THE REPRODUCTIVE BIOLOGY OF THE

DOLLY VARDEN CHAR

SALVELINUS MALMA WALBAUM

by

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of

BIOLOGY

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to the required standard

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October, 1969

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ABSTRACT

Migratory and reproductive behaviour of the non-anadromous Dolly Varden (Salvelinus malma Walbaum) was studied at Meadow Creek, a system in southeastern British Columbia which flows into the Duncan River approximately three miles upstream from its confluence with Kootenay Lake. The spawning migration lasted for more than two months (July 23 to September 26) with the peak period occurring during August. Data on several physical water properties as well as climatological information were collected during the migration and spawning periods. Body weight, length, and sex were recorded from Dolly Varden migrants at each of the fences. The total number of upstream migrants into the Meadow Creek system was 97 (81 mature, 16 immature or unclassified). The body weight to length relationship of the total upstream migrants was $\overline{Y}_x = 814.15 - 68.22x + 1.52x^2$. A site on John Creek approximately one mile above its confluence with Meadow Creek was chosen for the construction of two large aquaria (16' x 4' x 4'). For behavioural observations the aquaria simulated the natural spawning habitat. A total of 19 subjects were used for the reproductive behaviour study. Six spawning acts were observed (three documented in detail. The motor patterns of reproduction were described both quantitatively and qualitatively and compared to other salmonids. Generally Dolly Varden closely resembled the descriptions given for other salmonids with the exception of male trembling (unique to the Dolly Varden?), orgasm repetition, and certain post-spawning activity (both similar to other chars). Gravel analysis showed that Dolly Varden select redd sites which include larger aggregates (1-1/2" - 5"). This combined with post-spawning undulating (an activity which probably serves to sweep eggs located near the surface deep into redd crevices) and specialized post-spawn digging (higher frequency tail beats than in pre-spawn digging) appear to be functional adaptations related to egg survival in the unstable spawning and rearing environments exploited by this species in British Columbia.

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INTRODUCTION

Salmonid reproductive behaviour consists of several different activities; migration to a spawning area, the selection and defense of a territory, courtship behaviour, redd construction, egg laying, fertilization, and finally covering of the fertilized eggs.

The purpose of this study was to observe the migratory and reproductive behaviour of nonanadromous Dolly Varden char (*Salvelinus malma* Walbaum). More specifically, the objectives were: (1) to determine the temporal pattern of migration preceeding spawning; (2) to describe both qualitatively and quantitatively, the motor patterns of reproductive behaviour and; (3) to compare these patterns to those of other salmonids.

Needham and Vaughan (1952) appear to have been the first to describe the spawning behaviour of the Dolly Varden. Their field observations were based on a single pair of fish at Twin Creek, Idaho where light and weather conditions made detailed observations impracticable. The spawning colouration of the pair and a description of the nest site are mentioned. Blackett (1968) provides a somewhat more detailed account of the spawning activities of anadromous Dolly Varden in Hood Bay Creek, Alaska. Once again field conditions made it difficult to follow the spawning activities in detail. Aggression, female digging, quivering (body pressing) and sexual dimorphism are discussed.

MATERIALS AND METHODS

Study Areas

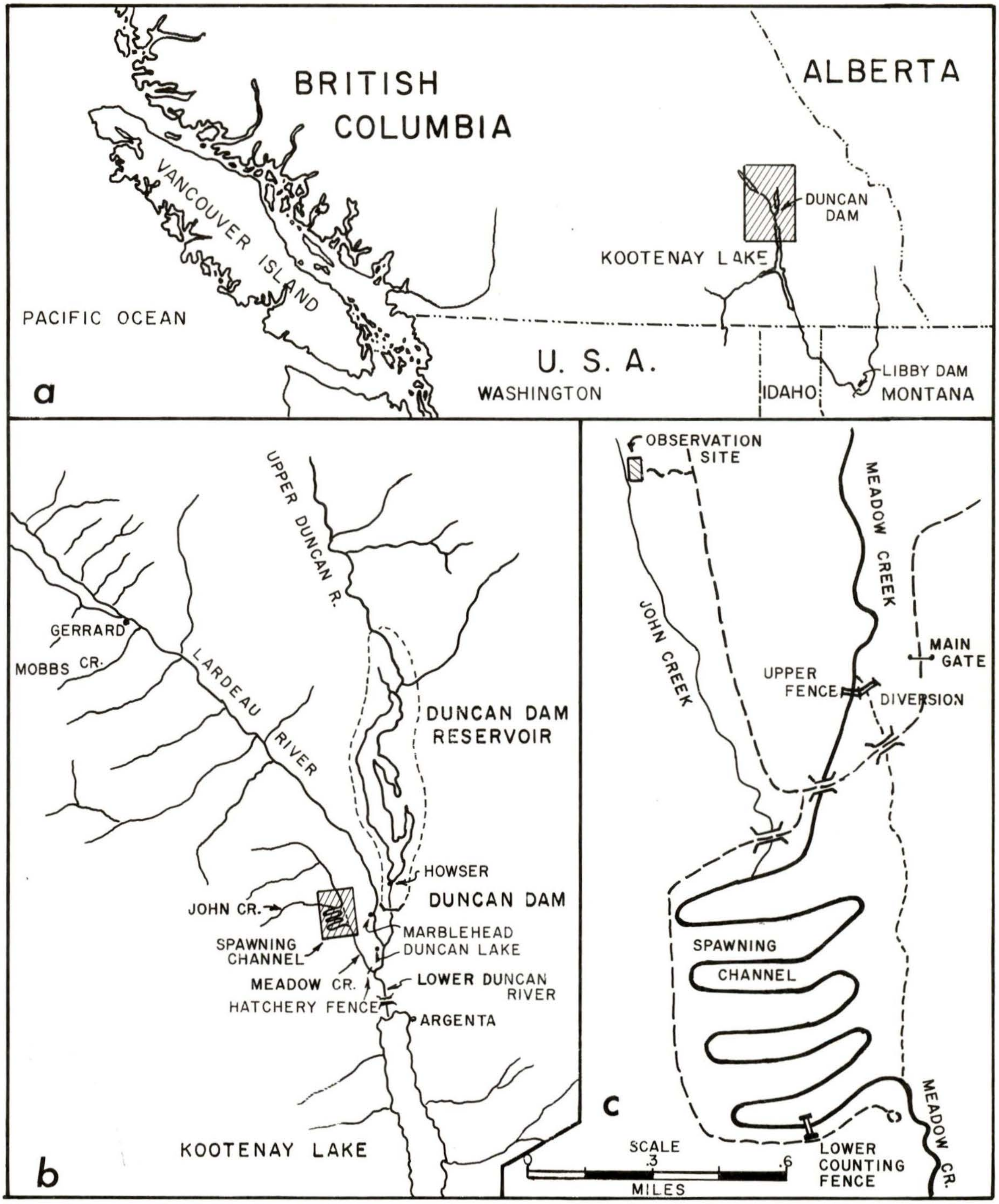
Kootenay Lake situated in southeastern British Columbia (Fig. 1-a) some 25 miles north of the United States border and supporting a population of large (weighing up to 25 pounds) Dolly Varden was selected as the general study area. In the summer of 1967 a field station was established at Coffee Creek, a precipitous stream with its headwaters originating in Kokanee Glacier Park. Initial observations on migration and spawning were made during this period. Flood conditions in the spring of 1968 destroyed these facilities and all subsequent work was carried out at Meadow and John Creeks, tributaries of the Duncan River.

Meadow and John Creeks

The Meadow and John Creek systems drain a mountain area of approximately 52 square miles into the Duncan River, approximately three miles upstream from its confluence with Kootenay Lake (Fig. 1-b). Meadow Creek and the Duncan River support populations of kokanee (*Oncorhynchus nerka* Walbaum) as well as mountain whitefish (*Prosopium williamsoni* Girard) and Dolly Varden.

To compensate for the building of a large storage dam on the Duncan River which threatened to eliminate the Duncan River kokanee population, an artificial spawning channel (11,500 ft. long by 30 ft. wide) and counting fences were constructed on Meadow Creek in 1967 by the British Columbia

Fig. 1. Study area showing location of (a) Kootenay Lake (b) Lardeau and Duncan river systems and (c) John and Meadow Creek systems and the spawning channel.


BRITISH
COLUMBIA
ALBERTA
VANCOUVER ISLAND
DUNCAN
DAM
KOOTENAY LAKE
PACIFIC OCEAN
U. S. A.
WASHINGTON
IDAHO
LIBBY DAM
MONTANA
a
UPPER DUNCAN R.
GERRARD
MOBBS CR.
LARDEAU
RIVER
DUNCAN DAM
RESERVOIR
HOWSER
DUNCAN DAM
JOHN CR.
SPAWNING
CHANNEL
MARBLEHEAD
DUNCAN LAKE
MEADOW CR.
LOWER DUNCAN
RIVER
HATCHERY FENCE
ARGENTA
KOOTENAY LAKE
b
OBSERVATION
SITE
MEADOW
CREEK
JOHN CREEK
MAIN
GATE
UPPER
FENCE
DIVERSION
SPAWNING
CHANNEL
MEADOW CR.
c
SCALE
0
.3
.6
MILES
LOWER
COUNTING
FENCE

Hydro and Power Authority in cooperation with the British Columbia Department of Recreation and Conservation. With slight modification these enumerating facilities were employed for capturing and observing the migratory movements of Dolly Varden.

John Creek drains approximately 10 square miles of the Meadow Creek system and flows into the spawning channel approximately 1,000 feet downstream from the upper fence and diversion facilities (Fig. 1-c). Originating in precipitous terrain, John Creek flows through a level area for approximately two miles before its juncture with Meadow Creek. This lower stretch, a productive spawning area, was chosen as a site for observing the spawning behaviour of the Dolly Varden.

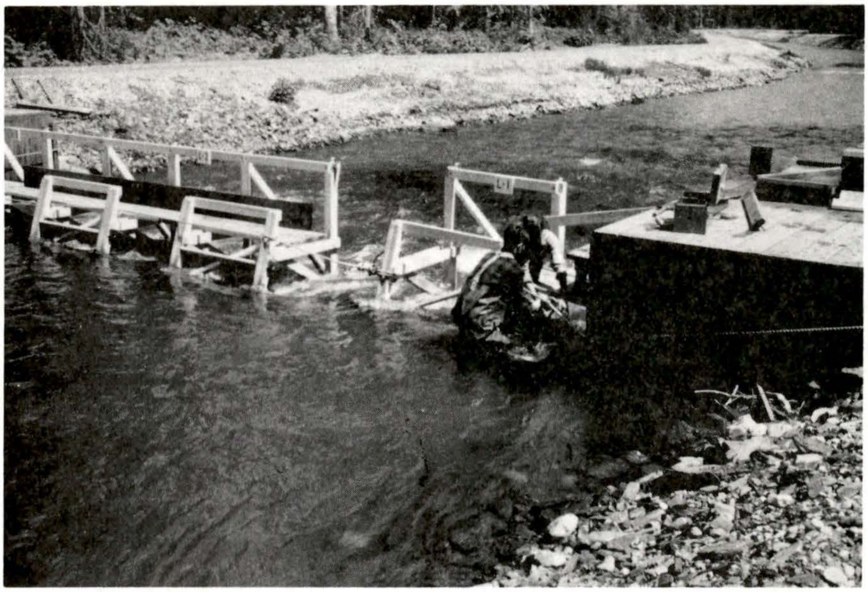
Migration Study Methods

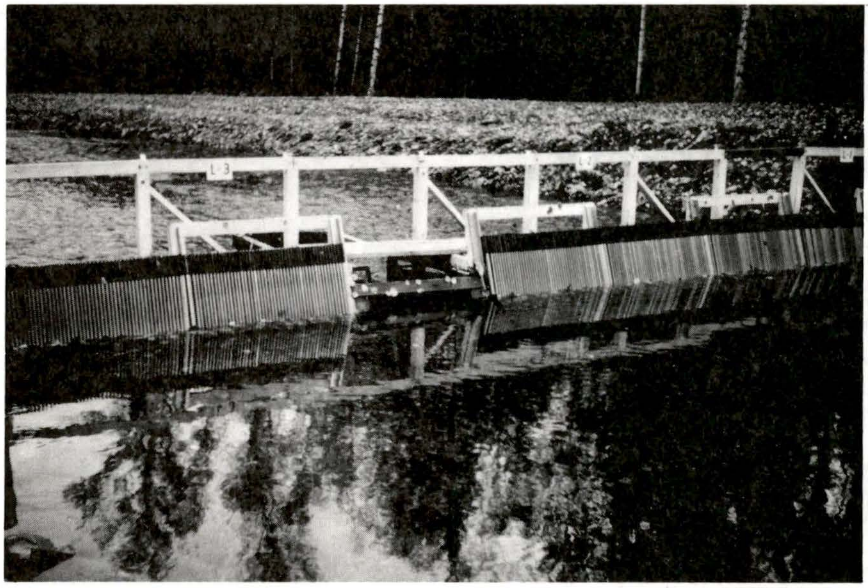
The two spawning channel fences, one above and one below John Creek, each consisted of nine interlocking 'L' shaped frames that spanned the 30 foot channel (Fig. 2). The frames were supported at the bottom by metal cleats on a submerged wooden foundation. Wooden decking and handrails added extra strength to the fence. Interchangeable panels constructed of wooden cedar slats and measuring three feet across fitted vertically in the frames (Fig. 3).

Traps permitting both upstream and downstream movement were provided at each of the fences. The upstream traps measured three feet wide and eight feet long. The sides and top were panelled with plywood and the bottom as well as the ends were covered with 1-inch square wire mesh.

Fig. 2. Installation of 'L' shaped frames for lower enumeration fence.

Fig. 3. Lower enumeration fence showing interchangeable panels and downstream trap entrance.




L-3

The entrance or "lead" into the trap was constructed in an 'V' shape (Fig. 4). Flexible, tapered, equally spaced cedar slats covered the sides of the "lead". Migrating fish were able to penetrate the small opening, created by the flexible wooden slats. Once through the opening, the pressure of the water reduced the size of the opening minimizing the chances of escape. Wooden baffles at the front of the trap directed water to the trap opening as well as provided resting areas for impounded fish (Fig. 5).

The somewhat larger downstream traps (three feet by ten feet) were constructed of wooden frames with 1-inch square wire mesh lining the bottom and sides. A wooden 'V' shaped lead funneled water into the trap.

Traps were checked and cleaned several times daily, usually in the early morning, afternoon, and evening and more frequently during high water conditions.

Recording and Fish Handling

All Dolly Varden migrants were recorded as they passed through the traps with a minimum of handling. Methods of measurement were standarized as follows:

1. Body lengths - measured to the nearest millimeter from the tip of the snout to the fork of the caudal fin.
2. Body weight - measured to the nearest gram.
3. Sex - determined from external features.

Nineteen fish were selected for later use in behavioural observations and either held in a covered pen above the upper fence or transported

Fig. 4. Upstream trap, showing the 'V' shaped entrance and flexible cedar slats.

Fig. 5. Wooden baffles directing water to trap opening and providing a resting area for upstream migrants.

directly to the observation aquaria. Transportation of all fish was executed in a water-proof box placed in the back of a truck. No anaesthetic was administered.

Physical Data

Data on several physical water properties as well as climatological information was collected during the migration and spawning periods.

Temperature

Continuous automatic recorders were used to record water temperatures. One was located on John Creek approximately 2,500 yards upstream from the behavioural observation site and another at the Meadow Creek hatchery fence. A meteorological branch station (Canada Dept. of Transport) located on Duncan Lake approximately three miles from the Meadow Creek channel made available a daily record of air temperatures and precipitation.

Flow and Water Levels

Water levels at Meadow Creek above the upper fence and below the lower fence were recorded daily. In addition, the Water Research Branch of the Department of Energy Mines and Resources provided daily discharge rates for both John and Meadow Creek. These measurements were taken above the upper fence and at John Creek immediately above its juncture with Meadow Creek.

Dissolved Solids

The Department of Energy, Mines and Resources made available records of dissolved solids for the two systems.

Behavioural Observation Methods

John Creek was selected as the most convenient area for behavioural observations. A site approximately one mile above its confluence with Meadow Creek was chosen for the construction of two large aquaria. Once selected, an access road to the site was constructed and the site leveled and cleared of debris.

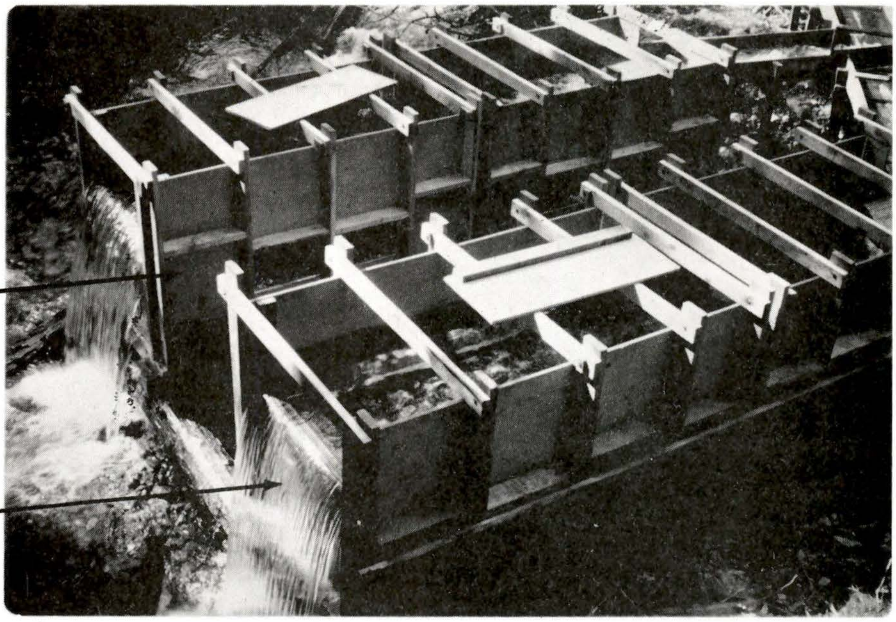
Two aquaria each measuring 16' x 4' x 4' were placed on three 4 x 10 inch timbers. A 2 x 6 inch framework was supported at the top by 2 x 4 inch wooden braces and lined with 3/4-inch waterproof plywood. A waterproof caulking compound was used to seal the aquariums. Two plexiglass windows measuring 4 feet by 18 inches in each aquaria faced a central observation area (Fig. 6). The floor of the observation area measured 16' x 6'. An 'A' frame covered with black polyethylene plastic provided the roofing and darkened the observation area (Fig. 7).

A flume (120' x 2') capable of holding water to a depth of eight inches was junctioned some 15 feet in front of the aquaria with the water supply equally divided to each of the two tanks (Fig. 7). A screen at the entrance of the flume prevented unwanted debris from reaching the aquaria. Baffles were placed at each of the screened intakes to the tanks to prevent excessive turbulence. Sliding gates at the rear of the aquaria

Fig. 6. View showing framework for the two aquaria.

Fig. 7. View showing the junction of the 120-foot flume and the black polyethylene plastic covering the viewing area.

II



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I II

were raised or lowered to adjust the water level. Holes drilled near the bottom of the gates permitted percolation of water through the gravel. A framed panel of one-inch square wire meshing prevented fish escape.

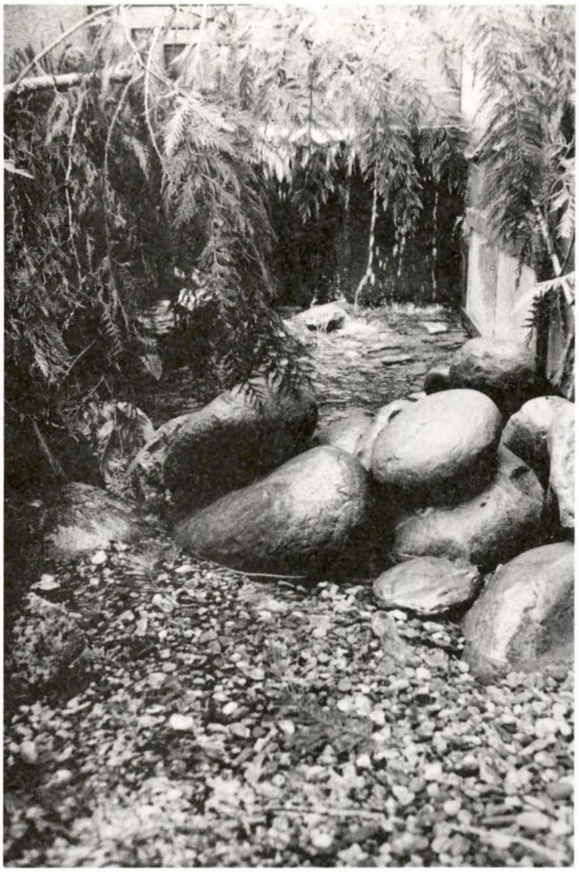
The aquaria were furnished with as natural a habitat as possible. Each aquarium was divided into two viewing areas (opposite observation ports) by means of large boulders (Fig. 8). The four areas were each provided with a different type of gravel (6-8" depth) obtained from the stream bottom and from nearby stock piles, one of which had been used for the artificial spawning channel. The gravel was raked, then thoroughly washed before the fish were introduced. Fifty pound samples taken before and after the study period were analysed for size composition to determine the preferred size for spawning. Cedar boughs (Thuja plicata) were tacked on the sides of the aquaria as well as suspended over the spawning area (Fig. 9) to provide cover and discourage the fish from jumping out of the aquaria. The water depth in the aquaria measured from the aquarium floor varied between 26.75 and 34.0 inches.

Behavioural Observations

Behavioural observations were begun on August 21. Initially, observations lasting an hour were conducted daily. Later, when the fish showed signs of becoming reproductively active, half hour observation periods divided into five-minute intervals were performed every hour when conditions permitted. During active courting and spawning, observations occasionally lasted for 1-1/2 hours or more. When observations became too frequent

Fig. 8. Aquarium divided into two viewing areas by means of large boulders.

Fig. 9. Cedar boughs tacked on the sides of the aquarium to provide cover.



for written records a Sony Cassette Tape Recorder 100 was used. A Beaulieu R16 movie camera equipped with a turret holding a 1:1.4 wide angle lens, a normal 1:1.4 lens and a 3-inch telephoto lens 1:1.9 was used to record fixed action patterns at 24 frames per second with Ektachrome type 7241 E. F. Daylight film. No filters were used.

Rainfall occasionally created rising water levels and turbid stream conditions which delayed observations for two or three days. An electric heater powered by a gasoline generator provided sufficient heat to evaporate the water condensed on the observation windows and warmth in the observation area.

Written and taped data were transposed to format data sheets for quantitative analysis. The 16 mm. coloured movie film was dubbed onto a 1-inch video tape by means of an Ampex Video tape recorder. The recorder was used for stopped-action viewings of stereotyped actions permitting a detailed descriptive analysis. Analysis of the original film by means of a stopped-action Athena T. V. 1900 projector provided duration and frequency measurements of specific patterns. Terms used to describe the behaviour patterns follow those used by Jones and Ball (1954), Jones (1959), Fabricius (1953), and Fabricius and Gustafson (1953) or are otherwise defined.

RESULTS

Migratory Movements

The Meadow Creek fences were operational from July 15 to October 22. From July 23 to September 26, 97 Dolly Varden (81 classed as mature) moved upstream through the lower fence and 29 (21 mature) proceeded through the upper fence which indicates that 49 (41 mature) fish either entered John Creek or remained in the spawning channel. Foot surveys confirmed the presence of Dolly Varden in John Creek above the observation site. Downstream traps were installed on August 19 at the upper fence and September 5 at the lower fence. By October 22, seven (3 mature) Dolly Varden moved downstream through the upper fence and eight (6 mature) through the lower fence.

Composition of the Migratory Population

The numbers of each sex, mean lengths and weights as well as standard deviations during various periods are given in Tables 1 and 2. The fork length to body weight relationship of 85 Dolly Varden (male and female and immature) is shown in Figure 10, and the females and males separately in Figures 11 and 12.

Fish were sexed solely on the basis of external features, by colour, body configuration and kype development. Early arrivals were difficult to sex (Fig. 13) but by late August the two sexes became more distinct in appearance with changes more pronounced in the male than in the female.

LOWER FENCE

	MATURE FISH*							Immature Fish and Unclassified**	Total No. Fish Recorded
	Number Sampled	Male	Female	Average Wt.-gm.	Std. Dev.	Average Length-cm.	Std. Dev.		
July	12	5	7	1710.4	864.5	53.6	8.0	--	12
Aug.	55	29	26	1372.4	691.2	51.0	7.2	5	60
Sept.	14	5	9	1470.0	944.5	51.8	9.8	11	25
Total	81	39	42	1439.3	776.8	51.5	7.9	16	97

* Refer to text for description of sex identification

** Unclassified fish were those observed passing the fence during Kokanee enumeration

TABLE I

Composition of Migratory Population at the Lower Fence.

UPPER FENCE

	MATURE FISH*							Immature Fish and Unclassified**	Total No. Fish Recorded
	Number Sampled	Male	Female	Average Wt.-gm.	Std. Dev.	Average Length-cm.	Std. Dev.		
July	1	1	-	875	-	47.0	-	3	4
Aug.	16	6	10	1172.8	459.0	49.82	7.32	2	18
Sept.	3	1	2	1050.0	70.7	47.8	1.3	2	5
Oct.	2	2	-	850	50.0	42.9	0.4	-	2
Total	22	10	12	1113.2	407.6	48.3	6.5	7	29

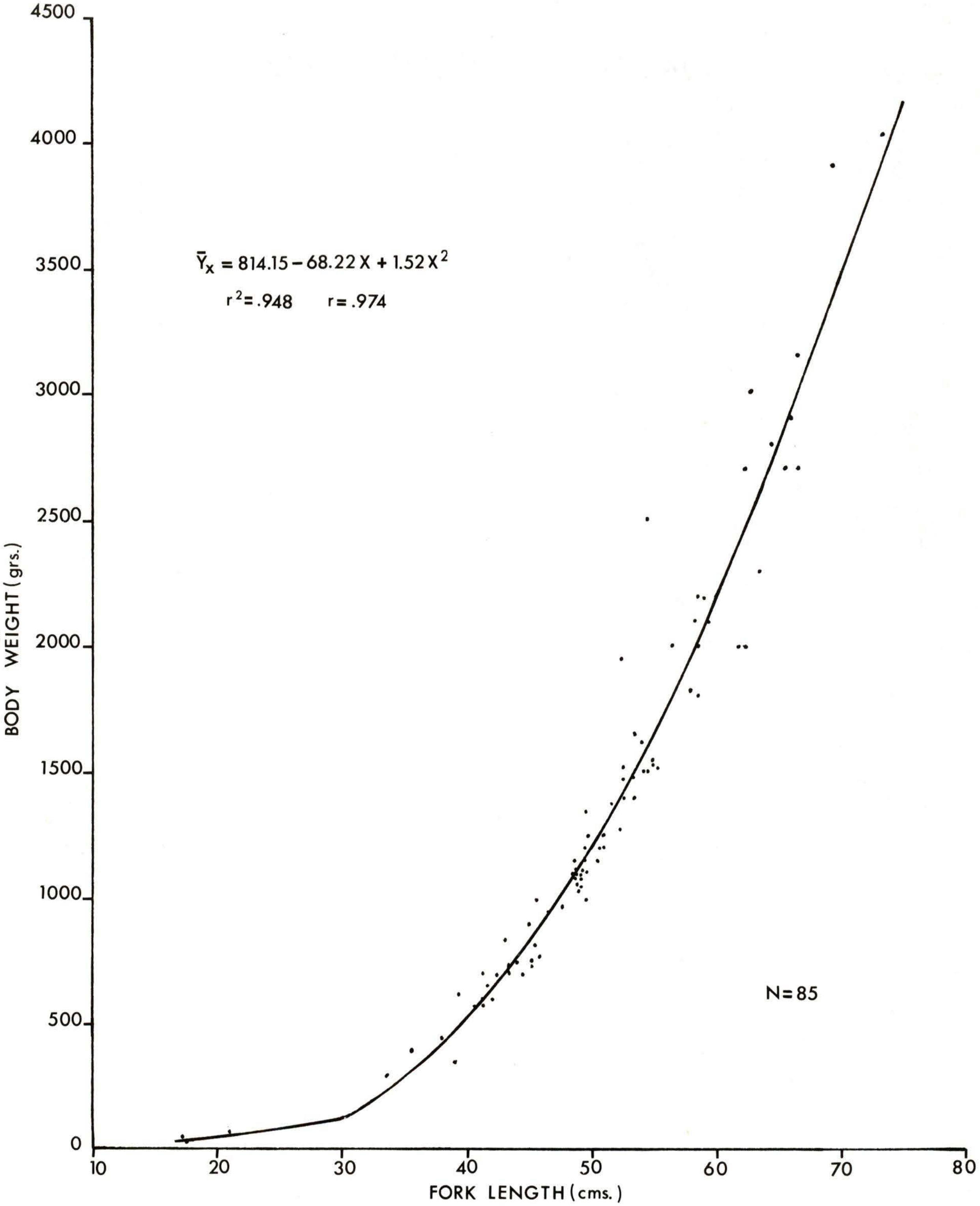
* Refer to text for description of sex identification

** Unclassified fish were those fish passing the fence during Kokanee enumeration

TABLE II

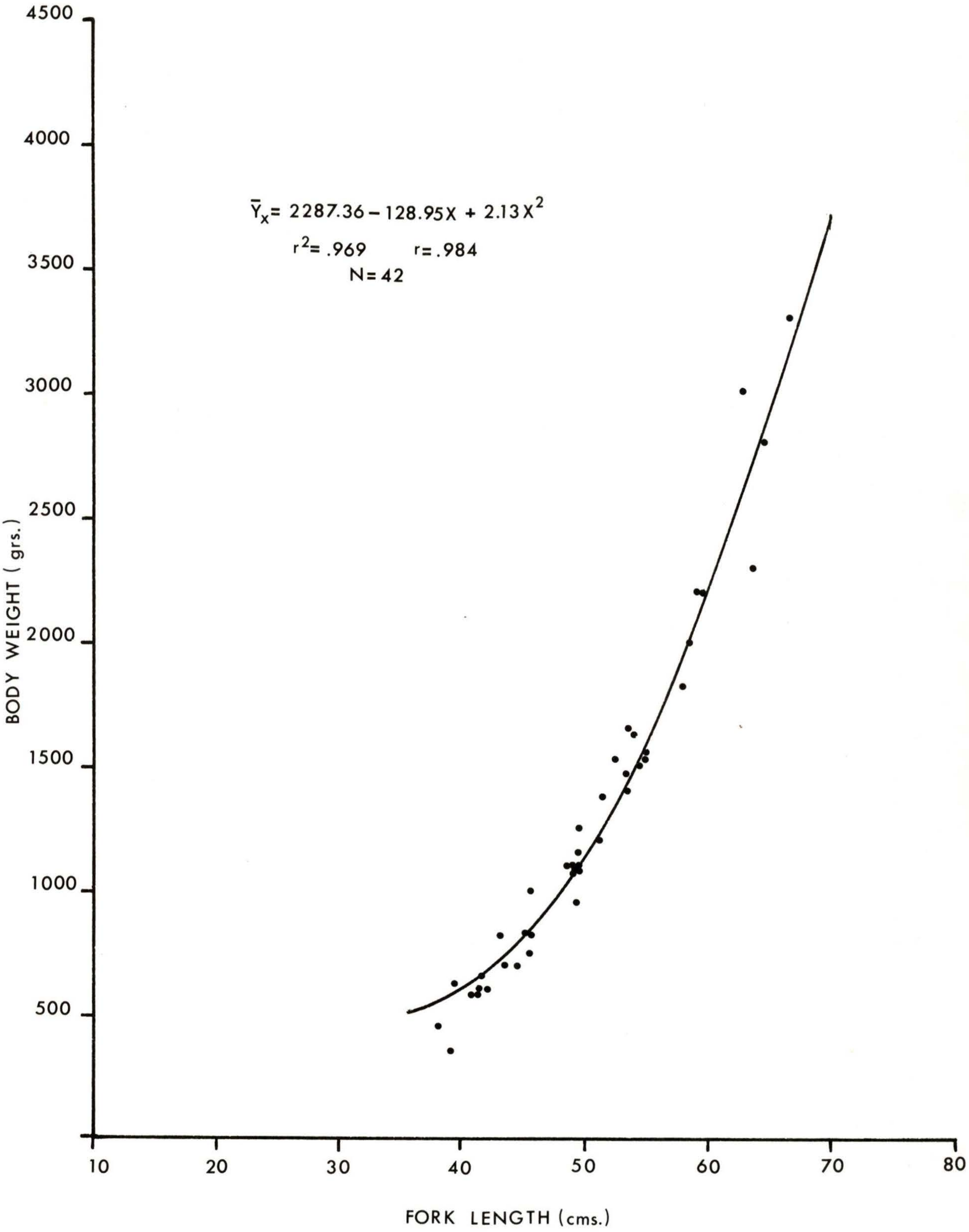
Composition of Migratory Population at the Upper Fence.

