Sockeye Salmon (*Oncorhynchus nerka*) Utilization of Quesnel Lake, British Columbia

K.F. Morton and I.V. Williams

Department of Fisheries and Oceans
Biological Sciences Branch
Cultus Lake Research Laboratory
Cultus Lake, British Columbia, VOX 1HO

August 1990

**Canadian Technical Report of
Fisheries and Aquatic Sciences
No. 1756**

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K.F. Morton and I.V. Williams[1]

Department of Fisheries and Oceans
Biological Sciences Branch
Cultus Lake Research Laboratory
Cultus Lake, British Columbia, VOX 1HO

[1]Department of Fisheries and Oceans
Biological Sciences Branch
Pacific Biological Station
Nanaimo, British Columbia, V9R 5K6

Cat. No. Fs 97-6/1756E ISSN 0706-6457

Correct citation for this publication:

Morton, K.F. and I.V. Williams. 1990. Sockeye salmon (*Oncorhynchus nerka*) utilization of Quesnel Lake, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1756: 29 p.

ABSTRACT

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Field studies investigating the utilization of nearshore and pelagic areas of Quesnel Lake British Columbia by underyearling sockeye salmon (*Oncorhynchus nerka*) were conducted during a dominant cycle year, 1982. Nearshore and pelagic sockeye distributions were documented using hydroacoustic and visual observations, while growth and diet information were obtained from samples captured with a midwater trawl. Zooplankton community structure was determined from stratified samples collected in horizontal tows. Sockeye distribution was highly variable with dense concentrations of fish occurring near shore before moving to the pelagic zone. Pelagic distribution was also highly variable with sockeye density ranging from <500 - 8000 fish$\cdot$ha^{-1}. Sockeye pelagic growth appeared to be density-dependant with lowest estimated growth rates occurring in areas of high fish concentrations. Zooplankton were the dominant prey of sockeye in both nearshore and pelagic areas with consumption shifting from *Leptodiaptomus* to *Daphnia* as sockeye juveniles became pelagic. Lake thermal structure had a substantial effect on the vertical distribution of both sockeye and their zooplankton prey. Sockeye remained within the hypolimnion while a major portion of the zooplankton community (75%) occurred in the epilimnion. The unequal vertical and areal distribution of sockeye in Quesnel Lake may play a key role in the rearing capacity and future production potential of the lake.

Key Words: (*Oncorhynchus nerka*) underyearlings, migration, distribution, feeding behaviour, growth rates, zooplankton.

RÉSUMÉ

Morton, K.F. and I.V. Williams. 1990. Sockeye salmon (*Oncorhynchus nerka*) utilization of Quesnel Lake, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1756: 29 p.

Des études sur le terrain concernant l'utilisation des zones prélittorales et pélagiques du lac Quesnel, en Colombie-Britannique, par le saumon rouge de moins d'un an (*Oncorhynchus nerka*) ont été effectuées au cours d'un cycle annuel dominant, soit 1982. Les distributions prélittorales et pélagiques du saumon rouge ont été déterminées à partir d'obsevations hydroacoustiques et visuelles, tandis que les données sur la croissance et le régime alimentaire ont été obtenues à partir d'échantillons prélevés à l'àide d'un chalut mésopélagique. La structure de la communauté zooplanctonique a été établie à partir d'échantillons stratifiés prélevés dans des traits horizontaux. La distribution du saumon rouge variait considérablement, les concentrations denses de poissons étant observées près du rivage avant la migration vers la zone pélagique. La distribution pélagique était également extrêment variable avec des densités de saumon rouge comprises entre moins de 500 à 8 000 poissons·ha^{-1}. La croissance pélagique du saumon rouge semblait être fonction de la densité, les taux de croissance estimés les plus bas ayant été observés dans les zones de concentrations élevées de poissons. Le zooplancton était la praie dominante du saumon rouge dans les zones prélittorales et pélagiques, la consemmation present de *Leptodiaptomus* à *Daphnia* au fur et à mesure que le saumon rouge juvénile devenait pélagique. La structure thermique du lac avait un effet notable sur la distribution verticale du saumon rouge et de leure proies zooplanctoniques. Le saumon rouge rectait dans l'hypolimnion tandis que la majeure partie de la communaute zooplanctonique (75%) se trouvait dans l'épilimnion. L'inégalité de la distribution verticale et en superficie pour le saumon rouge dans le lac Quesnel peut jouer un role olé dans la capacité d'élevage et la potential futur de production du lac.

Mots clé: alevins de moins d'un an (*Oncorhynchus nerka*), migration, distribution, comportement alimentaire, taux de croissance, zooplancton.

INTRODUCTION

Sockeye salmon (*Oncorhynchus nerka*) are commercially the most valuable of the five species of Pacific salmon in British Columbia, with the Fraser River system being the major producer of these anadromous stocks. Since juvenile sockeye spend from one to two years of their early life history in lakes prior to migrating to the sea, the freshwater environment is an important element affecting sockeye growth and survival.

Quesnel Lake is one of the major sockeye salmon producers in the Fraser system with total run size exceeding eleven million adults during recent peak years. In addition, there are proposals to further enhance Quesnel sockeye stocks by construction of artificial spawning channels, increasing natural spawning habitat and lake fertilization. Consequently, interest developed concerning the lake's ability to support increased numbers of juvenile sockeye. Further, logging activity next to Quesnel Lake raised some concerns regarding within lake distribution and dispersal of juvenile sockeye, particularly since logging could directly affect a substantial portion of the lake's littoral zone.

Although there is little published information on the early life stage of Fraser sockeye, there are numerous publications dealing with juvenile sockeye in other watersheds. Early investigations focused on the pelagic distribution of juvenile sockeye (Johnson 1958, 1961). Construction of an artificial spawning channel adjacent to Babine Lake led to numerous studies comparing growth and survival of fry reared in natural and artificial streams (Larkin and McDonald 1968, McDonald 1969). Diel vertical movements of juvenile sockeye as well as feeding behaviour were examined by Narver (1970), McDonald (1973) and Beacham and McDonald (1982). Recent studies have associated sockeye density with growth of Bristol Bay juvenile sockeye in Alaskan lakes (Rogers 1973, 1980) and later reported effects of fertilization on the food supply and growth of Little Togiak Lake juvenile sockeye (Rogers et al. 1982). More recently, Kyle et al. (1988) have linked increased sockeye density with reduced sockeye production in Frazer Lake, Alaska.

Studies of juvenile sockeye rearing in Fraser lakes have centred on determining zooplankton standing crop as a means of estimating the capacity of selected nursery lakes to support sockeye populations (Foerster 1925; Ricker 1934; Ward 1957, 1964; Geen and Andrew 1961; Goodlad et al. 1974). These estimates of rearing capacity relied on zooplankton measurements alone and assumed sockeye were distributed equally throughout the lake. To date, there are no published studies that focus on nearshore dispersal of juvenile sockeye, or on their pelagic distribution within Fraser nursery lakes. This study documents juvenile sockeye nearshore dispersal, offshore spacial distribution, and feeding in Quesnel Lake in order to identify areas where fish production may be limited. Implications of within lake sockeye distribution to future enhancement as well as potential effects of logging on sockeye production are reported.

STUDY LAKE DESCRIPTION

Quesnel Lake is a dimictic lake in the Columbia Mountain region of central British Columbia (52°N, 121°W) (Fig. 1). The interior climate and moderate elevation (725 m) result in a mean winter temperature of -10°C and ice cover over portions of the lake from January to May. A mean annual precipitation of <75 cm and a relatively small drainage area (5930 km^2) for a Fraser system lake of this size (surface area 270 km^2; mean depth 158 m) results in a low flushing rate and long theoretical water renewal time (10.8 y) (Stockner and Shortreed 1983). The lake is divided into three arms which converge at a central 20 km^2 junction area. Main Arm covers 87 km^2 and has a mean depth of 120 m; North Arm is 64 km^2 in area and has a mean depth of 130 m; and East Arm has an area of 100 km^2 and a mean depth of 218 m. Littoral areas are limited with the most extensively developed areas occurring in Main Arm. There are two major tributaries and sockeye spawning sites: the Horsefly River which empties into Main Arm, and the Mitchell River which discharges into North Arm. Adult sockeye escapement to the Quesnel system in 1981, the peak year of a 4-yr cycle, was 750,000 with 90% spawning in the Horsefly River; 9% in the Mitchell River; and 1% in small East Arm streams (IPSFC 1982). Most juveniles rear in the lake for 1 y before migrating seaward as smolts through the Quesnel River which flows 80 km Northwest to the Fraser River.

