

Changes in Glycogen and Lactate Levels in Migrating Salmonid Fishes Ascending Experimental "Endless" Fishways^{1,2,3}

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ABSTRACT

Certain aspects of the performance and biochemistry of adult migrating salmonid fishes were investigated during ascents of 1:16- and 1:8-slope experimental fishways which employed locking devices permitting the simulation of fishways of any length. Fish tested were chinook salmon (*Oncorhynchus tshawytscha*), sockeye salmon (*O. nerka*) and steelhead trout (*Salmo gairdneri*) diverted from their upstream migration on the Columbia river at the Bonneville dam fishways during the summer of 1959. Blood and muscle lactate, and muscle and liver glycogen levels were determined in control fish, and in fish following three types of activity. Records of individual performance were kept.

All species were willing to enter and capable of ascending fishways of either slope up to 1000 ft in height under favourable hydraulic conditions. Blood lactate and muscle glycogen determinations revealed the degree of exercise to be moderate even during prolonged ascents. Moderately high ascents (about 100 ft) in the steeper fishway apparently required the expenditure of some muscle glycogen whereas similar ascents in the 1:16 fishway did not. When muscle glycogen was utilized during prolonged ascents the expenditure appeared to be progressive. All species were apparently able to adapt to prolonged ascents of either fishway. Certain fish of each species tended to stop moving of their own volition in both fishways. After a 60-min volitional stop some evidence of recovery from the effects of exercise was observed. Discussion of the above data is presented.

INTRODUCTION

THE PRIMARY PURPOSES of the investigations were to study the behaviour and performance of salmonid fishes in fishways, and to determine the feasibility of using fishways of steeper than normal slope. The fishway slope accepted as standard on mainstem Columbia river dams until recently was 1:16 (i.e. 1 ft, or 30.5 cm, rise in 16 ft, or 4.88 m, of length). One exception is the 1:10-slope fishway system at Rock Island dam which has been in operation since 1933. The use of a 1:10- or 1:8-slope in new fishways could, under certain conditions, substantially reduce the costs of fishway construction.

Although many studies have been made on the effects of severe exercise on fish, very few have been carried out on fish subjected to moderate exercise. The experiments planned in order to study the effects of fishway design on swimming performance presented the opportunity to collect extensive data on the biochemistry of adult fish during moderate sustained exercise.

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Experiments were conducted at the Fisheries-Engineering Research Laboratory operated by the Bureau of Commercial Fisheries of the U.S. Fish and Wildlife Service in conjunction with the U.S. Army Corps of Engineers⁴ at North Bonneville, Washington, during 1958 and 1959.

In 1958, the work was primarily directed to studying the performance of salmon and trout in fishways of both 1:16- and 1:8-slope, and to determining the hydraulic conditions best suited to the passage of these fish in a 1:8 fishway. Preliminary studies on the biochemistry of fishes ascending both fishways were carried out. The results of the 1958 experiments have been published in detail by Collins *et al.* (1963). In summary, their conclusions were: (1) that the 1:8 fishway is as suitable for the passage of chinook salmon (*Oncorhynchus tshawytscha*), sockeye or blueback salmon (*O. nerka*), and steelhead trout (*Salmo gairdneri*) as is the conventional 1:16 fishway provided the proper hydraulic conditions are attained; (2) that the ability of these fishes (particularly chinook salmon) to pace themselves in a 1:8-slope fishway is dependent on the hydraulic conditions; and (3) that under the proper conditions, the ascent of either fishway constitutes only moderate exercise for salmonid fishes.

The 1959 studies which are reported here were designed to give more complete information on the biochemical aspects of the ascent of fishways by salmonid fishes under controlled conditions.

A report has been published by Collins *et al.* (1962) on the ability of salmonids to ascend extended fishways of 1000 ft or more. The report embodies some of the results from the 1959 studies. They concluded that high fishways are suitable for the passage of chinook, sockeye and steelhead under the conditions tested, and that the degree of muscular effort involved, as judged by the blood lactate response, is only moderate. No evidence of fatigue was found on the basis of either performance or blood lactate levels.

Studies by several workers (reviewed by Black *et al.*, 1961) have revealed that severe fatigue in fishes is accompanied by a marked and prolonged elevation of the blood and muscle lactate and pyruvate levels, and by a reduction of the muscle glycogen level. It has been concluded that, during strenuous exercise, fish rely primarily on the anaerobic breakdown of muscle glycogen to supply the energy for muscular contraction. The overall pattern is similar to that observed in mammals including man, but the time course of lactate removal from the blood and of restoration of muscle glycogen in certain fishes is extremely protracted when compared with warm-blooded animals. Black *et al.* (1962) postulated that inadequacy of tissue oxygenation due to several factors, including a possible impairment of circulation following severe exercise, may contribute to the delay in removal of lactate. Muscle glycogen appears to be restored in immature trout following severe exercise only when they are feeding. However, Fontaine and Hatey (1953) observed that in migrating, non-feeding Atlantic salmon (*S. salar* L.) ascending the Adour river the total stores of carbohydrate,

⁴Research financed by the U.S. Army Corps of Engineers as a part of a broad program of Fisheries-Engineering Research for the purpose of providing design criteria for fish-passage facilities at Corps projects on the Columbia river.

although redistributed throughout the body, remained more or less constant. They attributed this maintenance of carbohydrate reserves, despite the expenditure of considerable muscular effort, to an increased rate of conversion of lipid and protein to carbohydrate.

Controlled biochemical studies on moderate exercise in fishes are not very numerous nor complete since recovery patterns have not yet been fully investigated. In rainbow trout (*S. gairdneri*) following 30 min cruising in a rotating chamber, the blood lactate level is elevated approximately 3-fold, and the muscle glycogen may or may not be reduced (Black, 1957a; Black *et al.*, 1960 and 1962).

In the present studies on chinook and sockeye salmon and steelhead trout, blood and muscle lactate, and muscle and liver glycogen were measured in control fish, and in fish following ascents of various durations in both the 1:8 and 1:16 fishways in an attempt to determine the degree of muscular effort and fatigue which was involved.

METHODS AND MATERIALS

The fish used in the experiments were of three species: chinook salmon (*Oncorhynchus tshawytscha*), sockeye salmon (*O. nerka*) and steelhead trout (*Salmo gairdneri*). These fish were in the maturing, or fully mature, state and were diverted from their upstream migration 140 river miles (225.3 km) from the mouth of the Columbia river at the Washington-shore fishway of Bonneville dam.

The physical design of the laboratory and the experimental "endless" fishways has been described in detail by Collins *et al.* (1963). A brief resumé is given here.

In all procedures involving the passage of fish, the only stimulus employed was the apparently natural instinct of spawning salmonids to swim upstream against a current. The fish entered the laboratory collection pool at an elevation of 50 ft (15.24 m) above mean sea level. Fish showing obvious signs of recent severe injury or ill health were rejected. Most of the fish used in 1959 were held in the collection pool for 1–6 hr before testing. A small group of sockeye salmon was held overnight before use.

