Olsen 1968

FURTHER STUDIES OF ALASKA SOCKEYE SALMON

Edited by Robert L. Burgner

University of Washington
Publications in Fisheries
New Series, Volume III
$3.60

Seattle — University of Washington — 1968

PHYSICAL ENVIRONMENT AND EGG DEVELOPMENT IN A MAINLAND BEACH AREA AND AN ISLAND BEACH AREA OF ILIAMNA LAKE

by

JAMES C. OLSEN

CONTENTS

PHYSICAL ENVIRONMENT AND EGG DEVELOPMENT IN A MAINLAND BEACH AREA AND AN ISLAND BEACH AREA OF ILIAMNA LAKE

Abstract

The sockeye salmon spawning beaches of Iliamna Lake, Alaska, are of two types, mainland and island. Bottom composition, temperature regime, and source of water circulation in redds of an area of each type were determined. Sand comprised 85 per cent of the bottom materials in the mainland beach, whereas coarse gravel and boulders made up 95 per cent of bottom materials in the island area. Intergravel water temperatures in the mainland beach area were 1 to 4°C lower than lake temperatures during the period of August 26 to September 10, 1962, but little temperature difference was found in the island area. It seems conclusive that upwelling ground water is the source of water circulation in redds in the mainland beach area, whereas lake currents are the source in the island area.

The stages of development in embryos and alevins of sockeye salmon were related to thermal age in incubation experiments in the hatchery at the University of Washington College of Fisheries. Length attained and the first appearance and development of various morphological features were the criteria used to establish stages of development. Fifty per cent of the eggs hatched within 643 degree days, and yolk sac absorption terminated at 933 degree days. The rate of development of eggs planted in the study areas was determined with the development series as a guide. Development at the island beach area proceeded at a faster rate than at the mainland beach area because of earlier spawning and a warmer temperature regime. Hatching had commenced at the former by mid-November, but eggs planted at the latter had developed only halfway to hatching by this time.

Introduction

The Fisheries Research Institute, University of Washington, is conducting studies to determine the most productive population levels of sockeye salmon, *Oncorhynchus nerka* (Walbaum), in the lakes of the Bristol Bay region of Alaska. One of these studies is the identification and description of spawning races or colonies,[1] of which this work is part.

Iliamna Lake is the largest of several lakes in the Kvichak watershed. It lies on an east northeast-west southwest axis 15 m above sea level. The eastern half is bordered by mountains of the Aleutian and Alaskan ranges, and the western half lies in lowlands of the Alaska Peninsula. The lake has a shoreline development of 2.753, a maximum depth of 301 m, a mean depth of approximately 44 m, and a surface area of 2,622 km^2 (Lenarz, 1965).

The principal spawning beaches are located on the borders of the eastern half of the lake and of the islands within (Fig. 1). This region of the lake is deeply scoured by glaciation. It has a highly developed shoreline, with numerous bays and islands. The spawning beaches are of two types, mainland and island. Lacustrine grounds have supported, as a whole, an average of 24 per cent of the escapement to the Kvichak River system over the years. Mainland beaches support 53 per cent of the population spawning on beaches, and island beaches and shoals support the rest.[2] The fraction of lake spawners is more important when the escapement is large; of 24 million returning sockeye in 1965, 50 per cent spawned on lake grounds (McPhail, 1966).

Many of the mainland beach spawning areas adjoin lake tributaries, as in other sockeye-producing systems (Foskett, 1958; McConnell, and Brett, 1946; Owen, Conkle, and Raleigh, 1962). This type of location suggests that upwelling ground water is present. On the other hand, the location of island beach spawning areas suggests its absence. Visual observations of both types of spawning areas indicated that the bottom of mainland areas is composed of finer materials than are found in island areas. It was hypothesized that lake currents play the same role in sockeye redds in island areas that ground water does in

[1] *Race* is a genetically different subspecific group from the parent stock; *colony* is a group that may or may not be genetically different from the parent stock but that has transferred to a new environment (Thompson, 1962). *Race* in this paper means either *race* or *colony*.

[2] The average percentage of annual escapement was calculated from survey figures, 1956-1963; the average percentages of spawners that occupy the main types of areas were calculated from 1961-1963 survey figures (Demory, Orrell and Heinle, 1964).

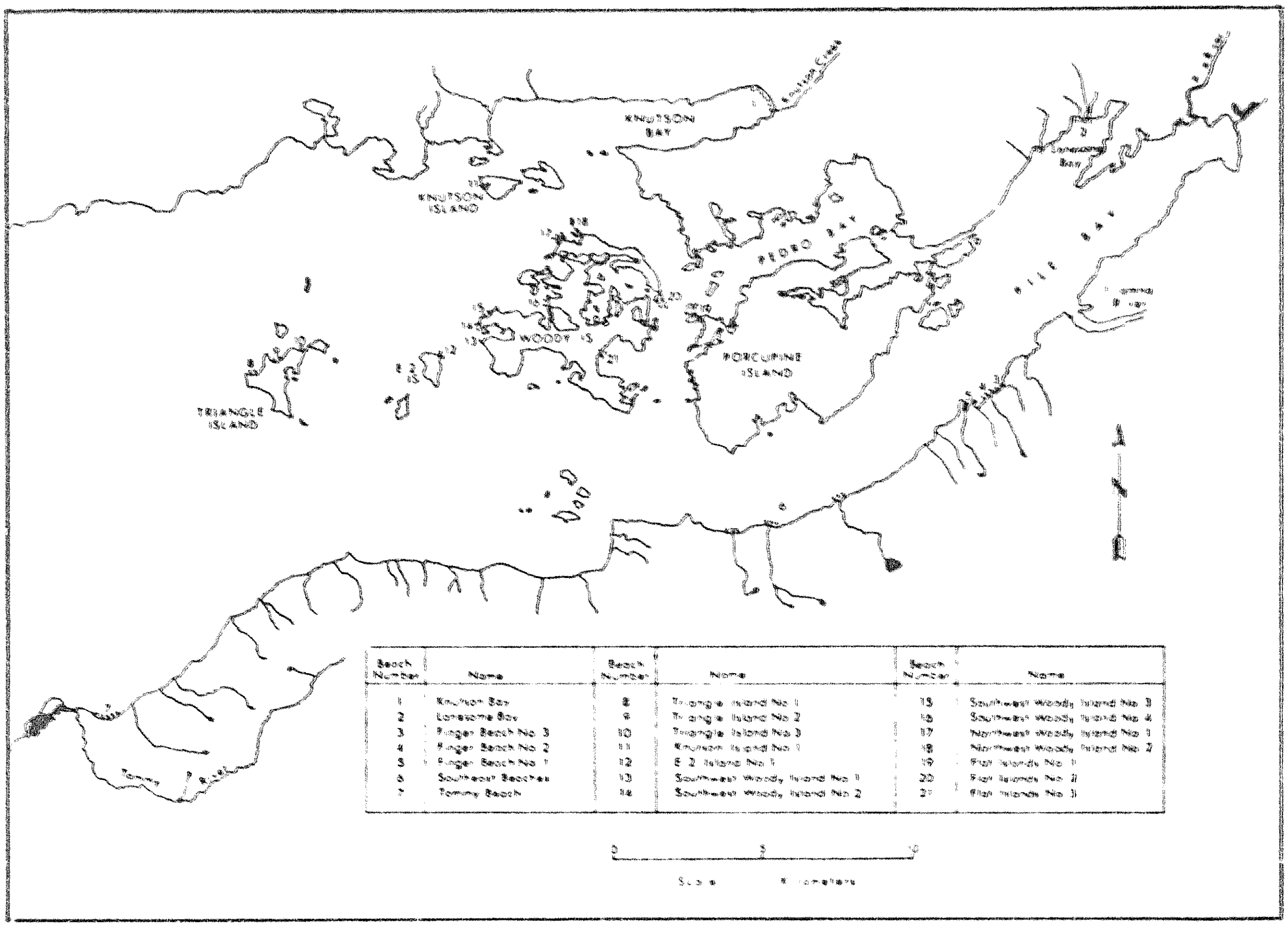


Fig. 1. Spawning beaches, eastern half of Iliamna Lake, Alaska.

mainland areas, and that consequently the rate of egg development differs in the two areas.

This study was made to compare the physical environments and rates of egg development in a mainland beach spawning area and in an island beach spawning area.

Physical Environment

The two study areas have been intensively utilized by sockeye salmon for spawning over the years. A portion of the extensive spawning ground in Knutson Bay was the mainland study area. The ground supports as much as 10 per cent of the spawning population of the Kvichak River system. Spawning takes place from early September to the end of October (Demory *et al.*, 1964). The neighboring steep mountains afford protection from easterly winds. An adjoining intermittent creek discharges only after heavy rains. The study area lies close to the deepest lacustrine spawning grounds known in the system. Triangle Island area 2 was the island study area. In 1961 the estimated escapement was 5,500 spawners. Spawning generally occurs during two weeks in August (*op. cit.*). Bordering rock cliffs shelter the area from easterly and southwesterly winds.

The size of each study area was determined from the time that could be spent underwater with SCUBA gear. The boundaries were defined and were marked on shore and underwater with white-painted rocks.

