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No. 949

PROGRESS REPORTS ON BABINE LAKE SOCKEYE SALMON STUDIES, FOR INCLUSION IN THE BABINE LAKE SOCKEYE SALMON DEVELOPMENT PROGRAM

PROGRESS REPORT NO. 1

Contents

Biological Station, Nanaimo, B.C.

December 1967

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THE DISTRIBUTION, GROWTH, AND SURVIVAL OF SOCKEYE FRY PRODUCED FROM THE FULTON RIVER AND ARTIFICIAL SPAWNING CHANNEL IN 1966

by J. McDonald

This report summarizes work carried out in 1966 and 1967 to answer two questions related to evaluation of the Babine Lake sockeye development project. These questions are, (1) how do fry produced from an artificial spawning channel compare to those produced from natural spawning grounds in their lake distribution, growth, and survival, and (2) what part of Babine Lake is utilized as a nursery area by Fulton River fry?

Sockeye fry were captured during their downstream movement from the Fulton River and the adjoining artificial spawning channel. The fry were marked distinctively by removing the right pelvic fin from the river fish and the left pelvic fin from the channel fish. Then both groups were released to enter the lake. A total of 203,754 river fry and 299,363 channel fry were marked and released between May 8 and June 23, 1966. Dates of 50% release of marked fish were June 6 for river fry and June 17 for channel fry.

Recoveries of marked fish were made by examining juvenile[1] sockeye caught by purse-seining in the main lake area throughout the summer and fall. In addition, marked smolts were recovered at the lake outlet the following spring.

Distribution in the lake

Figure 1 shows the location of mark recoveries for three periods in 1966, while Figure 2 shows the distribution of the total under-yearling population as indicated by catch-effort data. Fry from Fulton River dispersed rapidly and widely into the main lake area. Initially, most moved southward and occupied areas in the southern half of the lake. Later (August-September) a northward shift in distribution was evident and by October young sockeye were most abundant in the lake area adjacent to the Fulton River. Channel fry did not appear to disperse as widely as river fry - probably because lake entry of channel fry was, on the average, later.

Growth

No difference in the relative growth rates of channel and river fish could be detected by covariance analysis of mark recovery data obtained through-

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[1] The term juvenile as used in this report refers to sockeye during their lake residence prior to smolting.

out the first 4-5 months of lake residence. However, channel fry were smaller, on the average, probably due to late lake entry and thus a reduced growing period.

Survival

Survival rates of channel and river fish were examined by comparing the mark ratio at the time of release as fry (1 river mark to 1.47 channel marks) to the ratios observed in fish caught in the lake in three subsequent sampling periods (June-October). Analysis, using chi-square (Table I), did not reveal any significant departures from the expected ratio.

Table I. Chi-square tests of departures from expected ratio of river and channel recoveries, 1966 marking and recovery.

Fishing period		Marks actually recovered			Ratios		Chi-square
		River	Channel	Total	Expected	Observed	
I	June 25-July 27	35	62	97	1:1.47	1:1.77	0.69
II	August 16-September 9	52	75	127	1:1.47	1:1.44	0.03
III	October 6-25	23	28	51	1:1.47	1:1.22	0.32

Growth and survival to the seaward migrant stage

During the course of the 1967 smolt run, 482 marked river fish and 776 marked channel fish were recovered from 174,957 smolts examined. Preliminary analysis of the data indicates (1) that channel fish continued to be smaller than river fish (mean lengths of 76.9 and 78.9 mm respectively) and (2) differences in survival rate to the smolt stage were probably not statistically significant ($\chi^2 = 2.59$, $p > 0.10$).

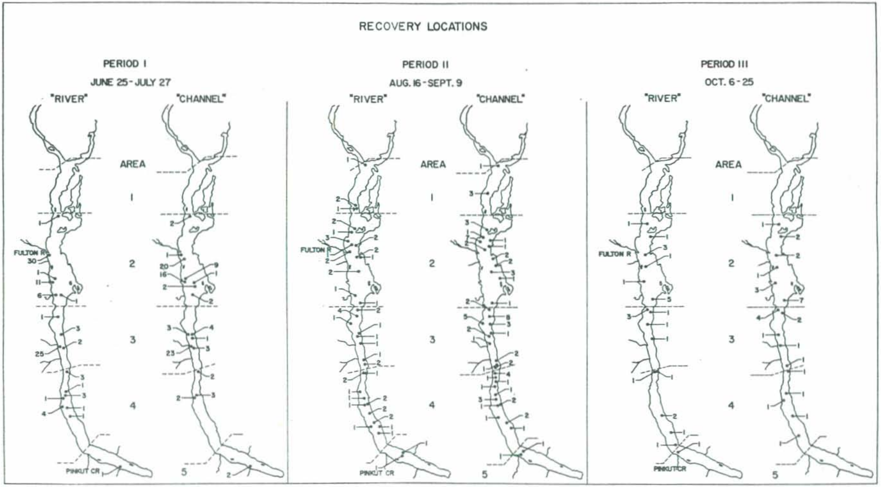

Fig. 1. Locations of marked sockeye recoveries in Babine Lake, 1966.

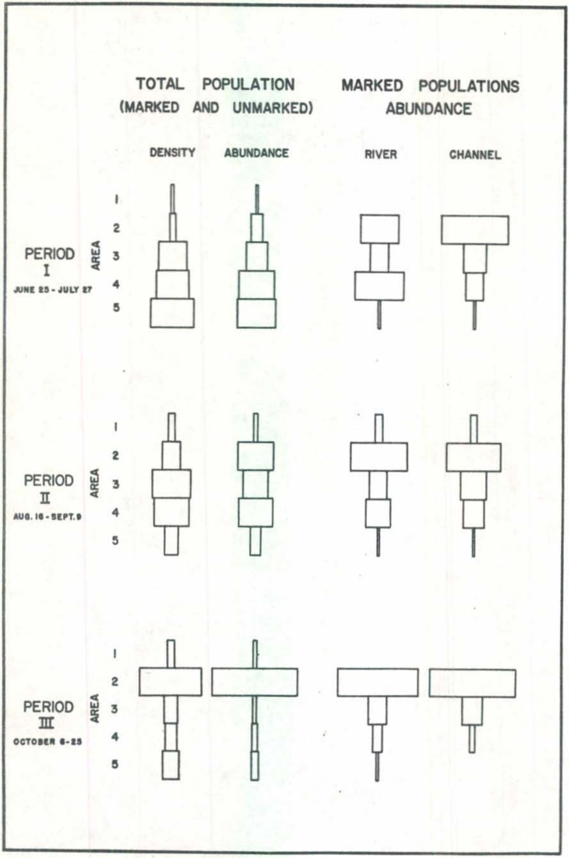

Fig. 2. Estimates of the relative density and abundance of marked and unmarked sockeye by lake area and fishing period. See Fig. 1 for location of areas.

