of sockeye and their predators, a combined antipredation window and bioenergetic hypothesis predicts a nocturnal occupation of the thermocline where temperatures optimize metabolic efficiency. Elements of three single factor hypotheses can thus be combined as a novel multifactor hypothesis.

The optimal metabolic temperature is dependent upon ration size (see above). On relatively low ration sizes, maximum net growth efficiency occurs between 8–10°C (Brett et al. 1969). Within Lake Washington, juvenile sockeye are in fact nocturnally associated with these temperatures (Fig. 2-3).

During daytime periods, this hypothesis predicts a descent into the hypolimnion (which would occur at the expense of metabolic efficiency) in order to minimize exposure to visual-feeding predators. Viewed from this perspective, diel vertical migration by juvenile sockeye would reflect a three-way compromise between foraging, predator avoidance, and metabolic efficiency.

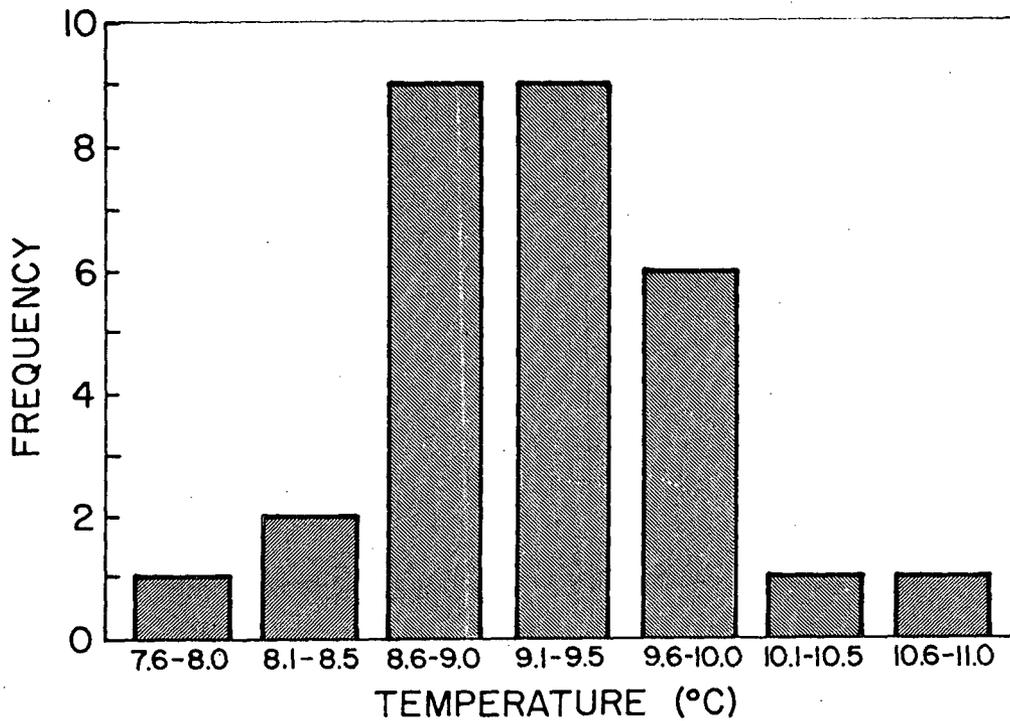


Figure 2-4. Frequency distribution of temperatures at which maximum nocturnal trawl catches of juvenile sockeye were made during the period of thermal stratification of Lake Washington in 1970; redrawn from Woodey (1972,fig.12).

III. Research Strategy

Diel vertical migrations by sockeye (and other aquatic organisms) are an established fact of aquatic life. There is a large body of theory (Table 3-1) concerning diel migratory behavior. The scientific challenge is to distinguish between the hypotheses and critically evaluate which are necessary and/or sufficient (*sensu* Hilborn and Stearns 1982) to provide a causal explanation for the behavior. This needs to be provided at both the proximate and ultimate levels.

Tests of a sensory mechanism hypothesis can be made through a series of descriptive laboratory experiments, or by observing the outcome of "natural experiments" under field conditions (e.g. Backus et al. 1965; Blaxter 1974). Considerable insight into the selective advantage of zooplankton diel migratory behavior has been provided by adopting experimental procedures (Huntley 1985; Johnsen and Jakobsen 1987). For sockeye within their nursery lakes, the relevant spatial scale for behavioral interaction is on the order of 10's of meters, making experimentation difficult. Several of the strongest hypotheses are multifactorial, further complicating experimental design and practicality (Hilborn and Stearns 1982).

In "The Growth of Biological Thought", Mayr (1982) suggests that experimental methodology is applicable in only certain branches of science, but not in others (e.g. geology, astronomy, paleontology). He further argues that observational-comparative methods are of major importance in evolutionary biology and emphasizes their scientific legitimacy, pointing out that "*observation in biology has probably produced more insights than all experiments combined*" (Mayr 1982, p. 32).

The role of technological advance in permitting meaningful comparative observations is paramount (Mayr 1982); one frequently cited example in biology is the role of the development of the microscope. In ecology, the lack of adequate sampling methodology is a major impediment and Gilbert et al. (1976) have stated (p. 56): "*By far the most serious problem in ecology today is not any difficulty of theory, analysis or interpretation: it is the difficulty of finding and implenting,*

Table 3-1. Predictions of juvenile sockeye diel vertical migration hypotheses.

Hypothesis	Prediction
Sensory mechanism	
Light controls daytime position Light controls migration timing Temperature controls nocturnal position	Daytime depth related to water clarity Crepuscular-timed vertical movements Narrow nocturnal temperature distribution
Adaptive Significance	
1) Foraging	Active zooplankton vertical migrations
2) Bioenergetics	Relaxation of migration under isothermal conditions
3) Predator avoidance	Sockeye occur under low light conditions (by day) corresponding to reduced predator visual acuity
4) Antipredation window	Brief crepuscular foraging excursions into surface waters Daytime occupation of depths with low light
5) Foraging and bioenergetics	Daytime zooplankton foraging Nocturnal descent to thermocline
6) Bioenergetics and predator avoidance	Occupation of deep hypolimnetic regions during non-feeding periods
7) Antipredation window and bioenergetics	Brief crepuscular foraging excursions into surface waters Daytime occupation of depths with low light Nocturnal descent to thermocline

accurate and unbiased sampling methods in the field". During the present study, a technological advance (development of SONAR hardware designed for fisheries research) was a necessary prerequisite to undertake the research.

The strategy during the present study was to define sets of environmental conditions where the predictions from theory were in conflict, and then assess sockeye diel migratory behavior. Large differences occur in the characteristics of sockeye lakes (Foerster 1968). An initial factorial sampling design (considering lakes as "treatments") was abandoned due to errors in lake classification status. The lakes that were eventually adopted were chosen to encompass wide differences in limnological characteristics. By exploiting lakes of different condition as "natural experiments" the observed behavior of the fish then provided a basis for accepting or rejecting a particular hypothesis.

An example is provided by Owikeno Lake. Owikeno is a glacially turbid lake (Secchi depths can be $< 1\text{m}$) which develops a deep thermocline in late-summer (Fig. 3-1). The lake serves as a nursery for the abundant Rivers Inlet sockeye run (Foskett 1958). The bioenergetic hypothesis predicts vertical migration below the thermocline in this lake (no temperature-related bioenergetic benefits can be achieved by migrating through an isothermal water column). In contrast, the predator avoidance hypothesis requires solely that the fish descend to daytime depth levels of low light intensity which, in a glacially turbid lake, would be relatively high in the water column. Assessment of sockeye diel migratory behavior in a lake like Owikeno can therefore quickly provide useful insight into the selective advantage of the behavior.

Replicated sockeye depth distribution and limnological observations from a large set of sockeye lakes provided the necessary statistical basis for examining the sensory mechanism hypothesis. The observations also provided the basis for testing the single factor selective advantage theories elaborated in Section II.

It is admittedly difficult to falsify a multifactor hypothesis on the basis of comparative field observations alone. One requirement of a multifactor theory in my case is that its predictions be consistent with observed fish behavior patterns in a large number of sockeye lakes representing

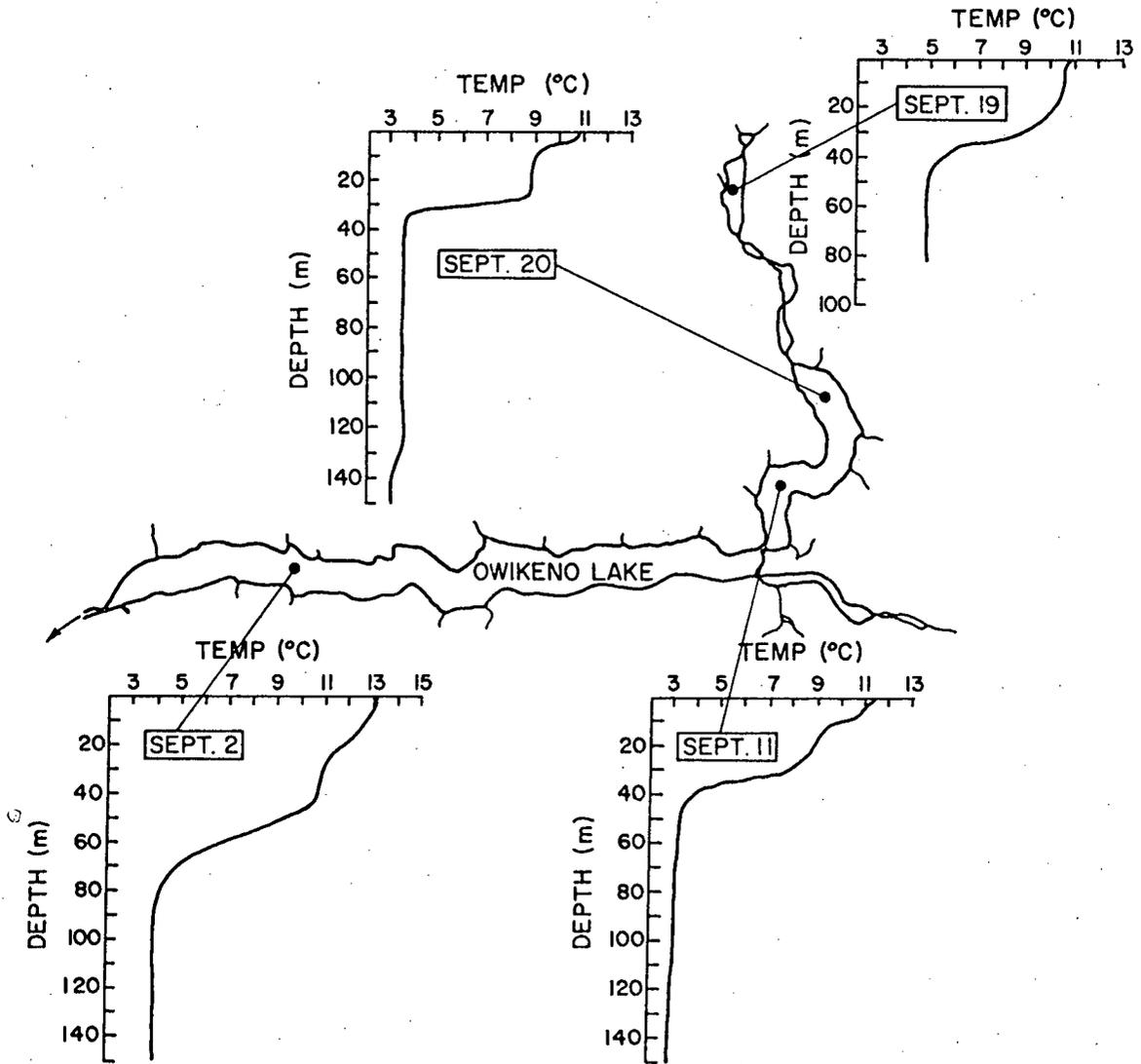


Figure 3-1. Temperature profiles from Owikeno Lake obtained during September of 1952. Data from Foskett (1958).

a wide range of conditions. Discrepancies between fish performance in the field and a theoretical model will suggest a need for further theoretical development.

Schedule and location of lake visits

I chose 15 lakes within the province of British Columbia as study lakes (Fig. 3-2). Limnological characteristics of the study lakes are summarized in Table 3-2 and are described by Goodlad et al. (1974), Stockner and Shortreed (1983, 1985) and Stockner (1987). Study lakes were visited on the dates shown in Appendix 1. Sampling sites are located on the lake maps contained in Appendix 2. Kokanee are present within the interior sockeye lakes but largely absent from the coastal systems studied. Due to historical events (Nelson 1968), sockeye are presently absent from three lakes within the Columbia River drainage basin (Okanagan, Skaha, Kootenay). Kokanee predominate in the pelagic zone of these latter 3 lakes (B.C. Fish and Wildlife Branch, UBC Research Office, unpublished data).

Sockeye lake visits were timed to coincide with relatively dense juvenile populations. During the period of study, large adult spawning escapements occurred within Fraser (1985), Meziadin (1985), Babine (1985), Quesnel (1985), Chilko (1986), and Shuswap (1986) lakes. These systems were visited during the year subsequent to the dense spawner population so that sampling coincided with a high density of juvenile sockeye within the lake's pelagic zone. Kokanee lakes were visited during the summer and fall months of 1987.



Figure 3-2. Location of study lakes within the province of British Columbia.

Table 3-2. Geographical and limnological characteristics of study lakes.

	Latitude (N)	Longitude (E)	Elevation (m)	Area (km ²)	Mean Depth (m)	Max Depth (m)	Volume (10 ⁹ m ³)	IOE (mg/L ² -1)	ph	Load (kg)	Secchi Depth (m)	Reference
Babine	54	122	708	490	55	186	21.6	62	7.0	---	5.0	d
Chilko	51	124	1170	200	109	362	---	---	---	---	10.5	d
Cultus	49	124	41	63	92	47	0.72	---	---	---	19.1	d
Fraser	49	124	670	55	13	30	---	23	6.9	14.7	---	d
Great Central	49	124	82	51	212	---	---	25	7.1	8.3	---	d
Kootenay	50	118	4	64	139	---	---	---	7.4	---	---	d
Lakelse	54	129	67	14	108	135	0.108	68	9.4	---	---	d
Meziedin	56	130	246	36	48	---	---	24	7.5	9.3	---	d
Nimkish	50	127	20	37	162	242	26.2	25	7.0	---	---	d
Kenogon	50	120	---	95	76	366	---	---	6.8	---	---	e
Quasnoy	51	125	720	28	159	460	48.0	---	---	---	11.0	f
Shuswap	52	119	347	310	162	199	10.56	---	---	---	7.9	g
Skaha	49	120	---	20	26	157	---	---	---	---	4.9	j

- a - total dissolved solids
- b - compensation depth (m)
- c - Levy and Hall (1985)
- d - Goodlad et al. (1974)
- e - K. Marton, Dept. of Fisheries and Oceans, unpublished data
- f - Stockner (1970)
- g - Stockner and Shortreed (1985)
- h - Platt (1950)
- i - Shortreed and Stockner (1981)
- j - Stockner and Northcote (1974)
- k - Foskett (1958); Chernoff (1971)

IV. Methods

Hydroacoustic methods

Information on fish diel distribution and migration behavior was derived by hydroacoustic methods (SONAR). Such methods are routinely used for stock assessment of pelagic fish species (Thorne 1983A) and have undergone recent refinements due to the development of multibeam hydroacoustic systems (Ehrenberg 1983; Burczynski and Johnson 1986; Thomas and Jackson 1987; Traynor and Ehrenberg in press), multifrequency systems (Simmonds and Armstrong in press), and the elaboration of appropriate statistical models (Rudstam et al. 1987). Moreover, independently derived salmon population estimates obtained by weir counts (Thorne 1979; Mulligan and Keiser 1986; Hyatt et al. in press) suggest that hydroacoustic methods are highly accurate in simple assessment situations (e.g. a single dominant fish species within a lake environment).

Description of fish diel vertical migration is a straightforward application of hydroacoustics. The first use of such methods for studying vertical migratory behavior occurred over 35 years ago (Hasler and Villemonte 1953) to document habitat shifts of perch within Lake Mendota. Other studies which have applied acoustic methods to the analysis of fish diel migratory activity include Northcote et al. (1964), Beamish (1966), Narver (1970), Dembinski (1971), Begg (1976), Bohl (1980), Janssen and Brandt (1980), and Hamrin (1986). Acoustic methods are also useful for describing invertebrate diel vertical migrations (Northcote 1964; Teraguchi and Northcote 1966).

Mathisen et al. (1977) have described juvenile sockeye as being ideally suited for acoustic enumeration because of their confinement to the limnetic zone, their relatively simple age-structure, the absence of a large number of co-habiting pelagic fish species, and the relatively simple physical properties of freshwater (compared to seawater). Many sockeye lakes are surveyed acoustically on a routine basis in order to provide juvenile population estimates and a basis for predicting adult returns. As a result, there is a wealth of experience and information concerning the application of hydroacoustic methods for the assessment of juvenile sockeye salmon populations.

In many of the study lakes (Babine, Chilko, Cultus, Fraser, Quesnel, Shuswap) trawling results (Narver 1970; Dept. of Fisheries and Oceans, Cultus Lake laboratory, unpublished data)

indicate that juvenile sockeye are numerically predominant in the pelagic zone, comprising over 90 % (and frequently 100 %) of trawl catches. Thus in these lakes, hydroacoustic targets can be safely identified as juvenile sockeye. Threespine sticklebacks (*Gasterosteus aculeatus*) co-occur with sockeye in the pelagic zone of 4 systems (Kennedy, Nimpkish, Owikeno, and Meziadin), potentially confounding the identification of acoustic targets in these lakes. Midwater trawl sampling and surface tow-net sampling (Chernoff 1971) suggests that sticklebacks in Owikeno Lake maintain a shallower diel vertical distribution than do juvenile sockeye.

Hydroacoustic methods are also applicable to kokanee (Northcote et al. 1964; Rieman and Bowler 1980; E.Parkinson, B.C.Fish and Wildlife Branch, unpublished observations. Kokanee maintain a pelagic distribution through most of their life cycle and predominate in the limnetic zone of several large lakes within British Columbia, including Okanagan, Skaha and Kootenay.

Field data collection procedures

A two-phased data collection-signal processing sequence was adopted during the present study (Fig. 4-1). Acoustic signals (0.4 msec pulse width generated at a rate of 2/sec) were digitized via a pulse code modulator (PCM) device and then taped on β -format video cassette recorder (VCR) tape in the field for subsequent laboratory analysis and data processing. Different BioSonics echosounder systems were employed during 1986 and 1987. During 1986, I used a single beam 420 kHz echosounder together with a 15 degree transducer (-3db, full angle) and amplified the electronic returns at 20 Log R time varied gain. During 1987, I used a dual beam 420 kHz echosounder together with a 6 degree/ 15 degree dual beam transducer, and amplified the electronic returns at 40 Log R time varied gain.

Echo signals were monitored in the field on an oscilloscope and chart recorder. By monitoring the detected output from the amplifier playback interface (Fig. 4-1), it was possible to ensure that echo signals were properly taped and that the receiver gain was adjusted so as to achieve echo voltages between 0.5-3 V (V_{rms}), thus maximizing signal: noise ratios and simultaneously avoiding tape saturation levels (10 V). Nunnallee (1973) describes the trade-off between system gain and tape saturation. At regular intervals during data collection, the voltage of a continuous wave

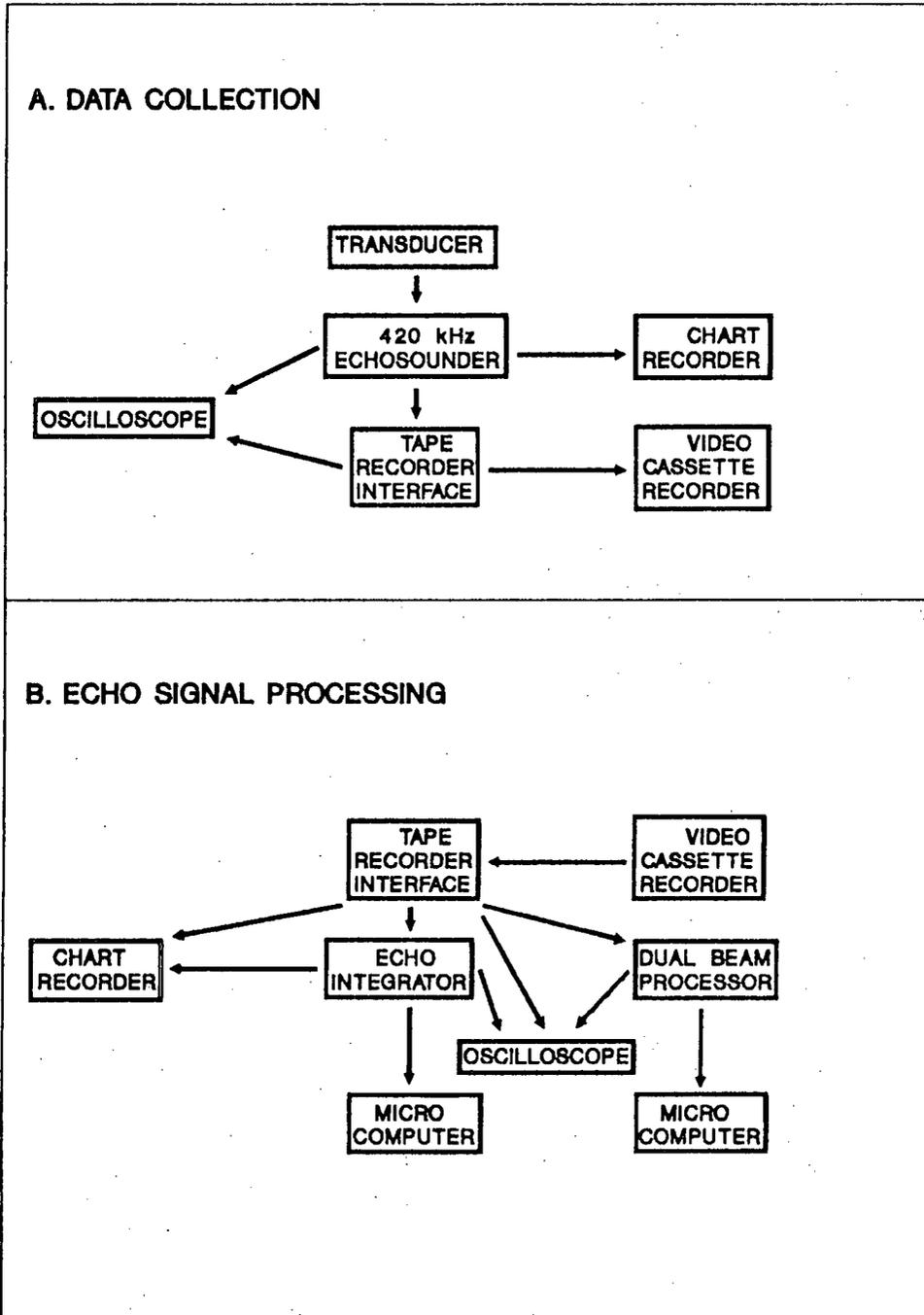


Figure 4-1. Block diagram showing analysis sequence during A) data collection and B) echo signal processing.

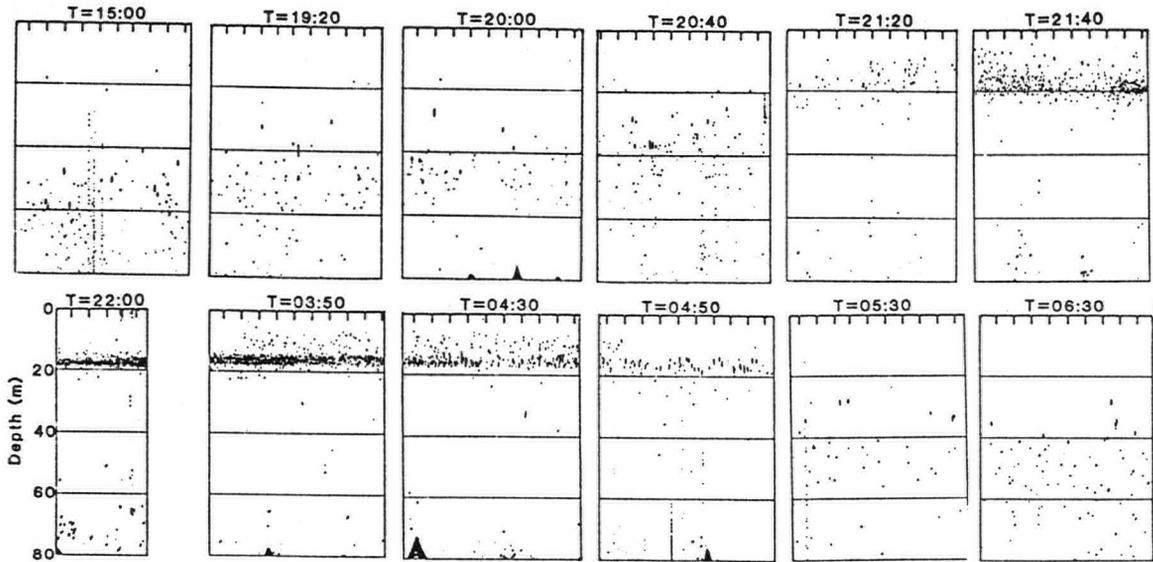
calibration tone was measured and taped. This procedure permitted standardized playback gain adjustment prior to echo signal processing.

The echosounder system was housed under the canvas cover of a 5m fiberglass outboard boat. The transducer was deployed from a rotatable pipe mount fixed amidships. After a relatively dense pelagic fish concentration was located, its movements were tracked over a 24 hour period. By transecting at a velocity of 2m/sec in an irregularly directed fashion, a large number of targets were encountered and electronic "surface noise" was minimized. Transects of 10 minute duration were undertaken to characterize the fish vertical depth distribution at a given point during the diel cycle. The transects were strategically distributed so as to detect changes in fish vertical distribution, with most intensive sampling at dusk and dawn when the fish were actively migrating. During the majority of surveys, a total of 20-25 10 minute transects were undertaken to characterize the diel cycle of migration. Examples of diel echogram sequences from Shuswap and Fraser lakes are shown in Fig. 4-2. The diel differences in echo target frequency apparent on the echograms result from diel changes in sockeye schooling behavior. Juvenile sockeye commonly occur in schools by day, and disperse as individuals at night (Narver 1970; Eggers 1978).

The down-looking deployment of the transducer provided an effective method for tracking sockeye and kokanee in most circumstances. However, when the fish were distributed in shallow surface waters most targets disappeared from the echograms. This effect is illustrated in Fig. 4-3, a diel sequence from Babine Lake. Juvenile sockeye on this date occurred between 25-30 m by day. At dusk, the fish ascended close to the surface, and there was a decrease in echo target frequency (T=2130 on Fig. 4-3). This was followed by an increase in target frequency as the fish descended to their nocturnal depth of 12-15 m (T=2340 on Fig. 4-3). At dawn, when many of the fish re-ascended to the surface there was again a decrease in echo target frequency (T=0510 on Fig. 4-3). Thereafter the fish began to school and descended to their daytime depth level. The reduction in target frequency in shallow water may have been due either to boat avoidance in shallow water (see below) or to near-field effects close to the face of the transducer (Shotton and Bazigos 1984).

Choice of the 420 kHz operating frequency reflected the freshwater application (for marine applications, lower operating frequencies would be appropriate for fish surveys due to the greater signal attenuation in seawater). Choice of transducer beam angle reflected the anticipated fish

A) Shuswap Lake July 18-19'87



B) Fraser Lake Aug.21-22'86

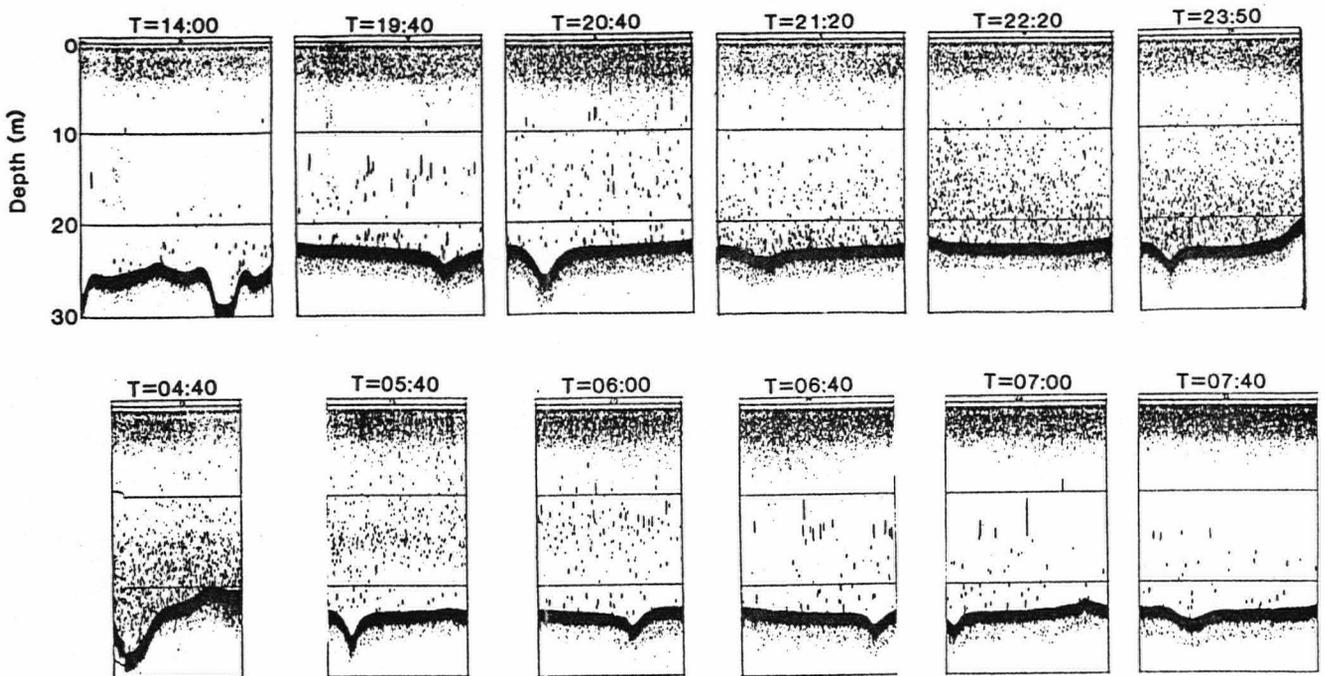


Figure 4-2. Diel sequence of echograms showing migration of juvenile sockeye salmon within A) upper 80 m of Shuswap Lake, July 18-19, 1987, and B) upper 30 m of Fraser Lake on Aug.21-22, 1986 (marks between 0-5 m due to sound reflections from zooplankton). Numbers shown above echograms indicate time of sampling (PDST).

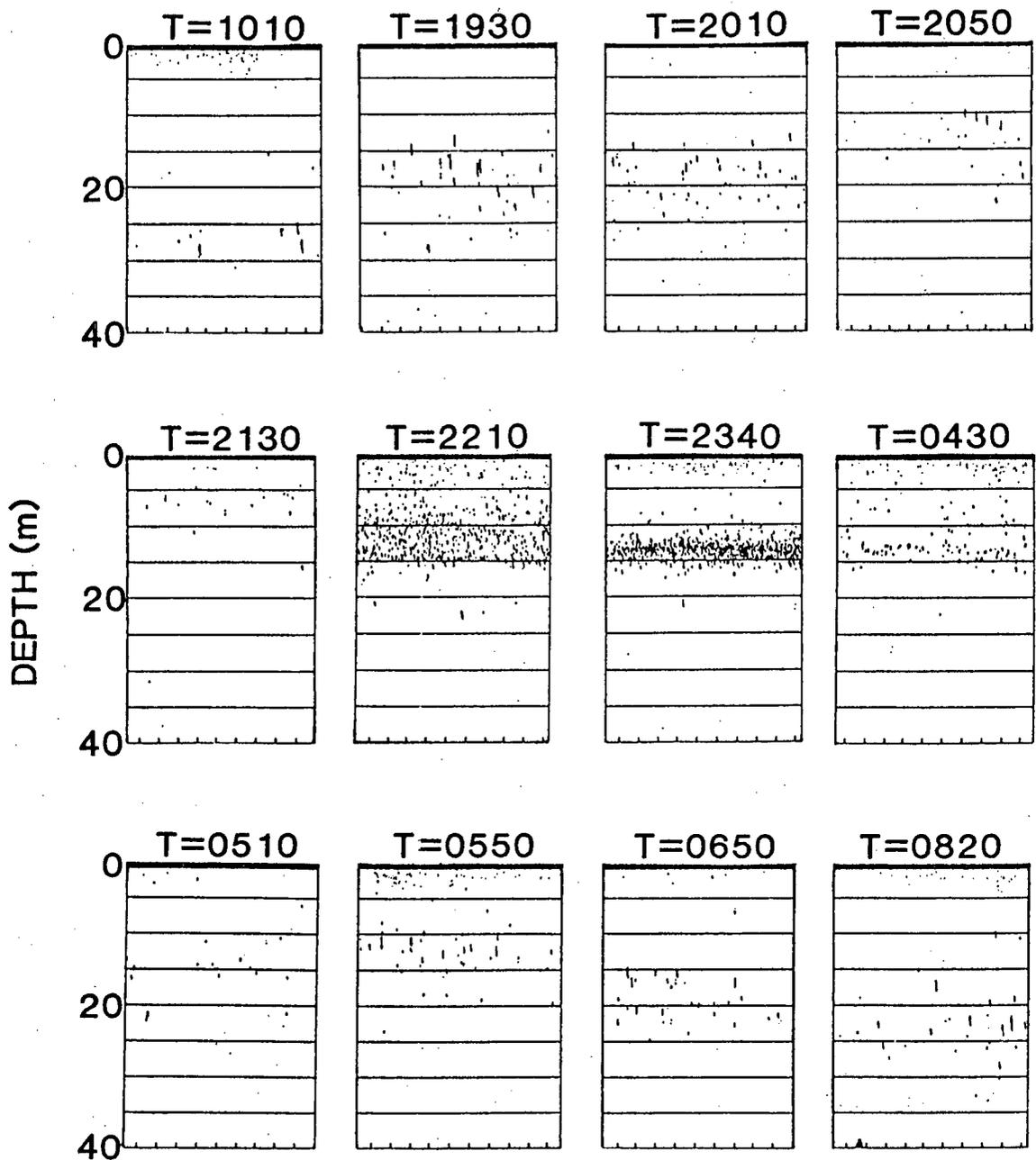


Figure 4-3. Diel sequence of echograms showing migration of juvenile sockeye salmon within upper 40 m of Babine Lake on Aug.19-20, 1986. Numbers above echograms indicate time of sampling (PDST).

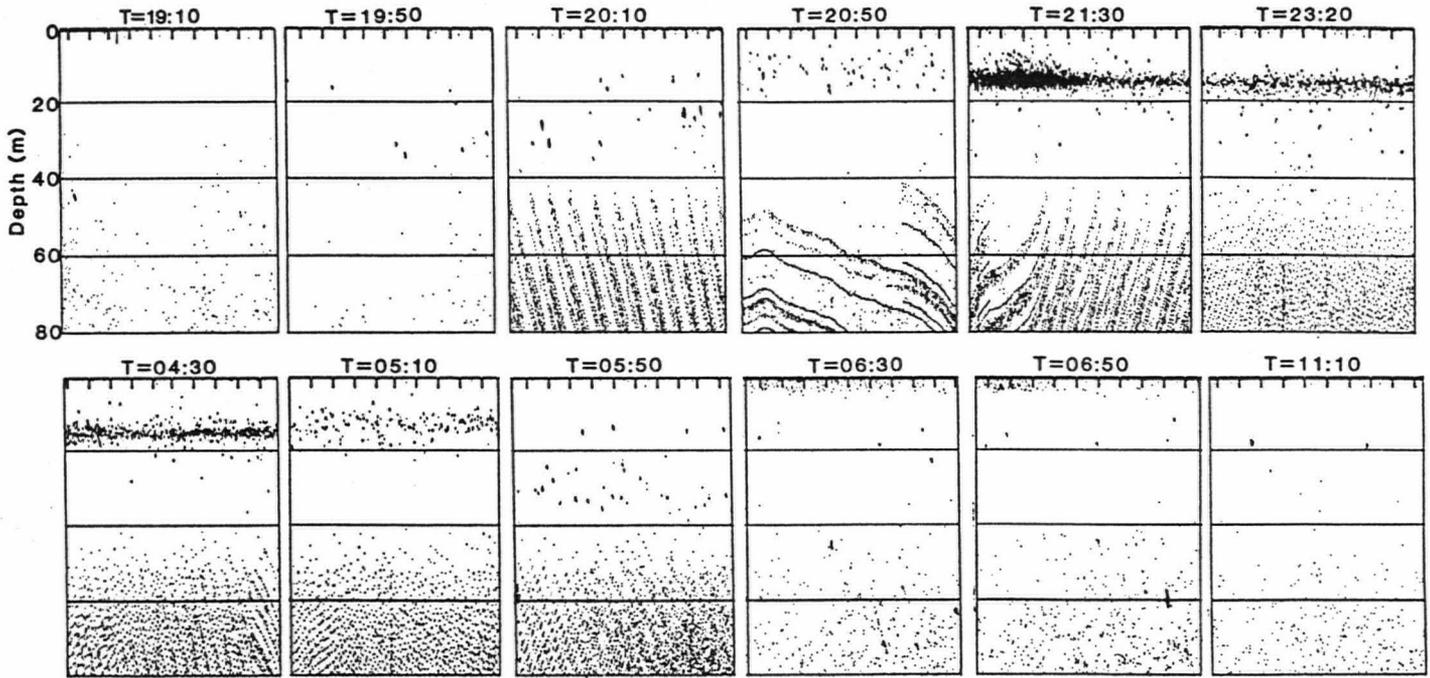
density and depth distribution since a trade-off exists between acoustic sampling power in shallow water, and depth penetration in deep water. With the acoustic system employed during 1986, it was possible to receive echoes from descending schools of sockeye down to a depth of 70 m (Fig. 4-4A). At deeper depths, voltage returns diminished to background noise levels, and it was not possible to track the fish. In clear lakes (e.g. Quesnel; August 1986 Secchi depth = 9.8m) where the fish descended beneath 70 m it was necessary to use a relatively narrow beam transducer (6 degrees) in order to estimate the daytime depth of the fish (Fig. 4-4B).

Some fish respond to the sound stimulus produced by an approaching vessel by altering their vertical distribution (Olsen et al. 1983). To evaluate vessel avoidance by juvenile sockeye, the nocturnal depth distribution of sockeye was compared under "quiet" (stationary) and "noisy" (mobile transect) conditions in Shuswap and Chilko lakes. On two dates in Shuswap Lake, sockeye had a similar vertical depth distribution during stationary deployments and mobile transects (Fig. 4-5A and B). In Chilko Lake, however, sockeye targets were present in shallow depths (0-10 m) on stationary echograms, but absent from mobile records (Fig. 4-5C). These observations suggest that active vessel avoidance occurs when the fish distribute in shallow water (0-10 m), but is probably negligible at depths below 10 m. Most observations during the present study, with the exception of those taken from Chilko, Babine and Owikeno lakes, involved juvenile sockeye populations deeper than 10 m.

Echo signal processing

1) Echo integration: The primary method of extracting fish depth distribution information was echo integration (Nunnallee 1973, 1980; Thorne 1971, 1983A; Burzynski 1982). This technique was developed for quantifying fish echo observations, and there are a number of echo integrators that are widely used in hydroacoustic research studies (compared in Johannesson and Mitson 1983). Most echo integrators produce squared voltage outputs within user-specified depth intervals such

A) DIEL ECHOGRAM SEQUENCE



B) DAYTIME ECHOGRAM



Figure 4-4. A) Diel echogram sequence from Quesnel Lake on Aug.23-24, 1986, indicating daytime disappearance of fish targets from field of 15 degree transducer (echogram marks between 40-80 m due largely to electrical noise), and B) daytime echogram with 6 degree transducer showing juvenile sockeye fish targets between 60-90 m.

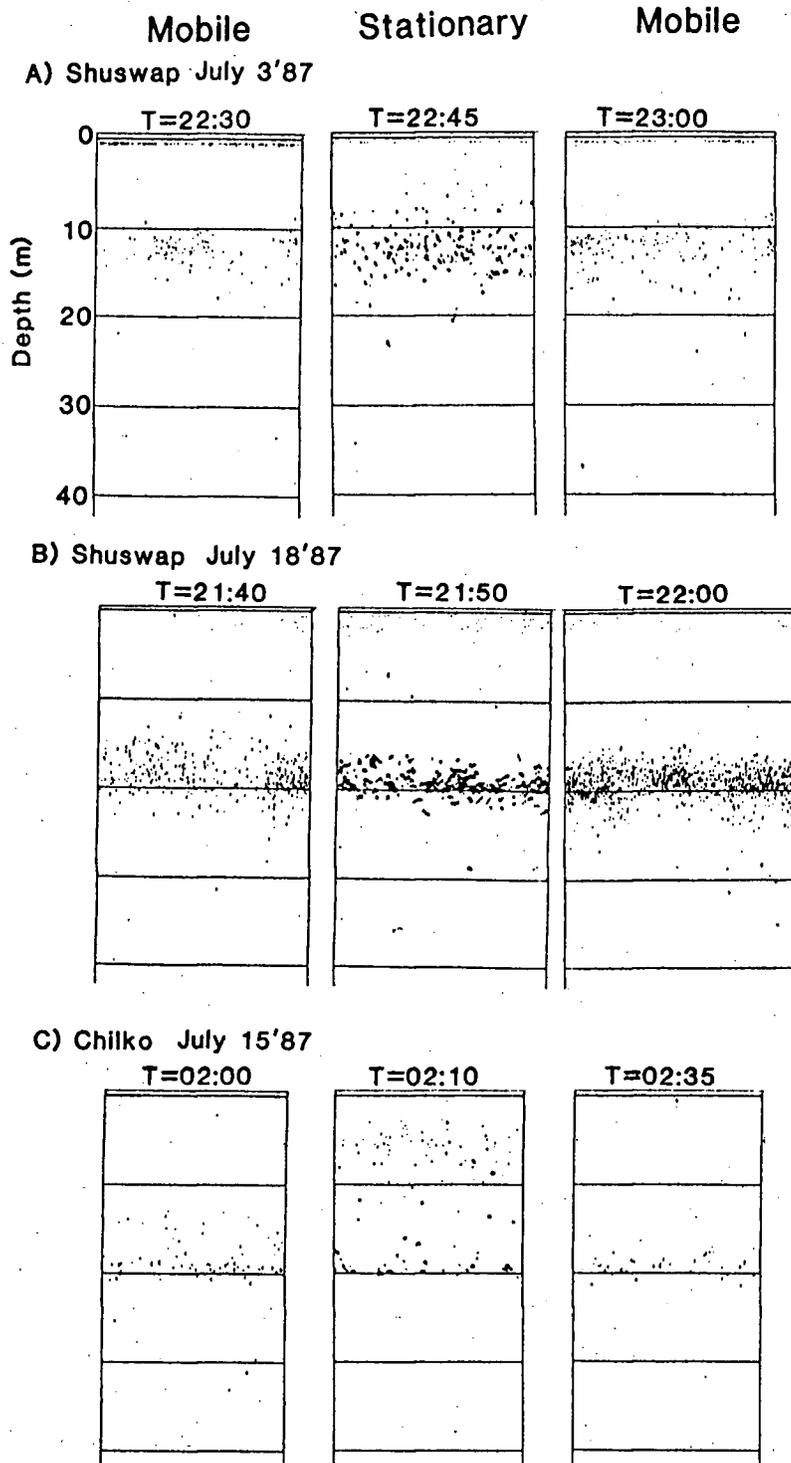


Figure 4-5. Comparison of echograms from Shuswap Lake on A) July 3, 1987 and B) July 18, 1987, and C) Chilko Lake on July 15, 1987, showing effect of vessel noise on juvenile sockeye nocturnal vertical distribution.

that the echo integrator output, V_{out} , is given by the product of fish density, D , and mean acoustic back-scattering cross-section, $\bar{\sigma}_{bs}$, multiplied by an equipment scaling constant, K :

$$V_{out} = K \cdot D \cdot \bar{\sigma}_{bs} \quad (4.1)$$

V_{out} is a mean value averaged over n sound pulses and is output in m discrete depth strata. During quantitative population studies, estimates of $\bar{\sigma}_{bs}$ (or alternatively, the decibel equivalent, target strength) are required in order to scale the echo integrator output, and these can be obtained in several ways (Ehrenberg 1983). During the present study, since juvenile sockeye of a single size-class predominated in most of the study lakes ($\bar{\sigma}_{bs}$ can be considered as a constant), the echo integrator output was directly proportional with sockeye density. Thorne and Ames (1987) have recently shown that juvenile sockeye abundance indices in Lake Washington, derived independently by echo integrator procedures and Isaacs-Kidd midwater trawls, have a strong positive correlation.