Materials and Methods

Bottom Sampling

Bottom samples were taken with a van Veen grab sampler with a volume of 21 liters and a weight of 50 kg. The maximum depth of sampling was 23 cm, and the maximum sampling area was 1100 cm^2. Samples were collected in the Knutson Bay study area along lines perpendicular to the shoreline and 15 m apart (Fig. 2). In the Triangle Island study area, samples were obtained along lines perpendicular to the shoreline and 30 m apart (Fig. 3). Divers accompanied the sampler to the bottom at Triangle Island, worked it into the gravel, and closed it. Depth of sample bite was measured by subtracting the dis-

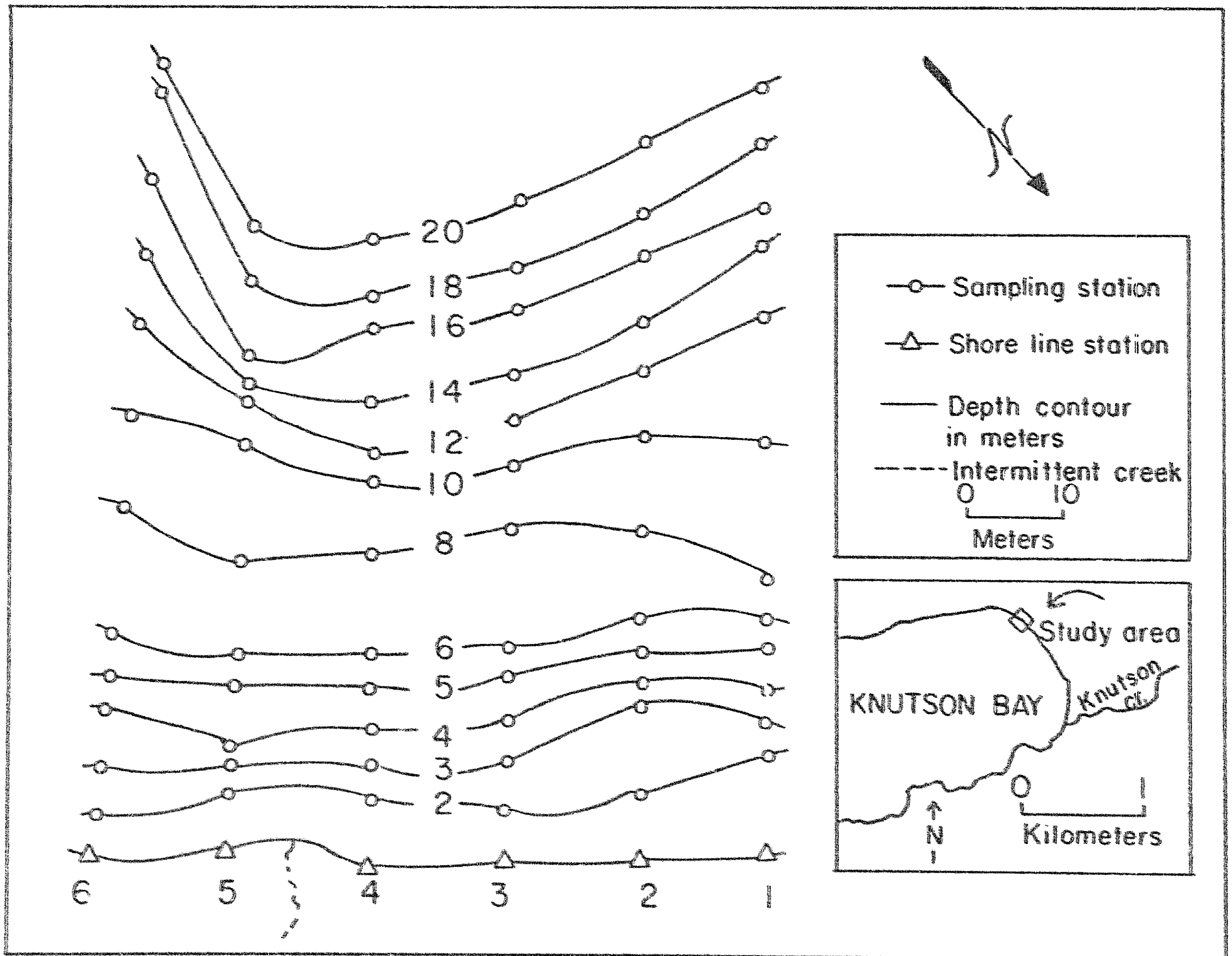


Fig. 2. Bathymetric map and map showing location (inset) of Knutson Bay study area, Iliamna Lake, Alaska.

tance from the top of the sampler to the top of the sample from the fixed maximum depth of sample bite. Water depth was recorded by a meter wheel attached to the sampler cable.

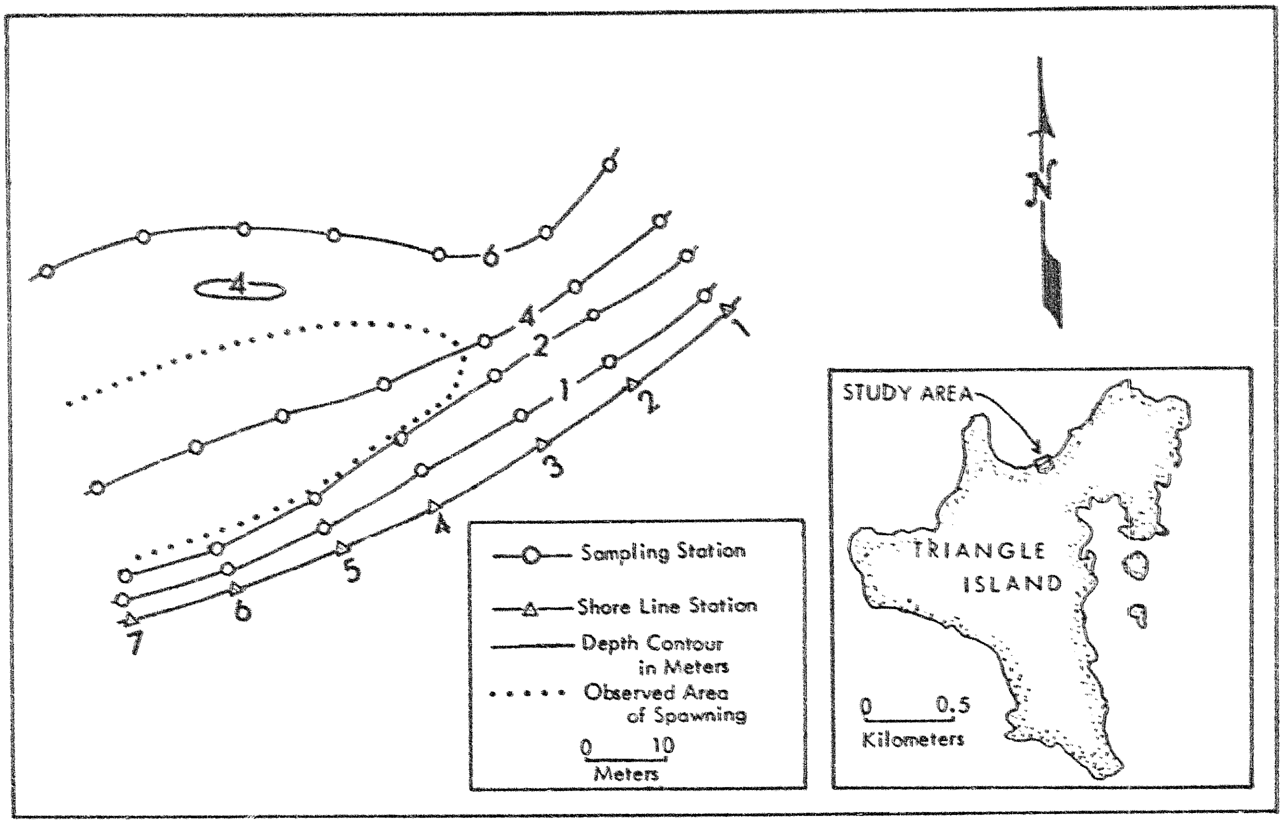


Fig. 3. Bathymetric map of Triangle Island study area, showing area of spawning in 1962, and location map (inset).

A subsample of about 800 ml of each sample from the Knutson Bay area was analyzed because of the prodigious quantity of sand and fine materials. Triangle Island samples were examined entire. The size composition of bottom materials was determined with Tyler sieves by the method described by McNeil (1962), expressed in per cent of the total sample. Solids passing the finest sieve (.104-mm mesh) were not measured.

Temperature Measurements

During the summer ground-water temperatures would be lower than lake temperatures. Intergravel and lake water temperatures were taken within each study area, and temperature differences were used as indicators of upwelling water. Stations were located in the Knutson Bay area by swimming on a compass course to a desired depth. A depth gauge with an accuracy of $\pm$ 0.3 m was used. Stations at Triangle Island were marked with painted rocks. At least one temperature measurement was taken at each station in the Knutson Bay area, but several measurements were taken at each station in the Triangle Island area.

Intergravel-water temperatures were measured at a depth of 23 cm with a Weston thermometer with a 30-cm probe and plexiglass housing, and were recorded to the nearest 0.5°C. Lake temperatures were taken just above the bottom with the thermometer on its side.

Results

Morphometric Measurements

The study area in Knutson Bay was 75 m long and extended to the 20-m depth contour. It included 5,238 m² (Table 1), or 3 per cent of the total area utilized for spawning in Knutson Bay in 1961. The bottom surface areas within contour increments of 2 m from 0 to 10 m ranged from 539 to 744 m². From 10 to 20 m, they ranged from 353 to 486 m². These ranges indicate a sharp increase in gradient below 10 m.

The Triangle Island study area was 90 m long and extended to the 6-m depth contour. It included 3,067 m² (Table 1), or 31 per cent of the total area of Triangle Island area 2 utilized by spawners in 1961. About one-half of the study area was between the 4-m and 6-m depth contours.

Bottom Composition

The differences in bottom composition between the study areas are shown in Table 2 and in Fig. 4. In the Knutson Bay area about 85 per cent of the bottom materials were granitic sand particles that were

Table 1. Bottom surface areas of study areas at 2-m depth intervals

Depth (m)	Knutson Bay (m²)	Triangle Island (m²)
0 – 2	539	797
2 – 4	609	708
4 – 6	670	1,562
6 – 8	744	
8 – 10	605	
10 – 12	486	
12 – 14	328	
14 – 16	481	
16 – 18	353	
18 – 20	423	
Total	5,238	3,067

Table 2. Average size composition of bottom materials (percentages) in each study area by depth

Depth, m	Number of samples	Mean depth of sample bite, cm	Diameter of material, mm						
			0.1–0.2	0.2–0.4	0.4–0.8	0.8–1.7	1.7–6.7	6.7–26.7	>26.7
Knutson Bay study area									
2– 3	4	14.7	4.5	24.1	49.5	18.0	1.6	0.4	2.0
5– 6	4	11.3	11.1	45.7	25.7	11.5	4.8	1.2	0
8– 9	4	11.0	4.8	19.1	38.3	16.0	12.2	6.9	2.8
10–11	4	10.2	6.0	25.2	34.4	15.2	11.8	5.2	2.2
14–15	4	—	6.6	27.1	23.5	15.5	15.1	8.4	3.8
19–20	5	10.3	12.7	45.0	23.6	9.7	5.9	2.5	0.7
Total	25		7.6	31.0	32.5	14.3	8.6	4.1	1.9
Triangle Island study area									
1	4	11.8					4.6	46.0	49.5
2	4	12.0	T	T	T	T	3.6	45.8	50.6
4	4	11.0	T	T	T	T	4.7	37.5	57.8
6	3	13.0	T	T	T	T	2.2	56.9	40.8
Total	15		T	T	T	T	3.8	46.6	49.7