Figure 10. Fork length to body weight relationship of Dolly Varden sampled from the lower Meadow Creek fence.



$\bar{Y}_x = 814.15 - 68.22X + 1.52X^2$
$r^2 = .948$ $r = .974$
N=85
BODY WEIGHT (grs.)
FORK LENGTH (cms.)
4500
4000
3500
3000
2500
2000
1500
1000
500
0
10
20
30
40
50
60
70
80

Figure 11. Fork length to body weight relationship of female Dolly Varden sampled from the lower Meadow Creek fence.



$\bar{Y}_x = 2287.36 - 128.95X + 2.13X^2$
$r^2 = .969$ $r = .984$
N=42
BODY WEIGHT (grs.)
4500
4000
3500
3000
2500
2000
1500
1000
500
10
20
30
40
50
60
70
80
FORK LENGTH (cms.)

Figure 12. Fork length to body weight relationship of male Dolly Varden sampled from the lower Meadow Creek fence.

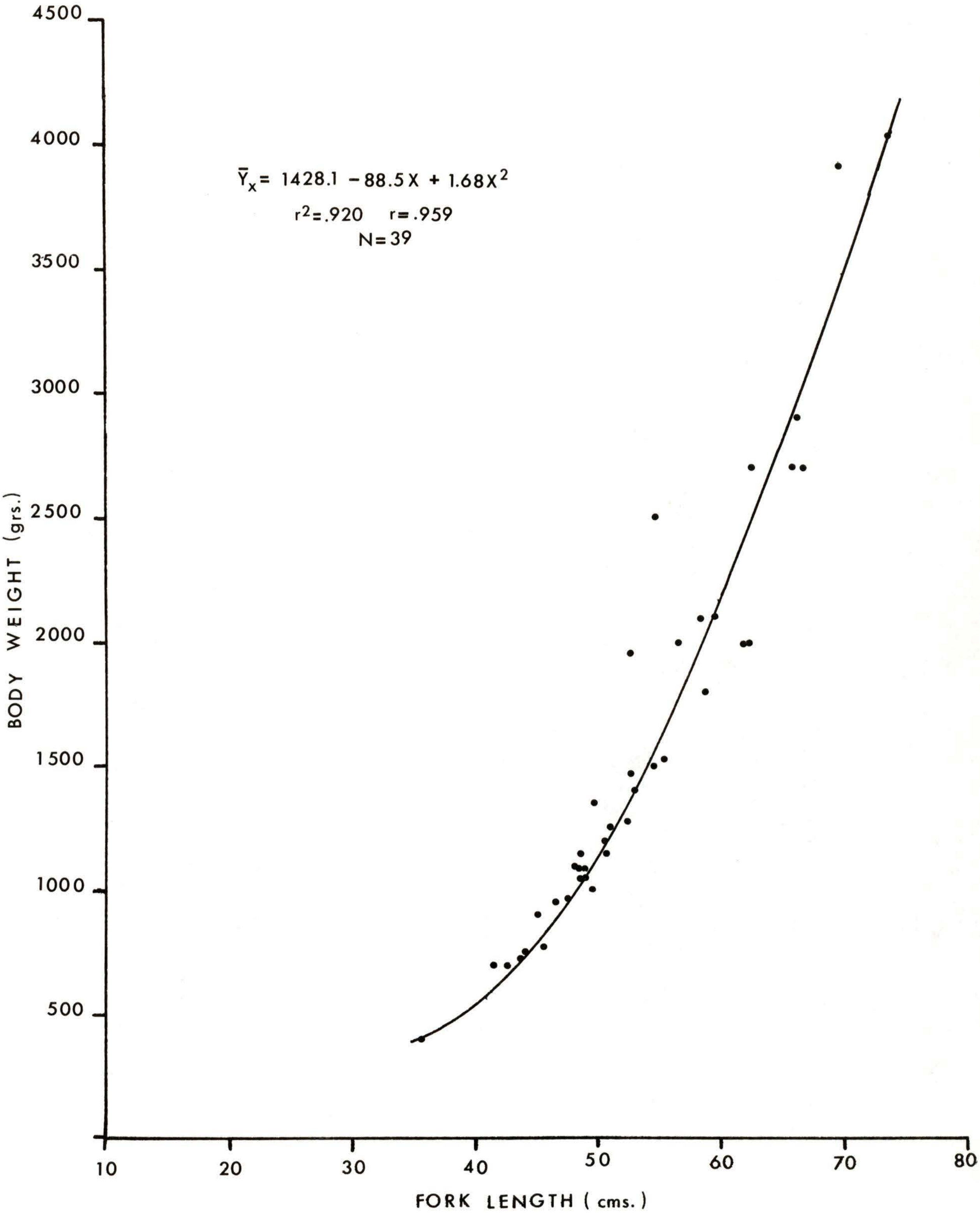
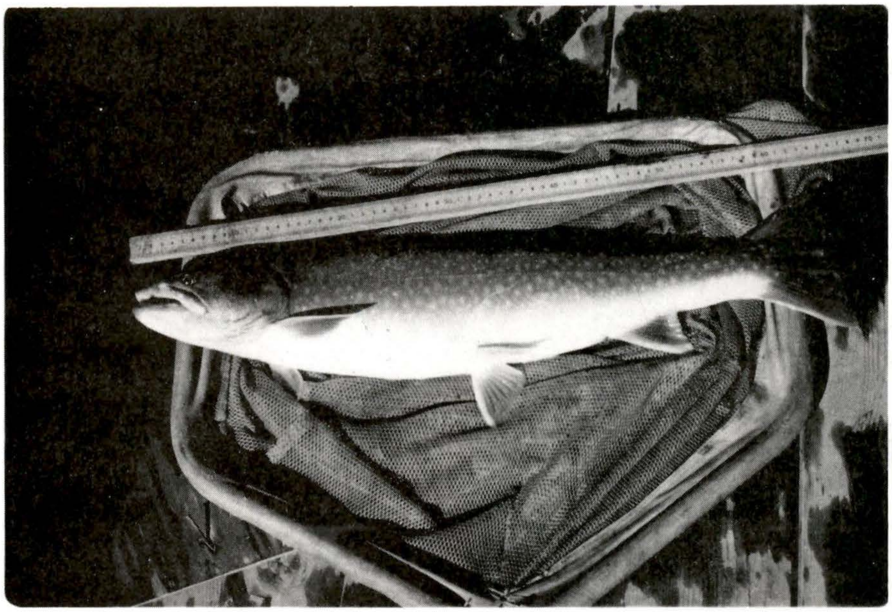
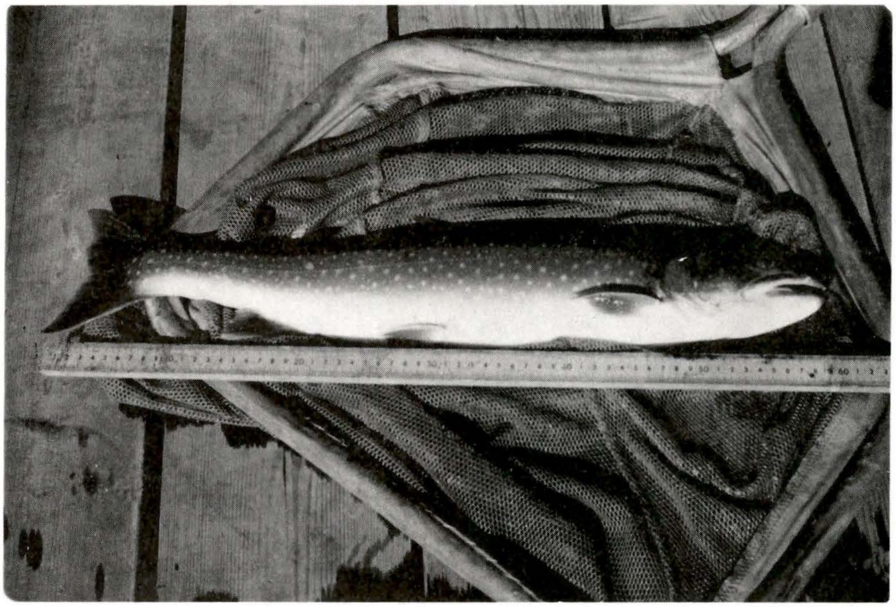

$\bar{Y}_x = 1428.1 - 88.5X + 1.68X^2$
$r^2 = .920$ $r = .959$
N=39
BODY WEIGHT (grs.)
4500
4000
3500
3000
2500
2000
1500
1000
500
10
20
30
40
50
60
70
80
FORK LENGTH (cms.)

Figure 13. Early migrant Dolly Varden; (a) female-stout body configuration with paired and anal fins lightly coloured (b) male-slender body configurations with paired and anal fins more darkly coloured than female.



a



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During migration Dolly Varden were light green on the dorso-lateral surfaces with light coloured spots (those close to the lateral line were light orange and larger than the rest) and white on the ventral surface. The pectoral, pelvic and anal fins all had white borders on their leading edges. As maturation proceeded males became orange on the ventral body surface and the pelvic, pectoral and anal fins became a dark reddish black which contrasted sharply with the outer white margins. Maturing females showed less marked changes.

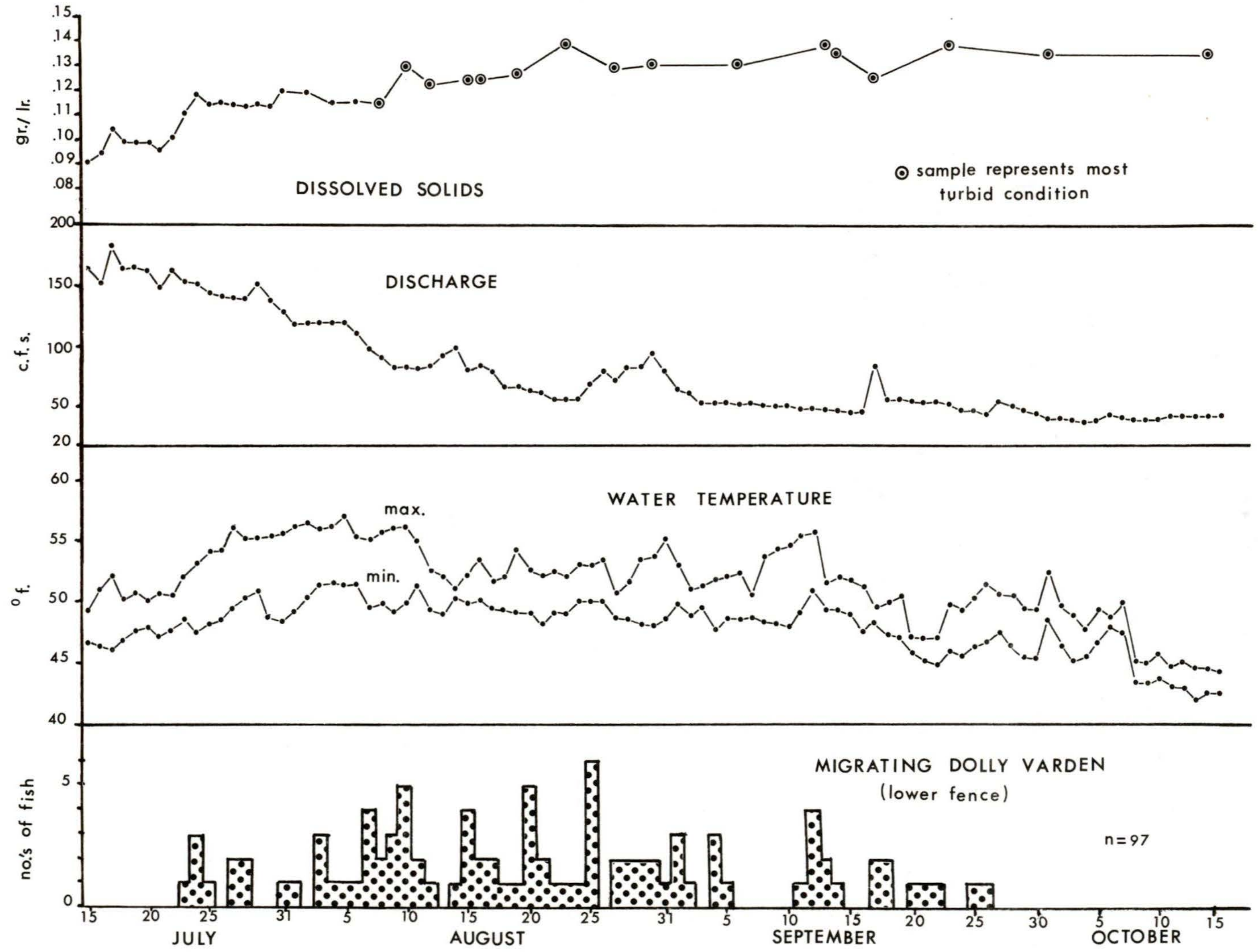
Both male and female develop kypes. In most cases the lower jaw of the mature male was longer than that of the female. However, some mature males had kypes similar to those of females so that kype size was not always a good criterion for sexing. Blackett (1968) reports the development of a kype in both sexes of anadromous Dolly Varden.

Migration in Relation to Physical Factors of Meadow and John Creeks

Physical data for Meadow Creek during the migration period is shown in Figure 14 and Table III. The main migration period (August) was characterized by peak water temperatures, declining discharge rates and increasing levels of dissolved solids. John Creek (Fig. 15 and Table IV) with a colder temperature régime and lesser discharge showed trends similar to those of Meadow Creek.

During August daily water temperatures in Meadow Creek ranged from a mean minimum of 49.7° F. to a mean maximum of 53.8° F. while temperatures at John Creek ranged from a mean minimum of 42.2° F. to mean maximum 46.25° F. (Tables III and IV). The mean discharge for Meadow and John

Figure 14. Migration frequency at lower Meadow Creek fence in relation to physical stream factors (dissolved solids, discharge, and water temperature).



MEADOW CREEK SPAWNING CHANNEL

TABLE III

Water Flow, Level, and Temperature
at Lower Meadow Creek Spawning Channel Fence

		July (15-31)	August (1-31)	September (1-30)	October (1-15)	Entire Period
Water Temperature (° F.)	Min.	$\bar{X}$ = 48.06	$\bar{X}$ = 49.70	$\bar{X}$ = 47.78	$\bar{X}$ = 44.88	$\bar{X}$ = 47.98
		S = 1.28	S = 0.92	S = 1.58	S = 2.18	S = 2.16
		R = 50.9-46.0	R = 51.5-48.1	R = 51.0-45.0	R = 48.9-42.6	R = 51.5-42.6
	Max.	$\bar{X}$ = 52.64	$\bar{X}$ = 53.78	$\bar{X}$ = 51.34	$\bar{X}$ = 47.16	$\bar{X}$ = 51.68
		S = 2.25	S = 1.74	S = 2.17	S = 2.18	S = 3.01
		R = 56.1-49.1	R = 57.0-50.9	R = 55.8-47.1	R = 52.5-44.4	R = 57.0-44.4
		r = 0.74	r = 0.42	r = 0.77	r = 0.95	r = 0.87
Flow (c.f.s.)		$\bar{X}$ = 152.94	$\bar{X}$ = 86.87	$\bar{X}$ = 54.53	$\bar{X}$ = 42.45	$\bar{X}$ = 81.35
		S = 13.70	S = 19.05	S = 7.5	S = 2.91	S = 40.10
		S^2= 187.56	S^2= 362.76	S^2= 56.24	S^2= 5.91	S^2= 1608.06
		R = 183-129	R = 120-58.4	R - 67.8-46.7	R = 45.4-38.9	R = 183-38.9
Gauge Level (feet)		$\bar{X}$ = 1.14	$\bar{X}$ = 0.83	$\bar{X}$ = 0.63	$\bar{X}$ = 0.55	$\bar{X}$ = 0.78
		S = 0.06	S = 0.10	S = 0.05	S = 0.02	S = 0.22
		S^2= 0.003	S^2= 0.01	S^2= 0.002	S^2= 0.0003	S^2= 0.05
		R = 1.27-1.04	R = 1.02-0.72	R = 0.72-0.58	R = 0.56-0.52	R = 1.27-0.52

$\bar{X}$ = Mean

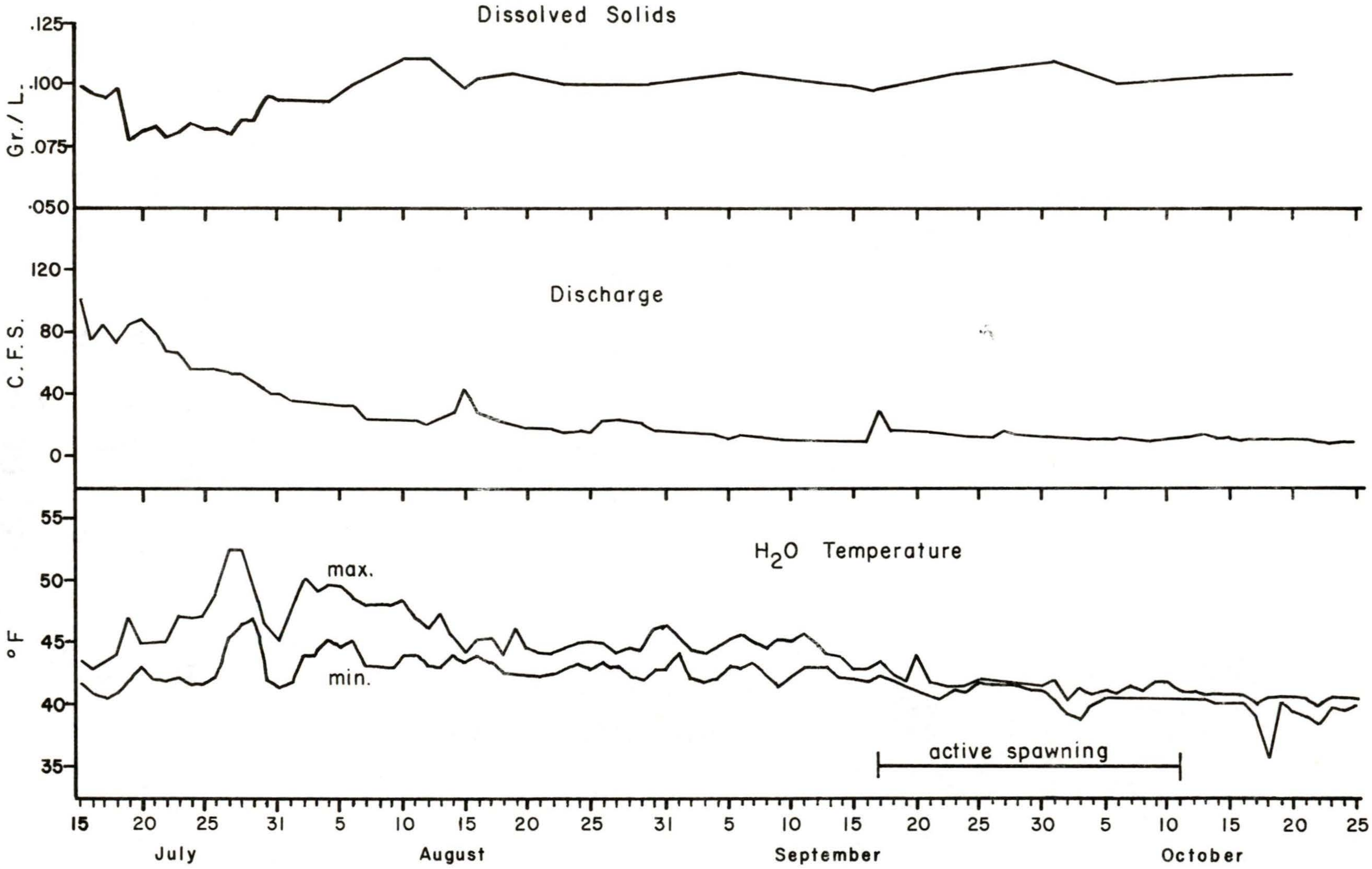
S^2= Variance

S = Standard Deviation

R = Range

r = correlation coefficient

Figure 15. Period of active spawning in observation aquaria in relation to physical stream factors, dissolved solids, discharge and water temperature of John Creek.



Dissolved Solids
Gr./L.
.125
.100
.075
.050
Discharge
C.F.S.
120
80
40
0
H_2O Temperature
°F
55
50
45
40
35
max.
min.
active spawning
15
20
25
31
5
10
15
20
25
31
5
10
15
20
25
30
5
10
15
20
25
July
August
September
October

TABLE IV

Water Flow, Level, and Temperature of John Creek with respect to Migration and Spawning Activity

		July (15-31)	August (1-31)	September (1-30)	October (1-20)	Entire Period
Water Temperature (° F.)	Min.	$\bar{X}$ = 42.5	$\bar{X}$ = 42.23	$\bar{X}$ = 42.11	$\bar{X}$ = 39.91	$\bar{X}$ = 42.08
		S = 1.88	S = 0.85	S = 0.839	S = 1.11	S = 1.65
		R = 40.5-47.0	R = 41.7-45.2	R = 41.2-44.2	R = 35.6-40.6	R = 35.6-47.0
	Max.	$\bar{X}$ = 46.59	$\bar{X}$ = 46.25	$\bar{X}$ = 43.38	$\bar{X}$ = 40.90	$\bar{X}$ = 44.34
		S = 2.80	S = 1.81	S = 1.56	S = 0.425	S = 2.814
		R = 42.8-52.5	R = 44.0-50.0	R = 41.3-45.8	R = 40.0-42.0	R = 40.0-52.5
		r = 0.827	r = 0.60	r = 0.80	r = 0.354	r = 0.815
Flow (c.f.s.)		$\bar{X}$ = 65.62	$\bar{X}$ = 24.89	$\bar{X}$ = 14.77	$\bar{X}$ = 12.45	$\bar{X}$ = 26.35
		S = 18.42	S = 6.84	S = 4.04	S = 0.917	S = 20.73
		S^2 = 339.13	S^2 = 46.73	S^2 = 472.97	S^2 = 0.842	S^2 = 429.93
		R = 103-40	R = 36.5-16.3	R = 31.5-10.4	R = 14.6-11.3	R = 103-10.4
Gauge Level (feet)		$\bar{X}$ = 2.11	$\bar{X}$ = 1.60	$\bar{X}$ = 1.39	$\bar{X}$ = 1.33	$\bar{X}$ = 1.57
		S = 0.157	S = 0.122	S = 0.089	S = 0.024	S = 0.293
		S^2 = 0.025	S^2 = 0.015	S^2 = 0.008	S^2 = 0.000	S^2 = 0.086
		R = 2.4-187	R = 1.90-1.43	R = 1.73-1.27	R = 1.39-1.30	R = 2.4-1.27

$\bar{X}$ = Mean

S^2 = Variance

S = Standard Deviation

R = Range

r = Correlation Coefficient

Creeks during August was 86.87 c.f.s. and 24.89 c.f.s. respectively; a decrease from the July figures of 66.07 c.f.s. at Meadow Creek and 40.93 c.f.s. at John Creek. Mean water levels during the month of August decreased 0.31 feet at Meadow Creek and 0.51 at John Creek from the mean July level.

Physical Features During Aquarium Spawning

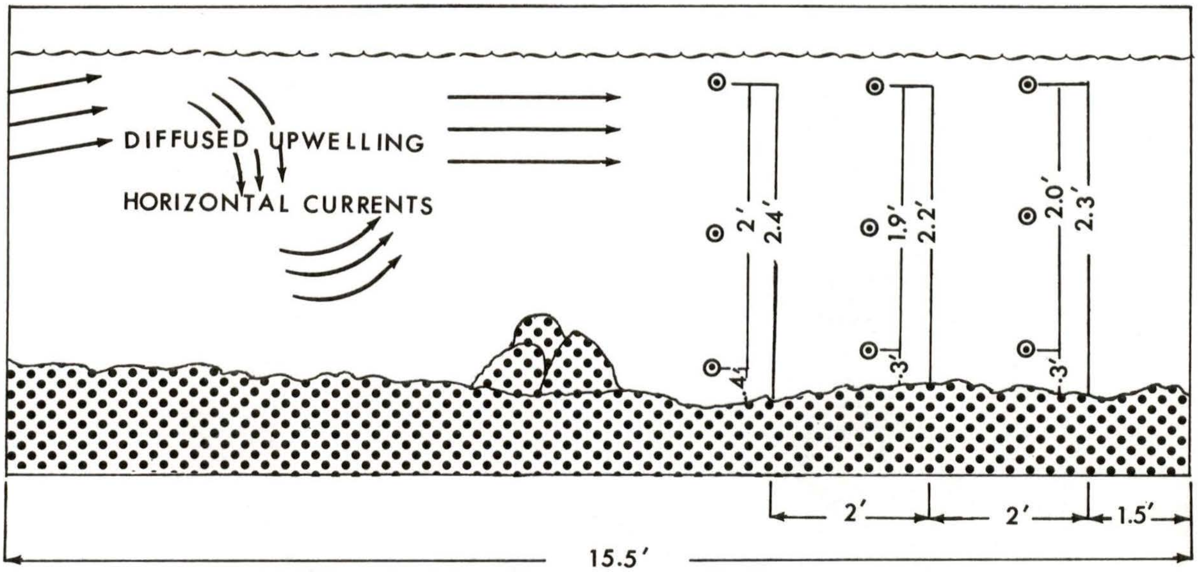
Stream temperatures during the aquarium spawning observation period (September 17 to October 11) remained relatively constant. On days when spawning was observed (September 18, 23, 26 and October 2 and 3) the mean temperature was 41.3° F. and fluctuations between maximum and minimum temperatures were small (between 0.2° and 1.0° F.). These temperatures correspond closely with those previously recorded for other Dolly Varden spawnings. Blackett (1968) reports that during the peak spawning period the water temperatures ranged from 42° - 44° F. Needham and Vaughan (1952) indicate the water temperature of Twin Creek, Idaho during spawning was 41° F.

Maximum daily air temperatures from September 18 to October 11 ranged from 47° F. to 67° F. and the minimum daily temperatures from 35° F. to 47° F.

Water velocity in the aquaria ranged from 1.92 to 0.13 feet per second (Figs. 16 and 17). Five inches above the sites in the aquariums where fish were observed to have spawned the velocities ranged from 0.27 to 0.53 feet per second. The water being discharged into the aquaria was calculated as 2.4 c.f.s. Water depths at which redd construction occurred varied from 26.75 to 30.75 inches.

Figure 16. Flow areas and velocities in aquarium one.