Echo integration of the taped echo data took place in the laboratory with a BioSonics Model 121 Digital Echo Integrator (Fig. 4-1). Since the objective was to monitor diel variation in relative (not absolute) fish density, values of 1 were adopted for the "A" and "B" constants (equipment scaling factors) required by the instrument. The A constant is computed from factors derived from the hydroacoustic hardware, the speed of sound in water, and the average back scattering cross section of the fish and has units of $fish/m^3 \cdot V^2$, while the B constant is a unitless scaling factor which corrects for variations in the time-varied gain of the echo sounder. The echo integrator output (V^2) was then used as a measure of the relative fish density in different depth strata. During all analyses, there was a direct correspondance between the echo integrator output, and the qualitative information present on the echogram (e.g. Fig. 4-6).

Mean depth of the fish population, \bar{Z} , for a given transect was computed as :

$$\bar{Z} = \frac{1}{V_t} \sum_{i=1}^m Z_i \cdot V_i \quad (4.2)$$

where

$$V_t = \sum_{i=1}^m V_i \text{ and } m \text{ is the total number of depth strata.}$$

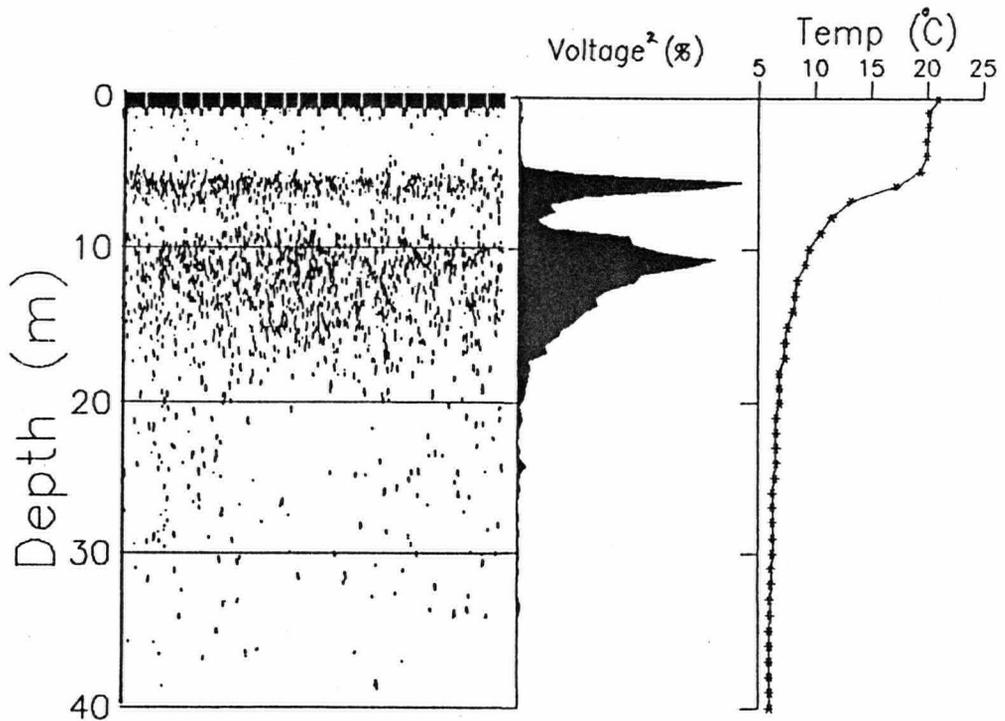


Figure 4-6. Comparison of nocturnal echogram from Kennedy Lake on Sept. 3, 1986, with echo integrator results.

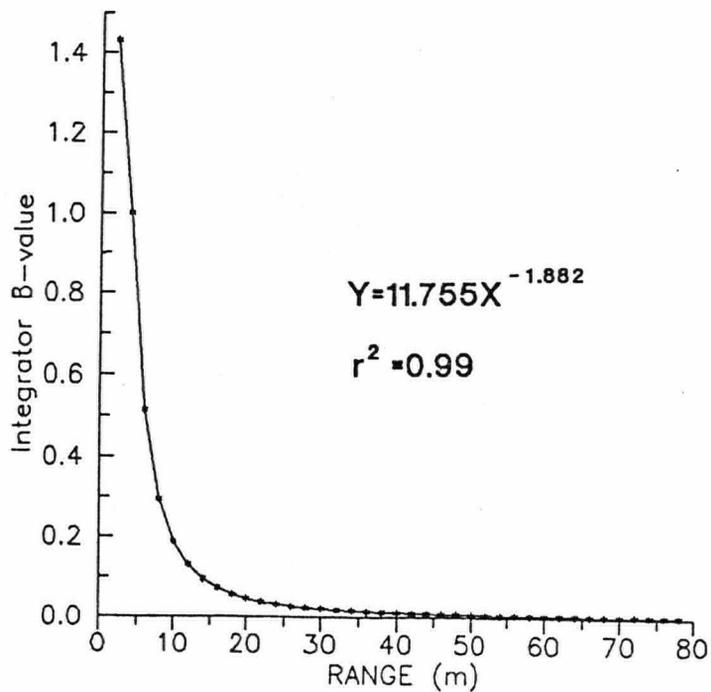


Figure 4-7. Echo integrator B values used for conversion of 40 Log R-amplified echo data to 20 Log R-amplified equivalents.

An alternative index of depth distribution, the depth of maximum echo integrator voltage, was used for analysis of juvenile sockeye depth preference when other species of fish targets were numerous in the transducer beam.

Echo integration requires 20 Log R-amplified echo data. Because the 1987 data were collected at 40 Log R amplification (for dual beam analysis), it was necessary to convert the results to their 20 Log R- amplified equivalents. This was achieved by echo integrating a 40 Log R-amplified calibration tone and computing adjusted B values (Fig. 4-7) according to a procedure outlined in Appendix B of the BioSonics Echo Integrator Manual. These values were entered into the instrument prior to echo integration of the 1987 echo data. The 6° (narrow beam) channel was used for echo integration purposes.

2) Target strength: Quantitative interpretation of echo amplitudes is confounded by the objects' spatial position within the transducer beam. It is not possible to easily distinguish the echo return of a large fish off-axis, from that produced by a small fish on-axis. For this reason, direct estimates of fish target strength (TS - a measure of an objects' acoustic reflecting power), are difficult to obtain with conventional single beam echo sounder systems (e.g. Rudstam et al. 1987). The SONAR equation (Thorne 1983A) relates the output voltage from an echo sounder, v_{out} (measured in decibels), to system operating parameters and physical parameters, as follows:

$$v_{out} = SL + TS + G_0 + 2B(\theta) \quad (4.3)$$

where SL is the source level, G_0 is the system gain, and $B(\theta)$ is the beam pattern factor derived from the directivity pattern of the transducer.

The 2 unknown parameters in the equation are TS and $B(\theta)$. The equation can be solved for TS provided $B(\theta)$ can be estimated; such estimates are obtainable *in situ* through the use of multi-beam systems, including split beam and dual beam techniques (Ehrenberg 1983). Use of such devices can in theory provide fish size information, since relationships can be derived which relate fish size and fish target strength (Love 1977; Dickie and Boudreau 1987). However, other factors, e.g spatial aspect (Buerkle 1987; MacLennan et al. in press) can also influence fish target strength

values and remote estimates of fish size need to be interpreted with caution. Initial application of dual beam techniques for estimating juvenile sockeye size distributions has produced favourable results (Burczynski and Johnson 1986).

In an attempt to establish whether kokanee undertake ontogenetic shifts in diel vertical migratory activity, dual beam hydroacoustic procedures were applied within Okanagan Lake during 1987. Dual beam data were acquired on a BioSonics Model 181 Dual Beam Processor, and transferred to computer disk (Fig. 4-1). Pulse amplitude and duration criteria used during analysis were the recommended values contained in the BioSonics Model 181 Manual. Fish target strength data were then computed using the BioSonics "TS" computer program.

In order to field test the dual beam system, a study was carried out in Shuswap Lake (Fig. 4-8) using suspended ping pong balls as standard targets. The results of computing target strength estimates (Fig. 4-9) suggest that the system provides reasonable values for a uniformly shaped target [the theoretical target strength of a ping pong ball is -40.54 db (J.E. Ehrenberg unpublished data)].

3) Echo counting: Due to the presence of abundant mysid populations which overlapped in space with the kokanee targets of interest within Okanagan Lake, it was not feasible to integrate the echo returns to estimate diel changes in depth distribution. Instead, echoes were counted using the dual beam system (see above) and an estimate of the number of echoes per m^3 was provided by an algorithm within the "TS" program which computes the effective sample volume within particular depth strata according to the mean target strength and the estimated beam pattern factor of the hydroacoustic system. Echo counting methods have also been used by Kelso et al. (1974) to quantify fish depth distributions.

Limnological methods

In order to accurately position temperature and light sensors in the water column, a hand-operated winch system, weighted with a 5 kg weight, was employed for all limnological measurements. Single temperature profiles were measured at mid-day, using a YSI-SCT meter, at 1m

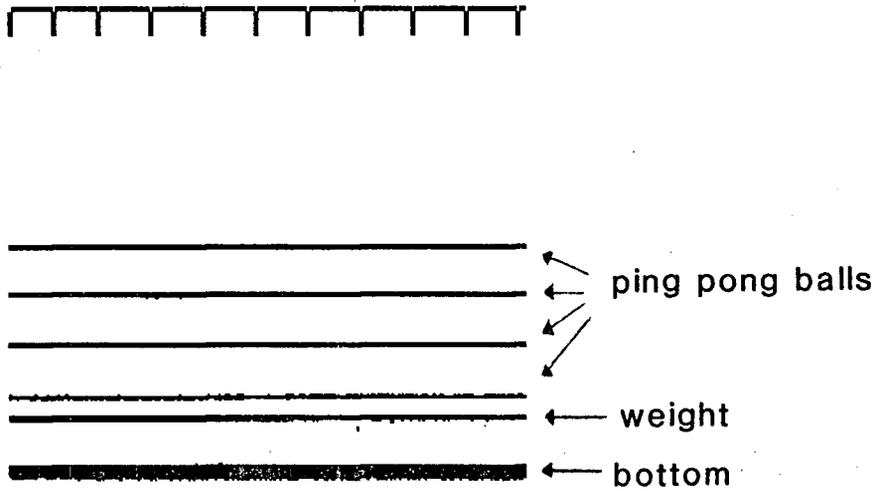


Figure 4-8. Echograms showing echo returns produced by ping pong balls suspended at different depth levels within Shuswap Lake, Sept. 29, 1987.

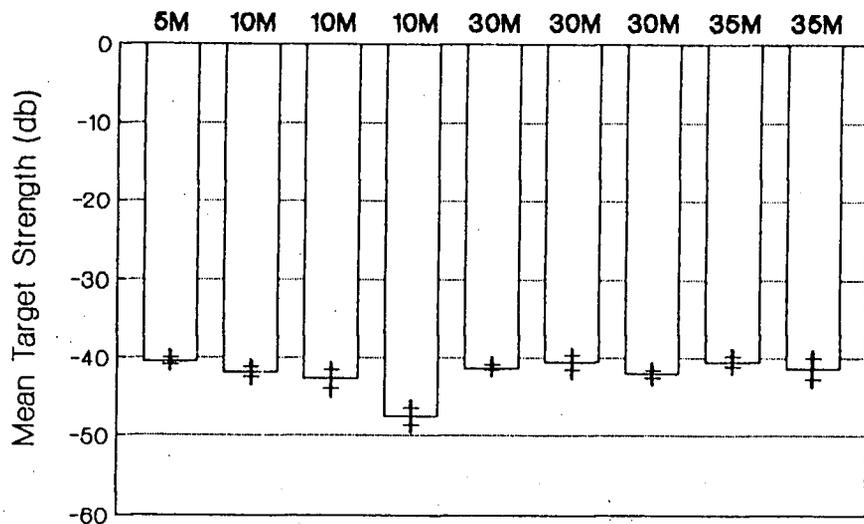


Figure 4-9. Mean and standard deviation (bars) for target strengths (measured in decibels) estimated for ping pong balls suspended in Shuswap Lake, Sept. 29, 1987.

depth intervals from the surface down to 50 m. Surface temperatures were also measured with a mercury thermometer accurate to $0.1^{\circ}C$ in order to derive a correction factor for inaccuracies of the SCT meter. Corrections (usually less than $0.5^{\circ}C$) were then applied to the vertical temperature profile.

Light profiles were measured at mid-day during time windows of constant atmospheric illumination. Light was measured in microeinsteins ($1\mu\text{einstein} = 6.02 \times 10^{17}\text{photons}$; $1lx \cong 5.17 \times 10^6\text{photons} \cdot m^{-2} \cdot s^{-1}$) with a Li-Cor 185-A Quantum Meter having an attached underwater quantum sensor. Measurements were taken at 1m intervals from the surface down to a depth corresponding to the maximum sensitivity of the sensor. Light extinction coefficients, K , were estimated by fitting regression lines to the standard formula for exponential light extinction (Wetzel 1983):

$$I_d = I_0 e^{-Kd} \quad (4.4)$$

where I_d is the measured illuminance at depth, d .

Secchi depths were recorded immediately prior to, or following, the light profile measurement using a 15 cm diameter white Secchi disk which was lowered adjacent to the illuminated side of the boat.

Zooplankton sampling methods

Replicate 75L zooplankton samples were taken at 5 depths (1, 7, 15, 22, and 30m) using a Par diaphragm pump powered by 12V battery. A funnel on the intake end of the pump tubing material was attached to the winch cable and lowered to the desired sampling depth. Because of observed variation in pump delivery rate, water was first pumped into a 75L vessel, and then siphoned through a 100μ plankton net. After concentrating the organisms in a small volume of water, the animals were poured into a glass jar and preserved in approximately 5% sugared formalin. Two vertical sampling series were taken on each sample date, the first at mid-day, and the second during the middle of the night.

In the laboratory, the preserved organisms were concentrated on a plankton seive made from 100 μ Nitex mesh material, and then transferred to a gridded counting vessel for enumeration under a stereo microscope at 10 \times magnification. All crustacea were identified to genus, and enumerated to compute the mean number of organisms per m^3 . Naupliar forms of copepods were subsampled during the counting procedure, by counting a subset of 14 (out of 84) regularly spaced grid squares, and multiplying the result by 6.

V. Test of the Sensory Mechanism

The sensory mechanism responsible for sockeye diel vertical migration is hypothesized (Section II) to involve the following components: 1) light controlling the daytime depth and the diel timing of vertical migration, and 2) nocturnal depth distribution due to thermoselection behavior. This hypothesis predicts between-lake differences in the daytime depth of juvenile sockeye corresponding to local water clarity conditions. Variations in sockeye nocturnal depth distribution within and between lakes should relate directly to the temperature structure of different pelagic water columns.

This section compares observations of sockeye depth distribution to limnological conditions in order to test this hypothesized mechanism.

Influence of light on vertical migration

To compare daytime depth with water clarity I considered only deep lakes where the presence of a lake bottom did not interfere with the daytime descent of the fish. In shallow systems (e.g. Cultus and Fraser) sockeye descents could be constrained by the presence of the lake bottom; data from such systems were not considered for this analysis.

There was a significant negative regression between water clarity and the mean daytime depth of juvenile sockeye (Fig. 5-1). Sockeye in transparent lakes (e.g. Quesnel and Shuswap) occupied deeper positions in the water column than did sockeye in more turbid lakes. Juvenile kokanee in Okanagan Lake (Section VIII) also fell close to the regression line relating fish depth and water clarity:

$$\overline{Depth} = 95.2K + 83.4 \quad (5.1)$$

where K is the light extinction coefficient. The regression had an r^2 value of 0.83. These field observations are consistent with the hypothesis that sockeye daytime depth distribution is influenced by water clarity conditions.

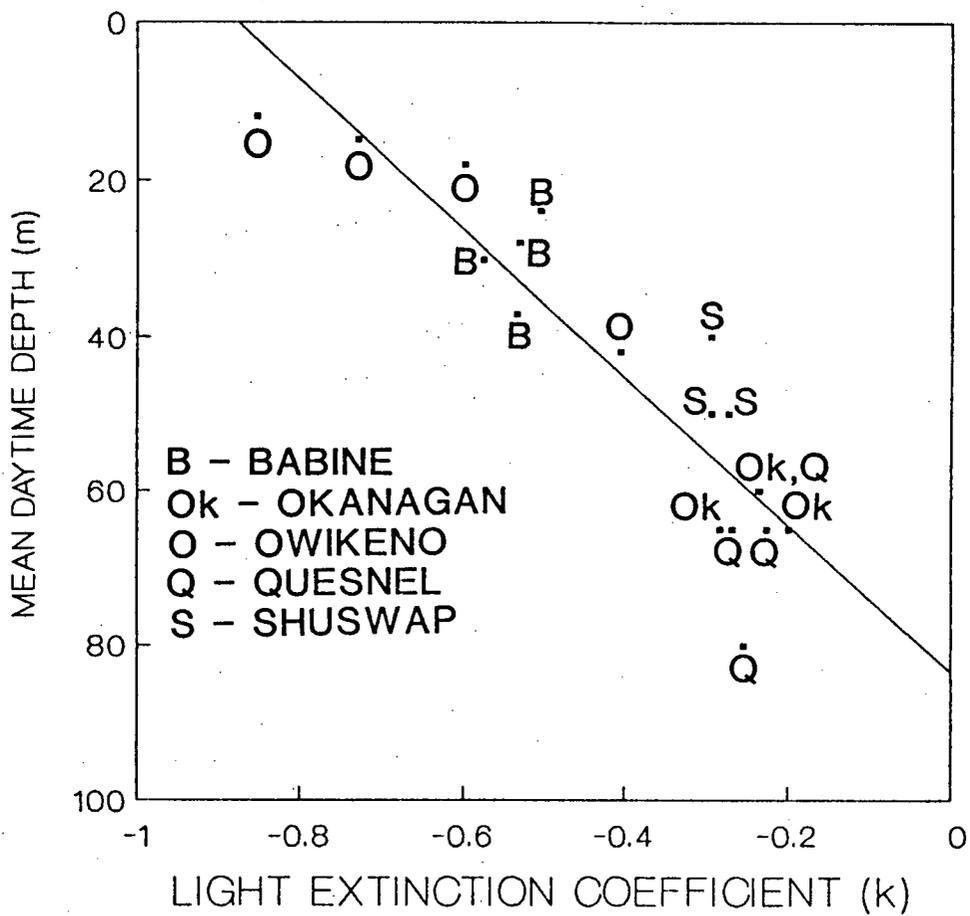


Figure 5-1. Mean daytime depth of fish targets plotted against the light extinction coefficient, K , in Babine, Owikeno, Quesnel, Shuswap and Okanagan lakes. Okanagan data for the lowermost mode of a bi-modally depth-distributed population (see Fig. 7-1).

Variations in daytime fish depth distribution could be caused by within-lake water transparency differences. To study the effect of altered water transparency on fish distribution, I compared the daytime depth of pelagic echo targets within Owikeno Lake. Owikeno is a glacial lake which supports abundant populations of both sticklebacks and sockeye (Ruggles 1966). The lake has a turbidity gradient extending between its relatively clear Upper Basin and its high turbidity lower reaches. Surface trawl catches of sockeye within Owikeno (Chernoff 1971) are consistent with a diel vertical migration. Fish targets within the turbid Basin 2 of Owikeno Lake migrate through a vertical amplitude of about 15m (Fig. 5-2). A 15 min surface tow net sample obtained from Basin 2 on the night of Oct. 2, 1985, produced a mixed catch of 5 juvenile sockeye and 37 sticklebacks.

Daytime acoustic transects indicated major differences in fish depth distribution between the major basins of Owikeno (Fig. 5-3). Within the turbid Basins 1 and 2, fish targets were centered around a daytime depth of about 15m. In contrast, fish targets were centered around a daytime depth of about 40m within the relatively clear Basin 4 (Fig. 5-3). Limnological measurements (Fig. 5-4) indicated inter-basin differences in water transparency. Light extinction coefficients were measured as 0.70 and 0.42 within Basins 2 and 4 respectively. These observations suggest a direct positive correlation between daytime depth distribution and water clarity. Fish targets in turbid areas of Owikeno Lake are higher in the water column, by day, than fish targets in more transparent water.

To evaluate crepuscular changes in water transparency, light conditions were monitored at dusk and dawn at Cultus and Great Central lakes respectively (Fig. 5-5). On both occasions, light extinction curves (Fig. 5-5) remained parallel to each other and there was no evidence for a crepuscular change in light transparency. One simple mechanism that would result in a crepuscular-timed diel vertical migration would be for sockeye juveniles to remain within a distinct light intensity preferendum.

Juvenile sockeye responded to seasonal changes in day length by altering the timing of their diel vertical movements. Vertical migrations always occurred at dusk and dawn, irrespective of the absolute timing of the crepuscular period. In Babine Lake (which remains ice-free between May and November in most years) juvenile sockeye maintained their nocturnal distribution for a

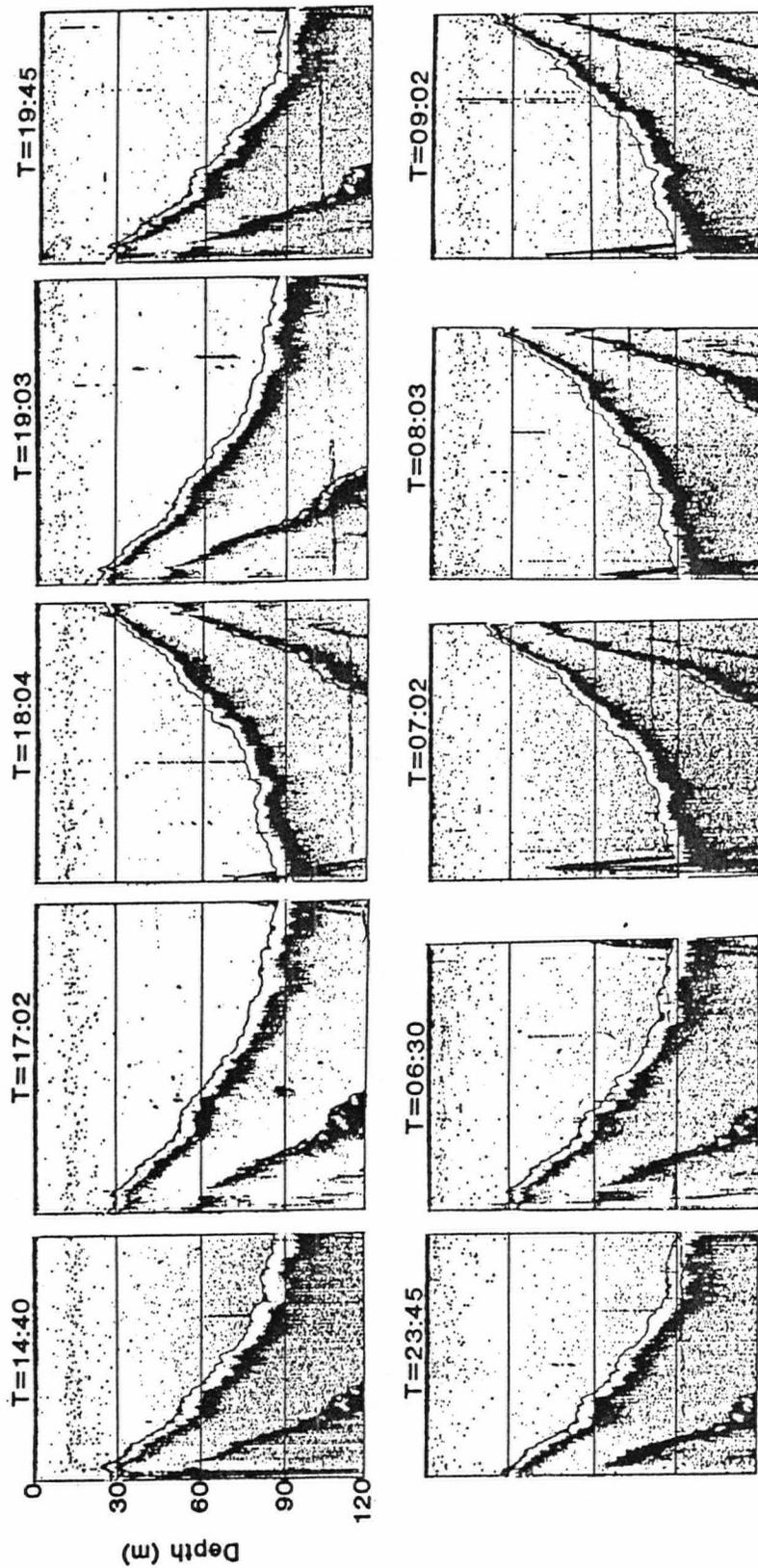


Figure 5-2. Diel sequence of echograms from Basin 2 of Owikeno Lake obtained on Oct. 1-2, 1985, with a 70kHz Simrad EY-M. Elongated vertical traces on echograms produced by gas bubbles within the water column.

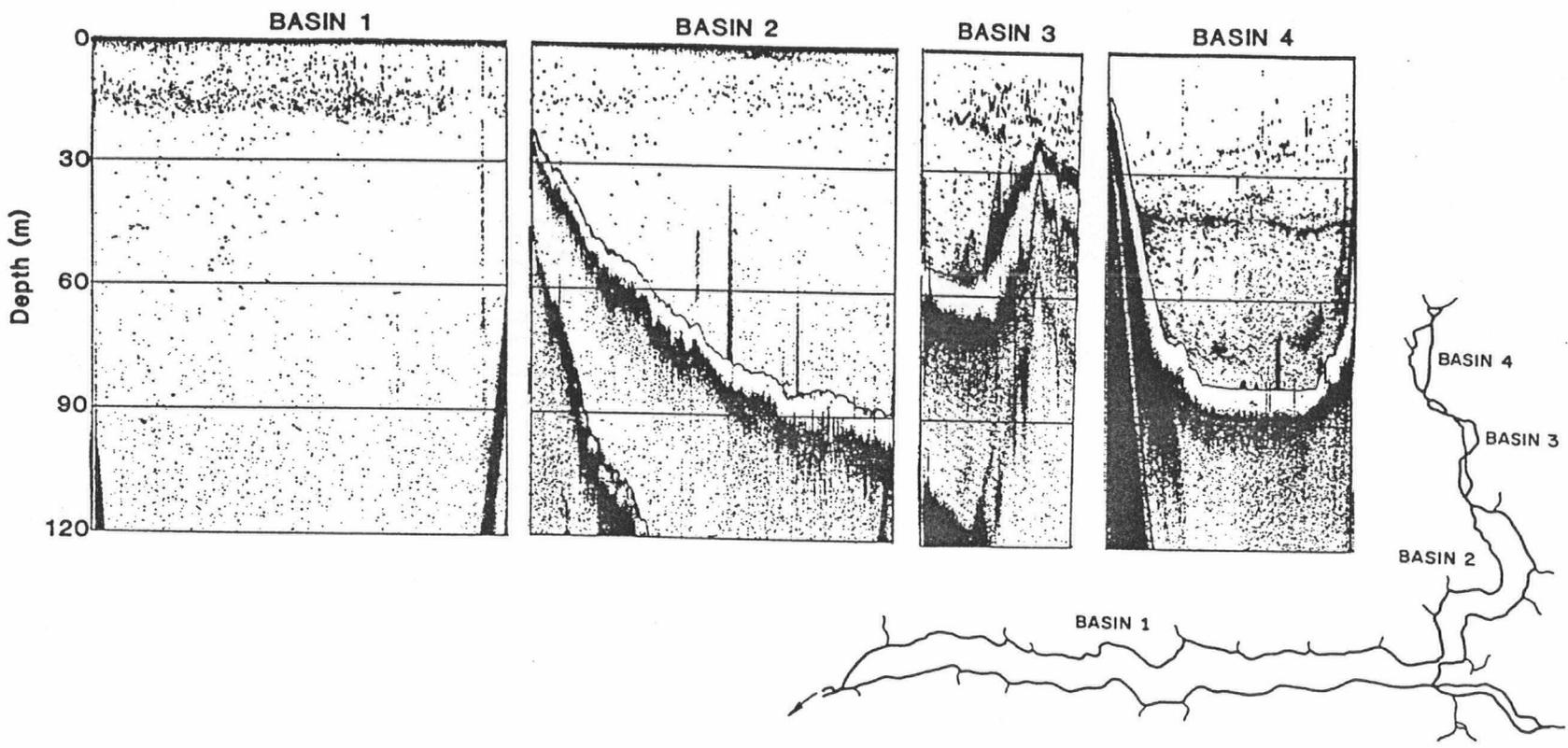


Figure 5-3. Daytime echograms obtained from the four different basins of Owikeno Lake on Oct. 2, 1985.

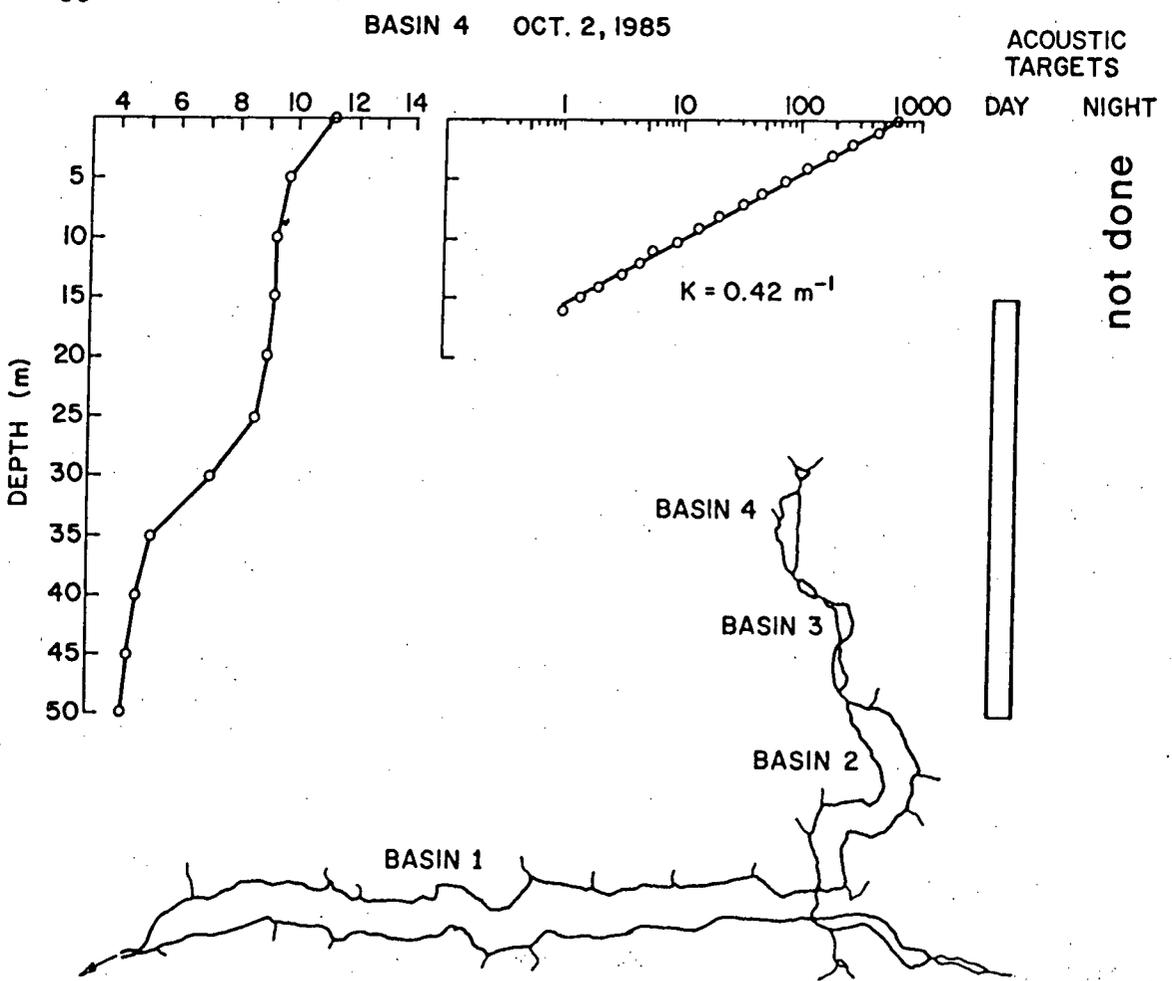
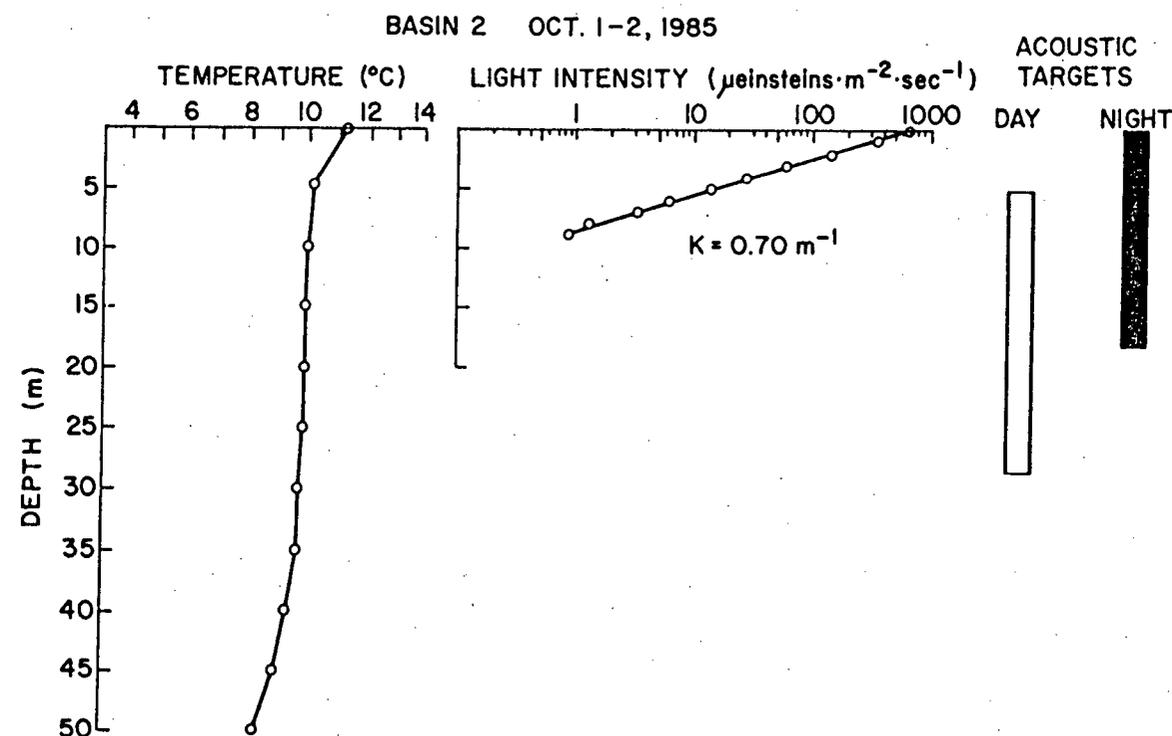
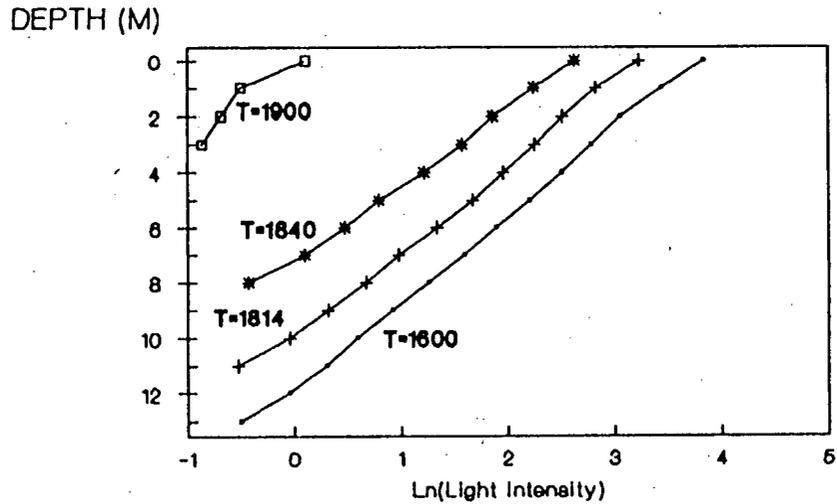


Figure 5-4. Light and temperature profiles for 2 different basins of Owikeno Lake on Oct. 1-2, 1985, shown in relation to the depth distribution of acoustic targets.

A) CULTUS LAKE APR. 15, 1986



B) GREAT CENTRAL LAKE MAY 27, 1986

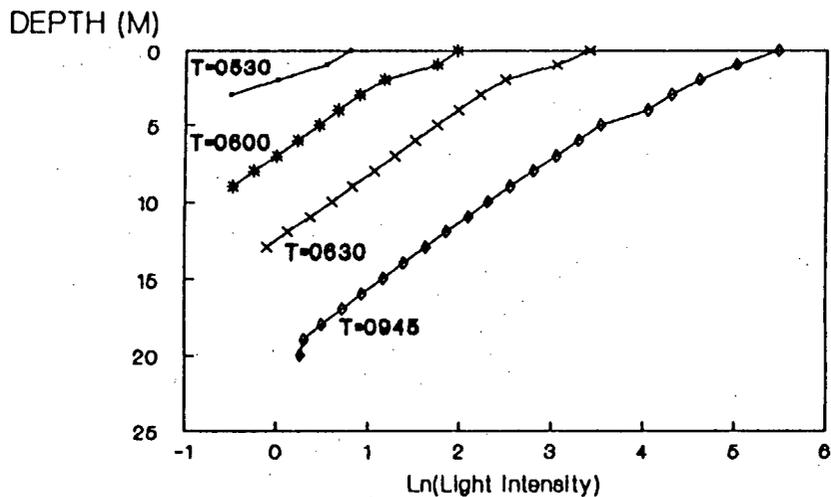


Figure 5-5. Sequential light extinction profiles during 2 crepuscular periods: A) dusk at Cultus Lake on Apr. 15, 1986, and B) dawn at Great Central Lake on May 27, 1986. Time of sampling shown adjacent to the curves.

considerably longer time period in October (12 h), than in mid- summer periods (8 h) (Fig. 5-6). These seasonal differences in migration timing correspond directly to seasonal changes in daylength.

Nocturnal observations suggested that moonlight can influence the depth distribution and behavior of sockeye juveniles. In Babine Lake, the depth distribution of echo targets was monitored before, during, and immediately after (Fig.5-7) the rise of a full moon on a calm night (June 26, 1986). Moonrise occurred at 01:10 h. Within 20 min, sockeye juveniles descended 10 m from surface waters, where they had been largely absent from the SONAR beam (due to near-field effects) and subsequently occupied a depth of 10-15 m. At dawn (04:10) they re-ascended into surface waters, and thereafter descended to their daytime depth (Fig. 5-7). On another calm moonlit night (Nov. 5, 1987) in Shuswap Lake, there was an unusual bi-modal depth distribution of echo targets (Fig. 5-8). A nocturnal transect across the lake suggested an upper, actively schooling group of fish in 10-25 m, and a deeper disaggregated group of individuals between 25-70 m. Schooling and feeding behavior of juvenile sockeye can occur on calm, moonlit nights (Narver 1970). Other freshwater planktivores also forage under moonlit conditions (Gliwicz 1986B).

Influence of temperature on vertical migration

The second component of the hypothesized sensory mechanism involves control of nocturnal sockeye depth by thermoselection behavior. This hypothesis predicts that between-lake differences in nocturnal depth distribution relate directly to the thermal structure of pelagic water columns.

The nocturnal temperature preference of juvenile sockeye was measured by first echo integrating nocturnal transects and establishing the depth of maximum echo integrator voltage (Appendix 4). The temperature at this depth was then extrapolated from the temperature profile to obtain a distribution of temperatures associated with the maximum fish biomass (Fig. 5-9). The results suggest a narrow distribution of preferred temperatures, centered around a mean of 10.9°C . These observations are slightly higher than the mean of 9.2°C observed in Lake Washington (Fig. 2-5), and somewhat lower than the preferred $12 - 15^{\circ}\text{C}$ which occurs in laboratory-induced vertical temperature gradients (Brett 1952). The thermocline in most temperate, stratified lakes will

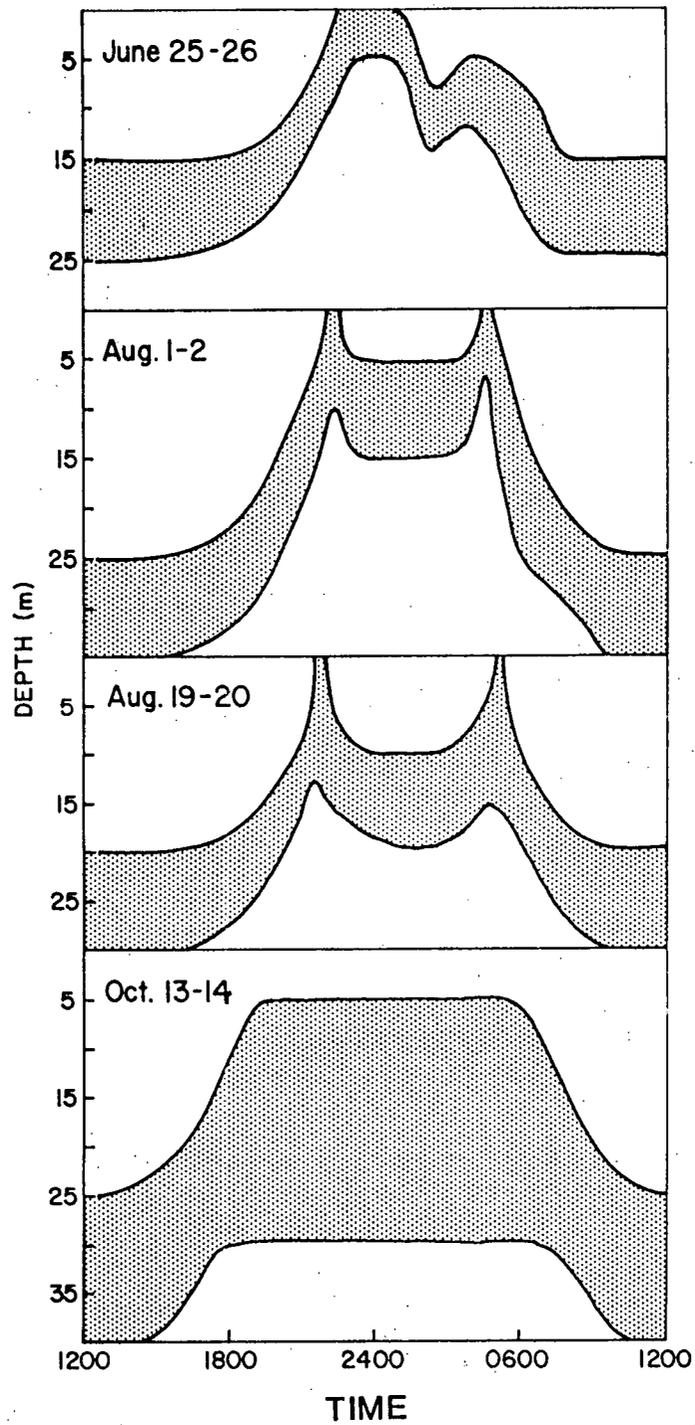
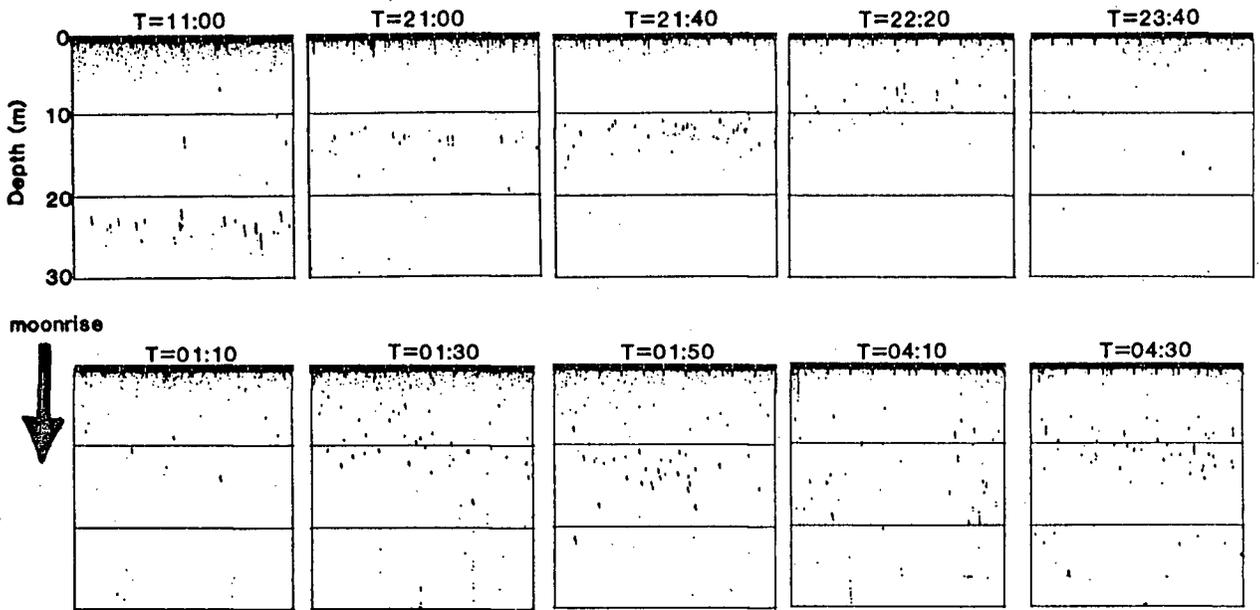


Figure 5-6. Diel patterns of juvenile sockeye depth distribution within Babine Lake during 1986. Diagrams based on diel echogram sequences shown in Appendix 3.