METHODS

LAKE TEMPERATURE

Lake temperature profiles were obtained at 2 pelagic stations in each arm with a mechanical bathythermogragh calibrated against a mercury thermometer. Recordings were taken every 5 m from the surface to 60 m. Surface water temperatures were recorded during May and June at 50 observation sites located along the lake shore.

ZOOPLANKTON

Zooplankton samples were collected using 158-um mesh size Clarke-Bumpus samplers (mouth area of 0.20 m^2) (Clarke and Bumpus 1940). Pelagic samples were collected at 1-, 5-, 10-, 15-, 20-, 25- and 30-m depths concurrently with mid-water fish trawls. Littoral samples were taken at 1 m. In addition, both day and night pelagic samples were taken in the junction area to determine diel vertical distribution. Replicate tows (n = 5) were taken on August 24 to determine sampling precision. Net filtration efficiency was assumed to be equal for all stations and sample dates (Ward 1957). Samples of 1200 L were concentrated into 150 mL glass jars and preserved in a borax-buffered, 4% formalin-sucrose solution (Haney and Hall 1973). Zooplankton were identified to genus from descriptions in Balcer et al. (1984). In addition, crustacea in 3 representative samples were identified to species to provide a detailed species list. Abundances were estimated from beaker-split subsamples (Van Guelpen et al. 1982) and converted to density per m^3.

SOCKEYE DISTRIBUTION

A description of sockeye littoral migration was based on weekly visual and hydroacoustic observations between May 12 and June 24, 1982. To facilitate analysis, observations were partitioned into six 1-wk intervals. Visual observations were made from 50 shore sites located uniformly around the lake perimeter and focused on estimates of sockeye density, swimming speed, direction of travel and orientation within the water column. Density was determined by classifying the numbers of sockeye underyearling present within the boundaries of a 1.0 m^2 quadrate into the following groups: none, no fish present; low, 1-100 fish present; medium, 100-1000 fish present; high, >1000 fish present. Swimming speed was determined by timing sockeye ($n = 10$) moving between two spikes set 5 m apart along the shoreline and direction was determined with a compass.

Day and night hydroacoustic data were collected along a series of transects perpendicular to the longitudinal axis of the lake to determine if sockeye moved off shore at any time during early migration (Fig. 1). Transects were marked with reflectors so they could be located during the night. Boat speed was held constant at 2.0 $m{\cdot}s^{-1}$ for each transect. In addition, hydroacoustic data were collected on August 18-25 and October 20-27 between 2230-0400 h to document juvenile sockeye pelagic distribution. These data were collected after sunset since juvenile sockeye in the pelagic zone are generally best distributed for acoustic detection during hours of darkness (Burczynski and Johnson 1986).

The hydroacoustic syst onsisted of a SIMRAD EY-M scientific echo sounder equipped with TVG cir uitry, a 70 kHz narrow beam (11°) transducer mount d in a v-fin towed body and a eel to reel tape recorder for storing data. Both the echo sounder and re rded data were monitored during sampling with a Tektronix 214 oscilloscope. Recorded data were echo integrated in 2 min segments and subsequent fish target density estimates were determined by the duration-in-beam signal processing technique (Thorne 1988). Fish target density was transformed to sockeye density estimates using species composition of trawl catches and expressed as abundance per hectare over the surface area represented by each transect.

Sockeye diel vertical distribution in the pelagic zone was determined on August 19 and October 21. On each occasion, hydroacoustic data were collected hourly for 24 hours along transect 6.

SOCKEYE GROWTH AND DIET

Pelagic sockeye were captured in August and October using a 3 m x 6 m mid-water trawl net at 6 mid-lake stations (Fig. 1). Tow speed was 0.5 $m{\cdot}s^{-1}$ and ranged from 5-20 min duration depending on fish density. Littoral samples were collected weekly during sockeye shore migration using a hand dipnet at various locations along the migration routes. All specimens were anaesthetized in 2-phenoxyethanol to avoid regurgitation of stomach contents, then were preserved in 10% formalin solution. Fork lengths were measured after one month in solution to stabilize shrinkage (Parker 1963), and instantaneous rates of growth (Ricker 1975) were computed from mean length values.

Twenty-five sockeye were randomly selected from each trawl and dipnet sample for stomach content analysis. Only food items in the esophagus and cardiac portion of the stomach were identified to avoid bias related to differential digestion of prey. Food preference was characterized by Ivlev's (1961) electivity index which is a ratio of food items ingested, to food items available in the environment. The index has a range of -1 to +1 with negative values indicating an avoidance of potential prey; zero indicating random selection; and positive values indicating active selection. Ivlev's index has been criticized for being biased for scarce prey (Strauss 1979). However an alternate index proposed by Strauss (1979) which reduces this bias is not appropriate for comparisons of field samples collected on different dates when the relative abundance of prey changes (Confer and Moore 1987). Therefore, we chose Ivlev's index for our analysis, but excluded uncommon zooplankton genera.

RESULTS

LAKE TEMPERATURE

Following ice breakup in mid May, the water column at all 6 pelagic stations was isothermal at 4°C. Surface water at stations in North and Main Arm warmed rapidly during the last 2 wks in May with temperatures reaching 10 and 12.5°C respectively. The water column was well stratified with an epilimnion depth of 4 m in Main Arm and 5 m in North Arm. By contrast, East Arm was still isothermal at the end of May with a temperature of 4°C. On the last sampling date, June 24, surface temperatures in Main Arm were 16.5°C and a strong thermocline occurred between 5-10 m. Thermal discontinuity was less pronounced at North Arm stations, with a weak thermocline between 5-14 m. Surface temperatures at East Arm stations were 8°C and thermal stratification was not evident. Shore temperatures varied from 4°C in early May to 18°C in June. In general, the littoral zone was 2°C warmer than offshore stations except in East Arm where there was no difference between offshore and nearshore temperatures.

In August, mean surface temperature in Main Arm was 16.5°C and 15°C in North Arm. The water column was well stratified with a strong thermocline occurring between 10-15 m in both arms. Mean surface temperature in East Arm was 12°C and a broader, less distinct thermocline was present between 10-30 m. The lake had cooled noticeably in October with mean surface temperatures in Main Arm of 8°C and a reduced thermocline present between 25-35 m. Surface temperatures at stations in North and East Arms in October varied between 5-6°C and thermal stratification was absent.

SOCKEYE NEARSHORE DISTRIBUTION

Sockeye fry were first seen entering Main Arm from the Horsefly River on May 17 when several schools of <100 individuals were sighted within 1 km of the river mouth. These low density schools remained within the influence of the turbid river plume and showed no clear directional movement. First observations of underyearling sockeye in North Arm occurred 5 days later (May

22) when low numbers were seen holding at the mouth of the Mitchell River (Fig. 2). By this time, high density schools were seen in littoral zone of Main Arm along the south shore up to 5 km east of the Horsefly River and several low density schools were sighted along the south shore of Cariboo Island. Fry in these areas were surface oriented, although they immediately sounded to the lake bottom when disturbed.

By the third week of observations (May 29), a continuous, surface oriented, high density band of migrating underyearlings extended eastward in Main Arm from the Horsefly River along the south shore for a distance of 12.5 km with low density schools dispersed a further 2.5 km. This band of fish was spread up to 5 m from shore. In North Arm, low density schools were present along both shorelines up to 5 km south of the Mitchell River.

Shoreline migration continued through the fourth and fifth weeks (June 5 and June 12) with high density schools extending along both north and south shores of Main Arm between the Horsefly River and junction area with only periodic sightings of low density schools in the western portion between the Horsefly and Quesnel Rivers. Low densities of Mitchell River sockeye extended south for 20 km along both east and west shores of North Arm.

In the sixth week (June 19), sockeye numbers in shore areas diminished as did their shore migration. Instead, large concentrations of fish were seen on the surface up to 200 m from shore in both Main and North Arms. Until this time, there was no evidence of sockeye in East Arm.

It was not possible to obtain reliable hydroacoustic estimates of sockeye numbers during early migration because of their shore orientation. However, it was possible to determine relative densities in different lake areas using hydroacoustics. These data confirmed that sockeye not only remained shore oriented during the day but during hours of darkness as well.