FLOW AREAS IN AQUARIUM ONE



FLOW [FT./SEC.] IN AQUARIUM ONE

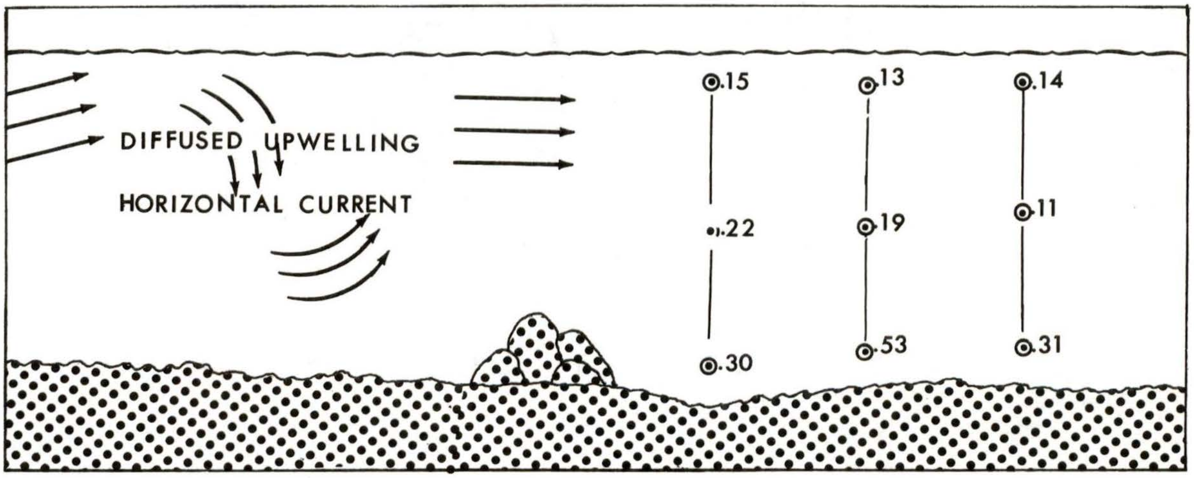
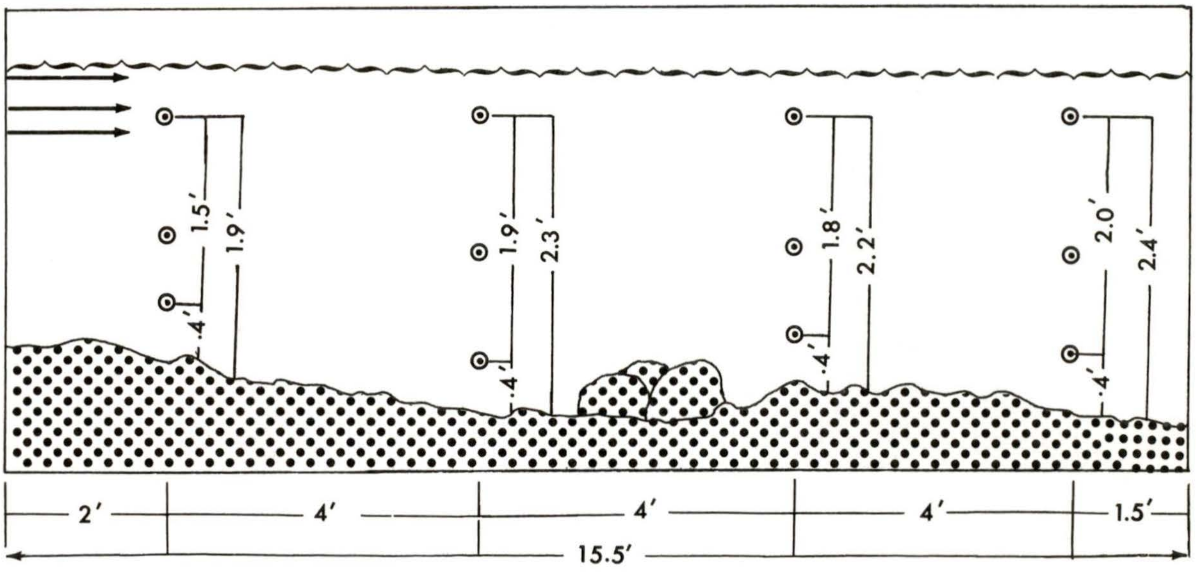
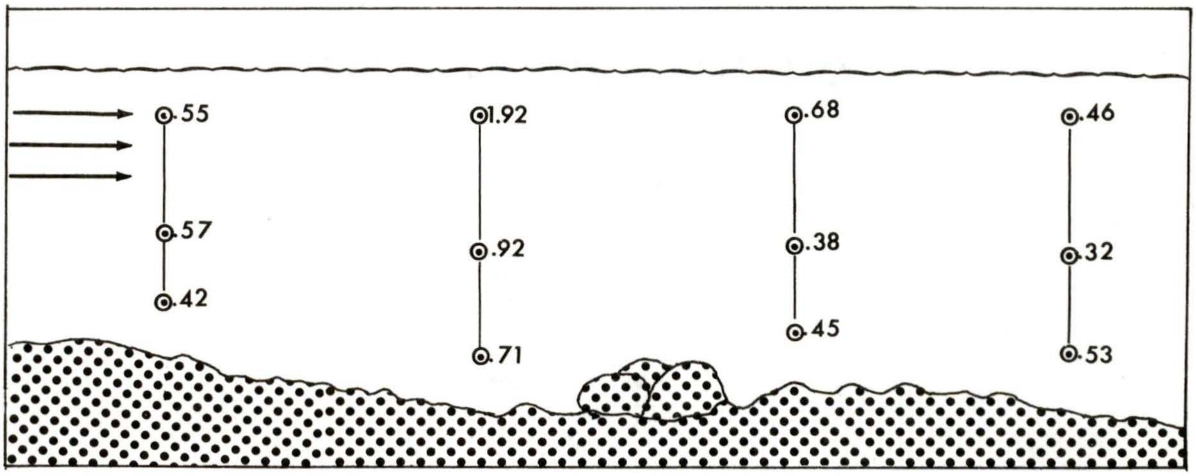


Figure 17. Flow areas and velocities in aquarium two.

FLOW AREAS IN AQUARIUM TWO



FLOW [FT./SEC.] IN AQUARIUM TWO



Reproductive Behaviour

A total of 19 subjects were used for the reproductive behaviour study with five to eight fish present in each aquarium at any one time. The first fish (five) were introduced into the aquarium on August 21. On September 13 the number of fish reached a maximum of 15 consisting of seven fish (three males and four females) in tank one and eight fish (two males and six females) in tank two. A total of five females were observed digging nests. Six spawning acts were observed and three were fully documented. The dominant male in each aquarium spawned two or more females.

General Description of Reproductive Behaviour

When first introduced into an aquarium the fish sought cover. Within a few hours they began to explore the environment. Males soon became involved in aggressive bouts with other males. The females remained near the bottom of the aquaria or leaped at the overfall created by water entering. Two escaped. After a fish had matured and commenced courtship there appeared to be little tendency to escape.

The general pattern of spawning behaviour can be summarized as follows. The males and females spent the first weeks resting near the gravel or in the aerated water entering the aquariums. Usually one male assumed dominance in aggressive interactions with other males. The first sign of female reproductive activities consisted of anal fin feeling and later non-localized digging movements. Gradually the digging became confined to a specific location and the male courted the female by quivering along her side.

Aggression by the male centered around the digging site and consisted of chasing, threatening and biting intruders. Occasionally the female reacted aggressively to other females but rarely was a female observed being displaced from her redd.

The digging produced a depression about 4-6 inches deep cleared of most of the fine aggregrates leaving crevices created by the larger stones. On one occasion a female was observed loosening a stone on the bottom of the nest with her snout after several futile attempts with the caudal fin failed (Fig. 18).

A shift in male behaviour from quivering to flanking appeared to be an indication that spawning was drawing near. With the nest completed after several hours of digging, the female began a series of crouching positions and the male became extremely attentive. The female then suddenly assumed an anchored position and was joined by the male. The male crouched, both opened their mouths wide, quivered violently, and the eggs and sperm were released simultaneously.

Immediately after the orgasm the male moved a short distance away from the female usually behind and to the side. The female then began a snake-like undulating movement forcing exposed eggs into the crevices in the bottom of the redd. This weaving motion was interrupted by an occasional digging movement in which the female positioned herself a

Figure 18. Female attempting to loosen a stone in the bottom of her redd with her snout.

foot or so in front of the redd and by vigorous digging moved gravel into the depression.

Coverings of the eggs sometimes continued until the commencement of the following spawning act. The eggs were found to be buried under six to eight inches of gravel. The size of the redds (depression in the gravelled substrate) appeared to vary with the size of the fish. The average redd was approximately 16-20 inches long and 10-12 inches wide. Blackett (1968) gives a size range for redd construction slightly smaller than the above. Detailed description of behaviours observed during reproduction follow.

Swimming and Comfort Movements

Such behaviours as swimming, yawning, snapping, chafing and gulping were observed to occur in both reproductively active and inactive fish.

Swimming

Leisure swimming was the most frequent mode of swimming observed and was achieved by the movement of the caudal fin, with the other fins partially extended. Rapid locomotion was accomplished with a quick thrust of the caudal fin and with all other fins depressed. Braking was achieved by extending the pectoral, pelvic and dorsal fins.

Yawning

Yawning consisted of rapidly opening the mouth (60° angle) for a second or two, usually with all of the fins depressed, the opercula extended, and hyoid apparatus depressed and the eyes directed forward (Fig. 19) followed by a more rapid closure accompanied by a slight lifting of the opercula, indicating that water may be pumped through the gill chamber. Following a yawn the opercula were often repeatedly opened and closed.

The mean number of male yawns per 30 minute observation period (n = 67) was 1.8 while the mean for females was 0.8. The difference might be due to the greater activity of females since yawning was rarely observed while a fish was active. Figure 20 which shows the frequency of male yawns suggests that yawning decreases as the spawning act is approached.

Snapping

The fish opened and closed the mouth in rapid succession with the head pointed slightly upward and the caudal fin downward. This activity was rarely observed.

Fabricius (1953) makes reference to a similar activity for the Swedish char which appears to comically resemble a little dog barking furiously. Hartman (1969) describes a similar activity among the Kootenay Lake rainbow.

Chafing

Chafing occurred when a fish swam so that some part of its body rubbed against branches, rocks, or other objects.

Gulping (Fabricius 1953 - air snapping)

This activity consisted in the fish swimming to the surface of the

Figure 19. Male yawning.

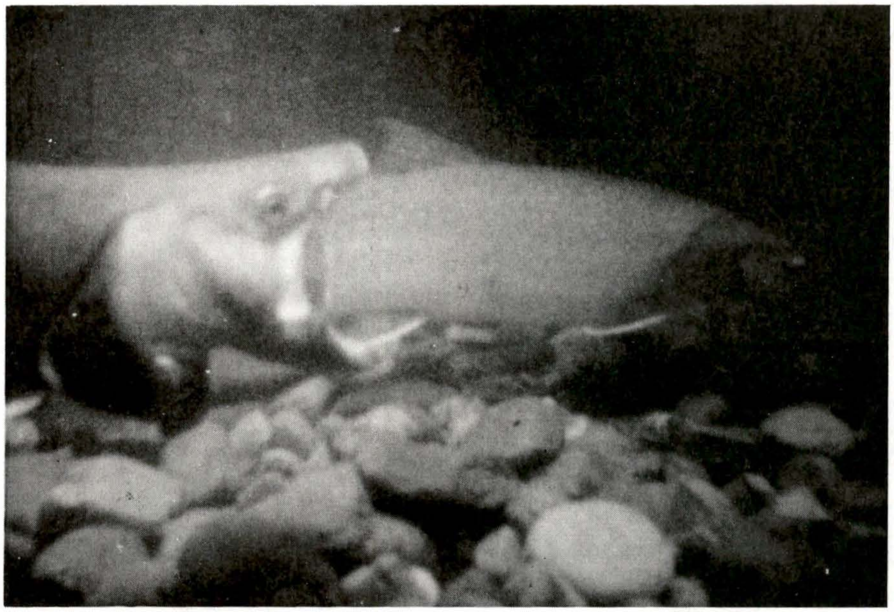
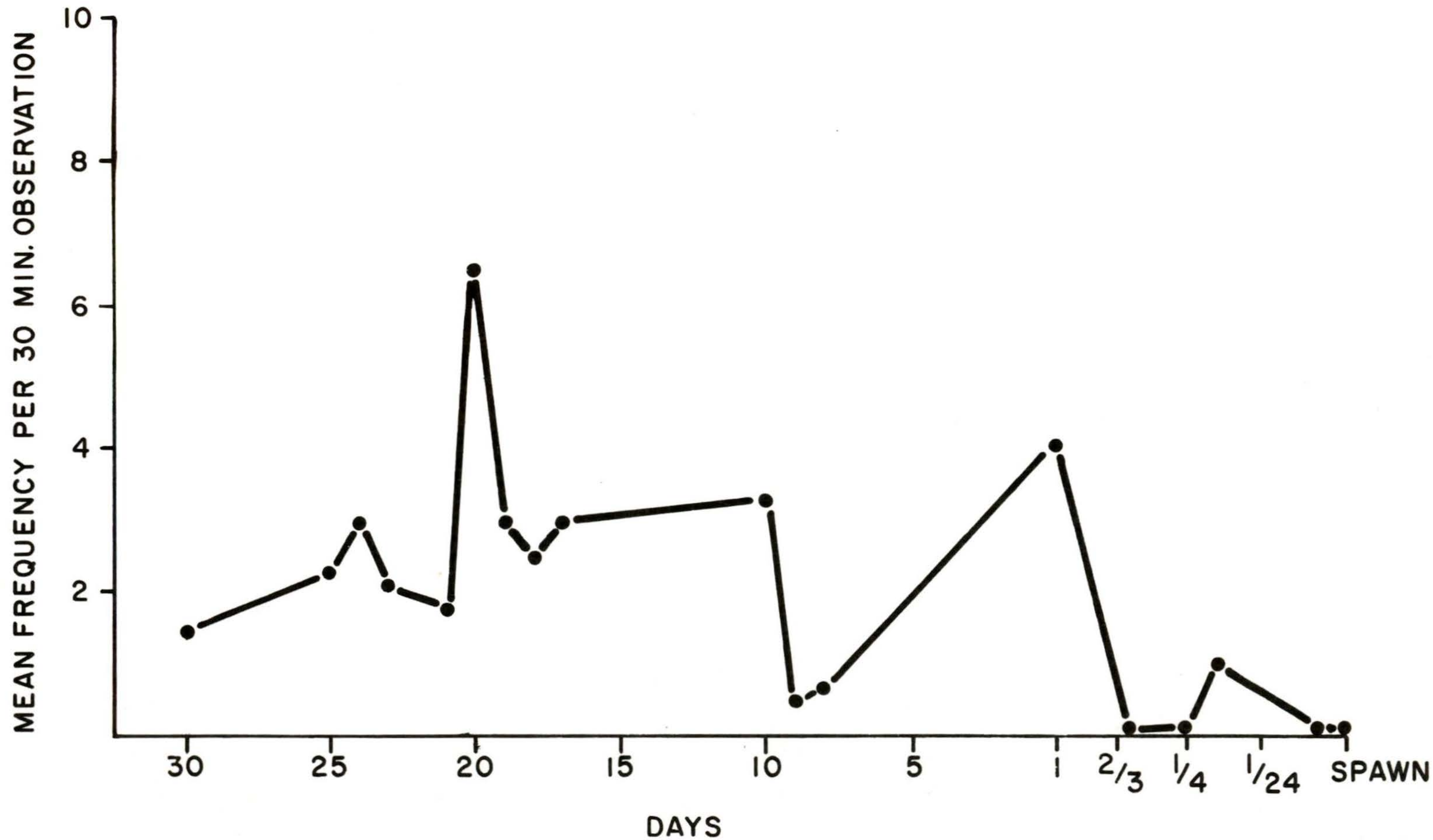


Figure 20. Frequency of male yawns.


MEAN FREQUENCY PER 30 MIN. OBSERVATION
10
8
6
4
2
30
25
20
15
10
5
1
2/3
1/4
1/24
SPAWN
DAYS

aquarium, briefly opening the mouth, gulping air at the surface, then returning to the bottom emmitting bubbles through the gills. Presumably this served as a buoyancy adjustment.

Fabricius (1953) makes reference to such an activity occurring among Dolly Varden shortly after being introduced into an aquarium.

Aggressive Behaviour

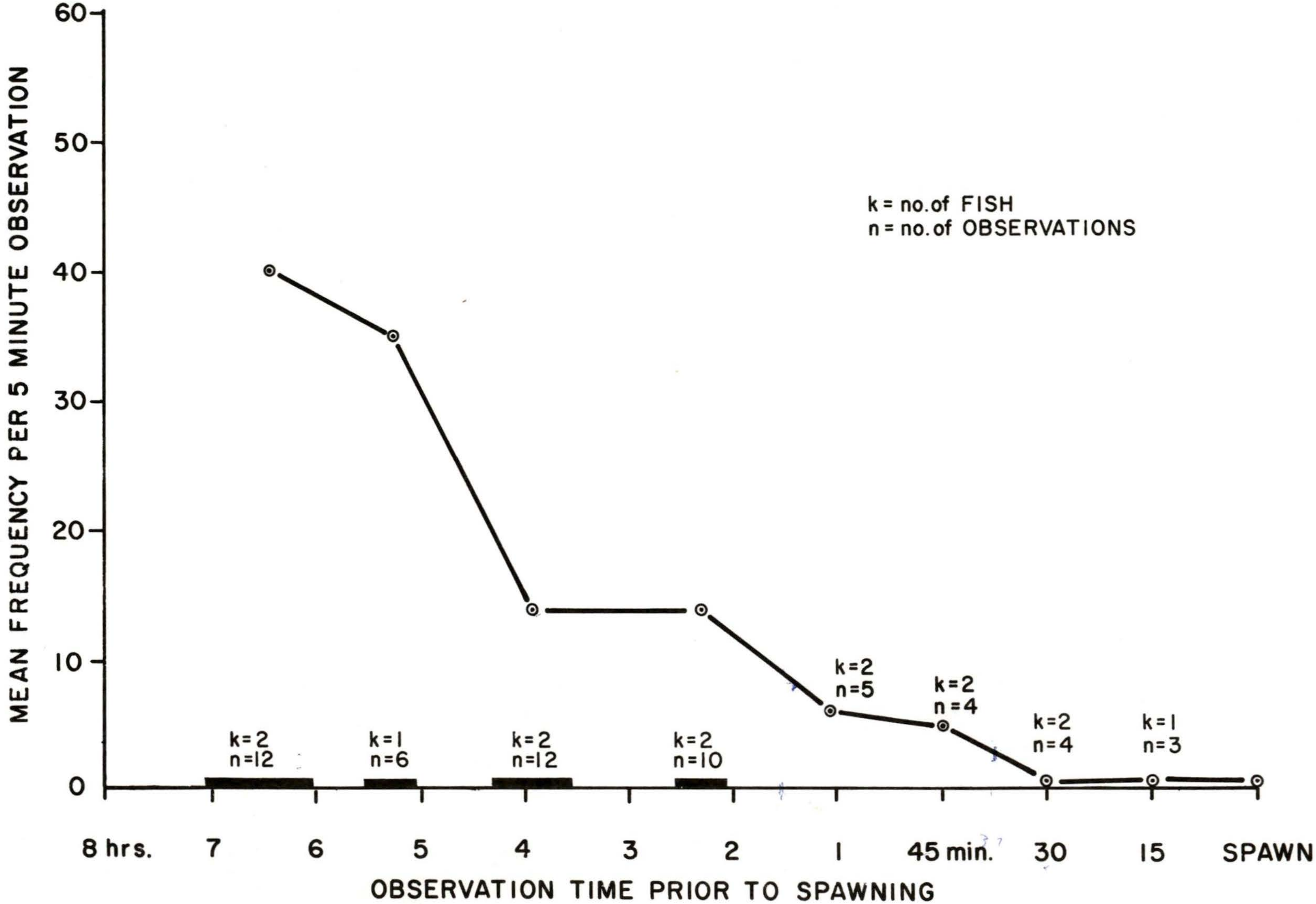
Territorial Behaviour

Only one territory was established within each aquarium at any one time. The dominant male tolerated other fish in the territory provided they were resting, but when they moved abruptly they were attacked.

During spawning activities both males and females occasionally interrupted their courtship to interact aggresively with intruders. If the intruder happened to be a male the female paid little attention, but if a female approached, she assumed a threat posture with fins fully erected or occasionally charged with open jaws. The intruding female usually darted away.

Males were more aggressive than females. They defended their territories by chasing, biting, or threatening (with fins fully erected) without obvious damage to intruders. The mean number of aggressive bouts (biting and chasing) per 30 minute observation period ($n = 67$) was 3.2 for males and 0.2 for females. Male aggression declined with the approach of the spawning act (Fig. 21). Fabricius (1953) indicates that among mountain char the frequency of male attack is high when the frequency of courtship activity is low and vice versa.

Figure 21. Mean frequency of male aggression (chasing and biting) per five minute observation period prior to spawning.


MEAN FREQUENCY PER 5 MINUTE OBSERVATION
60
50
40
30
20
10
0
k = no. of FISH
n = no. of OBSERVATIONS
k=2
n=12
k=1
n=6
k=2
n=12
k=2
n=10
k=2
n=5
k=2
n=4
k=2
n=4
k=1
n=3
8 hrs.
7
6
5
4
3
2
1
45 min.
30
15
SPAWN
OBSERVATION TIME PRIOR TO SPAWNING

The territorial behaviour of Kootenay Lake Dolly Varden closely paralleled the behaviour observed for the mountain char, S. alpinus (Fabricius, 1953). [By contrast the aggression displayed by both male and female Dolly Varden was much less intense than that observed among natural spawning Gerrard rainbow trout (Salmo gairdneri) Hartman (1969) where male rainbow became scarred from agonistic encounters. Jones (1959) states that Atlantic salmon fighting seldom results in bloodshed and the actual fighting of these animals is largely replaced by threats and chasing. Jones and Ball (1954) indicate that brown trout fight viciously, especially the dominant male who attacks all intruding males and females. Fabricius and Gustafson (1953) report that fighting mountain char males (S. alpinus) showed displacement feeding. A fish took a small stone or some sand in its mouth then spat it out again. No such displacement activities were observed to occur among the Kootenay Lake Dolly Varden. Blackett (1968) observed that male aggression in the natural environment became strongly developed during the spawning period.]

comparison to other spp

Frontal Threat (Fabricius 1953; Fabricius and Gustafson, 1953 - Frontal Threat Display)

The aggressor, preceding an encounter, and with fins maximally erect, positioned his body towards his opponent. In this posture the white anterior margins of the fins became more readily visible.

Lateral Threat (Fabricius, 1953; Fabricius and Gustafson, 1953 - Mutual Lateral Display)

In this activity two males swam side by side with heads and tails curved slightly upward, and all fins fully erected. During the preliminary study at Coffee Creek two large Dolly Varden, apparently males, were observed to drift backwards, both in lateral threat postures. This activity was not observed in the John Creek aquaria.

Fabricius and Gustafson (1953) speak of a similar aggressive pattern occurring among the mountain char while within the confines of an aquarium. Neither Smith (1941) nor Blackett (1968) makes reference to such a behaviour with cutthroat, eastern brook trout or Dolly Varden. Lateral threats were observed to be a common behaviour among the large Gerrard rainbow trout (Hartman, 1969). Pairs of rainbow have been observed to travel distances of 50 feet or more over the spawning grounds while in this position.

Biting

Biting was characterized by a quick body thrust in the direction of the opponent's body with fins erect and mouth open. In many instances no body contact occurred. On one occasion instead of attacking with an open mouth the aggressor butted the opponent with his snout. Biting was usually terminated with the opponent fleeing.

The mean frequency of biting bouts per 30 minute observation period (n = 67) were; male 1.7 and female 0.13.

Chasing

The territory holder with all fins erect, chased intruders who escaped by rapid swimming with all fins depressed.

The mean frequency of chasing bouts per 30 minute observation period (n = 67) were; male 1.5 and female 0.07.

Nest Construction

It appeared that the female was responsible for nest selection and that the male established his territory around the digging site. Nest construction by the female consisted of two basic motor patterns, digging and feeling. Digging was used to remove gravel from the nest and feeling served as a method of surveying the results of the digging activities.

Pre-Spawn Digging (Jones and Ball, 1953; and Jones, 1959 - cutting)

The female took up a position directly over the nest and with fins only slightly extended suddenly turned on her side. The eyes were turned forward so that the whites were readily visible. With the mouth partially opened the body was catapulted forward. Alternate bending and straightening of the body dislodged stones; the larger ones fell almost immediately while the finer pebbles were carried downstream beyond the nest site by water currents (Figs. 22, 23 and 24).

A bout of digging usually consisted of a series of rhythmic tail beats. The mean number of tail beats for 461 digging bouts was 3.28/bout. A

Figure 22. Sequence of pre-spawn digging movements (ventral view).

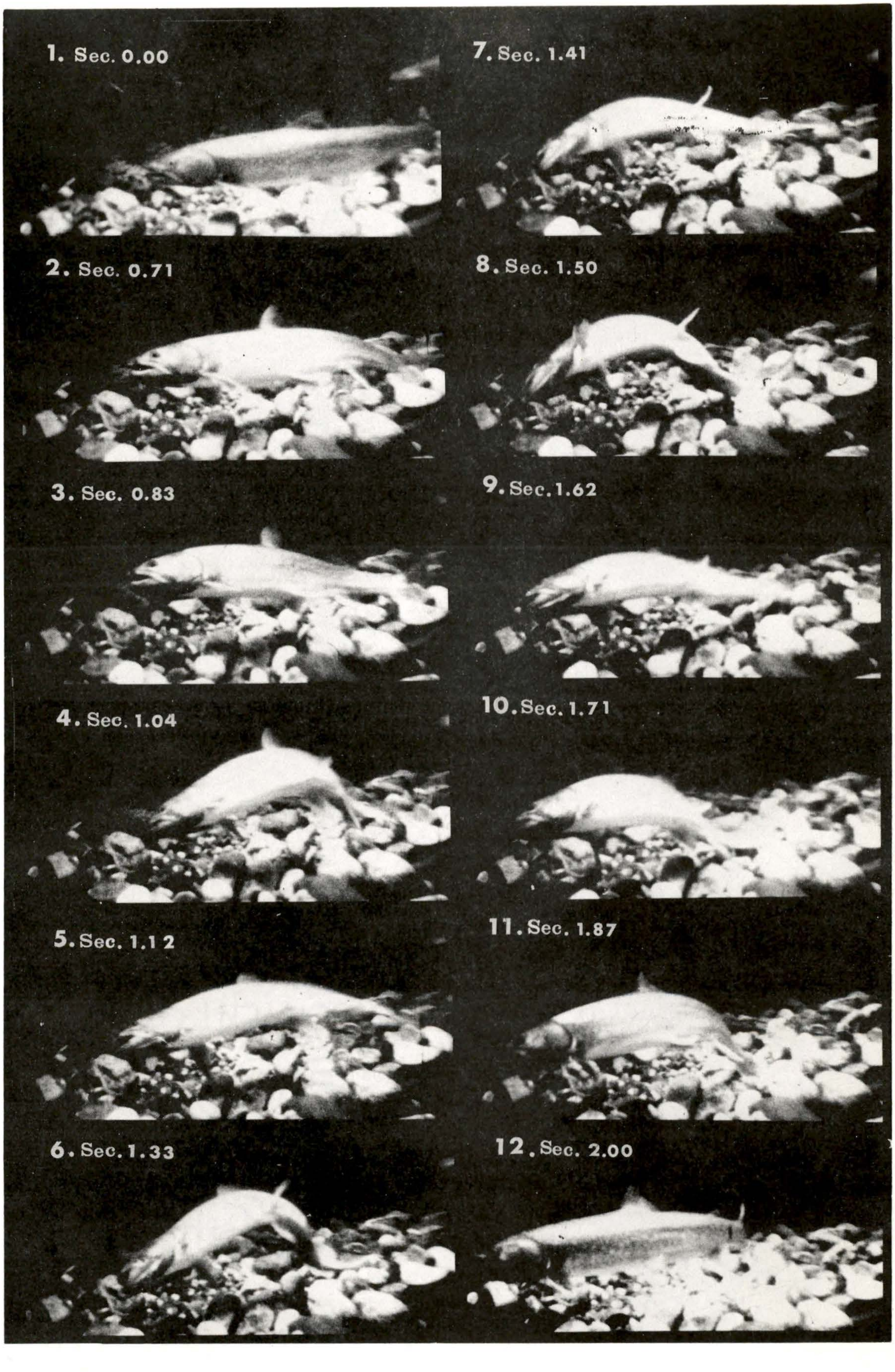
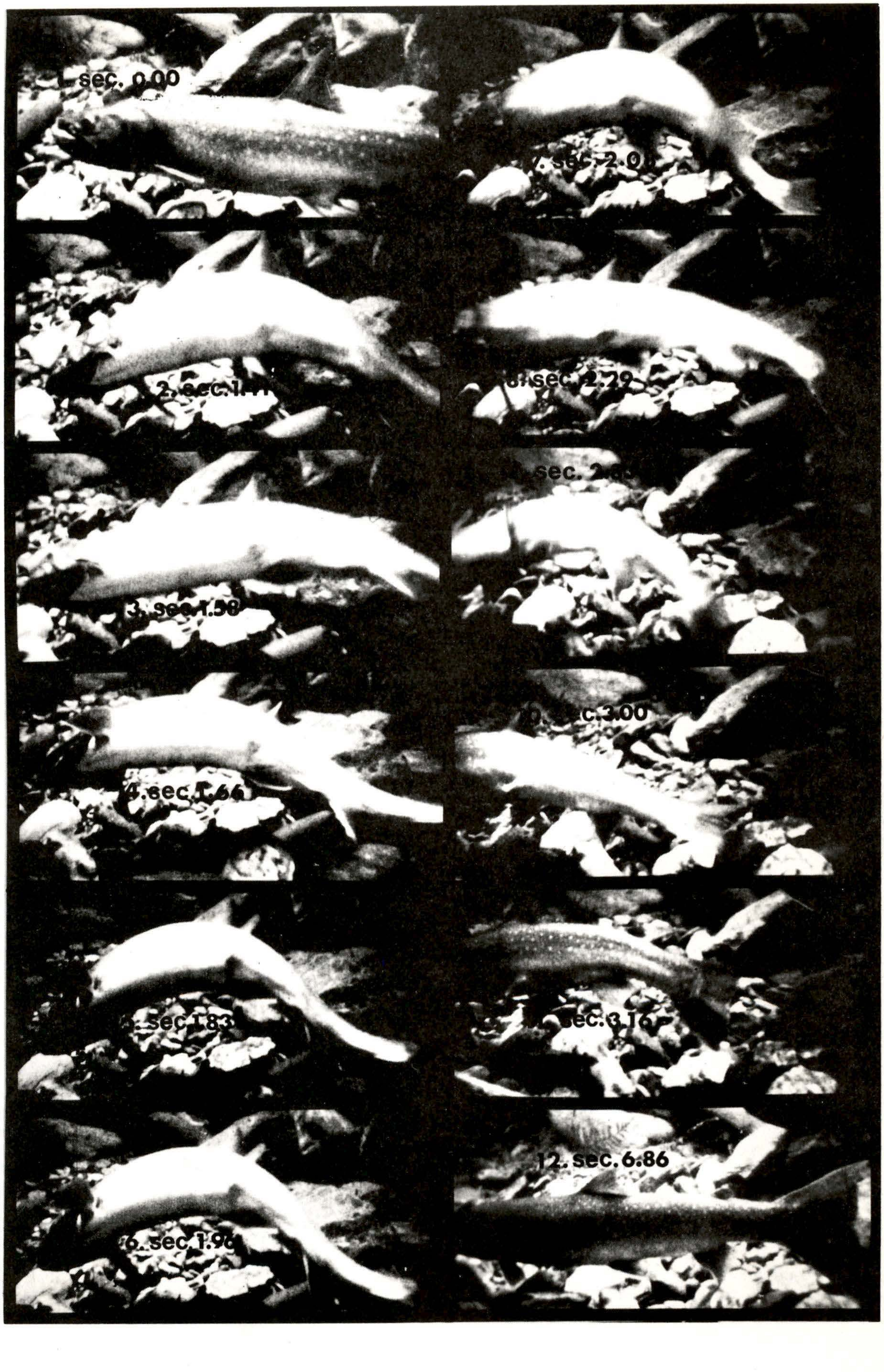

1. Sec. 0.00
2. Sec. 0.71
3. Sec. 0.83
4. Sec. 1.04
5. Sec. 1.12
6. Sec. 1.33
7. Sec. 1.41
8. Sec. 1.50
9. Sec. 1.62
10. Sec. 1.71
11. Sec. 1.87
12. Sec. 2.00

Figure 23. Sequence of pre-spawn digging movements (ventral view).