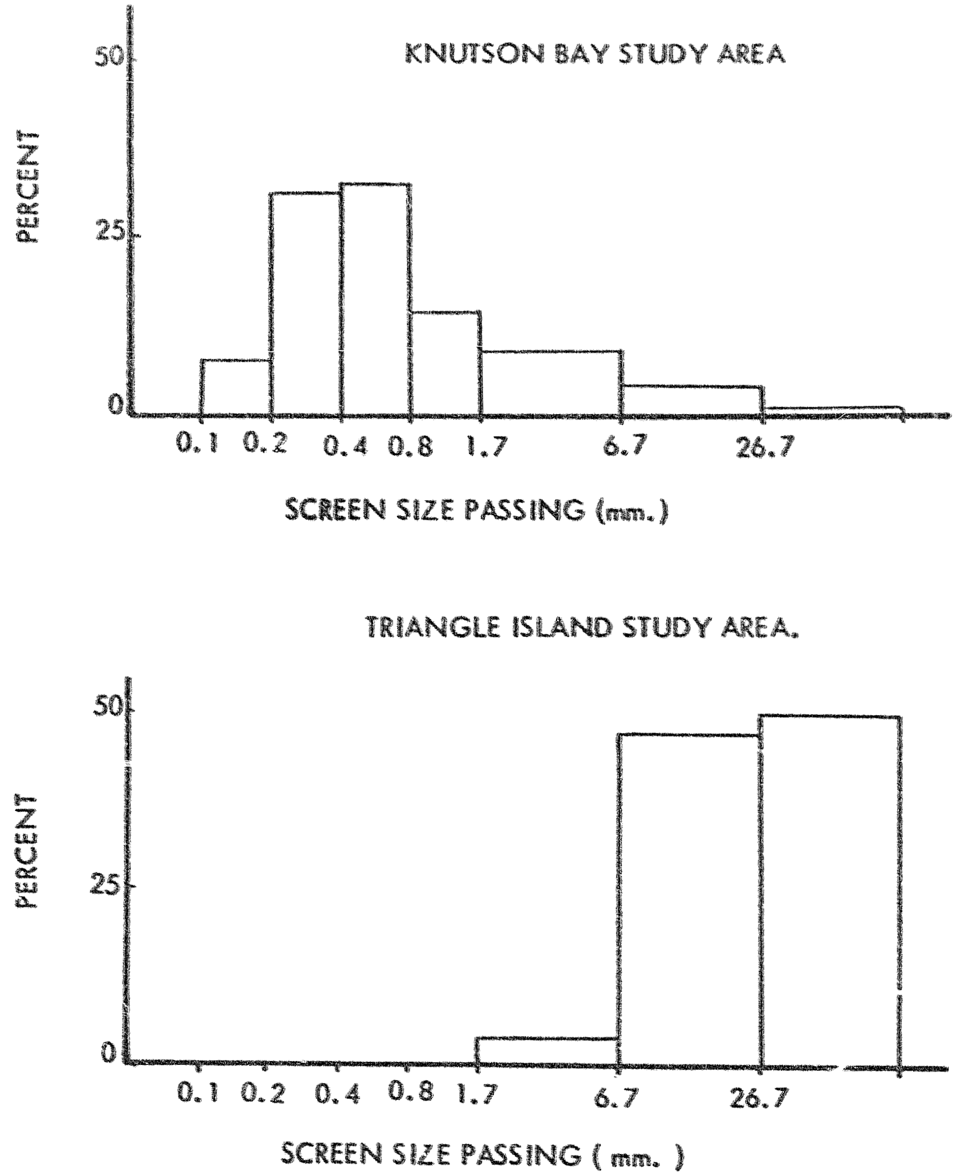


Fig. 4. Size composition of bottom materials in the two study areas.

less than 1.7 mm in diameter. The sand had apparently been formed by erosion of the bordering mountains. In Triangle Island area 2, coarse gravel and boulders greater than 6.7 mm in diameter predominated. The gravel had apparently been smoothed by wave action.

Temperature Measurements

Knutson Bay. Intergravel-water temperatures were taken over a period of 16 days at 43 of the 48 sampling locations to 12 m in Knutson Bay. Temperature isotherms are plotted in Fig. 5. Average lake temperatures near the bottom ranged from 9 to 11°C and averaged 10°C for the period. It was assumed that intergravel temperatures below 9°C indicated the presence of upwelling ground water. Intergravel-water temperatures ranged from 5 to 8°C, but were frequently 7 or 8°C. Areas with upwelling water were found at 2 m, but the majority were located below 3 m.

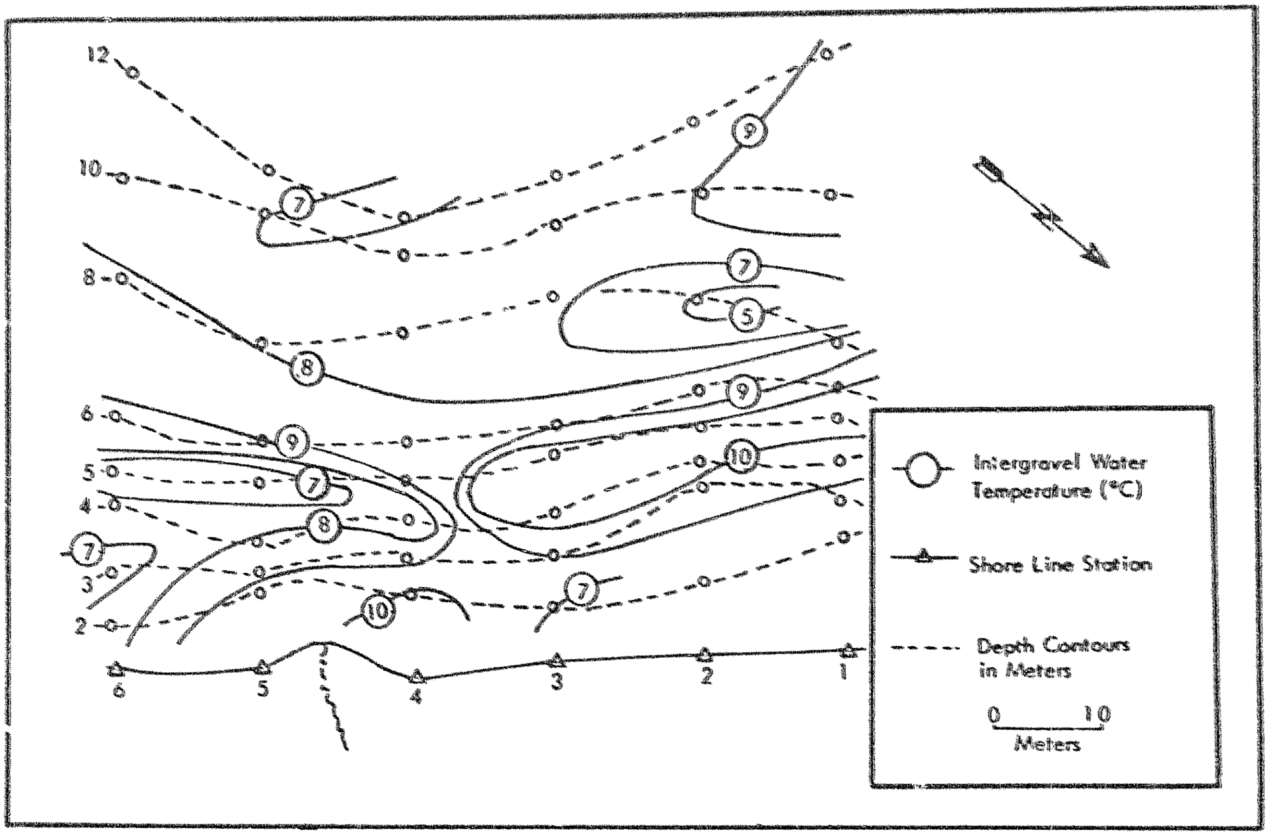


Fig. 5. Intergravel-water temperature isotherms for the Knutson Bay study area for the period August 26-September 10, 1962. Lake temperatures averaged 10°C.

The fluctuations in ground-water temperature from summer through winter would directly affect the rate of embryonic development. However, late fall and winter temperatures were not measured because of difficulties in sampling.

Triangle Island. Intergravel-water temperatures were measured at each of the 21 sampling stations on August 13 and 21 and September 3, and at stations 1, 3, 5, and 7 at 2, 4, and 6 m on September 14. All data were pooled for each sampling time and depth, and averages were calculated (Table 3).

Table 3. Lake temperatures and average intergravel-water temperatures (°C) at the Triangle Island study area, by date and depth of sampling

Depth m	August 13		August 21		Sept. 3		Sept. 14	
	Lake	Gravel	Lake	Gravel	Lake	Gravel	Lake	Gravel
1	—	—	—	—	—	—	9.5	9.5
2	13.5[a]	13.0	11.5	11.5	10.5	10.5	9.5	9.5
4	12.5[a]	12.0	10.5	11.0	10.0	10.0	9.0	9.0
6	12.0[a]	11.5	10.0	10.5	10.0	8.5	9.0	7.0

[a] Estimated from trends in data.

Intergravel-water temperatures at 2 and 4 m equalled or nearly equalled lake temperatures. Temperatures at 6 m differed slightly from lake temperatures during the first two observations, and differed by 1.5 to 2.0°C during the last two observations. The differences could not have been due to a constant flow of upwelling ground water because differences were not found during the first two sampling periods. They were not associated with areas of egg deposition since spawning was not noted at 6 m (Fig. 3). Apparently upwelling water does not occur in the spawning area and intergravel water circulation must be provided by lake currents.

Summary

The Knutson Bay spawning area has upwelling ground water and a bottom consisting largely of sand. The abundance of fine materials indicates the absence of strong lake currents. Apparently ground-water flows maintain water circulation in redds.

The Triangle Island spawning area apparently does not have upwelling water. The bottom is composed mainly of gravel and boulders. Apparently lake currents maintain water circulation in redds, and the lake temperature regime would largely determine the rate of egg development.

The differences found in source of water circulation, bottom composition, and time of spawning in the two study areas suggested that the rates of egg development and times of hatching and emergence would differ. These possible biological differences were examined in studies of egg development.

