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Factors Affecting the Production of Juvenile Sockeye Salmon (*Oncorhynchus nerka*) in Shuswap and Quesnel Lakes, British Columbia

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FACTORS AFFECTING THE PRODUCTION OF JUVENILE SOCKEYE SALMON (*Oncorhynchus nerka*) IN SHUSWAP AND QUESNEL LAKES, BRITISH COLUMBIA

by

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Abstract

Hume, J.M.B., I.V. Williams, and K.F. Morton, 1994. Factors affecting the production of juvenile sockeye salmon (*Oncorhynchus nerka*) in Shuswap and Quesnel Lakes, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1990:23p.

The 4-yr cycles in abundance, characteristic of many Fraser River stocks of sockeye salmon (*Oncorhynchus nerka*), provided an opportunity to study the effects of fry density on sockeye production. We examined juvenile sockeye density, growth, biomass, and survival, and the density and species composition of macrozooplankton over a wide variety of initial (emergent) sockeye densities in Shuswap and Quesnel lakes where spawning densities have respectively ranged from 0.5 - 45.8 and 2.8-19.6 spawners·ha^{-1} of lake surface area. Increased densities of emerged fry resulted in increased densities of autumn fry but only to an asymptote at 5,000 fry·ha^{-1}. Mean fry size decreased as fry density increased but was never less than 2 g. Thus autumn biomass also increased with density. The maximum estimated densities of 6,000 emergent fry·ha^{-1} and 22,000 fry·ha^{-1} in Quesnel and Shuswap lakes has not exceeded the rearing capacity of these lakes. Biomass and production of similarly sized spawning runs were positively correlated with mean growing temperature.

Résumé

Hume, J.M.B., I.V. Williams, and K.F. Morton. 1994. Factors affecting the production of juvenile sockeye salmon (*Oncorhynchus nerka*) in Shuswap and Quesnel Lakes, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1990:23p.

Les cycles d'abondance de quatre ans, caractéristiques de nombreux stocks de saumon rouge (*Oncorhynchus nerka*) du Fraser, ont permis d'étudier les effets de la densité, la croissance, la biomasse et la survie des saumons rouges juvéniles, et la densité et la composition en espèces du macrozooplancton sur une gamme très variée de densités initiales à l'émergence de saumon rouge dans les lacs Shuswap et Quesnel où les densités de géniteurs s'établissaient respectivement entre 0,5 et 45,8 et entre 2,8 et 19,6 géniteurs par hectare de l'aire de la surface du lac. Un accroissement des densités d'alevins émergés a entraîné une augmentation de la densité des alevins d'automne, mais seulement jusqu'à une asymptote à 5 000 alevins par hectare. La taille moyenne des alevins diminuait avec l'augmentation de la densité, mais elle n'était jamais inférieure à 2 g. A l'automne, la biomasse augmentait donc aussi avec la densité. Les densités maximales estimées de 6 000 alevins émergents par hectare et de 22 000 alevins par hectare dans les lacs Quesnel et Shuswap n'ont pas dépassé la capacité d'alevinage de ces lacs. On a établi des corrélations positives entre la biomasse et la production de remontes de taille similaire et la température moyenne de croissance.

INTRODUCTION

The lakes of the Fraser River system are some of the largest producers of sockeye salmon (*Oncorhynchus nerka*) in the world (Northcote and Larkin 1989). Within the Fraser system, Shuswap and Quesnel lakes receive the largest spawning escapements of sockeye and are of primary importance to the commercial fishery. Escapements to these lakes have increased to record levels in recent years but little is known about the effect successive years of high escapements may have on the community ecology of the lakes. A large body of sockeye ecology literature exists, but relatively few studies have focused on the ecology of juvenile sockeye in Fraser River lakes. Goodlad et al. (1974) reported on factors affecting growth in Shuswap, Chilko, Cultus and Fraser lakes. Williams et al. (1989) studied Shuswap Lake, and Morton and Williams (1990) investigated the early distribution of sockeye fry in Quesnel Lake.

In many Fraser River lakes, abundance of sockeye exhibit a 4-yr cycle (Ward and Larkin 1964; Walters and Staley 1987). In Shuswap and Quesnel lakes there is a cycle year of high abundance known as the dominant year (1974, 1978, etc., in Shuswap; 1973, 1977, etc., in Quesnel), followed by a cycle year of intermediate abundance (the subdominant year), followed by 2 years of very few fish (nondominant years). Recent total escapements range from 7,600 in nondominant years to 3,090,000 in dominant years in Shuswap lake and from 200 to 1,330,000 in Quesnel Lake (Fig. 1).

From 1975 to 1985, investigators with the International Pacific Salmon Fisheries Commission (IPSFC) conducted surveys of limnetic juvenile sockeye and the macrozooplankton community in various lakes of the Fraser River watershed. The main purpose of these surveys was to obtain population estimates of juvenile sockeye which could be used for the estimation of future adult run size. As a consequence, most sample dates were somewhat sporadic and only during years of high abundance. Few nondominant years were sampled in any Fraser River lake, but data sets useful for examining the effects of spawner density on juvenile growth and abundance are available for Shuswap and Quesnel lakes, where both dominant and subdominant years were sampled (Fig. 1). Escapements in the years sampled varied by 1:101 in Shuswap Lake and by 1:7 in Quesnel Lake.

The IPSFC surveys consisted of hydroacoustic population estimates of sockeye, trawl samples for species, age, and size compositon, and vertical net hauls for macrozooplankton density and species composition. We use these data to investigate how density, macrozooplankton and temperature affect growth and survival in Shuswap and Quesnel lakes.

STUDY AREA

Shuswap and Quesnel lakes are large oligotrophic lakes on the edge of the Columbia mountain ranges of British Columbia. Shuswap Lake located at 51°00'N, 119°00'W is 480 km upstream from the mouth of the Fraser River in the Straight of Georgia, while Quesnel Lake at 52°30'N, 121°00'W is 700 km upstream. The lakes have low concentrations of dissolved solids and total phosphorous (Stockner and Shortreed 1983). Shuswap is larger but shallower (area = 345 km^2; Mean depth = 62 m) than Quesnel Lake (area = 272 km^2; Mean depth = 158 m). Although both lakes are oligotrophic Shuswap is slightly more productive and is situated almost 400m lower in elevation.

Many fish species occur in both lakes but the abundance of pelagic species that compete with juvenile sockeye is very low. Of 3,923 fish caught in midwater trawls in Quesnel Lake 3,888 (99.1%) were underyearling *O. nerka*, and 34 (0.9%) were either older kokanee (lake resident *O. nerka*), lake whitefish (*Coregonus clupeaformis*), or were not identified (Mueller and Enzenhofer 1991; Enzenhofer et al. 1991). Of 19,419 fish caught in Shuswap Lake, 13,672 (70.4%) were underyearling *O. nerka*, 5,465 (28.1%) were age-1 *O. nerka*, 118 (0.6%) were older kokanee, 47 (0.2%) were lake whitefish ,