3. sec.1.58
6. sec.1.96
8. sec.2.29
12. sec. 6.86

Figure 24. Sequence of pre-spawn digging movements (dorsal view).


sec. 0.00
2. sec. 1.08
3. sec. 1.33
1.54
1.62
1.75
7. sec. 2.00
8. sec. 2.12
sec. 3.00
12. sec. 3.20

tail beat consisted of a complete bending and straightening of the body. Digging varied in quality from a series of weak listless tail beats to a series of strong rapid thrusts. The duration of 61 bouts analysed from projected film varied from 1.71 seconds to 3.67 seconds with a mean of 2.13 seconds. After a digging bout the female explored the substrate with the anal fin.

Figure 25 shows that the frequency of female digging per five minute observation peaks two to four hours before spawning and thereafter declines. Digging intensity (bout duration) of two females analysed from consecutively "filmed" observations before spawning showed no consistent temporal pattern (Fig. 26).

Fabricius and Gustafson (1953), Jones (1959) and Smith (1941) have observed similar digging behaviour including mouth opening and fin erection for the mountain char, Atlantic salmon, cutthroat and brook trout, respectively. Unlike the mountain char (Fabricius and Gustafson, 1953), there was no indication of eggs being liberated during digging movements of Dolly Varden and there was only one type of digging observed. This type appears to be much the same as that described for most salmonids. There was no indication of the "sweeping" digging movement described by Fabricius and Gustafson (1953). A stopped action movie analysis of the digging patterns indicated the digging of the Dolly Varden resembled the most frequently observed mode of digging described by Fabricius and Gustafson (1953). The Dolly Varden digging pattern appeared to differ slightly from

Figure 25. Frequency of female pre-spawn digging per five minute observation.

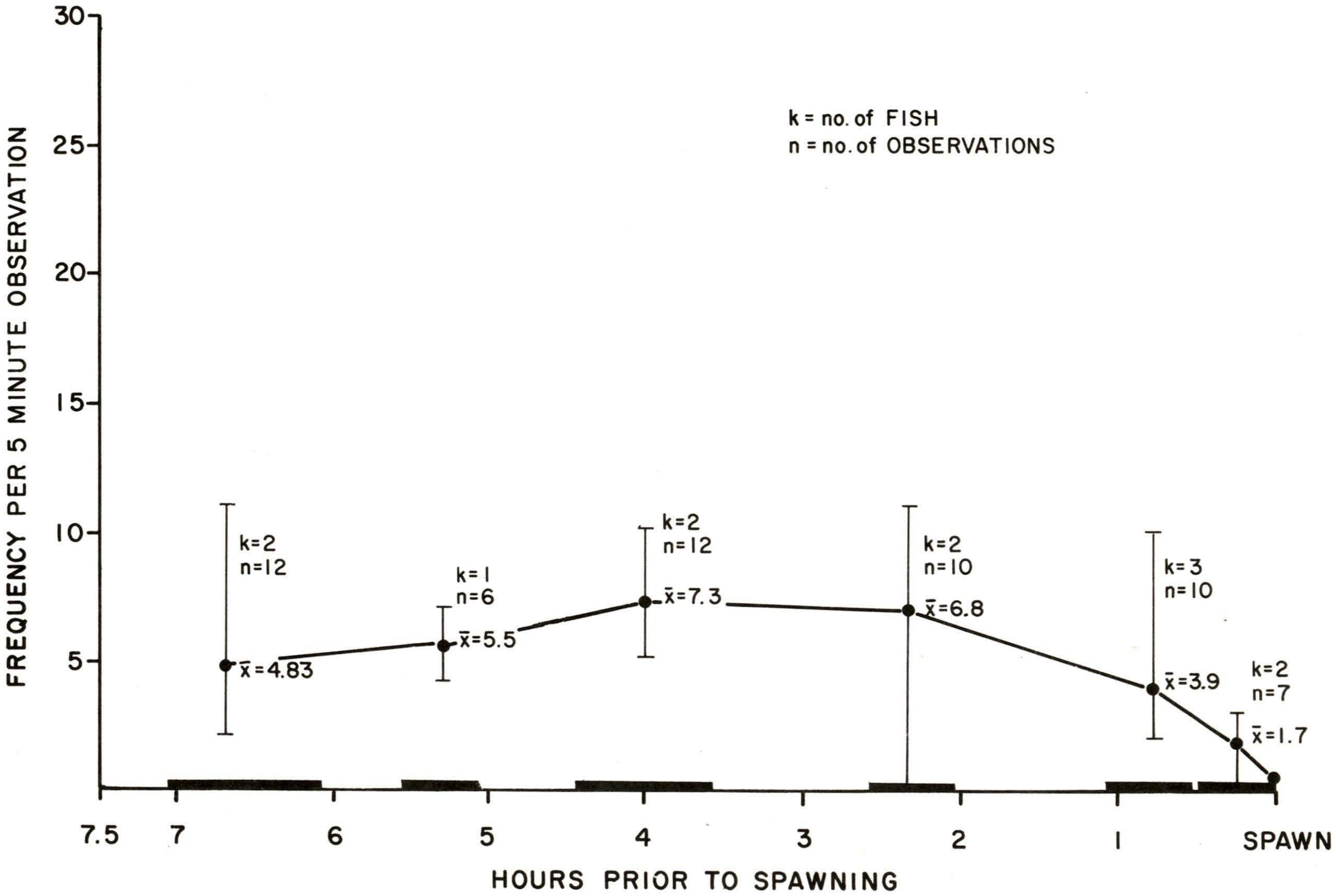
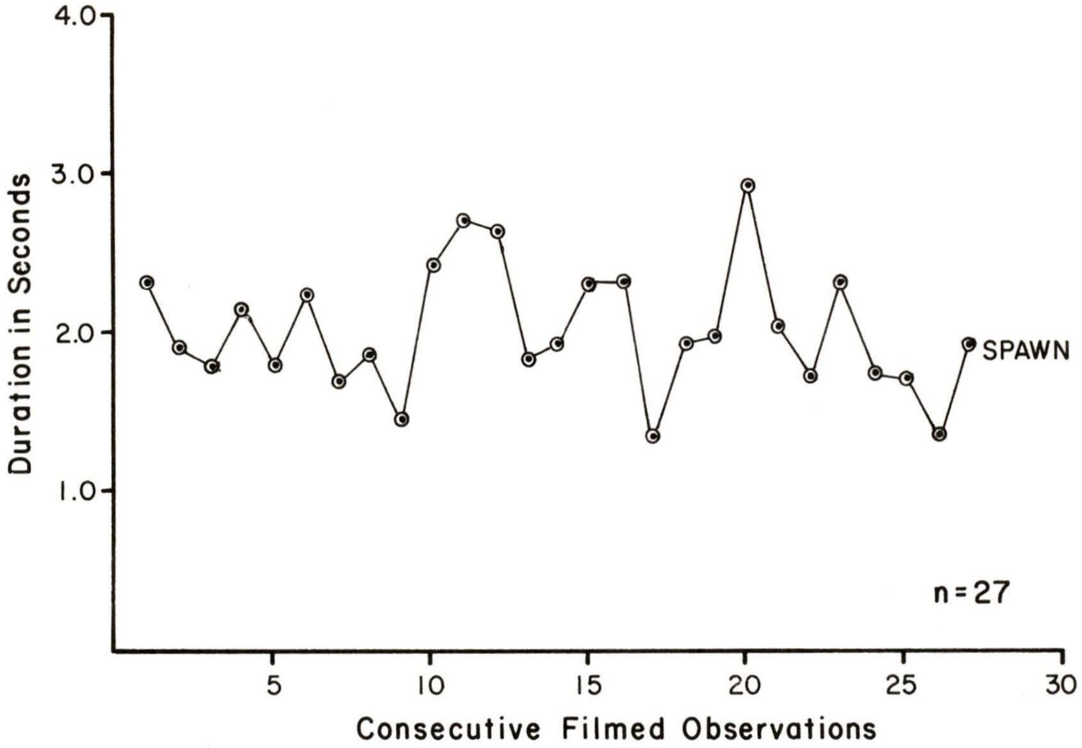
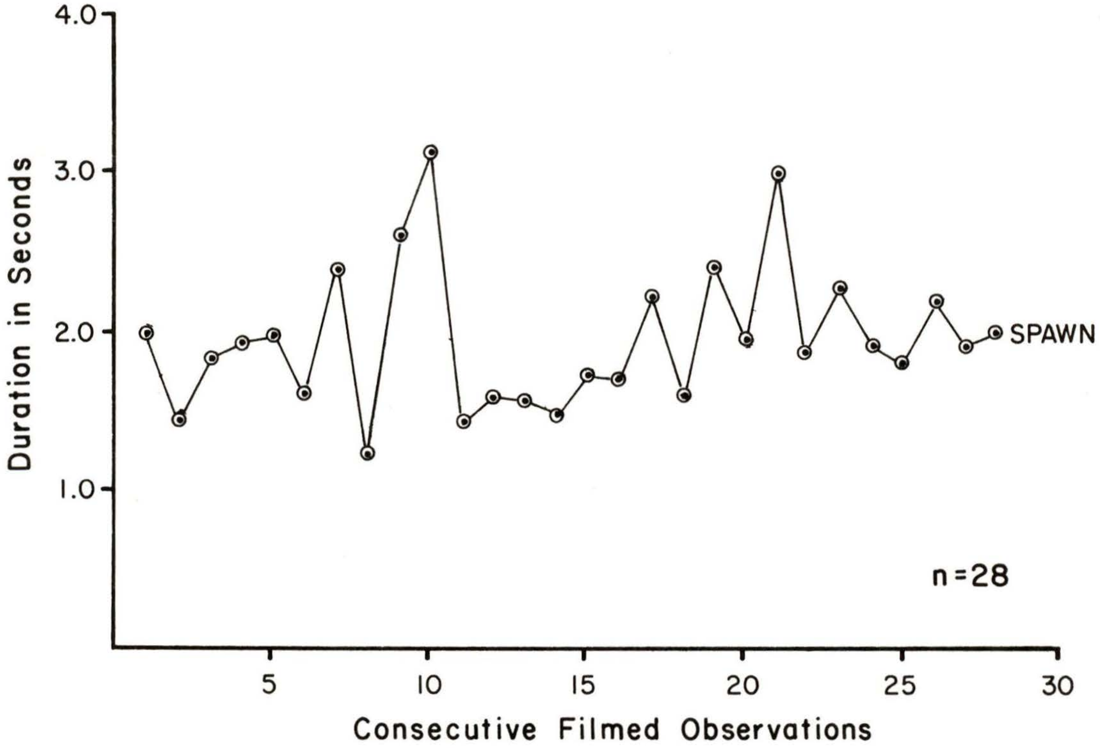

k = no. of FISH
n = no. of OBSERVATIONS
FREQUENCY PER 5 MINUTE OBSERVATION
30
25
20
15
10
5
k=2
n=12
x̄=4.83
k=1
n=6
x̄=5.5
k=2
n=12
x̄=7.3
k=2
n=10
x̄=6.8
k=3
n=10
x̄=3.9
k=2
n=7
x̄=1.7
7.5
7
6
5
4
3
2
1
SPAWN
HOURS PRIOR TO SPAWNING

Figure 26. Digging intensity of two females before spawning analysed from consecutively filmed observations.


4.0
3.0
2.0
1.0
Duration in Seconds
SPAWN
n=27
5
10
15
20
25
30
Consecutive Filmed Observations


4.0
3.0
2.0
1.0
Duration in Seconds
SPAWN
n=28
5
10
15
20
25
30
Consecutive Filmed Observations

the Atlantic salmon (Jones, 1959) in that the entire caudal region of the body was initially bent toward the gravelled substrate instead of only the caudal fin being rotated. The bending of the caudal region simultaneously pulled the tail forward. The head was bent in a direction away from the tail so that the body assumed an 'S' configuration.

Anal Fin Feeling (Fabricius, 1953; Jones and Ball, 1954; and Jones 1959 - Feeling)

The female, positioned close to the bottom of the nest, with the anal fin extended and touching the bottom substrate, moved her body gently from side to side. The anal fin and perhaps the paired pelvics and lower lobe of the caudal appeared to serve as tactile receptors for surveying the size and position of substrate materials in the nest site (Fig. 27). As it passed over the surface of a stone, the extended anal fin was compressed and after having passed over the obstruction suddenly became extended.

As the nest was deepened the female intensified her anal feeling by crouching. This posture was attained by raising the head and caudal region and pressing the mid section of the body snugly into the bottom of the nest with the extended anal fin almost completely hidden between the stones. The male responded to this activity by flanking or quivering. After a few moments, the female left the crouch position and continued to dig.

The mean frequency of anal fin feeling per five minute observation (n = 51) within eight hours of spawning was 6.94. During the two hours

Figure 27. Female feeling substrate with the anal fin.

prior to spawning there was an increased frequency. This increase coincided with an increase in male flanking (Fig. 28).

A similar type of anal feeling is described for other salmonids, the mountain char (Fabricius, 1953), the brown trout and salmon (Jones and Ball, 1954), the Atlantic salmon (Jones, 1959), the brook trout (S. fontinalis) and cutthroat trout (S. clarkii), (Smith, 1941).

Anchoring (Jones and Ball, 1954; Jones, 1959 - crouching)

At the moment of spawning the female maintained a prolonged crouch in the anal feeling position. This posture appeared to be the terminal signal to the male of the forthcoming spawning climax (Fig. 29). Jones (1959) states that among Atlantic salmon it is difficult to distinguish with certainty the crouch associated with feeling from the crouch which indicates the readiness for the orgasm. The same can be said of the Dolly Varden.

Male Courtship and Spawning

The elements of courtship and spawning included peduncle grasping, quivering, crossing-over, trembling, flanking and gamete release. The pattern for each of these activities consisted of the courting male approaching the female's flank and performing the courting activity at her side. Trembling deviated from this pattern in that it did not always occur close to the female's side. Courting was not always confined to the nest site and occasionally a male was observed courting two females at once.

Figure 28. Mean frequency trends of male flanking and female anal fin feeling before spawning.

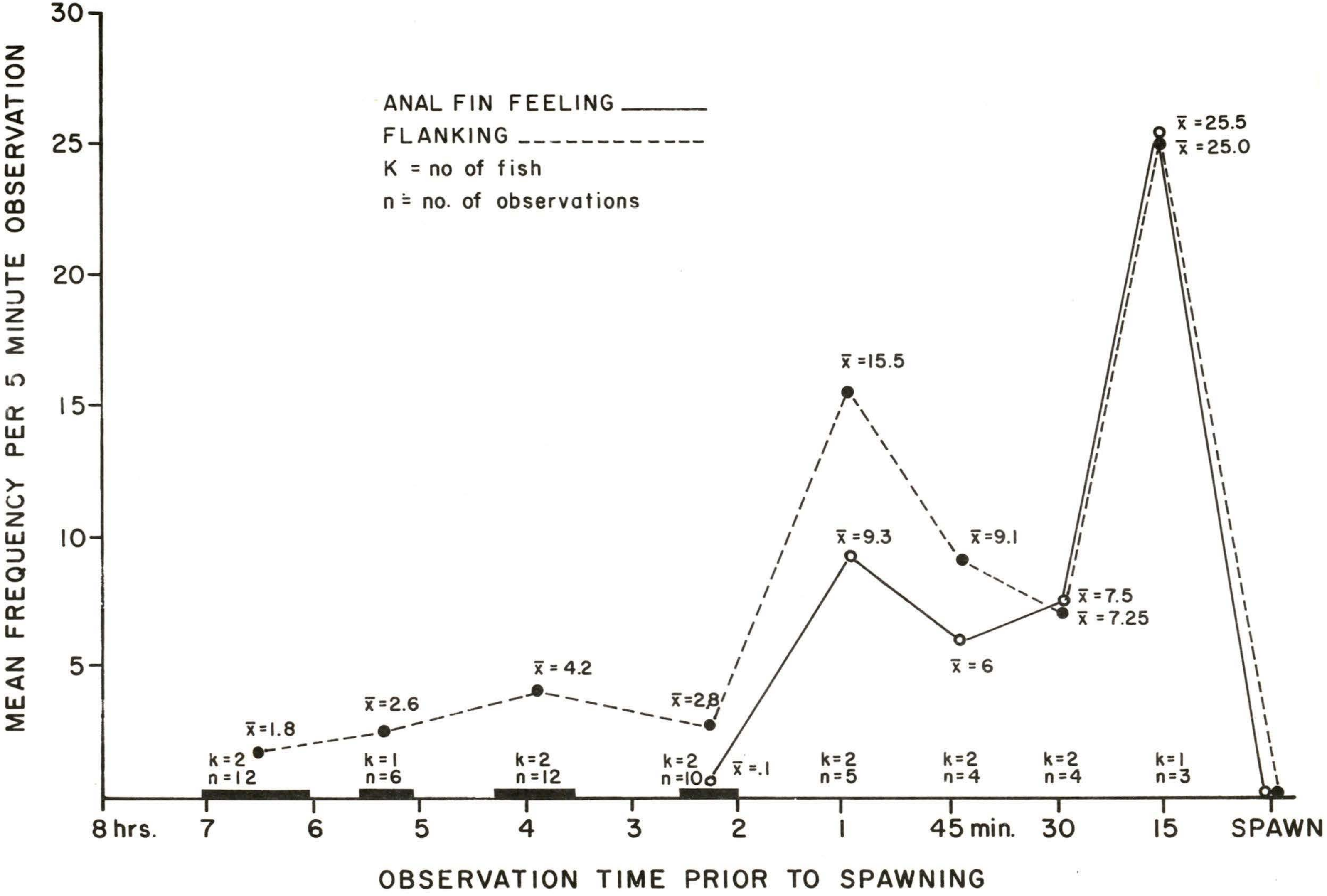

ANAL FIN FEELING
FLANKING
K = no of fish
n = no. of observations
MEAN FREQUENCY PER 5 MINUTE OBSERVATION
30
25
20
15
10
5
x̄ = 1.8
x̄ = 2.6
x̄ = 4.2
x̄ = 2.8
x̄ = .1
x̄ = 15.5
x̄ = 9.3
x̄ = 9.1
x̄ = 6
x̄ = 7.5
x̄ = 7.25
x̄ = 25.5
x̄ = 25.0
k = 2 n = 12
k = 1 n = 6
k = 2 n = 12
k = 2 n = 10
k = 2 n = 5
k = 2 n = 4
k = 2 n = 4
k = 1 n = 3
8 hrs.
7
6
5
4
3
2
1
45 min.
30
15
SPAWN
OBSERVATION TIME PRIOR TO SPAWNING

Figure 29. Female in anchored position just prior to spawning. Note also the large rocks in and around the redd.

Peduncle Grasping (Fabricius, 1953; Jones, 1959; Jones and Ball, 1954 - mentioned in passing)

Occasionally after a male had courted an inactive female for some time, he approached her with his mouth open, nipped her side or grasped her peduncle and shook her (Fig. 30). Typically the female responded to this activity by leaving the redd site. The male sometimes grasped the peduncle in his jaws again and dragged her back to the courting site.

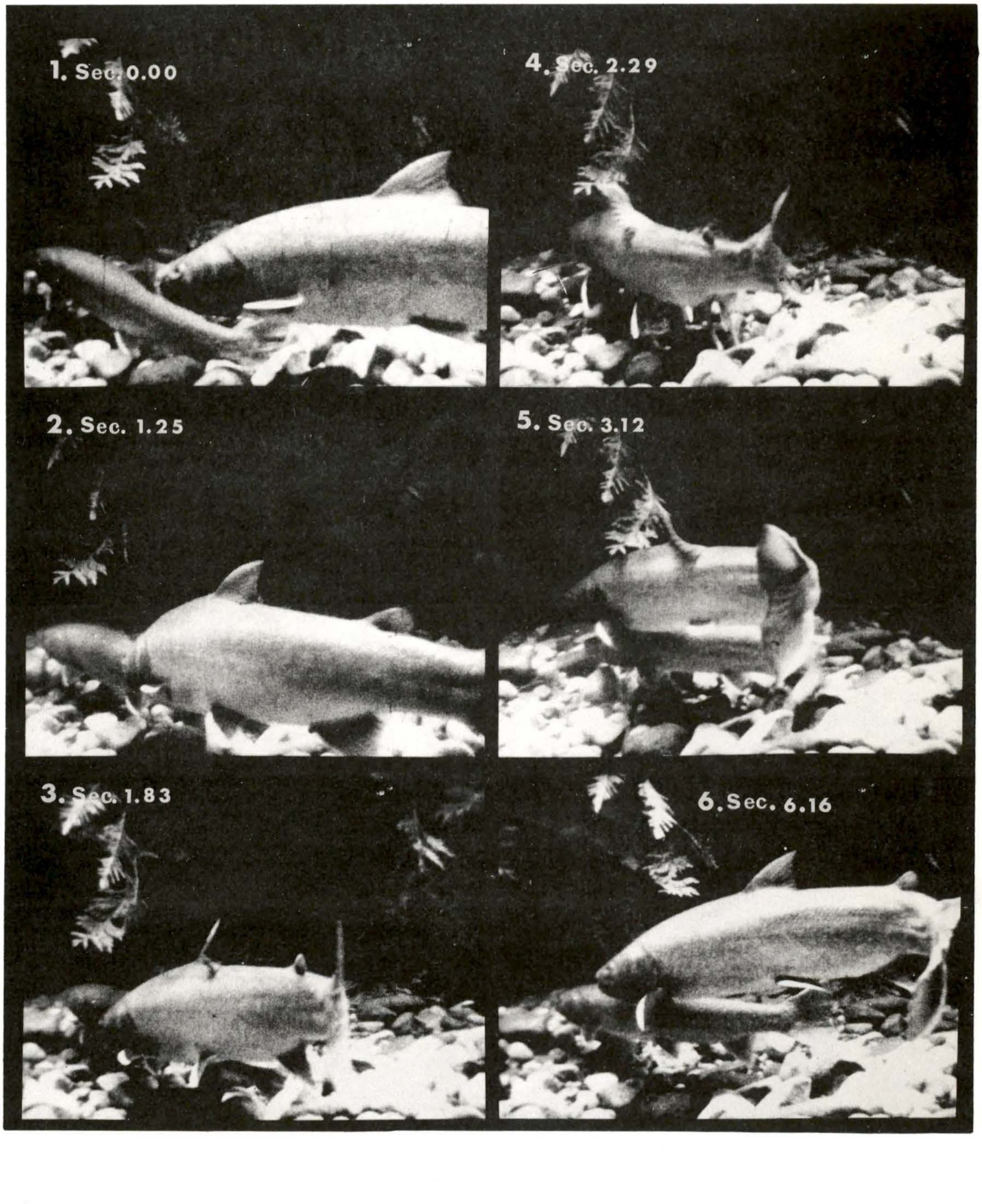
The Atlantic salmon according to Jones (1959) also bites inactive females. Blackett (1958) on the otherhand, implies that on several occasions male Dolly Varden were observed to grasp the peduncle region of other males for four to six seconds.

(Vibrating)
Quivering (Fabricius, 1953; Fabricius and Gustafson, 1953 - trembling)

This activity was characteristic of male courting behaviour (Fig. 31). Normally the male approached the female from the rear. When the head neared the middle of the female's body, the male began to quiver vigorously in a horizontal low amplitude movement of high frequency. The movement sometimes began before the male was beside the female and sometimes continued while he retreated back to a position behind her. It was occasionally observed to occur while the male was in a position directly above or while crossing-over the female. The fins were held partly erect during the act and periodically the mouth was slightly opened. The actual quivering movement appeared to begin in the male's head region and moved rapidly to the caudal region. The body became tense and the connective

Figure 30. Male grasping the peduncle of the female.

Figure 31. Sequence of courting male quivering to female.


1. Sec. 0.00
2. Sec. 1.25
3. Sec. 1.83
4. Sec. 2.29
5. Sec. 3.12
6. Sec. 6.16

tissue, (myocommata) separating the successive muscle segments (myomeres) became clearly visible. The amplitude of the oscillation appeared to be greater in the head region than in the caudal region.

On one occasion a smaller male was observed quivering to a larger male shortly after the latter had been introduced into the aquarium.

Quivering showed a temporal pattern of low frequency over a number of days prior to the first spawning act and a marked increase during the day of spawning (Fig. 32). This is in agreement with observations for the Atlantic salmon (Jones, 1959). An analysis of consecutive filmed observations of two males prior to spawning showed no consistent trend in quivering intensity (bout duration) (Fig. 33). For the Atlantic salmon, Jones (1959) mentions an increase in the intensity (not quantified) of quivering up to the time of orgasm which is at variance from the above observations. The duration of quivering bouts (n = 74) was observed to range from 0.5 seconds to 3.9 seconds with a mean of 1.82 seconds. The mean bout duration of male quivering when courting a digging female was 1.96 seconds and that not associated with female digging was 1.50 seconds, a difference significant at the 0.05 level (Appendix V).

Crossing-Over

After courting (quivering or flanking) the female on one side the male sometimes rose above her, crossed-over, and began courting her on the other side (Fig. 34). Occasionally the male back-peddled behind the female after attending her on one side then approached her on the other

Figure 32. Quivering frequency of a single male to several females over a number of days prior to the first spawning act.

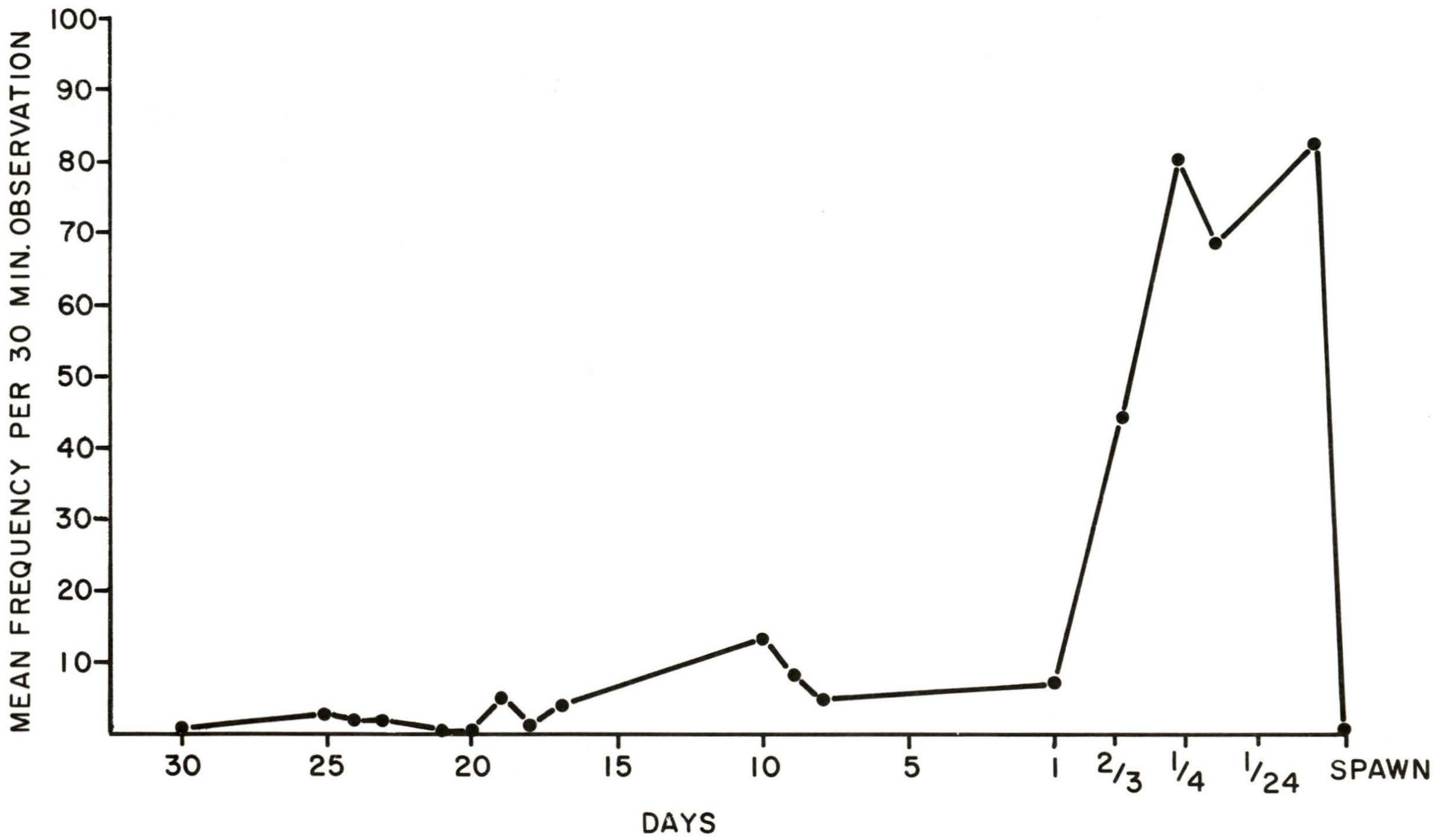
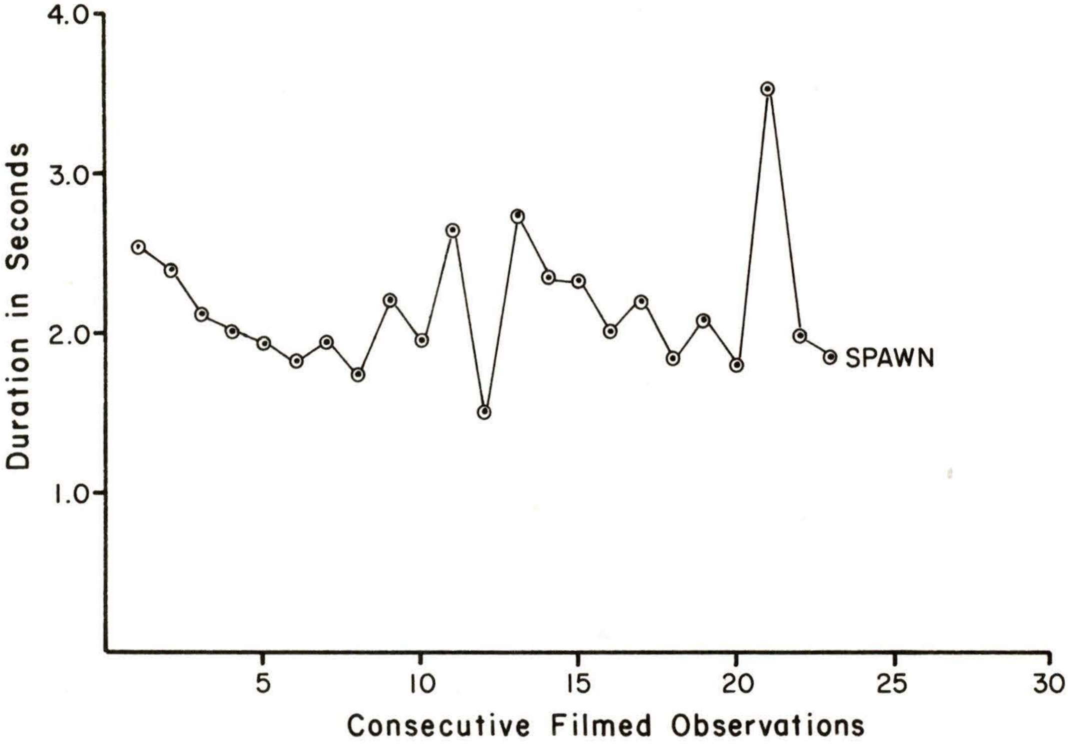

MEAN FREQUENCY PER 30 MIN. OBSERVATION
100
90
80
70
60
50
40
30
20
10
30
25
20
15
10
5
1
2/3
1/4
1/24
SPAWN
DAYS

Figure 33. Quivering intensity (bout duration) of two males prior to spawning. Note very low bout durations usually coincided with interruptions caused by intruders.