PRIMARY PRODUCTIVITY OF BABINE LAKE

by D. W. Narver

The rationale behind the Babine development program is that the main lake basin, on the average, rears only one-fifth as many sockeye as the North Arm-Nilkitkwa area while it is potentially equally productive. In 1966, relative primary productivity of the various basins of Babine Lake was assessed utilizing the C^{14} in situ method. It was found that primary productivity (as measured by this method) was slightly lower in the North Arm (outlet) and in Morrison Arm (an inlet) than in the main lake region (Narver, 1967). An unusually high rate of photosynthesis at one part of the main lake in September may have been related to the decomposition of salmon carcasses in a nearby stream.

Morrison Lake, a major tributary, was much lower in rate of photosynthesis, pH, alkalinity, compensation depth, and total dissolved solids than any part of Babine Lake. The rate of carbon fixation of Babine Lake was much less on a per unit area basis than those reported by other workers for the majority of 24 sockeye salmon lakes similarly tested in Southwestern Alaska but was similar to most per unit volume of the euphotic layer. Much of this difference is attributable to a shallower euphotic zone in Babine Lake. Ranked with the 24 Alaskan lakes, Babine was first in alkalinity, third in TDS, and fifth in pH.

The productivity measurements suggest that the carrying capacity for sockeye salmon per unit of nursery area of the main lake region is at least as great as that of the North Arm.

Reference

Narver, David W. 1967. Primary productivity in the Babine Lake system, British Columbia. J. Fish. Res. Bd. Canada, 24(10): 2045-2052.

ADULT AND SMOLT SOCKEYE ENUMERATIONS

by H. D. Smith

Among the measurements needed for assessment of the Babine Lake development project are adult escapements to Babine Lake and the smolt runs resulting from them. The relationship between these two parameters will serve as one measure of the success of year classes and may be quite sensitive to changes in the balance between the rearing capacity of the lake basins and the numbers of young introduced into them. Ultimately, a measure of spawning escapement and resulting smolt output from particular production units or stocks is needed and some progress is being made in this regard. Since 1946 total adult escapement has been counted annually at the Babine fence and spawning populations have been counted or estimated in individual streams. Tagging programs in 1958, 1962 and 1963 have demonstrated the approximate times of passage of adults of these particular stocks at the fence.

Populations of sockeye smolts migrating out of Babine Lake have been assessed since 1951: the "late run" produced by spawners in the main lake basins, 1951-1957; the entire run - including North Arm-Nilkitkwa production - after 1957. Assessment of reproductive success of individual stocks, however, will require better information than now exists on the timing of their smolt migrations. At the present time it is only possible to assess production from two groupings of fish, those contributing to the early and to the late runs.

Fin-clipped smolts of the Fulton River stock were recovered from the seaward migrations of 1967 and in 1968 and 1969 smolts from subsequent markings will be available. It is expected that the timing of this stock will become better known. Similar information for other stocks may be gained in the same way.

Counts of adult Babine sockeye passing through the fence and in the various streams for the years 1946-1966 are shown in Table I. The relationship between potential egg deposition (calculated from Table I and fecundity counts) and smolts produced is shown in Figure 1 for three groupings:

1. the entire system - assuming all females entering the lake spawned,
2. the North Arm-Nilkitkwa area, and
3. the main lake area including Morrison Arm.

The main lake and North Arm regions are calculated from a stream count base because differences in fence counts and summed stream counts cannot be safely attributed to a specific region. In each region there is a general trend but again a large variability in production per million eggs potential is apparent.

The 10 years of production data for the entire system suggests that some increase in smolts has usually accompanied increases in potential egg deposition, but they also reflect a great deal of variability in production at all levels. Brood years 1958 and 1961 had similar egg depositions but there was a fourfold difference in smolt production; brood years 1960, 1961 and 1965 had potentials ranging from 400 to 1600 million eggs but produced similar-sized smolt runs.

Factors governing age at maturity

Management of sockeye stocks is hampered by the difficulty of forecasting runs well in advance of commercial fishing seasons. Part of this problem is caused by the diverse and variable age at maturity of the species.

Two lines of investigation are being followed at Babine. First, sampling of the individual production units is providing a basis for study of parent-progeny age relationships. Figure 2 shows the age composition of these units for the years 1962-1966. Second, studies at Four Mile Creek on Babine Lake have shown that mating is not random with respect to the age composition of the fish present (Hanson and Smith, 1967). There are two factors which may limit the participation of 4-year-old males in the reproductive act. There is a strong tendency for sockeye of like size to mate, i.e. 5-year-old males mate with 5-year-old females, and 4-year-old males mate with 4-year-old females. On occasion the 4-year-old males are displaced by the larger 5-year-old males and relegated to a "satellite" status, but the inverse is seldom true. These factors limit the contribution of 4-year-old males to the population gene pool and could have a marked effect upon the ultimate ages of progeny if heritable factors are involved.

The age composition of sockeye stocks in other Skeena tributary systems (Table II) has been assessed whenever possible as an additional step in the search for cause and effect relationships in age at maturity studies.

Smolt size and post-lacustrine survival

Efforts to obtain efficient utilization of lake nursery areas and the forecasting of adult returning population will be aided by an understanding of the relation between smolt size and ocean survival. Both the numbers and the age composition of returning sockeye may be adversely affected by increasing the young salmon population beyond some optimum level.[2]

In 1966 and 1967 smolts in five separate size categories were marked by Bergman-Jefferts coded wire tags. Recoveries in the commercial fishery, at the Babine fence and on the spawning grounds will be used to measure marine

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[2] It has been estimated that the lake nursery area could support about 350 million more fry than can be produced from existing spawning grounds (Bab. Dev. Report). But it will be necessary to learn what numbers of fry will produce smolts of a size and quality likely to provide the largest fishable return.

survival rates. In 1966, 47,000 smolts were tagged and four tagged jacks were recovered in the escapement of 1967.

Survival of certain sizes of smolts may at times be influenced by parasitism. The tapeworm Eubothrium salvelini is associated primarily with smolts of small size (Dombroski, 1955; Margolis and Boyce, 1963) and was present in all daily samples in 1966 and 1967 (Fig. 3). Parasitized smolts succumb to routine handling more readily than unparasitized smolts and their scale patterns differ. The relation between this parasite and survival of sockeye is not yet known but is under study.

References

Dombroski, E. 1955. Cestode and nematode infection of sockeye smolts from Babine Lake, British Columbia. J. Fish. Res. Bd. Canada, 12(1): 93-96.

Hanson, A. J., and Howard D. Smith. 1967. Mate selection in a population of sockeye salmon (Oncorhynchus nerka) of mixed age groups. J. Fish. Res. Bd. Canada 24(9): 1955-1977.

Margolis, L., and N. Boyce. 1963. Fish. Res. Bd. Canada Annual Report of the Biological Station, Nanaimo, for 1962-1963.

Table I. Babine sockeye escapements, in thousands of fish, 1949-1966.