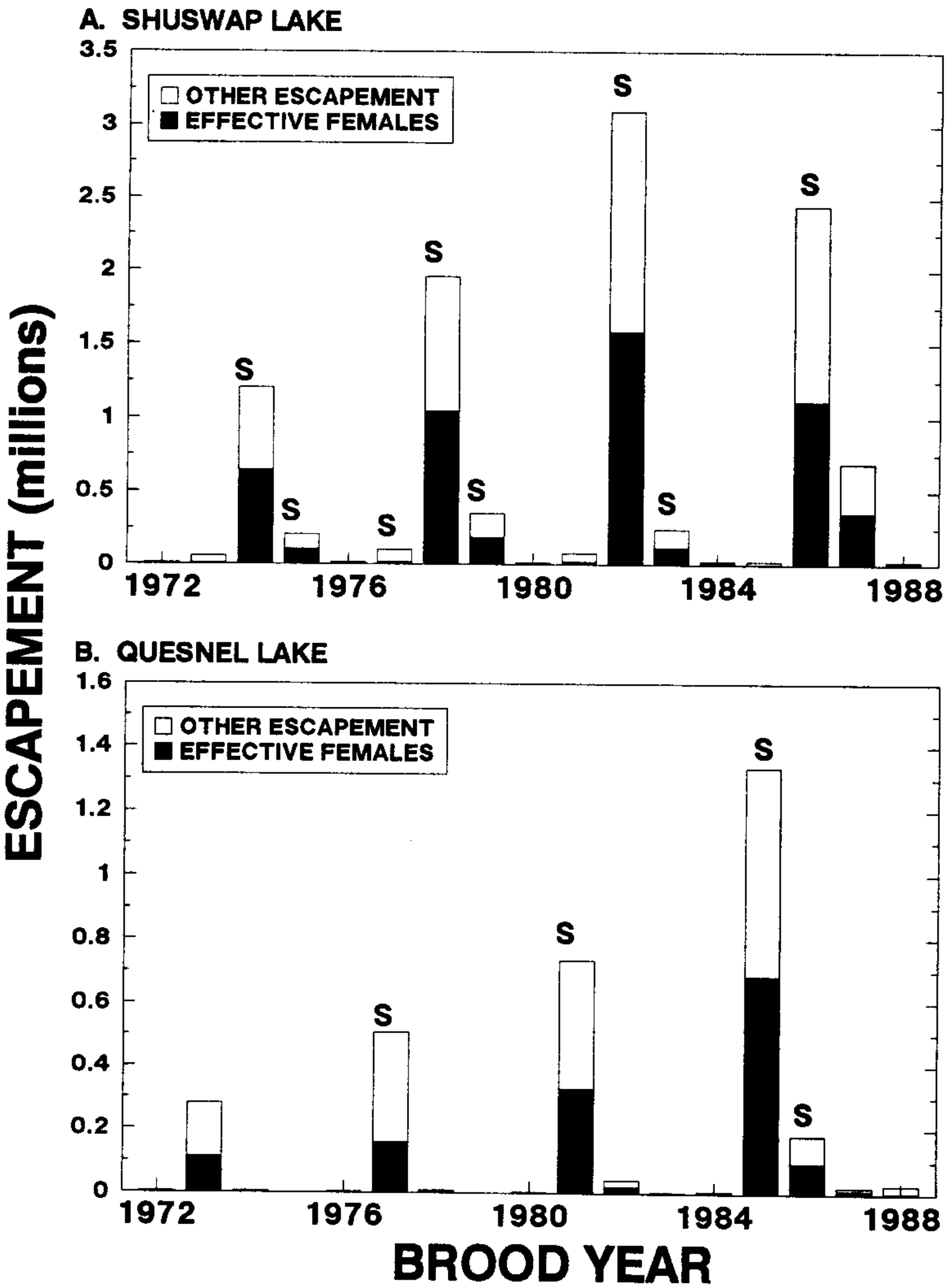


Fig. 1 Spawning escapements to Shuswap and Quesnel Lakes over the period of sampling. Sampled cohorts are indicated by an 'S'.

94 (0.5%) were sculpins (*Cottus asper*), and 20 (0.1%) were not identified.

Underyearling *O. nerka* (both sockeye and kokanee) are more susceptible to capture by midwater beam trawls than older age classes (mostly kokanee) because of their smaller size (Parkinson et al. 1993). Consequently, it was difficult to obtain unbiased estimates of kokanee abundance, in the underyearling and older age classes. Williams et al. (1989) estimated the total kokanee population at about 8,000,000 fish. They estimated the kokanee abundance by subtracting the expected fall juvenile sockeye abundance - based on a 5%$\cdot$mo^{-1} mortality rate (calculated from known survivals to smolts) to the emergent fry population (calculated from potential egg deposition) - from the October acoustic estimate. Using this figure, kokanee would account for about 5%, 20% and 80% of dominant, subdominant and nondominant populations of *O. nerka*, respectively.

Numerous predator species exist in these lakes (Northcote and Burwash 1991), including rainbow trout (*Oncorhynchus mykiss*), burbot (*Lota lota*), bulltrout (*Salvelinus confluentus*), northern squawfish (*Ptycocheilus orgeonensis*), lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*) and mountain whitefish (*Prosopium williamsoni*). Williams et al. (1989) found all of these species present in the early summer, near the mouth of the Adams River, the main spawning stream for Shuswap Lake, and all were feeding on sockeye fry to some extent.

METHODS

EMERGENT FRY

Escapements of sockeye salmon to Shuswap and Quesnel lakes were estimated from 1948 to 1985 by the IPSFC. Since 1986 escapements have been estimated by the Department of Fisheries and Oceans (DFO). Various techniques were used, including mark and recapture and counting of post-spawning mortalities, depending on the site (Wayne Saito, DFO, New Westminster). The number of effective females (females that spawned successfully) and age-specific mean fecundity were also recorded to estimate potential egg deposition (PED). The number of emergent fry each year has been estimated by applying egg-to-emergent-fry survival rates observed in key streams in each lake (e.g. Williams et al. 1989). In some dominant cycle years fry traps were used on both the Adams and Horsefly rivers to directly count emerging fry.

LAKE FRY

Survey Design

The lakes were divided into a number of sections, based on lake morphometry (Fig. 2). Within each section, two to three hydroacoustic transects were randomly established, depending on the size of the section for a total of 16 transects on Quesnel and 33 on Shuswap. The same transects have been used on all surveys since 1975. The acoustical estimates from each transect were used to estimate the mean density (n$\cdot$ha^{-1}) of a lake section and were expanded by surface area of the section to provide a section population estimate. These were summed to provide a total population estimate for the lake. Mean lake density was calculated by dividing the lake population estimate by the total surface area.

Fish samples were taken by mid-water trawl from each section to determine the size and species composition of the fish present.

Hydroacoustics

Prior to 1978 data were collected using a Ross 200A Fineline echosounder with a 105 kHz transducer producing a 10° beam at -20 dB (Nunnallee and Mathisen 1972). From 1978 to 1984 data were collected using a Simrad EY-M echosounder with a 70 kHz transducer producing a 11° beam at -3 dB (Johnson and Mathisen 1976; Johnson 1979). The transducer was mounted on a towed body suspended from the side of the boat. Data were recorded with a time varied gain (TVG) of 20 log(R) (where R is the distance from the transducer to the target) to correct for one-way propagation loss, on a 8 mm reel to reel tape recorder for later analysis. The