The design of the "endless" fishways is illustrated in Fig. 1. Each fishway comprised a circuit of 16 pools including 2 turn pools and a lock connecting the highest pool with the lowest, thus making possible the simulation of a fishway of any length. The fishway construction was of the pool-and-overfall type without submerged orifices. The dimensions of the pools were 3 ft (91.4 cm) in width, and 8 or 16 ft (2.44 or 4.88 m) in length depending on the fishway slope. The freeboard was 3 ft (91.4 cm) and the average water depth was 6.8 ft (2.07 m). The rise between pools was 1 ft (30.5 cm). The turn pools were coved and, because of the tendency of fish to use them as rest areas, were provided with a grill which limited the available depth to 2 ft (61.0 cm), and a system of floor baffles which created a turbulent, rapidly flowing water pattern. Lock pools in both fishways were 8 ft (2.44 m) in length, 23 ft (7.01 m) deep when filled and 7 ft (2.13 m) deep when emptied. The time required to empty the lock was approximately 30–40 sec. Refilling of the lock required about 1 min and was accomplished after a fish had left the lock pool on another circuit of the fishway.

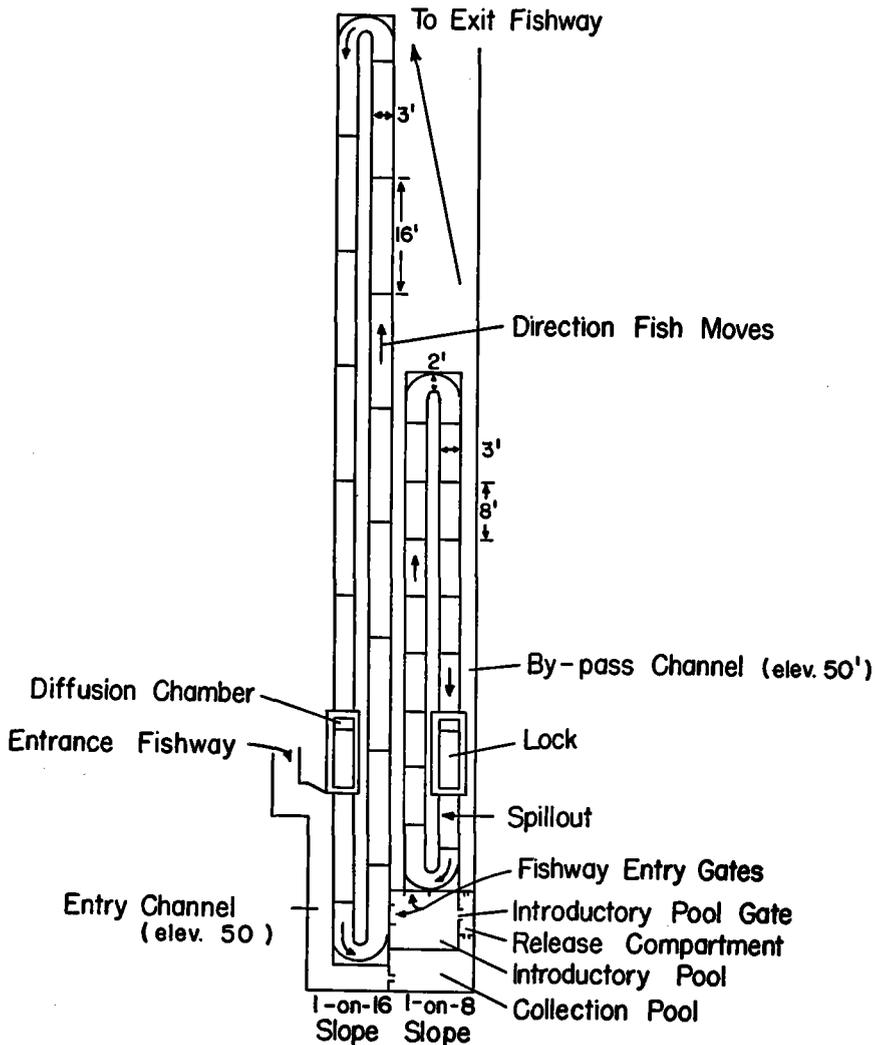


FIG. 1. Plan view of the 1:16- and 1:8-slope experimental "endless" fishways with auxiliary approach channels and pools. Bonneville, 1958-9. (Diagram courtesy of Bureau of Commercial Fisheries, Seattle.)

In the original design of the fishways, the weir crests were 3 ft (91.4 cm) long and 2 inches (5.08 cm) wide. During the 1958 experiments, it was found that many of the chinook salmon tended to ascend rapidly in the straight portions of the 1:8 fishway and rest in the turn pools (Collins *et al.*, 1963). When rest areas were eliminated by introducing a turbulent flow in the turn pools as described above, the chinook became unduly fatigued or stopped moving. Tests showed that the following modification in design provided more favourable hydraulic conditions. The weirs on the 1:8-slope fishway were restricted to

26½ inches (67.3 cm) by alternating baffles (Fig. 2) and, as a result, the turbulence in each pool was considerably reduced, and a definite lateral component was introduced into the flow pattern thus enabling the fish to rest during the ascent. The 1:16 fishway retained full 3-ft (91.4-cm) wide weir crests throughout 1958 and 1959.

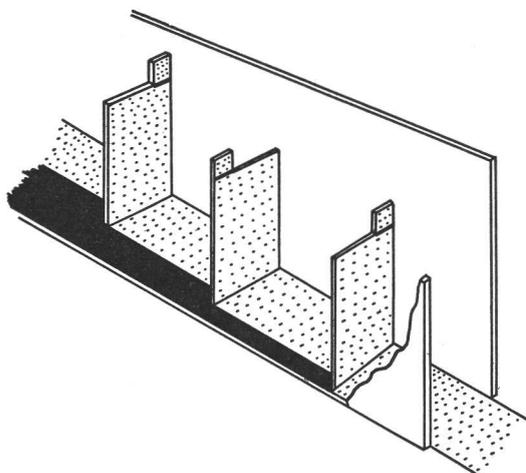


FIG. 2. Diagram of the 1:8-slope experimental "endless" fishway construction showing arrangement of alternate baffles to restrict the weir crests. Bonneville, 1958. (Diagram courtesy of Bureau of Commercial Fisheries, Seattle.)

With a single exception, both fishways remained structurally unchanged in 1959 from the conditions prevailing at the conclusion of the 1958 experiments. The minor change referred to consisted of a vertical stabilizer which was attached at right angles to each weir baffle in the 1:8-slope fishway only (Fig. 3 and 4). These stabilizers extended approximately 12 inches (30.5 cm) upstream and downstream into each pool. Their purpose was to reduce the draw-down of water over the weirs, and also to diminish the substantial air space beneath the weir overfall, thus providing more water depth for passage of large fish over the weir. The actual effect of the changed hydraulics on fish movement was not established in these tests, however, there was a possibility that the blind pocket created on the downstream side of each weir (Fig. 4) may have delayed the movement of some fish in this fishway.