Sockeye swimming speeds during nearshore migration ranged from 1.0 to 1.5 $m \cdot min^{-1}$ with a mean of 1.4 $m \cdot min^{-1}$ +/- 0.1. Based on a mean swimming speed of 1.4 $m \cdot min^{-1}$ for 24 h, Quesnel Lake sockeye had a nearshore dispersal rate of 2 $km \cdot day^{-1}$ +/- 0.15.

SOCKEYE OFFSHORE DISTRIBUTION

During August 18-25 sampling, sockeye underyearlings were well dispersed in the pelagic zone, making hydroacoustic estimates of fish abundance possible (Fig. 3). Densities in Main Arm ranged from <1000 $fish \cdot ha^{-1}$, between the Horsefly River and Quesnel River (transects 1, 2, and 3), to 7500 $fish \cdot ha^{-1}$ along transect 5. Moderate densities of 2000-3000 $fish \cdot ha^{-1}$ were found in the junction area and into East Arm at transects 11 and 12. Low densities of <1000 $fish \cdot ha^{-1}$ occurred in North Arm and even fewer, <500 $fish \cdot ha^{-1}$, were found in most areas of East Arm.

During the October 20-27 survey, sockeye distribution was concentrated in the 20 km^2 junction area with a density of 8000 $fish \cdot ha^{-1}$. In contrast, densities <1000 $fish \cdot ha^{-1}$ occurred in North and East Arms while densities in Main Arm reached only 1500 $fish \cdot ha^{-1}$.

VERTICAL DISTRIBUTION

The behaviour of sockeye underyearlings changed considerably after moving to the pelagic zone. Shore oriented sockeye found in shallow water did not avoid sunlight by seeking cover. In contrast, during their pelagic phase, sockeye undertook substantial diel vertical migrations descending to depths >80 m at dawn and ascending to relatively shallow depths at twilight (Fig. 4.) Although this migration was evident during both August and October surveys, there were obvious differences in the range of vertical distances travelled. In August, hydroacoustic fish targets observed along transect 6 remained below 80 m during daylight hours and ascended to the thermocline depth (12 m) at dusk. They remained distributed between 12-20 m during the night and descended at dawn to daytime depths at a rate of 0.9 $m \cdot min^{-1}$. In contrast, during the October survey, fish targets occurred higher in the water column (70 m) during the daytime and ascended to 5 m at dusk. At night, they were dispersed between 5-40 m, a much broader distribution than in August, then descended at a rate of 0.2 $m \cdot min^{-1}$ to daytime depths.

SOCKEYE DIET AND GROWTH RATES

Analysis of stomach contents indicated that Quesnel Lake sockeye utilize crustacean zooplankton as their primary food source. Benthic invertebrates and adult insects were not consumed. Prey were acquired selectively and Ivlev (1961) values show that consumption of specific zooplankton prey types shifted seasonally (Fig. 5). *Leptodiaptomus* was the primary prey in nearshore areas during early migration (May 12-June 10). However, during the later stages of migration (June 10-24) prey consumption shifted to *Daphnia* which remained the dominant prey of sockeye in the pelagic zone during August sampling. In October, although *Eubosmina* was the predominant prey numerically, stomach volume was comprised primarily of *Daphnia*.

Upon entering the lake, fry from the Horsefly were larger than Mitchell sockeye with mean fork lengths of 25.0 mm and 23.6 mm, respectively. Although sockeye were measured at various times and locations during shore migration, littoral growth rates were not determined because their was no way of assuring that samples were representative of the total sockeye population. Obtaining reliable growth estimates during shore migration was further hindered by the continuous immigration and emigration of different size groups of sockeye at sample sites. Pelagic sockeye growth estimates, however, were based on mid-water trawl catches. Assuming trawl efficiency was equal for all samples and movement of fish among lake arms was minimal, sockeye in the junction had the lowest August to October growth rate of 2.3 $\mu m \cdot d^{-1}$ while the highest rate of 5.0 $\mu m \cdot d^{-1}$ occurred in North Arm. Sockeye sampled in East Arm and at Stn 1 in Main Arm had estimated growth rates of 3.2 and 3.4 $\mu m \cdot d^{-1}$ respectively.

ZOOPLANKTON DISTRIBUTION AND COMMUNITY STRUCTURE

Two major groups of entomostracan zooplankton - *Copepoda* and *Cladocera* were present in Quesnel Lake (Fig. 6). Copepods included the species *Diacyclops bicuspidatus thomasi*, *Leptodiaptomus ashlandi*, and *Epischura nevadensis*. *Cladocerans* present included *Eubosmina coregoni longispina*, *Daphnia rosea*, *D. longiremis*, *D. longispina*, *Holopedium gibberum* and *Leptodora* *kindtii*. Replicate tows ($n = 5$) taken on August 24 to determine sampling precision resulted in a coefficient of variation (CV) for total copepod and cladoceran numbers of 12.8%. Counts of replicate beaker-splits ($n = 9$) resulted in a CV of 9.3%.

Leptodiaptomus and *Diacyclops* dominated the zooplankton community in all areas during all sample periods with numbers of *Diacyclops* in Main Arm ranging from 750 – 4000$\cdot m^{-3}$ and *Leptodiaptomus* from 1750 – 2650$\cdot m^{-3}$. The exception to this occurred in nearshore areas during sockeye migration when levels of *Leptodiaptomus* dropped to 350$\cdot m^{-3}$. Mean *Daphnia* abundance was highest in Main Arm ranging from 120$\cdot m^{-3}$ in early May to 1250$\cdot m^{-3}$ in mid June. Numbers then declined to 750$\cdot m^{-3}$ in August and <100$\cdot m^{-3}$ in October (Fig. 7). *Eubosmina* abundance was low (<300$\cdot m^{-3}$) until October when their numbers increased, ranging from 1125 – 1300$\cdot m^{-3}$. *Epischura* were rare (<50$\cdot m^{-3}$) during all sample periods.

Vertical distribution appeared to be influenced by temperature. During the second week of the study, before formation of a distinct thermocline, zooplankton were evenly distributed between the surface and 30 m. However, after formation of a stable thermocline, zooplankton distribution was stratified with 75% of the standing crop occurring between 0–10 m (Fig. 4). In October, after weakening of thermal stratification, zooplankton were more evenly distributed in the water column between 0-25 m. Vertical samples collected over 24 h in August and October gave no indication of zooplankton diel vertical movement.

DISCUSSION

NEARSHORE MIGRATION

This study, in documenting the littoral and pelagic distribution of juvenile sockeye in Quesnel Lake, has identified areas where sockeye production may be limited. After leaving the Horsefly and Mitchell rivers, juvenile sockeye utilized portions of the littoral zone in Main and North Arms for a period of six weeks or ca. 10% of their lacustrine life stage before moving off shore (Fig. 8). Initially, newly emerged sockeye fry congregated briefly within plumes of their respective nursery streams before beginning shore oriented migration 1-wk later. This type of behaviour has been suggested to have a survival benefit through predator "swamping" or depensatory mortality (Ward and Larkin 1964).

Shore migration began shortly after fry entered the lake (May 20) and continued uninterrupted for 5-wks (May 20–June 24). During this time, high concentrations of surface oriented sockeye dispersed along well defined migration routes within 5 m of shore for up to 25 km from the Horsefly River and 20 km from the Mitchell River. Fry densities occurring along these migratory were much greater than would later occur in the pelagic zone. Our observation of the nearshore migration of juvenile sockeye is consistent with reports in other sockeye lakes in British Columbia and Alaska (McDonald 1969; Rogers 1973; Simms and Larkin 1977). Migratory swimming speeds compared to mean swimming speeds for fry in Babine Lake of 1.0 $m\cdot min^{-1}$ (McDonald 1969) and

1.3 $m \cdot min^{-1}$ for sockeye fry in still water troughs (Hoar 1954). This behaviour may have the advantage of promoting rapid dispersal of fish away from areas of dense concentrations, effectively reducing intra-species competition. Additionally, as Ginetz and Larkin (1976) noted, large piscivore predation may be reduced since migration takes place in shallow water close to shoreline cover.

Regardless of these advantages, numerous studies have linked increased sockeye density and grazing to reduced zooplankton food supply and limited production (Johnson 1961; Mathisen and Kerns 1964; Burgner 1964; Brocksen et al. 1970; Rogers 1980; Kyle et al. 1988). In Quesnel Lake, crowding of sockeye in the littoral zone during shore migration was associated with a decline in nearshore abundance of *Leptodiaptomus*, while at the same time offshore abundance was increasing. We interpreted this as evidence of heavy sockeye grazing pressure. Therefore, since sockeye did not supplement their zooplankton diets with benthic invertebrates, there is a possibility that sockeye production in littoral areas was food limited. Unfortunately, it was not possible to obtain reliable growth estimates of littoral sockeye to provide quantitative evidence of production limitation.