A) DIEL ECHOGRAM SEQUENCE



B) ECHO INTEGRATION RESULTS

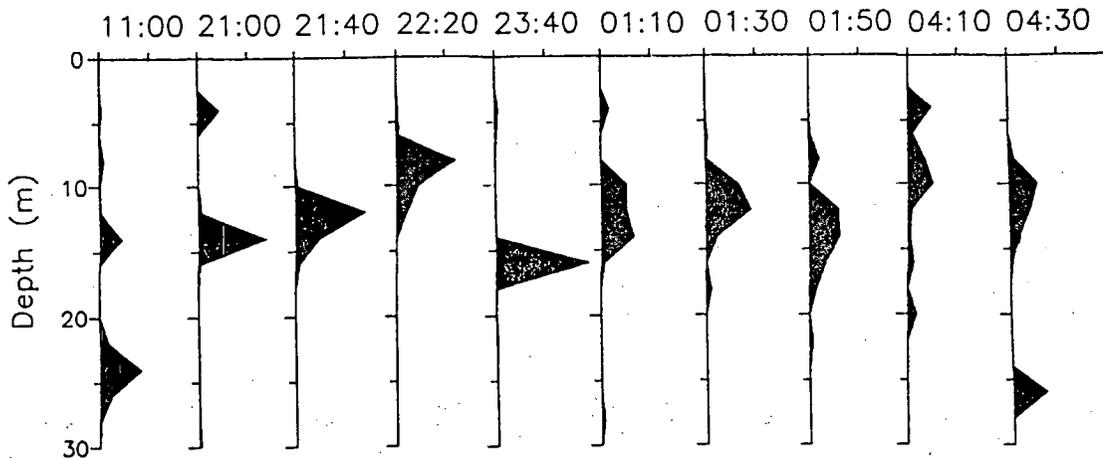


Figure 5-7. Effect of moonrise on juvenile sockeye depth distribution within Babine Lake on June 26, 1986. A) Diel echogram sequence (marks between 0-5 m due to surface noise), and B) echo integration results, showing proportion of voltage by depth in corresponding transects.

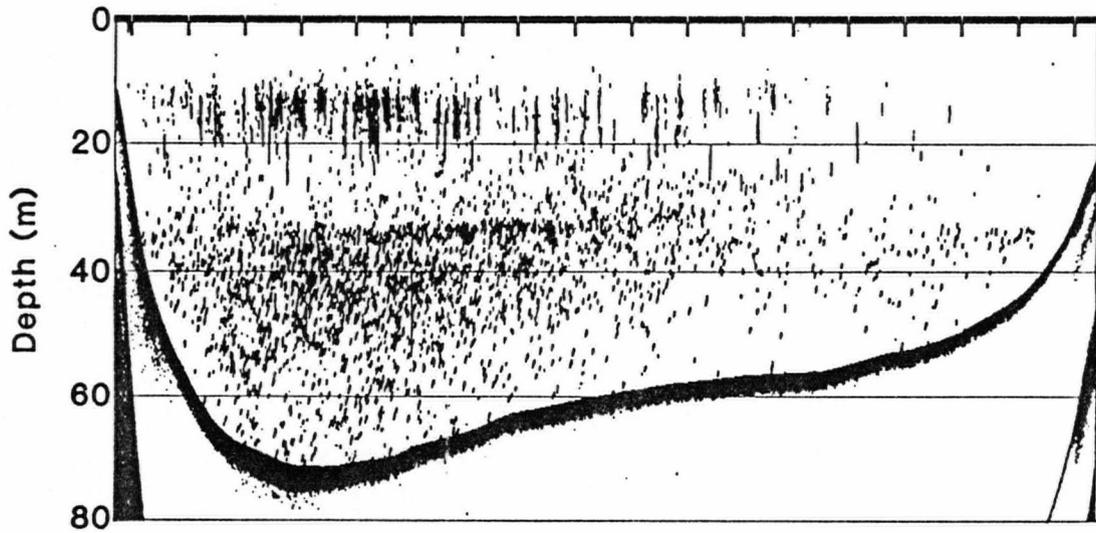


Figure 5-8. Echogram from nocturnal transect across Shuswap Lake on a calm, moon-lit night (Nov. 5, 1987).

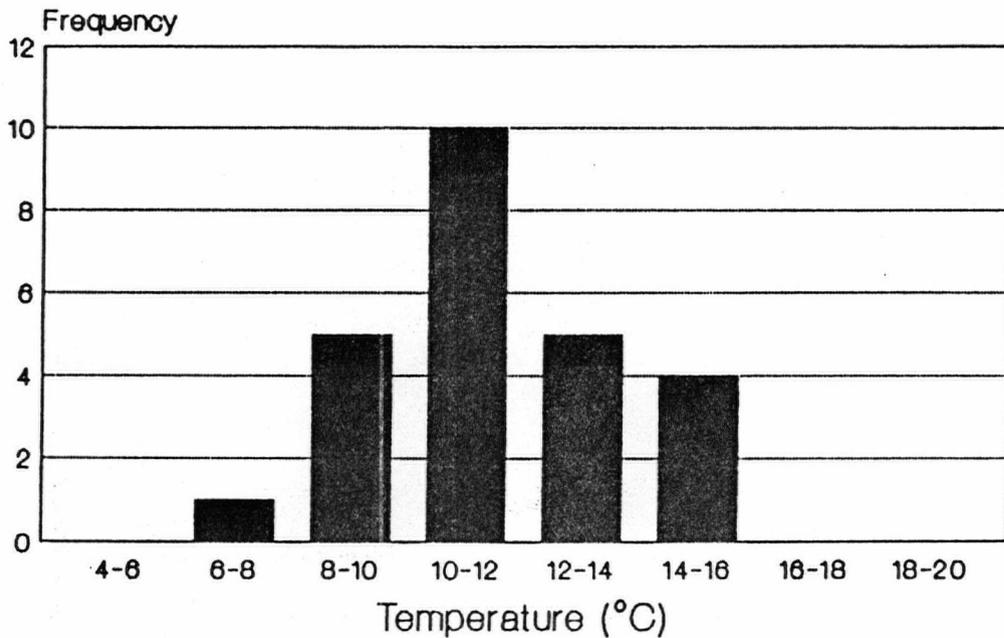


Figure 5-9. Temperature at the depth of maximum echo integrator voltage. Lake sampling dates and locations listed in Appendix 4.

occupy a relatively narrow depth range compared to the respective depth ranges of the hypolimnion and epilimnion. The relatively narrow distribution of preferred temperatures (Fig. 5-9), compared to the range of temperatures available in the entire water column, is consistent with the sensory mechanism as hypothesized above.

Seasonal changes in the temperature structure of a pelagic water column should affect sockeye nocturnal depth distribution if the fish are actively thermoselective. Seasonal comparisons of sockeye day and night distribution were undertaken at Babine and Shuswap Lakes (Figs. 5-10 and 5-11 respectively). The echograms indicate seasonal downward shifts in nocturnal vertical distribution, as well as seasonal expansions in the range of nocturnal depths occupied. Within Babine (Fig. 5-10), sockeye at night occupied shallow depths on June 25 (prior to moonrise; see Fig. 5-7), 10 m depth ranges during August, and a relatively wide 20 m depth range in October. Within Shuswap (Fig. 5-11) sockeye nocturnal depth distributions both shifted downward and expanded over greater vertical ranges during the 5 month period of study.

The most likely explanation for these seasonal shifts in nocturnal vertical depth distribution relates to the seasonal formation and progression of the thermocline within the water column. When the preferred temperature isotherms are situated within the thermocline, sockeye show a narrow depth distribution. Seasonally, as the thermocline descends within the water column and weakens, sockeye select deeper depth levels and a wider range of depths.

Numerous sockeye salmon lakes within B.C. are routinely surveyed hydroacoustically in order to obtain juvenile population estimates, and many thousands of nocturnal transects have been undertaken. During the course of a September 1986 Quesnel Lake survey undertaken on behalf of the Department of Fisheries and Oceans (DFO), a peculiar echogram was obtained from a transect oriented perpendicular to the main axis of the lake (Fig. 5-12A). Echo integration results (Fig. 5-12B) suggested a major "tilt" in the vertical distribution of sockeye juveniles within this particular region of Quesnel Lake. There was a 4 m difference in mean vertical position of sockeye across the transect. All of the other 15 transects undertaken during the 2 night survey produced "horizontal" echograms typical of sockeye salmon juveniles in freshwater nursery lakes.

If the nocturnal vertical distribution of sockeye is controlled by temperature, the distribution

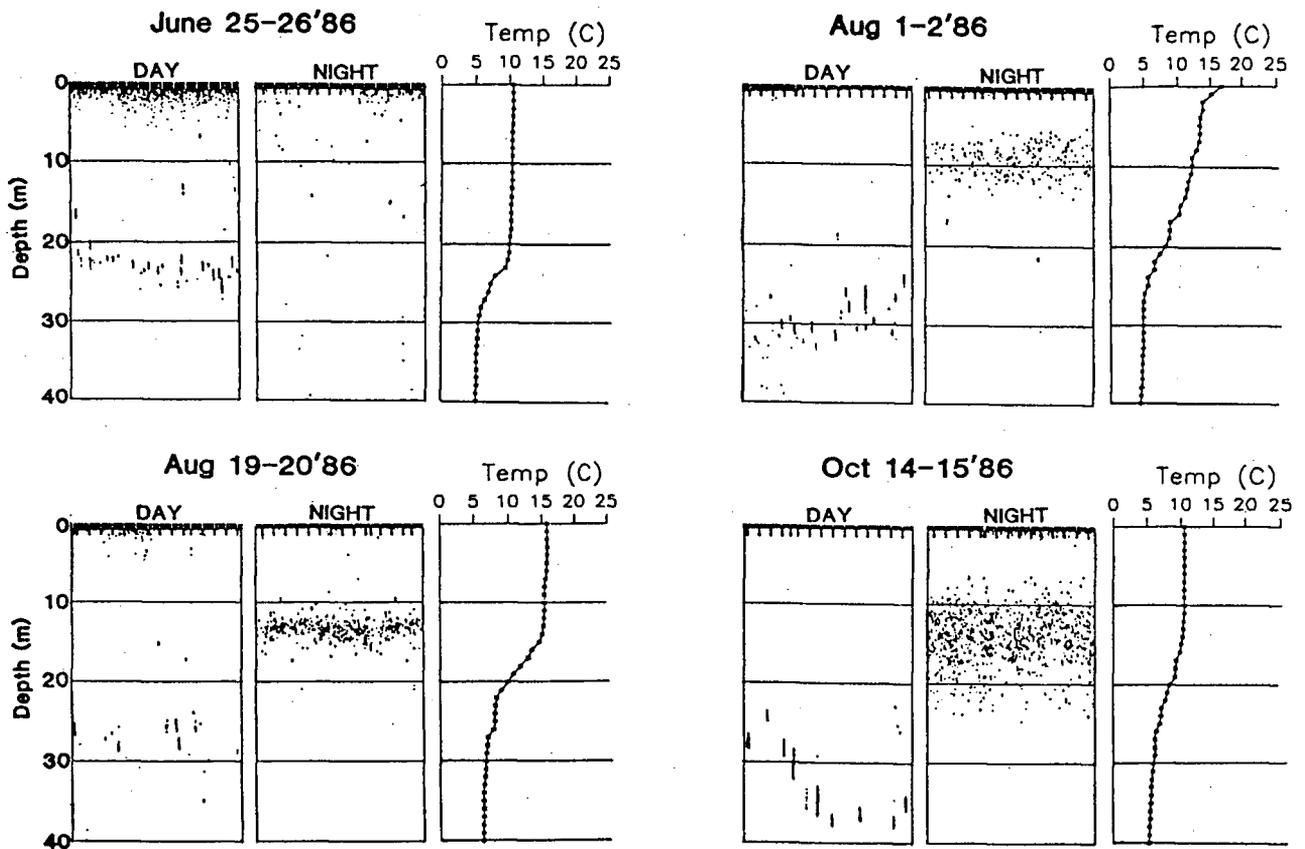


Figure 5-10. Day and night echograms obtained from Babine Lake, 1986, shown in relation to the temperature profiles.

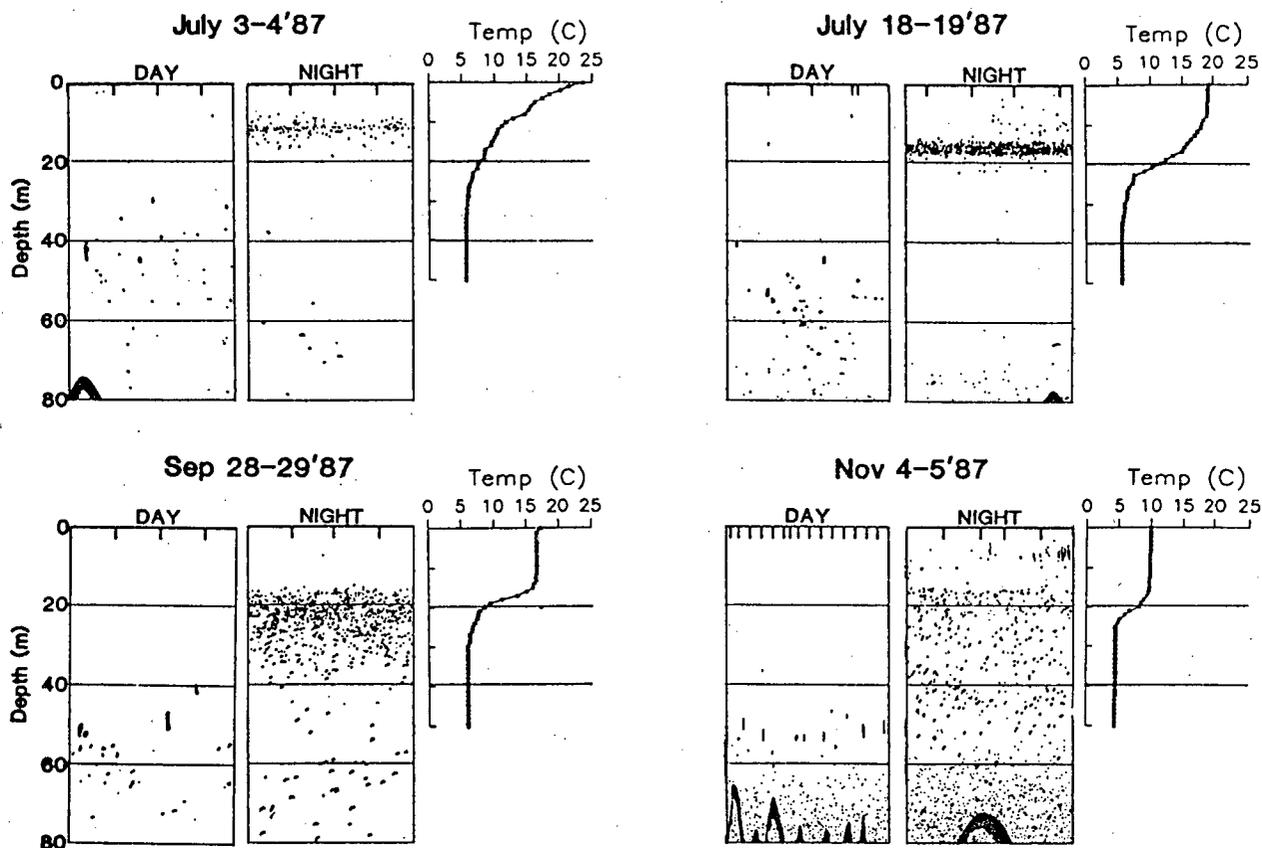


Figure 5-11. Day and night echograms obtained from Shuswap Lake, 1987, shown in relation to the temperature profiles.

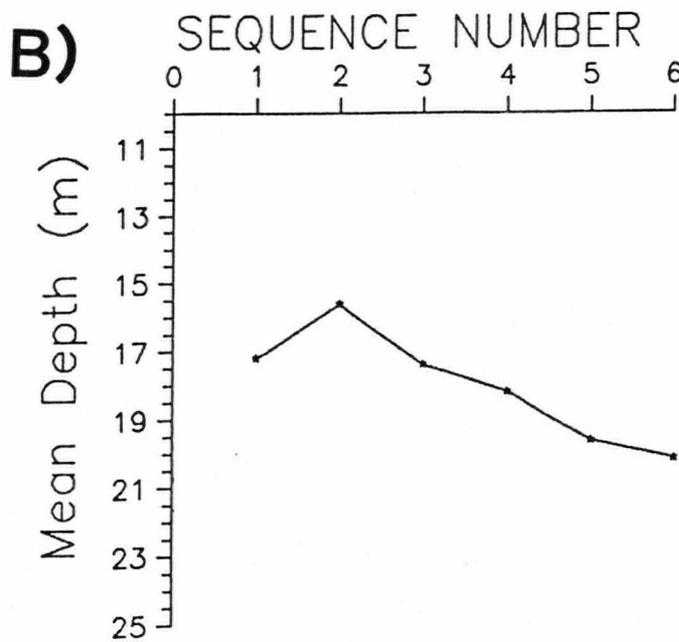
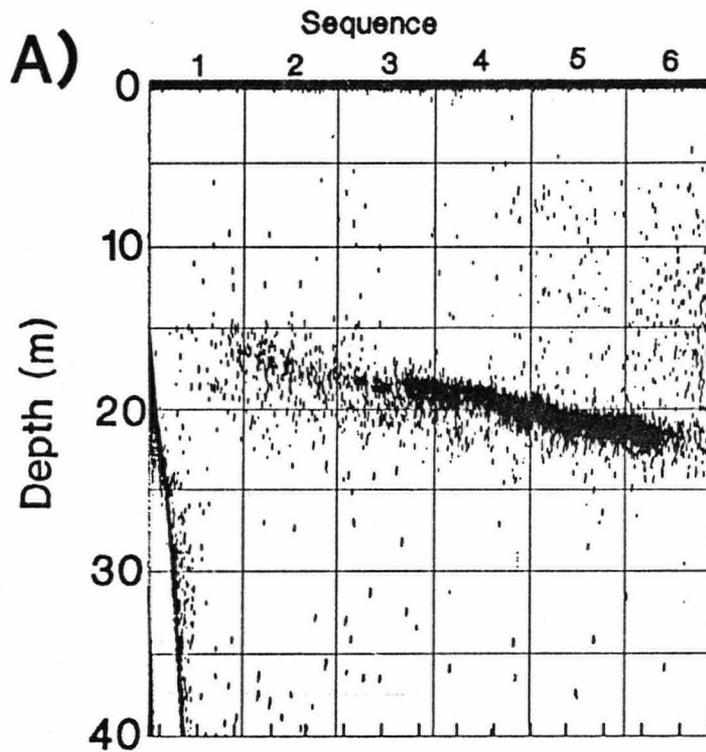


Figure 5-12. A) Juvenile sockeye nocturnal echogram from a transect across the main axis of Quesnel Lake on Sep. 22, 1986, and B) mean depth of acoustic targets as computed from 6 distinct echo integrator sequences.

of echo targets in Fig. 5-12 implies that the thermal distribution in this region of Quesnel Lake was tilted on Sep. 22, 1986. How could such a thermal distribution arise? Wind-driven thermocline seiche movements occur in large temperate lakes and can generate Kelvin waves when acted upon by the earth's Coriolis force (Goldman and Horne 1983). A two-layered lake model (Fig. 5-13) illustrates the potential tilting of the thermocline that can occur across the main lake-axis as a result of counterclockwise rotation (northern hemisphere) induced by Coriolis force.

An opportunity to test this model arose in August of 1987 when Quesnel Lake was again surveyed on behalf of DFO. The population of sockeye juveniles was much less dense in '87 than in '86; echograms taken during the '87 survey (Fig. 5-14) have been re-scaled to facilitate vertical distribution comparisons. During the day prior to the start of the survey (Aug. 10, 1987) a strong storm passed through the area causing minor damage to shoreline dock structures.

Differences in juvenile sockeye vertical distribution were evident both between and within transects (Fig. 5-14). On Transect 4, sockeye were centered at 15 m depth, several m shallower than sockeye on Transect 6 (sequences 1 and 2; Fig. 5-14B). Sockeye distributed across Transect 6 again showed a tilted vertical distribution, with a 3 m difference in mean vertical position across the transect. There was evidently an active seiche in Quesnel Lake at this time; temperature profiles taken at a monitoring site on Transect 6 showed a 10 m ascent of the thermocline position over a 25.5 h period between Aug. 11 and 12 (Fig. 5-15).

Comparison of the temperature distribution across Transect 6 at 05:00 on Aug.12 (Fig. 5-16) suggested a non-uniform temperature distribution across the transect. The thermocline was 5 m deeper in the middle part of the transect than at either the north or south sides (Fig. 5-16), suggesting the presence of an active Kelvin wave. There was no obvious correspondence between the tilted sockeye distribution on Transect 6 (Fig. 5-14) and the deeper thermal distribution at the middle of the transect. This discrepancy possibly relates to the 4 h timing difference between the acoustic transect and the temperature measurements.

These observations suggest that juvenile sockeye respond (nocturnally) to vertical differences in thermal distribution caused by wind-driven seiche movements. The response is consistent with the thermoselection mechanism hypothesized to control nocturnal vertical position.

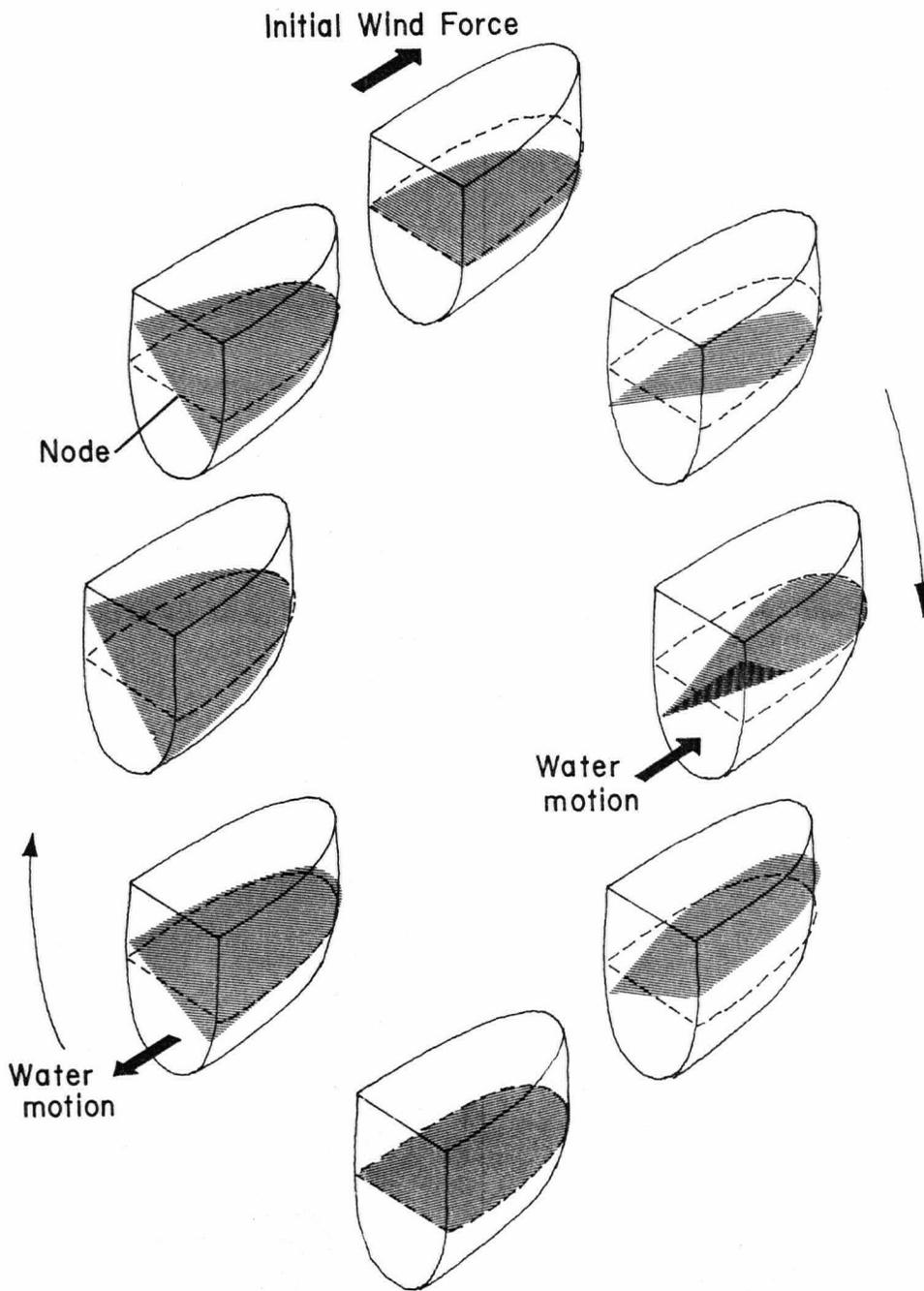


Figure 5-13. Establishment of a Kelvin wave in a temperate lake as a result of Coriolis force operating on a wind-driven seiche. Redrawn from Goldman and Horne (1983,fig.5-20).

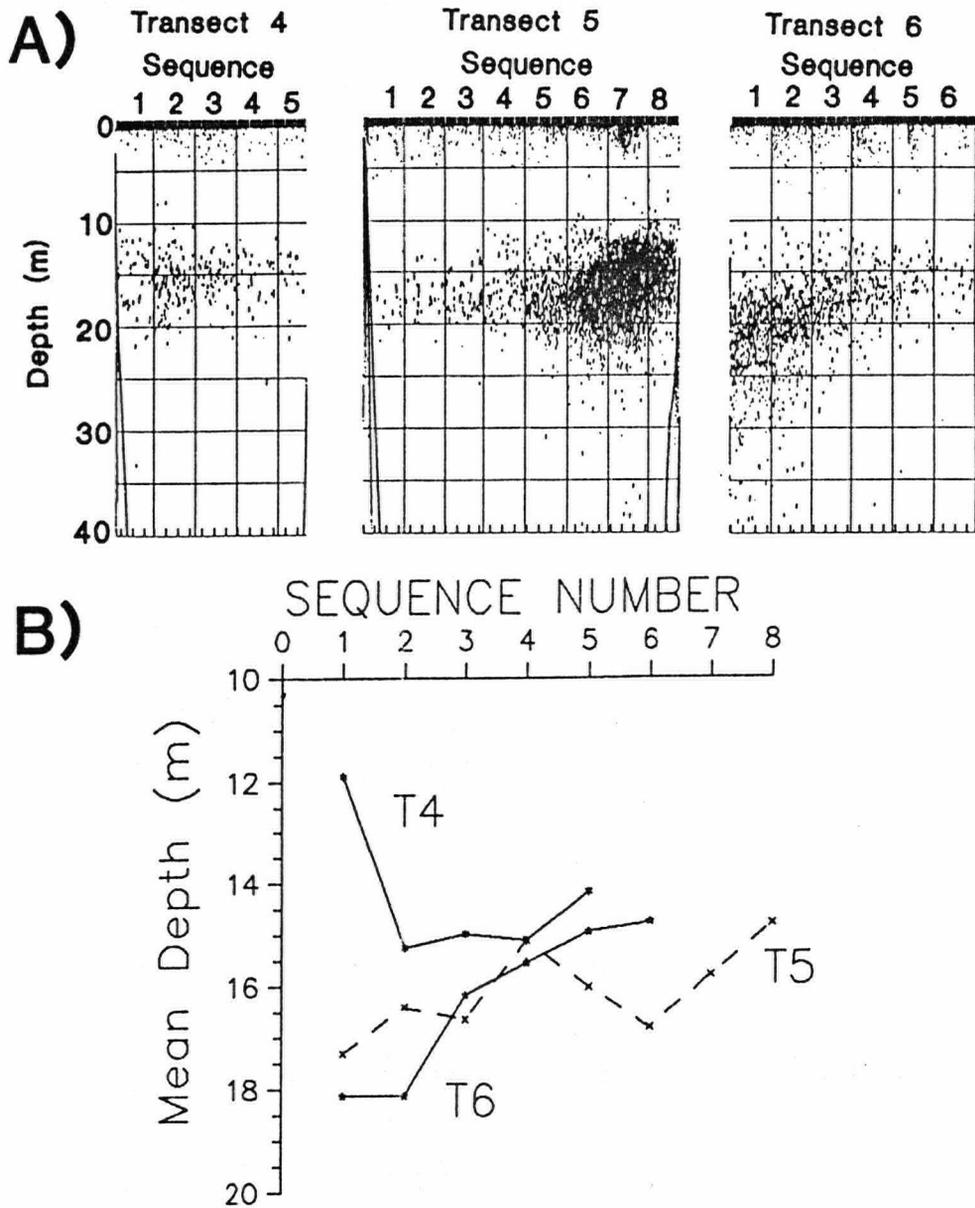


Figure 5-14. A) Juvenile sockeye nocturnal echograms, and B) echo integrator results, across the main axis of Quesnel Lake on Aug. 12, 1987.

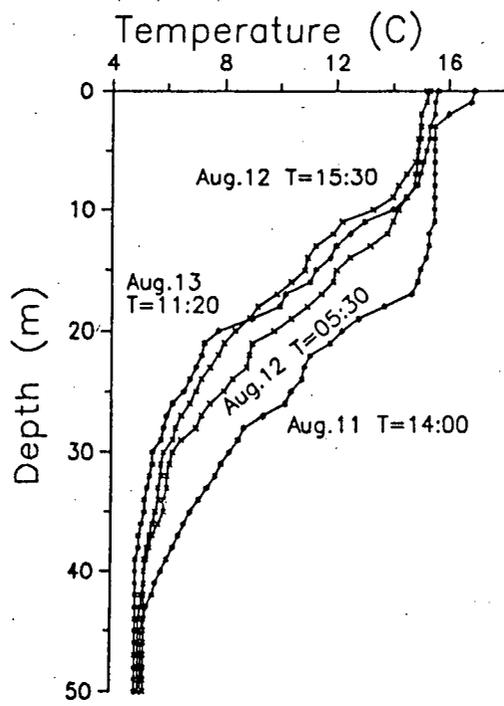


Figure 5-15. Alteration in Quesnel Lake temperature profiles over a 25.5 h period on Aug. 11-12, 1987.

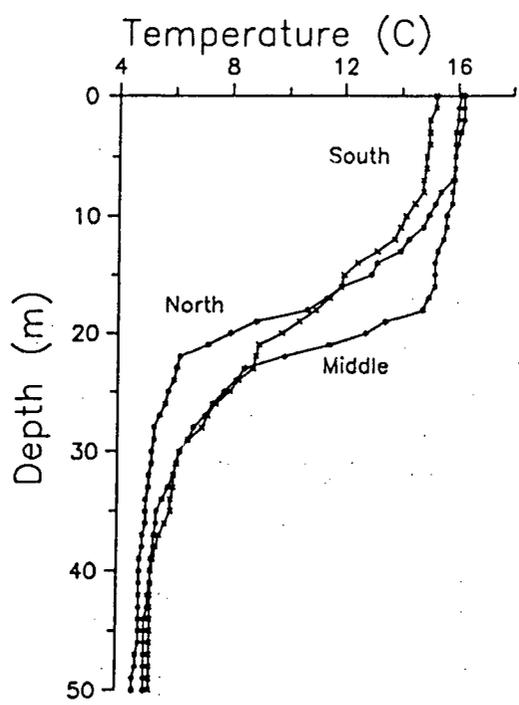


Figure 5-16. Quesnel Lake temperature profiles at 3 measuring points across Transect 6 on Aug. 12, 1987 at T=04:30-05:00 (PDST).

Discussion

The sensory mechanism controlling juvenile sockeye vertical migration must account for the day and night pelagic depth positions, as well as the diel timing of their migration. The hypothesized mechanism requires both thermoselection behavior and a light response to control the night and daytime vertical distributions respectively. The crepuscular timing is hypothesized to result from the sockeye light response. Field observations from B.C. sockeye lakes are in agreement with this sensory mechanism.

Daytime depth is related to water clarity, and field evidence suggests a direct effect of water clarity on daytime position. Sockeye in clear lakes tend to be deeper, and migrate over greater vertical distances, than sockeye in more turbid systems. During nocturnal periods, juvenile sockeye are evidently thermoselective, and associate with a narrow range of temperatures.

For ectothermic organisms in thermally stratified lakes, temperature will provide a strong and unambiguous environmental signal. Within laboratory-induced steep experimental gradients of temperature, most fish show strongly peaked, monomodal frequency distributions (Neill 1979). Wild juvenile sockeye populations under field conditions also demonstrate a strongly peaked distribution in temperature preference (Figs. 5-9, 2-3) in a fashion consistent with the hypothesized sensory mechanism.

Two different mechanisms capable of controlling the diel timing of fish vertical migrations were elaborated by Blaxter (1974). The first involved the fish 'following isolumes' whereby the animals remained within a distinct light intensity preferendum, while the second was a function of the fish responding to a specific rate of change in light intensity. Both of these mechanisms would result in a crepuscular-timed diel vertical migration. In a review of photoperiodic-induced shifts on marine animal behavior, McFarland (1986) concluded (p. 399): "*What is not clear is whether the trigger (for behavior) in each species is the result of the achievement of some absolute light threshold, or a directional and prolonged duration of rate of light intensity change, or the achievement of a specific rate of light intensity change, or some interactive combination of all of these factors.*"

Results from the present study support the importance of light in controlling the diel timing of juvenile sockeye vertical migration. However, the particular attributes of light to which the fish respond are difficult to specify. The simplest mechanism controlling the diel timing of migration is for the fish to maintain themselves within a distinct light intensity preferendum over the diel cycle. Such behavior would suffice to move the fish vertically up and down through the water column.

The potential usefulness of the diel cycle as an orienting mechanism in fish behavior was summarized by Smith (1985, p. 14): *“Although it may be modified by cloud cover, water clarity or eclipse, the daily cycle of light intensity is one of the most precise and regular cycles accessible to vertebrates. It is an appropriate timing stimulus for behavioural and physiological rhythms related to diel activity.”*

Other vertical migrators appear to respond directly to diel shifts in light intensity (Woodhead 1966; Blaxter 1974). Unusual light conditions can alter the normal timing of vertical migration; examples include solar eclipses, which may trigger vertical migration (Backus et al. 1965); artificial lights, which may alter normal migration patterns (Blaxter and Currie 1967); and the absence of darkness during polar summers, which may inhibit vertical migration altogether (Zusser 1958, cited in Blaxter 1974).

In summary, the combined light and temperature sensory mechanism is consistent with the observed patterns of juvenile sockeye migration within B.C. lakes. The physiological and ecological consequences of these behaviors are considered in Section IX.

VI. Tests of Selective Advantage Theories

The seven hypotheses concerning the selective advantage of diel vertical migration (Section II) make specific predictions concerning the movements of juvenile sockeye with respect to their zooplankton prey, limnological conditions, and diel cycles in light intensity. This section compares fish behavior to physical conditions and prey distributions in order to test the predictions of the various hypotheses and make inferences about the selective advantage of the behavior.

1) Foraging hypothesis

This hypothesis predicts that if crustacean zooplankton undertake diel vertical migrations, then so will juvenile sockeye to maintain a high degree of spatial overlap with their primary food source.

Comparison of day and night zooplankton vertical distributions provided the basis for assessing zooplankton diel migrations. Replicated, depth-stratified zooplankton pump samples were taken from the pelagic zone (both day and night) in the same vicinity as the echo sounding location. To evaluate pump sampler selectivity, zooplankton counts from Babine Lake were compared to results obtained by Narver (1970) using Miller net samplers, which by virtue of their rapid, towed deployment (Andersen and Narver 1968), accurately sample large crustacean zooplankton. *Heterocope septentrionalis* and *Bosmina coregoni* are the only two zooplankters that migrate vertically in Babine Lake (Fig. 6-1), the former migrating to a daytime depth of 15-30 m, and the latter undertaking a reversed diel vertical migration.

Zooplankton pump samples from Babine Lake (Fig. 6-2) produced results similar to those obtained by Narver (1970) with one notable exception. *Heterocope septentrionalis* were absent from daytime pump samples and only captured incidentally at night. *Heterocope* is a large (2-3 mm), predatory copepod evidently capable of avoiding capture by the pump sampler. The pump sampler adequately sampled the other genera in the lake, showing that copepods and *Daphnia* were

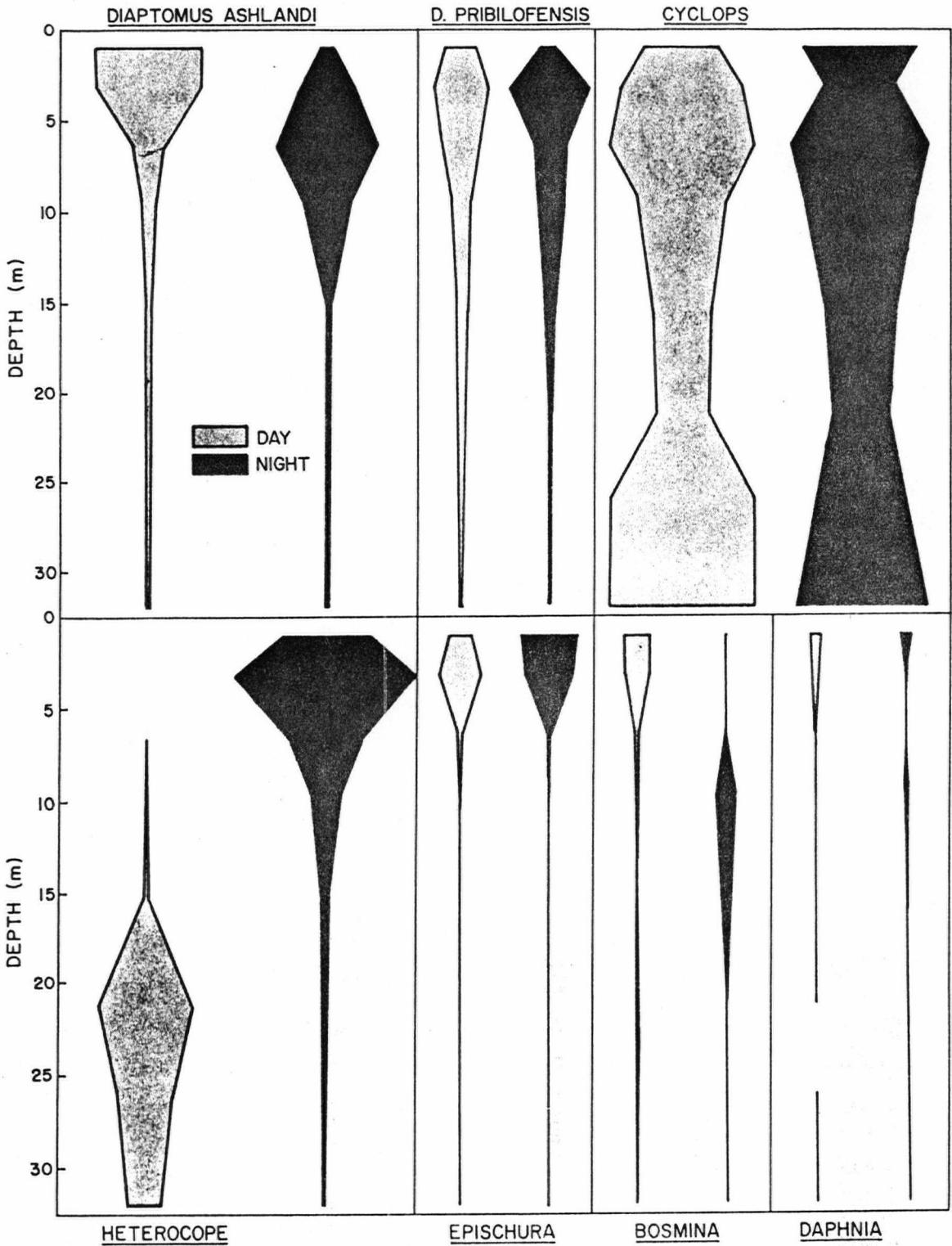
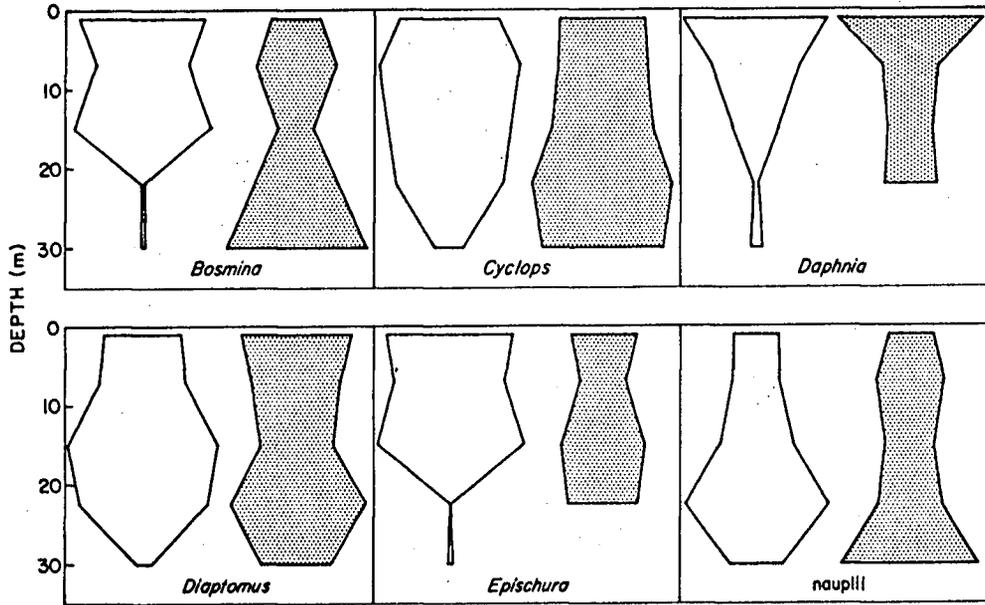


Figure 6-1. Day and night vertical depth profiles of the predominant zooplanktonic organisms within Babine Lake on Aug. 5-6, 1967, as indicated by averaging depth-stratified Miller samplers from 8 discrete depths; redrawn from Narver (1970,fig.11).