	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1949-1966	
																			Sums	Means
Babine fence count	461	364	141	349	687	494	71	355	433	812	783	263	942	548	588	828[1]	580	389	9088	504.9
Indian catch	29	27	19	34	27	22	10	31	20	39	17	17	32	18	20	20	19	19	420	23.3
Potential spawning stock (count less catch)	432	337	122	315	660	472	61	324	413	773	766	246	910	530	568	808	561	370	8668	481.6
<u>North Arm - Nilkitkwa Region</u>																				
Upper Babine River	216.0	65.0	13.3	78.2	147.0	136.7	9.7	66.5	117.8	156.8	156.7	36.9	196.0	192.0	119.3	222.0	120.4	69.0	2119.3	117.7
Lower Babine River	135.0	116.0	10.8	69.0	127.4	100.0	9.0	52.3	66.5	107.8	123.5	54.0	171.5	61.0	34.5	46.0	176.0	114.0	1574.3	87.5
9 Mile	0.9	1.0	0.4	0.1	2.5	1.0	0.1	0	4.0	0	2.4	1.8	2.5	0.5	1.0	1.5	0.5	0.8	21.0	1.2
5 Mile	0	0.1	0.1	0	0.3	0.3	0.1	0	0.2	0	0,6	0	0.5	0.1	0	0.1	0.2	0.2	2.8	0.2
Total spawners	351.9	182.1	24.6	147.3	277.2	238.0	18.9	118.8	188.5	264.6	283.2	92.7	370.5	253.6	154.8	269.6	297.1	184.0	3717.4	206.5
Per cent of potential spawners	81.5	54.0	20.2	46.8	42.0	50.4	31.0	36.7	45.6	34.2	37.0	37.7	40.7	47.8	27.3	33.4	53.0	49.7		42.9
<u>Main Lake Region</u>																				
Morrison system	1.6	5.9	4.1	1.2	24.7	24.0	1.8	27.0	28.9	18.0	35.9	9.9	23.6	12.5	41.8	27.0	8.5	8.8	305.2	17.0
Fulton River	33.9	42.0	15.2	31.5	134.4	105.6	16.7	81.0	108.0	76.0	114.0	36.0	170.1	86.4	98.6	117.0	123.3	59.1	1448.8	80.5
Pinkut Creek	10.5	12.0	4.9	7.5	23.5	25.0	3.2	22.8	29.1	44.0	77.6	27.0	44.1	21.4	40.0	135.3	22.0	21.4	571.3	31.7
Pierre Creek	4.2	17.9	11.5	3.3	19.2	17.0	3.2	18.0	21.2	29.4	33.0	9.9	24.5	4.1	28.4	22.0	10.0	8.8	285.6	15.9
Grizzly	1.5	2.7	2.1	3.5	6.0	3.1	0.5	4.8	7.0	30.0	14.0	10.8	23.5	4.6	11.4	8.0	5.0	4.5	143.0	7.9
Twin	2.3	7.6	4.8	0.4	9.8	14.0	2.4	4.5	5.4	12.0	9.0	5.4	6.9	1.3	11.4	9.0	3.0	2.0	111.2	6.2
4 Mile	1.6	4.2	0.9	0.2	2.0	2.2	0.4	0.4	2.5	6.0	5.4	1.8	1.0	2.8	2.8	2.5	1.4	1.7	39.8	2.2
Tachek	2.6	2.6	2.5	0	2.4	1.9	0.3	0	6.4	1.8	6.0	1.8	0	0.6	1.6	3.0	0.7	0.3	34.5	1.9
Sockeye	0.2	0.9	0.8	0	0.6	0.9	0.5	0	2.5	1.5	4.0	1.8	0	1.0	2.4	1.5	0.1	1.4	20.1	1.1
6 Mile	0.4	1.2	0	0	2.6	1.8	0.1	0.1	0.6	2.3	3.5	0.9	0	0.9	1.4	1.5	0.1	0.3	17.7	1.0
Pendleton	1.1	1.2	0	0	1.4	1.1	0	0	0.3	0	2.5	0	0	0.2	0	1.4	0	0	9.2	0.5
Others[a]	0	0	20.0	74.4	1.0	0	0	0	0.2	72.5	3.9	0.3	51.8	6.2	6.2	9.3	1.8	0	247.6	13.7
Total spawners	59.9	98.2	66.8	122.0	227.6	196.6	29.1	158.6	212.1	293.5	308.8	105.6	345.5	142.0	246.0	337.5	175.9	108.3	3234.0	179.7
Per cent of potential spawners	13.9	29.1	54.8	38.7	34.5	41.7	47.7	49.0	51.4	38.0	40.3	42.9	38.0	26.8	43.3	41.8	31.4	29.3		37.3
Total spawners accounted for	411.8	280.3	91.4	269.3	504.8	434.6	48.0	277.4	400.6	558.1	592.0	198.3	716.0	395.6	400.8	607.1	473.0	292.3	6951.4	386.2
Per cent accounted for	95.3	83.2	74.9	85.5	76.5	92.1	78.7	85.6	97.0	72.2	77.3	80.6	78.7	74.6	70.6	75.1	84.3	79.0		80.2
Potential spawners not accounted for	20.2	56.7	30.6	45.7	155.2	37.4	13.0	46.6	12.4	214.9	174.0	47.7	194.0	134.4	167.2	200.9	88.0	77.7	1716.6	95.4
Per cent not accounted for	4.7	16.8	25.1	14.5	23.5	7.9	21.3	14.4	3.0	27.8	22.7	19.4	21.3	25.4	29.4	24.9	15.7	21.0		19.8

[1] Estimate derived from stream counts, tag and recovery, av. "not accounted for" 1949-1963.

[a] Includes: <u>a</u> intermittent counts in small marginal streams
<u>b</u> counts of fish which died unspawned esp. 1951, 1952, 1958, 1961
<u>c</u> for Nanika egg take from Pinkut Creek; 1961 = 2050, 1962 = 6200, 1963 = 6200, 1964 = 9300; 1965 = 1800

Table II. Age composition of Skeena stocks outside Babine, 1963-1967.