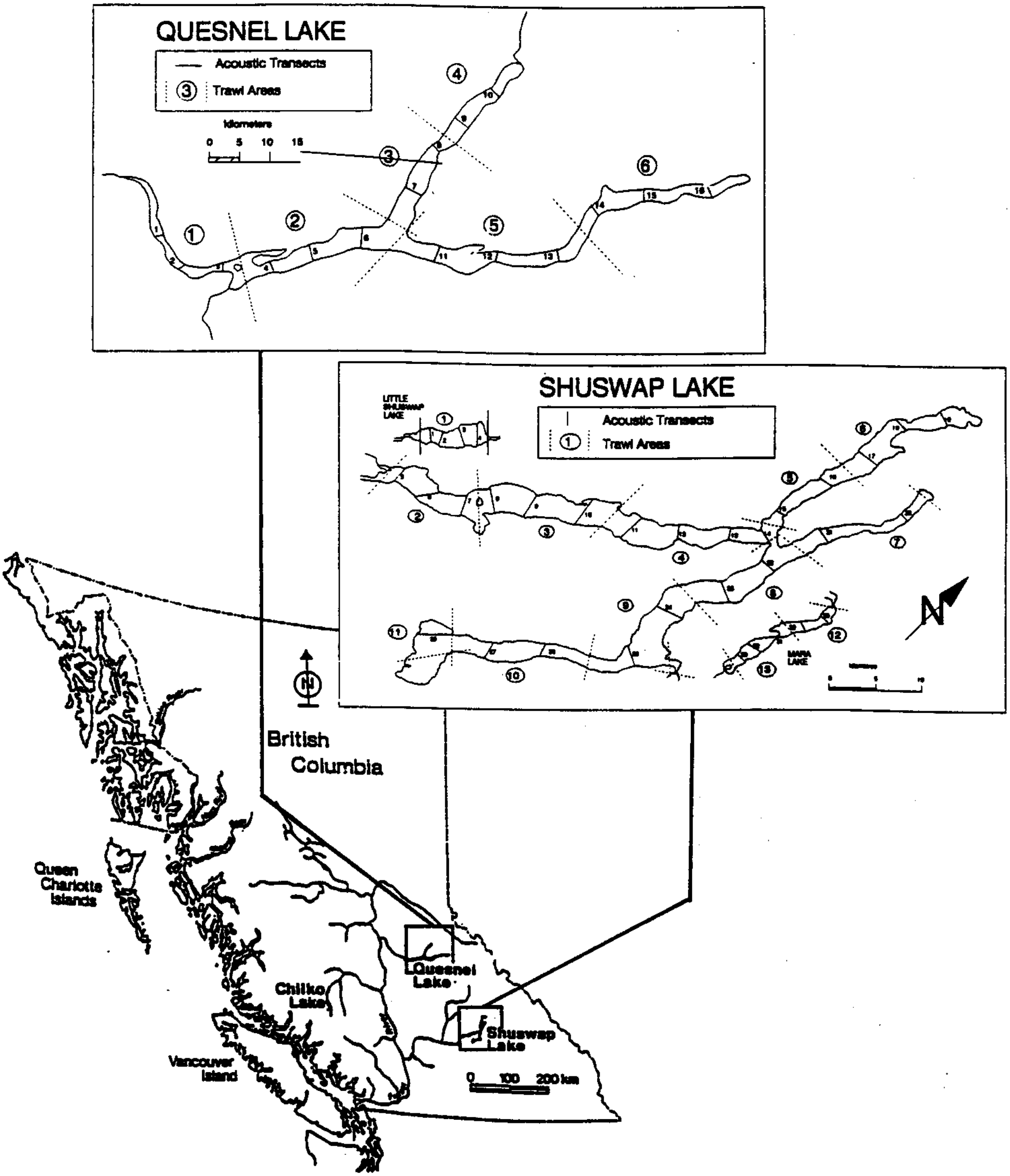


Fig. 2 Map of the Fraser River and study lakes, showing sampling locations.

hydroacoustic boat traversed each transect at approximately 2 $m \cdot sec^{-1}$.

Prior to 1985, data were analyzed in two stages using a technique developed by Nunnallee and Mathisen (1972) and Nunnallee (1973). First, the recorded voltages were integrated using either the digital hydroacoustic data processor at the University of Washington Applied Physics Laboratory or a Biosonics 121 integrator (from 1982) to give the relative uncalibrated density of fish in each transect. Second, targets were counted on an oscilloscope from selected transects in each lake. These counts were then regressed against the integrated data from the same transect. The regression line was then used to calibrate all the integrated transects to provide a density estimate for each transect.

In 1985 and 1986 data were collected using a Biosonics Model 105 dual beam echosounder, a 420 kHz dual beam (6°/15°) transducer mounted in a towed body, a Biosonics Model 115 chart recorder and a Model 171 tape recorder interface. The data were digitized and recorded on a Sony digital recording system for later processing. The data were collected using 40 log(R) TVG for target strength processing.

The later data were processed in two phases similar to the method used in Burczynski and Johnson (1986). First, the target strengths and mean backscattering cross sections were determined for each transect using a Biosonics Model 121 dual beam processor. Second, recorded data were echo integrated to give the relative density of targets using the narrow beam data with the TVG converted to 20 log(R). Target strength, mean backscattering cross section and equipment scaling factor (the "A constant") were then used to scale the echo integration to provide an estimate of the actual fish density in each transect. Estimates of the variance were calculated by the methods described in Burczynski and Johnson (1986).

Fish Sampling

Fish samples were collected using a 7 X 3m midwater trawl. Trawls of 5 to 45 min were made through the various layers of fish, as indicated on the echosounder. Trawl duration was chosen to give an adequate sample of fish for later measurements (100 - 200 fish). All fish were anaesthetized upon capture in 2-phenoxy-alcohol and then preserved in 10% formalin. Fish were kept in formalin for at least one month before length, weight and species were recorded. Instantaneous growth rates were calculated from:

$$G = ((\log_e W_2 - \log_e W_1)(t_2 - t_1)^{-1})100$$

where W = wet weight (g) and t = time in 30 day months.

MACROZOOPLANKTON

Macrozooplankton were collected in late summer or early fall using a 160-μm mesh size conical Wisconsin net with a mouth area of 0.05 m^2. Samples were taken from 10 stations in Shuswap Lake and from 6 stations in Quesnel Lake (Table 1). Four replicate vertical hauls were taken at each station from 30 m to surface. The 1,500-L samples were concentrated into 100-ml vials and preserved in 4% formalin solution. In the laboratory, samples were washed then subsampled using a Folsom plankton splitter. Subsamples were enumerated under a dissecting scope in a 6-cm diameter petri dish marked with 0.5-cm^2 grids. Macrozooplankton were identified to genus and dry weights were measured after drying at 90 °C for 24 h. Mean numbers of *Daphnia*, *Diacyclops* and total macrozooplankton (including copepod nauplii) are presented in this paper.

FRY REARING TEMPERATURE

We attempted to examine the growing temperatures experienced by the fry in the two lakes. We pooled temperatures across all years to provide a composite picture of temperatures in the two lakes because insufficient data were available from either lake on a yearly basis.

Table 1. Zooplankton sampling dates and locations.

BROOD YEAR	SAMPLE YEAR	DATE	NUMBER OF STATIONS
Shuswap Lake			
1974	1975	September 10	8
1975	1976	September 15	8
1977	1978	July 6	11
1978	1979	August 10	9
1979	1980	August 12	10
1982	1983	July 3	10
1983	1984	November 9	10
1986	1987	September 14	9
Quesnel Lake			
1978	1979	August 27	7
1985	1986	August 29	6
1986	1987	August 12	6

Mean growing temperature was calculated by first determining the amount of time the fish spent at various depths in the lake during different times of the year. This was done using echogram traces from surveys conducted over the course of this study. As in many sockeye lakes (Pella 1968; Narver 1970; Levy 1987), juvenile sockeye in Quesnel and Shuswap lakes undergo diel vertical migration. Fry are schooled at depths of 40-60 m during the day, rise to around 0-20 m at dusk, and return to day time depths at dawn. When a thermocline is present, fry usually spend the night below the thermocline with only brief excursions into the epilimnion at dawn and dusk. Weighted mean daily temperature was calculated from the time spent at each depth and the temperature at that depth at various times of the year. Mean growing temperature was determined by summing the weighted mean daily temperature over the growing season and dividing by the number of days in each growing season. The growing season was defined as the time when the weighted mean temperature was over 5°C.

RESULTS AND DISCUSSION

ADULT ESCAPEMENTS

Although most of our data are from brood years of moderate to high escapement, there was still considerable variation between years in numbers of effective females (Fig. 1). Highest variation occurred in Shuswap Lake where effective females varied between 0.5 to 45.8 spawners·ha^{-1} of lake area (a ratio of 1:101). In Quesnel Lake effective females ranged from 2.8 to 19.6 spawners·ha^{-1} (1:7) in the years sampled. Maximum escapement densities recorded during our study are not unusual for sockeye stocks. Similar escapement densities have occurred at Cultus Lake, in the Fraser watershed, while Chignik and Karluk lakes in Alaska, and Kuril and Dalnee lakes on the Kamchatka Peninsula have average escapements ranging from 100 to 266 spawners·ha^{-1}, approximately equivalent to 50 to 133 effective females·ha^{-1} (Burgner 1991). In our study, female escapements produced an estimated emergent fry density of 320 to 21,000 fry·ha^{-1} in Shuswap Lake and of 1,900 to 6,200 in Quesnel Lake (Appendix Table 1).

SURVIVAL AND MORTALITY

Fry survival from emergence to the fall was negatively correlated with density at emergence (Fig. 3a; arcsine transformation, $P = 0.05$, $r^2 = 0.33$, $n = 12$). Monthly instantaneous mortality tended to increase with density but no significant relationships existed, either within a single lake or with all lakes combined ($P > 0.05$, $r^2 = 0.278$, $n = 12$) (Fig. 3c). Overall survival averaged 37.9% from emergence to fall (range = 21 to 61%) and instantaneous mortality averaged 16.4%·mon^{-1} from emergence to fall (range = 7 to 24%·mon^{-1}) (Table 2). We believe that the relationship between density and survival appears weak due to the narrow range of densities examined and compounding of errors in the population estimates between time periods.

There are few comparable studies of freshwater survival in the literature, probably due to the difficulties of obtaining population estimates. Koenings and Burkett (1987) stocked a lake barren of sockeye with known numbers of sockeye fry and found a strong negative relationship ($r^2 = 0.98$) between stocking density and freshwater survival to smolting, ranging from 47% at a stocking density of 5,000 fry·ha^{-1} to 11% at 20,000 fry·ha^{-1} (Fig. 3b). The lake is small (1,100 ha) compared to Shuswap and Quesnel lakes and consequently there would be much less variation in density within the lake than in the larger multibasin lakes.