The setting of the heads on the weirs, measured 4 ft (1.22 m) upstream of the weir crests, was 0.8 ft (24.4 cm), and a plunging flow was maintained with the non-orifice condition.

Fish were sampled from the holding pool in the control state, and from each fishway in 3 different conditions of exercise. The *control* fish were dipped from the holding pool or identification chamber 1-6 hr after entry, and were considered to be in a relatively unexercised state. The largest experimental group consisted

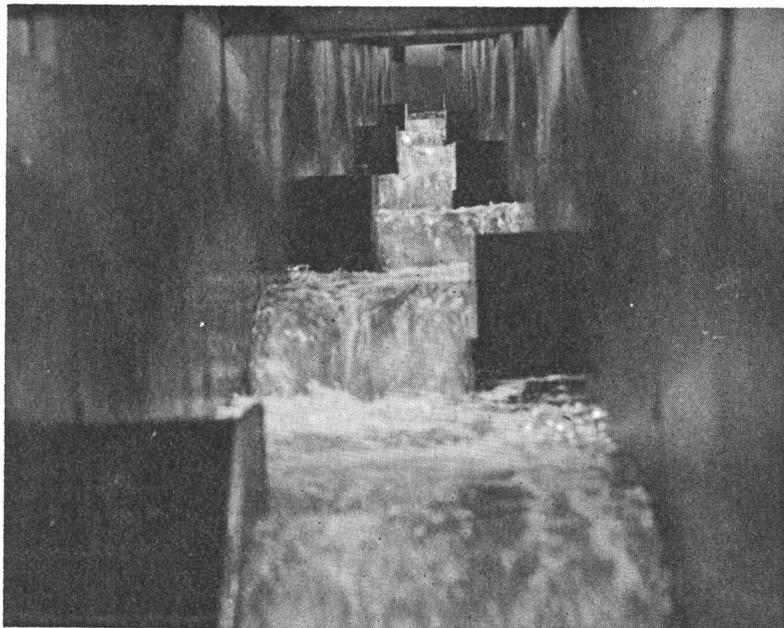


FIG. 3. View up the 1:8-slope experimental "endless" fishway showing the alternate baffle arrangement on weir crests, and the placement of the vertical stabilizers. Bonneville, 1959. (Photograph courtesy of Bureau of Commercial Fisheries, Seattle.)

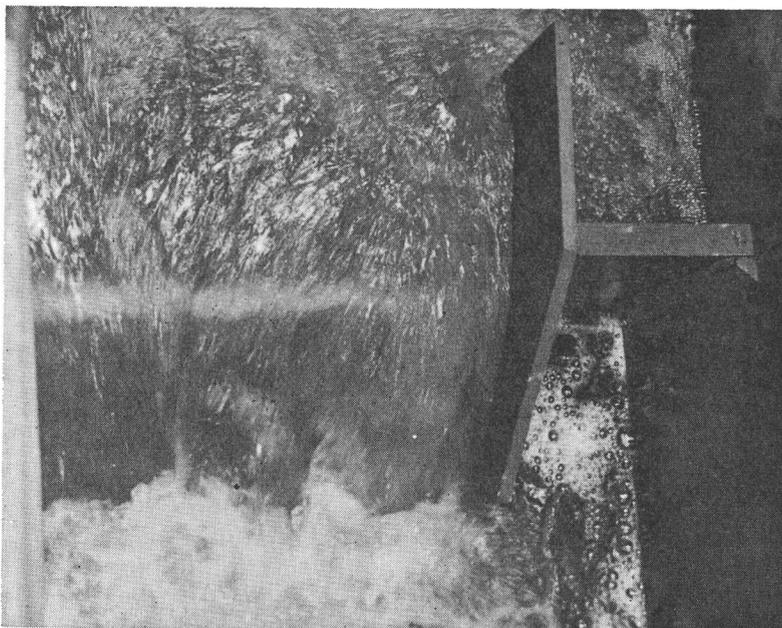


FIG. 4. View from above of a weir crest in the 1:8-slope experimental "endless" fishway showing the blind pocket created on the downstream face by the vertical stabilizer. Bonneville, 1959. (Photograph courtesy of Bureau of Commercial Fisheries, Seattle.)

of fish of each species which were sampled immediately upon entry into the 104th pool of either fishway (*104-pool terminated*). This standard ascent of 104 pools was arbitrarily chosen for its convenience (i.e. the upper turn pool on the 7th circuit of either fishway), and because it approximates the length of ascent in many existing fishways at low-head dams in the Columbia river basin. Another smaller group of fish of each species was sampled after completing various numbers of pools between 104 and 1000 in either fishway (*long-run terminated*). In both of the terminated treatments, the fish were considered to be in an actively moving state at the time of sampling. Under the hydraulic conditions described, a number of fish of each species showed a tendency to stop moving of their own volition and to remain in one pool for a considerable length of time during ascents of both fishways. These were called *volitional-stop* fish, and were sampled after they had remained for 60 min in any one pool. (A few fish were also sampled after a 30-min stop.) The volitional fish were considered to be in an inactive or recovery state at the time of sampling.

Sampling of fish was carried out as follows. The fish was lifted from the terminal pool with a dip net, stunned and carried quickly to the working area where it was placed ventral side uppermost in a V-shaped trough. The time required for this stage of sampling ranged from 10–35 sec except where difficulty was encountered in netting.

A blood sample of 2 ml was obtained by cardiac puncture, and transferred into a tube containing 18 ml of cold 10% trichloroacetic acid (TCA). After mixing, the filtrate was collected in a 1-oz polyethylene bottle in which it was stored in the frozen state until analyzed for lactate.

A muscle core was obtained with a punch from the left side of the fish between the lateral line and dorsal fin. Skin and scale were removed and the sample was divided into two portions and dropped into a freezing mixture of 95% ethanol and dry ice. The abdomen was opened and a liver sample of 1–2 g was removed and placed in the freezing mixture. Muscle and liver samples were kept frozen until extracts were prepared, in some cases overnight. In one series of experiments on chinook salmon, an additional muscle core was removed from a position near the tail of the fish for purposes of comparison.

For lactate determination, frozen muscle samples of approximately 2 g were weighed rapidly and placed in 18 ml of cold 10% TCA. A homogenate was prepared by grinding for 5 min in a Servall Omni-Mixer with the cup immersed in ice-water. The homogenate was then filtered and frozen as for blood.

For glycogen determination, frozen samples of muscle and liver (1–5 g) were weighed and dropped into 6 ml of hot 60% KOH. After 2 hr in a boiling water bath, the digests were transferred quantitatively while still hot to 1-oz bottles, using 10–15 ml of distilled water for rinsing. Digests were stored at room temperature.

Muscle and blood lactate were determined in the TCA filtrates by the method of Barker and Summerson (1941). Muscle and liver glycogen were determined in the KOH digests following dilution to a standard volume with distilled water and precipitation in 65% ethanol with the addition of Na_2SO_4 . The phenol-

sulphuric acid method of Montgomery (1957) was used for glycogen determinations of chinook and sockeye samples, and the anthrone method as described by Carroll *et al.* (1956) was used for steelhead samples.