Stock	Year	No. Sampled	1.2 (4_2)	1.3 (5_2)	1.4 (6_2)	2.2 (5_3)	2.3 (6_3)	2.4 (7_3)	3.2 (6_4)	3.3 (7_4)
Asitka Lake	1964	47		91.5		2.1	6.4			
	1966	4		100.0						
	1967									
Williams Creek	1964		47.6	51.5		0.6	0.3			
	1965		29.8	70.2						
	1966		17.8	80.4	0.9		0.9			
	1967									
Scully Creek	1964		19.0	80.8		0.2				
	1965		52.0	48.0						
	1966		46.8	52.2		0.7	0.3			
	1967									
Swan-Stephens Lake	1963	6	100.0							
	1964	62	85.5	11.3		3.2				
	1965	17	58.8	5.9		29.4	5.9			
	1966	143	50.3	37.8		9.1	2.8			
	1967									
Kitwanga Lake	1965	16	100.0							
	1967									
Bear Lake	1963	18	77.8	22.2						
	1964	73	10.9	89.1						
	1965	57	61.4	38.6						
	1966	45	13.3	86.7						
	1967									
Kalum Lake	1964	27	29.6	70.4						
	1965	51	68.6	27.5		3.9				
	1966	23		100.0						
	1967									
McDonnel Lake	1964	22	4.5	45.5		13.6	36.4			
	1965	230	9.6	79.2	0.4	4.3	6.5			
	1966	130	0.8	82.3		2.3	14.6			
	1967									
Johanson Lake	1963	35				31.4	65.7		2.9	
	1964	14		42.9		28.6	21.4			7.1
	1965	10				20.0	80.0			
	1967									
Sustut Lake	1963	90	24.5	44.4	1.1	16.7	13.3			
	1964	78	1.3	85.9		11.5	1.3			
	1965	65	4.6	78.5			16.9			
	1966	50	2.0	80.0	2.0	6.0	10.0			
	1967									
Azuklotz Creek	1965	19	89.5	10.5						
	1967									
Sicintine Lake	1964	2				50.0	50.0			
	1965	14		21.4			78.6			
	1966	4		25.0			75.0			
	1967									
Slamgeesh Lake	1964	5	80.0	20.0						
	1965	35	91.4	5.7		2.9				
	1966	7	22.2	77.8						
	1967									
Onerka Lake	1965	22		27.4	4.5	50.0	13.6	4.5		
	1966	6	83.3				16.7			
	1967									
Alistair Lake	1963	41	2.4	4.8		88.0	4.8			
	1964	113	1.8	47.8		9.7	40.7			
	1965	88	2.3	28.4		28.4	39.8			1.1
	1966		2.9	4.4		2.9	89.0		0.4	0.4
	1967									
Nanika River	1963	245				50.0	50.0			
	1964			6.7		93.3				
	1965		3.4	10.0		43.2	40.0		3.4	
	1966			1.9		81.4	16.7			
	1967									

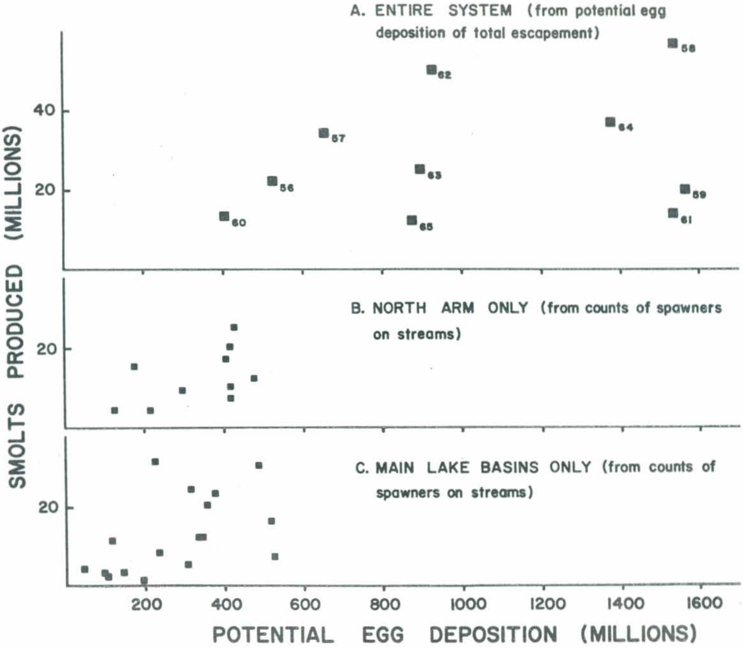

Fig. 1. Babine Lake sockeye smolt production.

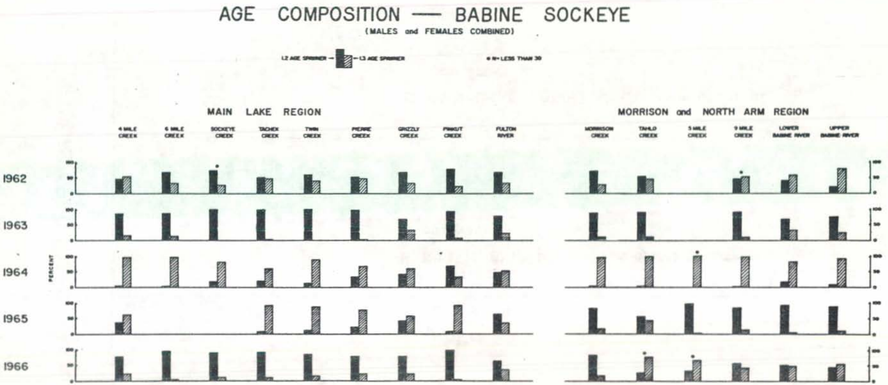

Fig. 2. Age composition - Babine sockeye.

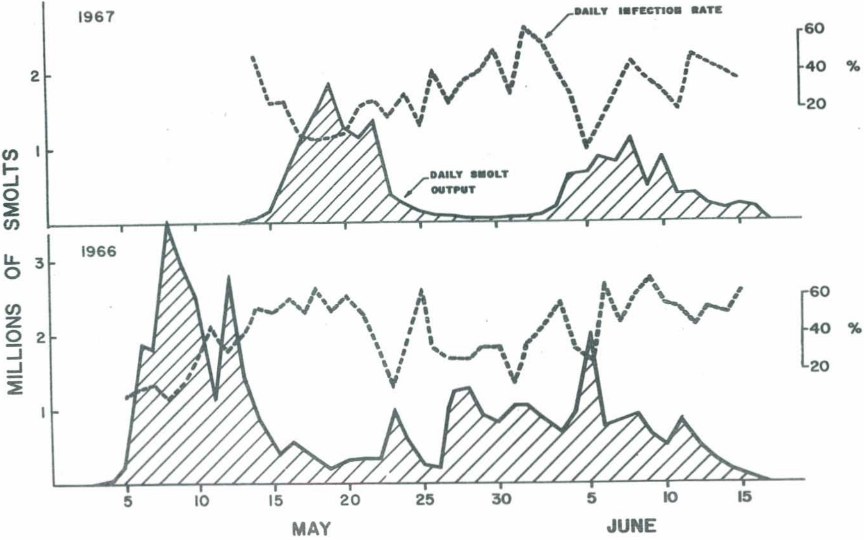

Fig. 3. Parasitism of Babine sockeye smolts by tapeworm Eubothrium salvelini in 1966 and 1967.

A REVIEW OF THE LITERATURE ON THE EFFECTS OF CHANGES IN TEMPERATURE REGIME ON DEVELOPING SOCKEYE SALMON EGGS AND ALEVINS

by R. A. Bams

INTRODUCTION

At a meeting of the Babine Lake Sockeye Development Sub-Committee, February 21, 1967, concern over a possible 10-15° F rise in temperature under certain conditions between the inlet and outlet points of the Fulton spawning channel was expressed. The biological consequences of temperature alteration in artificial spawning channels were not known to this group and a survey of literature was to be undertaken.