SOCKEYE OFFSHORE DISTRIBUTION

Our observation that sockeye were distributed unequally within the pelagic zone of Quesnel Lake is consistent with observations of sockeye distribution in other sockeye lakes (Foerster 1968; McDonald 1969; Hartman and Burgner 1972; Levy, 1989) (Fig 3). McDonald (1969) suggested that limited dispersal of sockeye which result in increased densities could effectively reduce the rearing capacity of a lake and limit fish production. We believe that the unequal pelagic distribution of sockeye in Quesnel Lake could influence fish production. Evidence of a density-dependent production relationship, resulting from limited dispersal, occurred in the junction area where high sockeye density was associated with low August - October growth rates and a decline in food (*Daphnia*) density. In this way, rearing capacity of Quesnel Lake could be reached sooner than expected from what its total area might indicate.

Diel vertical migration of sockeye in non-turbid lakes is not uncommon and has been the focus of many investigations which are review by Clarke and Levy (1988) and Levy (1989). Contrary to reports of sockeye migrating to the surface at dusk (Narver 1970), sockeye in Quesnel Lake ascended to the thermocline base and did not occur in the epilimnion. Effects of sockeye vertical distribution on production in Shuswap Lake have been reported by Goodlad et al. (1974) who have associated thermal stratification with reduced sockeye growth and production. Similarly, sockeye production in Quesnel Lake could be limited because sockeye appeared to be separated from a major portion (75%) of their potential zooplankton forage by a thermal barrier. In addition, an unequal vertical distribution of sockeye which resulted in high densities at the thermocline base could produce density effects which also limited production. Coupled with the unequal areal distribution of sockeye, we believe there is real concern for production limitation in Quesnel Lake.

SOCKEYE PRODUCTION AND POTENTIAL CONFLICTS WITH LOGGING

Levy and Hall (1985) have suggested that logging activity can potentially effect freshwater production of sockeye both directly by situating log storage facilities in littoral areas or indirectly through changes in pelagic water quality caused by nutrient loading. This study identified areas of Quesnel Lake utilized by sockeye during early migration where impacts of log storage are more likely to occur. These include nearshore areas of Main Arm between the Horsefly River and junction area as well as littoral areas in North Arm. Siting log storage facilities away from these areas would likely minimize possible conflicts with sockeye. In addition, effects of logging activity and nutrient loading on lake water quality should be monitored to document possible impacts on both littoral and pelagic sockeye production.

ENHANCEMENT IMPLICATIONS

The spacial heterogeneity of juvenile sockeye in both pelagic and littoral zones could play a key role in future enhancement strategies designed to increase sockeye production. For instance, lake enrichment schemes limited to areas where sockeye densities are high, such as the junction area and certain Main Arm littoral areas, are likely more appropriate than whole lake applications. Also, increasing the use of under utilized areas of the lake such as East Arm or portions of Main Arm could be beneficial. Moreover, strategies designed to increase fry recruitment such as improving spawning habitat or increasing adult escapement could cause over utilization of the pelagic forage base. Under these circumstances, increased fry recruitment should be coupled with lake enrichment.

Finally, the directional tendency of migrating sockeye is of prime concern if transplanting stocks to different lake areas. For instance, it may not be appropriate to transplant Horsefly sockeye which tend to migrate eastward, to East Arm streams. Alternately, it may be beneficial to move these same fish to locations in Main Arm, west of the Horsefly River. Regardless of the approach(s) taken to enhance sockeye production in Quesnel Lake, distribution and dispersal of juveniles are of prime concern.

ACKNOWLEDGEMENTS

Funding for this study was provided by the International Pacific Salmon Fisheries Commission. R. Johnson provided assistance in analysis of hydroacoustic data. B. Riddell, J. Stockner, K. Hyatt, K. Shortreed, J. Hume and D. Barnes provided critical reviews of this manuscript.

REFERENCES

Beacham, T.D., and J.G. McDonald. 1982. Some aspects of food and growth of fish species in Babine Lake, British Columbia. Fish. Res. Board Can. Tech. Rep. 1057: 23 p.

Blacer, M.D., N.L. Korda, and S.I. Dodson. 1984. Zooplankton of the Great Lakes. The Univ. of Wisconsin Press. Madison Wisconsin, 174p.

Brocksen, R.W., G.E. Davis, and C.E. Warren. 1970. Analysis of trophic processes on the basis of density-dependent functions. p. 468-498. In: Marine Food Chains, J.H. Steele (ed.), Edinburgh, Oliver and Boyd.

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.

Burgner, R.L. 1964. Factors influencing sockeye salmon (*Oncorhynchus nerka*) in lakes of southwestern Alaska. Verh. Int. Ver. Limnol. 15: 504-513.

Clarke, G.L., and D.F. Bumpus. 1940. The plankton sampler. An instrument for quantitative plankton investigations. Spec. Publ. No. 5. Limnol. Soc. Amer.

Clarke, C.W., and D.A. Levy. 1988. Diel vertical migration by juvenile sockeye salmon and the antipredation window. Amer. Nat. 131: 271-290.

Confer, J.L., and M.V. Moore. 1987. Interpreting selectivity indices calculated from field data or conditions of prey replacement. Can. J. Fish. Aquat. Sci. 44: 1529-1533.

Foerster, R.E. 1925. Studies in the ecology of the sockeye salmon (*Oncorhynchus nerka*). Contrib. Can. Biol. 2(16): 335-422.

Foerster, R.E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Bull. Fish. Res. Board Can. 162: 422p.

Geen, G.H., and F.J. Andrew. 1961. Limnological changes in Seton Lake resulting from hydroelectric diversions. I.P.S.F.C. Prog. Rep. No. 8, 76p.

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.

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.

Haney, J.F., and D.J. Hall. 1973. Sugar-coated *Daphnia*: A preservation technique for Cladocera. Limnol. Oceanogr. 18(2): 331-333.

Hartman, W.L., and R.L. Burgner. 1972. Limnology and fish ecology of sockeye salmon nursery lakes of the world. J. Fish. Res. Board Can. 29: 699-715.

Hoar, W.S. 1954. The behaviour of juvenile Pacific salmon, with particular reference to the sockeye (*Oncorhynchus nerka*). J. Res. Board Can. 11: 69-79.

International Pacific Salmon Fisheries Commission. 1982. Annu. Rep. 1981. Int. Pac. Salmon Fish. Comm. Annu. Rep.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven. 302p.

Johnson, W.E. 1958. Density and distribution of young sockeye salmon (*Oncorhynchus nerka*) throughout a multibasin lake system. J. Fish. Res. Board Can. 15: 961-982.

Johnson, W.E. 1961. Aspects of the ecology of a pelagic, zooplankton eating fish. Verh. Internat. Ver. Limnol. 14: 727-731.

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.

Larkin, P.A., and J.G. McDonald. 1968. Factors in the population biology of the sockeye salmon of the Skeena River. J. Anim. Ecol. 37: 229-258.

Levy, D.A., and K.J. Hall. 1985. A review of the limnology and sockeye salmon ecology of Babine Lake. Westwater Tech. Rep. No. 27.

Levy, D.A. 1989. The selective advantage of diel vertical migration behaviour in juvenile sockeye salmon and kokanee (*Oncorhynchus nerka*). Ph.D. Thesis. Univ. British Columbia, Vancouver, B.C. 118p.

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.G. 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.

Mathisen, O.A., and O.E. Kerns. 1964. Abundance, distribution, and size of juvenile red salmon of the 1960 year class in Iliamna Lake Alaska, p. 191-202. *In* George Dahlgren [ed.] Proc. 14th Alaskan Scientific Conf. Am. Assoc. Adv. Sci. Alaska Div.

Narver, D.W. 1970. Diel vertical movement and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Board Can. 27: 281-316.

Parker, R.R. 1963. Effects of formalin on length and weight of fishes. J. Fish. Res. Board Can. 20: 1441-1455.

Ricker, W.E. 1934. Plankton organisms and their relation to the sockeye of Cultus Lake. Biol. Board Canada, Pac. Prog. Rep. No. 21: 14-17.

RICKER, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382p.