BABINE LAKE

A. June 25-26, 1986



□ DAY ▨ NIGHT

B. Aug. 19-20, 1986

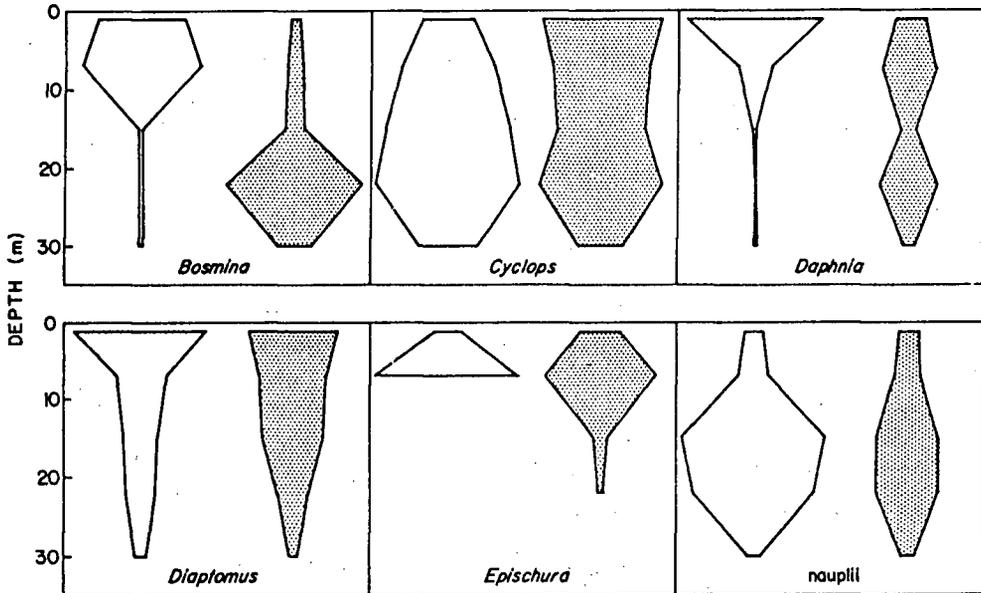


Figure 6-2. Day and night vertical depth profiles of the predominant crustacean zooplankton species captured in plankton pump samples from Babine Lake on 2 dates during 1986. Kites depict relative abundance of organisms at 5 particular depths throughout the upper 30 m of the water column.

static in the upper portion of the water column, while *Bosmina* undertook a reversed diel vertical migration. The reversed diel vertical migration of *Bosmina* was apparent during both June and August of 1986 (Fig. 6-2).

Zooplankton pump sampler results (Fig. 6-3) indicated static (non-migratory) zooplankton populations in Cultus, Quesnel and Shuswap Lakes. Day and night depth distribution patterns were similar in all 3 lakes. The occasional minor diel difference in depth distribution pattern can be ascribed to sampling error, rather than active vertical migration. These observations are inconsistent with the foraging hypothesis prediction of an active zooplankton vertical migration.

The foraging hypothesis prediction of a high degree of diel spatial overlap between sockeye and zooplankton was rejected. Sockeye diel vertical migration patterns in Babine (Fig. 5-6), Shuswap (Fig. 4-3), Quesnel (Fig. 4-4), and Cultus (Fig. 6-4) indicated that sockeye descended far below regions of concentrated zooplankton abundance in these lakes during daytime periods. The daytime descent effectively decreased zooplankton foraging opportunities.

The observed discrepancies in the distribution and movement patterns of fish and zooplankton invalidate the foraging hypothesis as an explanation of diel vertical movements by juvenile sockeye. To maximize foraging success, day and night residence in shallow water where zooplankton concentrate would be advantageous over a large amplitude diel vertical migration that segregates sockeye from their primary prey. Clearly, a selective agent other than foraging success alone is required to explain diel vertical migration behavior in juvenile sockeye salmon.

2) Bioenergetic hypothesis

This hypothesis suggests that migrating juvenile sockeye achieve an energetic advantage over non-migrants due to the effect of cyclic temperature fluctuations on growth rate. The hypothesis predicts a relaxation of diel migratory activity in isothermal water columns where temperature-related growth benefits cannot be achieved.

The temperatures experienced by sockeye migrants (Fig. 6-5) indicated that vertically migrating sockeye experienced average water temperatures of 6.9°C and 10.9°C during day and night periods respectively, with an average (absolute) diel temperature difference of 4.6°C . In most lakes,

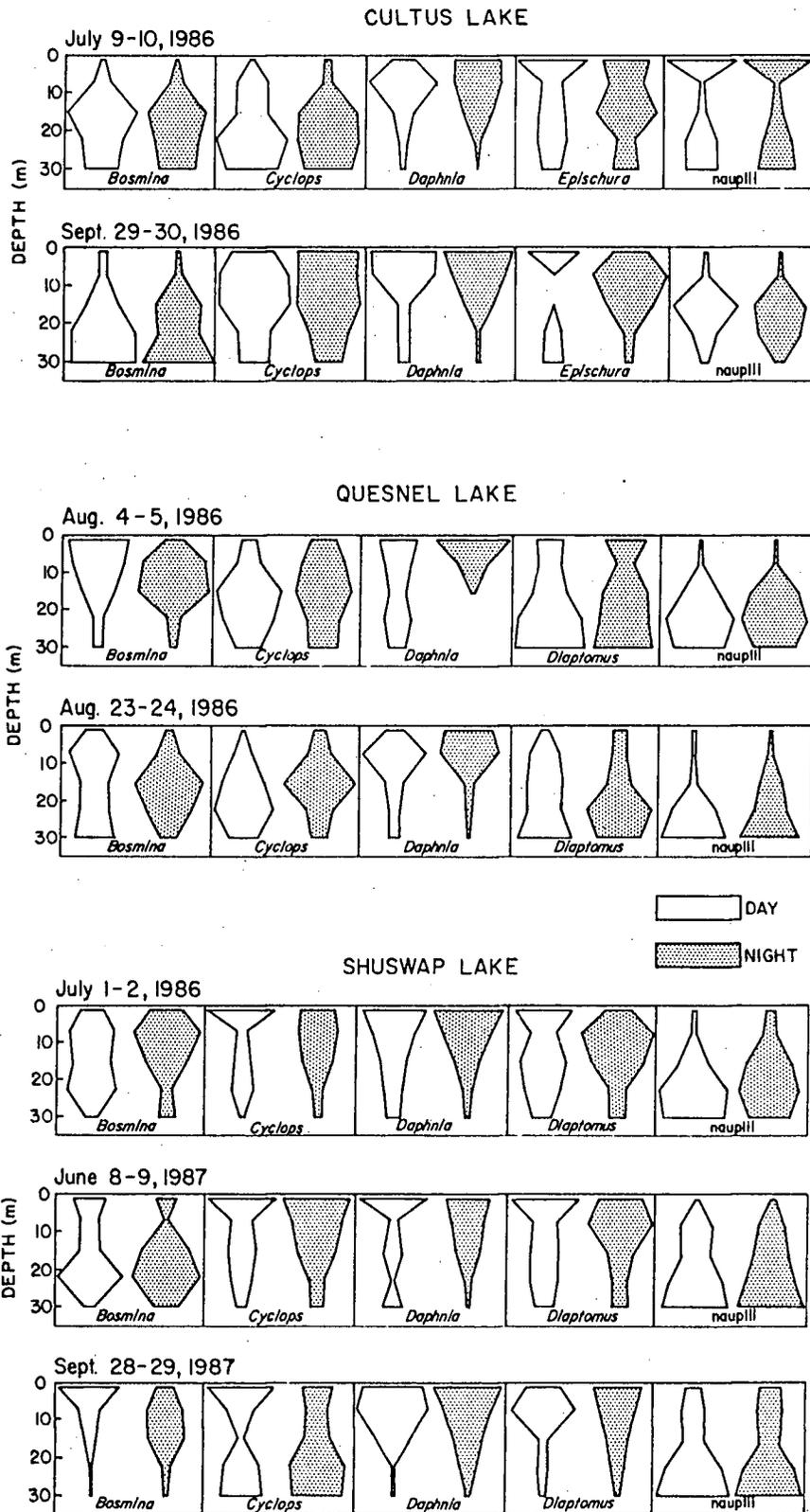


Figure 6-3. Day and night vertical depth profiles of the predominant crustacean zooplankton species captured in plankton pump samples from Cultus, Quesnel and Shuswap lakes.

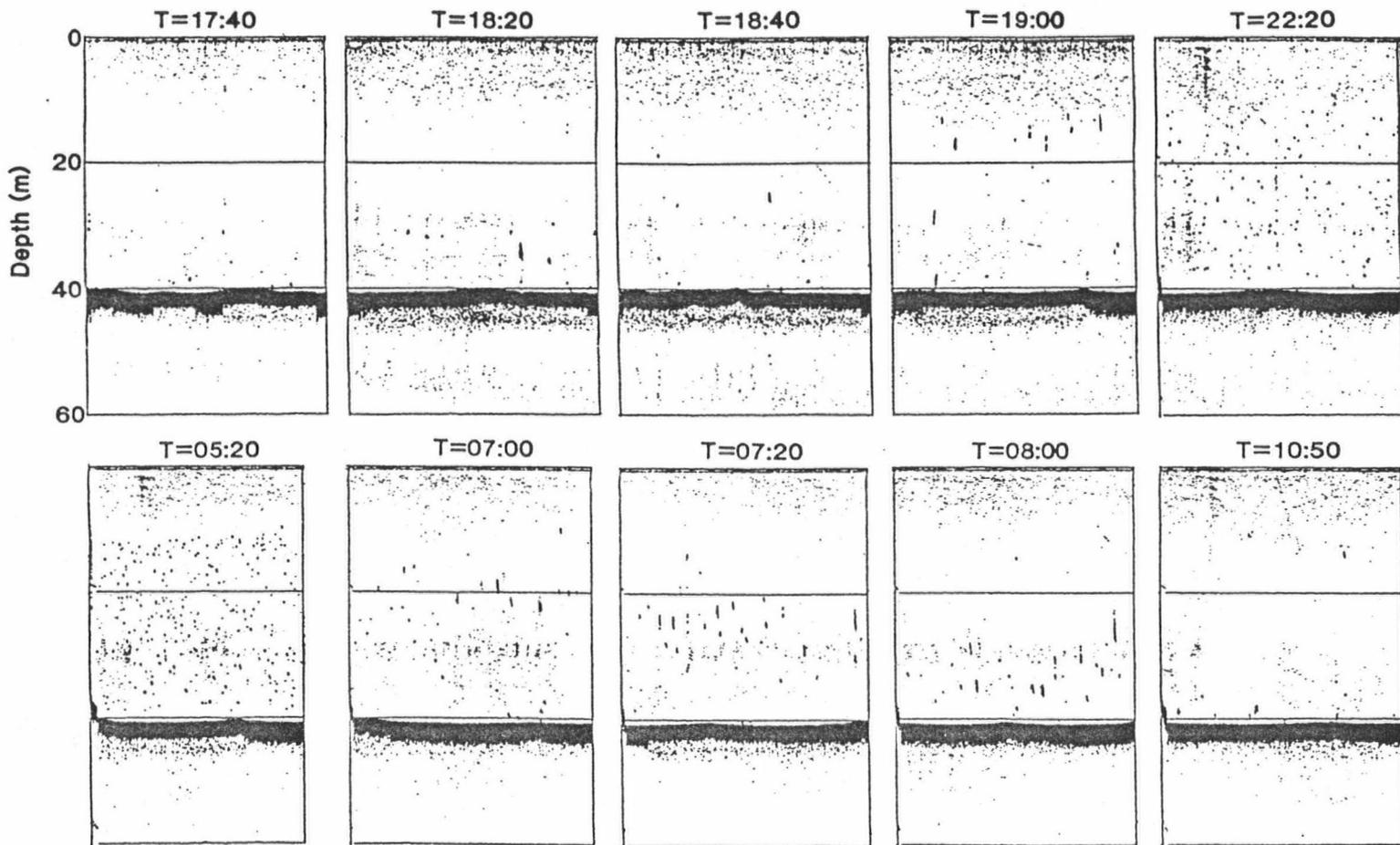
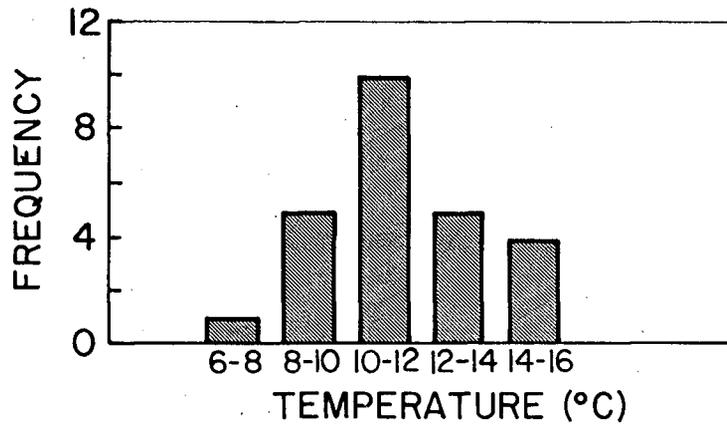
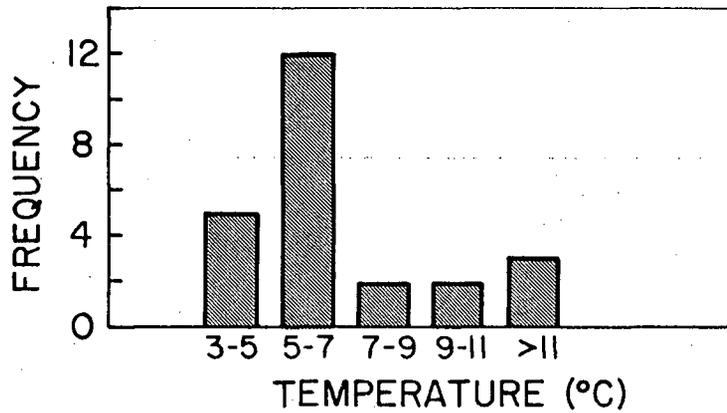


Figure 6-4. Diel vertical migration of juvenile sockeye in Cultus Lake on Sep. 29-30, 1986.

A. Nocturnal Temperature Distribution



B. Daytime Temperature Distribution



C. Diel Temperature Differences

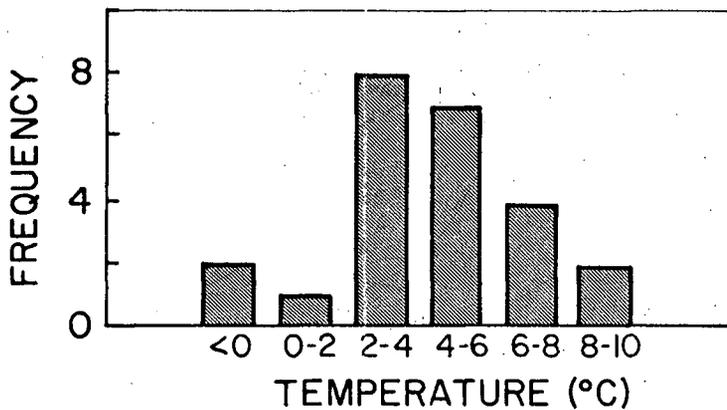


Figure 6-5. Distribution of temperatures experienced by migrating juvenile sockeye within B.C. sockeye lakes during A) nocturnal, and B) daytime periods. Diel temperature difference experienced by migrants indicated on distribution C).

sockeye were situated in cooler water by day than at night. However, in Nimpkish Lake (see below), sockeye diel vertical migrations were reversed, and the fish experienced warmer water by day than at night.

Juvenile sockeye in several lakes undertook diel vertical migrations under near-isothermal conditions. Such migrations were apparent in Lakelse, Babine, and Owikeno lakes. Lakelse Lake is subject to intense wind action which periodically disrupts the lake's thermal stratification (Brett 1950). During June of 1986, fish targets (presumed juvenile sockeye) were observed to undertake diel vertical migration under isothermal conditions (Fig. 6-6). Within Babine Lake, juvenile sockeye migrated vertically on June 25-26, 1986 (Fig. 5-6) within an isothermal water column (June 25'86 temperature profile is shown in Fig. 5-10). Lastly, the diel vertical migration of sockeye within Owikeno Lake observed in October of 1985 (Fig. 5-3) occurred in a water column that was close to isothermal (Fig. 5-4). Other observations of diel occupancy of similar temperatures by juvenile sockeye include those made by Woodey (1972) in Lake Washington.

These field observations suggest that thermal stratification of the pelagic water column is not a necessary prerequisite for diel vertical migration to occur. Moreover, within an isothermal water column, physiological functions occur at the same rate over all depths, and vertical migration under these conditions cannot provide temperature related bioenergetic benefits. I conclude therefore, that a simple bioenergetic hypothesis does not provide an adequate explanation for the selective advantage of diel vertical migration to juvenile sockeye salmon.

3) Predator avoidance hypothesis

This hypothesis predicts that sockeye vertical migrants will seek out particular irradiance isopleths where visual searching ability of the dominant piscivores is reduced or negligible. Thus the evolved light preference of vertical migrants should occur below the saturation irradiance threshold, *SIT*, of the dominant piscivore, where *SIT* is defined as the minimum quantity of irradiance that maximizes reaction distance to prey targets (Henderson and Northcote 1985).

Variations in the daytime depth distribution of sockeye (Fig. 5-1) are consistent with this prediction: sockeye in clear lakes occur deeper in the water column, by day, than sockeye in more

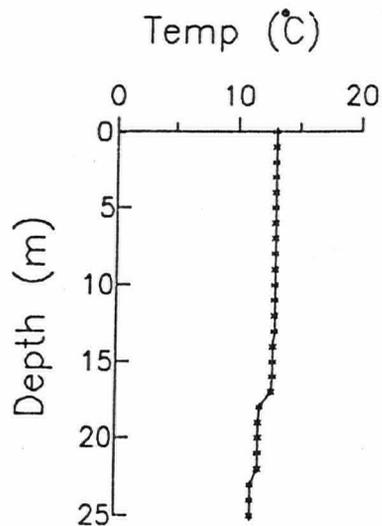
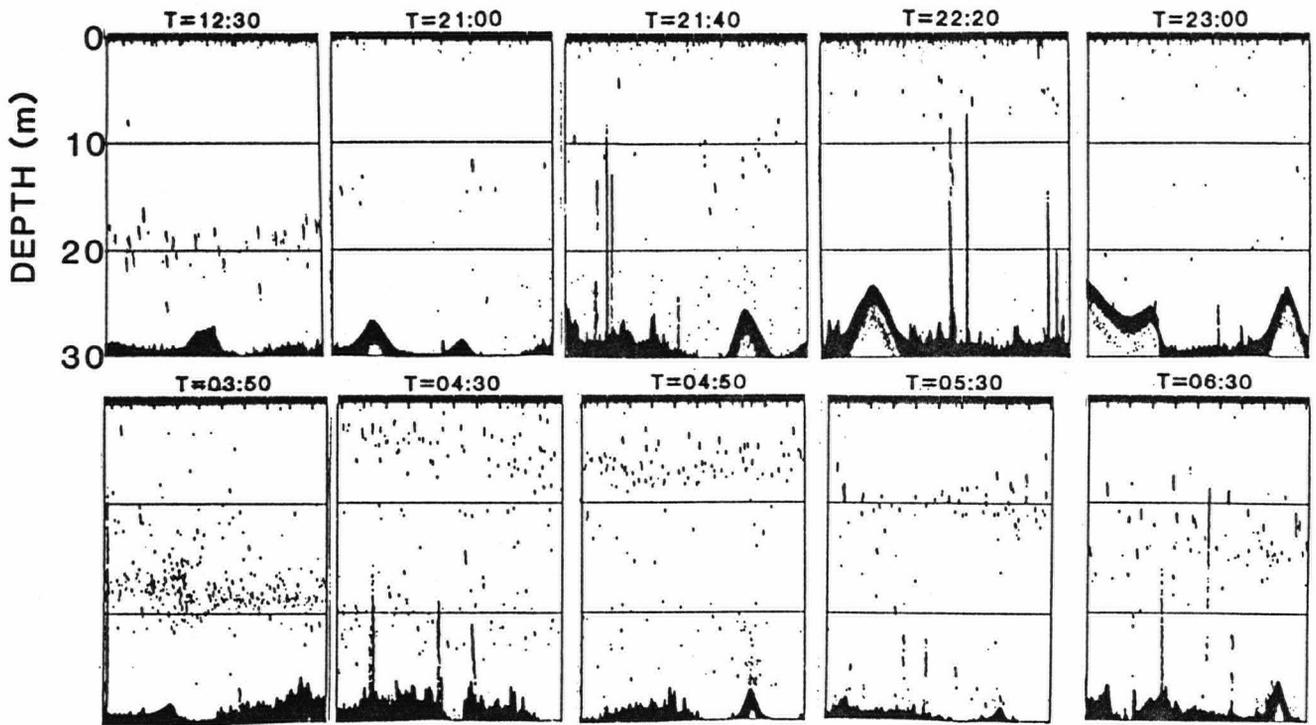


Figure 6-6. Diel vertical migration of echo targets under isothermal conditions within Lakelse Lake on June 21-22, 1986. Upper echograms show diel change in fish depth distribution, while lower graph shows the temperature for the upper 25 m of the water column.

turbid systems. During daytime periods (Fig. 6-7), sockeye experienced a mean irradiance level of $1.1 \times 10^{15} \text{ photons} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ (range = $10^{16} - 10^{11} \text{ photons} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$). Two important predators of juvenile sockeye, cutthroat trout and Dolly Varden char, have *SIT* values considerably higher than this level (Fig. 6-8). Based on the laboratory data collected by Henderson and Northcote (1985), sockeye at their daytime depth would be invulnerable to cutthroat and only marginally visible to Dolly Varden. Although comparison of laboratory results and pelagic field observations needs to be undertaken with caution, existing evidence is consistent with the main prediction of the predator avoidance hypothesis.

Considerable variation occurs in the mortality rates of juvenile sockeye within their nursery lakes. Predators are numerous in both Cultus and Lakelse lakes (Foerster 1968) and within-lake survival has been estimated as 5.5% (Foerster 1938) and 16% (Foerster 1968) respectively. In Babine Lake, fry-to-smolt survival rates varied between 7.5% and 49.9% during 16 years of study (McDonald and Hume 1984). Lakes where sockeye show exceptionally high within-lake survival include Port John Lake and Chilko Lake (Foerster 1968). Fry-to-smolt survival rates of sockeye within Chilko varied between 45.4% to 56.7% over the period 1949-1955, with a mean value of 52.6% (Foerster 1968, Table 86). In reference to Chilko Lake fry-to-smolt survival, Foerster (1968, p. 310-311) reported: *"In comparison with most findings elsewhere this high level of lake survival seems fantastic, but the figures for Port John Lake are of the same order if the 2- year lake life there is taken into account. No information is to hand regarding the prevalence of predator and competitor fishes in Chilko Lake."*

I surveyed Chilko Lake hydroacoustically during the daylight hours of July 28, 1986 and did not detect any fish targets within the pelagic zone at the northern end of the lake. Surface dimpling was observed in the afternoon suggesting a daytime surface orientation of juvenile sockeye on this date. On July 15-16'87, juvenile sockeye were detected by the SONAR equipment and they undertook a diel vertical migration covering at least 80 m of the water column (Fig. 6-9A). When the observations were repeated on August 14-15'87 (Fig. 6-9B), there was little evidence of substantial diel vertical migration, and sockeye schools were again observed dimpling the surface during hours of daylight. These visual surface observations suggest that at least some juvenile sockeye within Chilko have relaxed their diel vertical migratory activity for at least a portion of their lake

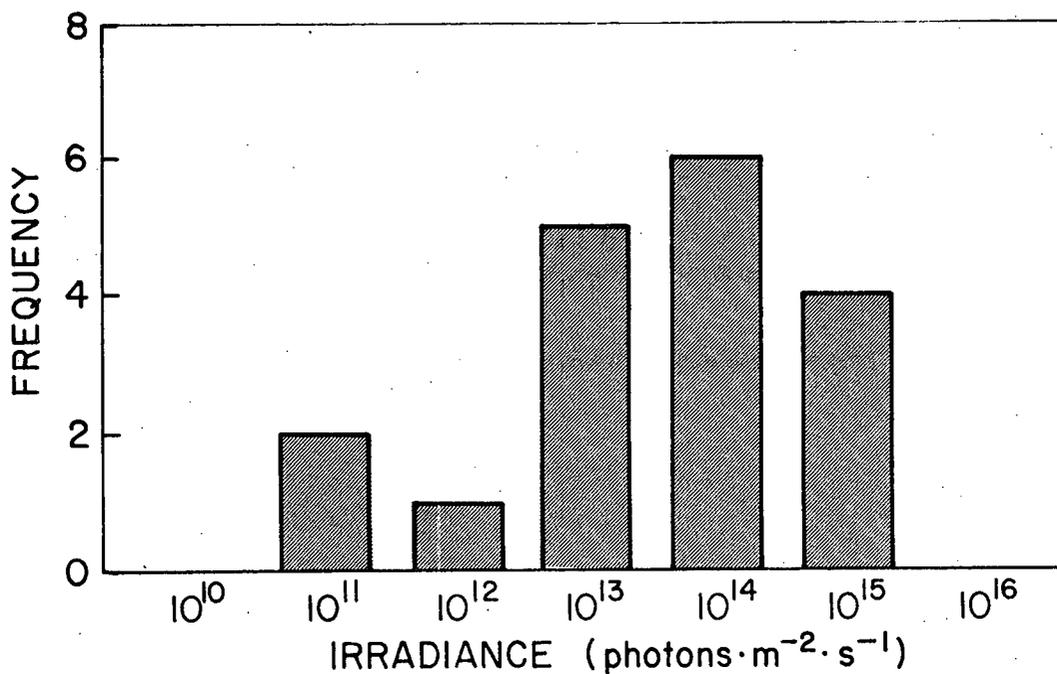


Figure 6-7. Frequency distribution of calculated light intensities at the daytime depth of maximum fish biomass (shown on Fig. 5-1).

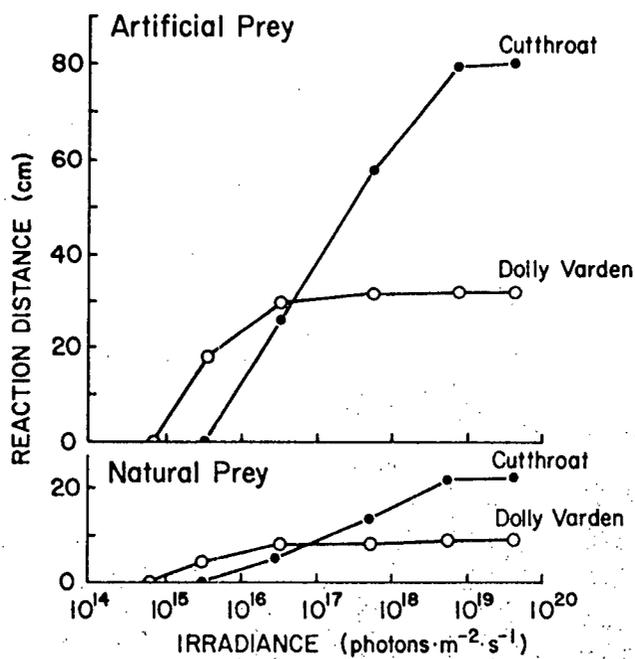
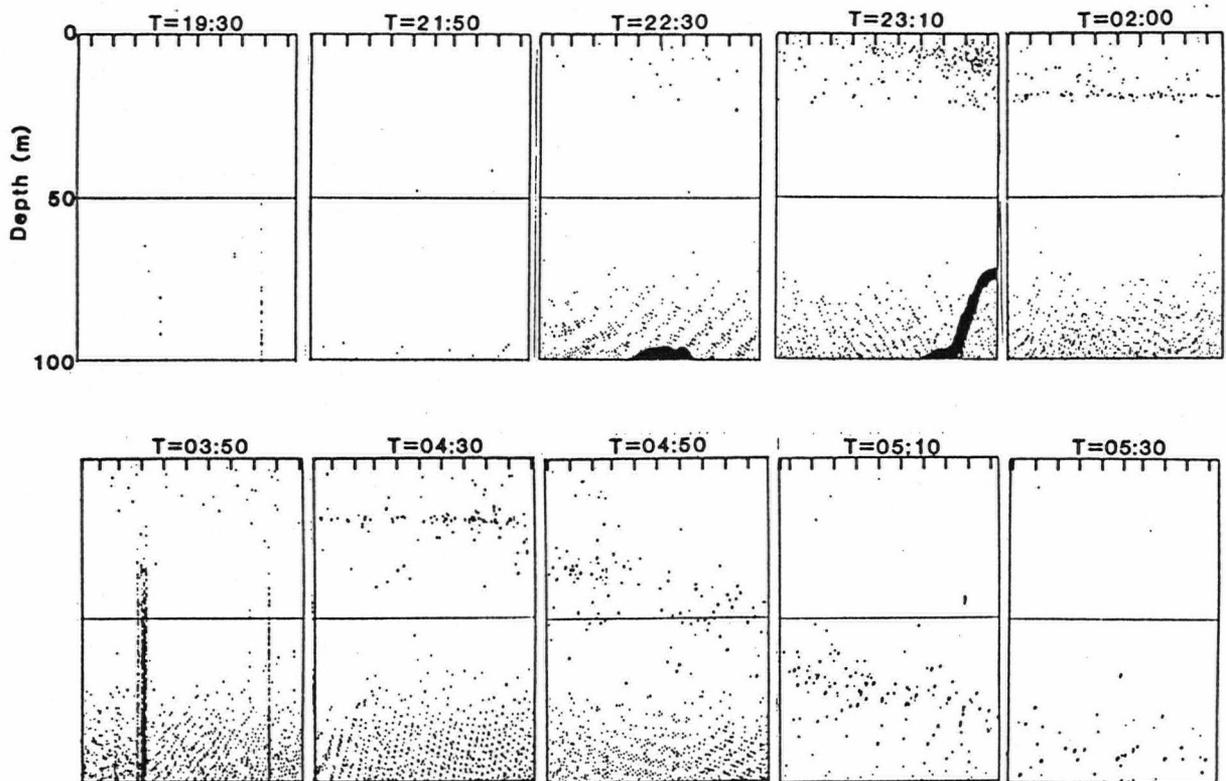


Figure 6-8. Effect of the quantity of irradiance on the mean reaction distance of cutthroat trout and Dolly Varden to artificial and natural prey; redrawn from Henderson and Northcote (1985,fig.2).

A) July 15-16'87



B) August 14-15'87

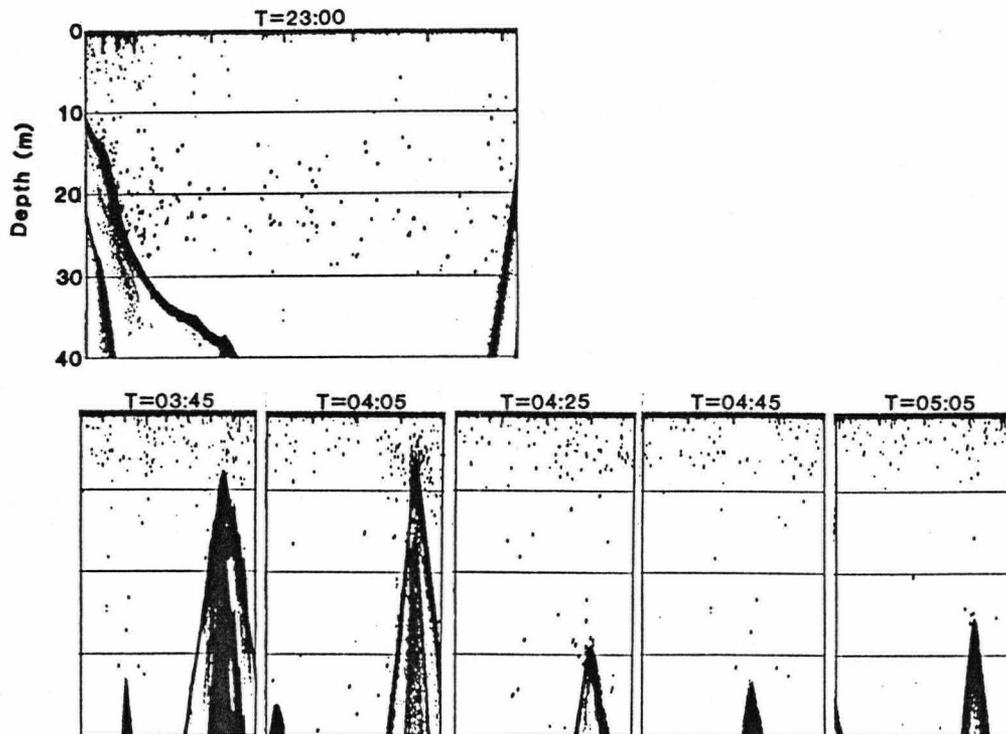


Figure 6-9. Diel echogram sequences from Chilko Lake obtained on A) July 15-16, 1987, and B) Aug. 14-15, 1987.

residency. The observations provide circumstantial support for the predator avoidance hypothesis in view of the low fry-to-smolt mortality that has been documented for Chilko. However, the observation of a large amplitude vertical migration (Fig. 6-9A) in a lake of moderate transparency (July '87 Secchi depth = 7.1 m), as well as the different vertical migratory behavior observed on different dates, remains puzzling. Unlike most Fraser sockeye lakes, substantial numbers of juveniles occupy Chilko Lake for a 2 year (vs. 1 year) freshwater residence period (Foerster 1968). Possibly the different migratory behaviors correspond to respective migratory patterns of different size classes of juvenile sockeye. Ontogenetic shifts in vertical migratory activity can occur in kokanee (Section VII).

During most diel hydroacoustic sampling sequences, sockeye were numerically predominant and few targets were observed that would qualify as "potential predators". Such was not the case within Little Shuswap Lake (Fig. 6-10) where diel sequences showed a group of echo targets that ascended from the lake bottom into the hypolimnion remaining largely segregated from the vertically migrating juvenile sockeye targets. When the target strengths of the 2 spatially distinct groups of echo targets were compared (sequence T=21:30 on Fig. 6-10), different distributions were evident (Fig. 6-11). Echo targets between 0-20 m and 40-60 m had mean target strength values of -50.6 and -46.7 db respectively. These target strength values correspond to fish of mean size 5.5 and 10 cm respectively, when fish sizes are estimated from the empirical regression equation derived by Love (1977):

$$TS = 19.1 \text{Log} L - 0.9f - 62.0 \quad (6.1)$$

where TS is the dorsal aspect target strength measured in decibels, L is the fish length in cm, and f is the frequency in kHz. Previous work within Shuswap (Williams et al. in prep.) has shown that the majority of fish species within the lake consume sockeye during years of dominant cycle residency. Many of the deeper fish targets within the hypolimnion of Little Shuswap can be considered potential consumers of juvenile sockeye, but predator species identification awaits further netting studies.

These observations suggest an alternative predator avoidance hypothesis which is partially consistent with observed patterns of juvenile sockeye diel vertical migration. Nocturnal avoidance of the hypolimnion might be a favourable survival strategy if there were a nocturnal predator which

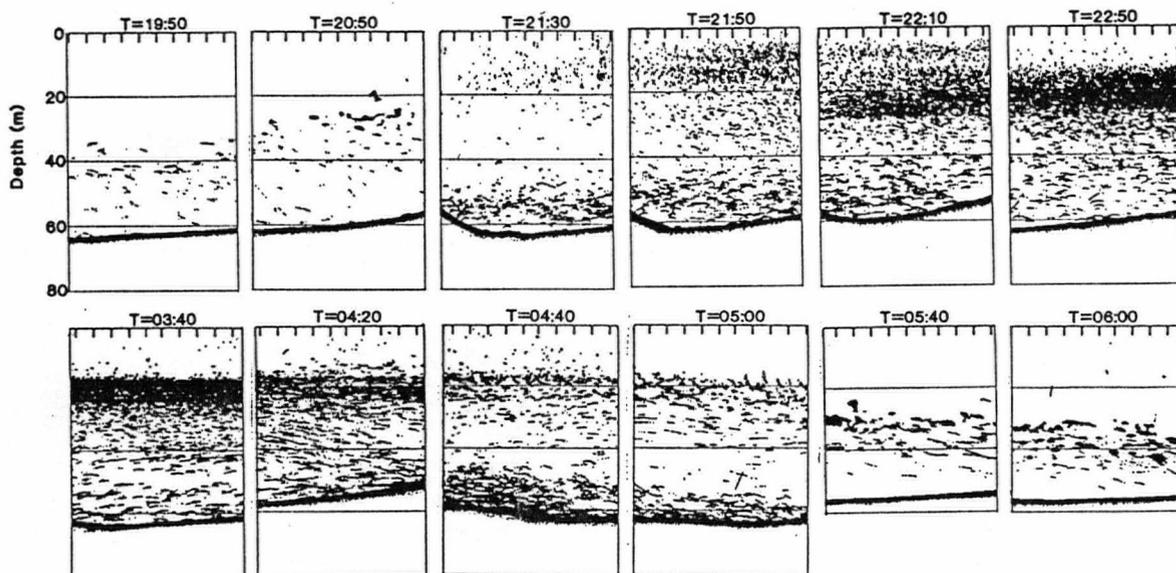


Figure 6-10. Diel echogram sequence from Little Shuswap Lake on July 19-20, 1987. Echograms obtained by drifting at slow velocity.

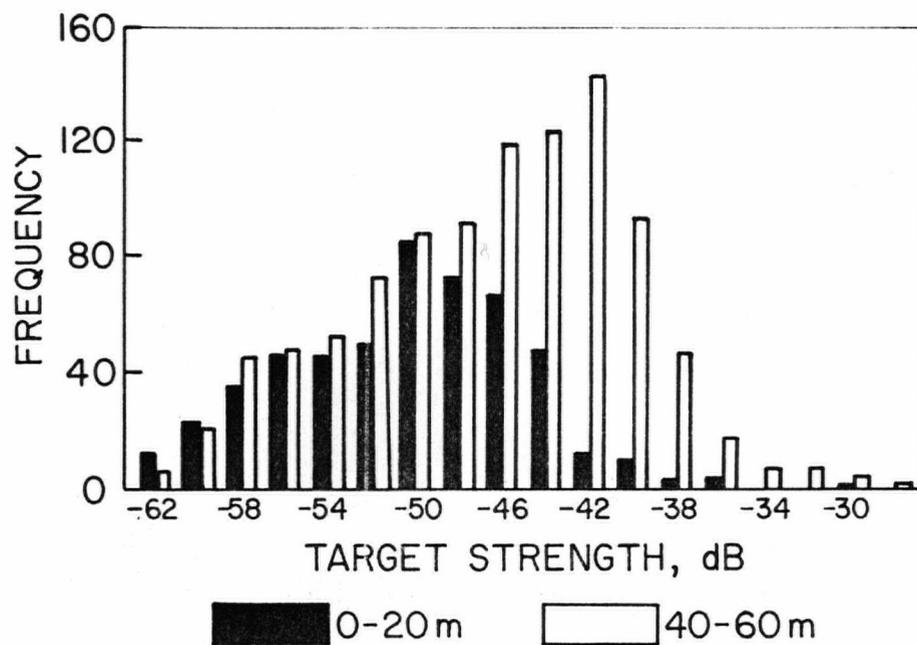


Figure 6-11. Comparison of target strengths of fish distributed in both shallow (0-20 m) and deep (40-60 m) water within Little Shuswap Lake at T=21:30 (PDST) on July 19, 1987.

relied on non-visual stimuli for sockeye capture. Squawfish (*Ptychocheilus oregonensis*) are in fact capable of capturing prey in complete darkness using olfactory stimuli (Chisholm 1975). However, this hypothesis cannot explain the full cycle of sockeye diel vertical migration, since, under this hypothesis, there would be no selective advantage for sockeye to descend into deep water during daylight hours. The nocturnal avoidance of hypolimnetic predators that hunt by non-visual stimuli could however re-inforce an established pattern of sockeye vertical migration.

The predator avoidance hypothesis is consistent with field observations of juvenile sockeye diel vertical migration. However, the hypothesis is incomplete (Section II) since it does not explicitly consider the trade-off between food intake and predation risk. Below, I consider predator avoidance as a component of multifactor hypotheses of diel vertical migration.

4) Multifactor hypotheses

There are 4 multifactor hypotheses (Table 3-1), three of which involve 2-way interactions between 3 factors (foraging, bioenergetics, and predator avoidance) and one of which involves a 3-factor combination. A combined foraging and bioenergetic hypothesis has been dismissed (Section II) since it predicts neither the diel timing, nor the observed amplitude of vertical migration. A combined bioenergetics and predator avoidance hypothesis is not valid since juvenile sockeye actively feed during the course of their diel vertical migration (Narver 1970; Doble and Eggers 1978). I here evaluate the remaining 2 multifactor hypotheses in light of the recent field observations.

The antipredation window model (Clark and Levy 1988) combines foraging and predator avoidance. The main novel prediction of the hypothesis is that planktivores which hunt by sight and which are subject to visual predation will undertake diel vertical migrations to feed on zooplankton in surface waters for relatively brief crepuscular periods. The model does not make any explicit nocturnal migration predictions. Field observations (Section V) suggest that juvenile sockeye are nocturnally thermoselective and associated with temperatures that optimize metabolic efficiency (Brett et al. 1969).

In addition to Chilko Lake where diel vertical migration is (periodically) relaxed, fish targets within Nimpkish Lake (both sticklebacks and juvenile sockeye are present within the pelagic zone)

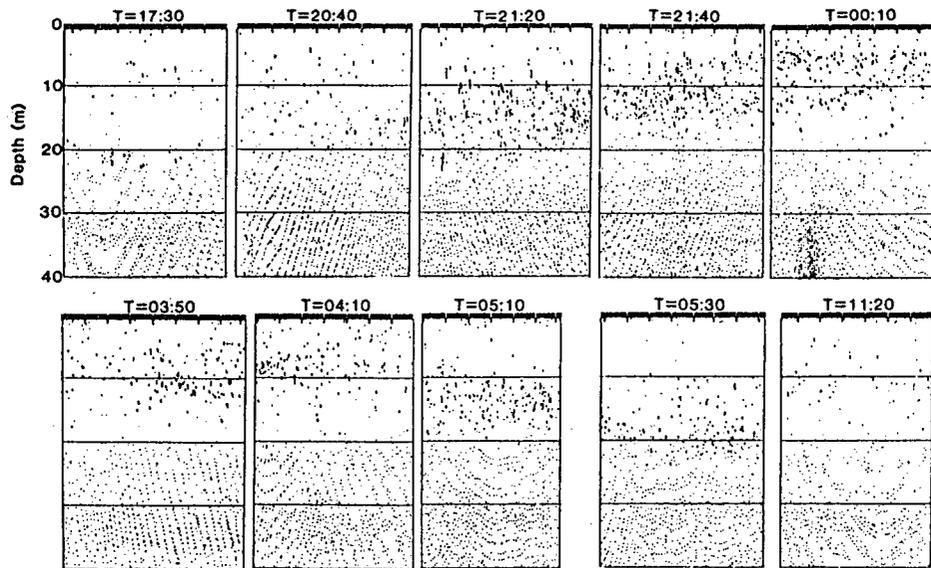
undertook altered diel vertical migrations (Fig. 6-12). On June 17-18'86 (Fig. 6-12A) most of the fish targets undertook a diel vertical migration, ascending at dusk, and descending at dawn. However, the pattern of movement was radically different on Sept. 8-9'86 (Fig. 6-12B) when fish targets *descended* at dusk and *ascended* at dawn. A similar reversed diel vertical migration of pelagic fish targets was observed on Sept. 16-17'86 (Fig. 6-12C).

Comparison of fish depth distributions with temperature profiles (Fig. 6-13) suggested that the most dense group of fish targets were nocturnally associated with the thermocline in a manner consistent with the hypothesized sensory mechanism (Section V). During hours of daylight, however, fish targets were concentrated in brightly illuminated shallow water. The deeper nocturnal depth distribution of the main group of fish targets on Sept. 16-17'86, compared to Sept. 8-9'86, probably corresponds to the deeper thermocline distribution on this date.