4.0
3.0
2.0
1.0
Duration in Seconds
SPAWN
5
10
15
20
25
30
Consecutive Filmed Observations

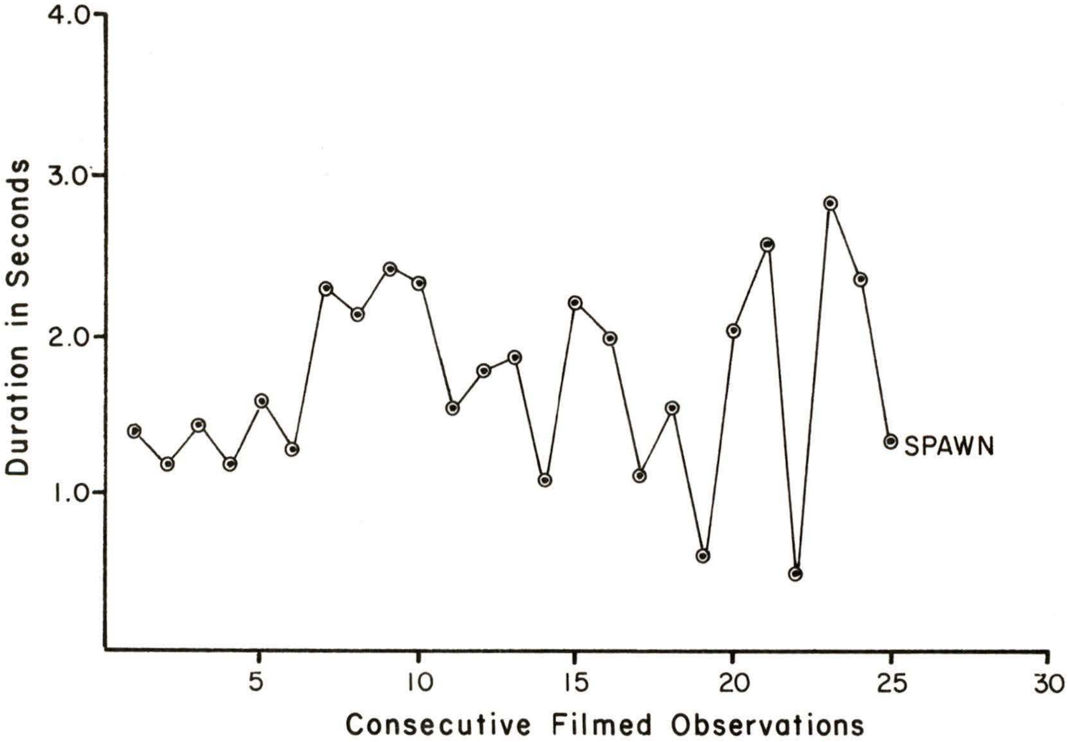
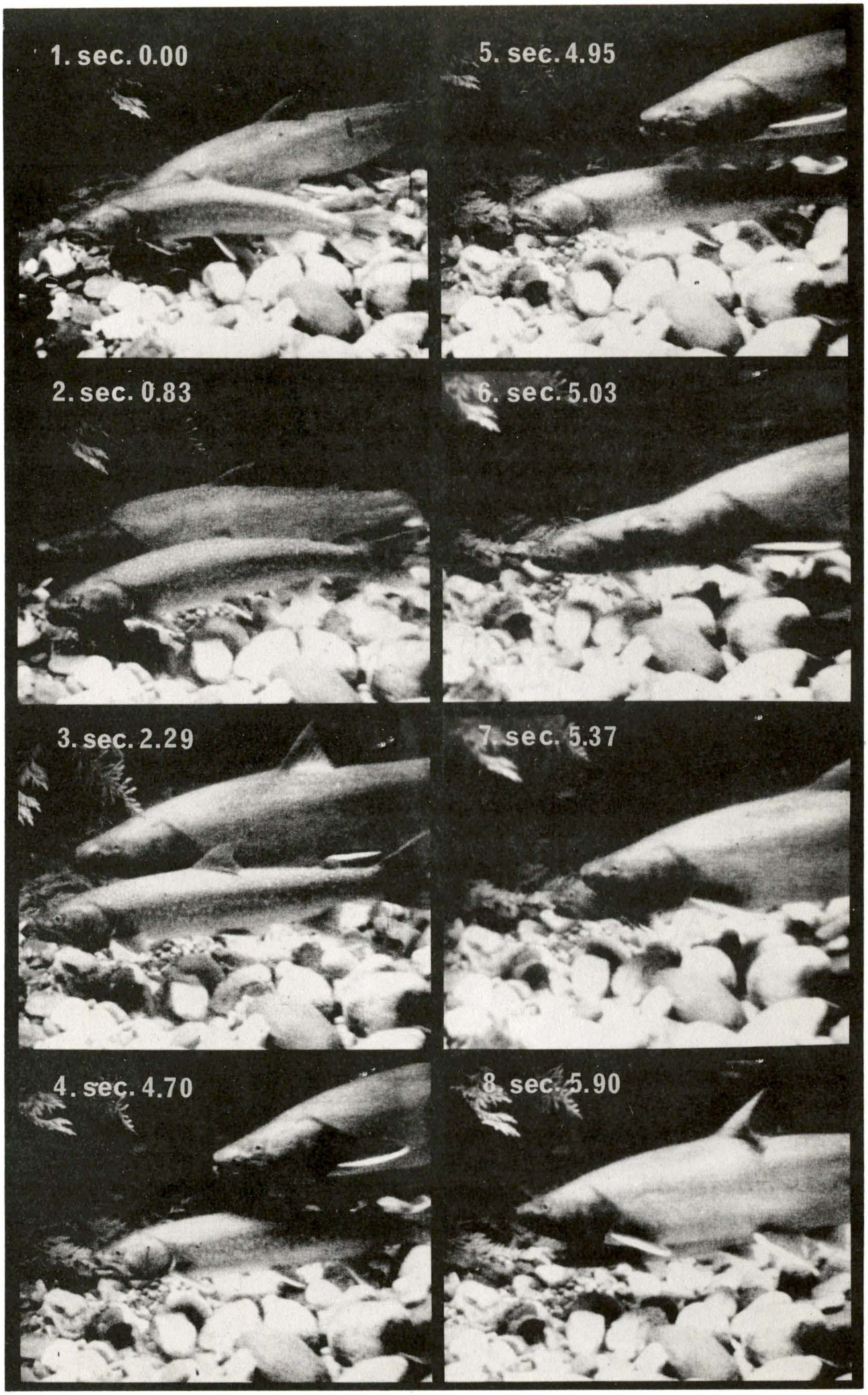

4.0
3.0
2.0
1.0
Duration in Seconds
SPAWN
5
10
15
20
25
30
Consecutive Filmed Observations

Figure 34. Sequence of courting (quivering) male crossing-over the female.


1. sec. 0.00
2. sec. 0.83
3. sec. 2.29
4. sec. 4.70
5. sec. 4.95
6. sec. 5.03
7. sec. 5.37
8. sec. 5.90

without crossing-over. Figure 35 shows the mean frequency of male crossing-over per five minute observation during the period of eight hours to spawning.

Crossing-over during pre-spawn courting appears to be common among the Gerrard rainbow trout (Hartman, 1969).

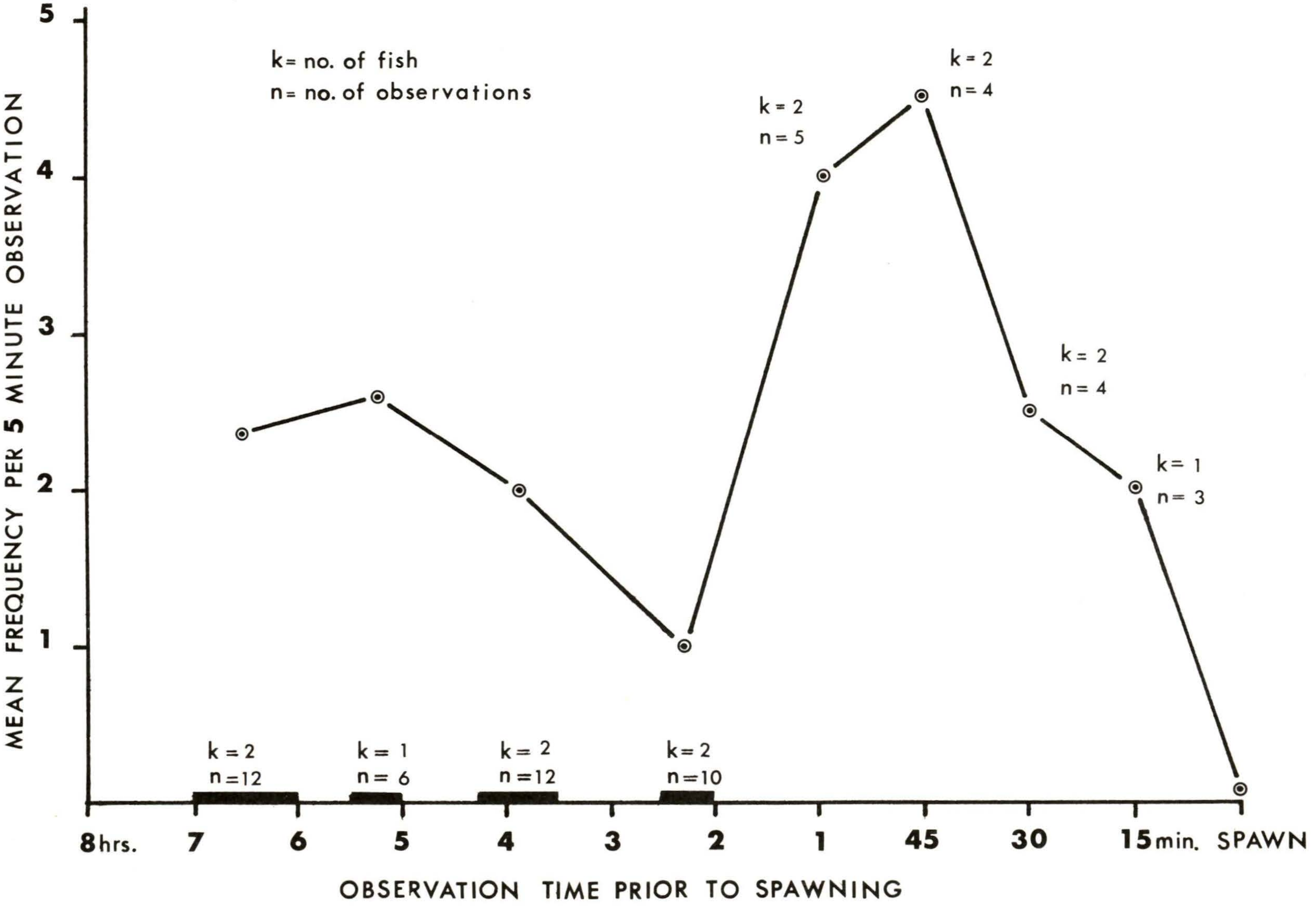
Trembling (Fabricius, 1953; Jones, 1959 - both used in another context)

The male trembled in a position beside and slightly behind the female. In contrast to quivering, trembling consisted of a low frequency, high amplitude lateral movement with the greatest amplitude in the head region. With the fins fully extended, the male raised his head so that the snout angled upward, and with the mouth open he began a spasmotic shudder, combined with a yawning and pitching movement. The opercula were repeatedly opened and closed during a trembling bout and their movements coincided with the opening and closing of the mouth. The gills were visible during the flexing of the opercula (Fig. 36).

This activity was observed to occur infrequently within two hours of spawning and as often as two or three times subsequent to the spawning act. The duration of two trembling bouts (n = 2) were 0.5 and 2.33 seconds.

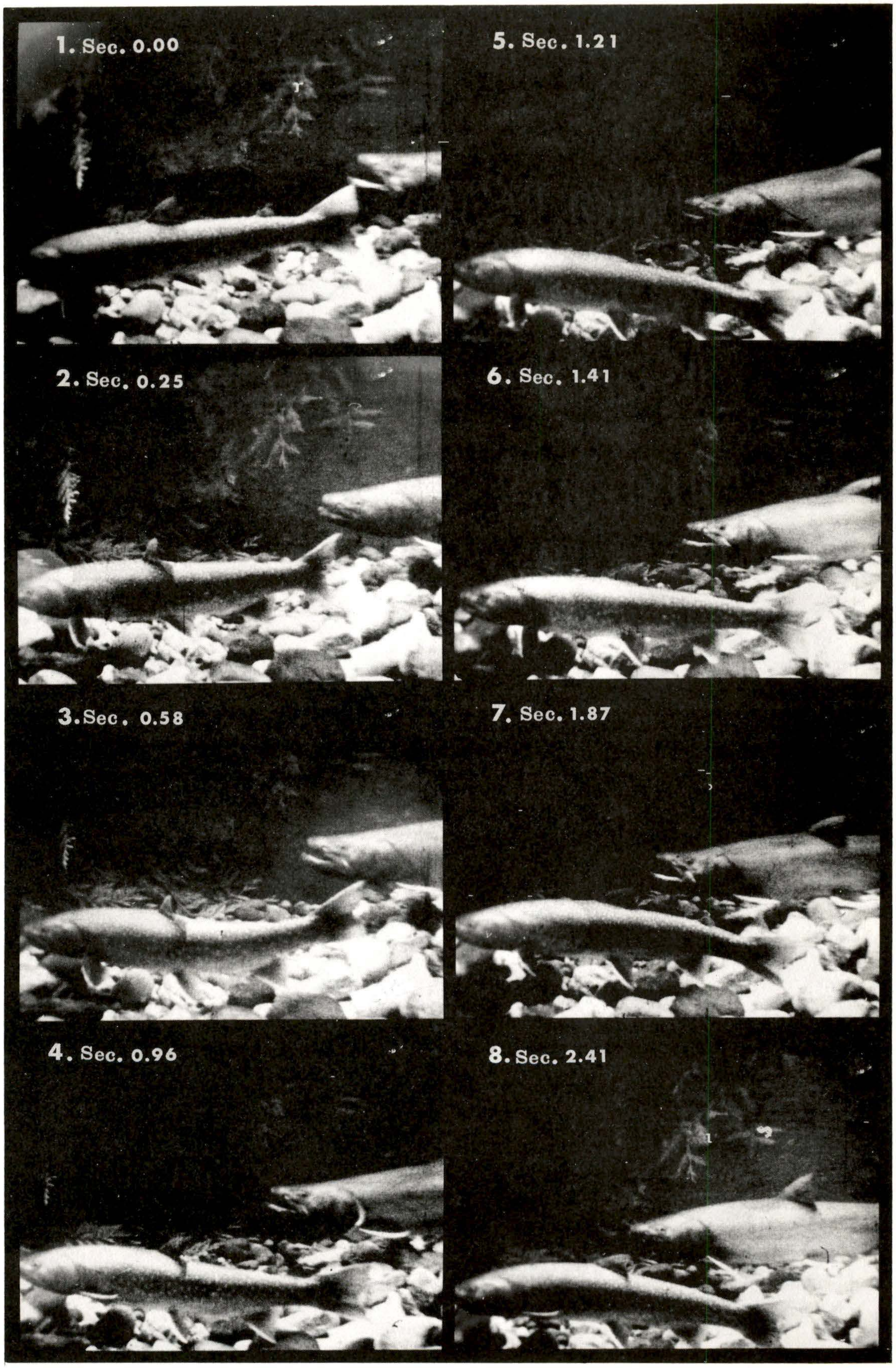
There is no description of this type of activity in the available literature on other spawning salmonids.

Figure 35. Mean frequency of crossing-over during the hours before spawning.



k= no. of fish
n= no. of observations
MEAN FREQUENCY PER 5 MINUTE OBSERVATION
5
4
3
2
1
k = 2
n =12
k = 1
n = 6
k = 2
n =12
k=2
n=10
k = 2
n = 5
k = 2
n = 4
k = 2
n = 4
k = 1
n = 3
8hrs.
7
6
5
4
3
2
1
45
30
15min.
SPAWN
OBSERVATION TIME PRIOR TO SPAWNING

Figure 36. Sequential bout of trembling.


1. Sec. 0.00
5. Sec. 1.21
2. Sec. 0.25
6. Sec. 1.41
3. Sec. 0.58
7. Sec. 1.87
4. Sec. 0.96
8. Sec. 2.41

Flanking (Fabricius, 1953 - gliding)

Just prior to spawning the male became very attentive to the female. When the female crouched in the redd or began to feel the bottom of the redd with her anal fin, the male moved alongside her in much the same fashion as when quivering (Fig. 37). The approach was usually made from above and behind. The male moved his body alongside the female occasionally making contact. After a brief pause in this position, he back-peddled with the pectoral and pelvic fins to a position above and behind the female.

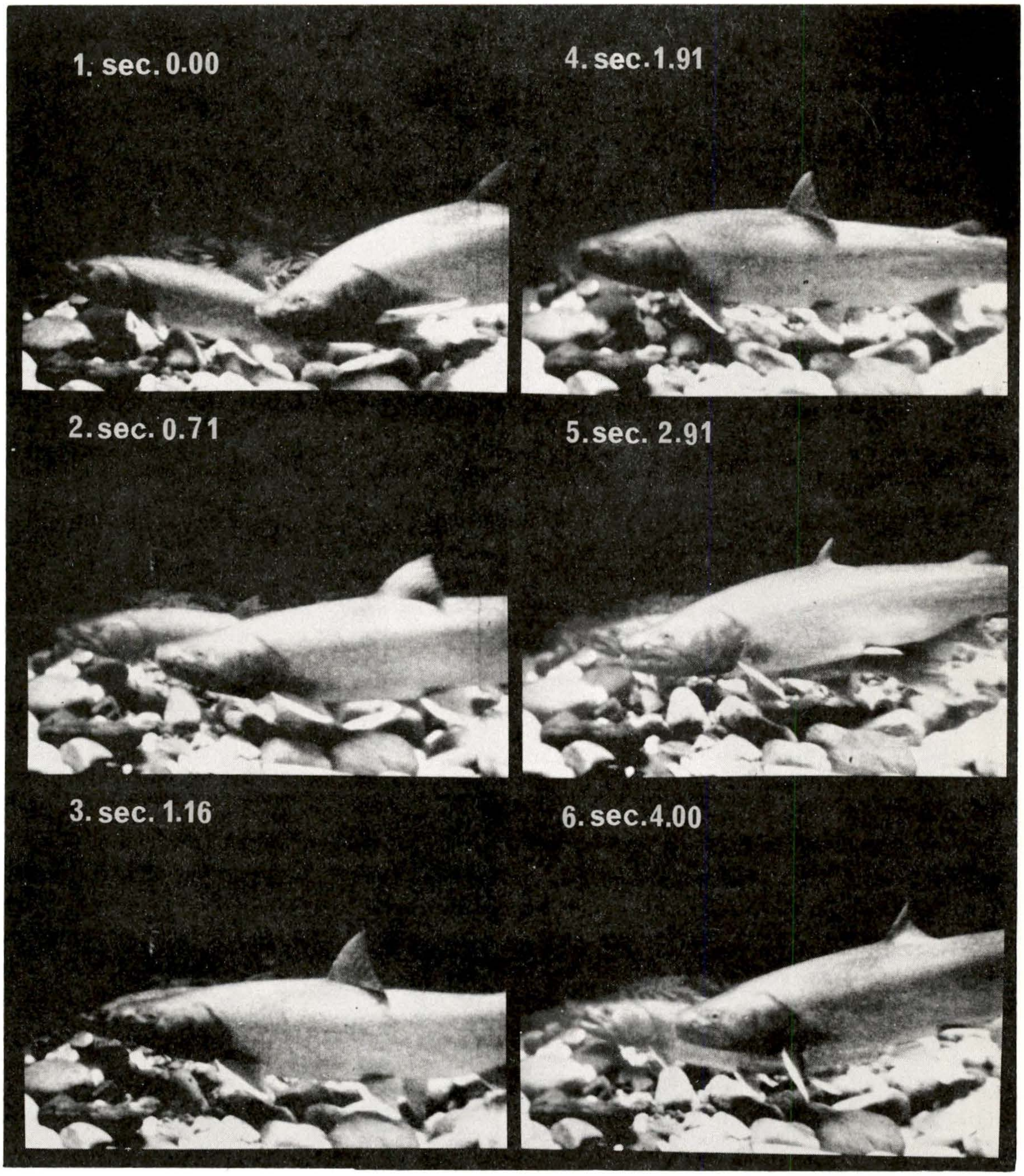
The mean bout frequency of flanking per five minute observation during the one hour period prior to spawning was 10.94. First indications of flanking occurred two hours before spawning. Figure 38 shows that as flanking frequency increased there was a decrease in quivering during the two hours preceeding spawning.

Fabricius (1953) refers to flanking as gliding or a low intensity quiver and maintains that if the fish is observed closely, a slight undulating movement in the lateral musculature can sometimes be seen. Jones (1954) states that the male Atlantic salmon becomes extremely attentive to the female prior to spawning and attends the female at each crouch and quivers vigorously.

Shedding of Gametes (Jones, 1959 - orgasm; Fabricius, 1953 - spawning act)

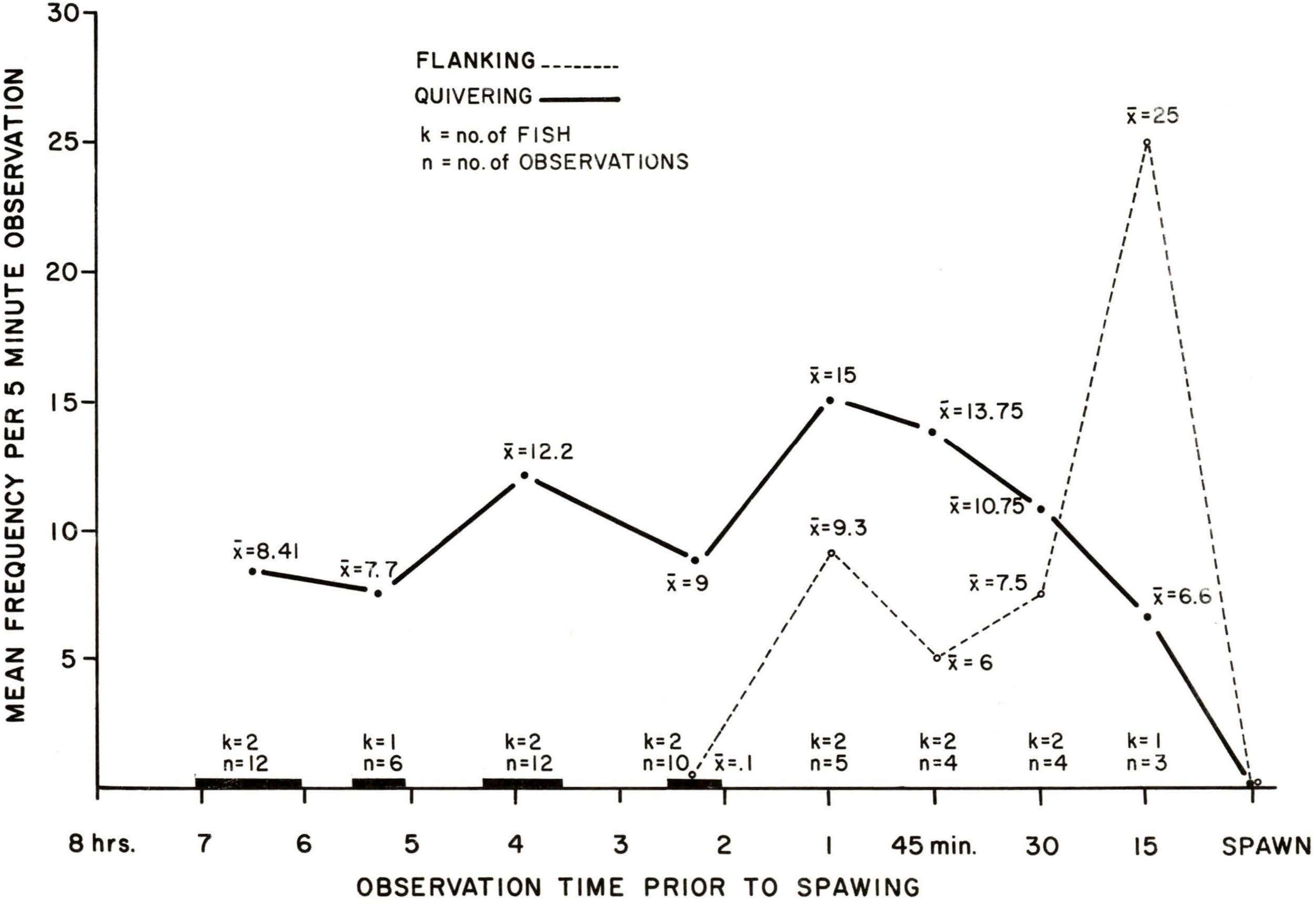
The female opened her mouth wide and gaped in the anchored position

Figure 37. Sequence of male flanking to the female.



1. sec. 0.00
4. sec. 1.91
2. sec. 0.71
5. sec. 2.91
3. sec. 1.16
6. sec. 4.00

Figure 38. Mean frequency of flanking and quivering during the hours before spawning.

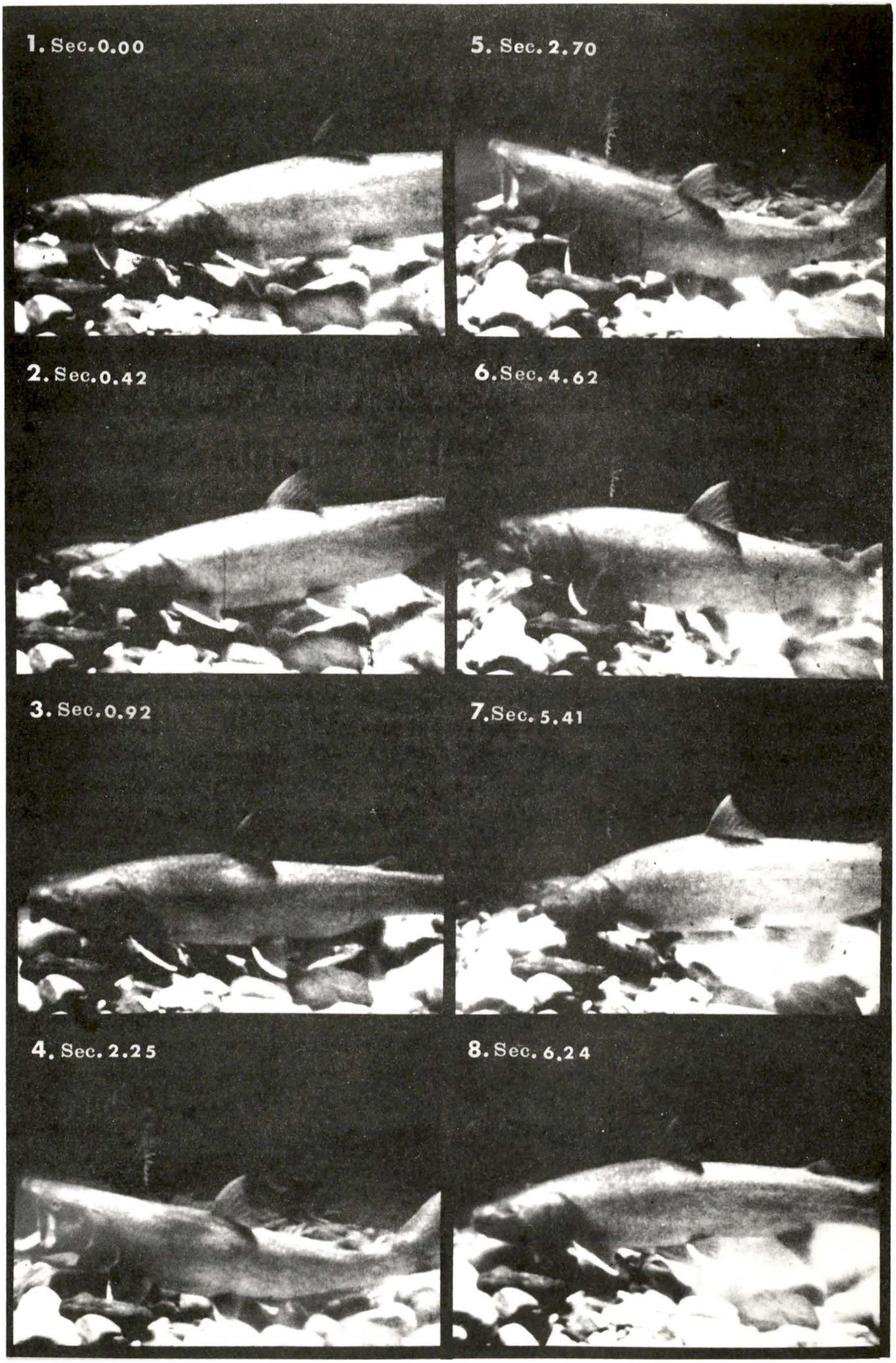

FLANKING
QUIVERING
k = no. of FISH
n = no. of OBSERVATIONS
MEAN FREQUENCY PER 5 MINUTE OBSERVATION
30
25
20
15
10
5
x̄=8.41
x̄=7.7
x̄=12.2
x̄=9
x̄=15
x̄=13.75
x̄=10.75
x̄=6.6
x̄=9.3
x̄=6
x̄=7.5
x̄=25
x̄=.1
k=2 n=12
k=1 n=6
k=2 n=12
k=2 n=10
k=2 n=5
k=2 n=4
k=2 n=4
k=1 n=3
8 hrs.
7
6
5
4
3
2
1
45 min.
30
15
SPAWN
OBSERVATION TIME PRIOR TO SPAWING

The male responded to the female by immediately moving to her flank so that their heads were adjacent. Quickly anchoring himself, the male tilted his body toward the female and with fins erect he too opened his mouth and gaped (Fig. 39). Quivering violently the pair shed their gametes simultaneously. The duration of three filmed orgasms ranged from seven to eight seconds (mean = 7.6 sec.).