Fishway water temperatures, measured daily, ranged from 56 to 70°F (13.3–21.1°C) throughout the 3 months of the experiment (June 2 to September 2, 1959). These temperatures were slightly lower than those prevailing during the 1958 experiments discussed by Collins *et al.* (1963).

The body weight of each fish was recorded. Accurate records were kept of the duration of each ascent and of the individual time per pool for every fish. Other measurements included daily water turbidity, and fork length and gonad weight of each fish. These latter data are not discussed in the present paper, since no correlation was found between observed variations and the biochemical properties under consideration.

Standard error of the mean was calculated for each condition, and is recorded in the tables. Where comparisons were made between means, Snedecor's "F" test for homogeneity of variance was applied to the mean squares of each group ($F = \text{greater mean square/lesser mean square}$; Snedecor, 1956, p. 96). Where the variances proved to be homogeneous at the 5% level, a standard Fisher "t" test was applied to estimate the probability of a significant difference between means (Snedecor, 1956, pp. 87–91). In many cases, where the treatments appeared to have affected the standard deviations of the sample groups, as shown by an F value exceeding the 5% level, "t'" was calculated from the formula $t' = (\bar{x}_1 - \bar{x}_2) / s \sqrt{\frac{1}{n_1} + \frac{1}{n_2}}$ and the 5% probability level of "t'" was estimated by Cochran's approximation (Snedecor, 1956, pp. 97–99). A probability of a larger value of "t'" or "t'", sign ignored, of 5% (0.05) or less was considered to be significant.

RESULTS

METHODOLOGY

Results of a comparison of lactate and glycogen levels in muscle cores taken near the tail with those in cores taken from the usual position below the dorsal fin are presented in Table I. Samples were obtained from chinook salmon upon

TABLE I. Comparison of lactate and glycogen levels in muscle cores taken from the "front" and the "back" positions of migrating Columbia river chinook salmon (*O. tshawytscha*) sampled after ascents of 104 pools (104 ft) in the experimental fishways. Bonneville, 1959.

| | | Muscle lactate | | Muscle glycogen | |
|------------|-------------|----------------|------------|-----------------|----------------|
| | | Front | Back | Front | Back |
| 1:16-slope | Mean ± SE | 315 ± 31.1 | 324 ± 31.3 | 0.154 ± 0.0275 | 0.190 ± 0.0387 |
| | No. of fish | (7) | (7) | (7) | (7) |
| | Range | 192–421 | 225–459 | 0.079–0.304 | 0.094–0.331 |
| 1:8-slope | Mean ± SE | 413 ± 55.8 | 332 ± 48.2 | 0.126 ± 0.0139 | 0.153 ± 0.0205 |
| | No. of fish | (4) | (4) | (4) | (4) |
| | Range | 247–475 | 257–470 | 0.089–0.154 | 0.106–0.203 |

TABLE II Mean sampling times, the standard error of the means and the range of sampling times (in seconds) measured from the time of capturing fish. Data are for migrating Columbia river chinook salmon (*O. tshawytscha*), sockeye salmon (*O. nerka*) and steelhead trout (*S. gairdneri*) taken from the holding pool (controls), from the experimental fishways during active ascent (terminated), and from the experimental fishways after a 60-min stop (volitional). Bonneville, 1959.

| | | Chinook | | | Sockeye | | | Steelhead | | |
|-------------------------------------|---------------|-----------------|------------------|------------------|-----------------|-----------------|-----------------|-----------------|-----------------|------------------|
| | | Blood | Muscle | Liver | Blood | Muscle | Liver | Blood | Muscle | Liver |
| Controls | Mean \pm SE | 73.8 \pm 6.48 | 108.1 \pm 7.33 | 126.0 \pm 8.43 | 50.1 \pm 2.31 | 72.5 \pm 2.91 | 82.3 \pm 3.57 | 72.2 \pm 5.33 | 95.6 \pm 5.93 | 104.5 \pm 6.29 |
| | No. of fish | 35 | 35 | 35 | 21 | 22 | 22 | 25 | 25 | 24 |
| | Range | 43-200 | 59-220 | 71-233 | 32-90 | 53-110 | 61-130 | 46-171 | 63-200 | 76-210 |
| Terminated (all con- ditions) | Mean \pm SE | 61.2 \pm 4.08 | 91.8 \pm 4.65 | 107.4 \pm 5.14 | 43.0 \pm 4.24 | 66.3 \pm 4.39 | 75.1 \pm 4.37 | 51.8 \pm 2.70 | 74.0 \pm 3.01 | 83.1 \pm 3.27 |
| | No. of fish | 80 | 81 | 81 | 46 | 46 | 46 | 86 | 88 | 88 |
| | Range | 29-235 | 45-270 | 52-298 | 26-220 | 45-240 | 51-245 | 24-182 | 42-209 | 46-217 |
| Volitional (all con- ditions) | Mean \pm SE | 72.4 \pm 5.04 | 112.4 \pm 6.81 | 129.2 \pm 7.39 | 43.0 \pm 2.46 | 64.9 \pm 3.62 | 74.6 \pm 4.56 | 68.2 \pm 7.58 | 96.6 \pm 8.58 | 108.7 \pm 9.60 |
| | No. of fish | 30 | 30 | 30 | 14 | 14 | 14 | 21 | 22 | 22 |
| | Range | 35-167 | 50-225 | 56-240 | 29-53 | 45-90 | 49-107 | 34-150 | 55-180 | 60-210 |

completion of ascents of moderate length (104 ft) in both fishways. Differences in muscle lactate and muscle glycogen levels between "front" and "back" core samples were not significant. There was no evidence that the degree of muscular contraction was greater near the tail of the fish during swimming. In fact, the ratio of lactate to glycogen was actually lower in the "back" core than in the "front". These findings are similar to those observed in 1½-year-old rainbow trout by Black *et al.* (1962) who concluded that no appreciable error would result from the routine use of the "front" position for sampling.

The average times taken to sample blood, muscle and liver in each species in the control, terminated and volitional conditions are shown in Table II. The shortest sampling times were recorded for the terminated conditions (both 104-pool and long-run) mainly because the fish were easier to reach and closer to the working area than those in the holding pool or those that stopped volitionally in certain areas of the fishways. It is also possible that fish terminated during active ascent struggled less upon capture than those in the control state or after 60 min in one pool.

CONTROL FISH

BLOOD LACTATE. Blood lactate for the control chinook salmon averaged 17.8 mg per 100 ml blood (mg%); the average for sockeye (blueback) salmon was 17.4 mg%; and the average for steelhead trout was 12.2 mg% (Table III). These values are somewhat higher than most of those reported by other workers for various species of fish (Black *et al.*, 1961, table VIII). The slightly higher value noted here for salmon as compared with trout is in keeping with the observations referred to above.