The Development of Sockeye Salmon Embryos and Alevins in Relation to Thermal Age

The development of embryos and alevins of sockeye salmon in relation to thermal age is not fully described in the literature, although various workers have studied phases of development. Rucker (1937) described the growth in weight and length of embryos of landlocked sockeye salmon from fertilization to hatching at four constant incubation temperatures. Ievleva (1951) described the stages of development in sockeye salmon from fertilization to hatching. Eggs were incubated in a hatchery, and samples were examined 6 and 24 hr after fertilization, on the third, fifth, tenth, and fifteenth day of development, and subsequently every 15 days until hatching occurred. The relative amounts of thermal units received to the time of first appearance of different morphological features can be determined from her data. Hanamura (1961, citing Semko, 1953) reported that hatching took place in 150 days at an average water temperature of 3.2°C. Smirnov (1958) noted the first hatch in 55 days at an average incubation temperature of 11.4°C, and the first hatch in 148 days at an average temperature of 4.6°C.

Studies on the relation of temperature during incubation to the development of Pacific salmons other than sockeye are summarized by Seymour (1956) and Rockwell (1956). Rockwell plotted the reciprocal of incubation time against temperature in several experiments on various species of salmonids. He noted a linear relationship between total development time and temperature over the middle portion of a sigmoid curve, and a curvilinear relationship over the extreme portions.

The purpose of this study was to describe stages in the development of sockeye salmon from fertilization to yolk sac absorption and the thermal ages attained at these stages in incubation experiments at the University of Washington hatchery to serve as standards in evaluating the thermal ages of embryos sampled in the field where continuous recording of temperature is not feasible.

Materials and Methods

Fertilization and Incubation

The eggs from one 2-ocean sockeye female were fertilized with milt from two males. The fish were taken from Lake Washington. The eggs averaged 5.3 ± 0.1 mm in diameter.[3] A standard vertical flow incubator was used. To determine degree-day[4] units received, the temperature within the incubation tray was measured every other day early in the experiment, and at intervals of four days later. Missing data were estimated from a continuous record of water temperatures at the hatchery inlet, which averaged 0.5°C lower than tray-water temperatures during the experiment. Incubation temperature fell from 11.1°C to 6.9°C, then rose to 9.1°C (Fig. 6).

[3] Eggs from mainland-spawning 2-ocean female sockeye in Iliamna Lake in 1965 had a mean diameter of 5.3 mm; it was 5.6 mm for eggs of island-spawning fish.

[4] *One degree day* is one degree Centigrade above freezing (0°C) for a period of 24 hr (a modification of Wallich's [1901] definition of *one temperature unit* as one degree Fahrenheit above freezing [32°F] for a period of 24 hr).

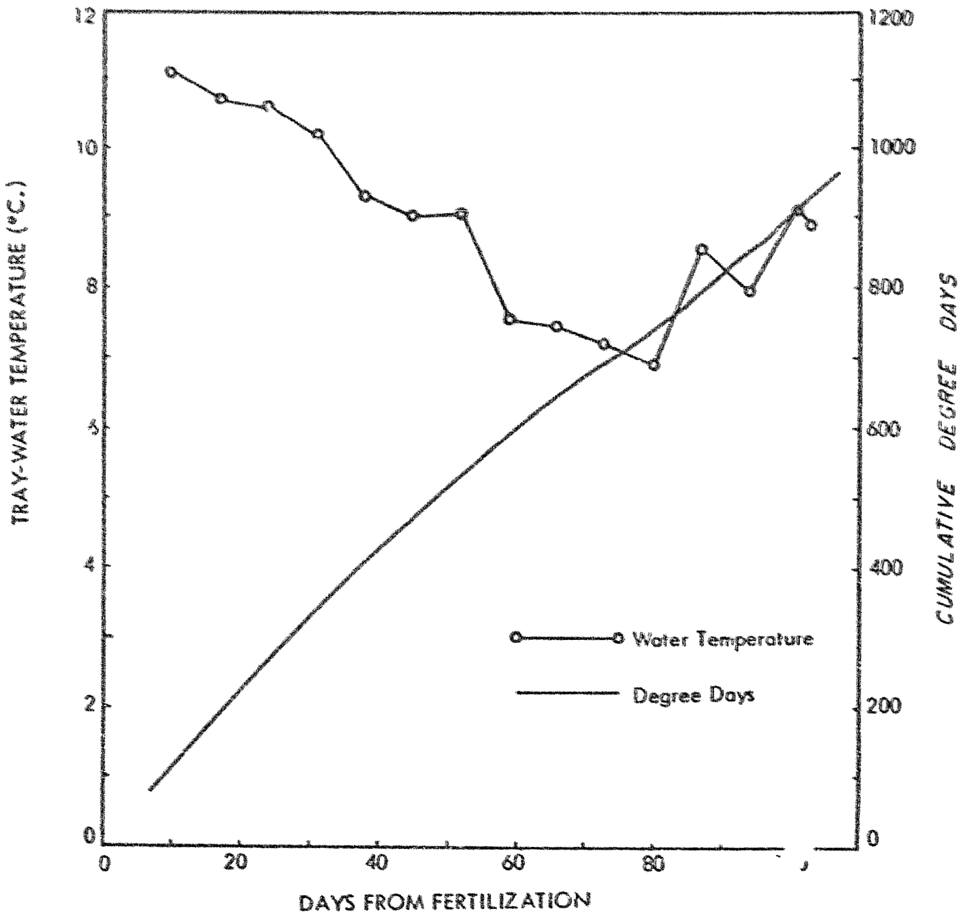


Fig. 6. Average 7-day tray-water temperatures and cumulative degree days during incubation.

Sampling

In this paper *embryo* denotes the stage of development from fertilization to hatching. *Alevin* denotes the stage of development from hatching to yolk sac absorption. *Yolk sac absorption* is the stage of development in which the yolk sac disappears from view.

Samples of 5 to 12 eggs were taken at random from the tray at intervals of 2 or 3 days from seven days after fertilization until hatching terminated. The majority of samples numbered 10 to 12 eggs. Eggs were exposed to diffused light during sampling, but this exposure never exceeded 5 min at any time. Samples of 10 alevins were taken when possible from the first day of hatching until yolk sac absorption terminated. Only those alevins that appeared healthy were removed for examination.

Embryos were immediately preserved in Stockard's solution. Alevins were preserved in 70-per cent alcohol.

Determination of Stages of Development

Length attained and first appearance and development of morphological features were the criteria used to establish stages of develop-

ment be
Length
in millin
All m
graph e
with a C
a 50-wa
to the y
the yolk
was det
yolk. O
dissectin
mencem
phores
Alevi
a vernie
microgr
were tal
few hou
pigmen
preserv
preserv

Growth
The
tive cu
7. The
7) cou
hatchir

Embry
It w
a defin
regime
the dev
(1911
and ap

ment because of their practicability of application to field samples. Length was measured from the tip of the snout to the end of the tail in millimeters.

All measurements of embryos were from traced outlines of photograph enlargements three times the natural size. Tracings were taken with a Goodkin Model A vertical camera under transmitted light from a 50-watt bulb. Embryos in samples 1 to 12 were measured attached to the yolk. Embryos in samples 13 to 35 were each detached from the yolk and measured after enlargement. Embryonic development was determined from preserved embryo samples detached from the yolk. Only those structures that could be identified under a binocular dissecting microscope were observed. The development of fins, commencement of pigmentation of the eyes, and appearance of melanophores on the body were noted.

Alevins were measured lying flat. Measurements were taken with a vernier caliper, and were recorded to the nearest 0.1 mm. Photomicrographs of alevins (approximately seven times the natural size) were taken with a Bausch and Lomb Model L vertical camera from a few hours to several days after sampling. The development of fins and pigmentation of the body were noted. Photographs before and after preservation indicated no loss in fin definition or pigmentation due to preservation.

Results

Growth in Length with Increase in Thermal Age

The average lengths of embryos and alevins in samples and respective cumulative degree days are shown in Table 4 and plotted in Fig. 7. The overlap in length measurements of embryos and alevins (Fig. 7) could be due to error in measurement or physiological effects of hatching.

Embryonic Development Related to Thermal Age

It was assumed that a particular stage of development is attained in a definite number of degree days regardless of prevailing temperature regime and racial origin. Rockwell (1956), who reviewed studies of the development of various species of fish by Wallich (1901), Apstein (1911), and Johansen and Krogh (1914) accepted the assumption and applied it in developmental studies of chum salmon.

Table 4. Length measurements of sockeye salmon embryos and alevins in samples, University of Washington hatchery experiment

Sample no.	Degree days	Sample size, n	Mean length, mm	Standard error $s_{\bar{x}}$	Sample no.	Degree days	Sample size, n	Mean length, mm	Standard error $s_{\bar{x}}$
				Embryos					
1	80.6	5	1.8	.06	19	397.2	10	12.0	.09
2	92.2	6	2.3	.10	20	406.7	10	11.8	.23
3	103.3	10	2.2	.10	21	423.9	10	11.7	.15
4	114.4	11	2.7	.05	22	440.6	10	12.7	.21
5	125.0	9	2.8	.11	23	457.8	10	12.7	.14
6	135.6	11	3.3	.14	24	466.7	10	13.3	.10
7	146.7	7	3.9	.16	25	485.6	12	13.7	.15
8	157.8	8	4.5	.17	26	504.4	12	13.8	.14
9	168.3	9	4.9	.08	27	522.8	10	14.1	.15
10	178.9	10	5.2	.10	28	549.4	9	14.7	.13
11	211.1	10	6.3	.16	29	567.2	9	15.1	.30
12	232.2	10	7.2	.19	30	588.3	10	15.9	.20
13	253.3	8	7.5	.18	31	603.3	10	15.8	.24
14	285.0	10	9.0	.09	32	618.9	10	16.1	.23
15	305.6	10	9.5	.13	33	634.4	10	16.8	.24
16	337.2	8	10.4	.10	34	648.9	9	18.1	.14
17	357.2	8	10.7	.08	35	663.3	10	17.9	.20
18	377.2	8	11.2	.22					
				Alevins					
1	558.3	9	16.6	.16	8	762.2	10	22.7	.32
2	588.3	5	17.9	.22	9	793.9	10	22.9	.34
3	618.9	10	18.4	.24	10	830.0	7	23.9	.22
4	648.9	10	19.7	.12	11	868.9	10	24.0	.25
5	677.8	10	20.0	.30	12	896.7	10	24.2	.19
6	706.7	10	21.5	.23	13	932.8	10	25.2	.15
7	732.8	10	21.9	.19	14	968.3	10	25.8	.16

Fig

MEAN TOTAL LENGTH (mm.)