Smolt size and numbers were collected from Babine Lake for a 25-yr period (from 1959 to 1983). Emergent fry density ranged from 900 to 8,700 fry·ha^{-1} (McDonald and Hume 1984; MacDonald et al. 1987). Even though there was a three-fold increase in average smolt density and nearly a ten-fold increase in maximum fry density during this period there was no significant change in measured survival rates (MacDonald et al. 1987). Babine is a large lake and densities vary considerably throughout the lake. Emergent fry to smolt survival in Babine Lake averaged 37% (range = 8 - 68%). This corresponds to an instantaneous mortality of about 7.5%·mon^{-1} (range = 3-17%). Mortality was significantly lower than the average mortality measured in Quesnel and Shuswap lakes ($P < 0.001$, Fig. 3d).

The Babine mortality rates include an overwintering period not examined in our study, which may explain the difference between instantaneous mortality rates in Babine and our study. Our data indicates a decline in mortality from the spring to fall periods that may continue throughout the winter. We divided the spring to fall into three periods: from emergence to summer (May to July or August); summer to fall (July or August to September or November); and within the fall (September to November) (Table 3). No significant relationship was found between instantaneous mortality and density in any of these seasons ($P > 0.05$) (Fig. 4). In general mortality declined from emergence to the fall in Shuswap lake but there was considerable variation and no significant differences among seasons ($p > 0.05$). In some cases the hydroacoustic estimates indicated increased abundance from one time period to the next, possibly due to continued recruitment to the pelagic area.

GROWTH AND PRODUCTION

Burgner (1991) listed eight factors affecting freshwater sockeye growth, including intra-specific competition (density), food abundance, and temperature. Koenings and Burkett (1987) separated sockeye rearing lakes into those that are recruitment limited and those that are rearing limited. Rearing limited lakes were further classified as: a) density dependent forage limited (e.g. not enough food); b) density independent forage limited (eg. poor overlap of fish and food) and; c) density independent environment limited (e.g. unfavourable temperature).

Density dependent growth is well known in sockeye rearing lakes (Burgner 1987). Fry size declined with increased fry density in both

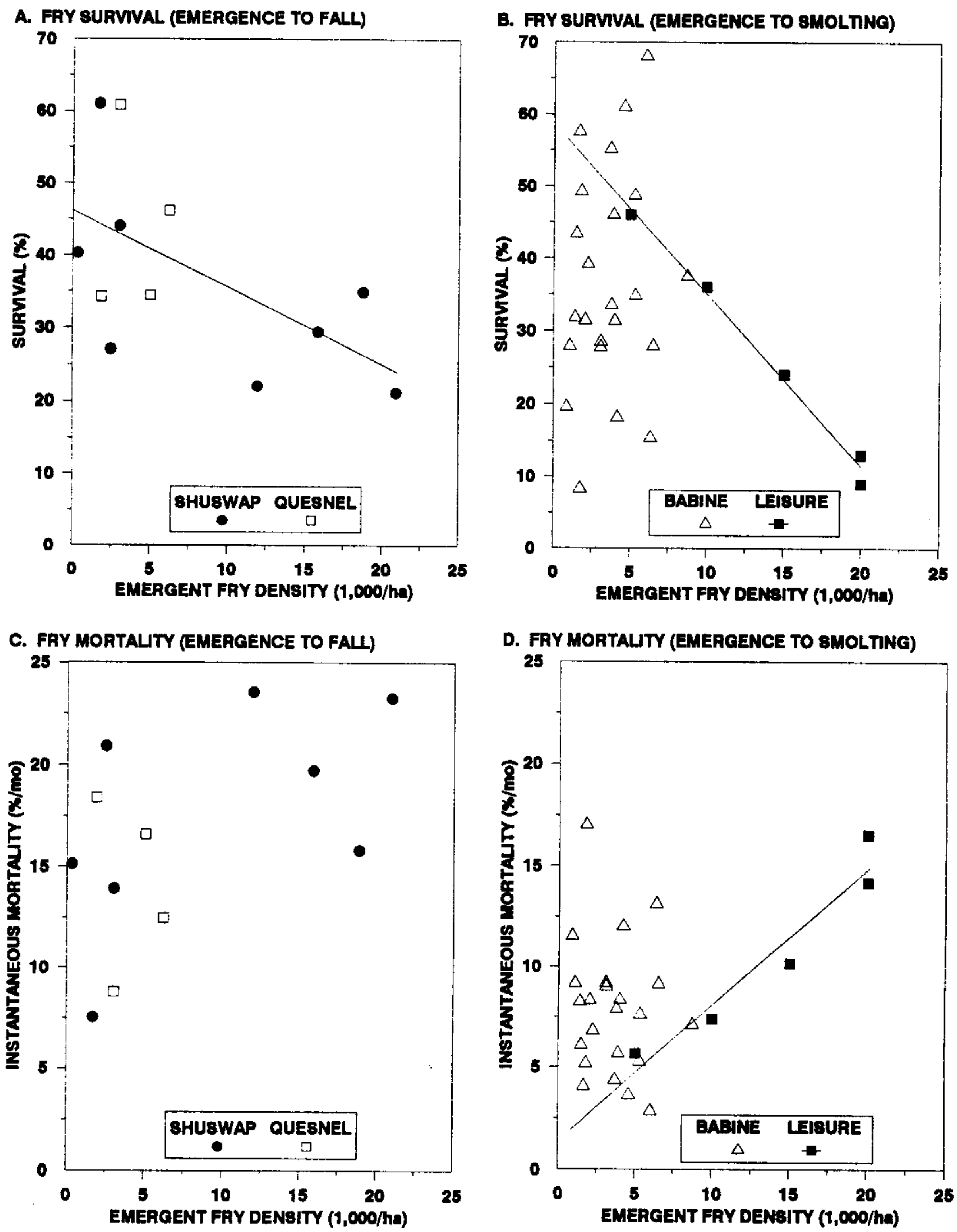


Fig. 3 Relationships between fry survival and instanteous mortality (time in months) and emergent fry density in Shuswap, Quesnel, Babine, and Leisure Lakes. See text for data sources.

Table 2. Total survival and instaneous mortality (time in months) of sockeye fry from emergence to autumn.

Brood Year	Starting Density ($N \cdot ha^{-1}$)	Total Survival (%)	Monthly Mortality (%)
Shuswap			
1974	11,939	22.0	23.6
1975	2,484	27.1	20.9
1977	324	40.3	15.2
1978	15,849	29.4	19.7
1979	3,017	44.0	13.9
1982	20,942	21.1	23.3
1983	1,694	61.0	7.5
1986	19,280	34.8	15.8
Quesnel			
1977	2,997	60.8	8.8
1981	6,199	46.2	12.5
1985	5,029	34.4	16.6
1986	1,876	34.2	18.4
MEAN		37.9	16.4