Blood lactates for the control fish probably represent values higher than those for the completely unexercised condition. The previous history and degree of activity in the holding pool for individual fish are not known. The flow of water used to stimulate fish to enter the experimental fishways frequently rendered all fish in the holding pool more active. Sockeye salmon which had been held overnight showed a significantly lower ($0.025 > P > 0.01$) blood lactate value (10.9 ± 1.44 mg%) than fresh fish which had been held 1-6 hr (19.5 ± 1.99 mg%). The lowering of blood lactate levels may be attributed to the longer holding period and the absence of disturbance during the night, together with a probable nocturnal reduction in metabolism and activity. Similar tests in 1958 failed to show any difference between lactate levels of fresh and heldover chinook salmon (Collins *et al.*, 1963).

The amount of struggling during netting and the completeness of stunning after capture undoubtedly varied between fish. However, no correlation was found between the sampling times (Table II) and the blood lactate values on an individual basis, probably because of the multiplicity of factors in this situation which may influence the lactate level. The values are presented as controls for subsequent experiments and are not intended to represent the true blood lactate levels for unexercised fish.

TABLE III. Body weights and levels of blood and muscle lactate, and muscle and liver glycogen in migrating Columbia river chinook salmon (*O. tshawytscha*), sockeye salmon (*O. nerka*) and steelhead trout (*S. gairdneri*) taken from the holding pool in the control state. Bonneville, 1959.

| | | Body weight | Lactate | | Glycogen | |
|-----------|---------------------------------------|------------------|-----------------|----------------|--------------------|------------------|
| | | | Blood | Muscle | Muscle | Liver |
| | | kg | mg% | mg/100 g | % | % |
| Chinook | Mean \pm SE | 5.28 \pm 0.421 | 17.8 \pm 1.37 | 394 \pm 17.3 | 0.127 \pm 0.0101 | 0.69 \pm 0.101 |
| | No. of fish | 35 | 35 | 35 | 35 | 35 |
| | Range | 1.39-10.53 | 5.7-38.5 | 238-600 | 0.053-0.346 | 0.04-2.62 |
| | Male mean (<i>n</i>) | 3.59 (17) | 15.3 (17) | 385 (17) | 0.123 (17) | 0.99 (17) |
| | Female mean (<i>n</i>) | 6.64 (18) | 20.1 (18) | 402 (18) | 0.131 (18) | 0.42 (18) |
| Sockeye | Mean \pm SE | 1.19 \pm 0.054 | 17.4 \pm 1.74 | 391 \pm 23.7 | 0.086 \pm 0.0063 | 0.61 \pm 0.105 |
| | No. of fish | 22 | 21 | 22 | 22 | 22 |
| | Range | 0.57-1.58 | 5.5-35.8 | 219-574 | 0.037-0.151 | 0.04-1.64 |
| | Male mean (<i>n</i>) | 1.21 (9) | 18.6 (9) | 394 (9) | 0.100 (9) | 1.03 (9) |
| | Female mean (<i>n</i>) | 1.17 (13) | 16.6 (12) | 390 (13) | 0.076 (13) | 0.31 (13) |
| | Fresh (held 1-6 hr) mean (<i>n</i>) | 1.16 (17) | 19.5 (16) | 391 (17) | 0.086 (17) | 0.52 (17) |
| | Held overnight mean (<i>n</i>) | 1.27 (5) | 10.9 (5) | 393 (5) | 0.087 (5) | 0.89 (5) |
| Steelhead | Mean \pm SE | 2.93 \pm 0.252 | 12.2 \pm 0.87 | 416 \pm 19.4 | 0.079 \pm 0.0055 | 1.31 \pm 0.197 |
| | No. of fish | 25 | 25 | 25 | 25 | 25 |
| | Range | 1.61-5.72 | 4.9-19.9 | 290-665 | 0.035-0.134 | 0.18-4.78 |
| | Male mean (<i>n</i>) | 2.24 (7) | 12.5 (7) | 450 (7) | 0.068 (7) | 2.19 (7) |
| | Female mean (<i>n</i>) | 3.19 (18) | 12.2 (18) | 403 (18) | 0.083 (18) | 0.97 (18) |

MUSCLE LACTATE. The average muscle lactate values for control fish were as follows: chinook salmon, 394 mg/100 g wet tissue; sockeye salmon, 391 mg/100 g; and steelhead trout, 416 mg/100 g (Table III). There was no significant difference between the values for fresh sockeye and those held overnight.

These values are much higher than those reported in the literature for unexercised fish (Nakatani, 1957; Leivestad *et al.*, 1957; Tomlinson *et al.*, 1961; Fraser *et al.*, 1961; Black *et al.*, 1962). The values are in fact similar to those reported by most of these authors for severely exercised or exhausted fish. However, the data of Tomlinson *et al.* (1961), for sockeye which had been commercially netted both at sea and in fresh water, and were probably exhausted, show lactate levels 100–200 mg/100 g higher than those in the control sockeye studied here.

There are several factors which may contribute to the high muscle lactate levels in these experiments. The average sampling times for muscle ranged from 72.5–108.1 sec (Table II). A time curve for the production of muscle lactate during strenuous exercise prepared by Black *et al.* (1962) for rainbow trout indicates that muscle lactate had reached over $\frac{3}{4}$ of its eventual maximum value within the first 2 min, whereas blood lactate had risen to only $\frac{1}{5}$ of its eventual peak value in the same period. The increase in blood lactate is delayed due to the time required for diffusion from muscle. Thus a large part of the muscle lactate found in the present experiments could have been generated during the sampling interval before the blood level had risen appreciably, especially since blood samples were taken first. Severe struggling of the fish during capture and stunning could contribute significantly to this increase in muscle lactate. Other factors which may have influenced the muscle lactate levels are the age and endocrine status of the fish, the recent environmental change from salt to fresh water, the relatively high water temperatures in the river, and the initial levels of the precursor, muscle glycogen.

High muscle lactate values were observed throughout the entire experiment and no significant differences appeared in any of the 104-pool, long-run or volitional groups in response to exercise, despite significant alterations in blood lactate and muscle glycogen. Muscle lactate data are included in the tables, but are not discussed further since they do not appear to be meaningful in terms of these experiments.

MUSCLE GLYCOGEN. The average levels of muscle glycogen in control fish were as follows: chinook 0.127 g/100 g wet tissue (%); sockeye, 0.086%; and steelhead, 0.079% (Table III). These values fall within the ranges reported for various species of fish in the literature (reviewed by Black *et al.*, 1961, and Tomlinson and Geiger, 1962), but appear somewhat low for adult fish. Earlier studies (Greene, 1921; and Fontaine and Hately, 1953) reported low levels of 0.01–0.15% in adult salmon at the start of the spawning migration, however, the methods of capturing and sampling employed were such that considerable loss of glycogen through struggling or autolysis could have occurred. Black *et al.* (1960) reported an average level of 0.378% in spawning Kamloops trout even without the use of quick-freezing techniques. Various studies of the *post-mortem* increase in muscle lactate such as those of Tomlinson *et al.* (1961)

indicate that the initial level of the precursor may have been considerably higher. These studies however should be interpreted cautiously since Tarr and Leroux (1962) have shown the existence of other intermediary metabolites in fish muscle capable of resulting in lactate formation. The factors mentioned above as tending to increase the control blood and muscle lactate levels during sampling would also lower the muscle glycogen levels. In view of the high muscle lactate levels, it is indeed probable that all muscle glycogen levels reported here are somewhat low. However, it was still found possible to demonstrate statistically significant changes in the muscle glycogen in response to exercise in most of the experimental situations, although the relative difficulty in sampling and the probability of greater struggling in control fish may have resulted in less apparent difference between control and exercised fish than actually existed.