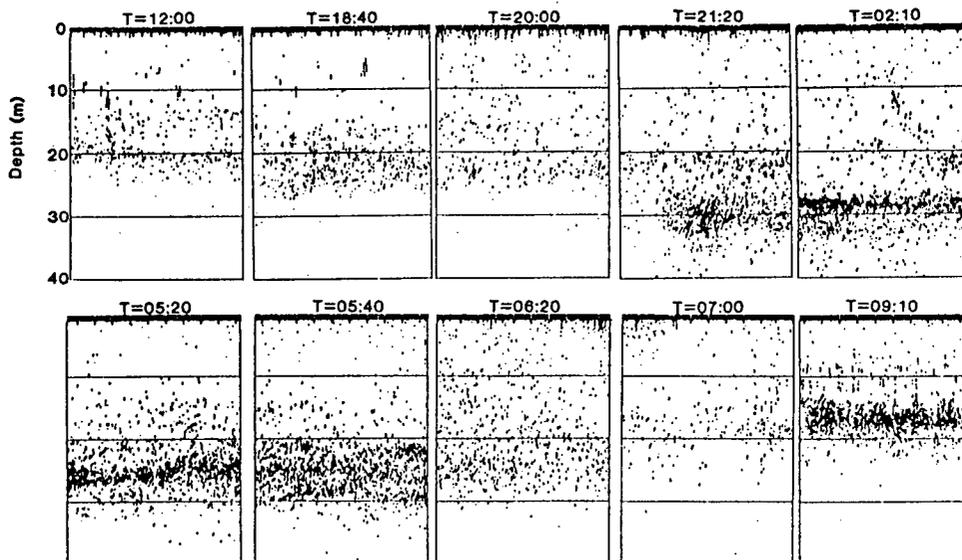
There are at least 2 possible explanations for the reversal of diel vertical migration behavior by juvenile sockeye within Nimpkish Lake. First, there could be a low predator-induced mortality rate since few predators have been observed within the pelagic zone, relative to other sockeye nursery lakes (K.Hyatt, Dept. of Fisheries and Oceans, Nanaimo, B.C., unpublished observations). Second, the presence of competition from threespined sticklebacks within Nimpkish Lake might select for a reversed diel vertical migration by juvenile sockeye within Nimpkish Lake. Pelagic sticklebacks are planktivorous and have been shown to compete with juvenile sockeye in enclosure experiments conducted at Kennedy Lake (O'Neill and Hyatt 1987). It is presently difficult to reject either explanation.

A reversed diel vertical migration is not predicted by the antipredation window hypothesis. In order to generate a reversed migration, it is necessary to postulate a bioenergetic influence on nocturnal distribution. Also, the nocturnal temperature observations (Fig. 5-9) suggest nocturnal selection of temperatures optimal for sockeye growth under restricted food rations (Brett et al. 1969). It is therefore apparent that the hypothesis which best explains the selective advantage of juvenile sockeye diel vertical migration, is a multifactor hypothesis combining the antipredation window and bioenergetics.

A) June 17-18'86



B) Sept. 8-9'86



C) Sept. 16-17'86

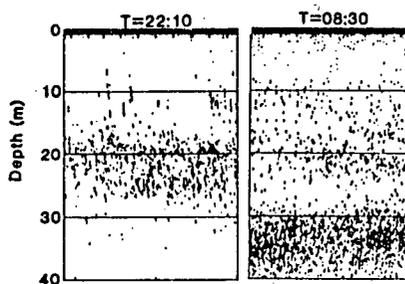
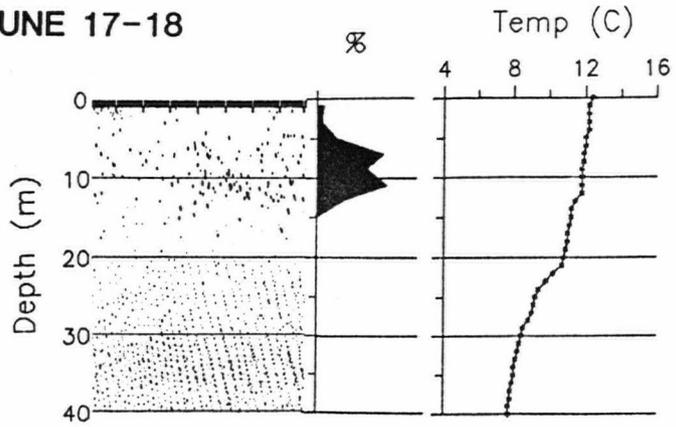


Figure 6-12. Diel echogram sequences from Nimpkish Lake on A) June 17-18, B) Sep. 8-9, and C) Sep. 16-17, 1986. Echogram marks between 20-40 m on June 17-18 caused by electrical noise.

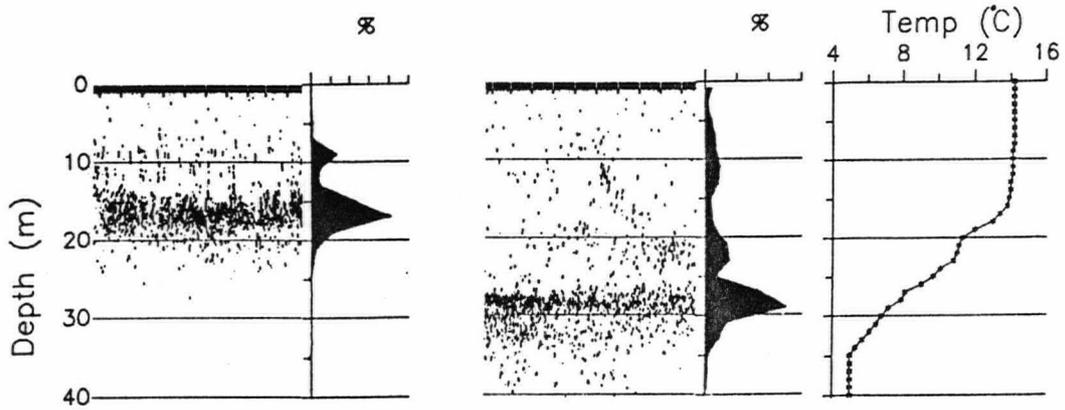
DAYTIME

NIGHT-TIME

JUNE 17-18



SEPT. 8-9



SEPT. 16-17

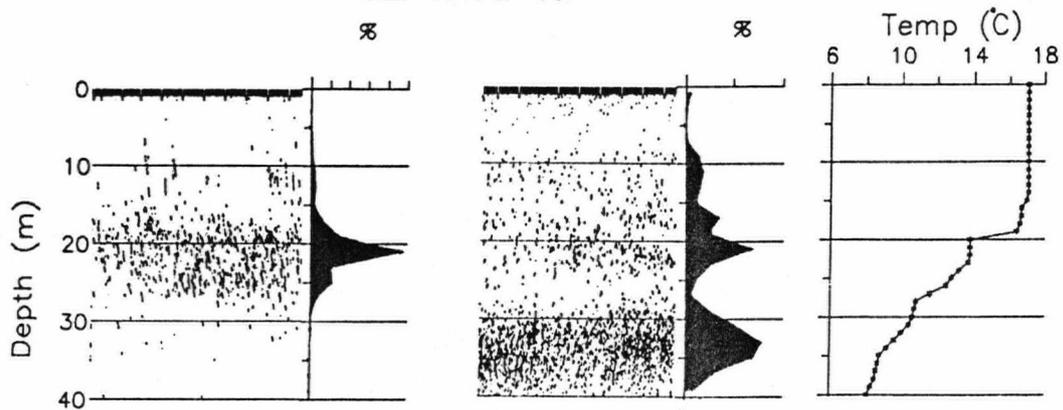


Figure 6-13. Day and night echograms and echo integrator depth profiles from Nimpkish Lake for 3 sampling dates in 1986.

Discussion

The major premise underlying this study is that there must be a selective advantage for juvenile sockeye which migrate compared to individuals which maintain a fixed depth in the water column. The exact nature of the selective advantage is not immediately apparent, and seven distinct hypotheses have been developed (Section II). In order to test the predictions of the various hypotheses (Table 3-1), vertical movements of juvenile sockeye were compared under a wide range of limnological and biological conditions.

The research has shown that diel vertical migration is a ubiquitous behavior in juvenile sockeye salmon. Detailed and quantitative descriptions of vertical migration behavior have been provided for most of the major sockeye salmon lakes of B.C. All of the populations studied undertook diel vertical migrations for at least a portion of their lake nursery residence. Variations in the normal diel pattern of migration were observed in 2 lakes where migrations were periodically relaxed (Chilko) or reversed (Nimpkish).

None of the three single factor hypotheses (foraging, bioenergetics, and predator avoidance) is capable of consistently predicting observed diel vertical migration behavior. The foraging hypothesis is inconsistent with the observed spatial segregation and dissimilarity in diel movement pattern between planktivore predator and zooplankton prey. The bioenergetic hypothesis does not account for the diel timing of vertical migration nor the observations of diel vertical migration under isothermal conditions. The predator avoidance hypothesis is consistent with field observations, but does not explicitly account for the trade-off between foraging and predator avoidance. In the absence of a single factor hypothesis which is sufficiently robust to account for the selective advantage of the behavior, it is necessary to consider multifactor explanations.

It is methodologically challenging to investigate processes caused by multiple factors (Hilborn and Stearns 1982). The approach followed during the present study was advocated by Gilbert et al. (1976) and involved modelling the process assuming multiple causes and then refining the model by testing each component. The antipredation window model (Clark and Levy 1988) served as the initial model and provided new insights into the selective advantage of juvenile sockeye diel vertical migration. However, even this model was incapable of predicting all of the observed

field observations. In order to account for juvenile sockeye nocturnal depth distribution it was necessary to invoke a bioenergetic influence on vertical distribution at light levels below the visual feeding thresholds of juvenile sockeye and their predators. The combined trade-off between foraging, predator avoidance, and metabolic efficiency at different temperatures provides the most realistic explanation for the selective advantage of diel vertical migration in juvenile sockeye salmon. This trade-off has yet to be modelled in a rigorous quantitative fashion.

Both Magnuson et al. (1979) and Crowder and Magnuson (1983) evaluated the distribution of fish in heterothermal environments and concluded that fish respond to both temperature and food according to bioenergetic expectations. However, the influence of predators on distribution was not even considered. The antipredation window model (Clark and Levy 1988) concluded that vertically migrating pelagic planktivores sacrifice growth in order to avoid predation. Predator avoidance considerations could easily modify, and even out-weigh, bioenergetic and feeding considerations in affecting the distribution and diel migratory behavior of fishes within the pelagic environment. Moreover, as pointed out by Mittelbach (1988), piscivores may have a greater impact on fish community organization through their indirect influence in modifying prey behavior, than through their direct consumption of a relatively small percentage of prey. More realistic models of aquatic population and community dynamics need to therefore incorporate predator avoidance as an important influence on prey distribution and abundance.

The daytime descent of juvenile sockeye evidently serves as a form of pelagic concealment from visual feeding piscivores. Future investigations of the selective advantage of diel vertical migration in juvenile sockeye should focus on estimating visual predation risk and foraging rate as a function of ambient light intensity. Empirical studies are required to quantify the trade-off between predator avoidance and the achievement of energetic returns (both foraging and bioenergetics).

VII. Ontogenetic Shifts in Diel Vertical Migration Behavior

Major ecological changes often coincide with the ontogeny of individual animals. Ontogenetic niche shifts in resource use are commonplace in fishes and are predictable on the basis of body size (Gilliam 1982; Werner and Gilliam 1984). Sockeye salmon show considerable variation in body size, commencing life as a fertilized egg weighing 0.013 g and terminating growth as a 2300 g adult (Brett 1983). Selective pressures undoubtedly change in importance across these extremes of body size.

Kokanee, the lake-locked form of sockeye salmon, complete their growth within the limnetic zone of a lake. Previous studies suggest that sub-adult kokanee undertake reversed diel vertical migrations. Kokanee in Nicola Lake were shown to have a reversed diel vertical migration during 8 out of 10 intensive 24 h netting series conducted during the summer and fall months (Northcote et al. 1964; Northcote 1967). In Babine Lake, McDonald (1969) captured kokanee in shallow (0-16 m) purse seine sets by day indicating that in this lake, kokanee are surface oriented during daylight hours. In Pend Oreille Lake, Idaho, summer echo sounding studies (Rieman and Bowler 1980) indicated that kokanee were distributed between 0-20 m during daylight hours and between 18-27 m during the night. While sub-adult kokanee evidently undertake reversed diel vertical migrations, there is no information available on juvenile kokanee diel vertical migrations from such systems. It is not known whether juvenile kokanee undertake reversed diel vertical migrations, or whether they behave like juvenile sockeye, shifting their diel vertical migratory behavior later in life. The occurrence (or absence) of an ontogenetic shift in vertical migratory activity has important implications for explanations of the selective advantage of the behavior in kokanee.

To establish whether an ontogenetic shift occurs in kokanee diel vertical migratory activity, diel echo sounding studies were undertaken in the pelagic zone of Okanagan Lake on four occasions during the summer and fall months of 1987. For comparative purposes, similar data were also collected on one occasion respectively from Skaha and Kootenay lakes. Previous trawling studies

(B.C. Fish and Wildlife Branch, unpublished data) have indicated that kokanee comprise virtually 100% of the fish vulnerable to an 3 X 5 m midwater trawl device operated within the pelagic zone of Okanagan, Skaha and Kootenay lakes.

Diel vertical migrations by kokanee

Echograms from Okanagan Lake showed major diel differences in appearance. Back-scattering was observed from objects throughout the upper 100 m of the pelagic water column (Figs. 7-1A and B). Moreover, back-scattering occurred at different vertical positions within the pelagic water column by day and night.

There were 3 distinct groups of echo targets present (Fig. 7-1). The predominant organism formed a dispersed group of targets centered at 100-120 m by day, ascending to within 15 m of the surface at night. This was followed by a dawn descent under low light intensities. The back-scattering was observed on the oscilloscope as a broad band of low voltage, suggesting the combined echo reflections from a large biomass of small-bodied organisms. This organism was tentatively identified as the mysid *Mysis relicta* which was introduced into Okanagan Lake in 1966 (Lasenby et al. 1986) and presently occurs there in high abundance. This species is a known vertical migrator in a number of lakes (Beeton and Bowers 1982).

In addition to the vertically migrating mysid layer, there were 2 distinct groups of fish targets present on echograms (Fig. 7-1). The first was present in shallow (15-25 m) water depths by day, while the second was observed to migrate vertically. The latter group evidently ascended from a daytime depth of 50-80 m and merged together with the shallow water group at night. At dawn, the second group descended away from the shallow water group, and gradually re-assumed the daytime depth level.

Observations of the fish targets were quantified by counting the echoes, scaling the counts by the estimated sample volume, and then expressing the number of echoes per m^3 within each depth strata as a proportion of the sum (Fig. 7-2). On all 4 sampling dates there was a distinct bi-modality in the daytime vertical depth distribution of echo targets. The shallow group of echo targets was "loosely" associated with the thermocline of the lake and appeared to shift its daytime

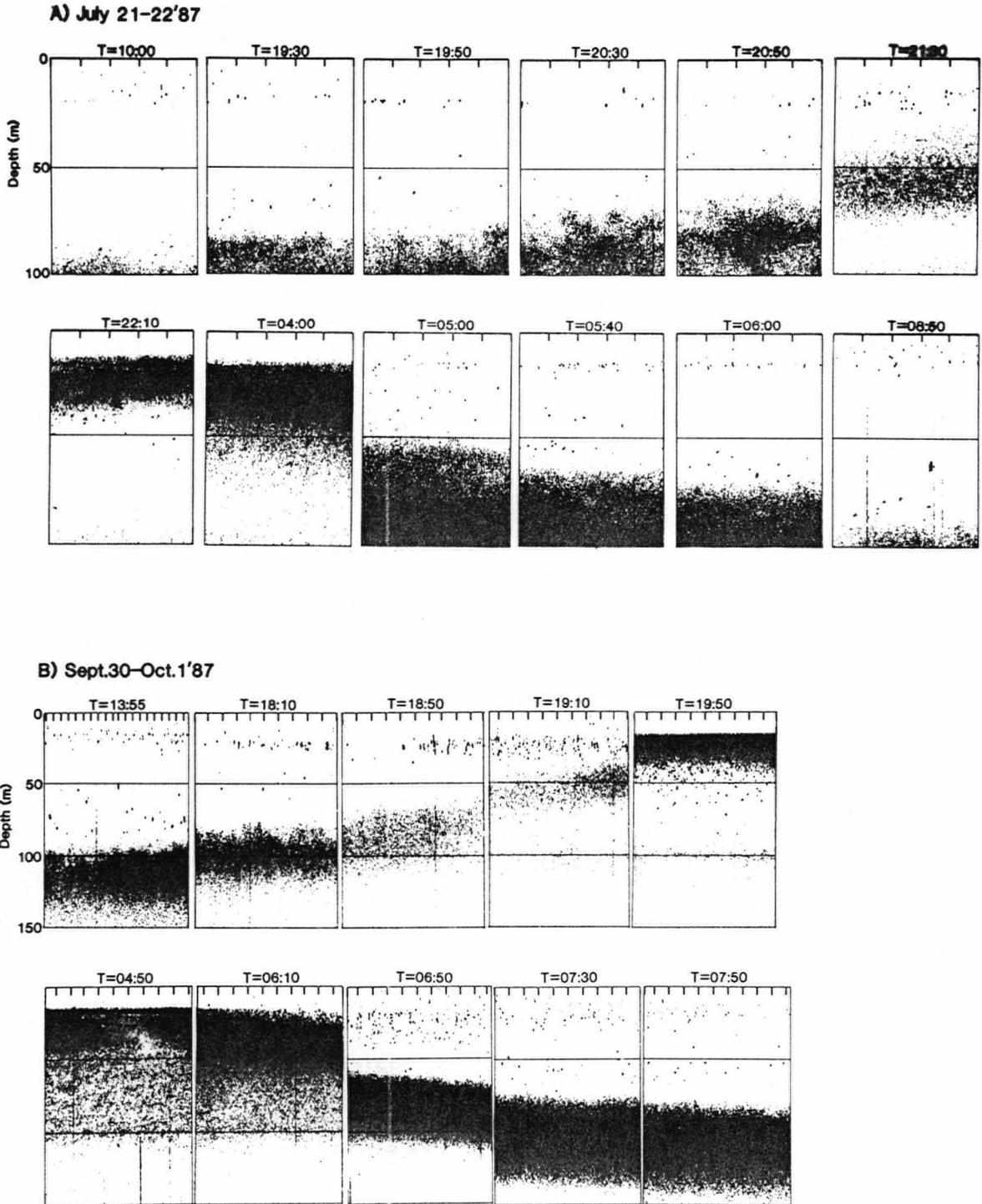


Figure 7-1. Diel echogram sequences from Okanagan Lake on A) July 21-22, and B) Sep. 30-Oct. 1, 1987. Dispersed marking on echograms due to echo returns from *Mysis relicta*.

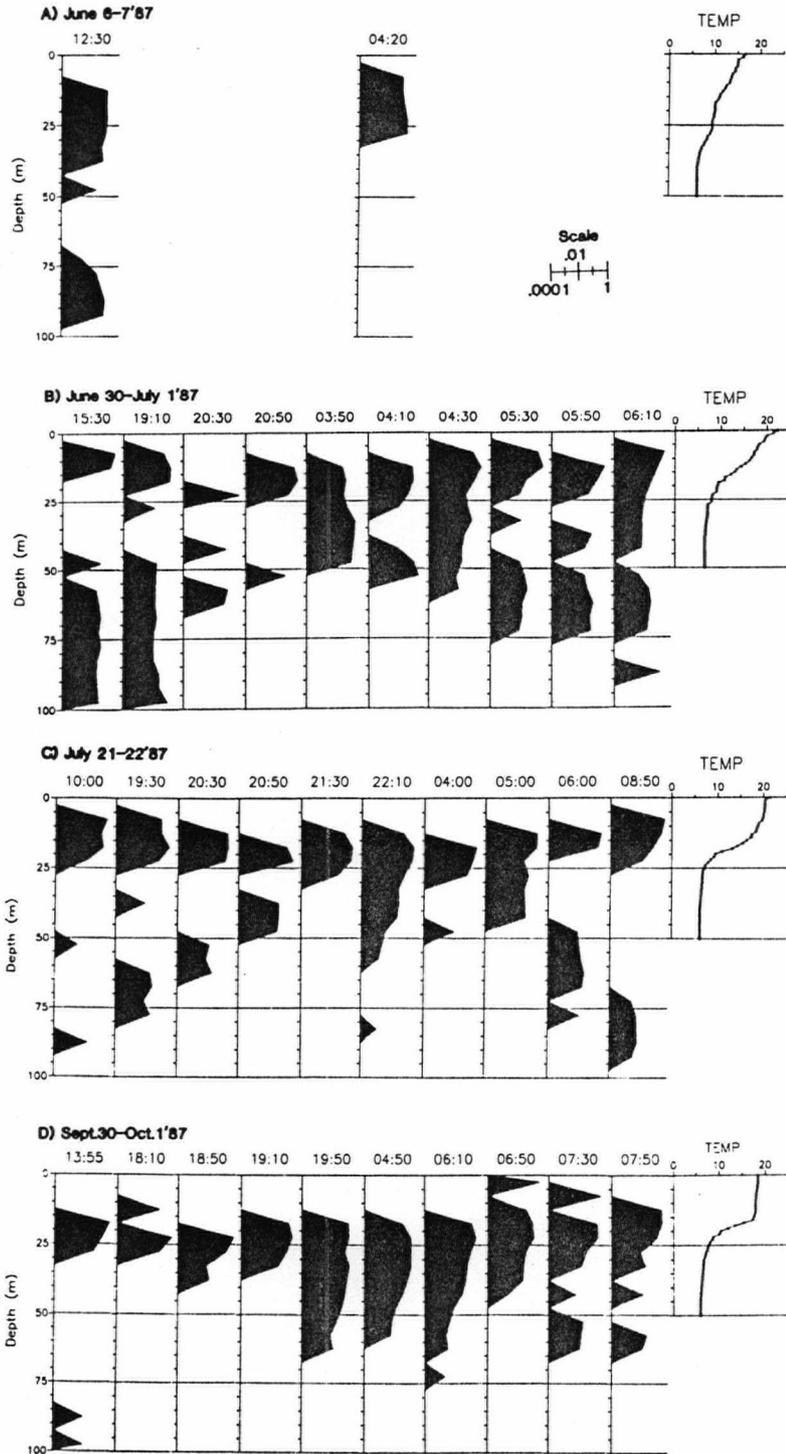


Figure 7-2. Results of counting echo targets in 5 m depth intervals within Okanagan Lake on 4 sampling dates of 1987. Count data are scaled by the effective sampling volume within each depth interval, and expressed as a proportion of the total target density within the pelagic water column. Note logarithmic scale. Temperature profile shown on the right.

vertical position in response to seasonal changes in the thermocline depth (Fig. 7-2). The deep group of echo targets was positioned at a depth of low light intensity and appeared to have a light preference comparable to juvenile sockeye, showing a similar relationship as juvenile sockeye between the mean daytime depth position and the light extinction co-efficient (Fig. 5-1).

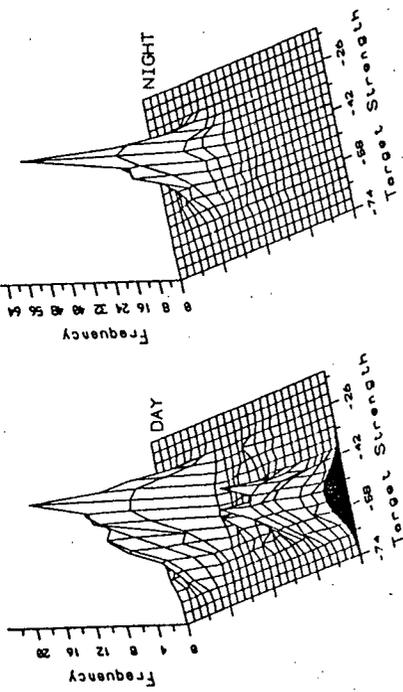
During nocturnal periods, kokanee within Okanagan Lake dispersed downwards, occupying a depth layer of 50 m thickness (Fig. 7-2). This nocturnal dispersal was evidently unrelated to thermal distribution, since the lake was well-stratified during three out of the four sampling dates, and many of the fish were situated in the isothermal hypolimnion (Fig. 7-2).

Target strengths of individual fish echoes were computed in order to make inferences about the size distribution of the two groups of fish echo targets. Separate results were computed for day and night transects (Fig. 7-3). During each of the four sampling dates there was a distinct bi-modal depth distribution in the frequency of daytime echo targets. There was also a difference in the mean target strength of the two groups of echo targets such that the mean of the deeper group of fish echoes was 8-14 db smaller than the mean of the shallow group (Fig. 7-3). These results suggest that the deeper group of migrating fish targets in Okanagan Lake were smaller in body size than the shallow targets.

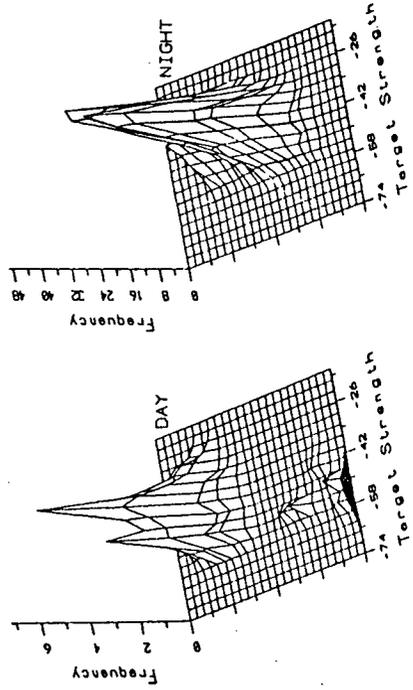
At night when the two groups of fish targets overlapped spatially, separate modes in target strength distribution could not be resolved (Fig. 7-3). This may be due to a homogeneous vertical depth distribution of different-sized animals, or alternatively to an inherent inability to resolve target strength modes when variance is high (variance in target strength is greater than variance in size due to effects of target attitude; see Burczynski and Johnson 1986).

These hydroacoustic results provide qualitative evidence for an ontogenetic shift in vertical migratory behavior of kokanee within Okanagan Lake. Small fish (juveniles) migrate vertically in a similar fashion as juvenile sockeye. Later in life, the fish alter their behavior and remain in shallow water during daylight hours. Angling practices within Okanagan Lake support this interpretation since sub-adult kokanee are vulnerable to shallow surface-deployed fishing gear during daylight hours.

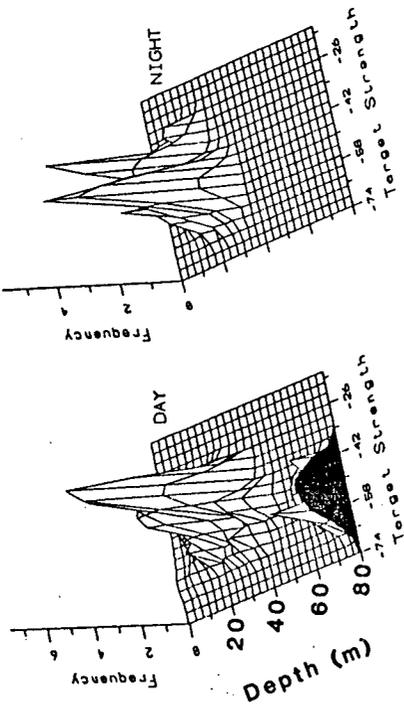
July 21-22'87



Sep 30-Oct 1'87



June 6-7'87



June 30-July 1'87

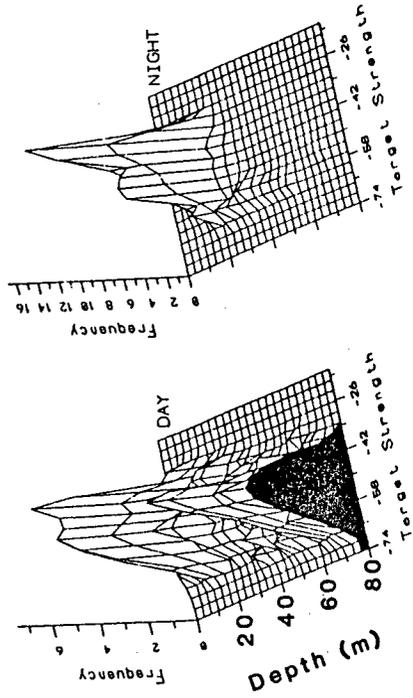


Figure 7-3. Target strength distribution within the water column of Okanagan Lake during 1987 day and night hydroacoustic transects.

Different diel patterns of echo target distribution were observed within Kootenay (Fig. 7-4) and Skaha (Fig. 7-6) Lakes. *Mysis relicta* are present within both of these lakes and undertook extensive vertical migrations which were evident on echograms. Within Kootenay Lake, there was evidence for separate modes in daytime fish depth distribution (Fig. 7-4A); however, the shallow daytime group was deeper in the water column (25-50 m) than the one observed in Okanagan. When target strength distributions were compared (Fig. 7-5), there was no clear evidence for depth-related differences in target strength distribution. Within Skaha Lake, diel differences in the vertical depth distribution of echo targets were slight (Fig. 7-6), and there was no indication of depth-related differences in target strength distribution (Fig. 7-7).

Discussion

There were two distinct groups of fish targets present within the pelagic zone of Okanagan Lake. The first occurred in relatively shallow water within the general vicinity of the thermocline, while the second undertook diel vertical migrations similar to those of juvenile sockeye. Daytime target strength estimates, obtained while the two groups were spatially segregated, indicated a lower target strength for the diel vertical migrants. These hydroacoustic results suggest the existence of an ontogenetic shift in diel vertical migratory behavior by kokanee within Okanagan Lake. Diel vertical migration behavior is evidently undertaken by small-bodied juveniles soon after they recruit into the pelagic zone. Later in life, at a larger body size, the behavior changes and the fish maintain a shallow orientation during the day and disperse downwards at night.

The occurrence of an ontogenetic shift in diel vertical migratory behavior is consistent with the Clark and Levy (1988) antipredation window model. If one assumes an inverse relationship between predator-induced mortality and body size, and a direct relationship between plankton food requirements and body size, it follows that larger-bodied individuals would spend a greater proportion of their diel time budget within shallow water. Moreover, since planktivorous kokanee are often food-limited within freshwater (their growth rate is generally much slower than that of their marine sockeye counterparts) bioenergetic benefits could be achieved by large-bodied kokanee

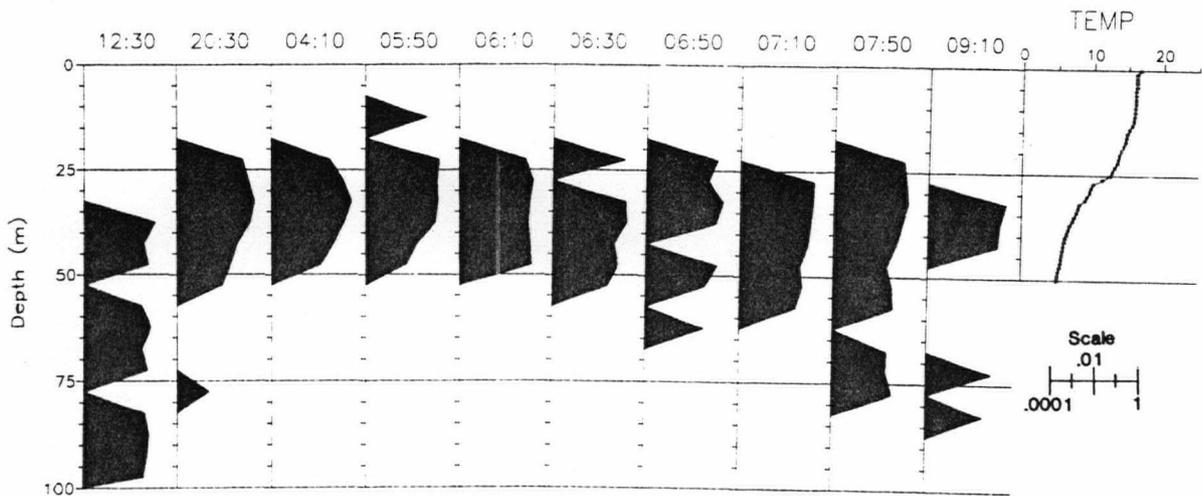
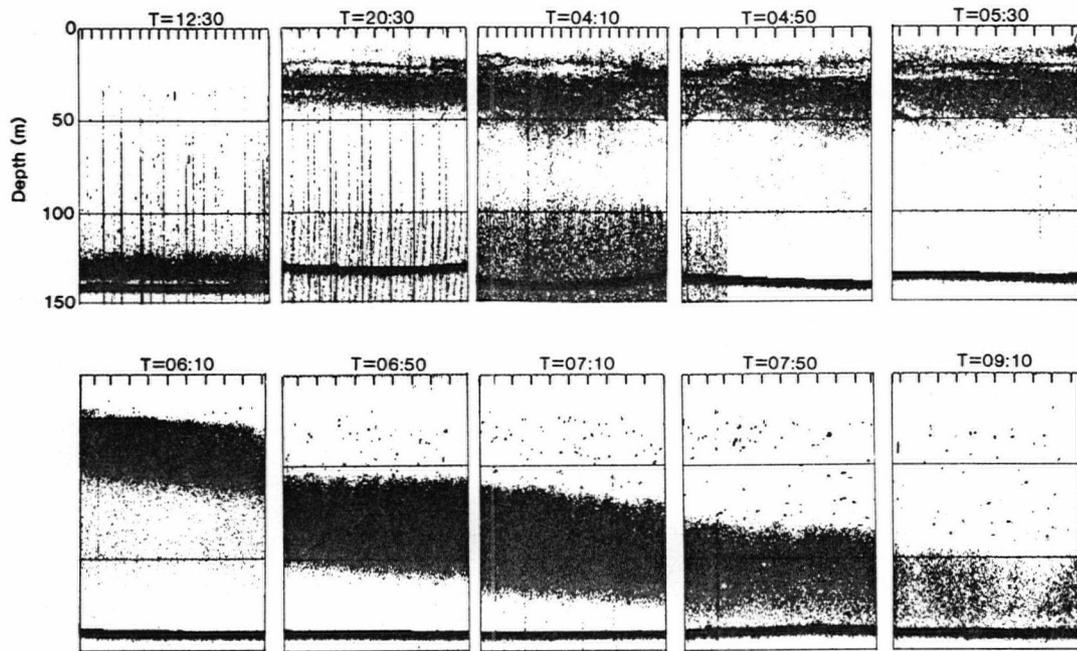


Figure 7-4. Diel echogram sequences and scaled echo count data for Kootenay Lake hydroacoustic transects on Sep. 25-26, 1987.

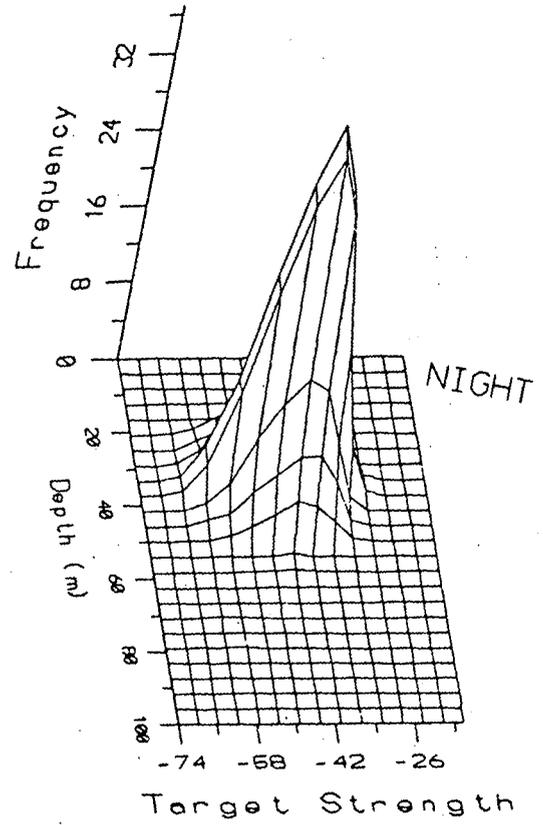
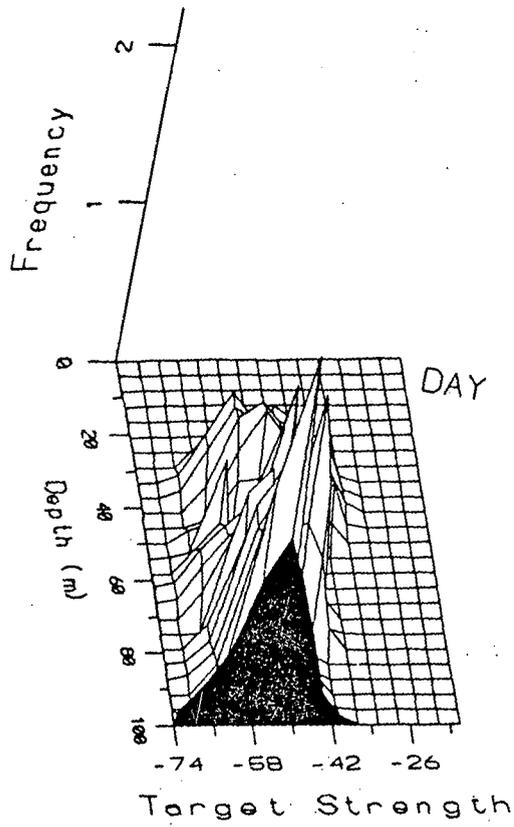


Figure 7-5. Target strength distribution within the water column of Kootenay Lake during day and night transects undertaken Sep. 25-26, 1987.

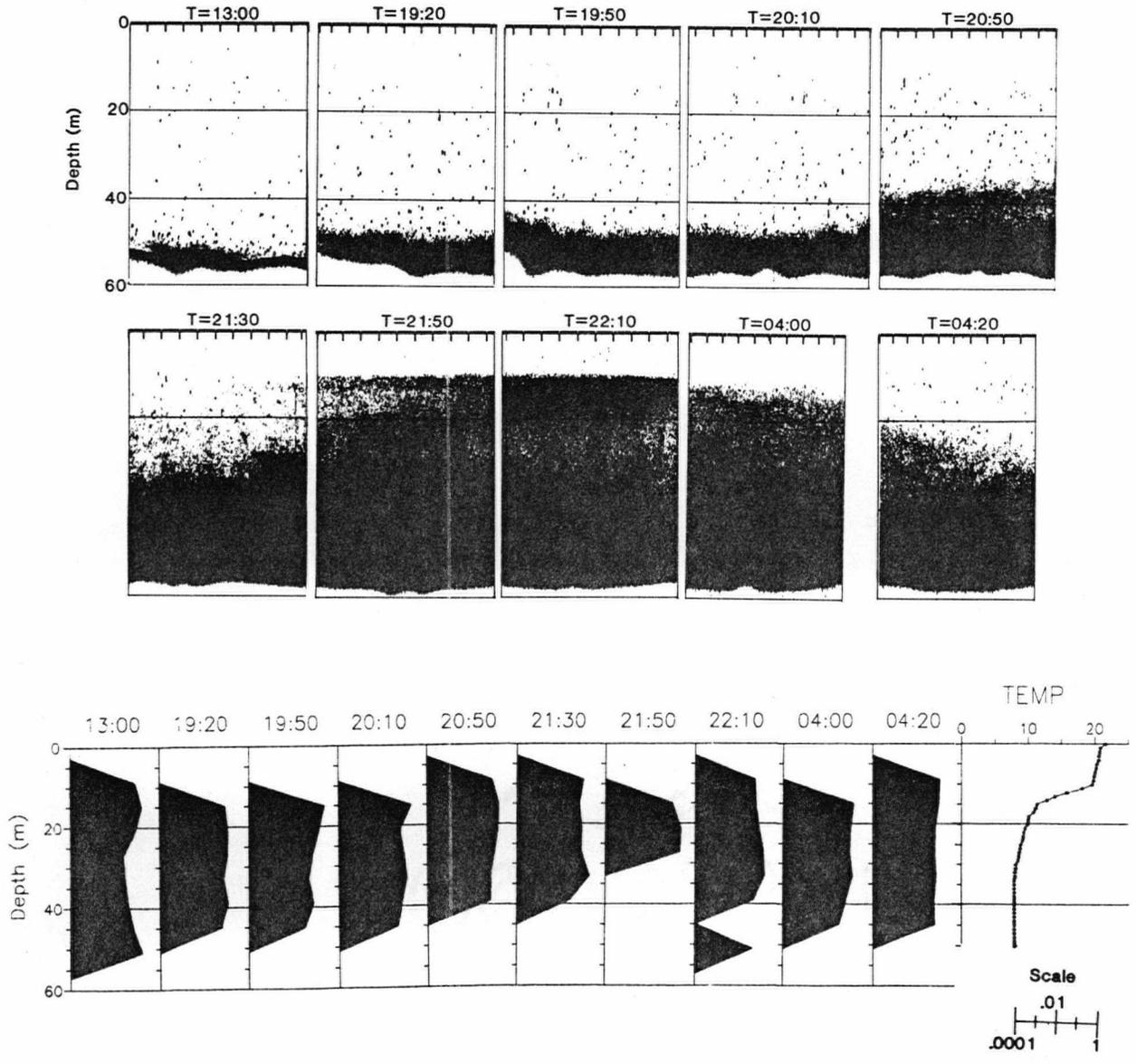


Figure 7-6. Diel echogram sequences and scaled echo count data for Skaha Lake hydroacoustic transects on July 23-24, 1987.

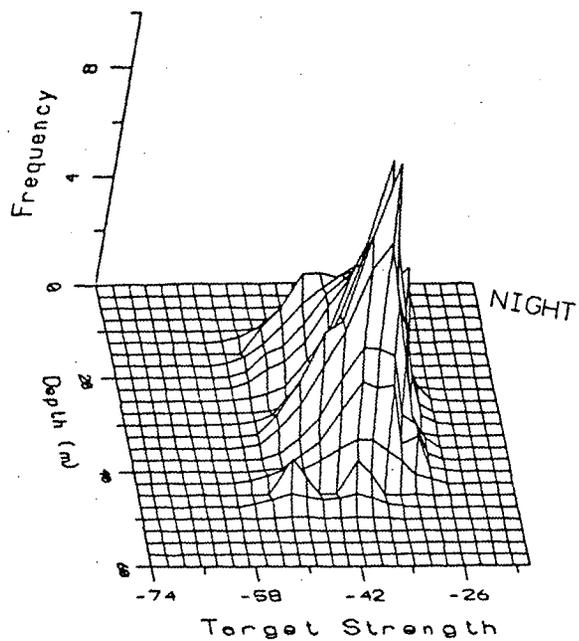
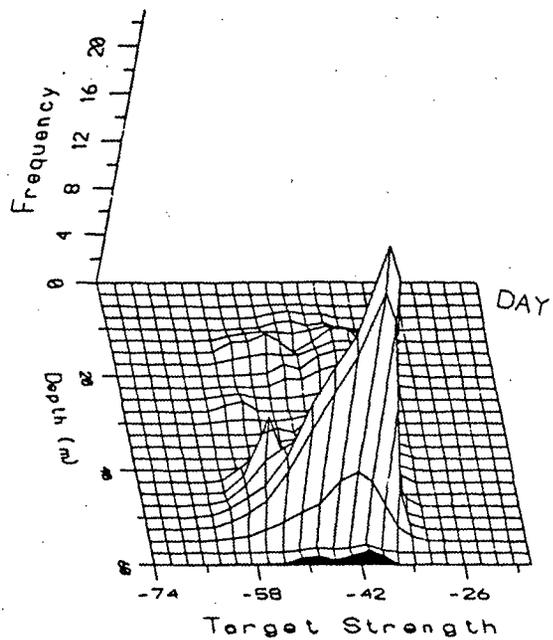


Figure 7-7. Target strength distribution within the water column of Skaha Lake during day and night transects undertaken July 23-24, 1987.

in the vicinity of the thermocline, provided these were not out-weighted by the additional predation risk from visual-feeding piscivores in shallow euphotic waters.

Kokanee within Kootenay and Skaha Lakes behaved differently from those within Okanagan. Kootenay fish were largely absent from the upper 25 m of the water column during daylight periods, and all kokanee size classes appeared to migrate vertically to some extent. There were no obvious diel changes in vertical distribution of kokanee within Skaha, suggesting a static diel vertical distribution. Sub-adult kokanee within Nicola (Northcote et al. 1964) and Pend Oreille (Rieman and Bowler 1980) lakes undertook reversed diel vertical migrations. This observed geographical variation suggests that kokanee diel vertical migratory behavior is variable from lake-to-lake, presumably in response to local selection pressures.

Sockeye salmon shift their diel vertical migratory behavior as they develop. Following their year-long pelagic zone residency (when diel vertical migration is well-developed), sockeye within Babine Lake become surface-oriented and are observable in shallow surface waters by day (Johnson and Groot 1963). During their coastal marine out-migration, sockeye maintain a shallow vertical distribution and are vulnerable to surface-operated purse seine devices during daylight hours (Groot and Cooke 1987). After reaching their marine nursery areas, sub-adult sockeye again undertake diel vertical migrations (Manzer 1964) which are presumably maintained until the fish commence their return migration. Within coastal waters, returning adult sockeye are distributed in shallow waters (Quinn and terHart 1987). It is likely that when sockeye are actively migrating between freshwater and marine sub-habitats, navigation and orientation requirements over-ride selective pressures associated with diel vertical migration.