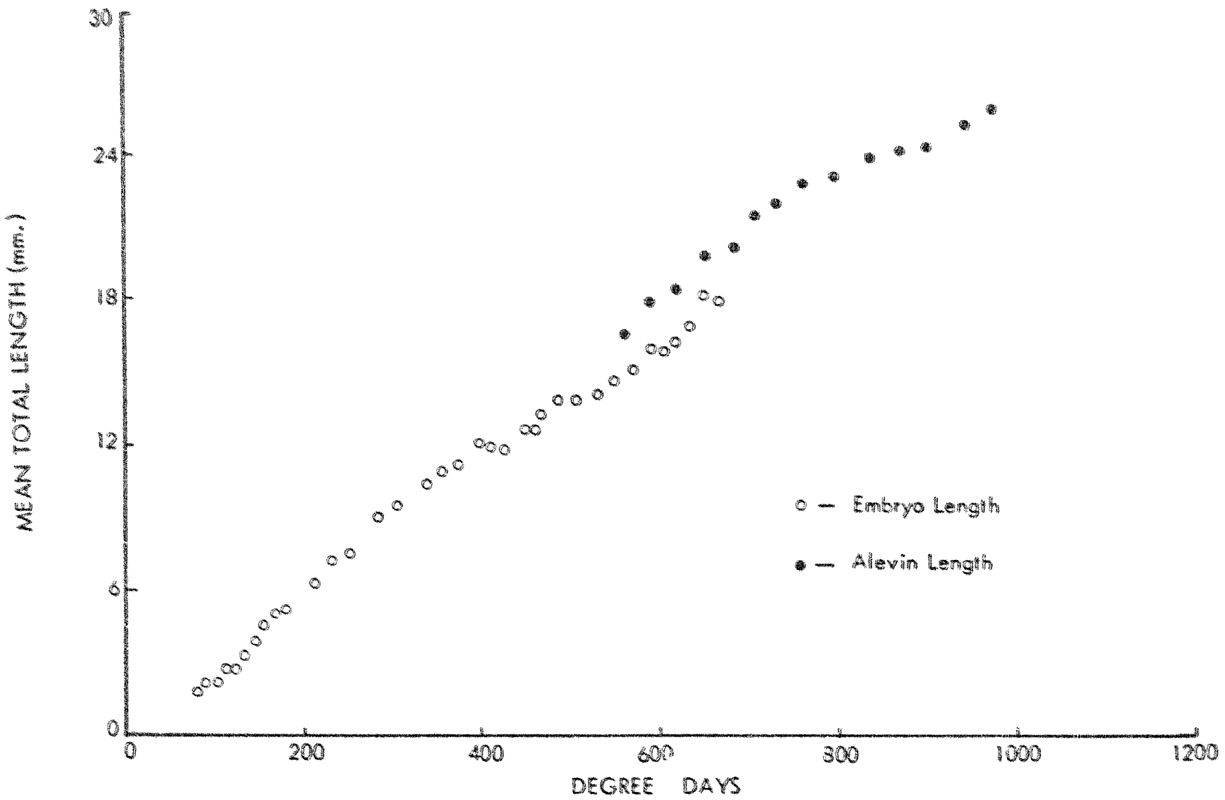


Fig. 7. Mean total lengths of sockeye salmon embryos and alevins in samples by cumulative degree days, University of Washington hatchery experiment.

The developmental stages and thermal ages follow:

Stage I—80.6 degree days. The germ ring of the blastoderm covers one-half of the yolk.

Stage II—125 degree days. The blastopore has closed, and the pectoral fins appear as small buds.

Stage III—157.8 degree days. The posterior end of the intestine is apparent in the ventral fin fold.

Stage IV—232.2 degree days. Melanophores have appeared in the eyes, and the posterior end of the notochord has begun to twist upward in the caudal region.

Stage V—305.6 days. Mesenchyme has appeared in the anal fin region of the ventral fin fold.

Stage VI—337.2 degree days. Pterygiophores have appeared at the base of the developing anal fin. Mesenchyme is apparent in the dorsal fin region of the dorsal fin fold.

Stage VII—357.2 degree days. Pterygiophores have appeared at the base of the developing dorsal fin.

Stage VIII—397.2 degree days. Fin rays have appeared in the caudal fin region.

Stage IX—406.7 degree days. Pigmentation is apparent on the head in the occipital region.

Thermal Age at Hatching

Hatching began at 467 degree days and continued until 685 degree days. The cumulative percentage of hatch was calculated for each sampling period and plotted (Fig. 8). The 5- to 95-per cent hatching

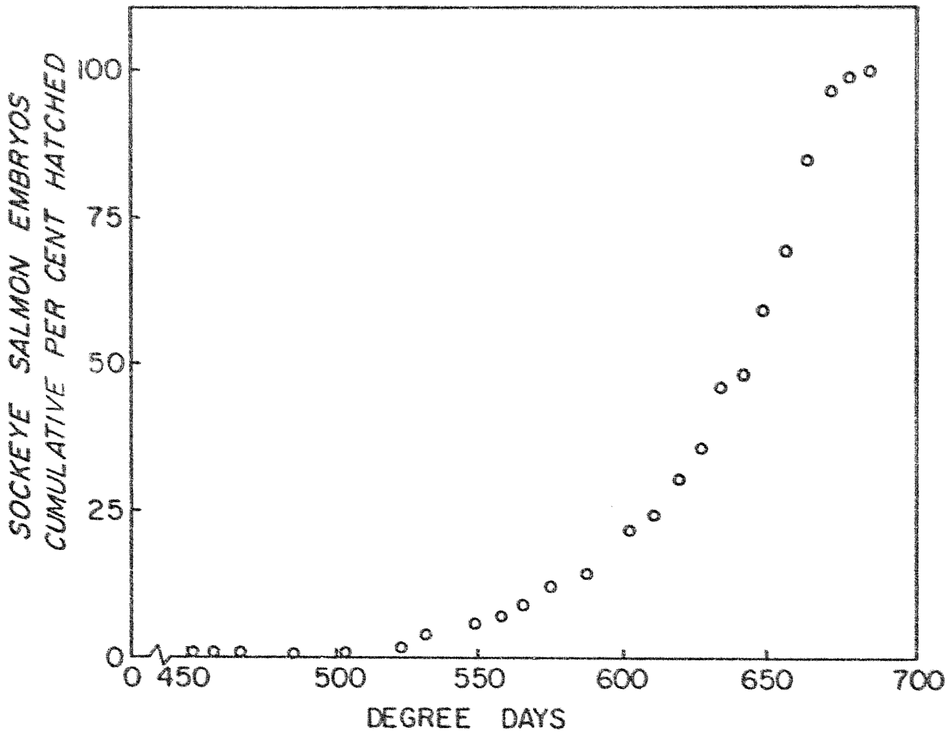


Fig. 8. Cumulative percentages of hatch by cumulative degree days, University of Washington hatchery experiment.

range was estimated at 546 to 668 degree days; the 90-per cent range eliminates early and late hatches. Fifty per cent of the eggs hatched within 643 degree days.

These results agree quite closely with data obtained by Ievleva (*op. cit.*) and by Church (1959). Hatching occurred at 591.6 degree days in an incubation experiment conducted by the former. Sockeye eggs studied by Church in Lake Nerka, Alaska, hatched within 555 to 720 degree days.

Alevin Development Related to Thermal Age

The development of fins and pigmentation in alevins in relation to thermal age is described below. A key was developed to describe the progression of fin development and pigmentation. Areas of pigmentation and final pigment pattern are illustrated in Fig. 9. Examples of the various stages of development are illustrated in Figs. 10-13. (Terminal numbers are guides to steps in the key.)

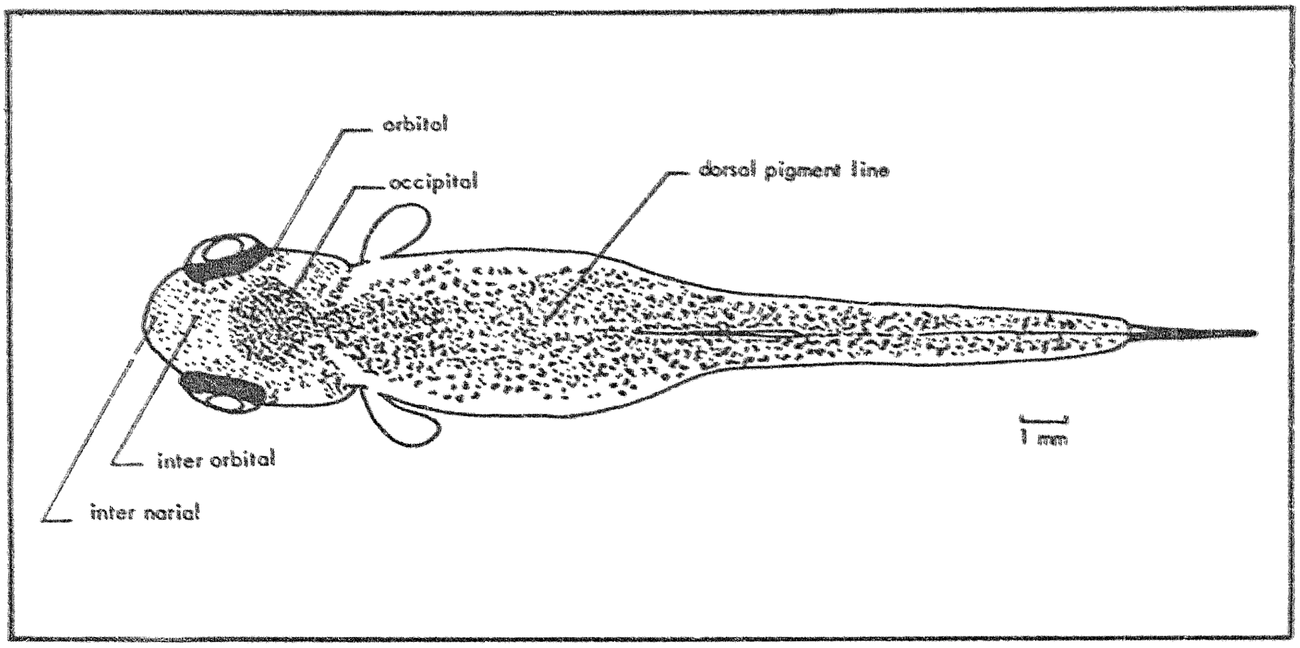


Fig. 9. Dorsal view of sockeye salmon alevin at 830 degree days; the pigment pattern is fully developed.