LIVER GLYCOGEN. The average liver glycogen level in control chinook was 0.69% wet weight (Table III). Male chinook had a significantly higher ($0.025 > P > 0.01$) average level ($0.99 \pm 0.171\%$) than female chinook ($0.42 \pm 0.065\%$). The average level in sockeye salmon was 0.61%. The mean level was again significantly higher ($P < 0.001$) in males ($1.03 \pm 0.147\%$) than in females ($0.31 \pm 0.070\%$). In steelhead trout, the average level of liver glycogen was 1.31%. The difference between male ($2.19 \pm 0.502\%$) and female ($0.97 \pm 0.129\%$) steelhead was not significant.

Since liver glycogen does not appear to respond immediately to muscular exertion (Black *et al.*, 1960, 1962), it is possible to make comparisons with other data with some degree of confidence. As noted by Fontaine and Hatey (1953), the levels of glycogen in both muscle and liver in migrating, non-feeding Atlantic salmon represent an equilibrium between forces tending to mobilize carbohydrate and the demands made upon stored glycogen. The present values for liver glycogen are markedly lower than values obtained in 1958 at Bonneville. Collins and Elling (1958, unpublished data) found the following levels of liver glycogen in control fish under conditions similar to those prevailing in the present experiments: chinook, $1.26 \pm 0.281\%$; sockeye, $2.37 \pm 0.299\%$; steelhead, $2.01 \pm 0.348\%$. The 1959 data reported here are also lower than those recorded by Fontaine and Hatey (1953) for migrating adult Atlantic salmon. No explanation is available for the low levels of liver glycogen found in these experiments. However, Black *et al.* (1960, 1962) found marked variations in the average level of liver glycogen in hatchery reared, juvenile trout in the unexercised condition in different years which they attributed, at least in part, to a difference in diet. The higher levels in male than in female salmon noted here were also observed by Fontaine and Hatey (1953), and by Chang and Idler (1960) in migrating sockeye on the Fraser river. The liver glycogen level in the 1959 steelhead trout was nearly twice as high as in either of the salmon species.

The liver glycogen levels of terminated and volitional fish in the experimental fishways did not differ significantly from each other or from the control levels. This finding is in accordance with earlier reports by Black *et al.* (1960, 1962) on rainbow trout. Liver glycogen levels in salmonid fishes do not appear to be affected by muscular activity, at least on a short-term basis. However, a high

degree of variation between individual levels seems to be characteristic, and may be sufficient to mask slight changes in response to exercise. Liver glycogen levels are recorded in the tables for all conditions, but will not be discussed.

COMPARISON OF MALE AND FEMALE FISH

Except for higher liver glycogen levels in male than in female salmon, no sex-related differences in lactate and glycogen levels or in performance were observed in either control or 104-pool terminated fish. In the long-run and volitional groups, there were not enough fish to permit a comparison between males and females. Collins *et al.* (1963) observed a higher blood lactate level in female than in male chinook following ascent of the fishways, but this was not confirmed in the present study.

104-POOL TERMINATED FISH

CHINOOK. Average blood lactate level in chinook salmon sampled immediately upon entering the 104th pool (i.e. 104 ft or 31.7 m ascent) in the 1:16-slope fishway was 29.4 mg% (Table IV) as compared with 17.8 mg% in control chinook (Table III). In chinook sampled after 104 pools in the 1:8 fishway the average was 32.4 mg%. The 1½- to 2-fold increase over the control levels was significant in both fishways ($P < 0.001$) and is typical of fish travelling at a cruising rate involving moderate exercise (Black, 1957a; Black *et al.*, 1960, 1962). The difference between the blood lactate levels in the 1:16 and 1:8 fishways was not significant.

Muscle glycogen levels for 104-pool terminated chinook averaged 0.135% in the 1:16 fishway and 0.092% in the 1:8 fishway (Table IV) as compared with 0.127% in control fish (Table III). The level in the 1:16 fishway does not differ significantly from the control level, however, the level in the 1:8 fishway is significantly lower than both the control ($0.01 > P > 0.005$) and the 1:16 ($P < 0.001$) levels. The relative ease of sampling fish from the 104th pool (i.e. the upper turn pool on the 7th circuit) and the possibility that fish struggle less after exercise than in the control state may account for the fact that level of muscle glycogen in 104-pool terminated chinook in the 1:16 fishway appears higher than the control level, and may mean that the actual reduction in the 1:8 fishway was somewhat greater than indicated. Black *et al.* (1962) have shown that 2 min of strenuous exercise may result in a 50% reduction in muscle glycogen levels. Since there was no difference in sampling 104-pool fish from the two fishways, the significant lowering of muscle glycogen after 104 pools in the 1:8 fishway as compared with the 1:16 fishway is apparently real and probably related to the greater degree of exercise in the steeper fishway.

The mean time taken for ascent of 104 pools in the 1:16 fishway was 209 min, and in the 1:8 fishway was 227 min (Table V). This difference, while not significant, may have been due to the creation of blind pockets on the downstream weir faces by the installation of vertical stabilizers in the 1:8 fishway (Fig. 3 and 4). In the previous season's work (Collins *et al.*, 1963) when the vertical stabilizers were not used (condition 2C, Fig. 2) the mean passage time of chinook in the 1:8 fishway (151 ± 9.6 min) was actually slightly less than that

TABLE IV. Body weights, blood and muscle lactate levels, and muscle and liver glycogen levels in migrating Columbia river chinook salmon (*O. tshawytscha*) at the completion of ascents of 104 pools (104 ft) in the experimental fishways. Bonneville, 1959.