This report specifically deals with the effects of alteration or variation of temperature from optimal conditions for larval development of sockeye salmon. It is beyond the scope of this review to speculate about changes in temperature regime which might be expected in a particular facility. Little of the available literature is specifically directed to the species in question hence it is necessary to apply generalities resulting from studies on a broad spectrum of species. Excellent reviews regarding the effects of temperature on development are already available: Hayes (1949), Seymour (1956), Rockwell (1956) and Kinne and Kinne (1962). A large segment of the applicable literature has been reviewed for this report, but the survey was not exhaustive. It is believed, however, that the more essential aspects are covered, and that little would be gained from further searching. Because many physiological processes, such as rate of growth, are influenced by more than one environmental factor, many of which interact (e.g. O_2 and temperature), treatment of the effects of temperature alone is not entirely satisfactory. For the immediate purposes of this report this simplification appears necessary.

There are many aspects to a particular temperature regime, such as the mean value, maxima and minima, the order and frequency of fluctuations, the rate of change, the duration at a certain level, etc., which can directly affect an organism. Not only may any one aspect influence one or more biological processes or events, but biological effects may be accumulative or interdependent. In general, effects of a temperature change are many, and extremely varied. They can range from a simple, direct relationship, such as the accelerating influence of an increase of temperature (within a certain range) on the basic metabolic rate, to extremely complex and multi-order effects. For example, the final effect of a rise in temperature on the survival potential of a particular migrant fry may go through the following chain of events: (a) an increase in the numbers of aerobic organisms in part of the channel, (b) a subsequent reduction in O_2-concentration, (c) mortality of part of the brood, (d) decomposition of these dead larvae by microorganisms, and (e) pollution of the environment in which this fry migrant developed. The final outcome may be death or lowered viability.

Clearly effects of this nature will be determined by local conditions and cannot be predicted in advance. However, they are of importance as they affect the environment and hence may limit the population.

EFFECTS DURING PERIOD BEFORE EGG DEPOSITION

Pacific salmon spawn during the declining phase of the annual temperature cycle. At Babine, sockeye generally spawn at temperatures between 55° and 45° F. If the decline in temperature, after summer maximum, is delayed a similar delay may be expected in spawning (Sheridan, 1962). Some immediate effects may be: (1) initiation of development of the embryos is delayed; (2) the sexual products become "overripe" and reduced egg survival results, particularly through loss of eggs (before fertilization) and reduced fertilization due to reduced viability of either eggs or sperm, or both. Extensive prespawning mortality in sockeye adults has been correlated with high water temperature (Royal, 1953). From Brett's work (1952, 1967) on thermal resistance in sockeye salmon, the zone of thermal resistance is known; generally speaking, temperatures become lethal at around 25°C (= 77°F). However, temperatures between the optimum level at around 15°C (= 59°F) and the upper lethal level become increasingly stressing and the scope for further activity is reduced, as evidenced by a gradual decrease in swimming performance (Brett, 1967). Further consequences of temperature levels above the physiological optimum can be expected, e.g. a reduced life span due to accelerated metabolism, and higher incidence of disease, particularly attack by Saprolegnia spp.

EFFECTS DURING THE LARVAL STAGES

Changes in sensitivity during development

Not all larval stages are equally sensitive to similar amounts of stress. In relation to O_2 and temperature the most sensitive periods are the period between early cleavages to the closing of the blastopore, and the period immediately prior to hatching (cf. Battle, 1944; Hayes and Armstrong, 1942; Hayes, 1949; Garside, 1959; Swift, 1965). Apparently both heat and cold tolerance of developing fish larvae is limited at the early stages and gradually increases during development (e.g. Donaldson, 1955, and Olson and Foster, 1956).

Rates of differentiation and growth (development) and metabolism

Developing sockeye salmon larvae depend entirely on their yolk supply as a source of energy during the full period of larval development. This supply must satisfy all physiological needs, i.e. various additive demands must share the available reserve. During normal development a rather precise balance is struck between the competing demands for activity, metabolism, and growth. A fully developed fry is formed at a time, stage of development, and size, optimally adapted to the average conditions experienced by the stock during succeeding stages. If, due to unusual circumstances during development, the demand of any one of the competing functions increases, one or both of the others must suffer if the supply rate remains constant, or, alternatively, the developing larva will use up its supply before development is complete.

The effect of temperature alone on the larval rate of development is an important consideration. In general a rise in temperature increases the rate of development, thus decreasing the developmental time period. Developmental rate is expressed as the reciprocal of developmental time. The relationship between this rate and a variety of constant temperatures is nearly linear over most of the normal developmental range, and such an interpretation forms the basis for the commonly used constant "Day-Degree" rule used by most investigators (Hayes, 1949; Seymour, 1956; Rockwell, 1956). These authors have extrapolated the linear approximation to obtain an estimate of the temperature at which developmental rate is zero. Over extended temperature ranges, however, the relationship is definitely curvilinear, and such extrapolations are in error.

Experimental evidence for developmental rates at temperatures below 2.5°C is scarce. Embody's work on Salvelinus fontinalis and Salmo trutta, however, clearly demonstrates a gradual slowing in deceleration of the growth rate with decreasing temperature at these low levels.

Garside's data for lake trout (Garside, 1959) have been selected to illustrate the changes in rate of development at lower temperatures. Garside ignored the non-linearity of his data, and indicated a development rate [100/(days from fertilization to hatching)] at 0°C of between 0.2 and 0.3, corresponding to a time period of some 380 days. From his data a decelerating rate of 13 days per 2.5°C decrease is estimated and, extrapolating, the rate of development would be 0.503 at 0°C, corresponding to a period of 198 days. The following table expresses expected increases in rate of development, starting with 0°C for increments of 2.5°C.

Table I. Expected relationship between development rate, fertilization to hatching, and temperature.

Temperature (°C)	Days	Rate (100/da)	Rate change over temperature interval - Δ rate and percent increase -							
			From 0.0 to		2.5 to		5.0 to		7.5 to	
			Δ	%	Δ	%	Δ	%	Δ	%
0.0	198	.503	-	-	-	-	-	-	-	-
2.5	141	.709	.206	41.0	-	-	-	-	-	-
5.0	97	1.031	.528	105	.322	45.4	-	-	-	-
7.5	67	1.493	.990	197	.784	111	.462	44.8	-	-
10.0	50	2.000	1.497	298	1.291	182	.969	94.0	.507	34.0

Note: The maximum relative increase in rate occurs around 5°C.

With this table the advance in days caused by a given temperature rise over a given number of days can be accurately determined. For example: with the river at 0°C and the channel at 2.5°C during a 20-day period, development in the channel is advanced by 41%, equivalent to 8.2 days. These 8.2 days, however, are based on a developmental rate of 0.503. In the spring when emergence occurs, the temperature is about 5°C, and at this temperature the developmental rate is about 1.031. Thus the early gain of approximately 8.2 days can be made up in about four days [8.2(503/1031)] by the river fry at the higher temperature. Emergence of the two groups of fry may occur at the same time because of factors other than temperature, e.g. daylight length and silt, however the relative stages of development of the two groups will have been altered. The developmental rates for many salmon species are quite similar and the lake trout data compare favourably with those available for sockeye at higher temperatures (Rucker, 1937).