1a—The posterior edge of the anal fin has not differentiated in the fin fold to insertion. 2

1b—The posterior edge of the anal fin has differentiated in the fin fold to insertion. 6

2a—The posterior edge of the dorsal fin has not differentiated in the fin fold to insertion. 3

2b—The posterior edge of the dorsal fin has differentiated in the fin fold to insertion. 5

3a—Orbital pigmentation has not appeared. 4

3b—619 degree days. Orbital pigmentation is apparent, but only posterior to the eye. (Fig. 11a, stage 3)

4a—558 degree days. Pigmentation has not appeared between the occipital pigment region and the dorsal pigment line. Pigmentation on the body is mainly concentrated on the dorsal surface and is scattered on the sides posterior to the pelvic fins. Pigmentation has not appeared on the dorsal surface of the yolk sac. The anal fin is identifiable in the fin fold but is not differentiated as yet. Pelvic fins appear as budlike protuberances. (Fig. 10a, stage 1)

4b—588 degree days. Pigmentation is present between the occipital pigmented region and dorsal pigment line, but is not as concentrated as in the final pigment pattern. Pigmentation is apparent on the body anterior to the pelvic fins, but not on the a

b

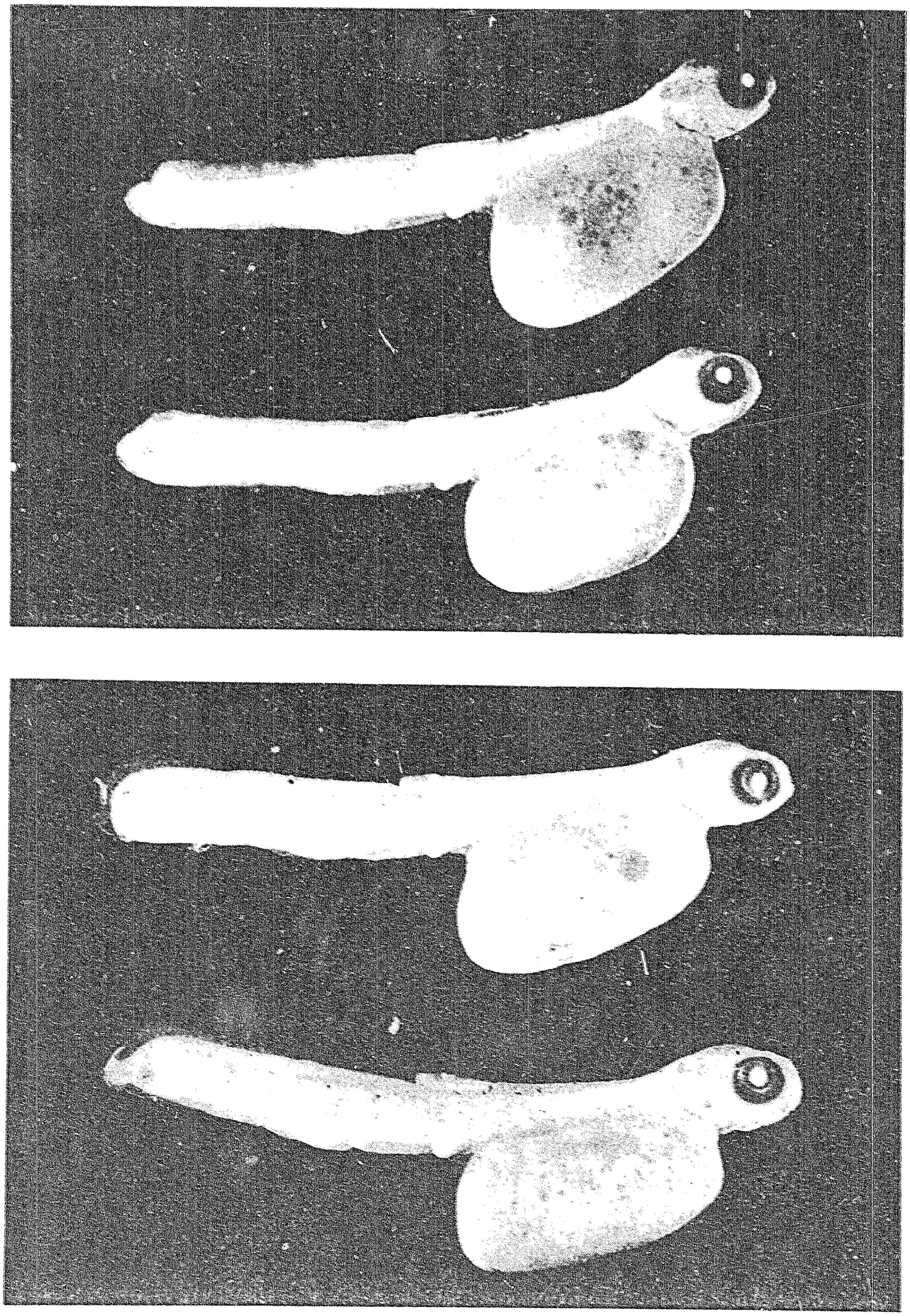
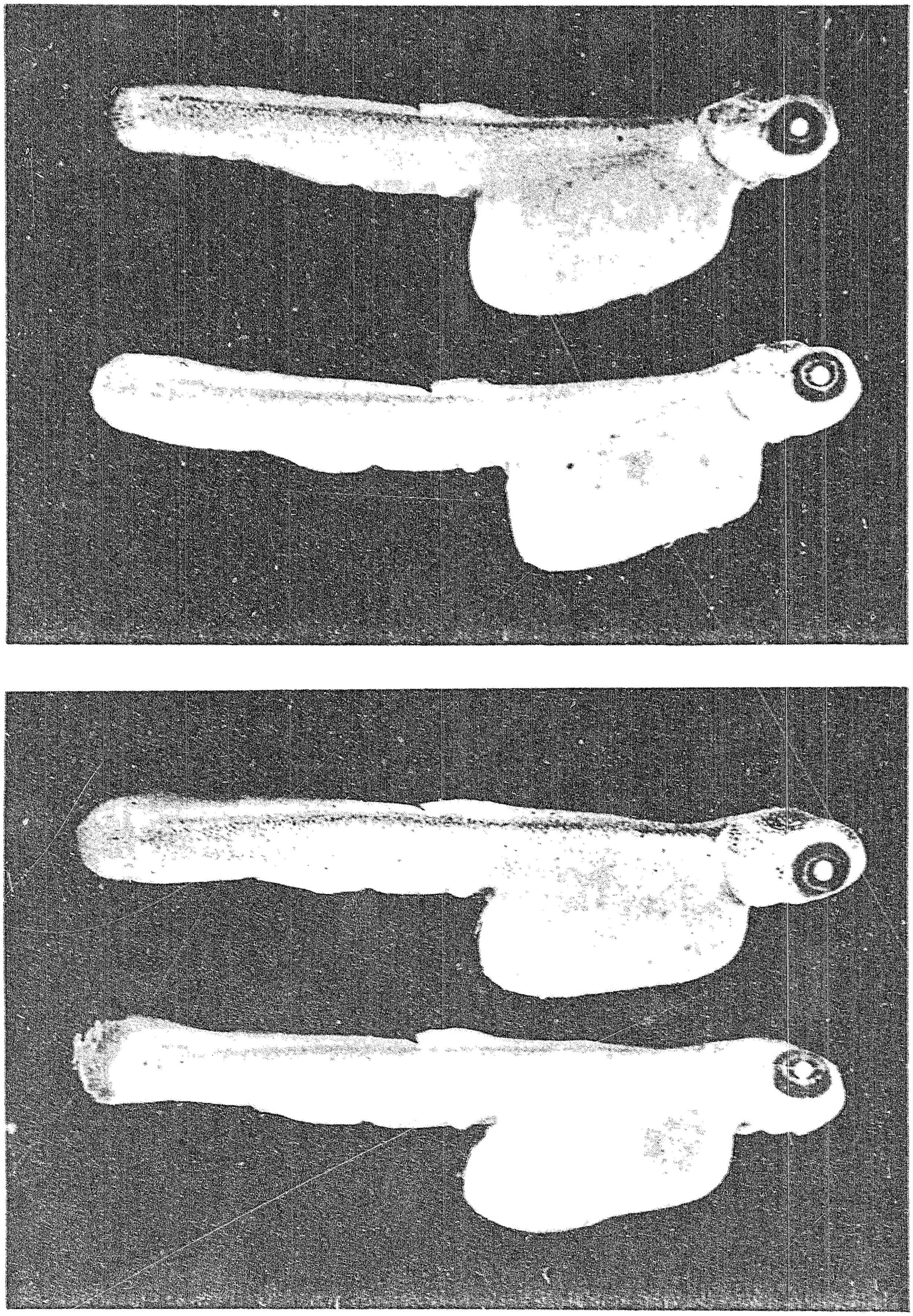