| | | Body weight | Lactate | | Glycogen | |
|------------|--------------------------|--------------|-------------|-----------------|----------------|--------------|
| | | | Blood | Muscle | Muscle | Liver |
| | | <i>kg</i> | <i>mg%</i> | <i>mg/100 g</i> | <i>%</i> | <i>%</i> |
| 1:16-slope | Mean ± SE | 8.17 ± 0.550 | 29.4 ± 1.54 | 384 ± 16.3 | 0.135 ± 0.0094 | 0.78 ± 0.164 |
| | No. of fish | 33 | 32 | 33 | 33 | 33 |
| | Range | 2.27-14.32 | 13.7-51.4 | 192-561 | 0.053-0.304 | 0.07-4.96 |
| | Male mean (<i>n</i>) | 6.95 (12) | 32.3 (12) | 442 (12) | 0.127 (12) | 1.35 (12) |
| | Female mean (<i>n</i>) | 8.87 (21) | 27.7 (21) | 351 (21) | 0.139 (21) | 0.45 (21) |
| 1:8-slope | Mean ± SE | 7.54 ± 0.509 | 32.4 ± 1.92 | 403 ± 16.5 | 0.092 ± 0.0069 | 0.55 ± 0.096 |
| | No. of fish | 34 | 34 | 34 | 34 | 34 |
| | Range | 1.89-15.65 | 15.9-59.6 | 225-597 | 0.022-0.188 | 0.04-2.78 |
| | Male mean (<i>n</i>) | 7.26 (14) | 30.1 (14) | 397 (14) | 0.094 (14) | 0.94 (14) |
| | Female mean (<i>n</i>) | 7.73 (20) | 34.1 (20) | 408 (20) | 0.091 (20) | 0.27 (20) |

TABLE V. Mean passage times (in *minutes*) of migrating Columbia river chinook salmon (*O. tshawytscha*), sockeye salmon (*O. nerka*) and steelhead trout (*S. gairdneri*) which completed 104 pools (104 ft) in the experimental fishways. Bonneville, 1959.

| | Chinook | | Sockeye | | Steelhead | |
|---------------------|---------|---------|---------|---------|-----------|---------|
| | 1:16 | 1:8 | 1:16 | 1:8 | 1:16 | 1:8 |
| Mean time 104 pools | 209 | 227 | 141 | 181 | 136 | 158 |
| ± SE | ±8.3 | ±7.1 | ±6.1 | ±7.1 | ±6.3 | ±4.7 |
| No. of fish | 84 | 84 | 26 | 26 | 49 | 49 |
| Range | 104-526 | 121-456 | 82-210 | 137-262 | 83-331 | 103-276 |
| Mean time per pool | 2.01 | 2.18 | 1.36 | 1.74 | 1.31 | 1.52 |

in the 1:16 fishway (160 ± 15.9 min). The latter data apply to fall-run fish only, while the former represent an average of all runs (spring to fall). It is impossible to state what effect the delay may have had on the biochemistry of fish in the 1:8 fishway, since there is not sufficient data for any single group of fish under the same conditions (i.e. alternating weir crests) in 1958 to compare with the present data.

SOCKEYE. Average blood lactate values in sockeye salmon after 104 pools were 31.2 mg% in the 1:16 fishway, and 42.4 mg% in the 1:8 fishway (Table VI) as compared with a control level of 17.4 mg% (Table III). The increase over the control value was significant for both fishways ($P < 0.001$), and the 1:8 level was significantly higher than the 1:16 level ($0.01 > P > 0.005$). As in the case of the chinook, the increase in lactate is of the order found in young trout during moderate sustained exercise. A significant difference between the 1:16 and 1:8 blood lactate levels was found only in sockeye salmon, and was not apparent in the previous year's experiments (Collins *et al.*, 1963).

Muscle glycogen levels of sockeye after 104 pools in the 1:16 fishway averaged 0.074% (Table VI). This value was not significantly different from the control level of 0.086% (Table III). In the 1:8 fishway the average muscle glycogen level for 104-pool terminated sockeye was 0.053% which was significantly lower than both the control ($P < 0.001$) and the 1:16-slope ($0.005 > P > 0.001$) values. The greater reduction of muscle glycogen in the steeper fishway is concordant with the greater degree of activity reflected in the blood lactate increase above. The situation is similar to that seen in chinook salmon, but is more pronounced in the sockeye.

There were no significant differences in lactate or glycogen levels of fresh as compared with heldover sockeye. The effects of exercise in both fishways were evidently sufficient to overcome the reduction in blood lactate seen in control sockeye when they were held overnight.

Mean passage time for sockeye ascending 104 pools in the 1:8 fishway was 181 min, a value which was significantly longer ($P < 0.001$) than the mean time of 141 min in the 1:16 fishway. No data are available from the 1958 experiments

TABLE VI. Body weights, blood and muscle lactate levels, and muscle and liver glycogen levels in migrating Columbia river sockeye salmon (*O. nerka*) at the completion of ascents of 104 pools (104 ft) in the experimental fishways. Bonneville, 1959.

| | | Body weight | Lactate | | Glycogen | |
|---------------------------------------|--------------------------|------------------|-----------------|----------------|--------------------|------------------|
| | | | Blood | Muscle | Muscle | Liver |
| | | kg | mg% | mg/100 g | % | % |
| 1:16-slope | Mean \pm SE | 1.31 \pm 0.037 | 31.2 \pm 1.91 | 396 \pm 19.6 | 0.074 \pm 0.0041 | 0.89 \pm 0.119 |
| | No. of fish | 18 | 18 | 18 | 18 | 18 |
| | Range | 1.02-1.58 | 20.7-54.6 | 235-583 | 0.043-0.110 | 0.15-1.76 |
| | Male mean (<i>n</i>) | 1.40 (8) | 31.8 (8) | 383 (8) | 0.076 (8) | 1.29 (8) |
| | Female mean (<i>n</i>) | 1.24 (10) | 30.8 (10) | 407 (10) | 0.072 (10) | 0.57 (10) |
| Fresh (held 1-6 hr) mean (<i>n</i>) | | 1.34 (10) | 31.1 (10) | 393 (10) | 0.080 (10) | 0.77 (10) |
| Held overnight mean (<i>n</i>) | | 1.25 (6) | 32.5 (6) | 396 (6) | 0.066 (6) | 1.04 (6) |
| 1:8-slope | Mean \pm SE | 1.36 \pm 0.058 | 42.4 \pm 3.17 | 382 \pm 15.5 | 0.053 \pm 0.0048 | 0.75 \pm 0.169 |
| | No. of fish | 18 | 18 | 18 | 18 | 18 |
| | Range | 1.07-2.15 | 17.6-63.2 | 282-522 | 0.032-0.112 | 0.06-2.51 |
| | Male mean (<i>n</i>) | 1.42 (10) | 40.8 (10) | 370 (10) | 0.058 (10) | 1.15 (10) |
| | Female mean (<i>n</i>) | 1.29 (8) | 42.3 (8) | 398 (8) | 0.046 (8) | 0.25 (8) |
| Fresh (held 1-6 hr) mean (<i>n</i>) | | 1.40 (12) | 43.0 (12) | 391 (12) | 0.051 (12) | 0.70 (12) |
| Held overnight mean (<i>n</i>) | | 1.26 (5) | 43.4 (5) | 357 (5) | 0.055 (5) | 1.00 (5) |

TABLE VII. Body weights, blood and muscle lactate levels, and muscle and liver glycogen levels in migrating Columbia river steelhead trout (*S. gairdneri*) at the completion of ascents of 104 pools (104 ft) in the experimental fishways. Bonneville, 1959.