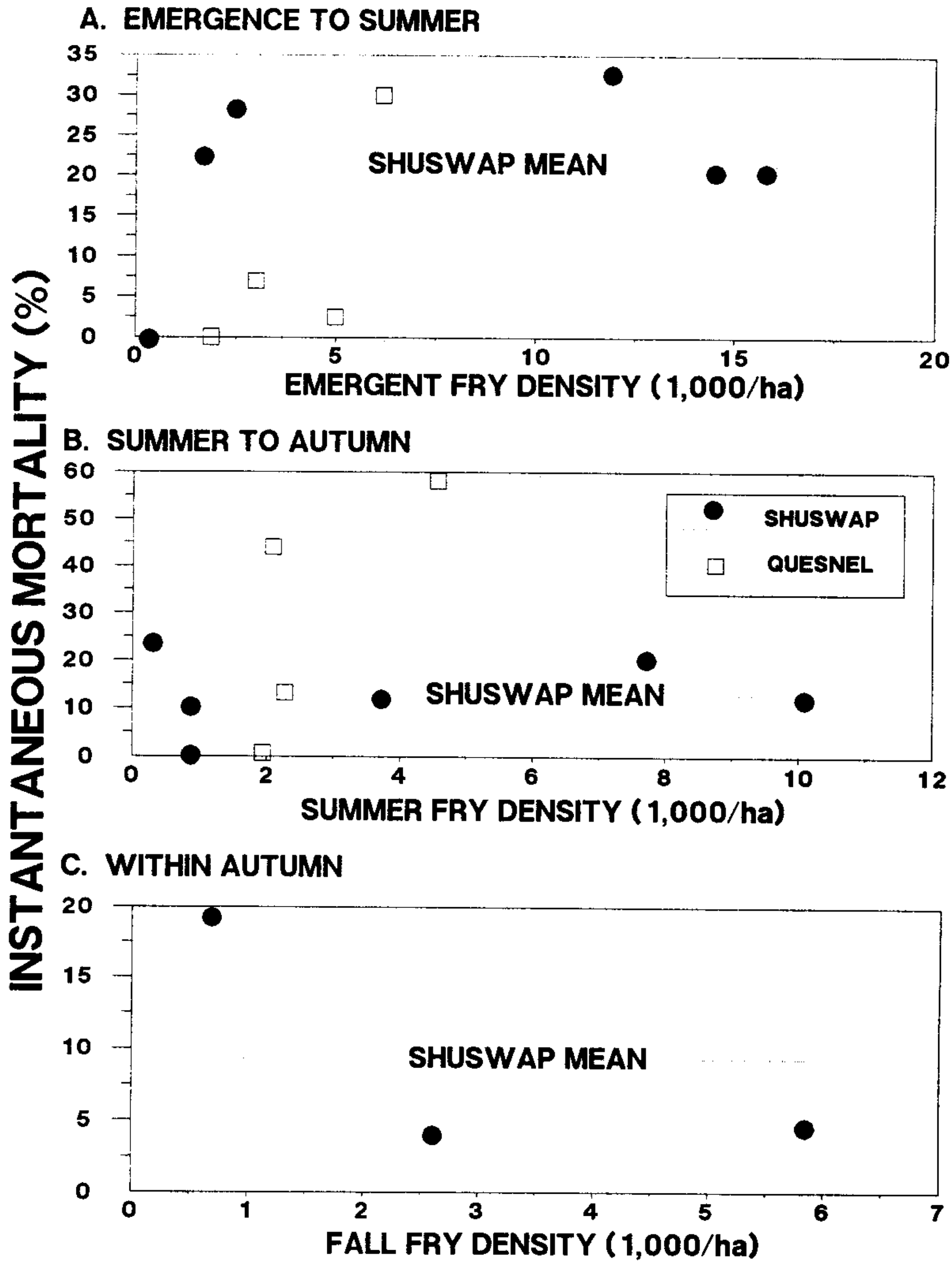


Fig. 4 Fry instantaneous mortality be season in Shuswap and Quesnel Lakes; (A) emergence (May) to summer (July and August); (B) summer to autumn (October and November, and; (C) within autumn (September to November).

Table 3. Instantaneous mortality (time in months) of sockeye fry by season.

	Emergence to Summer		Summer to Autumn		Within Autumn	
Brood Year	Starting Density ($N \cdot ha^{-1}$)	Instan. Mortality (%)	Starting Density ($N \cdot ha^{-1}$)	Instan. Mortality (%)	Starting Density ($N \cdot ha^{-1}$)	Instan. Mortality (%)
Shuswap						
1974	11,939	32.8	3,814	12.6	2,629	3.7
1975	2,484	28.0	858	9.9	672	19.3
1977	324	0.0	324	24.1		
1978	15,849	20.0	7,696	19.3		
1982					5,846	4.7
1983	1,694	22.2	868	-4.9		
1986	19,280	20.4	10,093	11.7		
Quesnel						
1977	2,997	6.9	2,276	13.2		
1981	6,199	29.8	1,975	-15.6		
1985	5,029	2.4	4,589	57.7		
1986	1,876	-2.9	2,057	44.1		
Mean		16.0		17.2		9.2

Shuswap and Quesnel lakes, suggesting density dependent growth but the relationship was significant only in Shuswap Lake (Fig. 5). Emergent fry density in Shuswap Lake explained 54% of the variation in fall fry size ($P < 0.05$, $n = 8$) and 87% of variation in instantaneous growth rates ($P < 0.001$, $n = 8$).

No density dependent growth response in either fall fry or smolt size was detected for emergent densities ranging from 900 to 5,400 fry$\cdot$ha^{-1} in Babine Lake (Fig. 5, McDonald and Hume 1984). However a significant response to density was detected when emergent densities were increased to as high as 8,800 fry$\cdot$ha^{-1} (Macdonald et al. 1987). Koenings and Burkett (1987) found a much stronger relationship between density and growth in Leisure Lake, Alaska. With stocking densities ranging from 5,000 to 20,000 fry$\cdot$ha^{-1}, the decrease in smolt size with density was much steeper than seen in the three B.C. lakes. But in Tustumena Lake, Koenings and Burkett (1987) found no density dependency between smolt size or age of smolting at densities ranging from 1,500 to 3,700 fry$\cdot$ha^{-1} (Fig. 5). We estimated these emergent densities in Tustumena Lake from spawning adult numbers given in their Table 4 and applying a 50:50 sex ratio, a mean fecundity of 4,000 eggs/ female and a 15% egg to fry survival rate. They attributed the small size of these smolts to low rearing temperatures rather than food limitation.

Density could not explain the differences in the size of fall fry in Quesnel and Shuswap lakes. Fry were considerably smaller in Shuswap Lake than in Quesnel Lake at the same emergent densities (Fig. 5). Consequently we examined both food supply and growing temperatures as possible explanations for the difference between the two lakes.

In Shuswap Lake, total seasonal macrozooplankton density (length > 0.25 μm, including some copepod nauplii) ranged from 5,900 to 19,000$\cdot$m^{-3} with *Daphnia* comprising between 3 - 12 % of the total and *Diacyclops* comprising 12 - 26% (Fig 6). In Quesnel Lake total plankton density ranged from 2,400 to 6,200$\cdot$m^{-3} for the three years we have data. *Daphnia* made up 15 to 33% of the total and *Diacyclops* were 25 to 40%. *Daphnia* (160 to 1,700$\cdot$m^{-3}) and *Diacyclops* (600 to 3,400$\cdot$m^{-3}) densities were similar in both lakes. There was a slight decrease in *Daphnia* and *Diacyclops* density and total zooplankton densities and biomass with increasing sockeye densities but this was not significant ($P > 0.05$, $r^2 < 0.20$). In contrast, Kyle et al. (1988) found that there were major declines in total macrozooplankton in Frazer Lake as escapement increased. While density of zooplankton did not decline with increasing densities, the number of zooplankton$\cdot$fish^{-1} (using fall fry densities) was strongly negatively associated with emergent fry density (Fig. 7, $r^2 = 0.89$, $P < 0.001$). This relationship was curvilinear such that a change in fry density had more effect on zooplankton$\cdot$fish^{-1} at low emergent fry densities than at high densities.

Fish size was not strongly associated with either zooplankton density or the number of zooplankton$\cdot$fish^{-1} in either Shuswap or Quesnel lakes (Fig. 7, $P > 0.05$) and there was no apparent difference between lakes either. This is in sharp contrast with the results of other studies. Both Kyle et al. (1988) in Frazer Lake and Hyatt and Stockner (1985) in coastal British Columbia lakes showed that as the number of zooplankton per fish decreased so did smolt length. There was however considerable variation in smolt length that was not explained (56%) by this normalized zooplankton abundance in the coastal lakes (Hyatt and Stockner 1985). Thus our sample size may have been too small to detect a significant relationship between food supply and smolt length. Also during summer, zooplankton may have thermal refuges in the epilimnetic water (LeBrasseur et al. 1978) and we may have overestimated available plankton density by using total vertical hauls.