VIII. Coevolution of Vertical Migratory Behavior in *O. nerka* and Zooplankton Prey

Both planktivores and zooplankton often undertake diel vertical migrations. Zooplanktonic diel vertical migrants can achieve survival benefits by reducing spatial and visual contact with their visual-feeding planktivore predators (Zaret and Suffern 1976; Stich and Lampert 1981; Gliwicz 1986A). In arguing that vertical migration of zooplankton in alpine lakes is an adaptation to predation pressure, Gliwicz (1986A) presented evidence showing that vertical migration is often absent in lakes devoid of planktivorous fishes. The introduction of planktivores to such lakes can rapidly deplete or exterminate populations of zooplankton that have not evolved vertical migratory behavior.

A zooplankton survival benefit through diel vertical migration is only possible, however, if the predominant planktivore preys on zooplankton during illuminated portions of the diel cycle. Where visual-feeding planktivores undertake diel vertical migrations, this will preclude a standard vertical migration by zooplankton as an effective predator avoidance mechanism. Alternatively, in lakes where planktivore diel vertical migrations are reversed there should be strong selective pressure for zooplankton to migrate vertically.

These predictions were tested by comparing the diel vertical migratory behavior of zooplankton in several lakes where fish vertical migration studies were undertaken. This section reviews available information on juvenile sockeye and kokanee feeding habits and then relates the diel vertical movements of the zooplankton to those of the predominant planktivore.

Juvenile sockeye and kokanee feeding behavior

Juvenile sockeye and kokanee dietary observations, both published and unpublished, are summarized in Table 8-1. Sockeye and kokanee are largely planktivorous, although both occasionally exploit juvenile and adult stages of insects. Crustacean zooplankton, including most of the

Table 8-1. Occurrence of prey in the stomach contents of juvenile sockeye and kokanee within northwest Pacific lakes.

LAKE	CLADOCERA				COPEPODA				ROTIFERA	MYCIDACEA		REFERENCE	
	<i>Bosmina</i>	<i>Daphnia</i>	<i>Diaphanosoma</i>	<i>Holopedium</i> <i>Leptodora</i>	<i>Cyclops</i>	<i>Diaptomus</i>	<i>Epischura</i>	<i>Heterocope</i> unidentified nauplii	<i>Asplanchna</i>	<i>Neomysis</i>	<i>Mysis</i>		Insecta Arachnida
A. SOCKEYE LAKES													
Babine	x	x					x					x	Narver (1970)
Babine		x			x	x	x	x				x	McDonald (1973)
Babine	x	x			x	x	x	x					Rankin (1977)
Cultus	x	x			x	x							Ricker (1937)
Fraser	x	x			x	x		x					¹ DFO (unpublished)
Frazer	x	x											Kyle et al (1988)
Great Central	x	x	x		x	x	x					x	Barracough ¹ / Robinson (1972)
Harrison	x				x								DFO (unpublished)
Iliamna	x				x			x					Hoag (1972)
Lakelse	x				x	x							McMahon (1948)
Owikeno		x			x	x			x			x x	Chernoff (1971)
Pitt	x	x			x								DFO (unpublished)
Quesnel	x	x			x								DFO (unpublished)
Shuswap	x	x			x	x		x					DFO (unpublished)
Stuart	x	x			x	x							DFO (unpublished)
Takla	x	x			x	x							DFO (unpublished)
Trembleur	x	x			x	x		x					DFO (unpublished)
Washington	x	x	x		x	x	x			x		x	Woodey (1972)
Washington	x	x			x	x	x						Doble ¹ / Eggers (1978)
B. KOKANEE LAKES													
Kootenay								x				x	Northcote (1972)
Nicola		x		x	x	x						x	Northcote ¹ / Lorz (1966)
Okanagan								x				x	² BCFW (unpublished)
Pend Oreille	x	x	x		x	x	x					x x	Rieman ¹ / Bowler (1980)

1. Department of Fisheries and Ocean, Cultus Lake Laboratory

2. B.C. Fish and Wildlife Branch, Pentlcton Laboratory

predominant cladocera and copepods, form the basis of sockeye and kokanee diets in most lakes. Large bodied cladocerans, notably *Daphnia*, are heavily exploited by juvenile sockeye within many of the interior Fraser system lakes, including Cultus, Fraser, Quesnel, Shuswap, Takla, and Trembleur (Dept. of Fisheries and Oceans, Cultus Lake Laboratory, unpublished data). Rotifera are noticeably absent from sockeye and kokanee diets, except for *Asplanchna* which has been recorded from the stomach contents of sockeye within Owikeno Lake (Table 8-1).

Variations, both spatial and temporal, have been recorded in the diets of sockeye within their nursery lakes. For example, Narver (1970) compared juvenile sockeye feeding behaviour within Babine Lake off Nine Mile Creek (northern basin) with those feeding off Pierre Creek (main basin). While *Heterocope septentrionalis*, *Daphnia longispina*, and *Bosmina coregoni* were predominant food of sockeye off Nine Mile Creek, adult insects (mainly Homoptera and Diptera) supplanted the former 3 zooplankters as the predominant food off Pierre Creek. Stomach analysis of main basin fry by McDonald (1973) also indicated the importance of *Daphnia* and *Heterocope* in the diet, as well as *Diaptomus*. Rankin's (1977) analysis showed that *Cyclops* were also eaten, especially in the northern part of the main arm. Within Babine Lake sockeye fry feeding habits also shift seasonally over time. Between July and September, the importance of *Heterocope* in the diet decreased, while the importance of *Bosmina* and especially *Daphnia* increased (Narver 1970; McDonald 1973). By October, sockeye shifted back to feeding on *Heterocope* (McDonald 1973). These observations suggest that all of the predominant crustacean zooplankton species within Babine Lake can be considered as potential sockeye prey organisms, but their relative importance shifts, probably in response to local and seasonal differences in abundance.

Barracough and Robinson (1972) have also recorded diel shifts in zooplankton feeding by juvenile sockeye within Great Central Lake. Over a 24 hour period in June of 1970, *Epischura*, *Daphnia*, *Cyclops*, and *Bosmina* all contributed substantially to the juvenile sockeye diet. However, the relative contribution of the four zooplankters to the diet shifted markedly over the diel cycle. These variations were probably due to diel shifts in predation rates.

Stomach analyses by Narver (1970), Barracough and Robinson (1972), McDonald (1973), and Doble and Eggers (1978) suggest that most zooplankton prey are captured during brief crepuscular foraging episodes. Within Lake Washington, sockeye feeding occurs during a single dusk

feeding period (Doble and Eggers 1978), while in other lakes, sockeye feed for brief periods both at dusk and dawn (Narver 1970; Barraclough and Robinson 1972). Feeding occasionally occurs during other portions of the diel cycle, notably on *Heterocope septentrionalis* at depth during daytime periods within Babine Lake, and also on several species of zooplankton in surface waters on calm, clear moon-lit nights (Narver 1970).

Sockeye juveniles are sufficiently abundant within their nursery lakes to exert a cropping effect on the zooplankton community. Examples include Babine Lake where zooplankton biomass is inversely related to sockeye biomass (Johnson 1961), and also Frazer Lake, where zooplankton community changes coincided with the establishment of a sockeye run over a 35 year period (Kyle et al. 1988). Moreover, it has been observed that sockeye growth rates are density-dependent within several systems including Babine (Johnson 1961), Owikeno (Ruggles 1966), and Frazer (Kyle et al. 1988).

In addition to cladocera and copepods, kokanee also feed heavily on *Mysis relicta* in lakes where they are present (Table 8-1). Analysis of kokanee stomach contents obtained from anglers on Okanagan Lake during May and June of 1987 and 1988 (B.C. Fish and Wildlife Branch, Penticton Laboratory, unpublished data) showed that small kokanee between 220-270 mm fork length (n=34) fed exclusively on microcrustacea, while those between 340-540 mm fork length (n=49) fed exclusively on *Mysis*. These data suggest that kokanee shift their feeding behavior as they develop, switching from microcrustacea to *Mysis* at a fork length of approximately 300 mm. Similar ontogenetic shifts in *Mysis* exploitation by kokanee over 300 mm also occur in Kootenay Lake (Northcote 1973).

The preceding review suggests that juvenile sockeye and kokanee both exploit the predominant microcrustacea within the limnetic zone of their nursery lakes. Large bodied zooplankters, particularly cladocerans, are selectively acquired where they are present. Juvenile sockeye are sufficiently numerous that they can affect zooplankton community structure. Lastly, in lakes where *Mysis* are present, kokanee apparently switch from feeding on microcrustacea to feeding on *Mysis* at an intermediate body size of about 300 mm.

Diel vertical movements of zooplankton in sockeye and kokanee lakes

Possible migration strategies for zooplankton in the presence of a vertically migrating planktivore were considered by Clark and Levy (1988). Three possible strategies were described and are diagrammed in Fig. 8-1. The first strategy ([1] on Fig. 8-1) involved refraining from vertical migration altogether, spending the entire 24 h period in surface waters and facing the risk of predation for brief intervals at dawn and dusk. Reversed diel vertical migration ([2] on Fig. 8-1) would be an effective strategy if the zooplankton was able to pass quickly through the zone of vertically ascending planktivores. A third strategy ([3] on Fig. 8-1) was for the zooplankton to undertake diel vertical migration, spending the day in deep water beneath the planktivore, and migrating to feed in shallow water at night, after the planktivore had ascended. Such behavior would largely evade the planktivore, but would also reduce considerably the time available for feeding in shallow water.

The majority of zooplankton in the sockeye lakes studied were evidently non-migratory in shallow surface waters. Such was the case for all of the dominant crustacean zooplankton species within Cultus, Quesnel and Shuswap Lakes (Fig. 6-3). Juvenile sockeye within these 3 lakes undertook diel vertical migrations, and occurred in dense numbers in 2 of the systems (Quesnel in 1986, Shuswap in 1987). Shuswap zooplankton diel vertical movements were compared in the vicinity of the mouth of the Adams River (an area of dense juvenile sockeye numbers) both in June and September of 1987, corresponding to respective time periods before and after juvenile sockeye had recruited into the pelagic zone of the lake. There was no evidence for zooplankton diel vertical migration at either of these time periods (Fig. 6-3C).

Whereas the majority of crustacean zooplankton were non-migratory within Babine Lake (Fig. 6-2), the cladoceran *Bosmina coregoni* was a notable exception and undertook reversed diel vertical migrations on both of the sampling dates considered. The same species was a non-migrator in the three Fraser system sockeye lakes (Fig. 6-3). Narver (1970) has also documented reversed diel vertical migrations of *Bosmina* within Babine Lake, and also well-developed diel vertical migrations by the large bodied (2-3 mm) predatory calanoid, *Heterocope septentrionalis* (Fig. 6-1). [The absence of *Heterocope* from zooplankton pump samples during the present study was probably a sampling artifact - see Section VI].

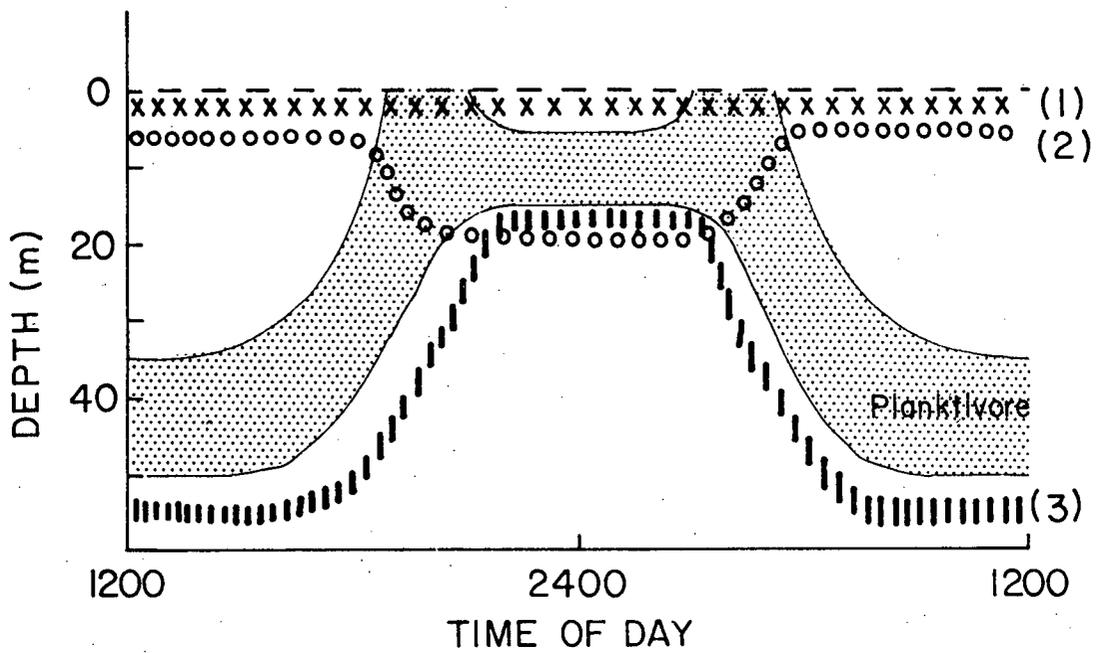


Figure 8-1. Three possible diel migratory patterns of zooplankton in relation to the diel movements of a predominant planktivore.

The presence of a planktivore which undertakes reversed diel vertical migrations should exert a strong selective pressure for zooplankton to avoid the euphotic zone during daylight periods. This prediction was tested by comparing the diel vertical movements of zooplankton within Nimpkish Lake, a lake where juvenile sockeye vertical migrations are on occasion reversed (Section VII), and where limnetic sticklebacks occupy shallow pelagic areas. Within Nimpkish Lake, most of the dominant zooplankton, including *Bosmina*, *Diatomus*, and *Daphnia*, all undertook diel vertical migrations (Fig. 8-2). Two genera (*Epishura* and *Cyclops*) were also distributed in shallower water at night than during the day (Fig. 8-2); however, diel movements of the latter two genera were not as pronounced as those of the former.

These field observations suggest that the diel vertical movements of zooplankton prey and their planktivorous predators are closely coupled. Zooplankton are evidently static in lakes where sockeye exhibit diel vertical migration. One exception to this pattern occurs in Babine Lake where *Heterocope* and *Bosmina* migrate vertically in opposite directions. It is suggested that in this lake, the *Bosmina* reversed vertical migrations are a response to *Heterocope* diel vertical movements (see Discussion below). Within Nimpkish Lake, where limnetic sticklebacks are present and where sockeye vertical migrations are periodically reversed, zooplankton vertical migrations are well developed.

Hydroacoustic surveys indicated the presence of high densities of vertically migrating *Mysis relicta* populations within Okanagan, Skaha and Kootenay Lakes, the three kokanee lakes that were surveyed. A diel echogram sequence from Okanagan Lake is shown in Fig. 8-3A. Mysids within this lake are concentrated between 90 - 125 m by day, and rise to within 15 m of the surface at night. The upper limit on the nocturnal distribution of *Mysis* is apparently set by temperature and there was a discrete discontinuity in the distribution pattern which occurred at the thermocline (Fig. 8-3B). Similar *Mysis* nocturnal distribution patterns were observed within Okanagan on three additional sampling dates, as well as within Kootenay and Skaha lakes (Figs. 7-4 and 7-6).

Compared to the vertically migrating kokanee within Okanagan Lake (Section VII), mysids ascended into shallow waters after the kokanee had ascended, and descended at dawn prior to the kokanee descent (Fig. 8-3). The rate of *Mysis* vertical ascent and descent was rapid, and there were detectable differences in vertical distribution even within the 10 minute hydroacoustic

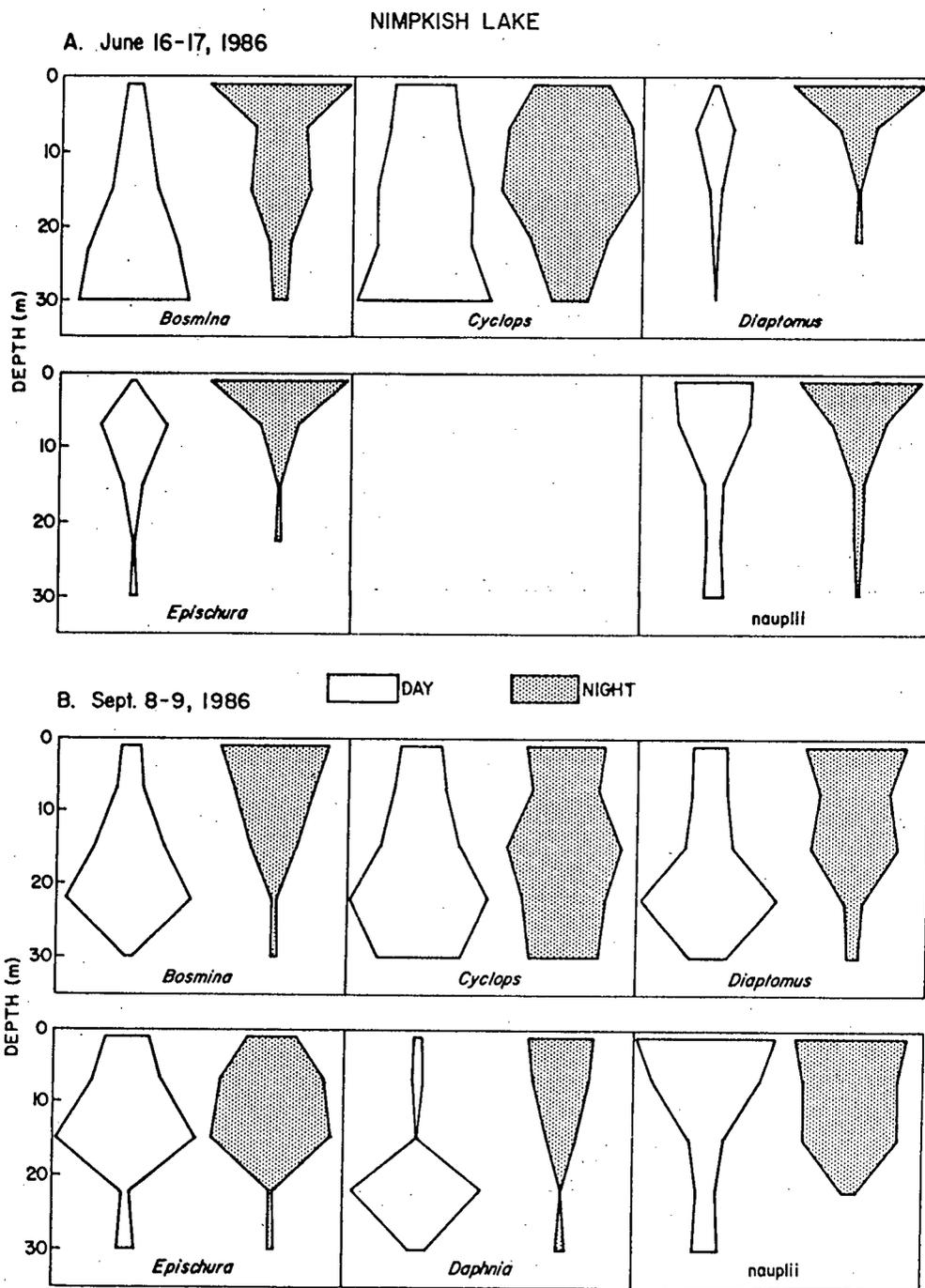


Figure 8-2. Day and night vertical depth profiles of the predominant zooplankton species captured in plankton pump samples from Nimpkish Lake on 2 dates during 1986.

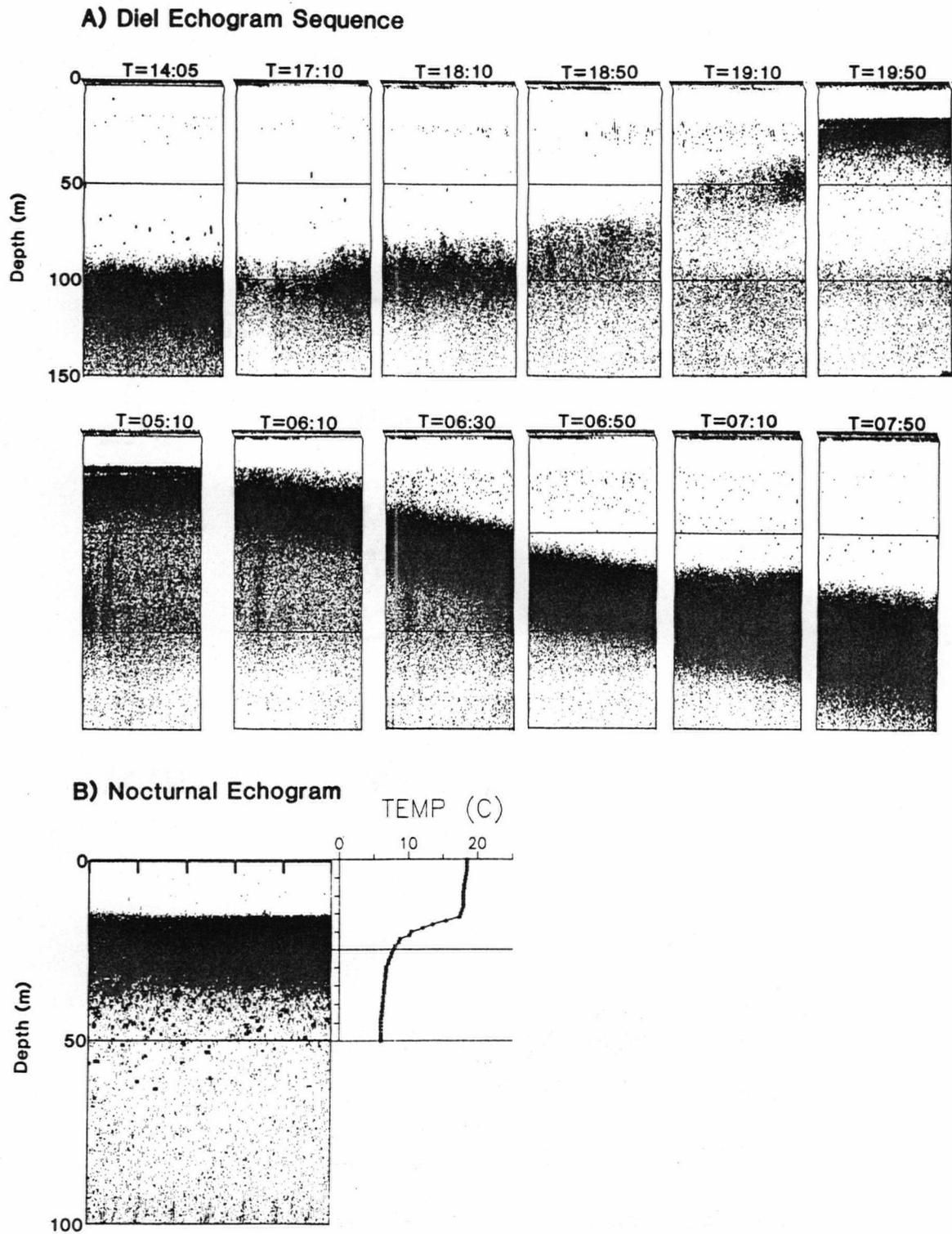


Figure 8-3. A) Diel vertical migration of *Mysis relicta* within Okanagan Lake on Sep. 30-Oct. 1, 1987, and B) nocturnal mysid distribution in relation to the temperature profile.

transect period (e.g. T=18:50 and T=06:30 on Fig. 8-3A). It would appear that the *Mysis* vertical migrations are timed so that the animals minimize contact with their kokanee predators, many of which are also vertical migrators. *Mysis* therefore provide an example of an evasive zooplankter which migrates vertically so as to minimize contact with their planktivorous predators (strategy [3] on Fig. 8-1). The result is that *Mysis* have minimal spatial overlap with kokanee and are largely unavailable as a food item for much of the diel cycle.

Discussion

Coevolution is defined as "...the joint evolution of two (or more) taxa that have close ecological relationships but do not exchange genes, and in which reciprocal selective pressures operate to make the evolution of either taxon partially dependent upon the evolution of the other." (Pianka 1974, p.175). The main conclusion from the preceding analysis is that coevolution has occurred in the vertical migratory behavior of zooplankton and their planktivorous predators. In the presence of non-migratory planktivores, freshwater zooplankton commonly undertake diel vertical migrations (Zaret and Suffern 1976; Stich and Lampert 1981; Gliwicz 1986A). However, in the presence of a vertically migrating planktivore like juvenile sockeye salmon, there is no selective advantage for zooplankton to migrate vertically, and the animals maintain a static distribution within the euphotic zone. *Daphnia longispina* for example, is a cladoceran which migrates vertically within Lake Kvernvatn, Norway, in order to balance predator avoidance and the risk of starvation (Johnsen and Jakobsen 1987). The same species maintains a shallow static distribution within Babine Lake (Figs. 6-1 and 6-2) where its main predator, juvenile sockeye salmon, is a diel vertical migrator.

The cladoceran *Bosmina longirostris* serves as prey for both juvenile sockeye (Table 8-1) as well as the predatory contact-feeding calanoid, *Heterocope septentrionalis* (O'Brien and Schmidt 1979). The absence of *Bosmina* from arctic ponds has been attributed to predator-induced mortality from *Heterocope* (Luecke and O'Brien 1983). Within sockeye lakes, three different vertical migratory patterns were evident in *Bosmina coregoni*. Depending upon the lake, this cladoceran was either static, a vertical migrator, or a reversed vertical migrator. The animals were static

within the Fraser system lakes where sockeye migrated vertically. Within Nimpkish Lake where sockeye vertical migrations were reversed, *Bosmina* undertook vertical migrations. Within Babine Lake where vertically migrating *Heterocope septentrionalis* were present, *Bosmina* was a reversed vertical migrator, presumably in order to minimize its spatial overlap with the copepod. It therefore appears that a tight coupling exists in the vertical migratory patterns of zooplankton and planktivores within sockeye salmon lakes.

It is likely that the vertical migrations of *Heterocope septentrionalis* within Babine Lake are a response to predation by juvenile sockeye. *Heterocope* within this lake probably adopt a strategy of entering shallow surface waters only under extreme light levels (strategy [3] on Fig. 8-1) in order to minimize contact with the vertically migrating sockeye juveniles. It is suggested that *Bosmina* within Babine undertake reversed vertical migrations in order to avoid the vertically migrating *Heterocope*. *Bosmina* are also susceptible to predation by sockeye juveniles, however, *Heterocope* probably exerts a more severe predation mortality than sockeye, and provides the selective pressure for *Bosmina* to avoid surface waters at night. Similar conclusions concerning the reversed vertical migration behavior of *Bosmina* were reached by Zaret (1980, p.77).

The findings of the present study suggest that freshwater zooplankton will adopt a static vertical distribution in the presence of vertically migrating planktivores. Pijanowska and Dawidowicz (1987) attributed the lack of vertical migration in *Daphnia* to a homogeneous seston distribution within Lakes Mikolajske and Majcz and concluded (p. 181): "... under conditions of homogeneously distributed food, there is no necessity to pay the energetic costs of diurnal vertical migration. Under these circumstances fish predation pressure does not promote migratory behavior and a stable pattern of vertical distribution results." However, two out of the three planktivores present within the lakes (*Coregonus albula* and *Osmerus eperlanus*) are diel vertical migrators (Northcote and Rundberg 1970; Dembinski 1971) and an alternative interpretation is that *Daphnia* within these two lakes are non-migratory because their planktivorous predators undertake diel vertical migrations. Under these circumstances, there would be no selective advantage for *Daphnia* to migrate vertically.

Mysis relicta undertook large amplitude vertical migrations within Okanagan, Skaha and Kootenay Lakes, effectively minimizing their encounters with kokanee. It is apparent that *Mysis*

within these lakes are sensitive to extremely low light intensities and vertical migration behavior in this species likely contributes to avoidance of visual predators. Similar vertical migration behavior is widespread in other *Mysis* populations (Beeton and Bowers 1982).

IX. Summary: The Selective Advantage of Diel Vertical Migration Behavior in *O. nerka*

In order for diel vertical migration behavior to evolve in sockeye salmon, selective benefits must be achieved by migrants which compensate for the reduced zooplankton foraging opportunities that accompany a daytime descent into the water column. Sockeye grow at rates substantially less than the maximum possible within their freshwater nursery lakes (Brett 1983). Since sockeye marine survival rates are positively correlated to smolt size at the time of downstream migration (Foerster 1954), there must be a selective advantage achieved by diel vertical migrants during their lake residency which compensates for the reduced opportunity for freshwater growth.

I interpret diel vertical migration in juvenile sockeye salmon as an adaptive compromise between foraging on zooplankton, minimizing exposure risk to visual-feeding piscivores, and promoting (nocturnal) metabolic efficiency. The mechanism underlying this trade-off is the diel change in the relative vulnerability of sockeye juveniles and zooplankton under different light intensities (Clark and Levy 1988). By ascending into shallow portions of the water column under low light conditions during crepuscular periods, sockeye achieve a measure of protection from their visual-feeding predators. This risk averse behavior results in reduced zooplankton foraging, and a reduced sockeye growth rate, compared to a continual occupation of the euphotic zone. Due to their potential susceptibility to visual-feeding piscivores, daytime occupants of the euphotic zone would suffer a high predation rate.

Although sockeye metabolize relatively inefficiently in the cold hypolimnion during hours of daylight, metabolic efficiency is optimized during nocturnal periods by associating with temperatures that provide maximum growth under restricted ration levels. Cyclic temperature fluctuations may also stimulate growth rate; however, such bioenergetic considerations are by themselves insufficient to account for the diel timing of vertical migration.

Major adjustments to diel vertical migratory behavior are also possible, and there is evidence from Nimpkish and Chilko lakes (this study) as well as from Lake Tustumena (Thorne 1983B),

that juvenile sockeye radically alter their diel migratory behavior under certain conditions. The observed relaxation of diel vertical migration behavior within Chilko and reversal of movement within Nimpkish suggest that juvenile sockeye are locally adapted to the particular conditions within their lake nurseries. The diel pattern of juvenile sockeye migration can evidently evolve in response to local selective pressures. Evidence for locally adapted differences in juvenile sockeye migratory behavior has been provided by Raleigh (1967) and Brannon (1972) who demonstrated that rheotactic responses of recently emergent juvenile sockeye served to facilitate lake-finding by the fish.

The sensory mechanism which controls diel vertical migration in juvenile sockeye is a simple one involving light and temperature. Daytime depth position and the diel timing result from the sockeye light response, while nocturnal depth position is due to thermoselection behavior. There is evidence that these light and temperature responses are themselves adaptive for juvenile sockeye. The isolumes associated with sockeye daytime depth (Fig. 6-7) are functionally related to the visual foraging capabilities of two of the dominant piscivores (Fig. 6-8). By associating with such low isolumes, the fish may be nearly invisible to their major predators. Likewise, the temperatures where sockeye concentrate at night (Fig. 6-5A) serve to maximize the metabolic efficiency of the animals (Brett et al. 1969).

The potential rate of change of diel vertical migration behavior depends whether the behavior is flexible (Dill 1983) or fixed (Sih 1987). Unlike bluegill sunfish which routinely encounter their bass predators in the littoral zone of a lake, pelagic planktivores like juvenile sockeye would only rarely encounter their predators in a lake's pelagic zone. Sih (1987) has argued that diel migratory behavior could be genetically fixed due to the high cost (potential death) of gathering information about predation intensity within the euphotic zone. Gilliam (1982) has suggested that habitat selection in aquatic animals which cannot monitor their predators visually would depend upon an evolved affinity for physical structure. Due to its critical importance in fish feeding behavior, the evolved sockeye light response may serve as the physical variable which directly controls the trade-off between zooplankton foraging and predator avoidance.

In sockeye lakes with different zooplankton and piscivore densities, it is easy to conceive how minor changes in the sockeye light response could affect the diel time budget and alter the balance

between foraging and predator avoidance. Juvenile sockeye could achieve a risk-prone vertical migration merely by associating with a higher light intensity. Conversely, they could achieve a risk-averse vertical migration by maintaining themselves at lower intensity isolumens. The specific sockeye light response would be affected by the relative zooplankton concentration and piscivore density, as well as the particular visual acuity of the predominant piscivore.

During the 1930's, a program of predator removal was implemented at Cultus Lake which resulted in more than a 3-fold increase in juvenile sockeye within-lake survival rates (Foerster and Ricker 1941). Predator control resulted in an increased number of seaward migrating smolts due to the reduced piscivore mortality. Interestingly, not only were the migrating smolts more numerous, but also, they were among the largest on record, and fish production calculations by Ricker and Foerster (1948) document a higher production rate of juvenile sockeye during years of predator control. Since there were no obvious changes in lake productivity during the predator control years, I speculate that juvenile sockeye relaxed their diel migratory behavior in the absence of piscivore predation pressure. If diel migratory behavior is genetically fixed in juvenile sockeye, this implies that there was (and probably still is) more than one vertical migratory phenotype present in the Cultus Lake population.

In many zooplanktonic species, adult forms migrate vertically, while the juvenile stages (e.g. nauplii) are static in shallow water (McLaren 1963). In contrast, juvenile kokanee from Okanagan Lake undertook diel vertical migrations, while older size-classes maintained a surface orientation. This behavioral shift might be accomplished by an altered light preference, with older stages associating with higher light intensities than younger stages. The ontogenetic shift in vertical migratory behavior is consistent with recent theories on fish foraging under mortality risk in size-structured populations (Gilliam 1982; Werner and Gilliam 1984; Clark and Levy 1988).

Results from this study rule out obvious single factor explanations for the selective advantage of vertical migration in *O. nerka*. While multifactor hypotheses are more difficult to test than traditional single factor explanations, they provide a more realistic interpretation of vertical migration behavior. Several recent studies on zooplankton also interpret vertical migration as an evolutionary compromise or "trade-off" between minimizing predation risk from visual foragers and exploiting surface food resources (Giguere and Northcote 1987; Johnsen and Jakobsen 1987; Vuorinen 1987).

Two recent review articles (Kerfoot 1985; Bayly 1986) conclude that vertical migrations in zooplanktonic grazers are related to the antagonistic selective pressures of maximizing foraging intake and avoiding visual predators within surface waters.

Comparisons of sockeye and zooplankton migratory patterns suggest that a tight coupling exists in the vertical migratory behavior of planktivores and zooplankton. In most sockeye lakes where the fish migrate vertically, zooplankton are static. In Nimpkish Lake where sockeye diel migrations can be reversed, zooplankton are active vertical migrators. It is therefore necessary to analyze the respective diel vertical movements of all trophic levels when considering the diel migratory behavior of a particular species. Fish can exert important "top-down" influences on aquatic communities (Northcote 1988). The present study provides an example of piscivore influence in modifying prey (planktivore) behavior, with consequent influences on lower zooplankton trophic levels.

It is important, from both theoretical and practical perspectives, to gain an improved understanding of the factors which regulate juvenile sockeye production in pelagic environments. The recent analysis by McQueen et al. (1986) considers the relative importance of both "bottom-up" and "top-down" processes in structuring pelagic aquatic communities. Evans et al. (1987) concluded that both "bottom-up" and "top-down" control processes operate in temperate fish communities and are nested such that overall productivity is determined by energy inputs, nutrients, edaphic factors, and habitat variables, but that the distribution of production by species is strongly influenced by interactions between species. Piscivores can evidently modify the vertical migratory patterns of planktivores, which in turn, can affect the migratory behavior of zooplankton. These behavioral interactions which extend across three (or more) trophic levels undoubtedly have important consequences for the pelagic community.

X. References

- Alexander, R.M. 1971. Swimbladder gas secretion and energy expenditure in vertically migrating fishes, p. 75-86. In G.B. Farquar [ed.] Proceedings of an International Symposium on Biological Sound Scattering in the Ocean. Maury Center for Ocean Science, Dep. of the Navy, Washington, DC.
- Alexander, R.M. 1972. The energetics of vertical migration by fishes. Symp. Soc. Exp. Biol. 26:273-294.
- Andersen, B.C., and D.W. Narver. 1968. Techniques for sampling zooplankton and underyearling sockeye salmon in the midwater of large lakes. Fish. Res. Board Can. MS Rep. 1009:5 p.
- Backus, R.H.R., R.C. Clarke, and A.S. Wing. 1965. Behavior of certain marine organisms during the solar eclipse of July 20, 1963. Nature 205:989-991.
- Backus, R.H., J.E. Craddock, R.L. Haedrich, D.L. Shores, J.M. Teal, A.S. Wing, G.W. Mead and W.D. Clarke. 1968. *Ceratoscopelus maderensis*: peculiar sound-scattering layer identified with this myctophid fish. Science 160:991-993.
- Barham, E. 1966. Deep scattering layer and composition: observations from a diving saucer. Science 151:1399-1403.
- Barracough, W.E., and D. Robinson. 1972. The fertilization of Great Central Lake III. Effect on juvenile sockeye salmon. Fish. Bull., U.S. 70:37-48.
- Bayly, I.A.E. 1986. Aspects of diel vertical migration in zooplankton, and its enigma variations. p. 349-368. In DeDecker, P. and W.D. Williams [ed.] Limnology in Australia. Monographiae Biologicae 61: 671p.
- Beamish, F.W.H. 1966. Vertical migration of demersal fish in the Northwest Atlantic. J. Fish. Res. Board Can. 23:109-139.
- Beeton, A.M., and J.A. Bowers. 1982. Vertical migration of *Mysis relicta* Lovén. Hydrobiologia 93:53-61.
- Begg, G.W. 1976. The relationship between the diurnal movements of some of the zooplankton and the sardine *Limnothrissa miodon* in Lake Kariba, Rhodesia. Limnol. Oceanogr. 21:529-539.
- Biette, R.M., and G.H. Geen. 1980. Growth of underyearling sockeye salmon (*Oncorhynchus nerka*) under constant and cyclic temperatures in relation to live zooplankton ration size. Can. J. Fish. Aquat. Sci. 37:203-210.
- Bilton, H.T., and G.L. Robins. 1973. The effects of starvation and subsequent feeding on survival and growth of Fulton Channel sockeye salmon fry (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 30:1-5.
- Blaxter, J.H.S. 1970. 2 Light. 2.3 Animals. 2.3.2 Fishes, p. 213-320. In O. Kinne [ed.] Marine Ecology. Part I. Wiley Interscience, London.

- Blaxter, J.H.S. 1974. The role of light in the vertical migration of fish - a review, p.189-210. *In* G.C. Evans, R. Bainbridge, and O. Rackham [ed.] Light as an Ecological Factor: II. British Ecological Society 16th Symposium. Blackwell Scientific Publications. Oxford, U.K.
- Blaxter, J.H.S. 1979. The effect of hydrostatic pressure on fishes, p.369-386. *In* M.A. Ali [ed.] Environmental Physiology of Fishes. Plenum Press. New York. 686p.
- Blaxter, J.H.S. 1985. The herring: a successful species? *Can. J. Fish. Aquat. Sci.* 42 (Suppl. 1):21-30.
- Blaxter, J.H.S., and R.I. Currie. 1967. The effect of artificial lights on acoustic scattering layers in the ocean. *Symp. Zool. Soc. Lond.* 19:1-14.
- Boden, B.P., and E.M. Kampa. 1967. The influence of natural light on the vertical migrations of an animal community in the sea. *Symp. Zool. Soc. Lond.* 19:15-26.
- Bohl, E. 1980. Diel pattern of pelagic distribution and feeding in planktivorous fish. *Oecologia* 44:368-375.
- Bowman, R.E., and E.W. Bowman. 1980. Diurnal variation in the feeding intensity and catchability of silver hake (*Merluccius bilinearis*). *Can. J. Fish. Aquat. Sci.* 37:1565-1572.
- Brandon, R. 1984. Adaptation and evolutionary theory p.58-82. *In* E. Sober [ed.] Conceptual Issues in Evolutionary Biology. MIT Press. Cambridge. 725p.
- Brannon, E.L. 1972. Mechanisms controlling migration of sockeye salmon fry. *Int. Pac. Salmon Fish. Comm. Bull.* 21:86p.
- Brett, J.R. 1950. The physical limnology of Lakelse Lake, British Columbia. *J. Fish. Res. Board Can.* 8:82-102.
- Brett, J.R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. *J. Fish. Res. Board Can.* 9:265-323.
- Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Board Can.* 21:1183-1226.
- Brett, J.R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am. Zool.* 11:99-113.
- Brett, J.R. 1983. Life energetics of sockeye salmon, *Oncorhynchus nerka*, p.29-63. *In* W.P. Aspey and S.I. Lustick [ed.] Behavioural Energetics: the Cost of Survival in Vertebrates. Ohio State University Press, Columbus, OH.
- Brett, J.R., and J.A. McConnell. 1950. Lakelse Lake sockeye survival. *J. Fish. Res. Board Can.* 8:103-110.
- Brett, J.R., J.E. Shelbourn, and C.T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *J. Fish. Res. Board Can.* 26:2363-2394.

- Buerkle, U. 1987. Estimation of fish length from acoustic target strengths. *Can. J. Fish. Aquat. Sci.* 44:1782-1785.
- Burczynski, J.J. 1982. Introduction to the use of sonar systems for estimating fish biomass. *FAO Fish. Tech. Pap.* 191 Rev. 1:89 p.
- Burczynski, J.J., and R.L. Johnson. 1986. Application of dual-beam acoustic survey techniques to limnetic populations of juvenile sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* 43:1776-1788.
- Cerri, R.D. 1983. The effect of light intensity on predator and prey behaviour in cyprinid fish: factors that influence prey risk. *Anim. Behav.* 31:736-742.
- Chernoff, B.W. 1971. Behaviour of underyearling sockeye salmon related to limnetic zooplankton in Owikeno Lake, British Columbia. *Can. Dep. Fish. For. Fish. Serv.* 1971-4:52p.
- Chisholm, B.A. 1975. An experimental study of nocturnal feeding in the northern squawfish (*Ptychocheilus oregonensis*). B. Sc. Thesis. Dept. of Zoology, The Univ. of British Columbia. 46p.
- Clark, C.W., and D.A. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *Am. Nat.* 131:271-290.
- Colwell, R.K. 1985. The evolution of ecology. *Amer. Zool.* 25:771-775.
- Crowder, L.B., and J.J. Magnuson. 1983. Cost-benefit analysis of temperature and food resource use: a synthesis with examples from the fishes, p. 189-221. *In* W.P. Aspey and S.I. Lustick (ed.) *Behavioural Energetics: Vertebrate Costs of Survival*. Ohio State University Press, Columbus.
- Curio, E. 1973. Towards a methodology of teleonomy. *Experientia* 29:1045-1180.
- Cushing, D.H. 1951. The vertical migration of planktonic Crustacea. *Biol. Rev.* 26:158-192.
- Dembinski, W. 1971. Vertical distribution of vendace *Coregonus albula* L. and other pelagic fish species in some Polish lakes. *J. Fish Biol.* 3:753-769.
- Dickie, L.M., and P.R. Boudreau. 1987. Comparison of acoustic reflections from spherical objects and fish using a dual-beam echosounder. *Can. J. Fish. Aquat. Sci.* 44:1915-1921.
- Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Can. J. Fish. Aquat. Sci.* 40:398-408.
- Dingle, H. 1980. Ecology and evolution of migration, p.1-101. *In* S.A. Gauthreaux, Jr. [ed.] *Animal Migration, Orientation, and Navigation*. Academic Press, New York, NY.
- Doble, B.D., and D.M. Eggers. 1978. Diel feeding chronology, rate of gastric evacuation, daily ration, and prey selectivity in Lake Washington juvenile sockeye salmon (*Oncorhynchus nerka*). *Trans. Am. Fish. Soc.* 107:36-45.