Dolly Varden appeared to differ from certain other species in that the spawning act sometimes included a number of orgasms before the female began to cover the eggs. On one occasion a female was observed to perform two successive orgasms. In this instance the total duration of the spawning act was 33 seconds (the first orgasm 8 seconds, an 18 second pause, second orgasm 7 seconds). Not more than two spawning acts per individual were observed to occur although it was quite possible that a larger number occurred as observations were intermittent and confined primarily to daylight hours.

Needham and Vaughan (1952) in their description of the spawning of a pair of Dolly Varden at Twin Creek, Idaho, noted that the spawning act consisted of two orgasms. The first lasted approximately two seconds and after an interval of about 10 seconds the second act lasted for a period of five seconds. Milt was observed on both occasions but no eggs were sighted which might be due to the angle from which the observations were made. Fabricius and Gustafson (1953) have observed in the mountain char as many as one to five orgasms in a series during a spawning act (mean 1.9). Blackett (1958) refers to the spawning act for anadromous Dolly Varden as

Figure 39. Sequential movements during the spawning act.


1. Sec. 0.00
5. Sec. 2.70
2. Sec. 0.42
6. Sec. 4.62
3. Sec. 0.92
7. Sec. 5.41
4. Sec. 2.25
8. Sec. 6.24

"body pressing". Body pressing involved one or more males pressing against the side of the female with the vents of the fish in close proximity. During a bout of body pressing both male and female were reported to quiver violently. Body pressing lasted for periods of one to five seconds and the frequency ranged from two to nine body presses per pair of fish. On one occasion as many as nine presses were recorded in thirty seconds. Smith (1949) in his description of brook trout reports only one orgasm per spawning act.

Post-Spawn Behaviour

The post-spawn behaviour of the Dolly Varden appeared to differ from most salmonid species in that the female did not cover the eggs immediately. Instead she began an undulating movement directly over the eggs. This movement gradually changed to a digging movement. Both activities occurred for a time until the characteristic post-spawn digging motion alone was employed. The male remained with the female during her post-spawn activities and defended the site from intruders, after which he began to court her again. He eventually left the female if she did not respond to his courting. Spent females were observed to remain at the nest site for as long as two days after spawning.

Undulating Movement (Fabricius and Gustafson, 1953)

Unlike salmon and trout, Dolly Varden females did not immediately cover the eggs after spawning. Instead they began a continuous rhythmic and slow snake-like undulating movement, dragging the pelvic, caudal and anal fin over the area where the eggs had been deposited (Figs. 40 and 41). The eyes protruded from the head and appeared to focus on the nest site where the eggs had been deposited. The mouth was continually opened and closed. The extended pectoral fins appeared to stabilize the body during this undulating movement. As a result of this movement the eggs on the surface substrate were swept into the crevices between the stones into the bottom of the redd. Smaller pebbles and sand displaced by this movement were swept into the crevices over the eggs.

Undulating bouts were recorded for 17, 27 and 56 minutes after spawning before any post-spawn digging. Indications of undulating movements were observed two hours or more after spawning.

Undulating movements have been observed in the eastern brook trout (Smith, 1941), the non-anadromous Dolly Varden (Needham and Vaughan, 1952) and the mountain char (Fabricius and Gustafson, 1953) but have not been described for other species of salmonids. Blackett (1968) makes no reference to this type of post-spawning activity for the anadromous Dolly Varden. For the brook trout (Smith, 1941), the duration of two bouts of undulating movement before any post-spawn digging were recorded for 52 and 37 minutes, respectively. Fabricius and Gustafson (1953) indicate that the duration of this movement for the mountain char in Sweden varied from 1 to 48 minutes (k = 12) and mean duration was slightly in excess of 12 minutes.

Figure 40. Sequence of female post-spawn undulating behaviour.

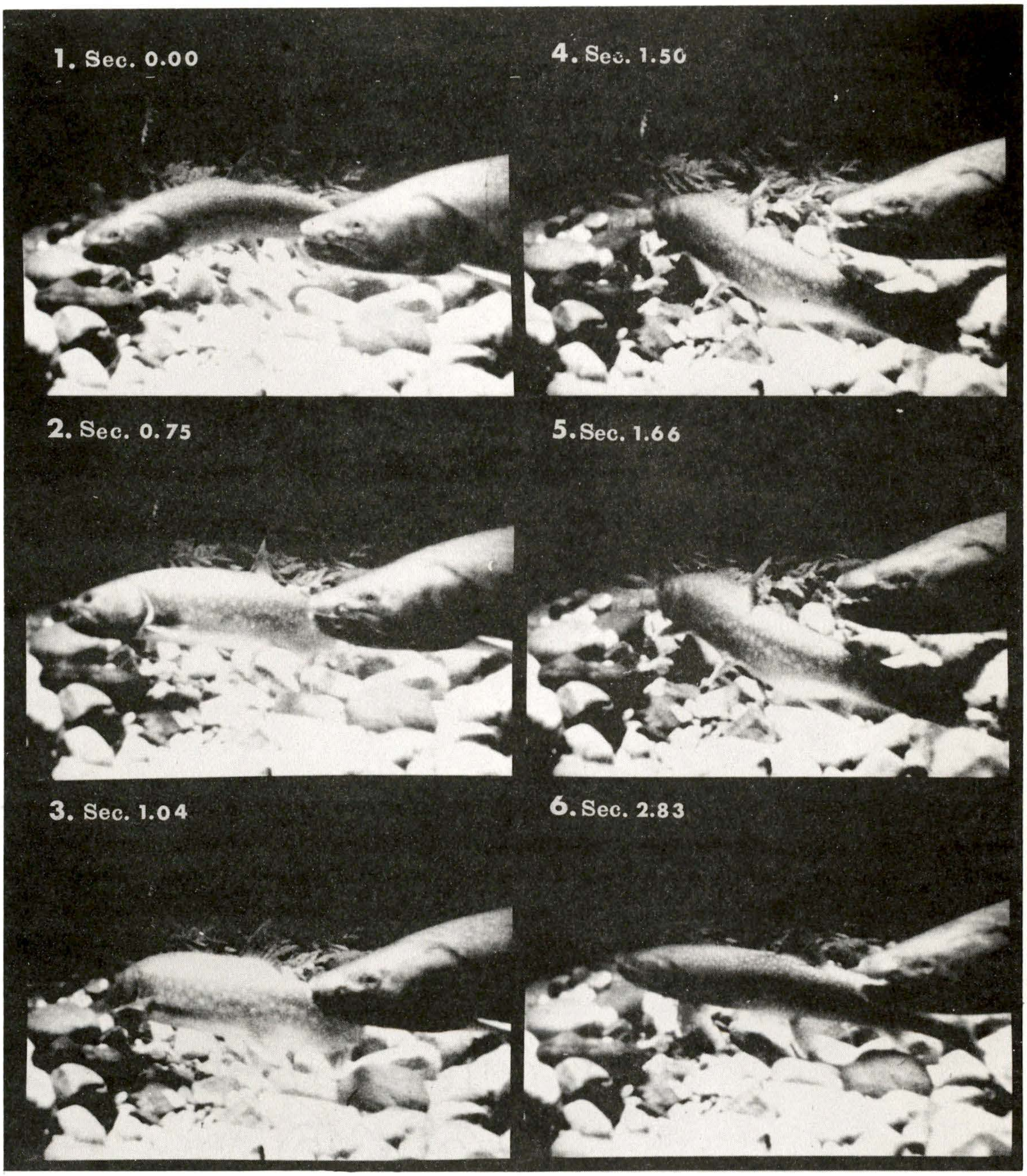
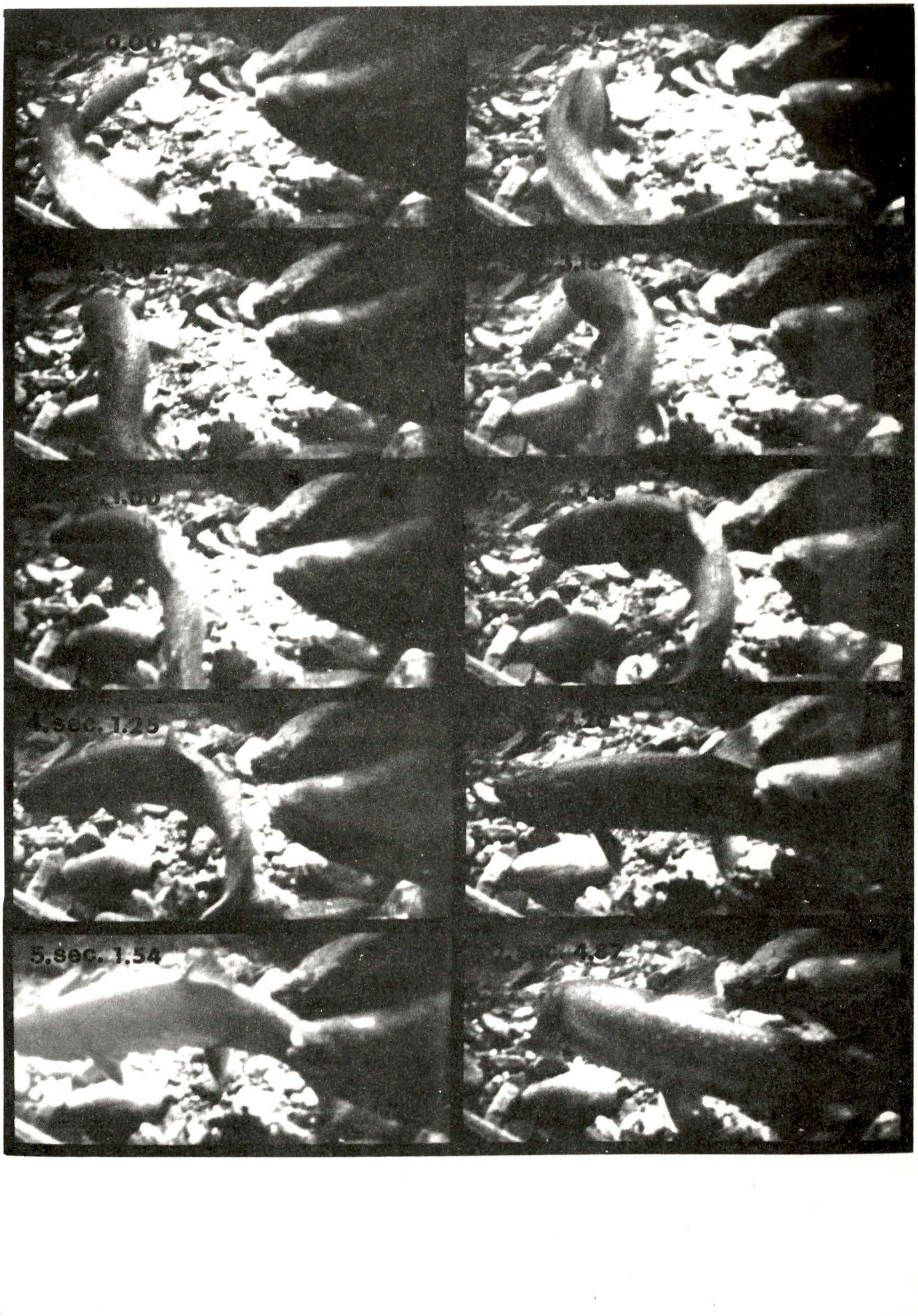

1. Sec. 0.00
4. Sec. 1.50
2. Sec. 0.75
5. Sec. 1.66
3. Sec. 1.04
6. Sec. 2.83

Figure 41. Sequence of female post-spawn undulating behaviour.


4.sec. 1.25
5.sec. 1.54

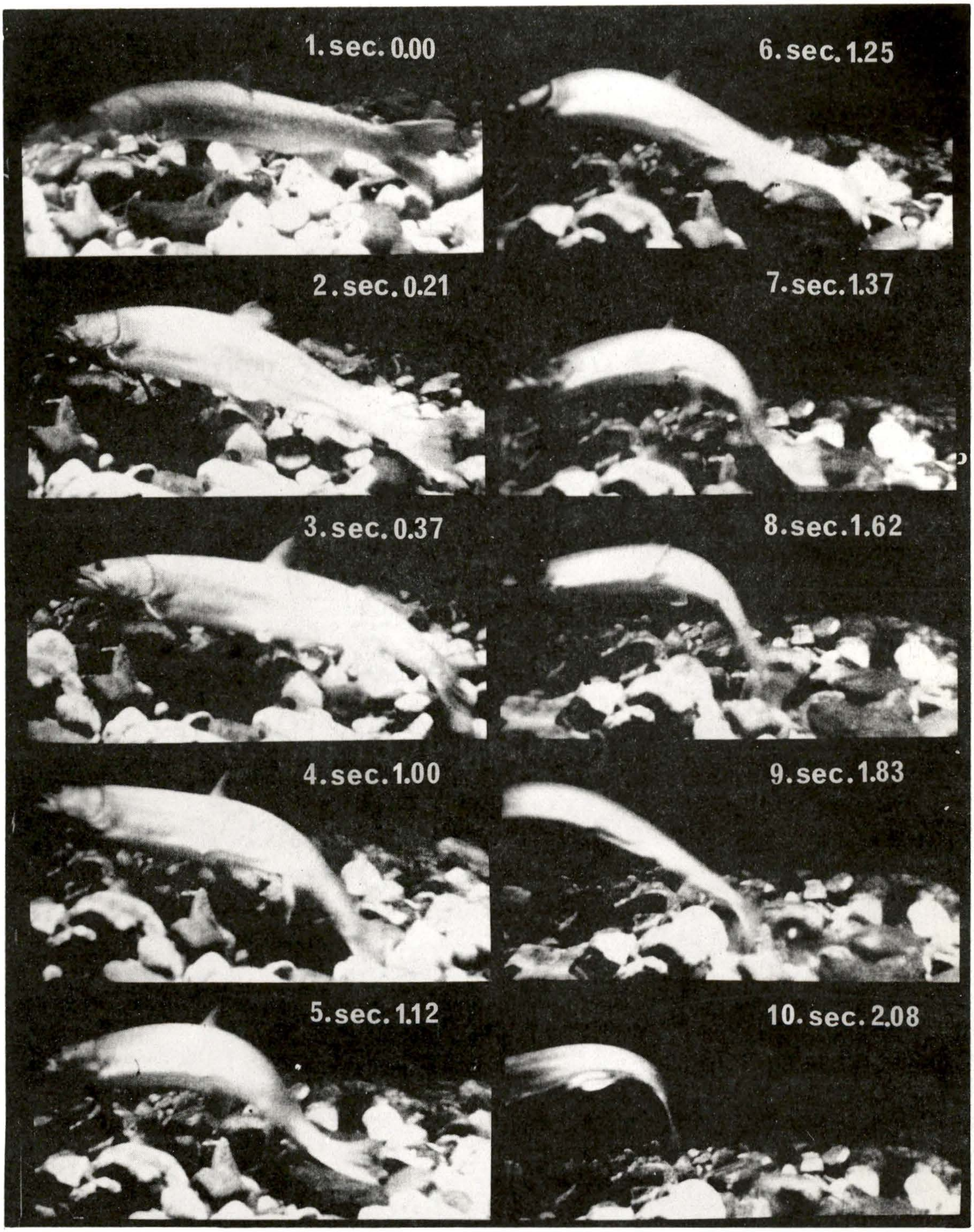
Post-Spawn Digging (Jones and Ball, 1953; and Jones, 1959 - cutting)

Female post-spawn activity, after a period of undulating, gradually changed to a digging movement. During a bout of post-spawn digging the female positioned herself over the redd, then moved to a position in front of the redd, turned on her side and by means of her caudal fin displaced gravel onto the nesting site (Fig. 42). This activity sometimes lasted for several hours, producing a mound of gravel two to four inches high over the redd. The female, while covering a previous redd, sometimes began the construction of a new nest.

The duration of seven post-spawn diggings ranged from 1.17 to 2.46 seconds with a mean of 1.83 seconds (Appendix X). Also for a given bout duration post-spawn digging always showed more tail beats.

Smith (1941) described a similar type of post-spawn digging for eastern brook trout. Needham and Vaughan (1952) report that nest sites of a pair of non-anadromous Dolly Varden at Twin Creek, Idaho was filled with pebbles and rocks and mounded to a height of three inches at the center. The mountain char of Sweden were observed to leave a similar mound of gravel (Fabricius and Gustafson, 1953).

Figure 42. Sequential movements of female during post-spawn digging.


1. sec. 0.00
2. sec. 0.21
3. sec. 0.37
4. sec. 1.00
5. sec. 1.12
6. sec. 1.25
7. sec. 1.37
8. sec. 1.62
9. sec. 1.83
10. sec. 2.08

Substrate Composition

Table V shows that a base of coarse gravel appeared to be essential for Dolly Varden spawning. On one occasion a female was observed to dig a nest for two days on gravel consisted of only small aggregates which continuously caved in. Finally the female moved to an upstream area of the aquarium, constructed another redd in coarse gravel and spawned. While the female was constructing her redd in the upstream area of the aquarium the gravel in the downstream area where she had begun digging earlier was supplemented with gravel of a size similar to that in the upstream area of the aquarium. After spawning in the front of the aquarium the female returned to the original area, constructed another redd and spawned.

A comparison of aquarium substrates on which spawning did and did not occur indicated that there was a significant correlation between gravel size composition and spawning. A Kolmogorov-Smirnov two sampled test showed that the spawn samples contained a significant (0.05 level 2 df.) amount of larger sized aggregate than the non-spawn samples (Table VI). A two-tailed student 't' test indicated that there was a significant (0.05 level) difference among gravel sizes between the spawn and non-spawn samples (Table VII).

TABLE V

Indicates Gravel Sites, Source, Number of Spawnings and the Presence or Absence of Coarse Gravel

Aquarium	Position	Gravel Source	No. of Spawnings	*Coarse Gravel 1" - 4"	Sample Numbers
One	Upstream Area	Meadow Creek Spawning Gravel	0	Absent	1, 5, 6
One	Downstream Area	Duncan Dam Gravel Pit 'B'	2	Present	4, 9, 11
Two	Upstream Area	John Creek	3	Present	2, 10
Two	Downstream Area	Screened Meadow Creek Spawning Gravel	0	Absent	7, 10
Two	Downstream Area	Screened Meadow Creek Spawning Gravel & John Creek Gravel	3	Present	3

* All Samples contained fine (< 1") gravel. For further detailed results see Table VI.

TABLE VI

A Kolmogorov-Smirnov Two Sampled Test Indicates that the Spawn and Non-spawn Samples are Significantly Different

Gravel Analysis
Mean Percentage Retained

U. S. Standard Sieve Size	Spawn Samples (n = 5) Mean	Cumulative	Non-spawn Samples (n = 6) Mean	Cumulative	Difference	
5 inch	2.33	99.88	0.00	99.96	.0012	
4 inch	6.43	97.55	0.00	99.96	.0241	
3 inch	7.82	91.92	0.62	99.96	.0804	
2-1/2 inch	12.30	83.30	0.86	99.34	.1604	
2 inch	18.02	71.00	4.60	98.48	.2248	
1-1/2 inch	19.07	52.98	8.90	93.88	.4090	
1 inch	7.63	33.91	7.62	84.98	.5107	D(max.)
3/4 inch	9.95	26.28	17.68	77.36	.5098	
1/2 inch	4.33	16.33	12.88	59.68	.4338	
3/8 inch	7.43	12.00	35.80	46.80	.3480	
No. 4	2.15	4.57	5.78	11.00	.0643	
No. 8	1.33	2.42	2.02	5.22	.0280	
No. 16	.56	1.09	1.12	3.20	.0211	
No. 30	.20	.53	.94	2.08	.0157	
No. 50	.10	.33	.48	1.14	.0081	
No. 100	.08	.23	.20	.66	.0043	
No. 200 decant	.15	.15	.46	.46	.0038	
	100%		100%			

$$\chi^2 = 4D^2 \frac{n_1 \cdot n_2}{n_1 + n_2}$$

*Kolmogorov-Smirnov Two Sample Test

$\chi^2 = 8.87$ ($p < .05$) for 2 d.f.

Ho - To determine whether the two distributions are from the same population.

Ha - At the 0.05 level of significance the two distributions are significantly different.

* See Siegal, page 131

TABLE VII

Spawning and Non-spawning Substrate Analysis
A Student 't' Test at the 0.05 Level of Significance with Nine Degrees of Freedom Indicates where there is a Significant Difference in Composition of the Various Gradients between the Two Samples

Gravel Test Results
Percentage Retained

U. S. Standard Sieve Size	Spawn Samples						Non-Spawn Samples				
	2	3	4	9	10	11	1	5	6	7	8
*5 inch	14.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
*4 inch	26.1	0.0	0.0	4.9	7.6	0.0	0.0	0.0	0.0	0.0	0.0
*3 inch	0.0	6.3	5.1	5.2	15.5	14.8	3.1	0.0	0.0	0.0	0.0
*2-1/2 inch	9.7	20.5	5.9	15.8	7.1	14.8	2.1	0.0	2.2	0.0	0.0
*2 inch	13.1	10.2	19.2	21.6	18.9	25.1	5.4	7.5	8.8	0.0	1.6
N.S.1-1/2 inch	9.9	12.1	30.5	25.5	13.6	22.8	11.9	14.0	17.6	0.0	1.0
N.S.1 inch	3.7	3.6	11.4	10.7	6.2	10.2	9.8	10.2	14.3	1.2	2.6
*3/4 inch	5.5	15.9	14.6	8.8	7.6	7.3	17.1	20.6	21.9	14.6	14.2
*1/2 inch	2.8	9.4	5.7	3.3	3.4	2.0	12.2	12.1	11.0	14.6	14.5
*3/8 inch	7.7	18.2	6.2	3.0	7.5	2.0	32.1	28.1	20.0	54.6	44.2
N.S. No. 4	3.0	2.4	0.6	0.8	5.4	0.7	4.6	4.1	1.7	7.5	11.0
N.S. No. 8	2.7	0.6	0.2	0.4	3.8	0.3	0.9	1.1	0.4	2.6	5.1
N.S. No. 16	1.2	0.3	0.2	0.0**	1.7	0.0**	0.3	0.6	0.4	1.6	2.7
N.S. No. 30	0.2	0.2	0.1	0.0**	0.7	0.0**	0.1	0.6	0.5	1.5	2.0
*No. 50	0.1	0.1	0.1	0.0**	0.3	0.0**	0.1	0.5	0.4	0.8	0.6
*No. 100	0.1	0.1	0.1	0.0**	0.2	0.0**	0.1	0.2	0.2	0.3	0.2
*No. 200	0.2	0.1	0.1	0.0**	0.5	0.0**	0.2	0.5	0.6	0.7	0.3

* A two-tailed Student 't' test at 0.05 level for 9 d.f. indicates that there is a significant difference among gravel sizes between the two samples.

** Insufficient amount of sand to warrant sieve analysis.

DISCUSSION

Migration

The movement of mature Dolly Varden into the Meadow Creek system took place during a period of approximately two months (July 23 - September 26) with the peak movement occurring during August. This compares favourably with Blackett's (1968) records for anadromous Dolly Varden entering Hood Bay Creek, Alaska.

During the main migration period conditions in the Meadow Creek system were characterized by peak water temperatures (mean temp. 51.7° F.) falling discharge levels and increasing levels of dissolved solids (Fig. 14). Armstrong (1965) recorded Dolly Varden movements into Eva Creek, Alaska in conjunction with rising water levels and peak seasonal temperatures. He also found that except during peak movements most Dolly Varden entered traps during the night hours, an observation confirmed in the present study.

The sex composition of potential spawners in Meadow Creek was 39 males and 42 females (Table I) a sex ratio similar to anadromous Dolly Varden entering Eva Creek, Alaska in 1964 (53 females and 49 males, Blackett, 1968).

Information on spawning frequency is sparse. Blackett (1968) in sampling Dolly Varden migrants at Lake Eva, Alaska found evidence of both repetitive spawning in consecutive years and non-consecutive repetitive spawning.

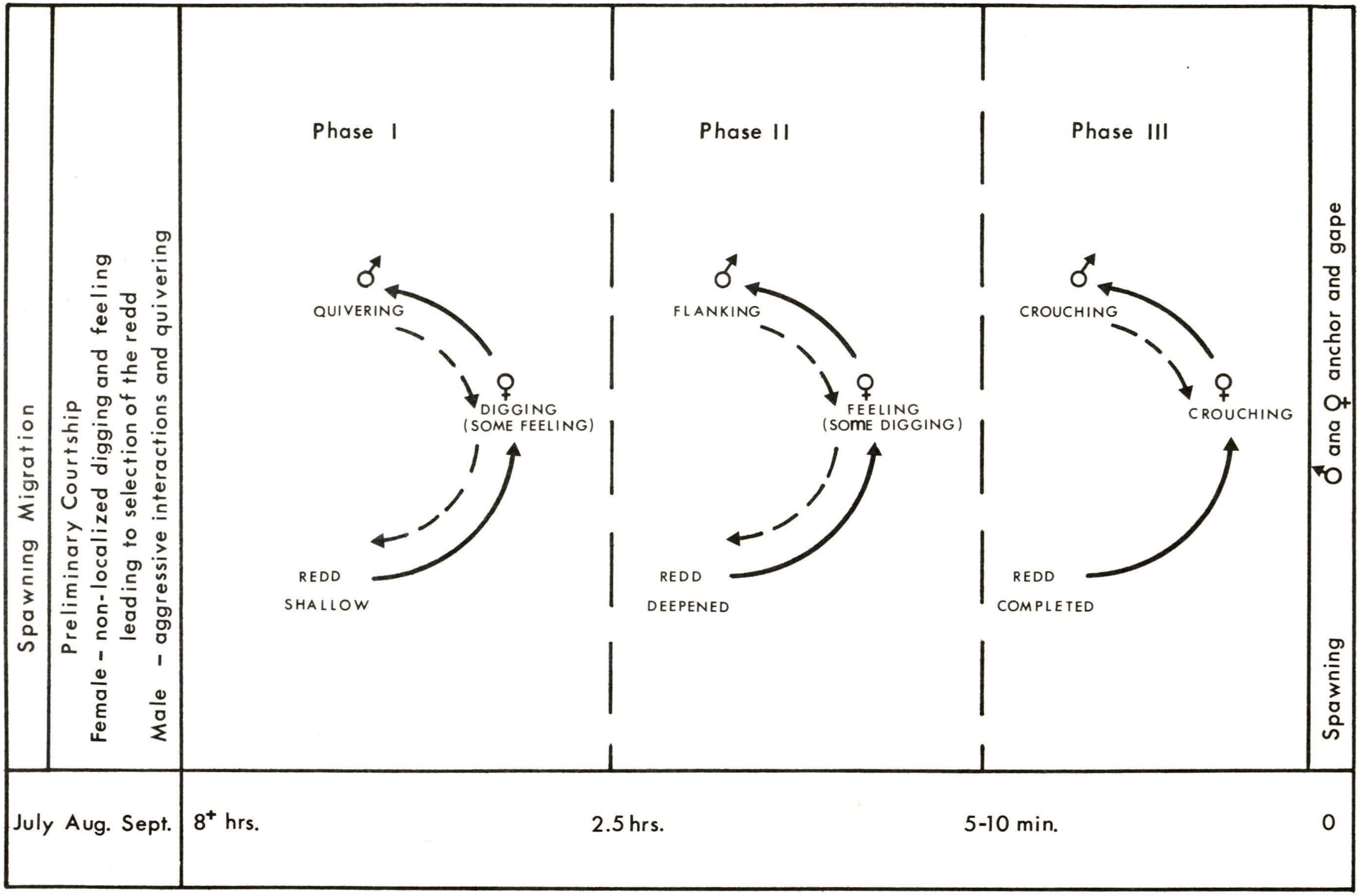
The limited period of trapping in the present study prevented a fuller description of migratory movements. It is possible that both upstream and downstream movements of adults occur at other times than those recorded. Armstrong's (1965) work on several Alaska streams showed evidence of repetitive seasonal movements of Dolly Varden between fresh-water and the sea prior to spawning. Until more complete documentation is available, comparisons with other salmonid migrations will be unsatisfactory.

Reproductive Behaviour

After migration, the first signs of reproductive behaviour appeared in the form of characteristic male aggressive behaviour and female digging and anal fin feeling, both unlocalized. In the observation aquaria courting interactions became more defined once the female's digging became more frequent and localized to a single area. The male responded to the female by centering his territorial behaviour around the redd. Male-female interactions beyond this point appeared to consist of a series of simple reciprocal behaviours which, for convenience, are divided into three phases. These phases and the associated predominant female activity and reciprocal male behaviours are shown in Figure 43.

Briefly the females' activities consists of two basic motor patterns digging and anal fin feeling, the latter changing in character (feeling → crouching → anchoring) with progress in redd excavation. Phase I activity consists predominantly of digging and to a lesser extent anal fin feeling.