Neither density of zooplankton nor zooplankton$\cdot$fish^{-1} can explain why fry in Quesnel Lake tend to be larger than fry in Shuswap Lake. Consequently, we attempted to examine the growing temperatures experienced by the fry in the two lakes. We pooled temperatures across all years to provide a composite picture of temperatures in the two lakes because insufficient data were available from either lake on a yearly basis

Temperature records showed that Quesnel Lake stratified at a much later date than Shuswap Lake and consequently hypolimnion temperatures were considerably higher in

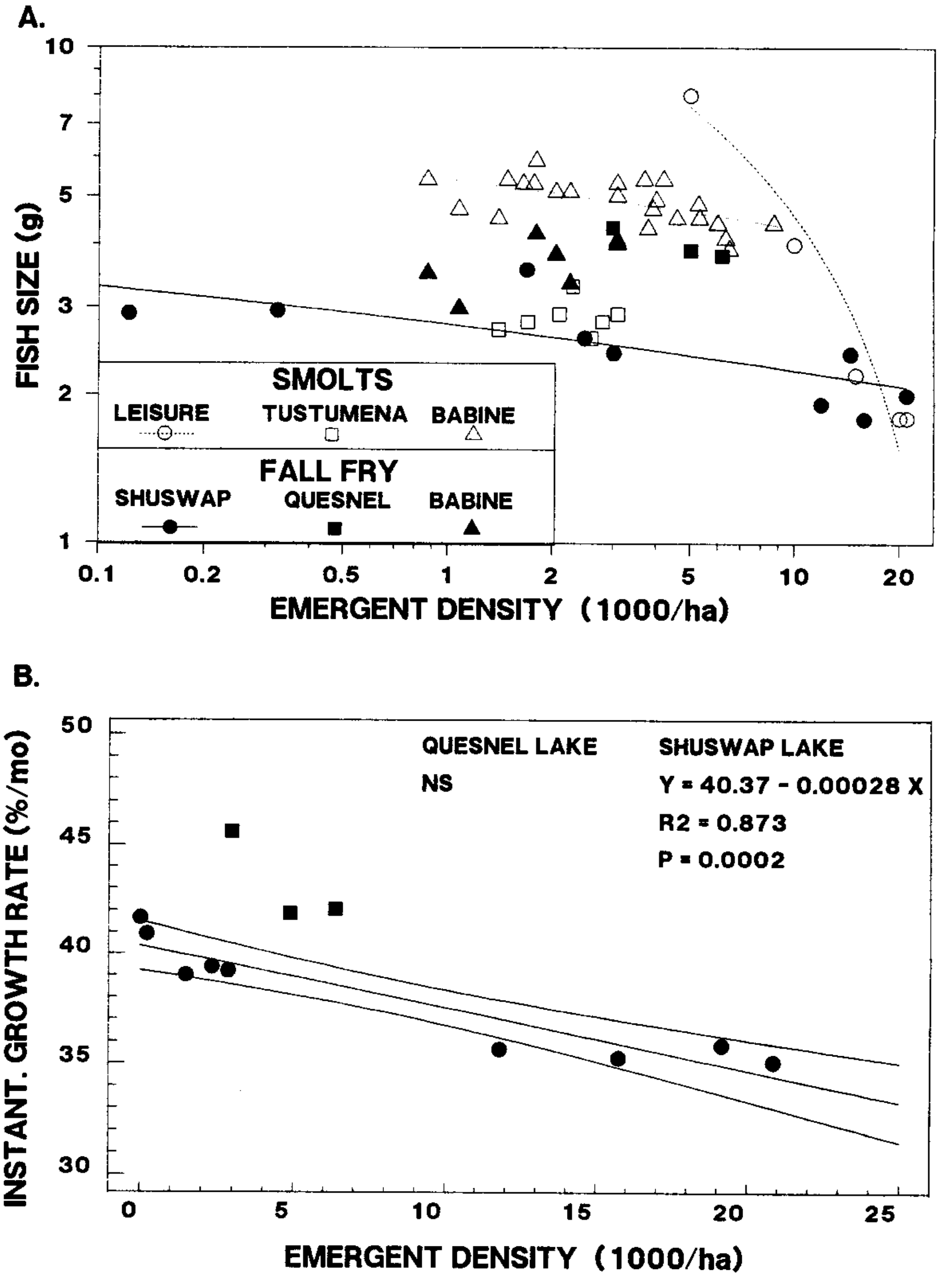


Fig. 5 Relationship between emergent fry density and (A) fall fry size, and (B) instantaneous growth rates (time in months). See text for data sources.

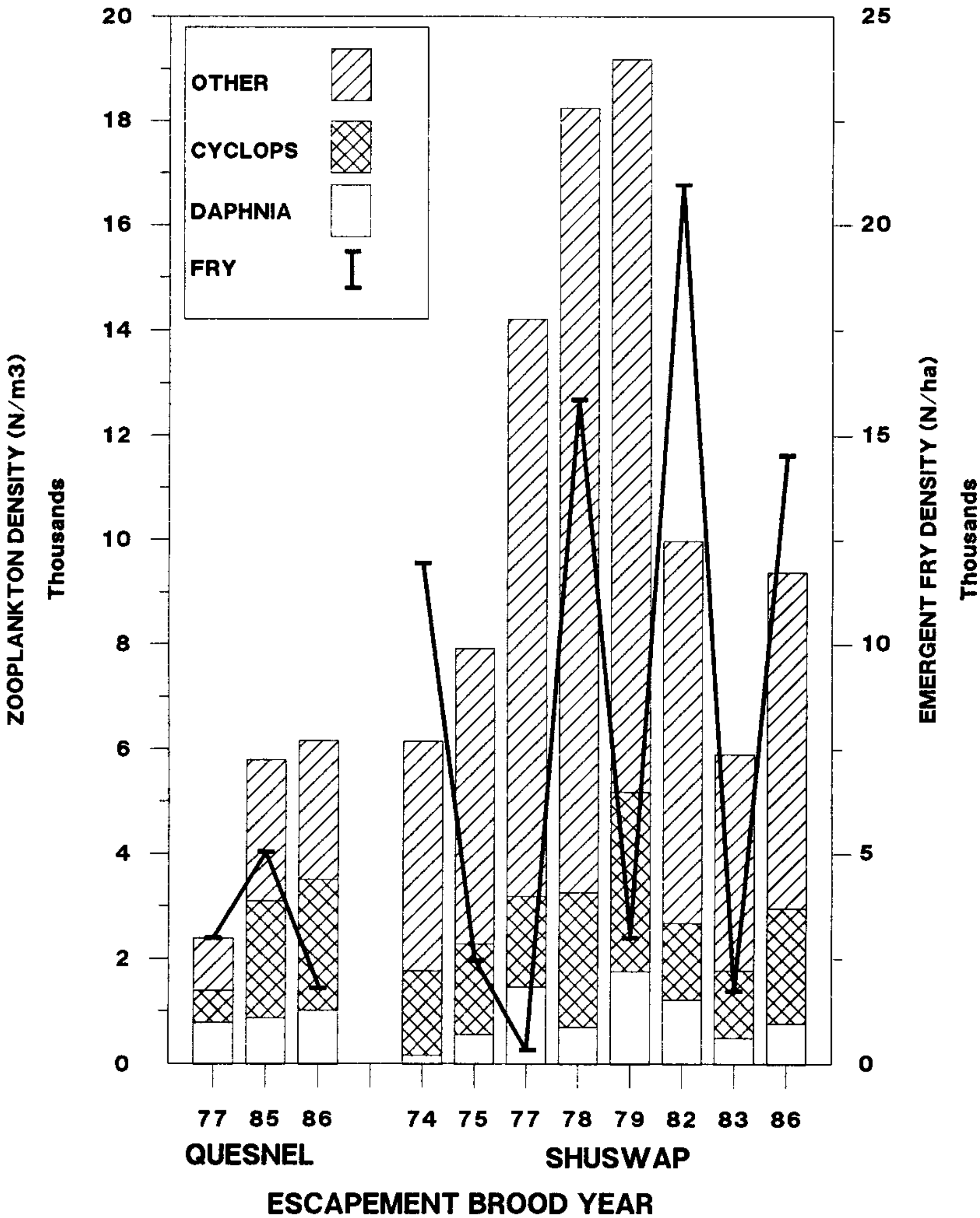
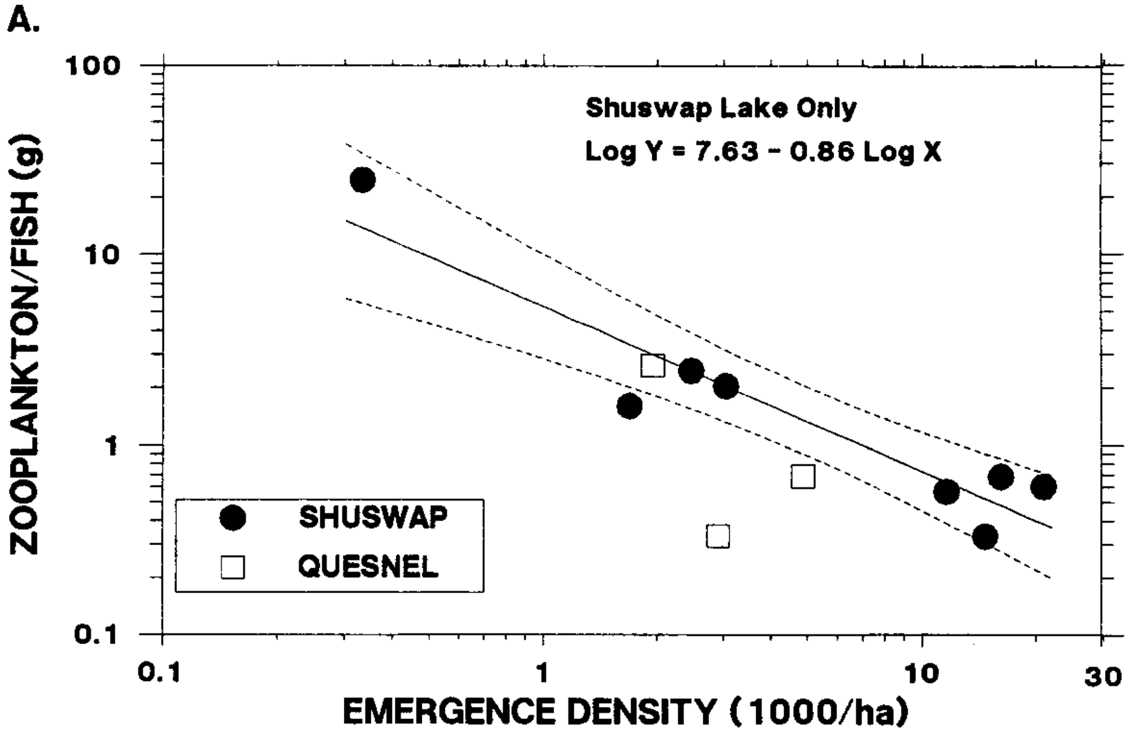