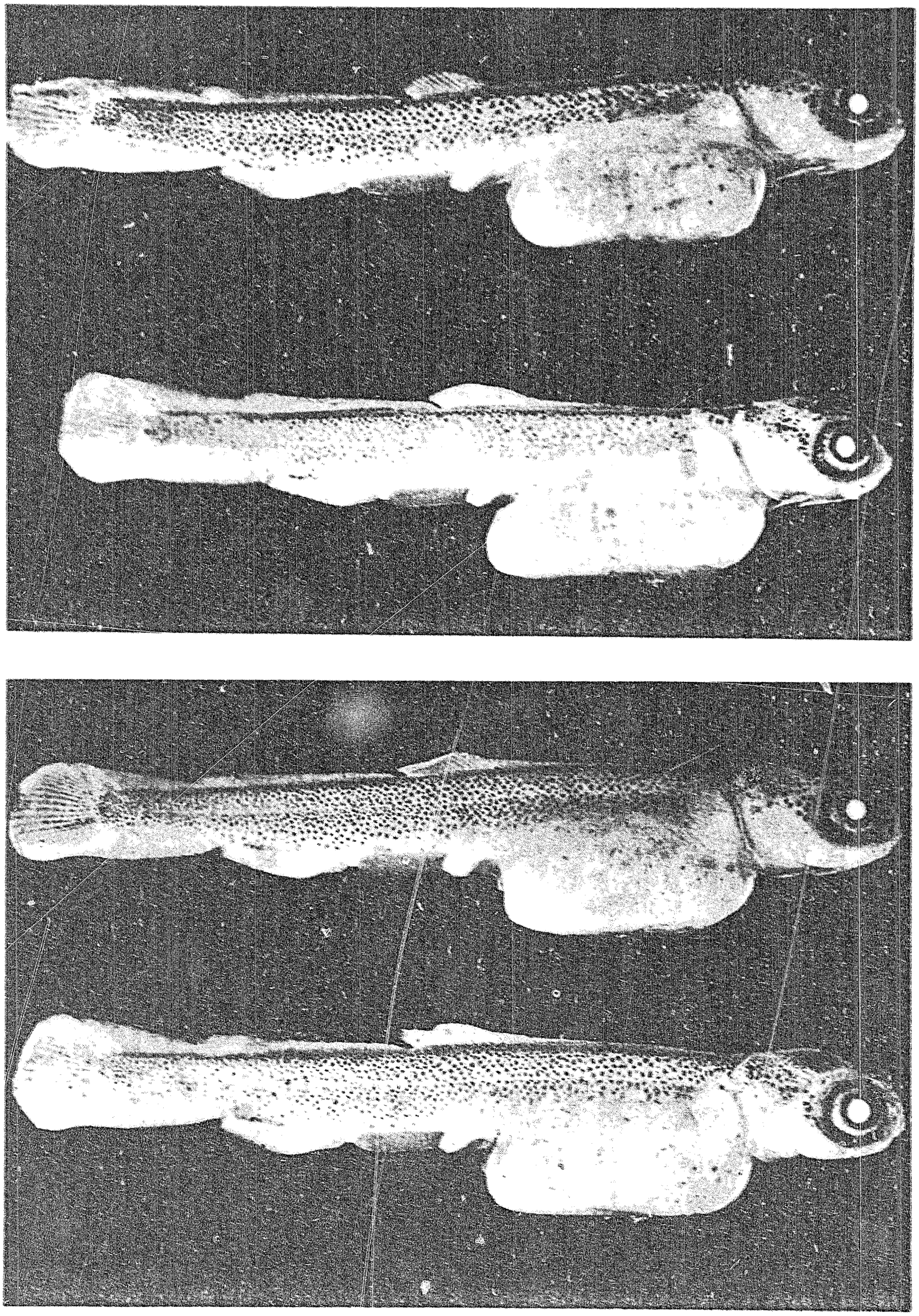
Fig. 10. Alevin, stages 1(a) and 2(b), 558 and 588 degree days, respectively. (5X) Note increased pigmentation on sides and on caudal fin in stage 2, and absence of orbital pigmentation in both stages.



a

b

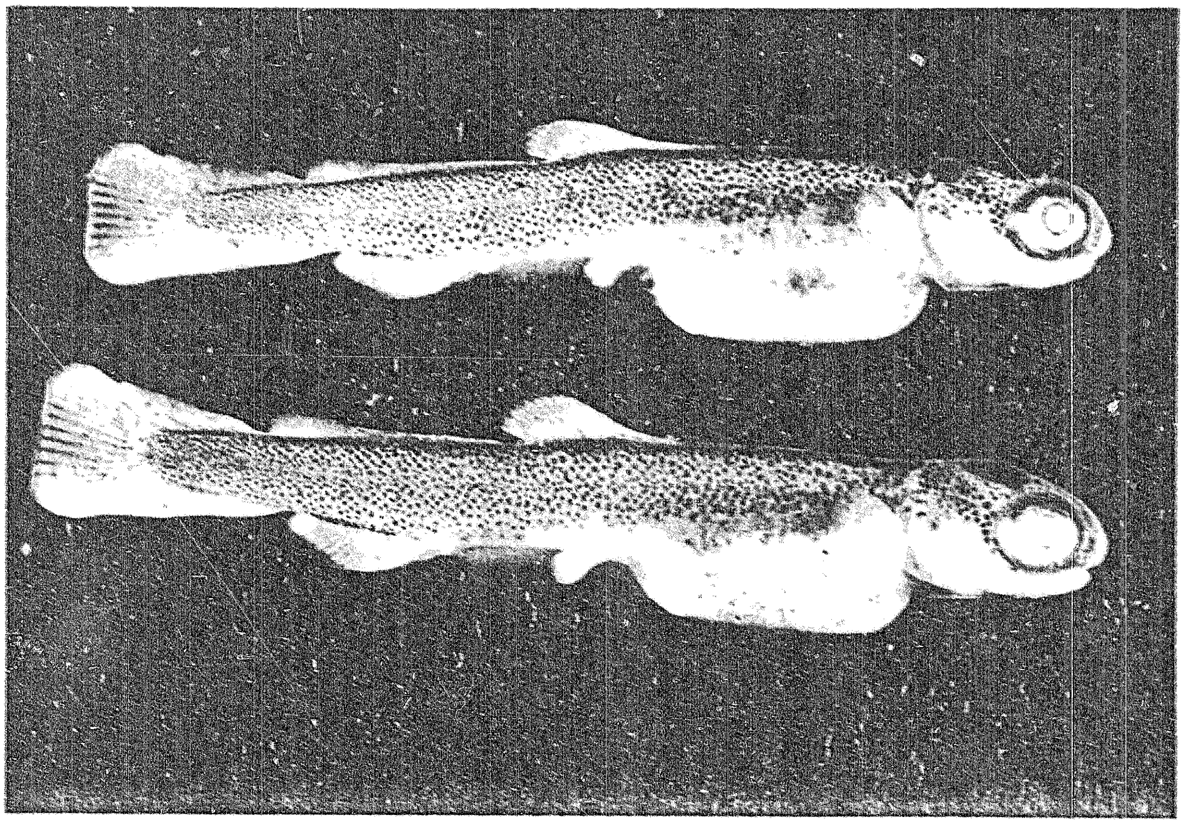
Fig. 11. Alevin, stages 3(a) and 4(b), 619 and 649 degree days, respectively. (5X) Note the appearance of orbital pigmentation and increased pigmentation of sides in stage 3. In stage 4 posterior differentiation of the dorsal fin is complete, and the adipose fin appears as a bulge in the fin fold.



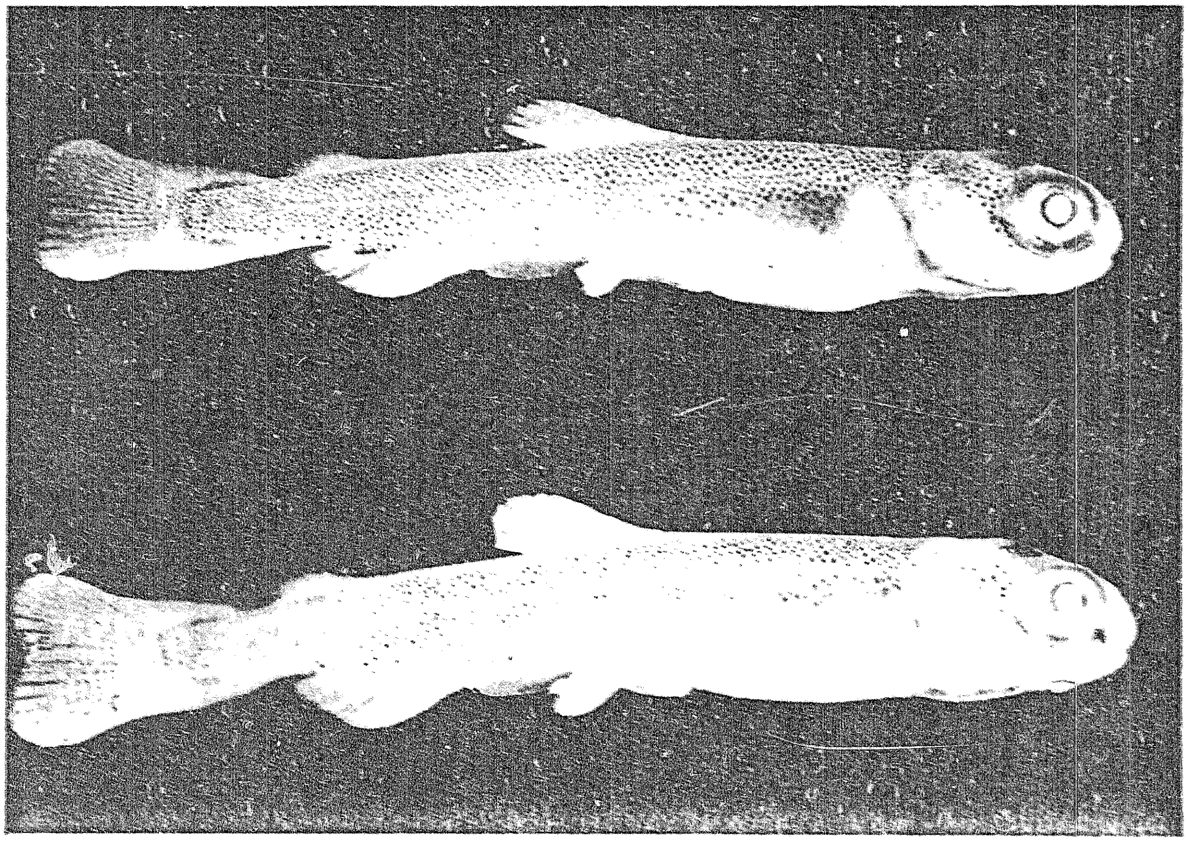
a

b

Fig. 12. Alevin, stages 5(a) and 6(b), 707 and 733 degree days, respectively. (5X) Note the beginning of anal fin differentiation and increase in orbital pigmentation in stage 5. In stage 6 the posterior edge of the anal fin is fully differentiated in the fin fold.



a



b

Fig. 13. Alevin, stages 7(a) and 8(b), 794 and 933 degree days, respectively. (4X) The posterior edge of the adipose fin has differentiated in stage 7 and a remnant of the fin fold remains between the dorsal and adipose fins. In stage 8 the yolk sac is no longer visible and all fins are well developed.

dorsal surface of the yolk sac. Pigmentation is apparent on the caudal fin. (Fig. 10b, stage 2)

5a—649 degree days. The anal fin has not differentiated in the fin fold. The adipose fin appears as a bulge in the dorsal edge of the fin fold. Pigmentation is scattered on the dorsal surface of the yolk sac. Orbital pigmentation does not extend into the dorsal region. The pigment pattern is incomplete in the interorbital and internarial regions. (Fig. 11b, stage 4)

5b—707 degree days. Differentiation of the posterior edge of the anal fin in the fin fold has begun. The posterior edge of the adipose fin is defined in the fin fold but is still not differentiated. Pigmentation extends throughout the orbital region. (Fig. 12a, stage 5)

6a—733 degree days. The posterior edge of the adipose fin is not completely differentiated in the fin fold. (Fig. 12b, stage 6)

6b—The posterior edge of the adipose fin is differentiated in the fin fold to its insertion. 7

7a—794 degree days. A remnant of fin fold remains between the adipose and dorsal fins. (Fig. 13a, stage 7)

7b—933 degree days. The fin fold is no longer apparent between the adipose and dorsal fins. The yolk sac is no longer visible. (Fig. 13b, stage 8)

Egg Development

Materials and Methods

Bags containing fertilized eggs were buried in each study area, and samples were taken at intervals to determine the rate of development. Stages of development and corresponding thermal ages established for sockeye salmon embryo and alevin in the hatchery study were the standards used for evaluating the thermal ages of embryos and alevins in samples.