Rogers, D.E. 1973. Abundance and size of juvenile sockeye salmon (*Oncorhynchus nerka*) and associated species in Lake Aleknagik, Alaska, in relation to their environment. Natl. Ocean. Atmos. Admin. Fish. Bull. 71(4): 1061-1075.

Rogers, D.E. 1980. Density-dependent growth of Bristol Bay sockeye salmon. *In* W.J. McNeil, D.C. Himsworth [ed.]. Salmonid ecosystems of the North Pacific. Oregon State Univ. Press, pp. 267-283.

Rogers, D.E., B.J. Rogers, and F.J. Hardy. 1982. Effects of fertilization of Little Togiak Lake on the food supply and growth of sockeye salmon. In *In* B.R. Melteff, R.A. Never [ed.] Proceedings of the North Pacific Aquaculture Symposium. Alaska Sea Grant Prog. ASG-82-2 pp. 125-142.

Simms, S.E., and P.A. Larkin. 1977. Simulation of dispersal of sockeye salmon (*Oncorhynchus nerka*) underyearlings in Babine Lake. J. Fish. Res. Board Can. 34: 1379-1388.

Stockner, J.G., and K.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: iv + 63 p.

Strauss, R.E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. Trans. Am. Fish. Soc. 108: 344-352.

Thorne, R.E. 1988. An empirical evaluation of the duration-in-beam technique for hydroacoustic estimation. Can. J. Fish. Aquat. Sci. 45: 1244-1248.

Van Guelpen, L., D.F. Markle, and D.J. Duggan. 1982. An evaluation of accuracy, precision, and speed of several zooplankton subsampling techniques. J. Cons. Perm. Int. Explor. Mer 40: 226-236.

Ward, F.J. 1957. Seasonal and annual changes in availability of the adult crustacean plankters of Shuswap Lake. I.P.S.F.C. Prog. Rep. No. 3. 56p.

Ward, F.J. 1964. Limnology of Kamloops Lake. I.P.S.F.C. Bull. 16. 47p.

Ward, F.J., and P.A. Larkin. 1964. Cyclic dominance in Adams River sockeye salmon. I.P.S.F.C. Prog. Rep. No. 11. 116p.

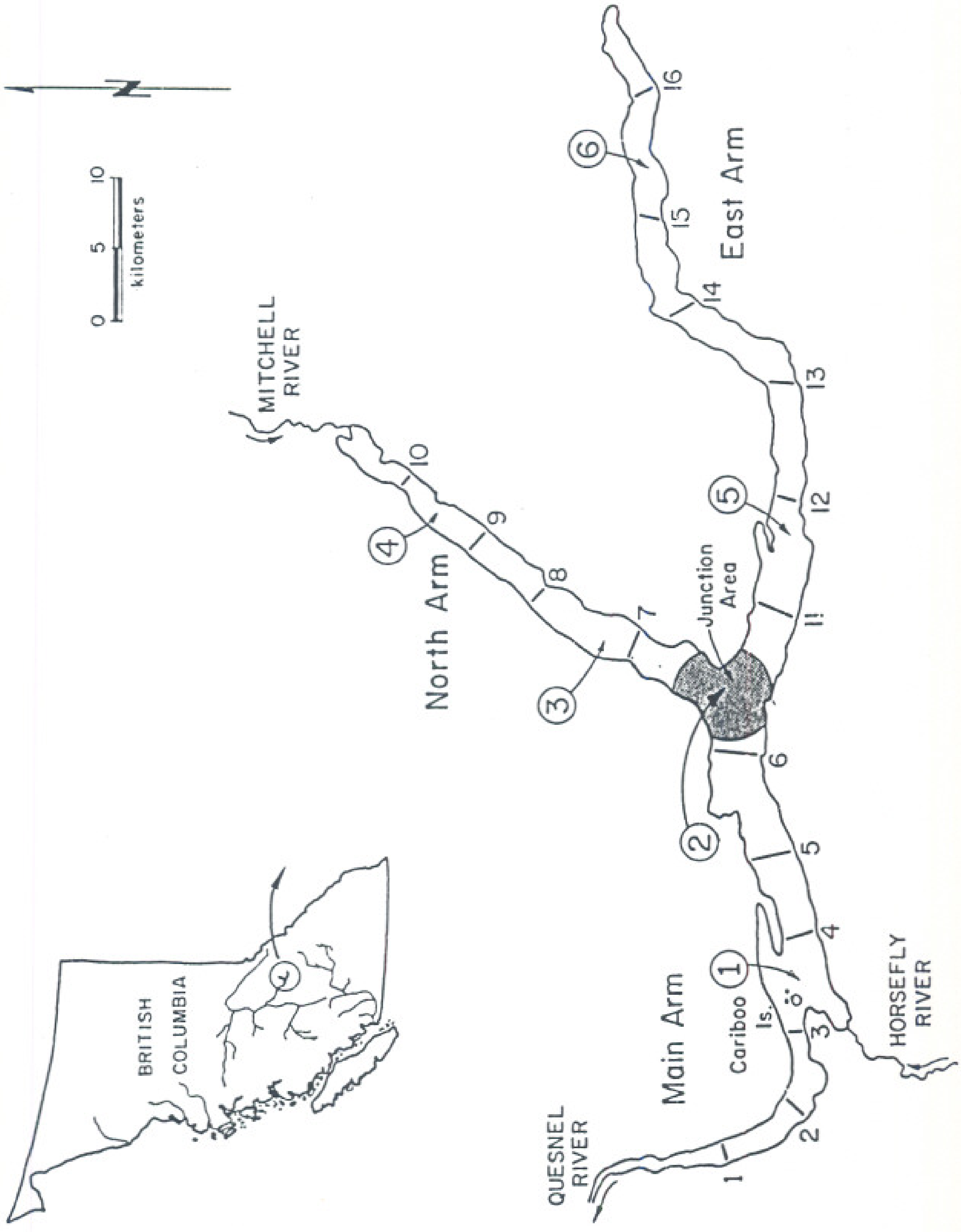

Fig. 1. Map of Quesnel Lake showing the location of hydroacoustic transects and trawl sampling sites.