Figure 43. Summary of courtship in the Dolly Varden


Spawning Migration
Preliminary Courtship
Female – non-localized digging and feeling leading to selection of the redd
Male – aggressive interactions and quivering
Phase I
♂
QUIVERING
♀
DIGGING (SOME FEELING)
REDD SHALLOW
Phase II
♂
FLANKING
♀
FEELING (SOME DIGGING)
REDD DEEPENED
Phase III
♂
CROUCHING
♀
CROUCHING
REDD COMPLETED
Spawning
♂ and ♀ anchor and gape
July Aug. Sept.
8+ hrs.
2.5 hrs.
5-10 min.
0

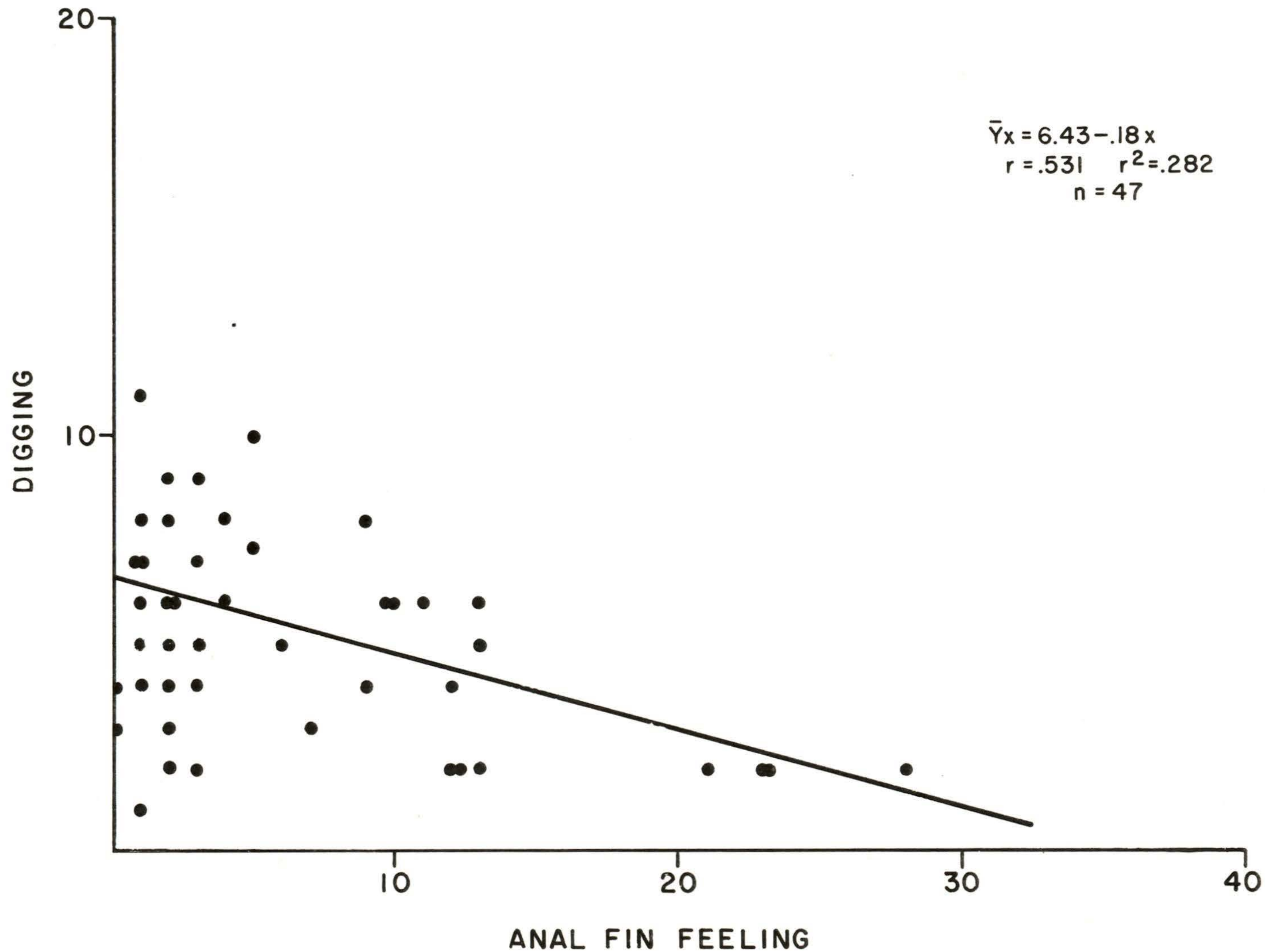
In phase II feeling became more frequent. Figure 44 shows the negative correlation between digging and anal feeling. Finally, in phase III the female assumes a progressively more crouched position prior to spawning. These temporal relationships are detailed in Figures 25 and 28.

The behaviour of the male during this period consists of one basic pattern--that of swimming to a position beside the female and in phase I, quivering; in phase II, not quivering (flanking); and in phase III, crouching in a position identical to the female's. These temporal patterns are shown in Figures 28, 32 and 38.

The sequence of female behaviour changes probably depends primarily on the developing state of the redd (depth and perhaps rock distribution). In turn, the male responds to changes in female behaviour. This sequence of action and reaction (redd development → female behaviour → male behaviour) is speculative since detailed changes in redd excavation were not followed. With regard to the male reacting to the females behaviour changes, Figure 28 shows that increasing anal fin feeling is clearly followed by male flanking. Likewise male anchoring clearly followed the same activity in the female. In this relationship the male's interaction with the female probably serves to coordinate the final stages of maturation leading to simultaneous gamete release and within each phase to stimulate the female in whatever activity she is pursuing. The character of the behavioural changes in both sexes through each phase leads to motor patterns progressively more similar to the actual spawning act.

The various phases of behaviour shown in Figure 43 are also supported

Figure 44. Frequency relationship of anal fin feeling to digging per five minute observation.



$\bar{Y}x = 6.43 - .18x$
$r = .531 \quad r^2 = .282$
$n = 47$
DIGGING
20
10
10
20
30
40
ANAL FIN FEELING

by two statistical correlations. Figure 45 shows the correlation between male quivering and female digging (r = .815) and Figure 46 shows flanking versus anal fin feeling (r = .846). These correlations also show that the male responds not only to the obvious visual features of particular female activity (other stimuli may also be involved) but also directly to the frequency of these patterns. Intensity (bout duration) changes appear to play no role in the temporal progression of the courtship pattern (Figs. 26 and 33) nor in the interactions between male and female. An analysis of 12 paired bouts of digging and quivering showed no significant correlation in duration (Appendix XI).

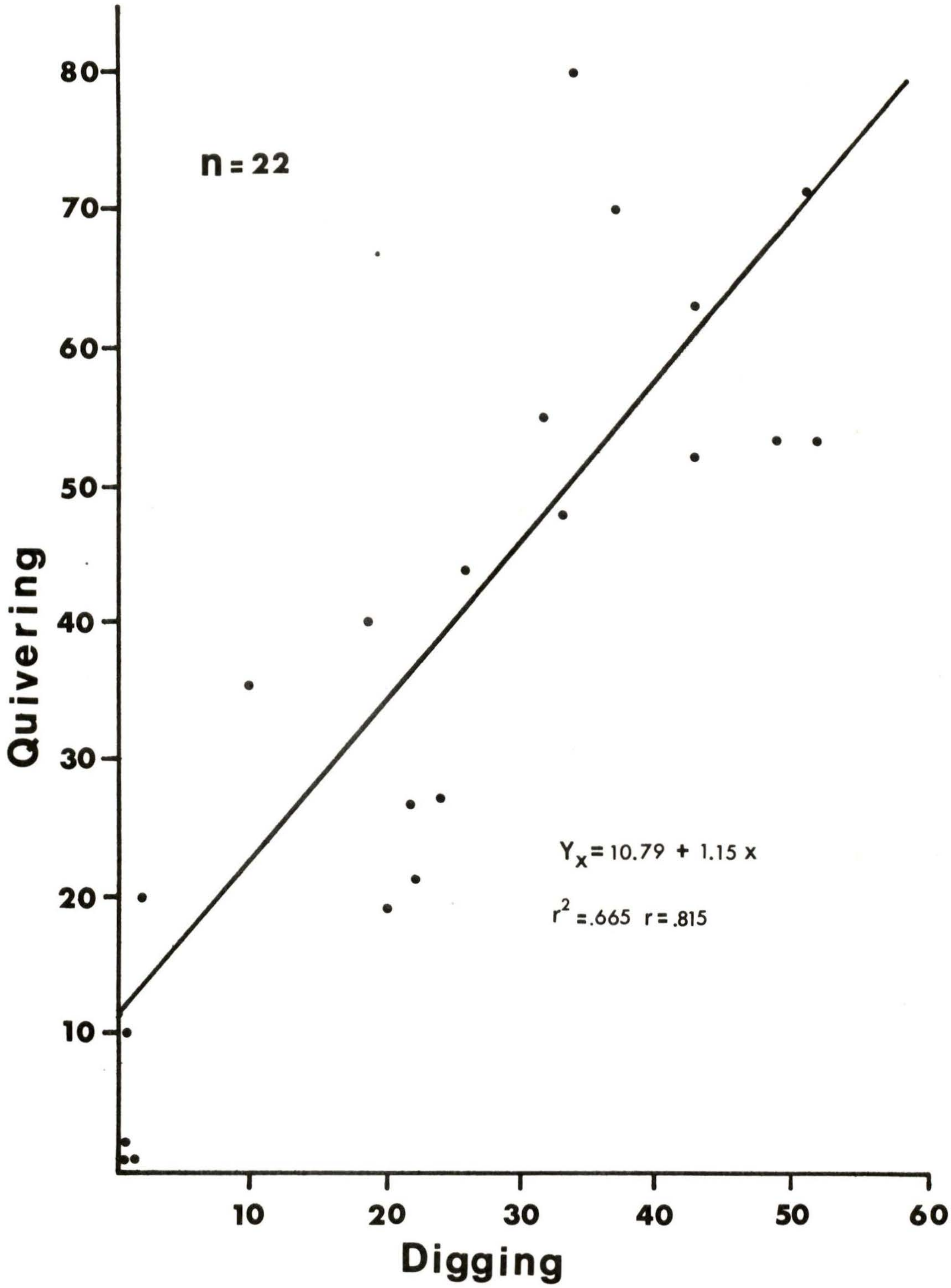
The temporal correlation of male and female activities, along with the prolonged repetition of behavioural interactions (phases I and II) suggests that the behaviours are mutually stimulating, i.e. that male quivering stimulated female digging and vice versa. The reciprocal influence of the male on the female and in phase I the subsequent indirect influence on the redd is suggested by the dotted lines in Figure 43.

In summary the changing interactions between male and female char are much less suggestive of a "chain reaction" than for example the courting sequence of the three-spine stickleback (Tingergen, 1951).

Certain other activities which occur during courtship are not so clearly a part of the developing interaction between male and female. These include peduncle grasping, crossing-over and trembling.

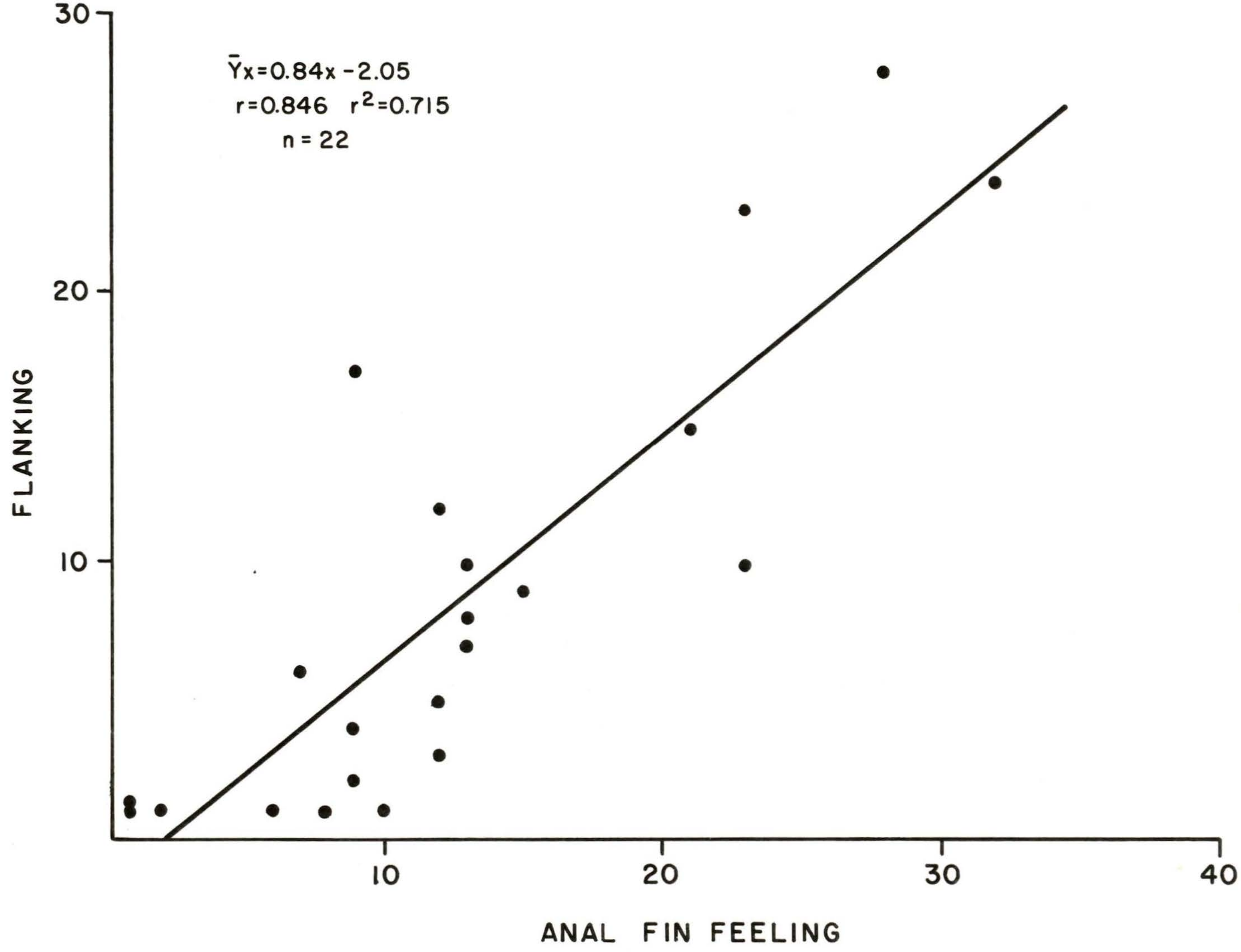
Peduncle grasping of the female by the male combines aggressive (motor pattern) and courting (sexual context) elements. Typically this activity

Figure 45. Frequency correlation of male quivering to female digging per 30 minute observation period.



n = 22
$Y_x = 10.79 + 1.15\,x$
$r^2 = .665 \quad r = .815$
Quivering
Digging
80
70
60
50
40
30
20
10
10
20
30
40
50
60

Figure 46. Frequency correlation of male flanking to female anal fin feeling per five minute observation during the two hour period prior to spawning.



$\bar{Y}x = 0.84x - 2.05$
$r = 0.846 \quad r^2 = 0.715$
n = 22
30
20
10
FLANKING
10
20
30
40
ANAL FIN FEELING

occurred in the early stages of courtship (prior to phase I) and was directed towards females showing a low digging frequency.

Crossing-over (the more or less regular alternation of male quivering and flanking from one side of the female to the other) persists throughout phases I and II. The data of this study suggests that this activity is not an important element of the courtship interaction. This conclusion is supported by an otherwise normal courtship sequence where a female's proximity to the observation window during redd construction curtails male crossing-over.

Male trembling occurs mainly during the later stages of phase II. While it is sometimes visible to the female it is not performed in physical contact with her. Its timing (late phase II), character (low frequency - high amplitude), and infrequent occurrence are suggestive of an act which either prepares the male for spawning (sperm transport or collection) or is a comfort movement uniquely associated with courtship and spawning. The fact that it was also seen occasionally after spawning may support the latter interpretation.

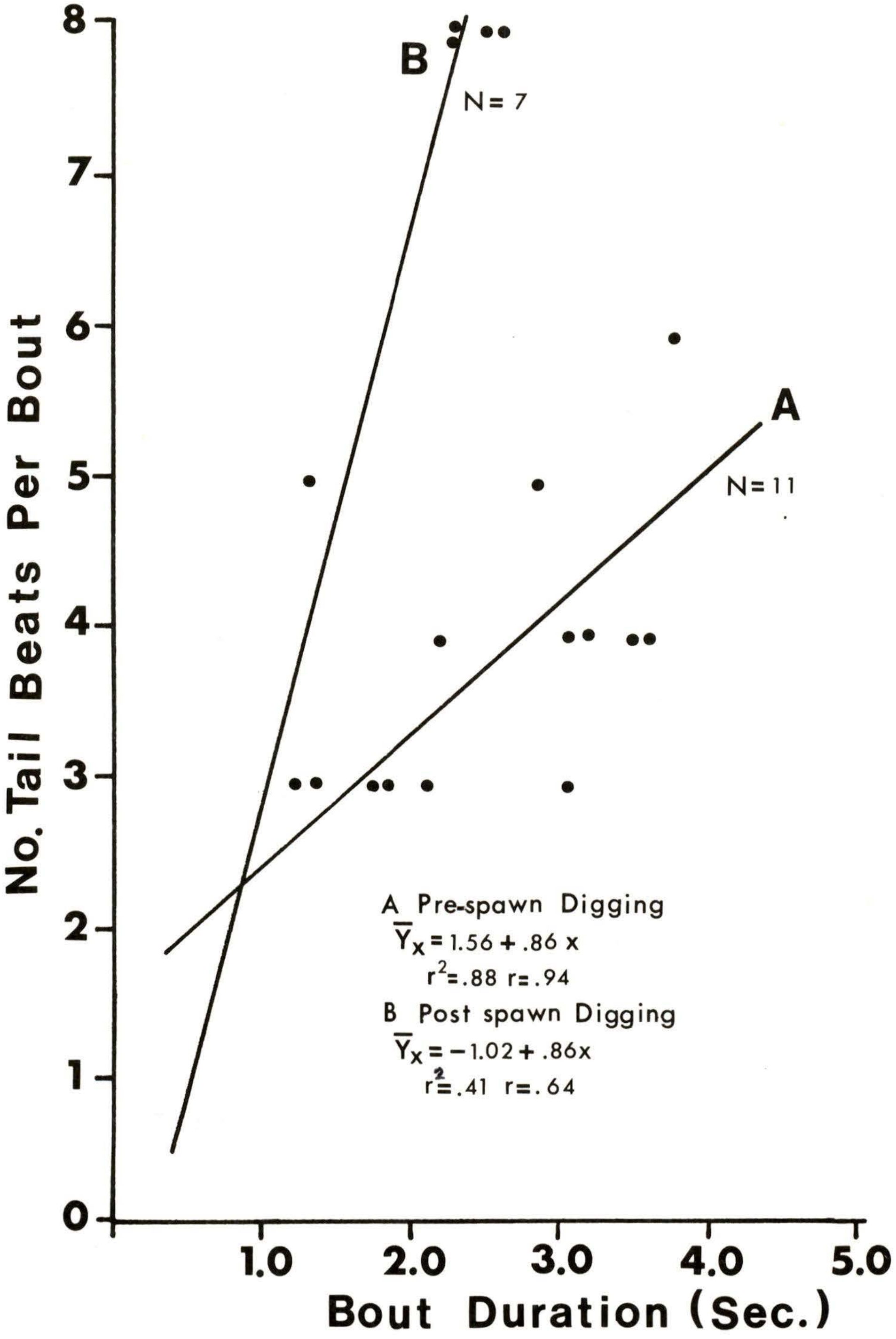
The final stages of the spawning act, female anchoring followed by male anchoring and then simultaneous gaping, quivering and gamete release, was not distinguishable from descriptions for other salmonids. The Dolly Varden resembles other chars and possibly differs from other salmonids in repeating the orgasm two or more times in rapid succession.

The post-spawn period showed certain features of female behaviour which are apparently unique to the chars. Two phases of post-spawning behaviour were recognized, first the undulating phase during which no digging was observed (1/2 - 1 hour) followed by the second or post-spawn digging phase during which the undulating movements gradually lessened in frequency and digging assumed prominence, sometimes for several hours.

The undulating movement, apparently a characteristic post-spawning behaviour of char probably serves to gradually transport loose eggs near the redd surface or around the redd circumference directly into the redd or into deeper crevices around the redd probably by generating horizontal water movements. In this species the adaptive significance of the behaviour may relate to the coarse gravel content preferred for redd construction. Such gravel leads to some eggs initially settling in exposed locations and later being shifted into less exposed sites.

Post-spawn digging begins after a more or less extended period of undulating in an area immediately in front of the redd. The character of this digging differed from that before spawning. Figure 47 shows that in both types of digging the number of tail beats (body flexures) shows a positive correlation with bout length. It also shows that for a given bout duration the number of tail beats (body flexures) is about fifty percent higher in post-spawn digging. Comparable bout frequencies were observed for both types of digging (Fig. 25 shows the mean frequency of pre-spawn digging to be about five bouts per five minute observation period: analysis of observations (28 minutes) for two females showing post-spawn digging produced a bout frequency of 5.14 per five minute observation period).

Figure 47. Correlation of bout duration and the number of tail beats for both pre-spawn and post-spawn digging of a female.



8
7
6
5
4
3
2
1
0
No. Tail Beats Per Bout
B
N= 7
A
N= 11
A Pre-spawn Digging
$\bar{Y}_x = 1.56 + .86x$
$r^2 = .88$ $r = .94$
B Post spawn Digging
$\bar{Y}_x = -1.02 + .86x$
$r^2 = .41$ $r = .64$
1.0
2.0
3.0
4.0
5.0
Bout Duration (Sec.)

The patterns of pre- and post-spawn digging outlined above differ considerably from those described by McCart (1969) for sockeye and kokanee salmon. These differences are summarized in Table VIII.

Dolly Varden do not show the marked increase in bout frequency that sockeye show shortly after spawning. Instead during this period they are performing the characteristic undulating movement of char. The most marked difference seems to be a post-spawn increase (Dolly Varden) rather than decrease (sockeye) in the number of tail beats per unit digging time. The higher frequency of body flexures suggest a movement of smaller amplitude leading to lower gravel lifting forces and the consequent movement of smaller gravel onto the eggs. An analysis of gravel showed that before spawning eighty percent of the gravel was three inches or less in size whereas after spawning ninety-five percent of the gravel was three inches or less (Appendix 12). This difference in digging seems particularly well suited to an egg-covering function.

The gravel size analysis of this study showing the importance of coarse aggregates characterizes more than any other physical factor, the kind of environment which is best suited to Dolly Varden spawning. While other salmonids, for example kokanee (*Oncorhynchus nerka*) may spawn under similar conditions of water temperature, turbidity and flow, Dolly Varden seem to be able to exploit for reproduction upstream segments of river systems unsuited to other species.

The area of a water shed characterized by coarse aggregates is also likely to show certain other physical features. For example, the bottom

TABLE VIII

Comparison of pre- and post-spawn digging patterns for Dolly Varden, Kokanee, and Sockeye salmon

	SOCKEYE		KOKANEE		DOLLY VARDEN	
Spawning	Before	After	Before	After	Before	After
Bout Frequency Per 5 Min. Obs.	1	10+	1.8	20+	5.2	4.5
Bout Duration (Sec.)	1.2	-	1.0	-	2.1	1.8
Tail Beats/Bout	5.0	initial decrease?	7.2	initial decrease?	3.3	4.3
Tail Beats/Sec.	4.2	?	7.2	?	1.3	2.4

gradient might be expected to be relatively steep, leading to higher water velocities and during some seasons, flash flooding. The latter feature may not be a problem during spawning but is likely to occur one or more times during the long incubation and pre-emergence period. The apparently deliberate selection of a redd area containing coarse aggregates, the unique undulating movements after spawning which probably serve to ensure that no eggs remain near the redd surface combined with the high mound of gravel covering the redd all seem particularly adapted to ensuring egg survival in an otherwise potentially highly unstable environment.

The almost circular cross-sectional configuration of the Dolly Varden body (both male and female) in contrast to the more laterally compressed configuration of other salmonids (exaggerated in mature females) may also be of adaptive significance in a spawning and rearing environment with high water velocities. The round configuration provides a better surface to volume relation and better control in turbulent flow.

In summary the reproductive behaviour of the Dolly Varden including migration is generally similar to other salmonids and in particular follows closely the patterns of other river spawning chars. Undoubtedly many behavioural differences of a quantitative nature will become apparent as the published literature in this area grows. Of the major qualitative differences in behaviour male trembling has been too seldom studied to permit either serious comparisons or a satisfactory functional interpretation. On the other hand the selection of coarse gravel for the redd combined with specialized, if not unique, post-spawning behaviours seem to be functionally suited to egg survival in the unstable spawning and rearing environments characteristic of Dolly Varden in British Columbia.

SUMMARY

1. Dolly Varden migrated from Kootenay Lake into the Meadow Creek system for a period of more than two months (July 23 to September 26). The peak migration period occurred during the month of August.
2. In 1968, the total number of Dolly Varden which migrated into the Meadow Creek system at the channel was 97 (81 mature, 16 immature or unclassified).
3. The sex ratio of the 81 mature fish consisted of 42 females and 39 males. The average length was 51.5 centimeters and the average weight 1439.3 grams.
4. Physical factors showed an increase in water temperature and dissolved solids and a decrease in water discharge for both John and Meadow Creek during the migration period.
5. Generally the Dolly Varden spawning behaviour as observed in aquaria, closely resembled the descriptions given for other salmonids with the exception of certain behavioural patterns such as trembling, repetitive orgasms, and some post-spawning activities.
6. Male aggression (biting and chasing) diminished as the spawning act approached.
7. Female digging peaked two to four hours before spawning. The frequency of male quivering correlated with the frequency of female digging. There appeared to be no temporal pattern of digging intensity.

8. The frequency of female anal fin feeling peaked during the hour preceeding spawning. Male flanking showed a positive linear correlation ($\overline{Y}_x = -2.05 + 0.84x$) with the frequency of female anal fin feeling.
9. Male quivering intensity (bout duration in sec.) of two males prior to spawning showed no temporal pattern.
10. A later stage of anal fin feeling (crouching) appeared to serve as a signal to the male for the approaching orgasm. Anchoring in the crouch position appeared to be the terminal signal for the spawning act.
11. A base of coarse gravel appears to be a prerequisite for spawning.

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APPENDICES

Appendix I. Program for Polynomial Regression Analysis.

```
C
C
C   I   ANALYSIS OF MALE BODY WEIGHT (GRS) VS FORK LENGTH (CMS)
C
C
C   II  ANALYSIS OF FEMALE BODY WEIGHT (GRS) VS FORK LENGTH (CMS)
C
C
C   III ANALYSIS OF MALE AND FEMALE BODY WEIGHT (GRS) VS FORK LENGTH (CMS)
C
C
      DIMENSION D(66)
      DIMENSION X(1500), DI(100), B(10), E(10), SB(10), T(10)
      DIMENSION XBAR(11), STD(11), CDE(11),SUMSQ(11), ISAVE(11), ANS(10)
      DIMENSION P(1100)
    1 FORMAT(A4,A2,I5,I2,I1)
    2 FORMAT(F3.1,F4.0)
    3 FORMAT(27H1POLYNOMIAL REGRESSION.....,A4,A2/)
    4 FORMAT(23HONUMBER OF OBSERVATIONS,I6//)
    5 FORMAT(32HOPOLYNOMIAL REGRESSION OF DEGREE,I3)
    6 FORMAT(12HO  INTERCEPT,E20.7)
    7 FORMAT(26HO  REGRESSION COEFFICIENTS/(6E20.7))
    8 FORMAT(1HO/24X,24HANALYSIS OF VARIANCE FOR,I4,19H  DEGREE POLYNOMI
     1AL/)
    9 FORMAT(1HO,5X,19HSOURCE OF VARIATION,7X,9HDEGREE OF,7X,6HSUM OF,9X
     1,4HMEAN,10X,1HF,9X,20HIMPROVEMENT IN TERMS/33X,7HFREEDOM,8X,7HSQUA
     2RES,7X,6HSQUARE,7X,5HVALUE,8X,17HOF SUM OF SQUARES)
   10 FORMAT(20HO  DUE TO REGRESSION,12X,I6,F17.5,F14.5,F13.5,F20.5)
   11 FORMAT(32H  DEVIATION ABOUT REGRESSION  , I6,F17.5,F14.5)
   12 FORMAT(8X,5HTOTAL,19X,I6,F17.5///)
   13 FORMAT(17HO  NO IMPROVEMENT)
   14 FORMAT(1HO//27X,18HTABLE OF RESIDUALS//16H OBSERVATION NO.,5X,7HX
     1VALUE,7X,7HY VALUE,7X,10HY ESTIMATE,7X,8HRESIDUAL/)
   15 FORMAT(1HO,3X,I6,F18.5,F14.5,F17.5,F15.5)
  100 READ(5,1) PR,PR1,N,M,NPLOT
      WRITE(6,3) PR, PR1
      L = N*M
      DO 110 I = 1,N
      J = L + I
  110 READ (5,2) X(I),X(J)
      CALL GDATA(N,M,X,XBAR,STD,D,SUMSQ)
      MM = M+1
      SUM = 0.0
      NT = N-1
      DO 200 I = 1,M
      ISAVE(I) = I
      CALL ORDER(MM,D,MM,I,ISAVE,DI,E)
      CALL MINV(DI,I,DET,B,T)
      CALL MULTR(N,I,XBAR,STD,SUMSQ,DI,E,ISAVE,B,SB,T,ANS)
      WRITE(6,5) I
      IF(ANS(7)) 140,130,130
  130 SUMIP = ANS(4)-SUM
      IF (SUMIP) 140,140,150
  140 WRITE(6,13)
      GO TO 210
  150 WRITE(6,6) ANS(1)
      WRITE(6,7) (B(J),J = 1,I)
      WRITE(6,8) I

      WRITE(6,9)
      SUM = ANS(4)
      WRITE(6,10) I,ANS(4),ANS(6),ANS(10),SUMIP
      NI = ANS(8)
      WRITE(6,11) NI,ANS(7),ANS(9)
      WRITE(6,12) NT, SUMSQ(MM)
      CDE(1) = ANS(1)
      DO  160 J = 1,I
  160 CDE(J+1) = B(J)
      LA = I
  200 CONTINUE
  210 IF(NPLOT) 100,100,220
  220 NP3 = N+N
      DO 230 I = 1,N
      NP3 = NP3+1
      P(NP3) = CDE(1)
      L=I
      DO 230 J = 1,LA
      P(NP3)=P(NP3)+X(L)*CDE(J+1)
  230 L = L+N
      N2 = N
      L = N*M
      DO 240 I = 1,N
      P(I)=X(I)
      N2=N2+1
      L =L+1
  240 P(N2)=X(L)
      WRITE(6,3) PR  , PR1
      WRITE(6,5) LA
      WRITE(6,14)
      NP2 = N
      NP3=N+N
      DO 250 I=1,N
      NP2=NP2+1
      NP3=NP3+1
      RESID=P(NP2)-P(NP3)
  250 WRITE(6,15) I,P(I),P(NP2),P(NP3),RESID
      GO TO 100
  602 CALL EXIT
      END
```

Appendix II. Analysis of male weight (grs.) and fork length (cms.).