Table II gives the estimated development rates between 0 and 10°C in 0.5° intervals. From it rate changes can be calculated for any temperature interval according to the method shown in Table I.

Table II. Development rates at different temperatures.

Temperature °C	Rate (100/days)	Temperature °C	Rate (100/days)
0.0	.503	5.5	1.111
0.5	.534	6.0	1.198
1.0	.570	6.5	1.293
1.5	.611	7.0	1.392
2.0	.657	7.5	1.493
2.5	.709	8.0	1.594
3.0	.765	8.5	1.695
3.5	.825	9.0	1.796
4.0	.889	9.5	1.898
4.5	.958	10.0	2.000
5.0	1.031		

Note: For rate values located between values listed use linear interpolation.

Admittedly these calculations are somewhat more involved than the Degree-Day method, but the greatly increased accuracy, particularly at the low end of the temperature range, dictates its use.

From the rates shown it is evident that even limited changes in temperature regime have a significant effect on the developmental rate. Hence, a consistently higher daily average temperature will result in earlier completion of development. Such a condition may lead to two alternatives: (1) early emergence and migration at a time that will not provide optimum conditions for further growth and development, or (2) remaining in the gravel with further depletion of critically low energy reserves, leading to poor condition at time of emergence. Both alternatives are considered undesirable: "premature emergence in good condition" because the lake environment (e.g. temperature and/or food) is not yet favourable, and "suboptimal condition at the right time" because such fry have been shown to exhibit a reduced survival potential (Bams, 1967).

Other effects

In addition to alteration of the developmental period, changes in temperature affect differentiation and growth in other aspects. A decrease in potential size of fry at the end of the incubation period from increased temperature is well documented (cf. Gray, 1928; Donaldson, 1955; Seymour, 1956). Gray attributes the reduction in size to differences in rates of reaction as these pertain to growth and maintenance: relatively more energy is required for the increased rate of maintenance metabolism, hence less yolk is available for growth. Sockeye fry of a reduced size are known to have a decreased viability as shown by Brett (1952) for low temperature tolerance, and by Bams (1967) for swimming performance and vulnerability to predation. It is now thought likely that such changes will lead to an alteration of life history and time of maturity.

Related effects are changes in morphological characteristics of the developing larvae. There are a number of critical stages during development when different levels of O_2 and/or temperature can affect the extent of various differentiation processes. Particularly the work of Hayes (cf. Hayes, 1949, Hayes et al., 1953) has shown that various differentiation processes have different temperature coefficients so that interacting processes affect each other differently at different temperatures. Much evidence is on hand regarding the effect of temperature level on the number of vertebrae, fin rays, morphometric relationships, etc. (cf. Alderdice et al., 1958; Garside, 1959; Kinne, 1963). Seymour (1956) indicates, for chinook fry, changes in vertebrae counts, dorsal fin rays, and anal fin rays. Related to these effects are the influence of temperature on the number of abnormal (deformed) fry and on hatching efficiency. From the limited body of information reviewed it can be concluded that changes will occur with changes in temperature level. Optimum values are indicated and temperature changes precipitate modifications of these characteristics in either direction.

Effects of substantial decreases in temperature are presumed to be limited to events that can occur during a matter of hours only. Direct lethal effects are perhaps unlikely. Brett (1952) and Brett and Alderdice (1958) investigated the lower lethal temperature limits of young chum and sockeye salmon. Their results indicate that exposure to 0°C is within the tolerance range of both species from the fry stage on. Exposure to temperatures far enough below zero to be harmful ($\leqslant$ -0.5°C) cannot occur in fresh water unless the intergravel water freezes. Survival under the latter conditions, even for limited exposure, is unlikely. Direct effects on morphological characters may possibly occur in cases where the duration of the critical phase of a differentiation process is sufficiently short to be influenced by a temporary cold wave. No data were found regarding the duration of any such critical phases.

Continuous low temperature, especially during early embryonic stages, is known to be harmful and to increase mortality. Brett and Alderdice, 1958, mention that fry and yearlings acclimated to 2.5°C showed less resistance to cold (below 0°C in salt water) than did fry acclimated to 5.0°C, and infer that the 2.5°C acclimation temperature imposed a stress on the fish.

The dependence of the effect of a change in temperature on previous thermal experience is well known from temperature tolerance work by various authors. In general, exposure to high or low temperature can be tolerated better if the fish is already acclimated to a high or low temperature level. The effect is much more pronounced (greater dependency) for the low than for the high temperature limit. Hence, a sudden decrease in temperature is potentially much more harmful than a slower decrease of the same magnitude; the rate of change of an increase in temperature is of much less importance.

The effects of temperature fluctuations are largely unexplored. As long as harmful extremes are not reached little effect of increased fluctuation around a common mean can be expected. In regard to morphological characteristics Lindsey and Ali (1965) established, in a temperature transfer experiment with medeka, that these characteristics followed the arithmetic mean temperature. It should be noted that, due to the previously mentioned reduced tolerance ranges during certain stages in larval development, increased daily fluctuations of a certain magnitude could be harmless during most of the developmental period but potentially harmful at certain times, particularly during the pre-eyed stages.

Indirect effects

An immediate effect of increased metabolic rate due to temperature increase is increased O_2 demand. The importance of O_2 to the brood and effects of changes in demand and/or supply are discussed below.

Most indirect effects of a change in temperature are expected to occur by means of changes in the environment. Both changes in physico-chemical and biotic elements of the environment are likely to occur. Of the former oxygen is of major concern. The direct influence of available O_2 on the fry is of prime importance, possibly more so than temperature per se. O_2 is known to affect differentiation rate, growth rate, efficiency of yolk conversion, mortality rate at all embryonic stages, hatching success, time of emergence, formation of abnormals and morphological characteristics. Temperature affects the O_2 content of the water directly by reducing the saturation level as temperatures increase. Indirectly O_2 content will be affected through increased consumption by the resident flora and fauna. Conversely, a lowering of the temperature could cause over-saturation, which is very harmful to fish, and increased ice formation, which could seriously interfere with the intergravel water flow pattern. Of the biotic factors possible, increases in algal and bacterial growth as correlates of increased temperature should be mentioned, both of which would have consequences regarding O_2 content, metabolic waste products, and possibly interference with the intergravel flow. Incidence and growth of fungus on dead eggs can also be expected to increase, with a subsequent higher mortality rate of adjacent eggs.