Eggs were taken and fertilized at the Triangle Island study area on August 17, 1962. Spawning activity was nearly at peak at the time. Eggs were obtained at Knutson Bay on September 12, 1962. Spawning had just commenced at the time. Bags of saran plastic screen were filled with washed gravel and 100 eggs each, and were buried at depths of 20 to 25 cm in the bottom of each study area. At Triangle Island six bags each were buried at water depths of 1, 2, 4, and 6 m at stations 1 and 5 (Fig. 3). In Knutson Bay, four bags each were buried at water depths of 3, 6, and 12 m at stations 2, 4, and 6 (Fig. 2).

Samples were taken on September 14 and on November 15 at Triangle Island. Samples were taken at Knutson Bay on November 11. Samples were not taken later because of ice cover.

The first appearance and development of morphological features rather than length was selected as the best index to stage of development and thermal age. Gray (1928) proved that the size of the embryo at hatching is proportional to the total amount of yolk in the fertilized egg and relative to the incubation temperature. Details on lengths and stages of development within samples are given in Olsen (1964).

Results

Samples recovered at all depths and stations at Triangle Island on September 14 except those from station 5 at 6 m had attained stages IV and V (230-300 degree days). Samples from station 5 at 6 m had reached a stage between I and II (100 degree days). All samples recovered on November 15 showed that hatching had commenced. Alevins in samples had thermal ages ranging from 590 to 730 degree days. Embryos at Knutson Bay had reached stages V and VI (300-340 degree days) by November 11. These samples probably indicated nearly maximum development possible to mid-November in Knutson Bay because the eggs were obtained from early spawners.

Development at Triangle Island proceeded at a faster rate than at Knutson Bay because of earlier spawning and a warmer temperature regime. Hatching had commenced at Triangle Island by mid-November, but eggs at Knutson Bay had developed only halfway to hatching by this time.

It may be essential that eggs hatch before winter ice cover is formed over island beach spawning areas, where intergravel water circulation is provided by lake currents rather than upwelling water. The eggs are not effectively buried in the coarse rocks (Kerns and Donaldson, in press), and alevins may be able to avoid possible suffocation from stagnation after ice formation. Upwelling ground water in mainland beach spawning areas probably provides adequate intergravel water circulation through the winter; thus hatching before freezeup does not seem essential.

It is not possible to determine precisely when hatching and emergence take place without winter temperature data. It was observed in the hatchery experiment that alevins that had accumulated thermal units ranging approximately from 890 to 1000 degree days could swim freely and had completed or nearly completed yolk sac absorption. At spring ponds, creeks, and lake grounds in Lake Nerka, alevins emerged at thermal ages ranging from 620 to 955 degree days (Church, 1959). If the temperature were monitored throughout winter in the future, it would be possible to determine the time periods of hatching and emergence from the data provided by this study supplemented with the data from this future sampling.

Summary

1. There are two types of lake spawning areas in Iliamna Lake, mainland beach and island beach.

2. Analysis of the bottom materials of a mainland beach spawning area and an island beach spawning area showed that the bottom of the mainland area is composed mainly of sand whereas the bottom of the island area is composed largely of gravel and boulders. Measurements of intergravel temperature at each study area indicated that ground-water flows maintain water circulation in redds in the mainland area, and lake currents maintain water circulation in the island area.

3. Stages in the development of embryos and alevins of sockeye salmon were related to thermal age in incubation experiments at the hatchery of the University of Washington College of Fisheries. Growth in length and first appearance and development of morphological features were the criteria used to establish stages of development. Thermal ages at hatching ranged from 546 to 668 degree days.

4. Eggs were planted in the two study areas. Degree-day units received by eggs in samples were calculated from the development standard. Hatching occurred before freezeup at Triangle Island, but it would not have occurred until after freezeup at Knutson Bay.

Acknowledgments

Support for this work was provided through the Fisheries Research Institute of the University of Washington. Dr. O. A. Mathisen assisted in the formulation of the study and reviewed the manuscript. Drs. R. L. Burgner and R. W. Moore also critically reviewed the manuscript. Mr. O. E. Kerns assisted in the field work and provided ideas and encouragement. Mr. Russell F. Orrell also assisted in the field work, and Mr. Ronald Lopp photographed alevins. Dr. Lauren Donaldson furnished sockeye salmon eggs for the hatchery studies and made available incubation facilities at the College of Fisheries.

Field facilities in Alaska were financed by members of the Bristol Bay salmon canning industry through the Association of Pacific Fisheries, Inc.

This study was part of a research program financed under Contract #14-17-0007-172(C), U.S. Fish and Wildlife Service.

Literature Cited

Apstein, Carl H. 1911. Die Verbreitung der pelagischen Fischeier und Larven in der Beltsee und den angrenzenden Meeresteilen 1908/09. Wissenschaftliche Meeresuntersuchungen. Abt. Kiel (Kommission zur wissenschaftlichen Untersuchung der deutschen Meere in Kiel und der biologischen Anstalt auf Helgoland, Berlin) N.F. Bd. 13, p. 225-284 (Laboratorium für internationale Meeresforschung in Kiel. Biologische Avt. Nr. 20). [Cited by Rockwell, 1956.]

Church, W. A. 1959. Report on the 1957-1958 studies on the effects of winter environment on red salmon eggs and larvae in the Wood River lakes. Intradep. Rep., Fish. Res. Inst., Univ. Washington, Seattle. 53 p.

Demory, Robert L., Russell F. Orrell, and Donald R. Heinle. 1964. Spawning ground catalog of the Kvichak River system, Bristol Bay, Alaska. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. No. 488. 292 p.

Foskett, D. R. 1958. The Rivers Inlet sockeye salmon. J. Fish. Res. Bd. Can. 15(5):867-889.

Gray, J. 1928. The growth of fish, II; The growth-rate of the embryo of *Salmo fario*. Brit J. Exp. Biol. 6:110-124.

Hanamura, Nobuhiko. 1961. General life history of sockeye salmon in the Far East. Int. N. Pac. Fish. Comm. Transl. No. 21. 49 p.

Ievleva, M. Ya. 1951. Morphology and rate of embryonic development of Pacific salmon, p. 236-244. *In* Pacific salmon. Israel Prog. Sci. Transl., Jerusalem, 1961. [Transl. from Russian.] (Izvestiya Tikhookeanskogo nauchno-issledovatel'skogo instituta rybnogo khozyaistva i okeanografii 34:123-130. 1951.)

Johansen, A. C., and August Krogh. 1914. The influence of temperature and certain other factors upon the rate of development of the eggs of fishes. Cons. Perma. Int. Explor. Mer, Copenhague. Publ. Circonstance, No. 68 (May). 44 p. [Cited by Rockwell, 1956.]

Kerns, Orra E., Jr., and John R. Donaldson. 1968. Behavior and distribution of spawning sockeye salmon on island beaches in Iliamna Lake, Alaska, 1965. J. Fish. Res. Bd. Canada 25(3):485-494.

Lenarz, William H. 1965. Bathymetric and thermal studies of Iliamna Lake, 1961-1964. Fish. Res. Inst. Circ. 230, Univ. Washington, Seattle. 15 p.

McConnell, J. A., and J. R. Brett. 1946. Lakes of the Skeena River drainage: III. Kitwanga Lake. Fish. Res. Bd. Can., Progr. Rep., Pac. Coast Sta. 68:55-59.

McNeil, William John. 1962. Mortality of pink and chum salmon eggs and larvae in Southeast Alaska streams. Ph.D. Thesis, Univ. Washington, Seattle. 270 p.

McPhail, J. D. [ed.]. 1966. Studies of salmon in freshwater in Alaska, p. 9-16. *In* Research in Fisheries, 1965. Contrib. 212, Coll. Fish., Univ. Washington, Seattle.

Olsen, J. C. 1964. Studies of sockeye salmon lake spawning grounds in Iliamna Lake, Bristol Bay, Alaska. M.S. Thesis, Univ. Washington, Seattle. 98 p.

Owen, John B., Charles Conkle, and Robert Raleigh. 1962. Factors possibly affecting production of sockeye salmon in Karluk River, Alaska. U.S. Fish Wildl. Serv., MR 62-8. 57 p.

Rockwell, Julius, Jr. 1956. Some effects of sea water and temperature on the embryos of the Pacific salmon, *Oncorhynchus gorbuscha* (Walbaum) and *Oncorhynchus keta* (Walbaum). Ph.D. Thesis, Univ. Washington, Seattle. 416 p.

Rucker, Robert Raymond. 1937. The effect of temperature on the growth of the embryos of *Oncorhynchus nerka* (Walbaum). M.S. Thesis, Univ. Washington, Seattle. 54 p.

Semko, R. S. 1953. Causes of fluctuations in abundance of Pacific salmon and problems concerning the rational utilization of their stocks. Trudy Soveshchanii 1:37-40. (Proceedings of an all-union conference on problems of the fishing industry.) [Cited in Hanamura, 1961.]

Seymour, Allyn H. 1956. Effects of temperature upon young chinook salmon. Ph.D. Thesis, Univ. Washington, Seattle. 127 p.

Smirnov, A. I. 1958. Certain peculiarities in the biology of propagation and development of the salmonid fish nerka—*Oncorhynchus nerka* (Walbaum). [Transl. from Russian by R. E. Foerster.] Fish. Res. Bd. Can. Transl. Ser. No. 229. 4 p.

Thompson, W. F. 1962. The research program of the Fisheries Research Institute in Bristol Bay, 1945-58. Univ. Washington Publ. Fish., New Ser. 1:1-36.

Wallich, Claudius. 1901. A method of recording egg development for use of fish-culturists. U.S. Bur. Fish., Rep. U.S. Comm. Fish., 1900, p. 185-194. [Fish. Doc. 452.]