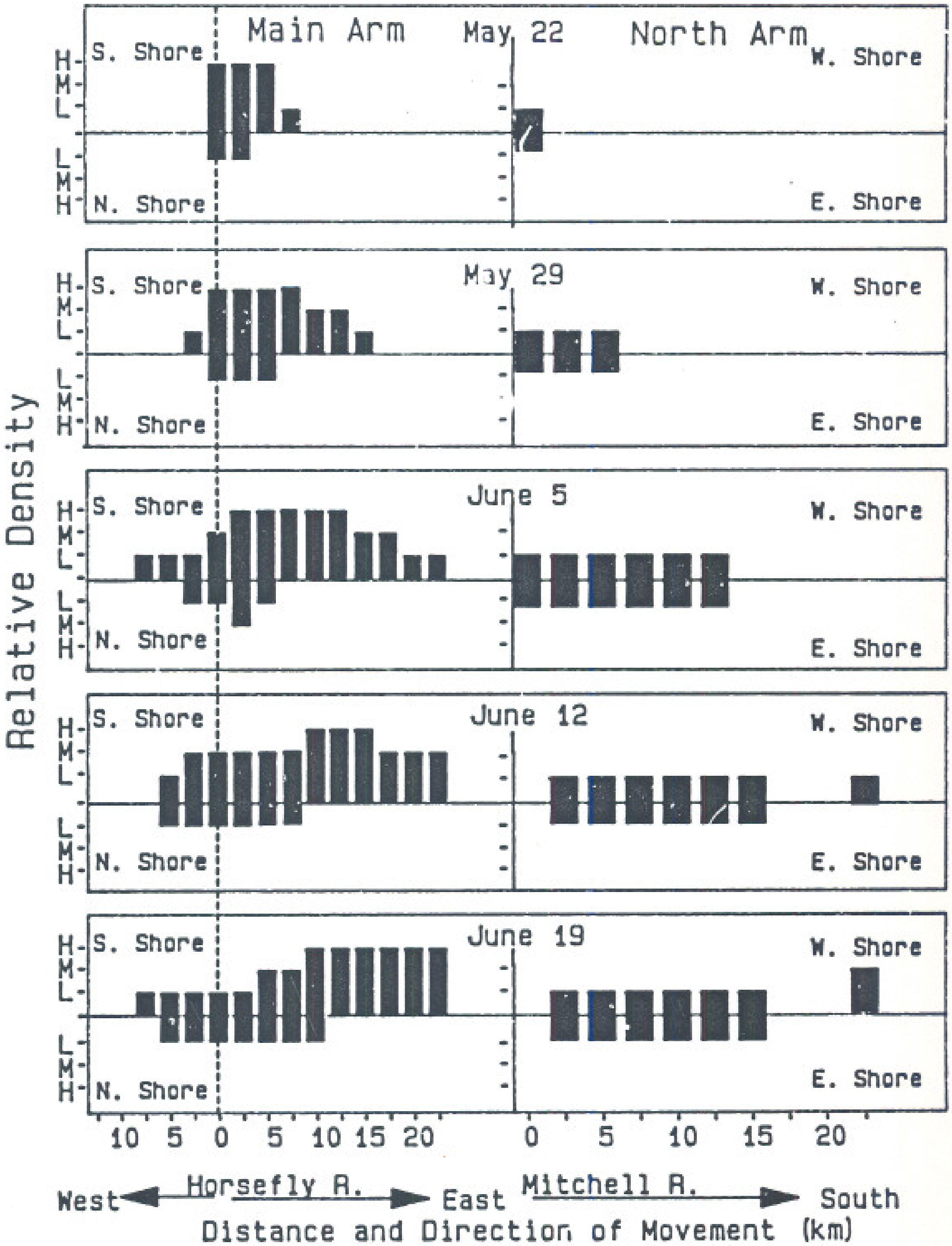

Fig. 2. Shore distribution of juvenile sockeye in Main Arm and North Arm determined by visual observations of High- (>1000 fish$\cdot m^{-2}$); Medium-(100-1000 fish$\cdot m^{-2}$); and low- (1-100 fish$\cdot m^{-2}$) sockeye abundance.

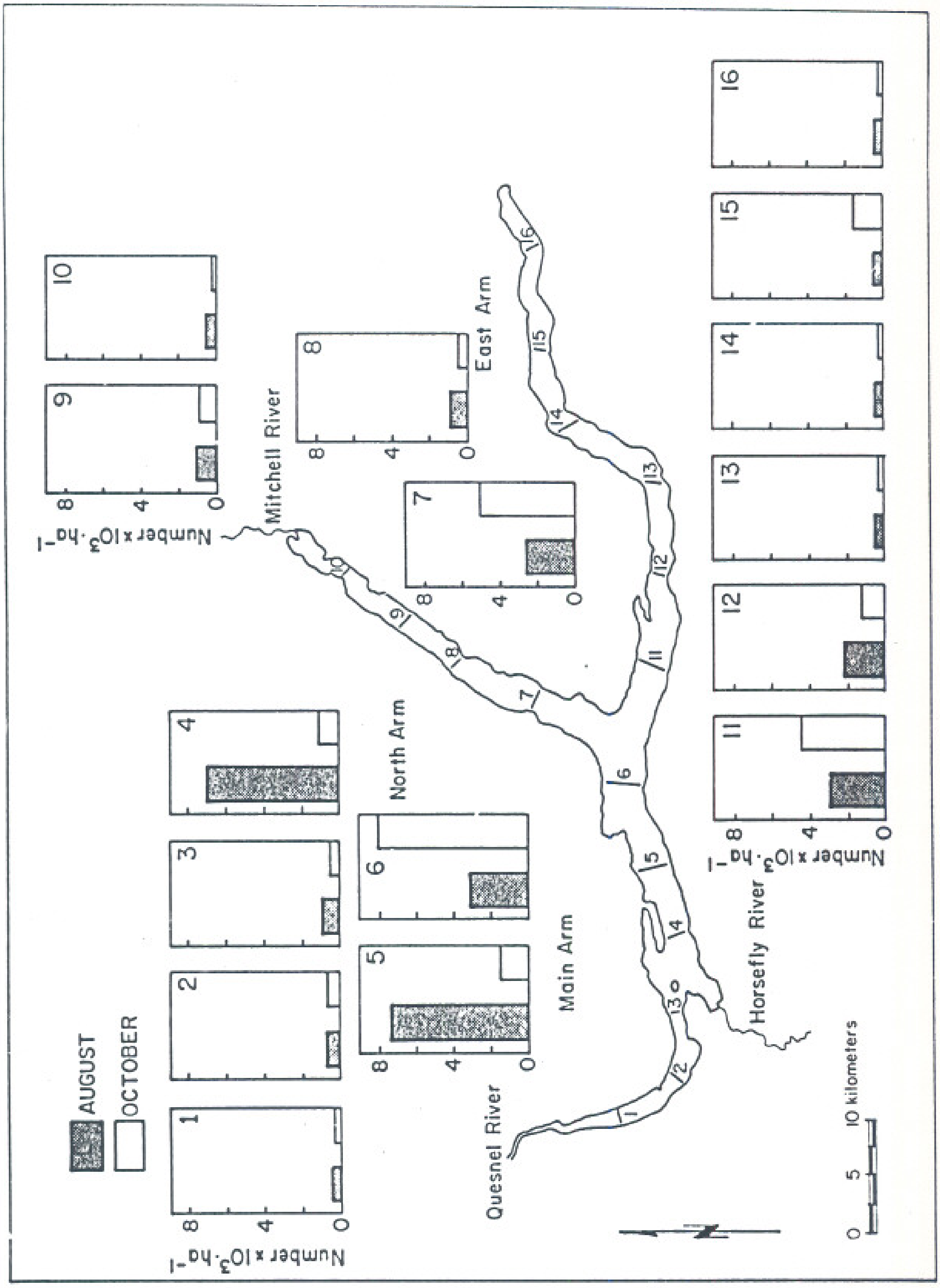

Fig. 3. Juvenile sockeye distribution during August and October determined by hydroacoustic echo integration.

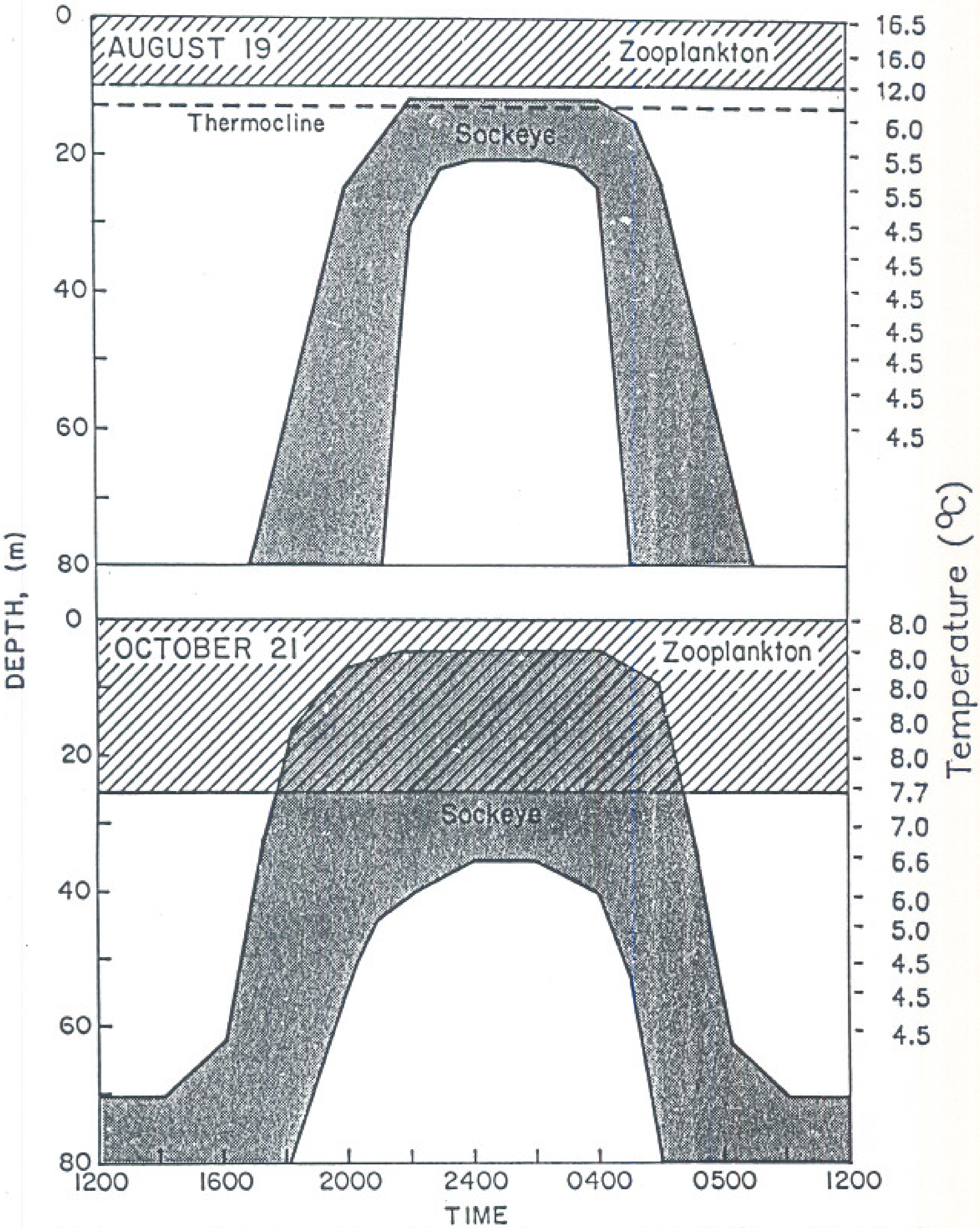

Fig. 4. Diel vertical distribution representing 75% of the juvenile sockeye population and 75% of the zooplankton biomass occurring in the junction area.