The effects of lowered O_2 content and reduced flow have been studied extensively by Garside (1959, 1966), Silver et al. (1963), Shumway et al. (1964). Small reductions in either temperature or O_2 were shown to measurably affect the fry, especially in respect to rate of development and size, and increasingly so as the absolute levels of these factors dropped. Of considerable interest here is the repeatedly established interaction of O_2 and temperature (Alderdice et al., 1958; Garside, 1959, 1966). A progressive increase of any effect (such as retardation of development rate) produced by a certain level of hypoxia was observed with increase of temperature. Also, with increasing temperature the effect occurs at progressively earlier stages in development, i.e. a certain level of hypoxia may not adversely affect the developing larva of a particular stage at a certain temperature, but it will do so at: (1) a later stage at the same temperature, and (2) at its present stage if the temperature is increased. These findings illustrate the earlier observation that the consideration of the effects of a single factor are not satisfactory, and that an integrated multifactor model is necessary to assess realistically the effects of any one factor, such as temperature.

Conclusions

1. The effects of changes in temperature regime on developing salmonid larvae are of great diversity, and many are potentially harmful.
2. Virtually all the effects mentioned are impossible to quantify beforehand because of (a) the body of data applicable to the stock under consideration is too limited, and (b) the extent of the expected temperature changes is unknown. Prediction of changes in second, or higher order events that are likely to affect the brood is also impossible due to the many, largely unknown, local conditions that will influence these events.

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PROGRESS REPORT ON A STUDY OF FACTORS ASSOCIATED WITH AGE AT MATURITY OF SKEENA RIVER SOCKEYE

by T. Bilton

Several correlated effects have led to a possible chain of events which may influence the age at maturity of Skeena River sockeye salmon. These are:

1. In general the size of 1.3 females is larger than that of 1.2 females.
2. A significant positive correlation exists between body size and egg size, hence eggs of 1.3 females are, on the average, larger than those of 1.2 females.
3. Results from reciprocal crosses of 1.2 and 1.3 sockeye indicate that size of resulting alevins and their subsequent growth as juveniles is positively correlated with egg size, and that this is a maternal effect.
4. Within each of four brood years of Skeena River sockeye, fish maturing as 1.2's had a higher number of freshwater circuli than those which matured as 1.3's.
5. Number of freshwater circuli is directly correlated with smolt size.

The evidence thus suggests that the size of the female parent may directly influence the age at which the progeny will mature. This further suggests that, where other influencing factors are equal, an alteration of generation time can exist, e.g. that 1.3 females will produce 1.2 females which will in turn produce 1.3 females. This hypothesis is now being tested.

DIEL VERTICAL MOVEMENT OF PELAGIAL SOCKEYE SALMON JUVENILES

by D. W. Narver

Problem and methods

A general pattern of vertical diel movement of pelagial sockeye salmon juveniles during the summer in Babine Lake was suggested from tow netting in 1956 to 1963 and from echo sounding, tow netting and purse seining in 1966. These sources indicated that (1) during the day juveniles were deeper than 50 ft, (2) at least some moved to the lake surface at dusk, (3) at least some remained within 50 ft of the surface at night, and (4) juveniles moved away from the surface soon after dawn. The objective of this research in 1967 was to answer specific questions about this apparent diel vertical movement of juveniles: "What is the precise pattern of movement? When does this behaviour first become evident and how does it change through the summer? Is this behaviour the same in the North Arm as in the main lake? What is the physical and biological environment associated with the behaviour? What is the feeding biology of juveniles and how does it fit into this behaviour?" The basic hypothesis was that juveniles seek a specific light intensity and hence light is the primary factor controlling the diel movement. To test this a prototype underwater light meter was designed and ordered, but unfortunately it was not delivered in time for field use in 1967.

The field study was based on observations and samples taken at intervals during ten 24-hr series (noon to noon). These series included transects with a 145 kc Sea Scanar (Honeywell) echo sounder, tows with a 3-ft Isaacs-Kidd midwater trawl, purse seine sets with a 600 × 35 ft net, horizontal zooplankton tows with Miller samplers at eight depths, secchi depth, and vertical temperature profile. These 24-hr series were conducted from mid-July to early October in the North Arm of Babine Lake (7) and in the main Babine Lake (3).

Early results

The success of this investigation lay primarily with the reliability of the echo sounder as a device to indicate the abundance of juvenile sockeye salmon at any depth. A correlation coefficient of .81 was obtained in the relationship between juvenile catch by trawling and the number of echo sounder targets (Fig. 1). Purse seine sets substantiated this since midday sets when there were no echo sounder targets above 35 ft resulted in no catches of juveniles; sets made in the evening, night, or early morning when targets were found above 35 ft resulted in catches of juveniles.

A precise, well-defined diel vertical movement is displayed by pelagial sockeye juveniles in Babine Lake from at least mid-July to September (Fig. 2). The maximum vertical movement in the North Arm was from the midday depth on the bottom or 130 ft to the lake surface just after sunset. (In the study area between Nine Mile and Five Mile creeks depth of bottom ranged from 100 to 170 ft.) A distinct and consistent double layer of targets, believed to be juveniles, during the day was found in the North Arm (Fig. 2). The two layers maintained a constant distance apart until the top layer reached the surface in the evening. The bottom layer (the majority of targets) continued to rise until it also reached the lake surface (Fig. 2). The pattern of diel vertical movement changed in the fall as indicated by the October 2-3 series. Juveniles no longer came to the surface but remained in midwater through the night and returned to deeper water during midday (Fig. 3). The double layer was no longer conspicuous during the day.

The July and August diel vertical behaviour of juveniles in the main lake was similar to that of the North Arm except the midday maximum depth was 150 to 170 ft.

The zooplankton of Babine Lake is composed of the Calanoid copepods Diaptomous (2 species), Epischura and Heterocope; the Cyclopoid copepod Cyclops; and the Cladocera Daphnia, Bosmina, and Holopedium. Only Bosmina and Heterocope displayed a pronounced diel movement and these were in opposite directions (Fig. 4). Daphnia, Holopedium, Epischura, and both Diaptomous were found almost entirely above 35 ft. Cyclops occurred in greatest concentrations below 35 ft (Fig. 4). The species are ranked in relative abundance from lowest to highest: Holopedium, Epischura, Heterocope, Bosmina, Daphnia, Diaptomous pribilofensis, Cyclops and Diaptomous ashlandi. Although Heterocope was relatively scarce it formed a major portion of the zooplankton biomass since an individual adult is about 4 mm long.

A preliminary examination has been made of juvenile stomach contents from one 24-hr series in North Arm. These data suggest that intensive feeding occurred at dusk as the juveniles reached the 0-35 ft stratum and again at dawn as the fish commenced to move away from the lake surface. There appears to have been no feeding during the hours of darkness when the fish were within 50 ft of the surface and little feeding in midday when the fish were mainly below 100 ft. The dominant food item was Heterocope followed by Daphnia.