POLYNOMIAL REGRESSION.....NO I

POLYNOMIAL REGRESSION OF DEGREE 1

INTERCEPT -0.3548665E 04

REGRESSION COEFFICIENTS
0.9677417E 02

ANALYSIS OF VARIANCE FOR 1 DEGREE POLYNOMIAL

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F VALUE	IMPROVEMENT IN TERMS OF SUM OF SQUARES
DUE TO REGRESSION	1	24606960.00000	24606960.00000	301.96069	24606960.00000
DEVIATION ABOUT REGRESSION ,	37	3015152.00000	81490.56250		
TOTAL	38	27622112.00000			

POLYNOMIAL REGRESSION OF DEGREE 2

INTERCEPT 0.1428112E 04

REGRESSION COEFFICIENTS
-0.8849507E 02 0.1683709E 01

ANALYSIS OF VARIANCE FOR 2 DEGREE POLYNOMIAL

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F VALUE	IMPROVEMENT IN TERMS OF SUM OF SQUARES
DUE TO REGRESSION	2	25423456.00000	12711728.00000	208.13724	816496.00000
DEVIATION ABOUT REGRESSION ,	36	2198656.00000	61073.77734		
TOTAL	38	27622112.00000			

POLYNOMIAL REGRESSION OF DEGREE 3

NO IMPROVEMENT

POLYNOMIAL REGRESSION.....NO I

POLYNOMIAL REGRESSION OF DEGREE 2

TABLE OF RESIDUALS

OBSERVATION NO.	X VALUE	Y VALUE	Y ESTIMATE	RESIDUAL
1	49.00000	1050.00000	1134.43994	-84.43994
2	62.00000	2000.00000	2413.59668	-413.59668
3	45.00000	900.00000	855.34521	44.65479
4	73.50000	4025.00000	4019.54297	5.45703
5	49.50000	1350.00000	1173.11621	176.88379
6	55.20000	1515.00000	1673.51465	-158.51465
7	43.50000	725.00000	764.57544	-39.57544
8	44.00000	750.00000	793.99023	-43.99023
9	52.29999	1275.00000	1405.25293	-130.25293
10	58.70000	1800.00000	2034.98730	-234.98730
11	59.50000	2100.00000	2123.40918	-23.40918
12	69.20000	3900.00000	3366.92578	533.07422
13	45.79999	775.00000	906.85254	-131.85254
14	65.50000	2700.00000	2855.21875	-155.21875
15	52.50000	1950.00000	1422.84668	527.15332
16	35.50000	400.00000	408.43164	-8.43164
17	46.50000	950.00000	953.69287	-3.69287
18	66.00000	2900.00000	2921.67578	-21.67578
19	42.50000	700.00000	708.27124	-8.27124
20	41.20000	700.00000	640.11035	59.88965
21	48.50000	1150.00000	1096.60913	53.39087
22	54.50000	1500.00000	1606.16699	-106.16699
23	52.50000	1475.00000	1422.84668	52.15332
24	48.79999	1050.00000	1119.20776	-69.20776
25	50.50000	1150.00000	1252.99121	-102.99121
26	62.20000	2700.00000	2437.72168	262.27832
27	50.59999	1200.00000	1261.16309	-61.16309
28	58.29999	2100.00000	1991.59277	108.40723
29	51.00000	1250.00000	1294.19043	-44.19043
30	49.79999	1000.00000	1196.72168	-196.72168
31	52.79999	1400.00000	1449.48340	-49.48340
32	48.59999	1090.00000	1104.10474	-14.10474
33	62.20000	2000.00000	2437.72168	-437.72168
34	56.50000	2000.00000	1802.96387	197.03613
35	66.50000	2700.00000	2988.97266	-288.97266
36	48.79999	1100.00000	1119.20776	-19.20776
37	47.79999	975.00000	1045.05347	-70.05347
38	48.50000	1100.00000	1096.60913	3.39087
39	54.50000	2500.00000	1606.16699	893.83301

Appendix III. Analysis of female body weight (grs.) and fork length (cms.).

POLYNOMIAL REGRESSION.....NO II

POLYNOMIAL REGRESSION OF DEGREE 1

INTERCEPT -0.3241568E 04

REGRESSION COEFFICIENTS
0.9069250E 02

ANALYSIS OF VARIANCE FOR 1 DEGREE POLYNOMIAL

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F VALUE	IMPROVEMENT IN TERMS OF SUM OF SQUARES
DUE TO REGRESSION	1	18318720.00000	18318720.00000	568.57227	18318720.00000
DEVIATION ABOUT REGRESSION ,	40	1288752.00000	32218.79687		
TOTAL	41	19607472.00000			

POLYNOMIAL REGRESSION OF DEGREE 2

INTERCEPT 0.2287362E 04

REGRESSION COEFFICIENTS
-0.1289497E 03 0.2136188E 01

ANALYSIS OF VARIANCE FOR 2 DEGREE POLYNOMIAL

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F VALUE	IMPROVEMENT IN TERMS OF SUM OF SQUARES
DUE TO REGRESSION	2	19007664.00000	9503832.00000	617.94678	688944.00000
DEVIATION ABOUT REGRESSION ,	39	599808.00000	15379.69141		
TOTAL	41	19607472.00000			

POLYNOMIAL REGRESSION.....NO II

POLYNOMIAL REGRESSION OF DEGREE 2

TABLE OF RESIDUALS

OBSERVATION NO.	X VALUE	Y VALUE	Y ESTIMATE	RESIDUAL
1	51.50000	1375.00000	1312.16016	62.83984
2	51.00000	1200.00000	1267.15625	-67.15625
3	45.50000	825.00000	842.59595	-17.59595
4	66.50000	3300.00000	3158.96484	141.03516
5	41.59999	650.00000	619.85547	30.14453
6	64.50000	2800.00000	2857.18359	-57.18359
7	59.00000	2200.00000	2115.40234	84.59766
8	62.79999	3000.00000	2614.10547	385.89453
9	49.50000	1150.00000	1138.54517	11.45483
10	45.20000	830.00000	823.15063	6.84937
11	49.29999	1200.00000	1122.12329	77.87671
12	43.00000	825.00000	692.33618	132.66382
13	39.39999	625.00000	522.87891	102.12109
14	43.39999	700.00000	714.58350	-14.58350
15	49.79999	1250.00000	1163.49609	86.50391
16	53.29999	1475.00000	1483.01562	-8.01562
17	58.00000	1825.00000	1994.41797	-169.41797
18	39.00000	350.00000	507.46753	-157.46753
19	49.50000	1100.00000	1138.54517	-38.54517
20	58.50000	2000.00000	2054.37500	-54.37500
21	54.00000	1625.00000	1553.20312	71.79688
22	53.50000	1650.00000	1502.85937	147.14062
23	55.00000	1525.00000	1657.09766	-132.09766
24	48.70000	1100.00000	1073.88501	26.11499
25	49.00000	1100.00000	1097.81470	2.18530
26	45.20000	750.00000	823.15063	-73.15063
27	54.50000	1500.00000	1604.61719	-104.61719
28	52.50000	1520.00000	1405.37109	114.62891
29	40.70000	575.00000	577.68433	-2.68433
30	53.50000	1400.00000	1502.85937	-102.85937
31	49.00000	1075.00000	1097.81470	-22.81470
32	55.00000	1550.00000	1657.09766	-107.09766
33	41.20000	575.00000	600.68823	-25.68823
34	45.39999	1000.00000	836.06860	163.93140
35	49.20000	1100.00000	1113.97876	-13.97876
36	44.50000	700.00000	779.28735	-79.28735
37	49.20000	1100.00000	1113.97876	-13.97876
38	38.00000	455.00000	471.93042	-16.93042
39	42.00000	600.00000	639.71338	-39.71338
40	59.00000	2200.00000	2115.40234	84.59766
41	63.50000	2300.00000	2712.70312	-412.70313
42	41.20000	600.00000	600.68823	-0.68823

Appendix IV. Analysis of male and female body weight (grs.) and fork length (cms.).

POLYNOMIAL REGRESSION.....NO III

POLYNOMIAL REGRESSION OF DEGREE 1

INTERCEPT -0.2317240E 04

REGRESSION COEFFICIENTS
0.7365782E 02

ANALYSIS OF VARIANCE FOR 1 DEGREE POLYNOMIAL

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F VALUE	IMPROVEMENT IN TERMS OF SUM OF SQUARES
DUE TO REGRESSION	1	46004944.00000	46004944.00000	395.95801	46004944.00000
DEVIATION ABOUT REGRESSION ,	83	9643472.00000	116186.37500		
TOTAL	84	55648416.00000			

POLYNOMIAL REGRESSION OF DEGREE 2

INTERCEPT 0.8141543E 03

REGRESSION COEFFICIENTS
-0.6822926E 02 0.1523730E 01

ANALYSIS OF VARIANCE FOR 2 DEGREE POLYNOMIAL

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F VALUE	IMPROVEMENT IN TERMS OF SUM OF SQUARES
DUE TO REGRESSION	2	52746320.00000	26373152.00000	745.18481	6741376.00000
DEVIATION ABOUT REGRESSION ,	82	2902096.00000	35391.41406		
TOTAL	84	55648416.00000			

POLYNOMIAL REGRESSION OF DEGREE 3

NO IMPROVEMENT

POLYNOMIAL REGRESSION.....NO III

POLYNOMIAL REGRESSION OF DEGREE 2

TABLE OF RESIDUALS

OBSERVATION NO.	X VALUE	Y VALUE	Y ESTIMATE	RESIDUAL
1	51.50000	1375.00000	1341.66089	33.33911
2	51.00000	1200.00000	1297.68433	-97.68433
3	54.50000	2500.00000	1621.51904	878.48096
4	45.50000	825.00000	864.22534	-39.22534
5	48.50000	1100.00000	1089.22949	10.77051
6	47.79999	975.00000	1034.27417	-59.27417
7	48.79999	1100.00000	1113.23730	-13.23730
8	66.50000	3300.00000	3015.22461	284.77539
9	66.50000	2700.00000	3015.22461	-315.22461
10	56.50000	2000.00000	1823.32593	176.67407
11	41.59999	650.00000	612.72266	37.27734
12	64.50000	2800.00000	2752.46680	47.53320
13	62.79999	3000.00000	2538.70117	461.29883
14	62.20000	2000.00000	2465.36133	-465.36133
15	48.59999	1090.00000	1097.20117	-7.20117
16	49.50000	1150.00000	1170.32593	-20.32593
17	45.20000	830.00000	843.23291	-13.23291
18	49.29999	1200.00000	1153.86182	46.13818
19	43.00000	825.00000	697.67334	127.32666
20	52.79999	1400.00000	1459.56421	-59.56421
21	39.39999	625.00000	491.29883	133.70117
22	43.39999	700.00000	723.04102	-23.04102
23	49.79999	1000.00000	1195.24756	-195.24756
24	51.00000	1250.00000	1297.68433	-47.68433
25	49.79999	1250.00000	1195.24756	54.75244
26	53.29999	1475.00000	1506.28149	-31.28149
27	58.29999	2100.00000	2015.37744	84.62256
28	50.59999	1200.00000	1263.05054	-63.05054
29	58.00000	1825.00000	1982.68530	-157.68530
30	39.00000	350.00000	470.80688	-120.80688
31	62.20000	2700.00000	2465.36133	234.63867
32	50.50000	1150.00000	1254.46973	-104.46973
33	48.79999	1050.00000	1113.23730	-63.23730
34	49.50000	1100.00000	1170.32593	-70.32593
35	54.00000	1625.00000	1572.96948	52.03052
36	52.50000	1475.00000	1431.89941	43.10059
37	58.50000	2000.00000	2037.32837	-37.32837
38	54.50000	1500.00000	1621.51904	-121.51904
39	53.50000	1650.00000	1525.18579	124.81421
40	48.50000	1150.00000	1089.22949	60.77051
41	41.20000	700.00000	589.54907	110.45093
42	42.50000	700.00000	666.64844	33.35156
43	55.00000	1525.00000	1670.82617	-145.82617
44	66.00000	2900.00000	2948.39258	-48.39258
45	46.50000	950.00000	936.17944	13.82056
46	35.50000	400.00000	312.29663	87.70337
47	48.70000	1100.00000	1105.20459	-5.20459
48	49.00000	1100.00000	1129.39673	-29.39673
49	52.50000	1950.00000	1431.89941	518.10059
50	65.50000	2700.00000	2882.32227	-182.32227
51	45.20000	750.00000	843.23291	-93.23291
52	54.50000	1500.00000	1621.51904	-121.51904
53	45.79999	775.00000	885.49023	-110.49023
54	52.50000	1520.00000	1431.89941	88.10059
55	69.20000	3900.00000	3389.28320	510.71680
56	40.70000	575.00000	561.26709	13.73291
57	59.50000	2100.00000	2148.89600	-48.89600
58	58.70000	1800.00000	2059.39771	-259.39771
59	52.29999	1275.00000	1413.60474	-138.60474
60	53.50000	1400.00000	1525.18579	-125.18579
61	44.00000	750.00000	762.00854	-12.00854
62	43.50000	725.00000	729.45996	-4.45996
63	49.00000	1075.00000	1129.39673	-54.39673
64	55.20000	1515.00000	1690.76270	-175.76270
65	55.00000	1550.00000	1670.82617	-120.82617
66	41.20000	575.00000	589.54907	-14.54907
67	45.39999	1000.00000	857.19727	142.80273
68	17.29999	25.00000	89.82544	-64.82544
69	21.00000	75.00000	53.30469	21.69531
70	17.20000	45.00000	91.39136	-46.39136
71	49.50000	1350.00000	1170.32593	179.67407
72	49.20000	1100.00000	1145.67676	-45.67676
73	44.50000	700.00000	795.31885	-95.31885
74	49.20000	1100.00000	1145.67676	-45.67676
75	73.50000	4025.00000	4030.87891	-5.87891
76	38.00000	455.00000	421.70874	33.29126
77	42.00000	600.00000	636.38550	-36.38550
78	59.00000	2200.00000	2092.72949	107.27051
79	33.50000	300.00000	238.48022	61.51978
80	63.50000	2300.00000	2625.65820	-325.65820
81	41.20000	600.00000	589.54907	10.45093
82	45.00000	900.00000	829.39136	70.60864
83	62.00000	2000.00000	2441.16211	-441.16211
84	49.00000	1050.00000	1129.39673	-79.39673
85	59.00000	2200.00000	2092.72949	107.27051

IHC217I

Appendix V. Analysis of the intensity (bout duration) of a male quivering to digging and non-digging females.

APPENDIX V

To determine whether there was a significant difference between the intensity (bout duration) of a male quivering to digging and non-digging females.

Quivering intensity to digging female		Quivering intensity to non-digging female
1.416 sec.	2.560 sec.	1.500 sec.
1.215	2.030	1.600
1.430	3.900	1.400
1.200	2.530	1.630
1.600	2.400	2.030
1.300	2.115	2.100
2.300	2.133	0.900
2.150	1.433	0.800
2.450	1.833	0.483
2.350	1.966	1.366
1.550	1.700	0.700
1.800	2.200	3.533
1.900	1.960	2.133
1.100	2.660	1.300
2.250	1.500	1.060
2.000	2.760	1.760
1.150	2.360	2.100
1.580	2.330	1.630
0.623	2.030	1.960
2.065	2.230	1.900
2.600	1.866	1.130
0.500	2.100	0.566
2.083	1.800	1.566
2.366	3.530	
1.350	2.000	
1.833		

Hypothesis: The intensity of a male quivering to a digging female is of the same intensity as quivering to a non-digging female.

Alternate Hypothesis: The intensity of a male quivering to a digging female is greater than quivering to a non-digging female.

Level of significance: 0.05

Critical Region: $(n_1 + n_2 - 2)$ 72 d.f.

Computed 't' = 2.90 lies within the critical region

Conclusion: Reject the hypothesis in favour of the alternate hypothesis.

Appendix VI. Analysis of anal fin feeling to flanking per five minute observation.

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C
C   (1) ANALYSIS OF ANAL FIN FEELING VS  FLANKING  PER 5 MIN OBSERVATION
C
C
C   (2) ANALYSIS OF DIGGING VS QUIVERING PER 30 MIN OBSERVATION
C
C
C   (3) ANALYSIS OF ANAL FIN FEELING VS DIGGING PER 5 MIN OBSERVATION
C
C
```

POLYNCMIAL REGRESSION.....LEGGET

POLYNOMIAL REGRESSION OF DEGREE 1

INTERCEPT -0.2048320E 01

REGRESSION COEFFICIENTS
0.8425199E 00

ANALYSIS OF VARIANCE FOR 1 DEGREE POLYNOMIAL

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F VALUE	IMPROVEMENT IN TERMS OF SUM OF SQUARES
DUE TO REGRESSION	1	1015.61792	1015.61792	50.09575	1015.61792
DEVIATION ABOUT REGRESSION ,	20	405.47070	20.27353		
TOTAL	21	1421.08862			

POLYNCMIAL REGRESSION.....LEGGET

POLYNOMIAL REGRESSION OF DEGREE 1

TABLE OF RESIDUALS

OBSERVATION NO.	X VALUE	Y VALUE	Y ESTIMATE	RESIDUAL
1	2.00000	1.00000	-0.36328	1.36328
2	6.00000	1.00000	3.00680	-2.00680
3	8.00000	1.00000	4.69184	-3.69184
4	9.00000	2.00000	5.53436	-3.53436
5	13.00000	10.00000	8.90444	1.09556
6	12.00000	13.00000	8.06192	4.93808
7	10.00000	1.00000	6.37688	-5.37688
8	12.00000	5.00000	8.06192	-3.06192
9	12.00000	3.00000	8.06192	-5.06192
10	23.00000	10.00000	17.32962	-7.32962
11	21.00000	15.00000	15.64460	-0.64460
12	13.00000	8.00000	8.90444	-0.90444
13	9.00000	4.00000	5.53436	-1.53436
14	13.00000	7.00000	8.90444	-1.90444
15	32.00000	24.00000	24.91231	-0.91231
16	28.00000	28.00000	21.54222	6.45778
17	23.00000	23.00000	17.32962	5.67038
18	15.00000	9.00000	10.58948	-1.58948
19	7.00000	6.00000	3.84932	2.15068
20	9.00000	17.00000	5.53436	11.46564
21	1.00000	1.00000	-1.20580	2.20580
22	1.00000	1.00000	-1.20580	2.20580

Appendix VII. Analysis of digging to quivering per thirty minute observation.

POLYNOMIAL REGRESSION.....LEGGET

POLYNOMIAL REGRESSION OF DEGREE 1

INTERCEPT 0.1079808E 02

REGRESSION COEFFICIENTS
0.1148968E 01

ANALYSIS OF VARIANCE FOR 1 DEGREE POLYNOMIAL

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F VALUE	IMPROVEMENT IN TERMS OF SUM OF SQUARES
DUE TO REGRESSION	1	8281.73828	8281.73828	39.62306	8281.73828
DEVIATION ABOUT REGRESSION ,	20	4180.26172	209.01308		
TOTAL	21	12462.00000			

POLYNOMIAL REGRESSION.....LEGGET

POLYNOMIAL REGRESSION OF DEGREE 1

TABLE OF RESIDUALS

OBSERVATION NO.	X VALUE	Y VALUE	Y ESTIMATE	RESIDUAL
1	20.00000	67.00000	33.77744	33.22256
2	32.00000	55.00000	47.56505	7.43495
3	37.00000	70.00000	53.30988	16.69012
4	33.00000	48.00000	48.71400	-0.71400
5	24.00000	26.00000	38.37331	-12.37331
6	49.00000	53.00000	67.09749	-14.09749
7	19.00000	40.00000	32.62846	7.37154
8	52.00000	53.00000	70.54440	-17.54440
9	51.00000	71.00000	69.39543	1.60457
10	34.00000	80.00000	49.86298	30.13702
11	0.0	10.00000	10.79808	-0.79808
12	1.00000	1.00000	11.94705	-10.94705
13	20.00000	19.00000	33.77744	-14.77744
14	22.00000	21.00000	36.07536	-15.07536
15	26.00000	44.00000	40.67123	3.32877
16	43.00000	63.00000	60.20369	2.79631
17	43.00000	52.00000	60.20369	-8.20369
18	2.00000	20.00000	13.09602	6.90398
19	10.00000	35.00000	22.28775	12.71225
20	22.00000	27.00000	36.07536	-9.07536
21	0.0	1.00000	10.79808	-9.79808
22	0.0	2.00000	10.79808	-8.79808

IHC217I

TRACEBACK FOLLOWS-	ROUTINE	ISN	REG. 14	REG. 15	REG. 0	REG. 1
	IBCOM		00008B84	00009828	00000017	00009070
	MAIN		00002BE0	700059D8	0000003C	0003FF1C

ENTRY POINT= 700059D8

Appendix VIII. Analysis of anal fin feeling to digging per five minute observation.

POLYNCMIAL REGRESSION.....LEGGET

POLYNOMIAL REGRESSION OF DEGREE 1

INTERCEPT 0.6434354E 01

REGRESSION COEFFICIENTS
-0.1819771E 00

ANALYSIS OF VARIANCE FOR 1 DEGREE POLYNOMIAL

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F VALUE	IMPROVEMENT IN TERMS OF SUM OF SQUARES
DUE TO REGRESSION	1	92.34749	92.34749	17.68898	92.34749
DEVIATION ABOUT REGRESSION	45	234.92790	5.22062		
TOTAL	46	327.27539			

POLYNOMIAL REGRESSION.....LEGGET

POLYNCMIAL REGRESSION OF DEGREE 1

TABLE OF RESIDUALS

OBSERVATION NO.	X VALUE	Y VALUE	Y ESTIMATE	RESIDUAL
1	1.00000	4.00000	6.25238	-2.25238
2	1.00000	11.00000	6.25238	4.74762
3	2.00000	3.00000	6.07040	-3.07040
4	1.00000	7.00000	6.25238	0.74762
5	1.00000	5.00000	6.25238	-1.25238
6	0.0	4.00000	6.43435	-2.43435
7	1.00000	7.00000	6.25238	0.74762
8	1.00000	8.00000	6.25238	1.74762
9	2.00000	9.00000	6.07040	2.92960
10	0.0	10.00000	6.43435	3.56565
11	2.00000	8.00000	6.07040	1.92960
12	3.00000	9.00000	5.88842	3.11158
13	7.00000	3.00000	5.16051	-2.16051
14	0.0	3.00000	6.43435	-3.43435
15	0.0	9.00000	6.43435	2.56565
16	2.00000	3.00000	6.07040	-3.07040
17	3.00000	2.00000	5.88842	-3.88842
18	2.00000	4.00000	6.07040	-2.07040
19	3.00000	5.00000	5.88842	-0.88842
20	5.00000	7.00000	5.52447	1.47553
21	1.00000	6.00000	6.25238	-0.25238
22	2.00000	5.00000	6.07040	-1.07040
23	2.00000	6.00000	6.07040	-0.07040
24	3.00000	4.00000	5.88842	-1.88842
25	10.00000	6.00000	4.61458	1.38542
26	11.00000	6.00000	4.43261	1.56739
27	6.00000	5.00000	5.34249	-0.34249
28	2.00000	6.00000	6.07040	-0.07040
29	4.00000	6.00000	5.70644	0.29356
30	4.00000	8.00000	5.70644	2.29356
31	9.00000	8.00000	4.79656	3.20344
32	10.00000	6.00000	4.61458	1.38542
33	1.00000	1.00000	6.25238	-5.25238
34	3.00000	7.00000	5.88842	1.11158
35	5.00000	10.00000	5.52447	4.47553
36	12.00000	2.00000	4.25063	-2.25063
37	12.00000	4.00000	4.25063	-0.25063
38	23.00000	2.00000	2.24888	-0.24888
39	21.00000	2.00000	2.61283	-0.61283
40	13.00000	6.00000	4.06865	1.93135
41	9.00000	4.00000	4.79656	-0.79656
42	13.00000	2.00000	4.06865	-2.06865
43	32.00000	0.0	0.61109	-0.61109
44	28.00000	2.00000	1.33900	0.66100
45	23.00000	2.00000	2.24888	-0.24888
46	12.00000	2.00000	4.25063	-2.25063
47	13.00000	5.00000	4.06865	0.93135

IHC217I

TRACEBACK FOLLOWS-	ROUTINE	ISN	REG. 14	REG. 15	REG. 0	REG. 1
	IBCOM		00008B84	00009828	00000030	00009070
	MAIN		00002BE0	700059D8	00000030	0003FF1C

ENTRY POINT= 700059D8

Appendix IX. Analysis of bout duration versus the number of tail beats for pre-spawn and post-spawn digging of a single female.

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C
C
C    I  PRESPAWN DIGGING  ANALYSIS OF BOUT DURATION VS NO. TAIL BEATS
C
C
C    II  POST-SPAWN DIGGING  ANALYSIS OF BOUT DURATION VS NO. OF TAIL BEATS
C
C
C
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POLYNOMIAL REGRESSION.....NO I

POLYNOMIAL REGRESSION OF DEGREE 1

INTERCEPT -0.1020821E 01

REGRESSION COEFFICIENTS
0.3902394E 01

ANALYSIS OF VARIANCE FOR 1 DEGREE POLYNOMIAL

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F VALUE	IMPROVEMENT IN TERMS OF SUM OF SQUARES
DUE TO REGRESSION	1	30.76759	30.76759	37.61771	30.76759
DEVIATION ABOUT REGRESSION ,	5	4.08951	0.81790		
TOTAL	6	34.85710			

POLYNOMIAL REGRESSION.....NO I

POLYNOMIAL REGRESSION OF DEGREE 1

TABLE OF RESIDUALS

OBSERVATION NO.	X VALUE	Y VALUE	Y ESTIMATE	RESIDUAL
1	1.17000	3.00000	3.54498	-0.54498
2	1.21000	5.00000	3.70107	1.29893
3	1.30000	3.00000	4.05229	-1.05229
4	2.17000	8.00000	7.44737	0.55263
5	2.37000	8.00000	8.22785	-0.22785
6	2.46000	8.00000	8.57907	-0.57907
7	2.17000	8.00000	7.44737	0.55263

IHC217I

TRACEBACK FOLLOWS-	ROUTINE	ISN	REG. 14	REG. 15	REG. 0	REG. 1
	IBCOM		00008B84	00009828	00000008	00009070
	MAIN		00002BE0	700059D8	00000030	0003FF1C

POLYNOMIAL REGRESSION.....NO II

POLYNOMIAL REGRESSION OF DEGREE 1

INTERCEPT 0.1557896E 01

REGRESSION COEFFICIENTS
0.8561131E 00

ANALYSIS OF VARIANCE FOR 1 DEGREE POLYNOMIAL

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F VALUE	IMPROVEMENT IN TERMS OF SUM OF SQUARES
DUE TO REGRESSION	1	3.67817	3.67817	6.32843	3.67817
DEVIATION ABOUT REGRESSION ,	9	5.23092	0.58121		
TOTAL	10	8.90909			

POLYNOMIAL REGRESSION.....NO II

POLYNOMIAL REGRESSION OF DEGREE 1

TABLE OF RESIDUALS

OBSERVATION NO.	X VALUE	Y VALUE	Y ESTIMATE	RESIDUAL
1	3.50000	4.00000	4.55429	-0.55429
2	3.00000	4.00000	4.12623	-0.12623
3	3.67000	6.00000	4.69983	1.30017
4	3.12000	4.00000	4.22897	-0.22897
5	3.00000	3.00000	4.12623	-1.12623
6	2.75000	5.00000	3.91221	1.08779
7	3.46000	4.00000	4.52005	-0.52005
8	2.17000	4.00000	3.41566	0.58434
9	2.04000	3.00000	3.30437	-0.30437
10	1.71000	3.00000	3.02185	-0.02185
11	1.79000	3.00000	3.09034	-0.09034

Appendix X. Analysis of pre-spawn and post-spawn digging durations.

APPENDIX X

To determine whether there is a difference between bout duration of post-spawning and pre-spawning digging.

Pre-spawning	Post-spawning
3.4980 sec.	1.1666 sec.
2.9920	1.2075
3.6652	1.2916
3.1229	2.1657
2.9992	2.3740
2.7499	2.4581
3.4559	2.1665
2.1656	
2.0406	
1.7076	
1.7916	
n = 11	n = 7

Hypothesis: That the duration of pre-spawn and post-spawn digging are equal.

Alternate Hypothesis: That the duration of pre-spawn digging is greater or less than the duration of post-spawn digging.

Level of significance: 5% level.

Critical Region: $(n_1 + n_2 - 2)$ 16 d.f.

$$t = < -2.12 \text{ and } > 2.12$$

Computed 't' = 2.8366

Conclusion: Reject the hypothesis in favour of the alternate hypothesis. The computed 't' lies within the critical region, the conclusion is that the pre-spawning digging is of a longer duration than post-spawning digging.

Appendix XI. Analysis of quivering versus digging (bout duration).

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C
C
C
C
C
C      QUIVERING  VS.  DIGGING (BOUT DURATION)
C
C
C
C
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POLYNOMIAL REGRESSION.....LEGGET

POLYNOMIAL REGRESSION OF DEGREE 1

INTERCEPT 0.1634147E 01

REGRESSION COEFFICIENTS
0.1580003E 00

ANALYSIS OF VARIANCE FOR 1 DEGREE POLYNOMIAL

SOURCE OF VARIATION	DEGREE OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F VALUE	IMPROVEMENT IN TERMS OF SUM OF SQUARES
DUE TO REGRESSION	1	0.04839	0.04839	0.60933	0.04839
DEVIATION ABOUT REGRESSION	10	0.79411	0.07941		
TOTAL	11	0.84250			

POLYNOMIAL REGRESSION.....LEGGET

POLYNOMIAL REGRESSION OF DEGREE 1

TABLE OF RESIDUALS

OBSERVATION NO.	X VALUE	Y VALUE	Y ESTIMATE	RESIDUAL
1	1.50000	2.00000	1.87115	0.12885
2	1.52000	2.00000	1.87431	0.12569
3	1.62000	1.85000	1.89011	-0.04011
4	2.00000	1.50000	1.95015	-0.45015
5	2.45000	1.75000	2.02125	-0.27125
6	1.95000	1.90000	1.94225	-0.04225
7	1.75000	2.30000	1.91065	0.38935
8	1.85000	2.00000	1.92645	0.07355
9	1.00000	1.60000	1.79215	-0.19215
10	2.45000	2.50000	2.02125	0.47875
11	1.75000	1.95000	1.91065	0.03935
12	2.25000	1.75000	1.98965	-0.23965

IHC217I

TRACEBACK FOLLOWS-	ROUTINE	ISN	REG. 14	REG. 15	REG. 0	REG. 1
	IBCOM		00008B84	00009828	0000000D	00009070
	MAIN		00002BE0	700059D8	00000030	0003FF1C

ENTRY POINT= 700059D8

Appendix XII. Composition analysis of pre-spawn and post-spawn gravel.

APPENDIX XII

Sieve size	Pre-Spawn (n = 2)	Cum.	Post-Spawn (n = 3)	Cum.
+5 inch	7.00	100	0.00	100
+4	13.05	93.00	4.17	99.98
-3	2.55	79.95	11.83	95.81
-2-1/2	7.80	77.40	12.57	83.98
-2	16.15	69.60	21.87	71.41
-1-1/2	20.20	53.45	20.63	49.54
-1	7.55	33.25	9.03	28.91
+3/4	10.05	27.70	7.90	19.88
+1/2	4.25	15.65	2.90	11.98
+3/8 or smaller	11.40	11.40	9.08	9.08

+ Average size composition per category in post-spawn gravel is smaller than in pre-spawn sample.

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