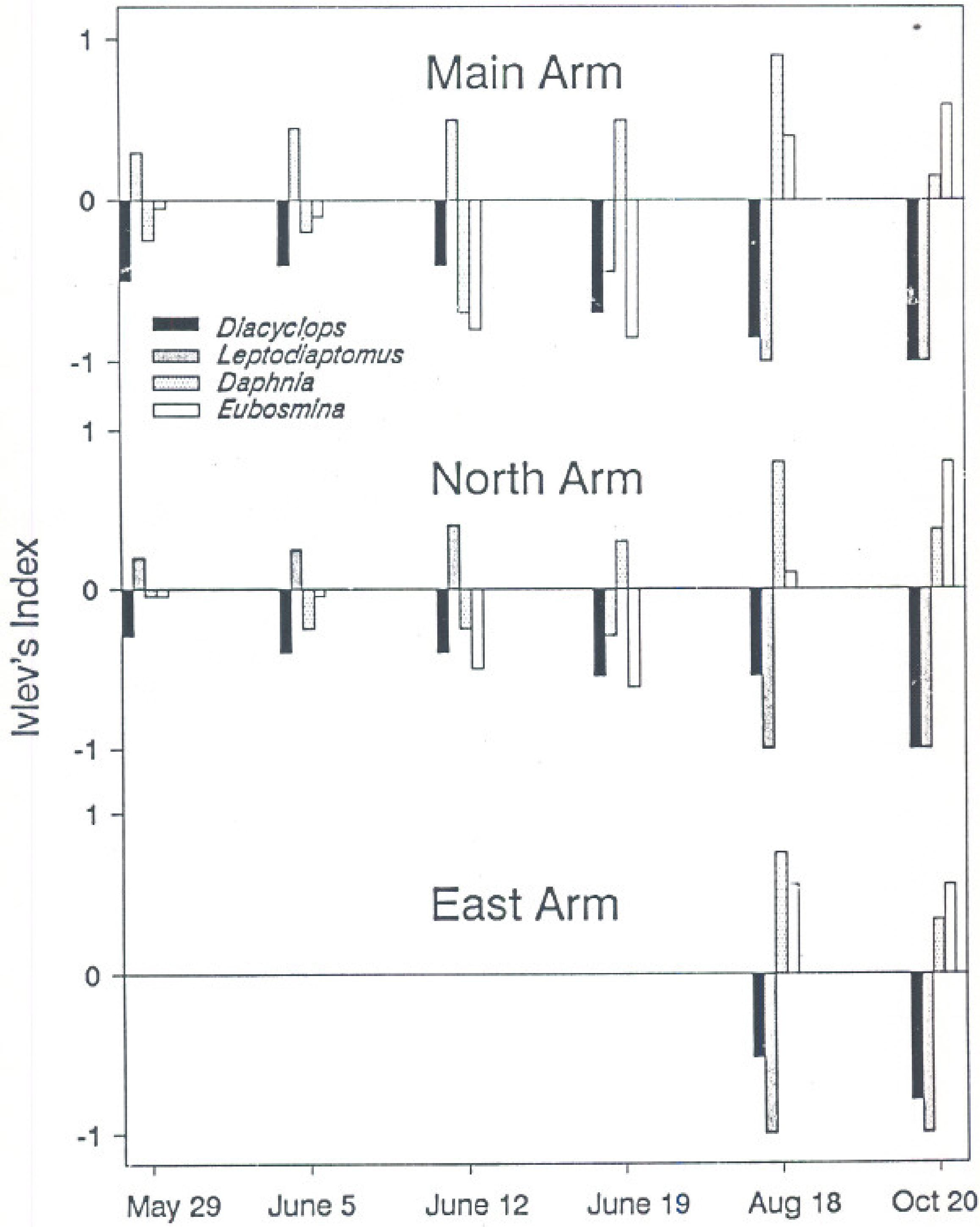

Fig. 5. Electivity indices determined for juvenile sockeye consumption of zooplankton prey in the 3 arms of Quesnel Lake.

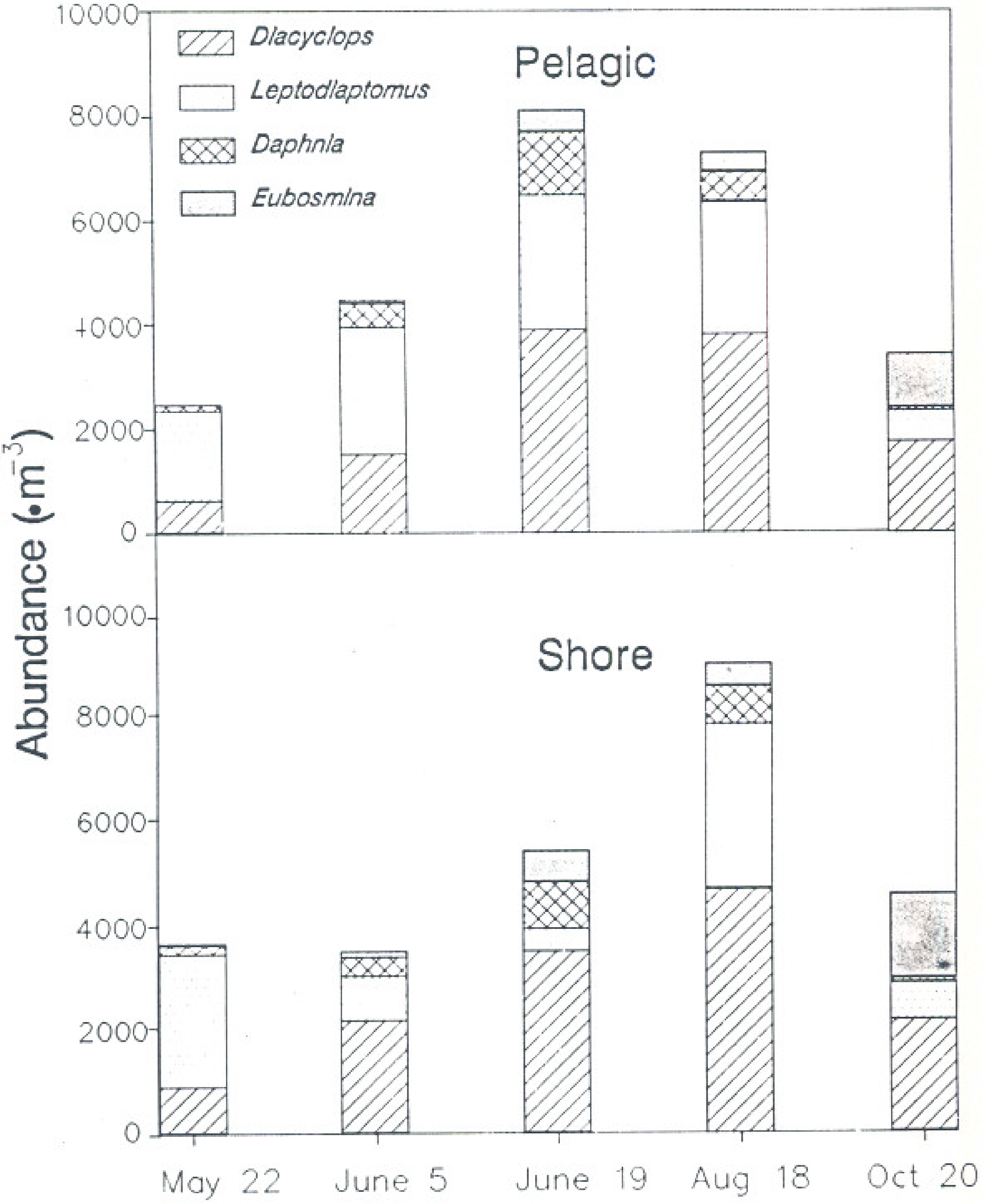

Fig. 6. Mean zooplankton abundance in shore and pelagic areas of Quesnel Lake.