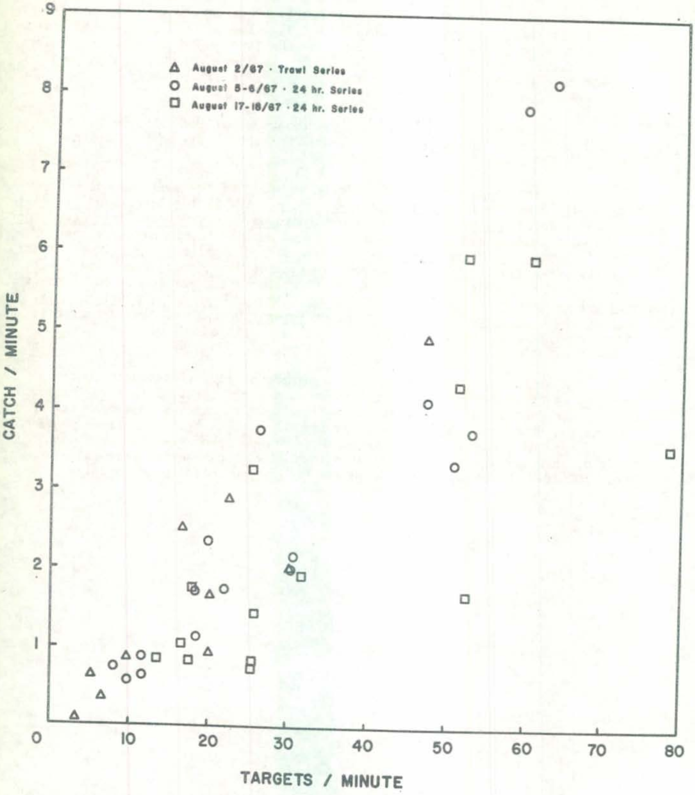

Fig. 1. Plot of midwater trawl catch per minute of juvenile sockeye and the simultaneous number of echo sounder targets per minute in the 10-ft stratum of water at the depth of the trawl. Data from August, 1967 in the North Arm of Babine Lake.

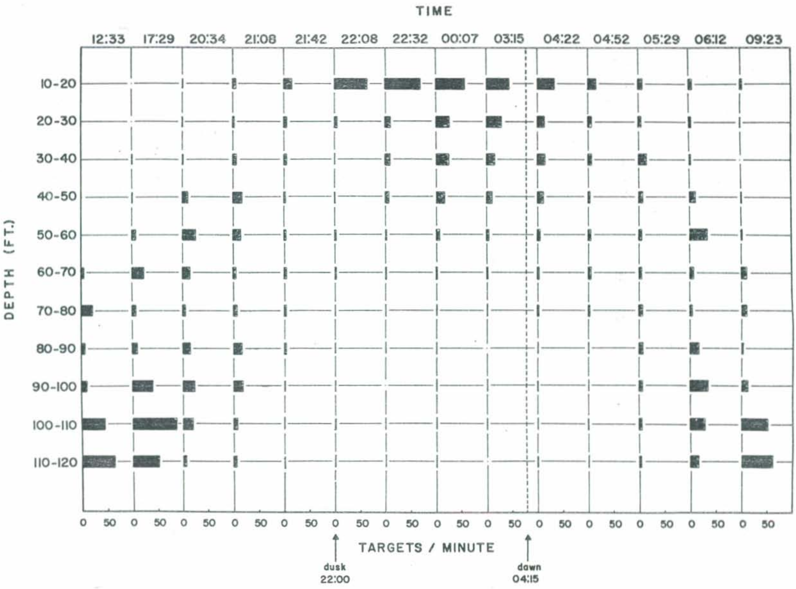

Fig. 2. Echo sounder targets per minute (.3 mile) by 10-ft strata during the 24-hr series of August 5-6 in the North Arm. (Note that time is not to scale.)

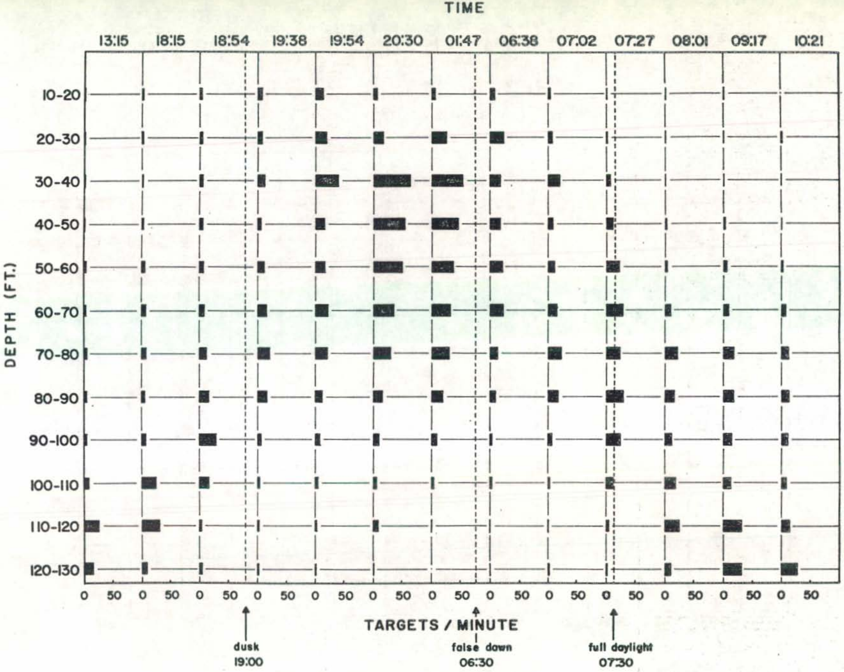

Fig. 3. Echo sounder targets per minute (.3 mile) by 10-ft strata during the 24-hr series of October 2-3 in the North Arm. (Note that time is not to scale.)

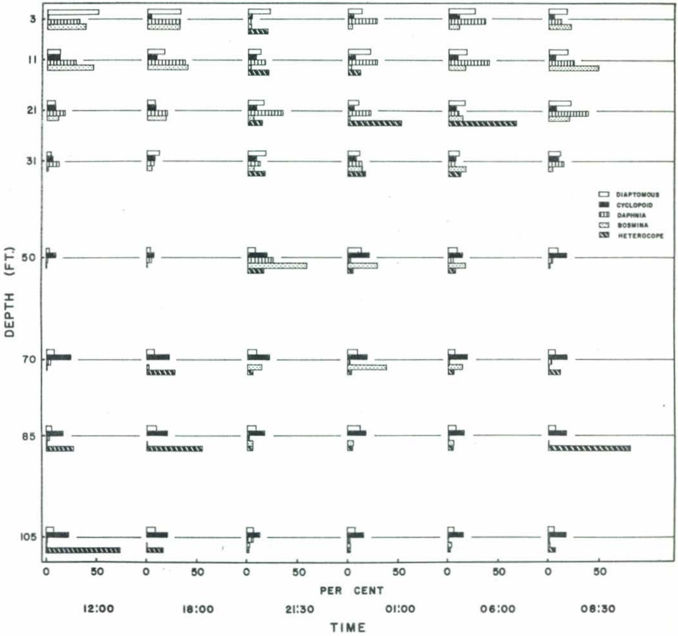

Fig. 4. The diel vertical distribution of zooplankton species in the North Arm of Babine Lake on September 22-23, 1967. Each depth is expressed as a per cent of the number of that species taken in a particular vertical profile.