Fig. 6 Trends in fall fry biomass (solid line) and fall zooplankton densities (histogram) in Quesnel and Shuswap Lakes.



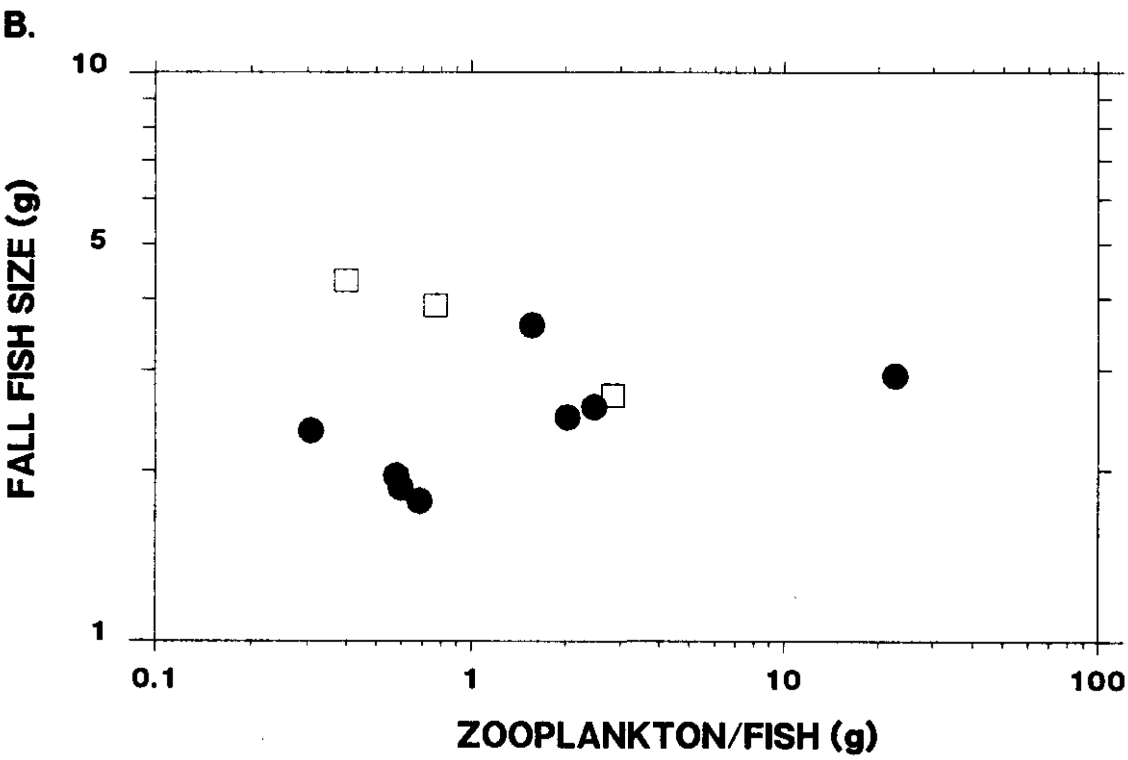


Fig. 7 Relationships between zooplankton·fish^{-1} (using fall fry densities) and (A) emergent fry density and (B) fall fry size.

Quesnel Lake. Because fry spent the majority of their time in the hypolimnion, the average seasonal growing temperature was almost 2 degrees higher in Quesnel lake (9.2°C) than in Shuswap Lake (7.6°C). Brett et al. (1969) in laboratory experiments and Johnston (1990) in field trials have shown that differences in temperature of this magnitude have a considerable effect on sockeye fry growth. Koenings and Burkett (1987) attributed the small size of smolts in Tustumena Lake to low rearing temperatures rather than food limitations.

In Shuswap Lake both the density and biomass of fall fry have increased linearly with emergent fry density (Fig. 8) but the measured biomass is highly variable at high densities. Total biomass is depressed in some years of high density but not in the 1986 brood year, despite the small size of fall fry (2.4 g). The 3 data points for Quesnel Lake give no indication that fry densities are limiting production in that system.

RELATIONSHIP OF SIZE TO SMOLTING

By pooling data from many different lakes Ricker (1962) showed that smolt-to-adult survival (SAS) increased with smolt length from 63 to 107mm, but not from 107 to 170 mm. Hyatt and Stockner (1985) re-analysed these data and found that smolt length explained 58% of SAS, after an arcsine transformation. Koenings et al. (1993) also re-analyzed Ricker's data together with more recent Alaskan data using non-parametric regression. They confirmed the curvilinear nature of the relationship but also found distinct thresholds or 'breakpoints'. SAS increased with smolt length at about 0.35-0.45 $\%\cdot mm^{-1}$ up to about 90-100 mm (6-9 g), but not above this size. They also found a strong relationship between broad geographical latitude and overall SAS. For smolts entering the ocean south of 55° N latitude SAS ranged from 5.9 to 17.1% compared with 17.7 to 41.7% for smolts entering north of 60° N latitiude. Analysis of SAS data for smolts grouped by 10-mm size categories only revealed significant differences in SAS between adjacent size classes at the 'breakpoints' identified by non-parametric regression (Koenings et al. 1993).

The minimum mean size of smolts in any population was about 60 mm (2 g) (Foerster 1968; Hyatt and Stockner 1985; Koenings and Burkett 1987) but the smolt size producing the maximum number of returning adults was between 90-100 mm (6-8 g) in Cultus and Leisure lakes (Ricker 1962; Koenings et al. 1993). Similarly, Henderson and Cass (1991) found that within a cohort larger smolts from Chilko Lake, in the Fraser River system, returned at a greater rate than the smaller ones but there was no relationship between SAS and mean smolt size amongst cohorts (Goodlad et al. 1974; Henderson and Cass 1991). It is probable that amongst cohorts any effect of smolt size in the range produced by Fraser River lakes is masked by effects caused by the long migration to the ocean, 640 km (Henderson and Cass 1991). Quesnel, and Shuswap lakes are also long distances from the ocean (750 and 480 km respectively) and as a consequence it is likely that any size effect of smolt size on SAS would also be undetectable.

At emergent densities of between 10,000 to 20,000 $fry\cdot ha^{-1}$ in Shuswap Lake, mean smolt size appears to be approaching the minimum required for smolting . On dominant years fall pre-smolts are only about 2 g (Fig. 5) so that smolts would be about 3 g assuming a late winter and spring growth increment of about 1g, as found in Babine Lake (McDonald and Hume 1984). Only in the years of lowest density do fall fry approach 5g, the size Koenings et al. (1993) found to produce the maximum adult return. Of course adult returns depend not only on SAS, which appears to be size related but also on smolt abundance. There is some indication that emergent densities greater than $20{,}000\cdot ha^{-1}$ do not produce more fall fry (Fig 8) but higher emergent fry numbers are required to test this hypothesis.