- Dobzhansky, T. 1956. What is an adaptive trait? *Am. Nat.* 90:337-347.
- Eggers, D.M. 1978. Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and predator avoidance. *Limnol. Oceanogr.* 23:1114-1125.
- Ehrenberg, J.E. 1983. A review of *in situ* target strength estimation techniques, p.85-90. In O. Nakken and S.C. Venema [ed.] Selected papers of the ICES/FAO Symposium on fisheries acoustics, Bergen, Norway, 21-24 June 1982. FAO Fish. Rep. 300: 331 p.
- Evans, D.O., B.A. Henderson, N.J. Bax, T.R. Marshall, R.T. Oglesby, and W.J. Christie. 1987. Concepts and methods of community ecology applied to freshwater fisheries management. *Can. J. Fish. Aquat. Sci.* 44(Suppl. 2):448-470.
- Foerster, R.E. 1938. Mortality trend among young sockeye salmon (*Oncorhynchus nerka*) during various stages of lake residence. *J. Fish. Res. Board Can.* 4:184-191.
- Foerster, R.E. 1954. On the relation of adult sockeye salmon (*Oncorhynchus nerka*) returns to known smolt seaward migrations. *J. Fish. Res. Board Can.* 11:339-350.
- Foerster, R.E. 1968. The sockeye salmon, *Oncorhynchus nerka*. *Bull. Fish. Res. Board Can.* 162:422p.
- Foerster, R.E., and W.E. Ricker. 1941. The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus Lake. *J. Fish. Res. Board Can.* 5:315-336.
- Foskett, D.R. 1958. The Rivers Inlet sockeye salmon. *J. Fish. Res. Board Can.* 15:867-889.
- Giguere, L.A., and T.G. Northcote. 1987. Ingested prey increases risks of visual predation in transparent *Chaoborus* larvae. *Oecologia* 73:48-52.
- Gilbert, N., A.P. Gutierrez, B.D. Fraser, and R.E. Jones. 1976. *Ecological Relationships*. W.H. Freeman. Reading.
- Gilliam, J.F. 1982. Habitat use and competitive bottlenecks in size-structured fish populations. Ph.D Thesis. Michigan State Univ., East Lansing, MI. 107p.
- Gilliam, J.F., and D.F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 68:1856-1862.
- Ginetz, R.M., and P.A. Larkin. 1976. Factors affecting rainbow trout (*Salmo gairdneri*) predation on migrant fry of sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Board Can.* 33:19-24.
- Gliwicz, Z.M. 1986A. Predation and the evolution of vertical migration in zooplankton. *Nature (Lond.)* 320:746-748.
- Gliwicz, Z.M. 1986B. A lunar cycle in zooplankton. *Ecology* 67:883-897.
- Goldman, C.R., and A.J. Horne. 1983. *Limnology*. McGraw Hill. New York. 464p.

- Goodlad, J.C., T.W.Gjernes, and E.L.Brannon. 1974. Factors affecting sockeye salmon (*Oncorhynchus nerka*) growth in four lakes of the Fraser River system. J. Fish. Res. Board Can. 31:871-892.
- Gould, S.J., and R.C. Lewontin. 1979. The spandrels of San Marco and the Panglossian Paradigm: a critique of the adaptationist programme. Proc. Roy. Soc. Lond. B 205:581-598.
- Groot, C., and K. Cooke. 1987. Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related? p. 53-60. In H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.
- Hall, D.J., E.E. Werner, J.F. Gilliam, G.G. Mittelbach, D. Howard, C.G. Doner, J.A. Dickerman, and A.J. Stewart. 1979. Diel foraging behavior and prey selection in the golden shiner (*Notemigonus crysoleucas*). J. Fish. Res. Board Can. 36:1029-1039.
- Hamrin, S.F. 1986. Vertical distribution and habitat partitioning between different size classes of vendace, *Coregonus albula*, in thermally stratified lakes. Can. J. Fish. Aquat. Sci. 43:1617-1625.
- Hardy, A.C. 1958. The Open Sea: Its Natural History. Part 1. The World of Plankton. Collins, London.
- Hasler, A.D., and J.R. Villemonte. 1953. Observations on the daily movements of fishes. Science 118:321-322.
- Hemmings, C.C. 1974. The visibility of objects underwater. p. 543-545. In G.C. Evans, R. Bainbridge and O. Rackham [ed.] Light as an Ecological Factor:II. British Ecological Society 16th Symposium. Blackwell Scientific Publications. Oxford, U.K.
- Henderson, M.A., and T.G. Northcote. 1985. Visual prey detection and foraging in sympatric cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*). Can. J. Fish. Aquat. Sci. 42:785-790.
- Hester, F.J. 1968. Visual contrast thresholds of the goldfish (*Carassius auratus*). Vision Res. 8:1315-1336.
- Hilborn, R., and S.C. Stearns. 1982. On inference in ecology and evolutionary biology: the problem of multiple causes. Acta. Biotheoretica 31:145-164.
- Hoag, S.H. 1972. The relationship between the summer food of juvenile sockeye salmon, *Oncorhynchus nerka*, and the standing stock of zooplankton in Iliamna Lake, Alaska. Fish. Bull. 70:355-362.
- Hokanson, K.E.F., C.F. Kleiner, and T.W. Thorslund. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 34:639-648.
- Howick, G.L., and W.J. O'Brien. 1983. Piscivorous feeding behavior of largemouth bass: an experimental analysis. Trans. Am. Fish. Soc. 112:508-516.

- Huntley, M. 1985. Experimental approaches to the study of vertical migration of zooplankton. p.71-90. In M. Rankin [ed.] Migration: Mechanisms and Adaptive Significance. Contrib. Mar. Sci. Suppl. 27:868p.
- Hutchinson, G.E. 1967. A treatise on limnology, volume 2. Wiley.
- Hyatt, K.D., and J.G. Stockner. 1985. Responses of sockeye salmon (*Oncorhynchus nerka*) to fertilization of British Columbia coastal lakes. Can. J. Fish. Aquat. Sci. 42:320-331.
- Hyatt, K.D., J. Candy, M. Wright, and D.P. Rankin. 1989. An appraisal of the potential utility of hydroacoustic techniques for routine estimation of sockeye salmon (*Oncorhynchus nerka*) escapements in British Columbia coastal lakes. Can. J. Fish. Aquat. Sci. (in press).
- Janssen, J., and S.B. Brandt. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. Can. J. Fish. Aquat. Sci. 37:177-184.
- Johannesson, K.A., and R.B. Mitson. 1983. Fisheries acoustics. A practical manual for aquatic biomass estimation. FAO Fish. Tech. Pap. 240: 249 p.
- Johnson, W.E. 1961. Aspects of the ecology of a pelagic, zooplankton-eating fish. Verh. Int. Ver. Limnol. 14:727-731.
- Johnson, W.E., and C. Groot. 1963. Observations on the migration of young sockeye salmon (*Oncorhynchus nerka*) through a large, complex lake system. J. Fish. Res. Board Can. 20:919-938.
- Johnsen, G.H., and P.J. Jakobsen. 1987. The effect of food limitation on vertical migration in *Daphnia longispina*. Limnol. Oceanogr. 32:873-880.
- Kelso, J.R.M., E.E. Pickett, and R.G. Dowd. 1974. A digital echo-counting system used in determining abundance of freshwater pelagic fish in relation to depth. J. Fish. Res. Board Can. 31:1101-1104.
- Kerfoot, W.C. 1985. Adaptive value of vertical migration. In M.A. Rankin [ed.] Migration: Mechanisms and Adaptive Significance. Contrib. Mar. Sci. Suppl. 27:92-113.
- Krebs, J.R., and N.B. Davies. 1981. An Introduction to Behavioural Ecology. Sinauer Associates. 292p.
- Kyle, G.B., J.P. Koenings, and B.M. Barrett. 1988. Density-dependent, trophic level responses to an introduced run of sockeye salmon (*Oncorhynchus nerka*) at Frazer Lake, Kodiak Island, Alaska. Can. J. Fish. Aquat. Sci. 45:856-867.
- Lasenby, D.C., T.G. Northcote, and M. Fürst. 1986. Theory, practice, and effects of *Mysis relicta* introductions to North American and Scandinavian lakes. Can. J. Fish. Aquat. Sci. 43:1277-1284.
- Levy, D.A., and K.J. Hall. 1985. A review of the limnology and sockeye salmon ecology of Babine Lake. Westwater Research Centre Tech. Rep. 27:78p. The University of British Columbia.

- Longhurst, A.R. 1976. Vertical migration, p.116-136. In D.H. Cushing and J.J. Walsh [ed.] The Ecology of the Seas. W.B. Saunders, Philadelphia, PA.
- Love, R.H. 1977. Target strength of an individual fish at any aspect. J. Acoust. Soc. Am. 62:1397-1403.
- Luecke, C., and W.J. O'Brien. 1983. The effect of *Heterocope* predation on zooplankton communities in arctic ponds. Limnol. Oceanogr. 28:367-377.
- Lythgoe, J.N. 1979. The Ecology of Vision. Clarendon Press. New York. 244p.
- McDonald, J.G. 1969. Distribution, growth, and survival of sockeye fry (*Oncorhynchus nerka*) produced in natural and artificial stream environments. J. Fish. Res. Board Can. 26:229-267.
- McDonald, J. 1973. Diel vertical movements and feeding habits of underyearling sockeye salmon (*Oncorhynchus nerka*), at Babine Lake, B.C. Fish. Res. Board Can. Tech. Rep. 378:55 p.
- McDonald, J., and J.M. Hume. 1984. The Babine Lake sockeye salmon enhancement program: testing some major assumptions. Can. J. Fish. Aquat. Sci. 41:70-92.
- McFarland, W.N. 1986. Light in the sea - correlations with behaviors of fishes and invertebrates. Amer. Zool. 26:389-401.
- McLaren, I.A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. J. Fish. Res. Board Can. 20:685-727.
- MacLennan, D.N., A.E. Magurran, T.J. Pitcher, and C.E. Hollingworth. In press. Behavioural determinants of fish target strength. Rapp. P. -v. Reun. Cons. int. Explor. Mer
- McQueen, D.J., J.R. Post, and E.L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. Can. J. Fish. Aquat. Sci. 43:1571-1581.
- Magnuson, J.J., L.B. Crowder, and P.A. Medvick. 1979. Temperature as an ecological resource. Amer. Zool. 19:331-343.
- Manzer, J.I. 1964. Preliminary observations on the vertical distribution of Pacific salmon (genus *Oncorhynchus*) in the Gulf of Alaska. J. Fish. Res. Board Can. 21:891-903.
- Mathisen, O.A., T.R. Croker, and E.P. Nunnallee. 1977. Acoustic estimation of juvenile sockeye salmon. Rapp. P. -v. Reun. Cons. int. Explor. Mer 170:279-286.
- Mayr, E. 1974. Behavior programs and evolutionary strategies. Am. Sci. 62:650-659.
- Mayr, E. 1982. The Growth of Biological Thought. Diversity, Evolution, and Inheritance. Harvard University Press. Cambridge. 974p.
- Mittelbach, G.G. 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. Ecology 69:614-623.

- Mulligan, T.J., and R. Kieser. 1986. Comparison of acoustic population estimates of salmon in a lake with a weir count. *Can. J. Fish. Aquat. Sci.* 43:1373-1385.
- Murray, R.W. 1971. Temperature receptors, p. 121-133. *In* W.S. Hoar and D.J. Randall [ed.] *Fish Physiology*, Vol. 5. Sensory Systems and Electric Organs. Academic Press. New York, NY.
- Narver, D.W. 1970. Diel vertical movements and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. *J. Fish. Res. Board Can.* 27:281-316.
- Neill, W.H. 1979. Mechanisms of fish distribution in heterothermal environments. *Amer. Zool.* 19:305-317.
- Neill, W.H., J.J. Magnuson, and G.D. Chipman. 1972. Behavioural thermoregulation by fishes: a new experimental approach. *Science* 176:1443-1445.
- Nelson, J.S. 1968. Distribution and nomenclature of the North American kokanee, *Oncorhynchus nerka*. *J. Fish. Res. Board Can.* 25:409-414.
- Northcote, T.G. 1964. Use of a high-frequency echosounder to record distribution and migration of *Chaoborus* larvae. *Limnol. Oceanogr.* 9:87-91.
- Northcote, T.G. 1967. The relation of movements and migrations to production in freshwater fishes, p. 315-344. *In* S.D. Gerking [ed.] *The Biological Basis of Freshwater Fish Production*. Blackwell Scientific Publications, Oxford, U.K.
- Northcote, T.G. 1972. Some effects of mysid introduction and nutrient enrichment on a large oligotrophic lake and its salmonids. *Verh. Internat. Verein. Limnol.* 18:1096-1106.
- Northcote, T.G. 1973. Some impacts of man on Kootenay Lake and its salmonoids. *Great Lakes Fish. Comm. Tech. Rept.* 25:46p.
- Northcote, T.G. 1988. Fish in the structure and function of freshwater ecosystems: a "top-down" view. *Can. J. Fish. Aquat. Sci.* 45:361-379.
- Northcote, T.G., and H.W. Lorz. 1966. Seasonal and diel changes in food of adult kokanee (*Oncorhynchus nerka*) in Nicola Lake, British Columbia. *J. Fish. Res. Board Can.* 23:1259-1263.
- Northcote, T.G., H.W. Lorz, and J.C. MacLeod. 1964. Studies on diel vertical movement of fishes in a British Columbia lake. *Verh. Internat. Verein. Limnol.* 15:940-946.
- Northcote, T.G., and H. Rundberg. 1970. Spatial distribution of pelagic fishes in Lambarfjärden (Mälaren, Sweden) with particular reference to interaction between *Coregonus albula* and *Osmerus eperlanus*. *Inst. Fresh. Res. Drottningholm* 50:133-167.
- Nunnallee, E.P. Jr. 1973. A hydroacoustic data acquisition and digital data analysis system for the assessment of fish stock abundance. *Univ. Washington, Fish. Res. Inst. Circ.*, 73-3. 48 p.
- Nunnallee, E.P. Jr. 1980. Application of an empirically scaled digital echo integrator for assessment of juvenile sockeye salmon (*Oncorhynchus nerka* Walbaum) populations. Ph.D Thesis. Univ. of Washington, Seattle, WA. 151p.

- O'Brien, W.J., and D. Schmidt. 1979. Arctic *Bosmina* morphology and copepod predation. *Limnol. Oceanogr.* 24: 564-567.
- Olsen, K., J. Angell, F. Pettersen and A. Løvik. 1983. Observed fish reactions to a surveying vessel with special reference to herring, cod, capelin and polar cod, p.131-138. In O.Nakken and S.C. Venema [ed.] Selected papers of the ICES/FAO Symposium on fisheries acoustics, Bergen, Norway, 21-24 June 1982. FAO Fish. Rep. 300: 331p.
- O'Neill, S.M., and K.D. Hyatt. 1987. An experimental study of competition for food between sockeye salmon (*Oncorhynchus nerka*) and threespine sticklebacks (*Gasterosteus aculeatus*) in a British Columbia coastal lake, p. 143-160. In H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.
- Pianka, E.R. 1974. *Evolutionary Ecology*. Second Edition. Harper and Row. New York. 397p.
- Pijanowska, J., and P. Dawidowicz. 1987. The lack of vertical migration in *Daphnia*: the effect of homogenously distributed food. *Hydrobiologia* 148: 175-181.
- Pitcher, T.J. 1986. Functions of shoaling behaviour in teleosts. p.294-337. In T.J. Pitcher [ed.] *The Behaviour of Teleost Fishes*. Croom Helm. London.
- Quinn, T.P., and B.A. terHart. 1987. Movements of adult sockeye salmon (*Oncorhynchus nerka*) in British Columbia coastal waters in relation to temperature and salinity stratification: ultrasonic telemetry results, p. 61-77. In H.D. Smith, L. Margolis, and C.C. Wood. [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.
- Qutob, Z. 1962. The swimbladder of fishes as a pressure receptor. *Arch. Neerl. Zool.* 15:1-67.
- Raleigh, R.F. 1967. Genetic control in the lakeward migrations of sockeye salmon (*Oncorhynchus nerka*) fry. *J. Fish. Res. Board Can.* 24:2613-2622.
- Rankin, D.P. 1977. Increased predation by juvenile sockeye salmon (*Oncorhynchus nerka* Walbaum) relative to changes in macrozooplankton abundance in Babine Lake, B.C. M.Sc. Thesis. Dept. of Zoology. The Univ. of British Columbia. 101p.
- Reynolds, W.W. 1977. Temperature as a proximate factor in orientation behavior. *J. Fish. Res. Board Can.* 34:734-739.
- Reynolds, W.W., and M.E. Casterlin. 1979. The role of temperature in the environmental physiology of fishes, p.497-518. In M.A. Ali [ed.] *Environmental Physiology of Fishes*. Plenum Press. New York. 686p.
- Ricker, W.E. 1937. The food and the food supply of sockeye salmon (*Oncorhynchus nerka* Walbaum) in Cultus Lake, British Columbia. *J. Biol. Board Can.* 3:450-468.
- Ricker, W.E. 1941. The consumption of young sockeye salmon by predaceous fish. *J. Fish. Res. Board Can.* 5:293-313.
- Ricker, W.E., and R.E. Foerster. 1948. Computation of fish production. *Bull. Bingham Oceanog. Collection* 9:173-211.

- Rieman, B.E., and B. Bowler. 1980. Kokanee trophic ecology and limnology in Pend Oreille Lake. Idaho Dep. Fish and Game Fish. Bull. 1:27 p.
- Robinson, D.G., and W.E. Barraclough. 1978. Population estimates of sockeye salmon (*Oncorhynchus nerka*) in a fertilized oligotrophic lake. J. Fish. Res. Board Can. 35:851-860.
- Rozin, P.N., and J. Mayer. 1961. Thermal reinforcement and thermoregulatory behavior in the goldfish, *Carassius auratus*. Science 134:942-943.
- Rudstam, L.G., C.S. Clay, and J.J. Magnuson. 1987. Density and size estimates of cisco *Coregonus artedii* using analysis of echo peak PDF from a single-transducer sonar. Can. J. Fish. Aquat. Sci. 44:811-821.
- Ruggles, C.P. 1966. Juvenile sockeye studies in Owikeno Lake, British Columbia. Can. Fish. Cult. 36:3-22.
- Shortreed, K.S., and J.G. Stockner. 1979. Limnological results from the 1979 British Columbia Lake Enrichment Program. 1981. Can. Tech. Rep. Fish. Aquat. Sci. 995: 71p.
- Shotton, R., and G.P. Bazigos. 1984. Techniques and considerations in the design of acoustic surveys. Rapp. P.-v. Reun. Cons. int. Explor. Mer 184:34-57.
- Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview, p. 203-224. In W.C. Kerfoot and A. Sih [ed.] Predation. Direct and Indirect Impacts on Aquatic Communities. Univ. Press of New England. Hanover.
- Simmonds, E.J., and F. Armstrong. In press. A wide band echosounder: measurements on cod, saithe, herring and mackerel from 27 to 54 kHz. Rapp. P.-v. Reun. Cons. int. Explor. Mer.
- Smith, R.J.F. 1985. The Control of Fish Migration. Springer-Verlag. Berlin.
- Steigenberger, L.W. 1972. Observations on the predation by squawfish (*Ptychocheilus oregonensis*) on sockeye salmon (*Oncorhynchus nerka*), with particular reference to Cultus Lake, British Columbia. M.Sc. Thesis, Dept. of Zoology, The Univ. of British Columbia.
- Stich, H.B., and W. Lampert. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. Nature 293:396-398.
- Stockner, J.G. 1987. Lake fertilization: the enrichment cycle and lake sockeye salmon (*Oncorhynchus nerka*) production, p. 198-215. In H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96
- Stockner, J.G., and T.G. Northcote. 1974. Recent limnological studies of Okanagan Basin lakes and their contribution to comprehensive water resource planning. J. Fish. Res. Board Can. 31:955-976.
- Stockner, J.G., and K.R.S. Shortreed. 1983. A comparative limnological survey of 19 sockeye salmon (*Oncorhynchus nerka*) nursery lakes in the Fraser River system, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1190:63 p.

- Stockner, J.G., and K.R.S.Shortreed. 1985. Whole-lake fertilization experiments in coastal British Columbia lakes: empirical relationships between nutrient inputs and phytoplankton biomass and production. *Can. J. Fish. Aquat. Sci.* 42:649-658.
- Sullivan, C.M. 1954. Temperature reception and responses in fish. *J. Fish. Res. Board Can.* 11:153-170.
- Teraguchi, M., and T.G. Northcote. 1966. Vertical distribution and migration of *Chaoborus flavicans* larvae in Corbett Lake, British Columbia. *Limnol. Oceanogr.* 11:164-176.
- Thorne, R.E. 1971. Investigation into the relation between integrated echo voltage and fish density. *J. Fish. Res. Board Can.* 28:1269- 1273.
- Thorne, R.E. 1979. Hydroacoustic estimates of adult sockeye salmon *Oncorhynchus nerka* in Lake Washington, 1972-75. *J. Fish. Res. Board Can.* 36:1145-1149.
- Thorne, R.E. 1983A. Hydroacoustics. In Neilsen, L.A., and D.L. Johnson [ed.] *Fisheries Techniques*. Am. Fish. Soc. Bethesda.
- Thorne, R.E. 1983B. Application of hydroacoustic assessment techniques to three lakes with contrasting fish distributions, p.269-277. In O. Nakken and S.C. Venema [ed.] *Symposium on fisheries acoustics*. Bergen, Norway, 21-24 June 1982. *FAO Fish. Rep.* 300: 331p.
- Thorne, R.E. and J.J. Ames. 1987. A note on the variability of marine survival of sockeye salmon (*Oncorhynchus nerka*) and effects of flooding on spawning success. *Can. J. Fish. Aquat. Sci.* 44:1791-1795.
- Thomas, G.L., and D.R. Jackson. 1987. Acoustic measurement of fish schools using array phase information. *Can. J. Fish. Aquat. Sci.* 44:1544- 1550.
- Traynor, J.J., and J.E. Ehrenberg. In press. Fish and standard sphere target strength measurements obtained with a split beam-dual beam system. *Rapp. P. -v. Reun. Cons. int. Explor. Mer.*
- Vuorinen, I. 1987. Vertical migration of *Eurytemora* (Crustacea, Copepoda): a compromise between the risks of predation and decreased fecundity. *J. Plankton Res.* 9:1037-1046.
- Ware, D.M. 1971. The predatory behaviour of rainbow trout (*Salmo gairdneri*). Ph.D Thesis. Dept. of Zoology. The Univ. of British Columbia.
- Werner, E.E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *Am. Nat.* 128:319-341.
- Werner, E.E., and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.* 15:393-425.
- Wetzel, R.G. 1983. *Limnology*. Second Edition. W.B. Saunders Co. Philadelphia.
- Williams, G.C. 1966. *Adaptation and Natural Selection*. Princeton University Press. Princeton. 307p.

- Williams, I.V., D. Brock, P. Gilhousen, T. Gjernes, K. Morton, R. Johnson, and W. Saito. In preparation. Studies of the lacustrine biology of the sockeye salmon (*Oncorhynchus nerka*) in the Shuswap system.
- Woodey, J.C. 1972. Distribution, feeding, and growth of juvenile sockeye salmon in Lake Washington. Ph.D Thesis, Univ. of Washington, Seattle, WA. 174p.
- Woodhead, P.M.J. 1965. Effects of light upon behaviour and distribution of demersal fishes of the North Atlantic. ICNAF Spec. Publ. 6:267-287.
- Woodhead, P.M.J. 1966. The behavior of fish in relation to light in the sea. Oceanogr. Mar. Biol. Ann. Rev. 4:337-403.
- Wurtsbaugh, W.A., and H. Li. 1985. Diel migrations of a zooplanktivorous fish (*Menidia beryllina*) in relation to the distribution of its prey in a large eutrophic lake. Limnol. Oceanogr. 30:565-576.
- Wurtsbaugh, W.A., and D. Neverman. 1988. Post-feeding thermotaxis and daily vertical migration in a larval fish. Nature 333:846-848.
- Zaret, T.M. 1980. Predation and Freshwater Communities. Yale University Press, New Haven, Conn.
- Zaret, T.M., and J.S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr. 21:804-814.

Appendix 1. Timing of Lake Visits

Babine:

June 25-26'86
Aug. 1-2'86
Aug. 19-20'86
Oct. 13-14'86

Chilko:

July 27-28'86
July 14-15'87
Aug. 15-16'87

Cultus:

Apr. 14-16'86
July 9-10'86
Sept. 29-30'86

Fraser:

June 27-28'86
Aug. 21-22'86
Oct. 14-15'86

Great Central:

May 26-27'86
July 20-21'86
Sept. 6-7'86

Kennedy:

May 28-29'86
July 20-21'86
Sept. 4-5'86

Kootenay:

Sept. 25-26'87

Lakelse:

June 21-22'86
Aug. 13-14'86

Meziadin:

June 23-24'86
Aug. 10-11'86

Nimpkish:

June 16-17'86
Sept. 8-9'86
Sept. 16-17'86

Okanagan:

June 6-7'87
July 1-2'87
July 21-22'87
Oct. 1-2'87

Owikeno:

Oct. 1-3'85
Sept. 11-14'86

Quesnel:

Aug. 4-5'86
Aug. 23-24'86
Sept. 20-21'86
Aug. 11-12'87

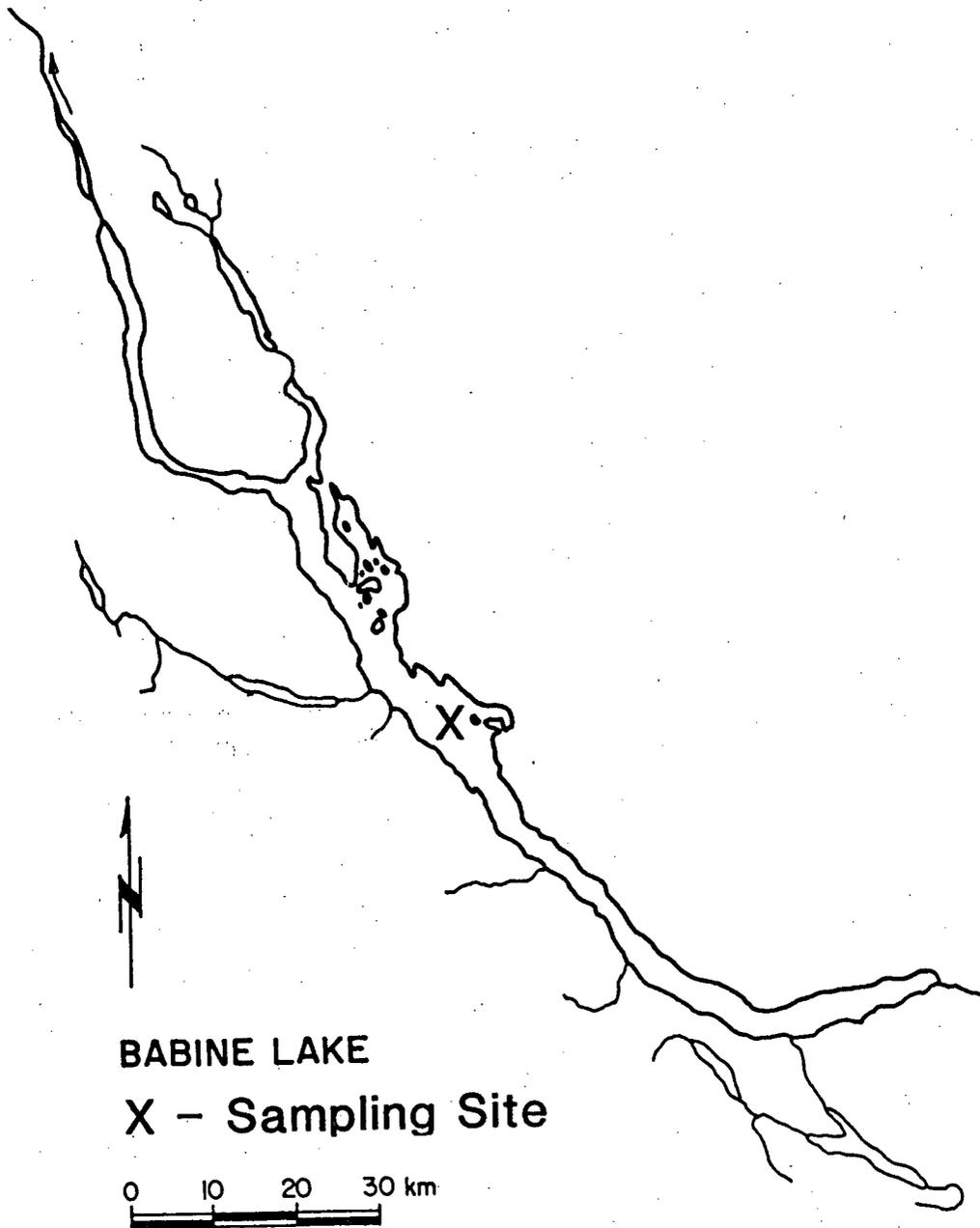
Shuswap:

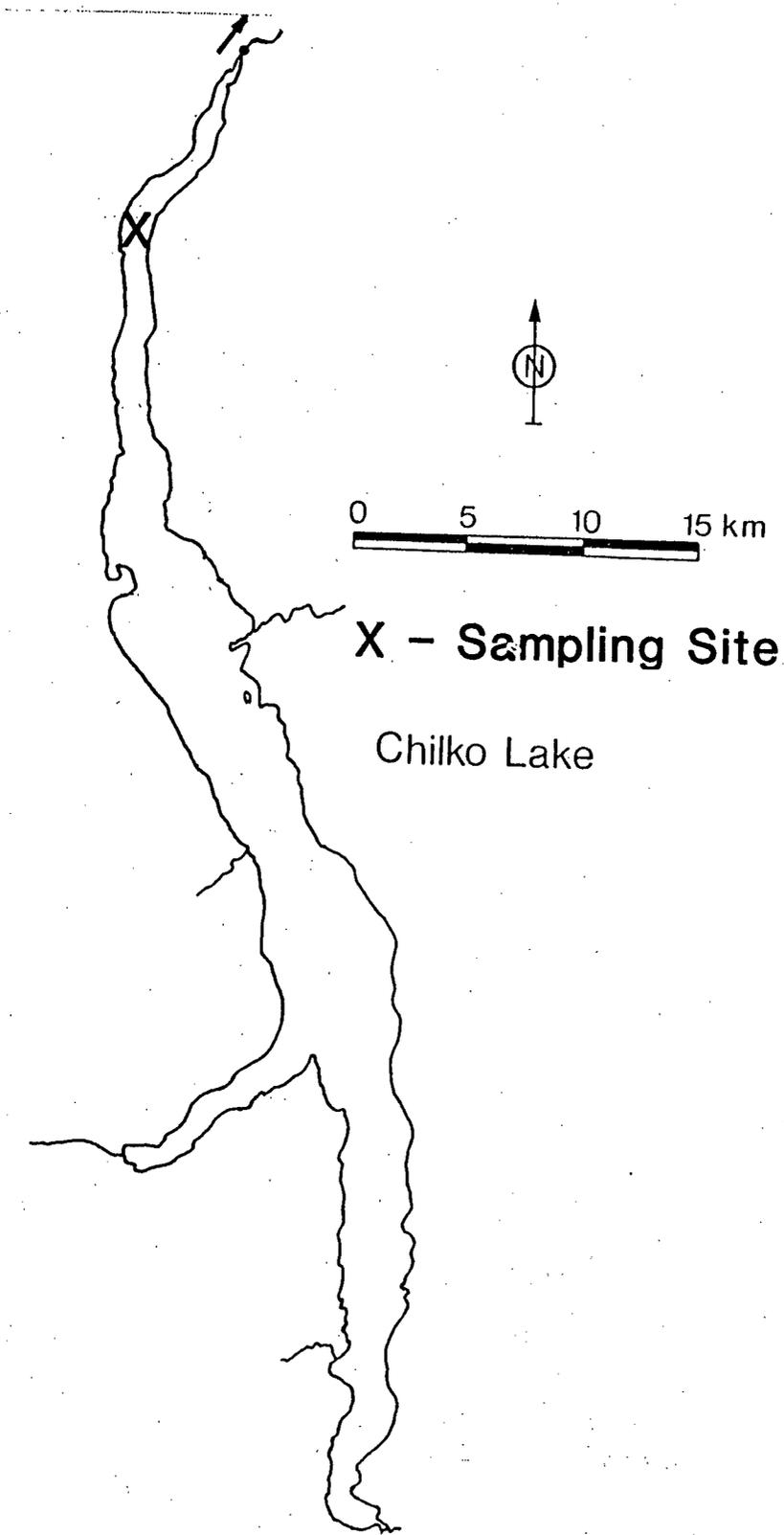
Sept. 23-25'85
July 1-2'86
July 2-4'87
July 18-20'87
Sept. 28-29'87
Nov. 4-5'87

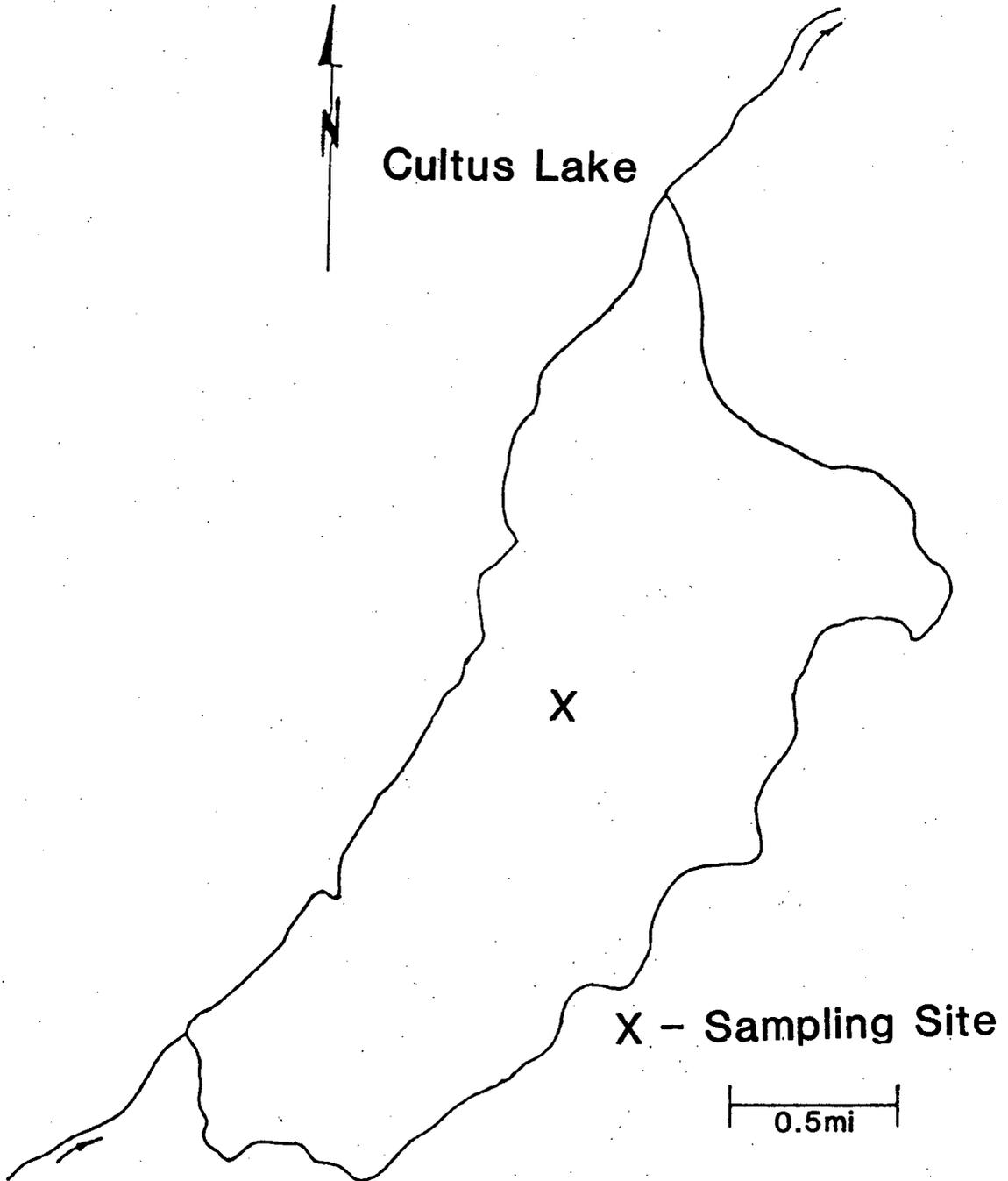
Skaha:

July 23-24'87

Appendix 2. Location of Sampling Sites

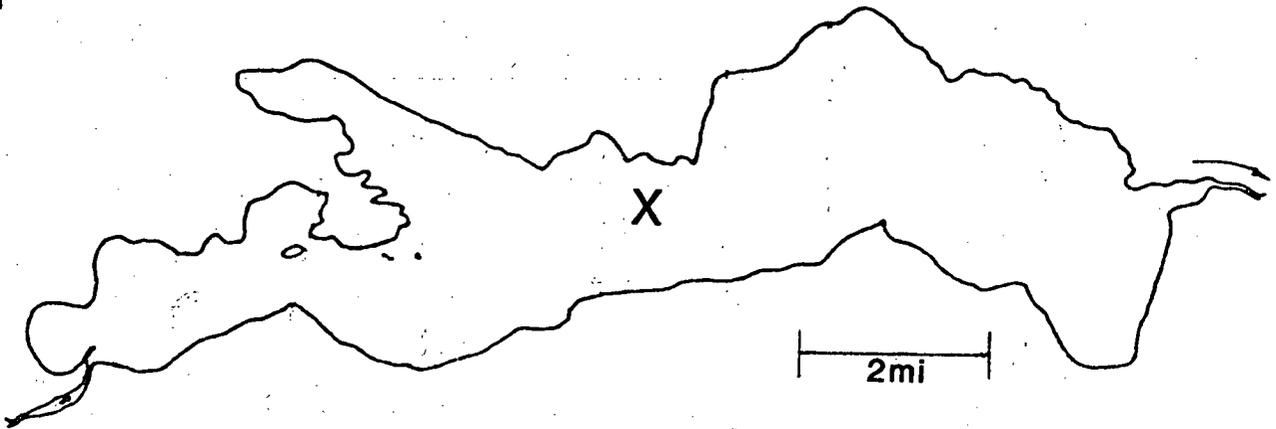




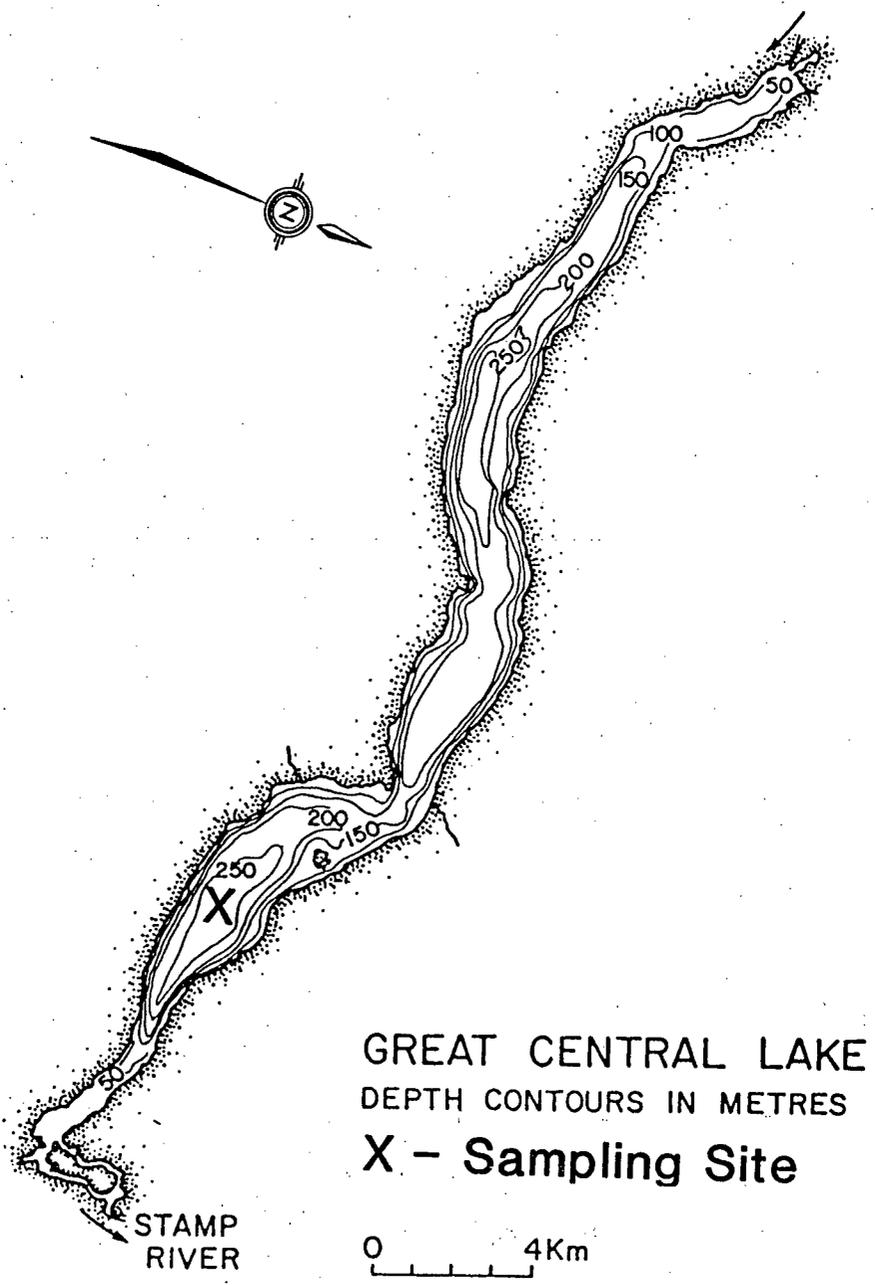




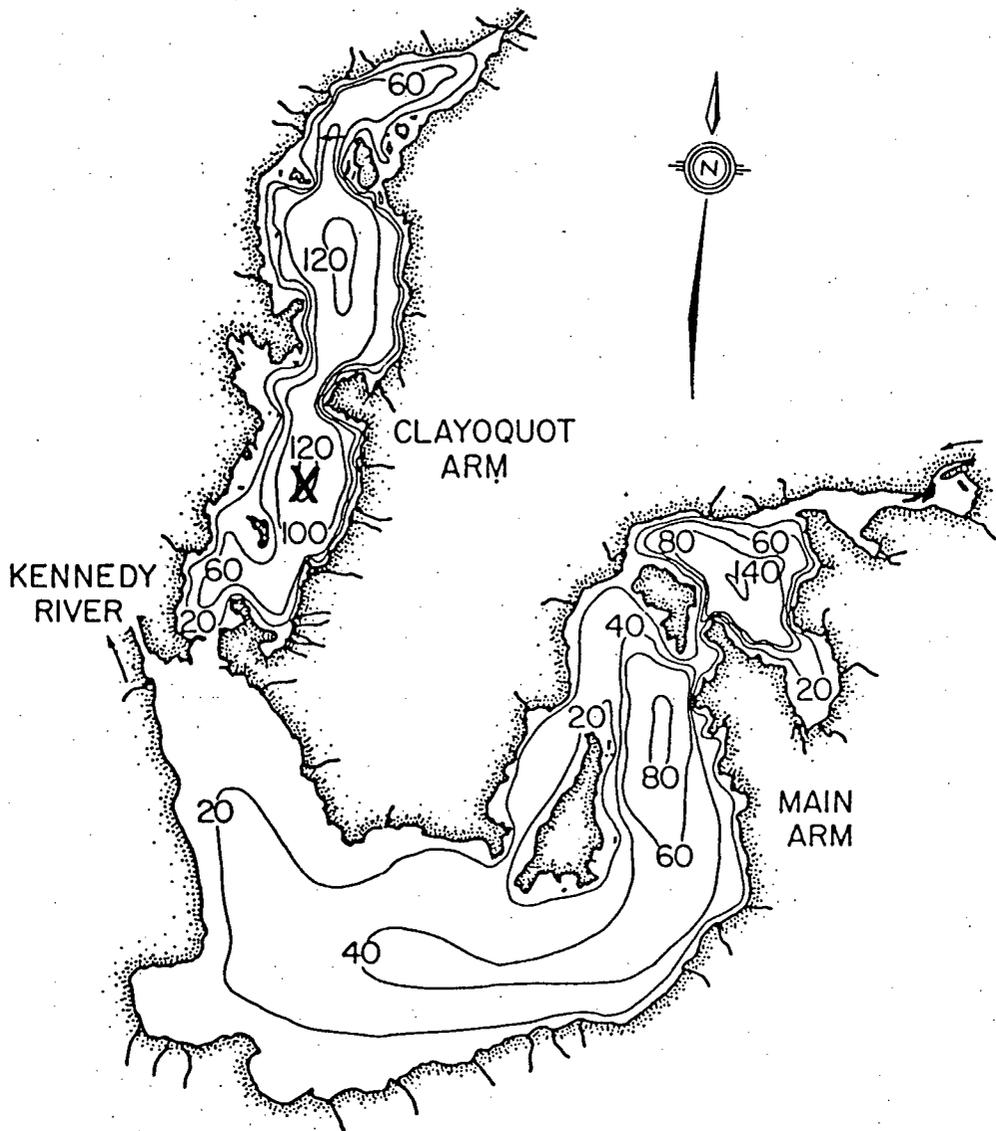
Fraser Lake



X - Sampling Site

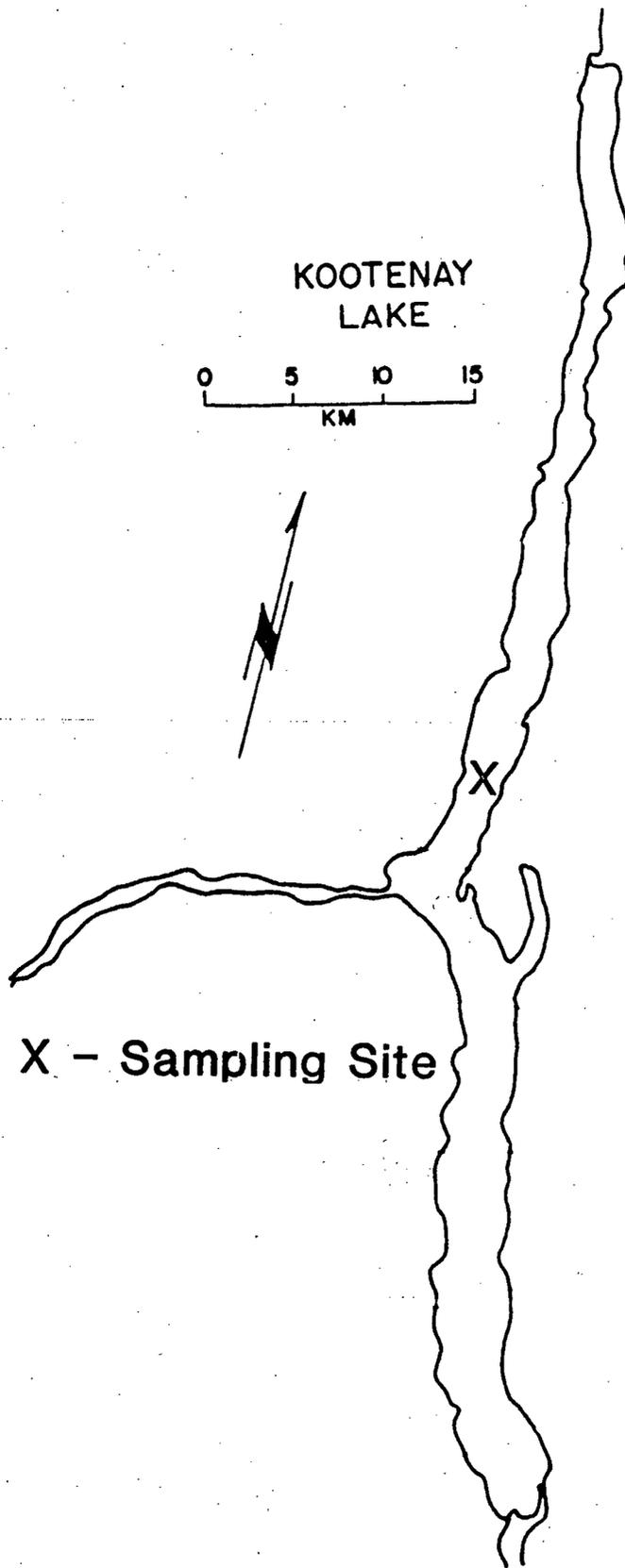


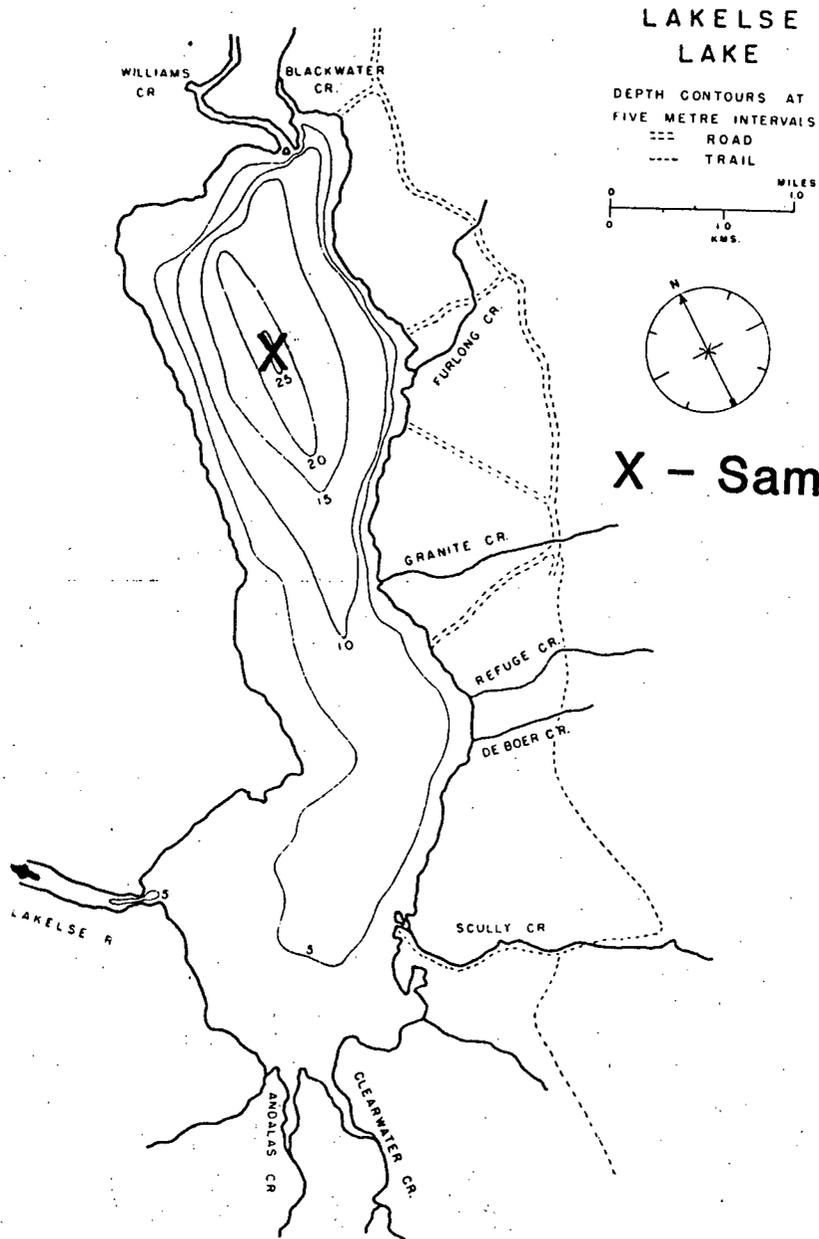
GREAT CENTRAL LAKE
DEPTH CONTOURS IN METRES
X - Sampling Site