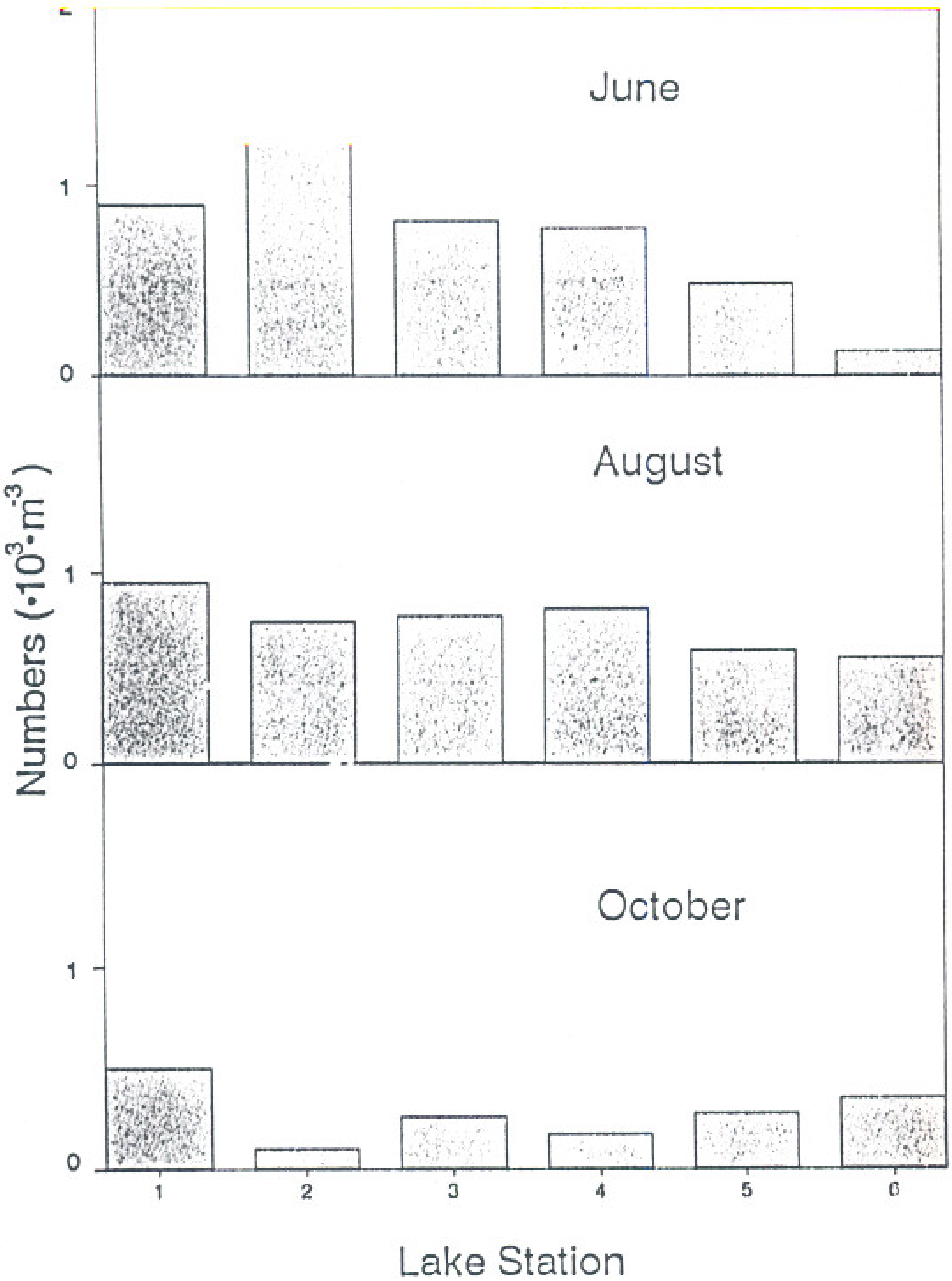

Fig. 7. Seasonal abundance of *Daphnia*, the primary forage of Quesnel Lake juvenile sockeye.

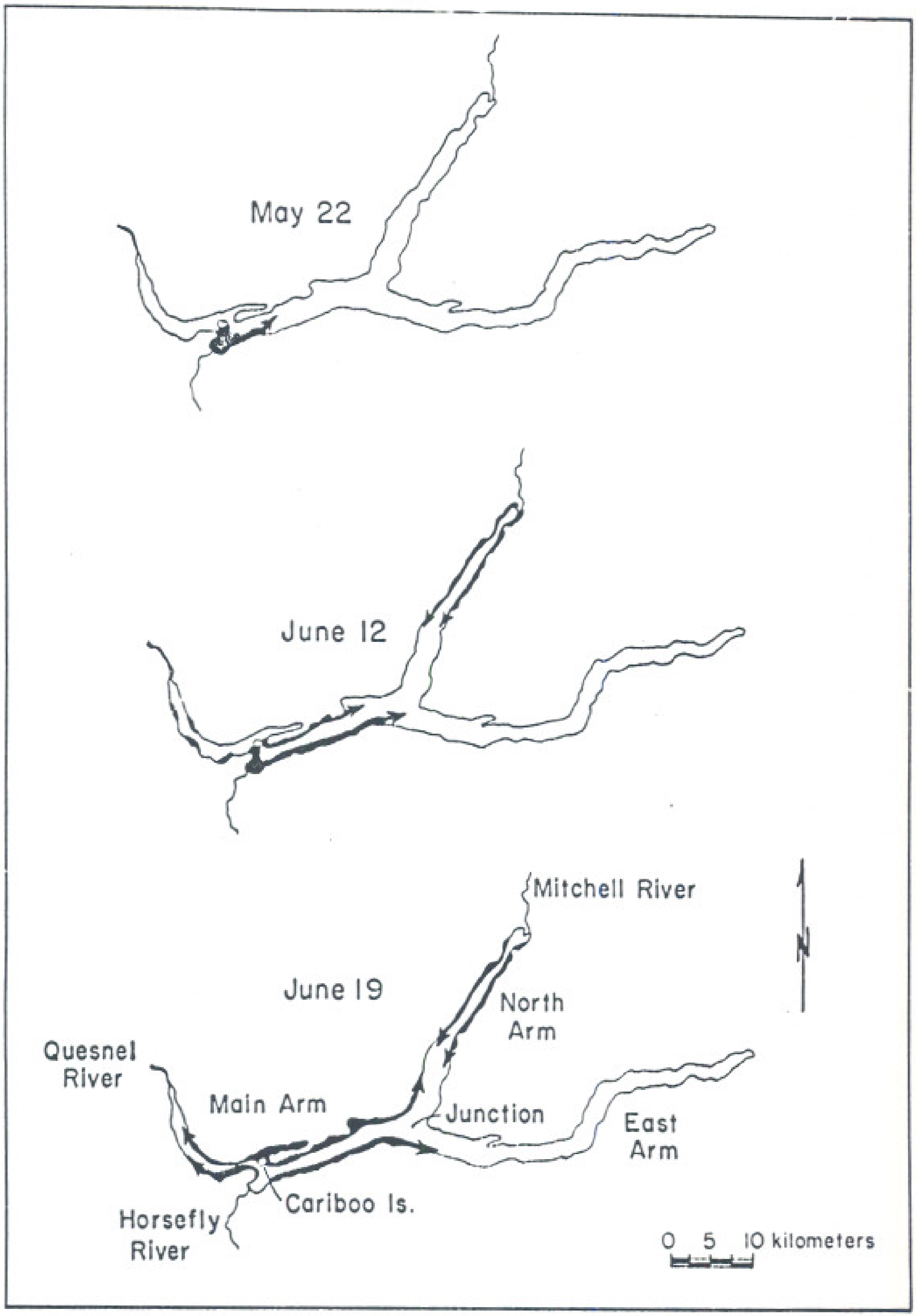

Fig. 8. Map of Quesnel Lake summarizing the early nearshore migration of juvenile sockeye.