Long term management goals are to increase dominant and subdominant returns to Shuswap and Quesnel lakes. Close monitoring of both the fry and their zooplankton food base will be required to prevent potentially disastrous consequences of over escapement. Frazer Lake showed a dramatic drop in sockeye fry growth when fry density exceeded the forage capacity of the lake (Kyle et al. 1988). Sockeye production in Frazer lake failed to recover when escapements were subsequently reduced. The evidence suggests that fry production has yet to exceed the forage capacity in Shuswap and Quesnel (up to 1986). However pre-smolt sizes are reduced at high fry densities in both lakes. In addition fry size in Shuswap decreased to the

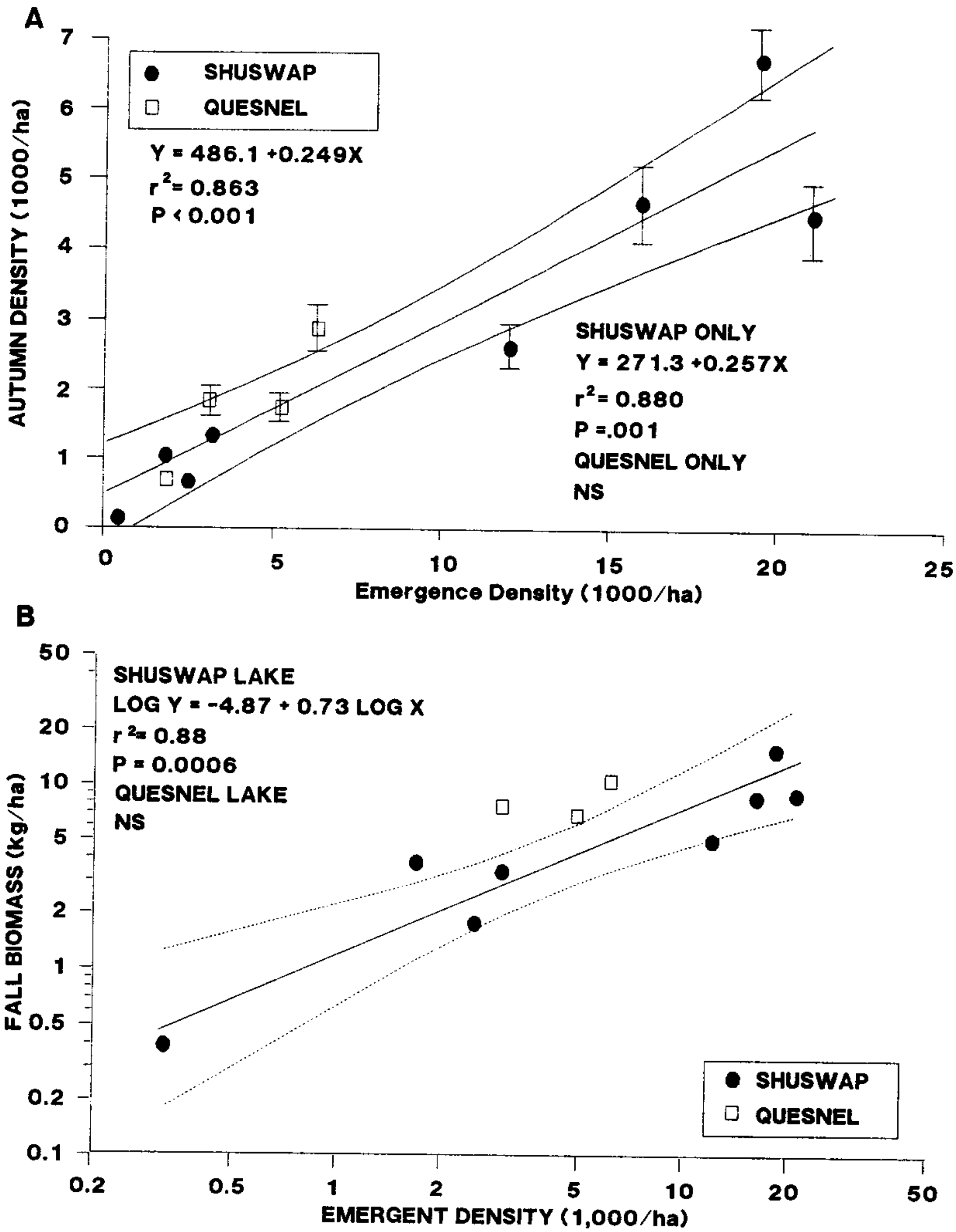


Fig. 8 Relationships between emergent fry density and (A) autumn fry density and (B) autumn fry biomass.

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Appendix Table 1. Sockeye fry abundance, density, and survival estimates for Shuswap and Quesnel lakes.

Brood Year	Effective Females	Sample Date	Population Estimate (N)	+/-95%	Density (N·ha^{-1})	+/-95%	Survival (%) From Emerg.	Mortality (% mo^{-1}) From Emerg.	Mortality (% mo^{-1}) Between Dates
Shuswap Lake									
1974	644,093	05-May-75	411,900,000		11,939				
		29-Jul-75	131,600,000	15,489,320	3,814	449	31.9	32.8	32.8
		20-Oct-75	90,700,000	10,675,390	2,629	309	22.0	23.6	12.6
		29-Nov-75	86,300,000	10,157,510	2,501	294	21.0	20.1	3.7
1975	102,284	05-May-76	85,700,000		2,484				
		09-Aug-76	29,600,000	3,483,920	858	101	34.5	28.0	
		18-Oct-76	23,200,000	2,730,640	672	79	27.1	20.9	9.9
		28-Nov-76	17,300,000	2,036,210	501	59	20.2	20.6	19.3
1977	15,649	05-May-78	11,170,000		324				
		10-Jul-78	11,170,000	1,314,709	324	38	100.0	0.0	0.0
		17-Oct-78	4,500,000	529,650	130	15	40.3	15.2	24.1
1978	1,040,978	05-May-79	546,800,000		15,849				
		09-Aug-79	265,500,000	31,249,350	7,696	906	48.6	20.0	20.0
		18-Oct-79	160,900,000	18,937,930	4,664	549	29.4	19.7	19.3
1979	186,639	05-May-80	104,087,000		3,017				
		15-Oct-80	45,850,000	5,396,545	1,329	156	44.0	13.9	13.9
1982	1,581,171	05-May-83	722,513,000		20,942				
		19-Sep-83	201,700,000	23,740,090	5,846	688	27.9	24.2	24.2
		27-Oct-83	152,800,000	17,984,560	4,429	521	21.1	23.3	4.6
1983	114,840	05-May-84	58,430,000		1,694				
		23-Jul-84	29,940,000	3,523,938	868	102	51.2	22.2	22.2
		09-Nov-84	35,670,000	4,198,359	1,034	122	61.0	7.5	-4.9
1986	1,114,577	05-May-87	665,170,000		19,280				
		28-Jul-87	348,212,000	40,383,253	10,093	1,171	52.3	20.4	20.4
		04-Nov-87	231,271,398	15,997,665	6,704	464	34.8	15.8	11.7
Quesnel Lake									
1977	151,758	05-May-78	81,517,387		2,997				
		27-Aug-78	61,900,000	7,285,630	2,276	268	75.9	6.9	
		13-Oct-78	49,600,000	5,837,920	1,824	215	60.8	8.8	13.2
1981	323,266	05-May-82	168,583,589		6,199				
		09-Aug-82	53,720,000	6,322,844	1,975	232	31.9	29.8	
		25-Oct-82	77,860,000	9,164,122	2,863	337	46.2	12.5	-15.6
1985	683,020	05-May-86	136,781,205		5,029				
		23-Aug-86	124,800,000	14,688,960	4,589	540	91.2	2.4	
		27-Oct-86	47,100,000	5,543,670	1,732	204	34.4	16.6	57.7
1986	94,493	05-May-87	51,026,760		1,876				
		10-Aug-87	55,954,257	7,046,247	2,057	259	109.7	-2.9	-2.9
		09-Oct-87	17,460,000	3,192,777	642	117	34.2	18.4	44.1