KENNEDY LAKE
 DEPTH CONTOURS IN METRES
X - Sampling Site

0 1 2 3 4 Km

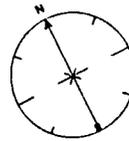
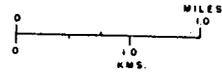




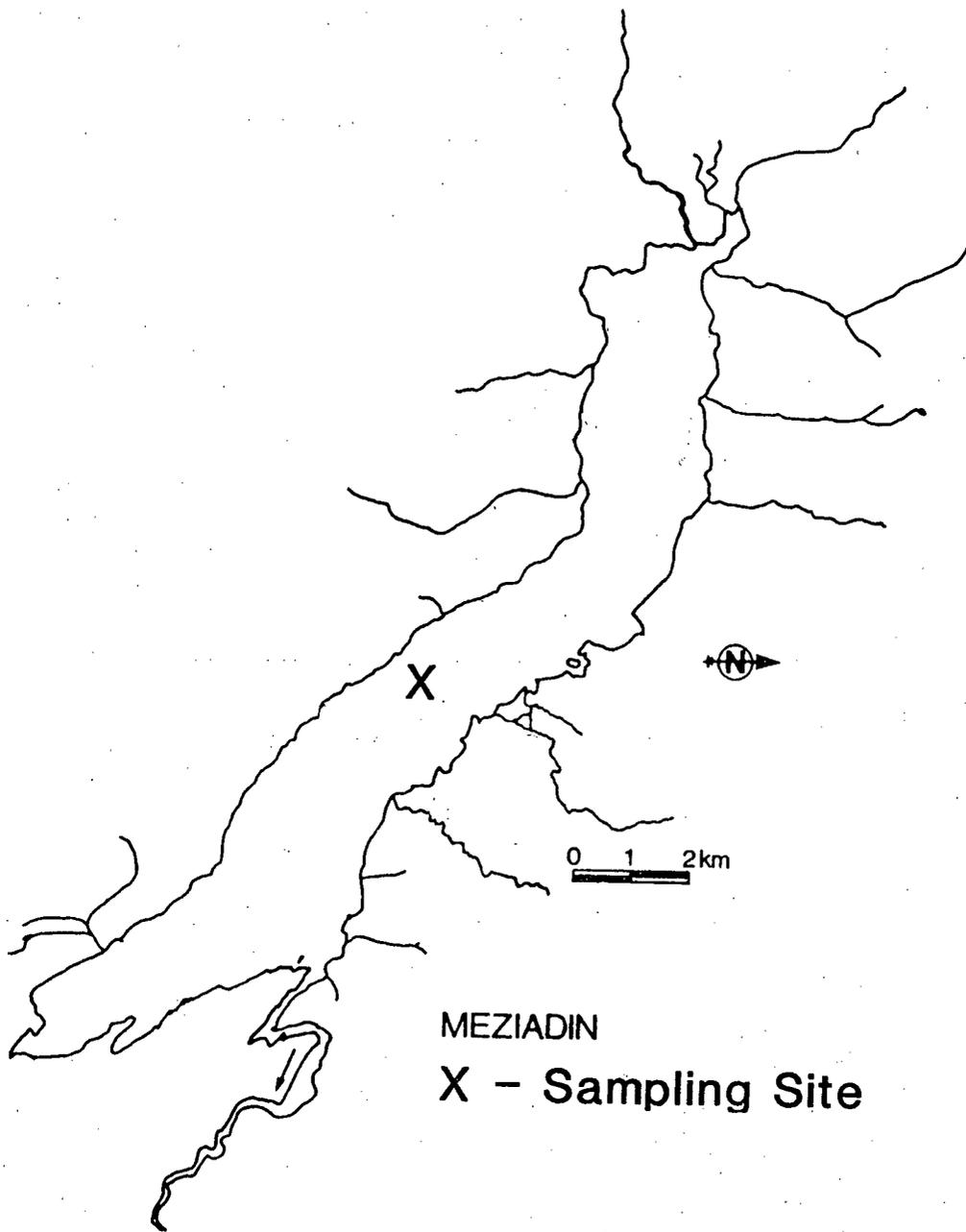
LAKELSE
LAKE

DEPTH CONTOURS AT
FIVE METRE INTERVALS

--- ROAD
... TRAIL

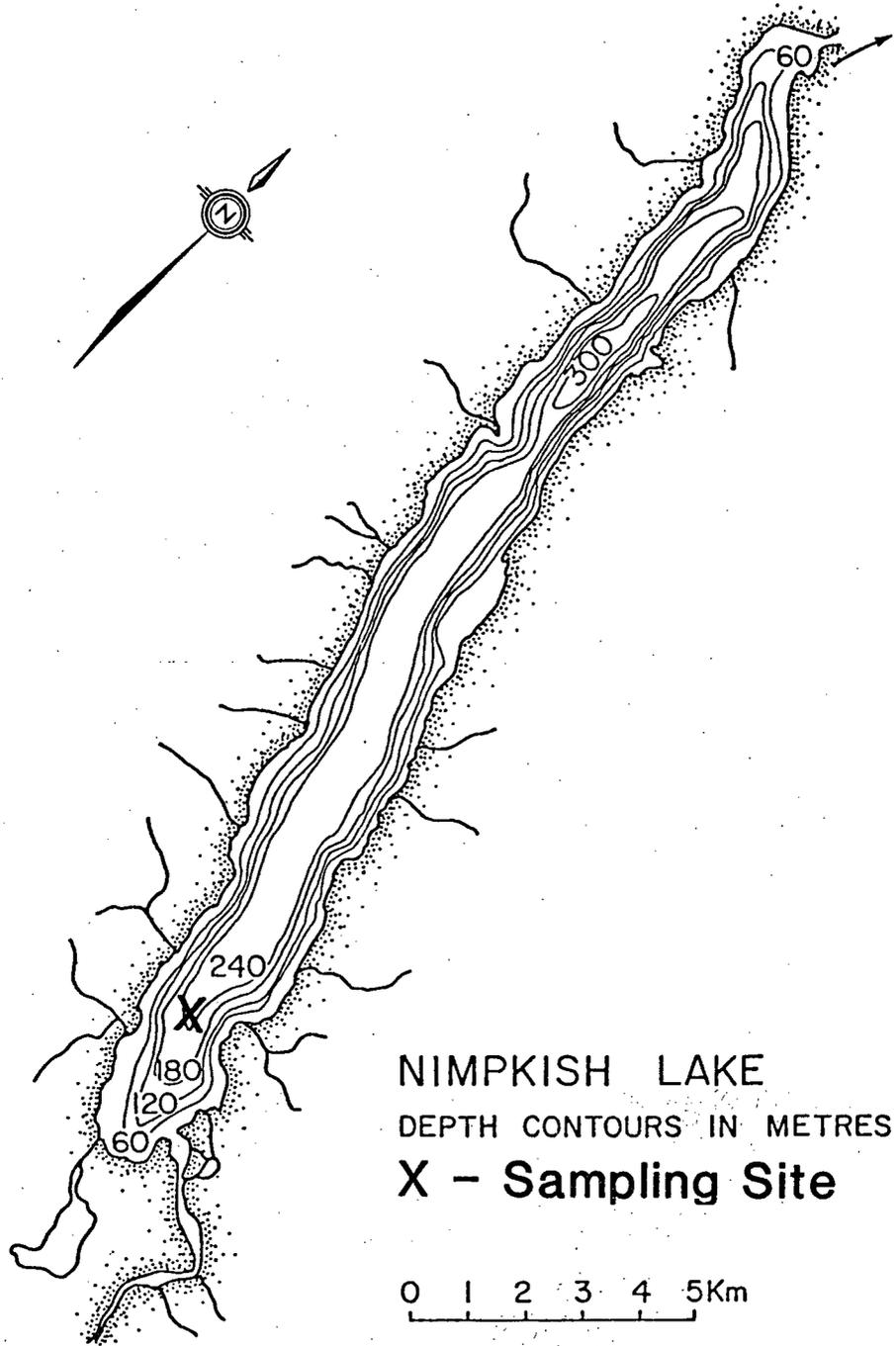


X - Sampling Site



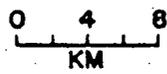
MEZIADIN

X - Sampling Site

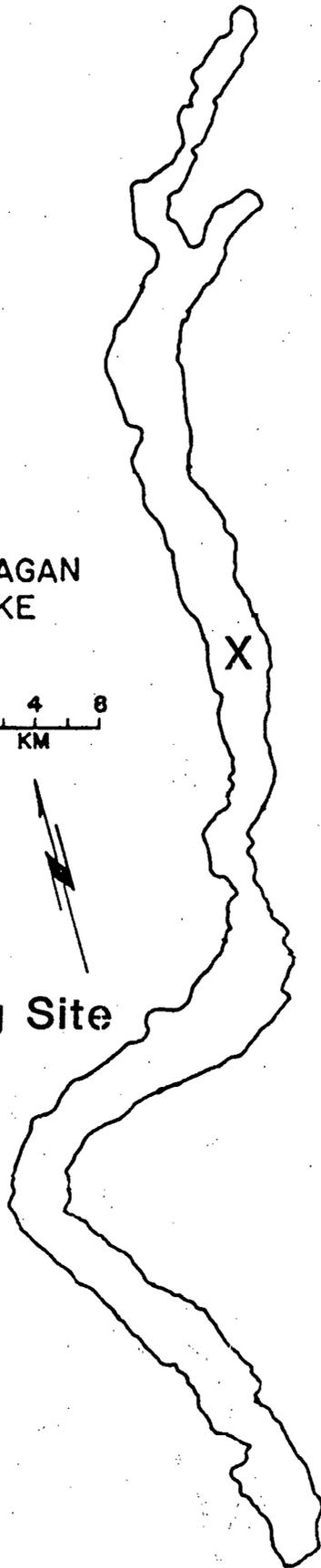


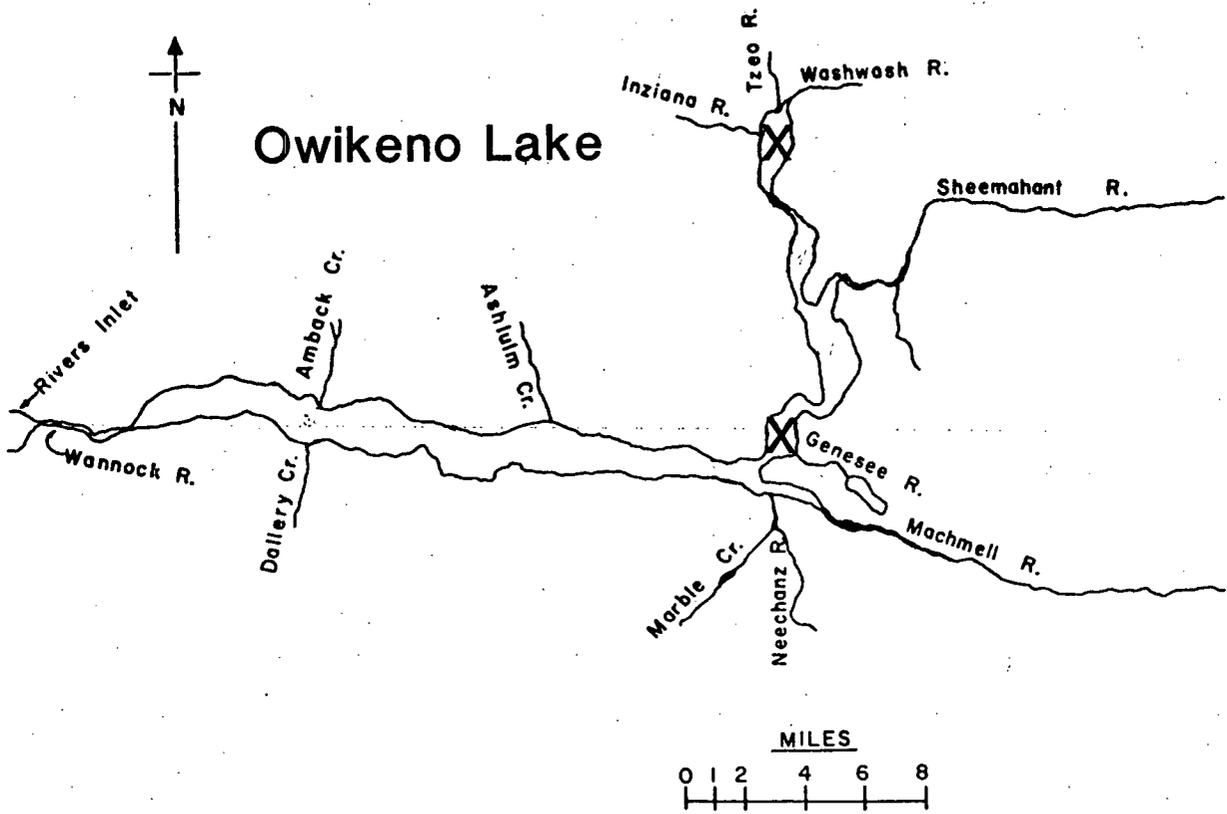
NIMPKISH LAKE
DEPTH CONTOURS IN METRES
X - Sampling Site

OKANAGAN
LAKE

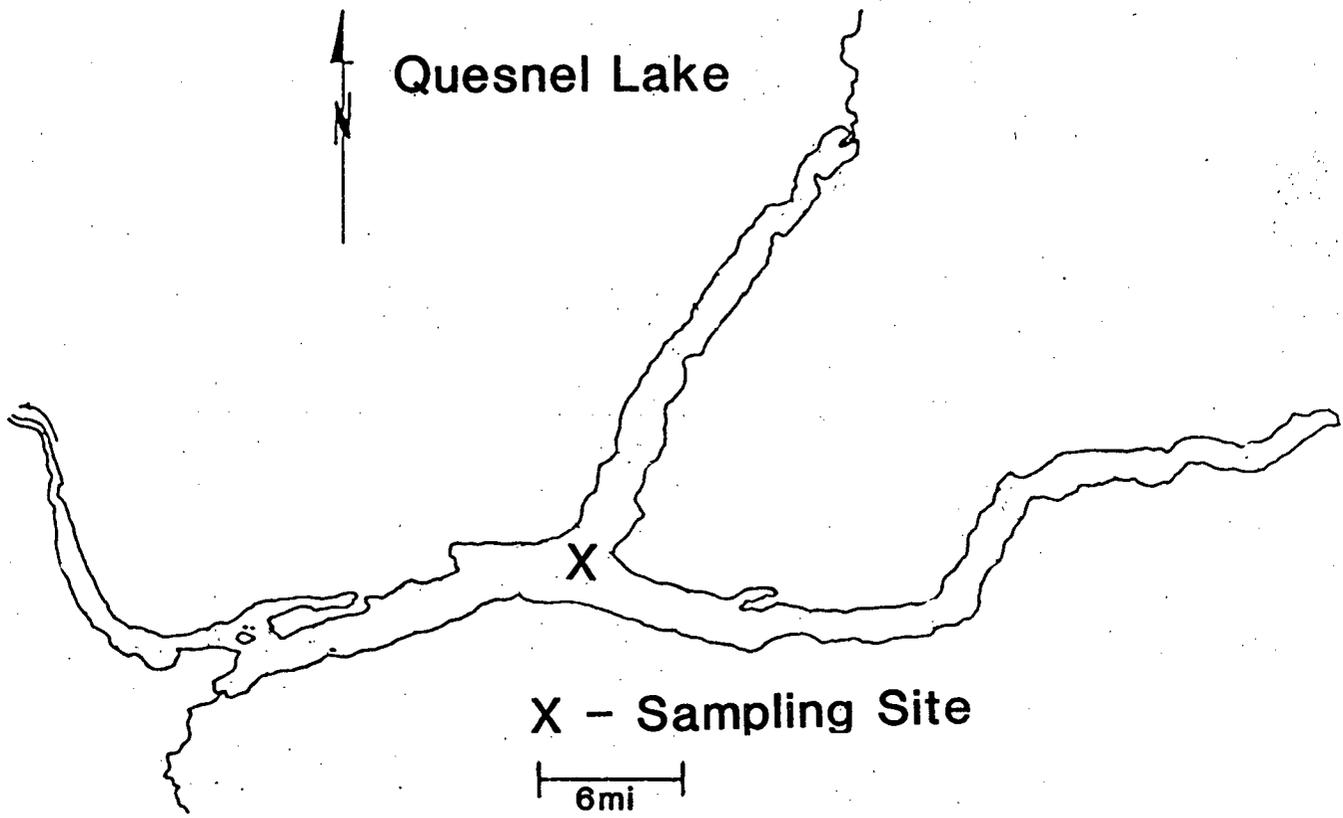


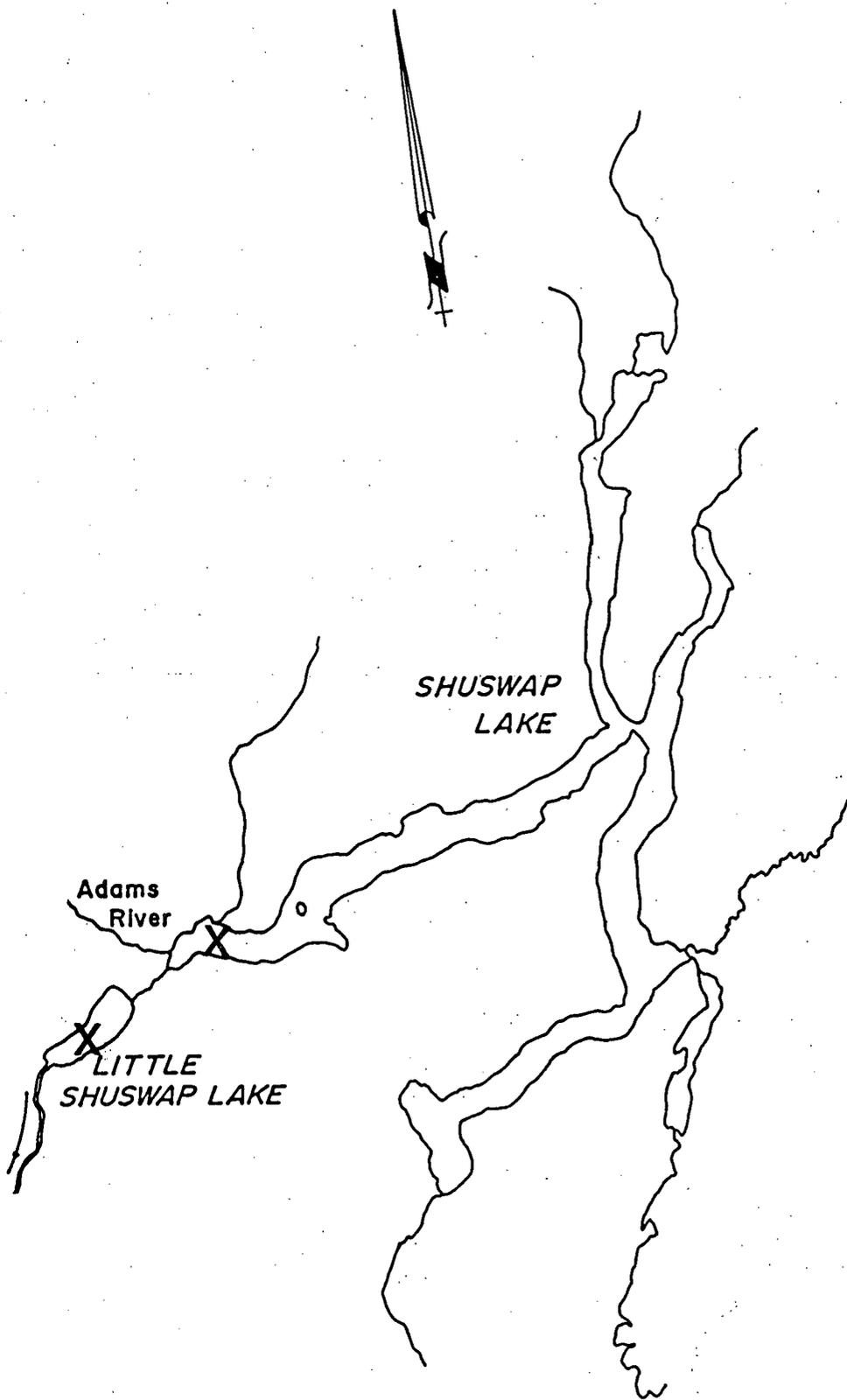
X - Sampling Site





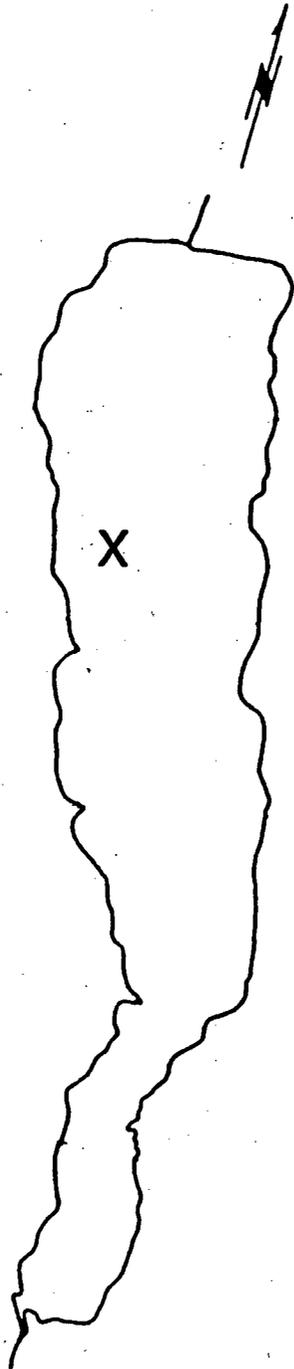
X - Sampling Site



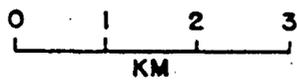


Scale-Kilometres
0 10 20

X - Sampling Site



X - Sampling Site

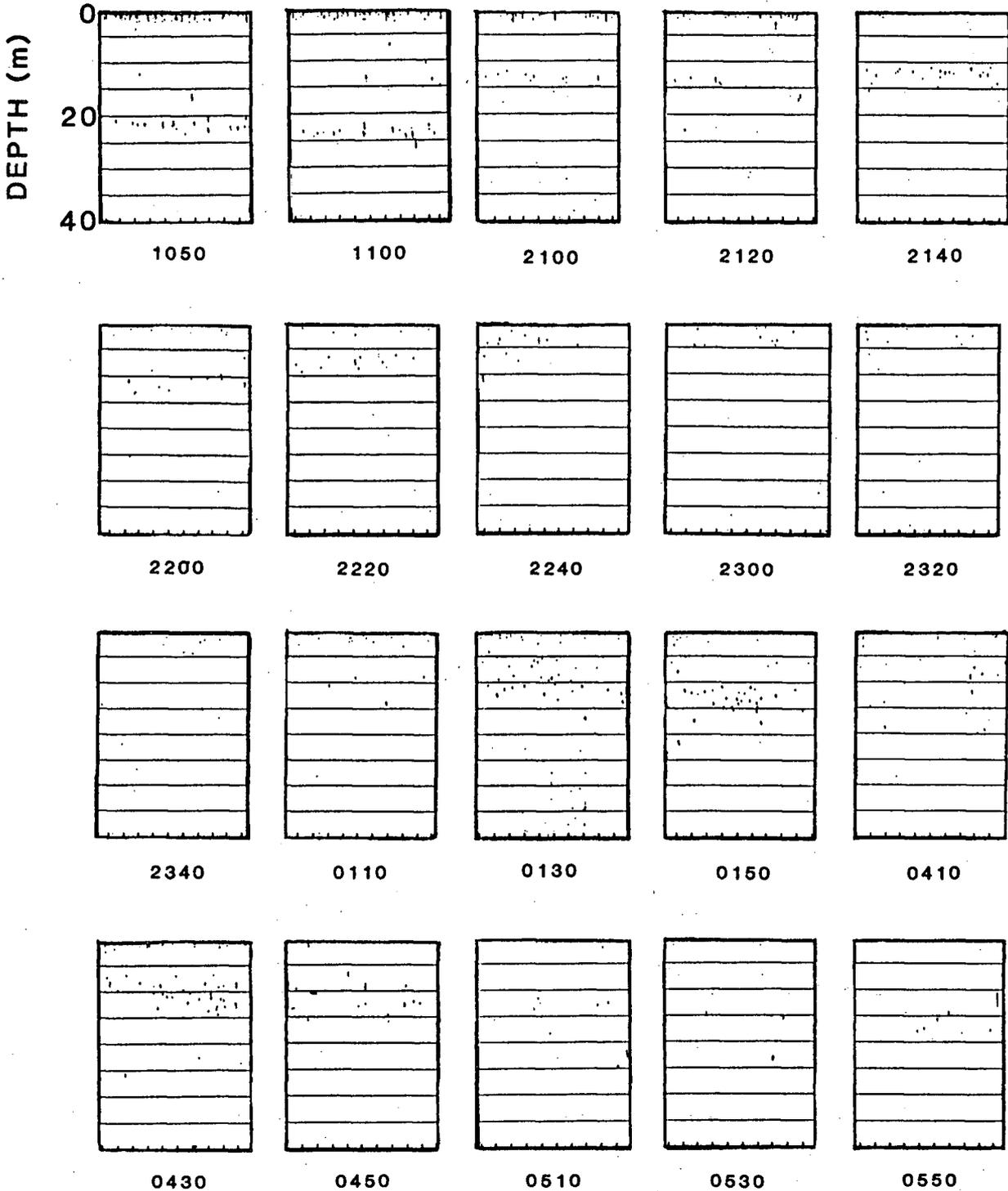


SKAHA LAKE

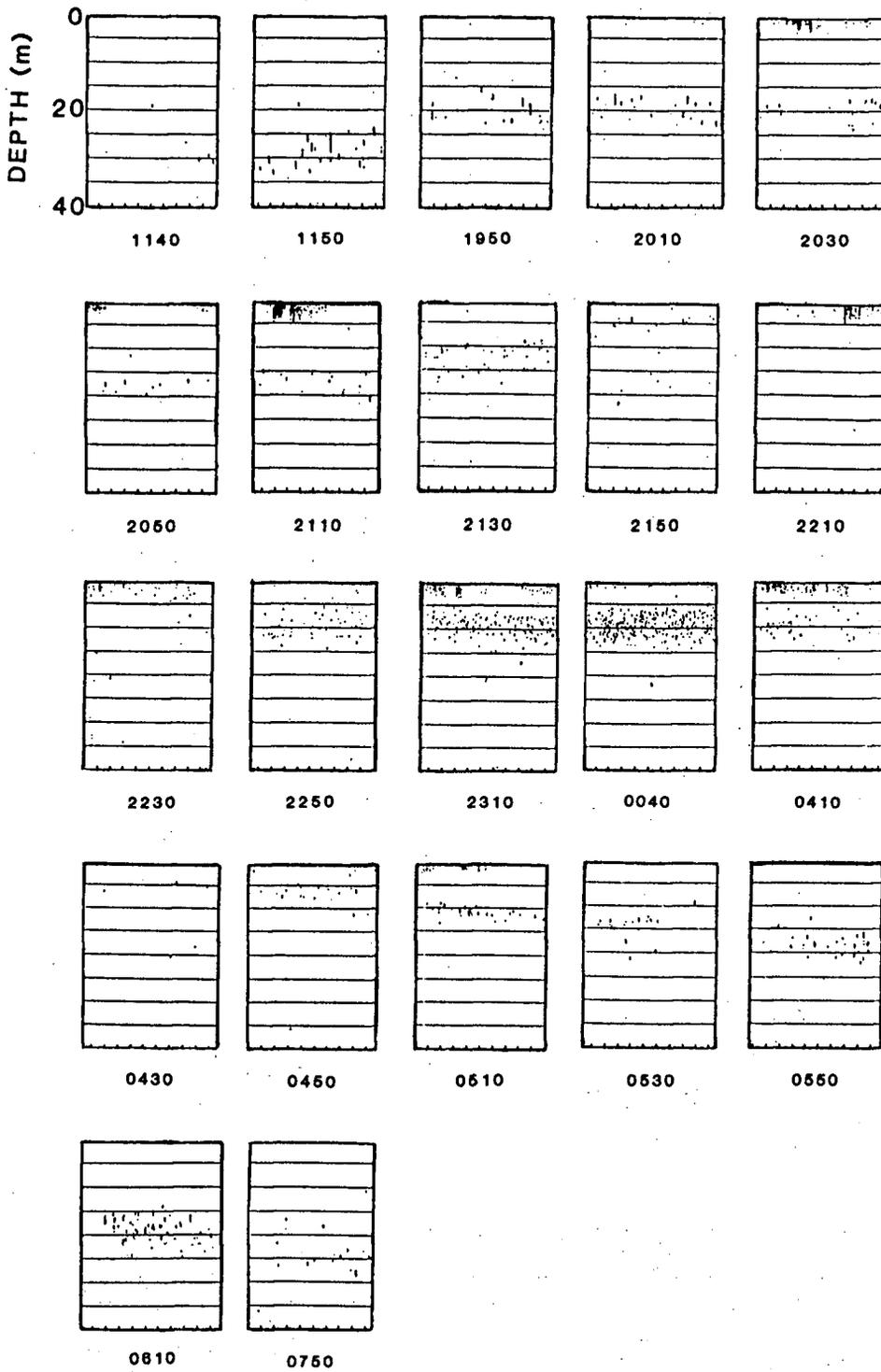
Appendix 3. Diel Echogram Sequences from Babine Lake

BABINE LAKE

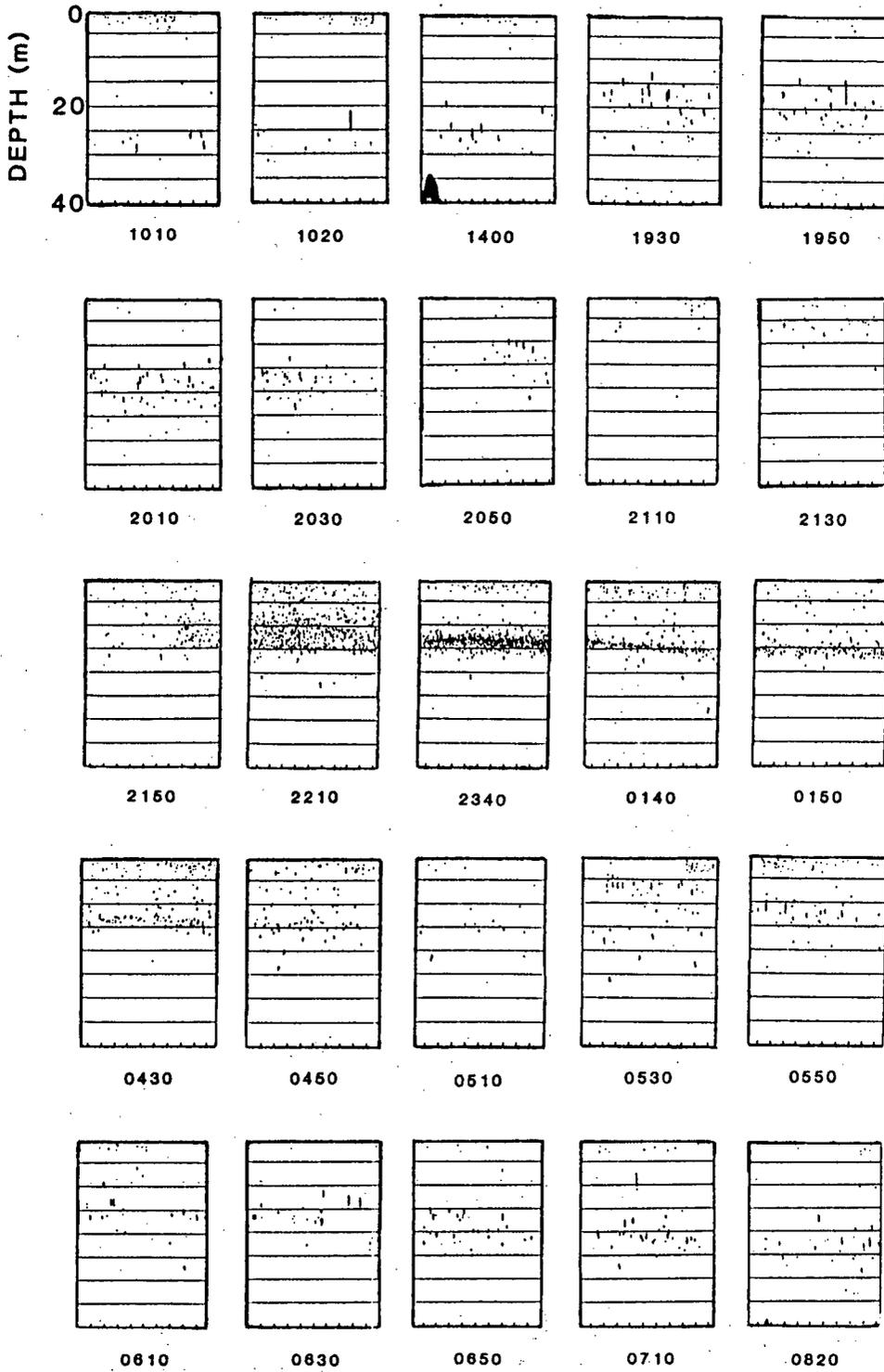
June 25 - 26, 1986



BABINE LAKE August 1-2, 1986

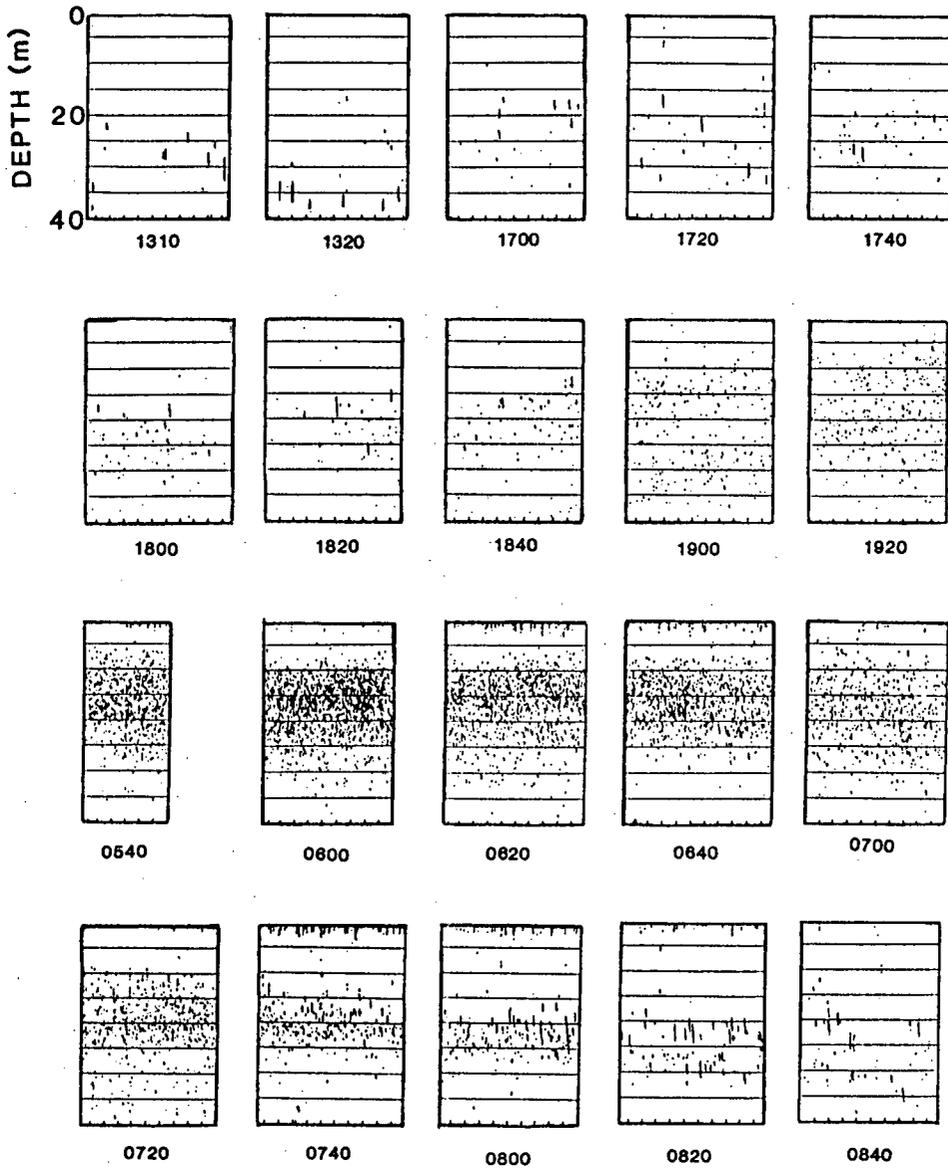


BABINE LAKE August 19 - 20, 1986



BABINE LAKE

Oct. 13-14, 1986



Appendix 4. Temperature at Maximum Nocturnal Echo Integrator Voltage

Lake	Date	Nocturnal transect	Depth (m) of maximum integrator voltage	Temperature (°C)
Babine	June 26'86	T13	12	10.5
Babine	Aug.2'86	T14	10.5	12.2
Babine	Aug.20'86	T25	14	15.1
Babine	Oct.13'86	T11	15	10.1
Cultus	July 9'86	T12	6	11.7
Cultus	Sep.29'86	T11	14	8.3
Chilko	July 15'87	T2	14	12.5
Fraser	June 27'86	T13	14	11.8
Fraser	Aug.21'86	T12	24	11.8
Fraser	Oct.14'86	T10	19	12.2
Great Central	July 22'86	T20	9	12.5
Great Central	Sep.6'86	T12	15	7.8
Kennedy	July 20'86	T12	11	10.1
Kennedy	Sep.4'86	T12	12	8.5
Meziadin	Aug.10'86	T12	7	12.0
Nimpkish	Sep.8'86	T11	26	9.0
Nimpkish	Sep.16'86	T2	32	10.0
Quesnel	Aug.5'86	T11	9	14.0
Quesnel	Aug.23'86	T11	17	10.2
Quesnel	Sep.20'86	T1	18	8.6
Shuswap	Sep.23'85	T8	17	11
Shuswap	July 3'87	S4	14	10.1
Shuswap	July 18'87	T12	16	10.2
Shuswap	July 19'87	T12	19	14.2
Shuswap	Sep.28'87	T2	20	8.6