| | | Body weight | Lactate | | Glycogen | |
|------------|-----------------|--------------|-------------|------------|----------------|--------------|
| | | | Blood | Muscle | Muscle | Liver |
| | | kg | mg% | mg/100 g | % | % |
| 1:16-slope | Mean ± SE | 3.12 ± 0.204 | 20.0 ± 1.05 | 424 ± 14.4 | 0.070 ± 0.0041 | 1.16 ± 0.114 |
| | No. of fish | 37 | 37 | 38 | 38 | 38 |
| | Range | 1.56-6.11 | 5.8-23.8 | 261-607 | 0.025-0.132 | 0.22-3.03 |
| | Male mean (n) | 2.98 (13) | 22.2 (13) | 453 (14) | 0.064 (14) | 1.33 (14) |
| | Female mean (n) | 3.20 (24) | 18.9 (24) | 407 (24) | 0.074 (24) | 1.07 (24) |
| 1:8-slope | Mean ± SE | 2.62 ± 0.147 | 20.5 ± 1.17 | 395 ± 14.7 | 0.065 ± 0.0037 | 1.14 ± 0.137 |
| | No. of fish | 36 | 36 | 36 | 36 | 36 |
| | Range | 1.70-5.55 | 8.2-36.5 | 232-623 | 0.026-0.121 | 0.27-2.87 |
| | Male mean (n) | 2.55 (13) | 18.5 (13) | 370 (13) | 0.067 (13) | 1.13 (13) |
| | Female mean (n) | 2.66 (23) | 21.6 (23) | 410 (23) | 0.065 (23) | 1.15 (23) |

for sockeye passage times or biochemistry in the 1:8 fishway with alternating weir crests without vertical stabilizers. As in the case of the chinook above, it is possible that the modification in design caused a delay in the 1:8 fishway.

STEELHEAD. Average blood lactate levels in 104-pool terminated steelhead trout were 20.0 mg% in the 1:16 fishway and 20.5 mg% in the 1:8 fishway (Table VII). These values both represent significant increases ($P < 0.001$) over the control level of 12.2 mg% (Table III), but are not significantly different from each other. It should be re-emphasized that all blood lactate increases observed during 104-pool terminated ascents were of the order of magnitude associated with moderate sustained exercise, and did not approach the levels found in trout which have been chased to exhaustion for periods up to 15 min (Black, 1957a, b, c; Black *et al.*, 1959, 1960, 1962).

Average muscle glycogen levels in 104-pool terminated steelhead were 0.070% in the 1:16 fishway and 0.065% in the 1:8 fishway (Table VII). The 1:16 mean level does not differ significantly from the control level of 0.079% (Table III), but the 1:8 level is significantly lower ($0.05 > P > 0.025$) than the control, again indicating the probability of a slightly greater drain on metabolic stores in the steeper fishway. The 1:16 and 1:8 muscle glycogen levels do not differ significantly from each other.

The average passage time for steelhead completing 104 pools in the 1:16 fishway was 136 min which was significantly less ($0.01 > P > 0.005$) than the average time of 158 min in the 1:8 fishway (Table V). The delay may have been due to the use of vertical stabilizers in the steeper fishway. Although the passage times of steelhead and sockeye were similar in the 1:16 fishway, the time taken for steelhead to complete 104 pools in the 1:8 fishway was significantly less ($0.01 > P > 0.005$) than for sockeye. Yet the steelhead did not show any greater lactate increase in the steeper fishway, whereas the sockeye did.

LONG-RUN TERMINATED FISH

CHINOOK. Long-run chinook salmon were terminated at an average of 522 pools (range, 232–1000) in the 1:16 fishway, and 527 pools (range, 248–1000) in the 1:8 fishway. Several of the extremely long ascents were interrupted by the fish stopping volitionally during the night for periods totalling up to $7\frac{1}{2}$ hr. This occurred only in chinook and mainly during the spring-run. Since these fish were in an actively moving state at the time of sampling, they are included in the terminated category.

In the 1:16 fishway, the blood lactate of long-run chinook was elevated to 27.6 mg% (Table VIII). However, presumably because of the high degree of individual variation (S.E. ± 7.30) this value was not significantly different from the control level (Table III), nor did it differ from the level in 104-pool terminated chinook (Table IV). Muscle glycogen in long-run chinook in this fishway averaged 0.145% (Table VIII) and showed no significant change from either the control or 104-pool terminated levels.

In the 1:8 fishway, the average blood lactate level of long-run chinook was 29.6 mg% (Table VIII), a value which is significantly higher ($0.005 > P > 0.001$)

TABLE VIII. Body weights, blood and muscle lactate levels, and muscle and liver glycogen levels in migrating Columbia river chinook salmon (*O. tshawytscha*), sockeye salmon (*O. nerka*) and steelhead trout (*S. gairdneri*) at the completion of long-run terminated ascents (between 105 and 1000 ft) in the experimental fishways. The average numbers of pools completed are given in column 2. Bonneville, 1959.

| 1 | | 2 | 3 | 4 | | 5 | | 6 | | 7 | |
|-----------|-------------|------------------------|--------------|-------------|-------------|----------------|----------------|--------------|--|---|--|
| | | | | Lactate | | Glycogen | | | | | |
| | | No. of pools completed | Body weight | Blood | Muscle | Muscle | Liver | | | | |
| | | | | kg | mg% | mg/100 g | % | % | | | |
| Chinook | Mean ± SE | 522 ± 108.8 | 7.56 ± 1.377 | | 27.6 ± 7.30 | 364 ± 41.0 | 0.145 ± 0.0463 | 0.51 ± 0.127 | | | |
| | No. of fish | 7 | 7 | 7 | 7 | 7 | 7 | | | | |
| | Range | 232-1000 | 1.30-11.58 | 7.1-67.1 | 223-482 | 0.023-0.336 | 0.07-1.01 | | | | |
| 1:8-slope | Mean ± SE | 527 ± 124.4 | 8.50 ± 0.823 | 29.6 ± 3.07 | 375 ± 32.6 | 0.068 ± 0.0107 | 0.41 ± 0.091 | | | | |
| | No. of fish | 7 | 7 | 7 | 7 | 6 | 7 | | | | |
| | Range | 248-1000 | 4.73-11.38 | 20.4-41.6 | 237-493 | 0.042-0.101 | 0.07-0.74 | | | | |
| Sockeye | Mean ± SE | 839 ± 93.9 | 1.41 ± 0.049 | 19.7 ± 6.50 | 328 ± 54.8 | 0.028 ± 0.0082 | 0.59 ± 0.280 | | | | |
| | No. of fish | 4 | 4 | 4 | 4 | 4 | 4 | | | | |
| | Range | 648-1000 | 1.33-1.53 | 7.9-37.5 | 214-444 | 0.015-0.052 | 0.22-1.42 | | | | |
| 1:8-slope | Mean ± SE | 772 ± 131.7 | 1.25 ± 0.083 | 30.6 ± 3.84 | 317 ± 37.0 | 0.024 ± 0.0026 | 0.49 ± 0.194 | | | | |
| | No. of fish | 4 | 4 | 4 | 4 | 4 | 4 | | | | |
| | Range | 536-1000 | 1.07-1.44 | 21.9-40.5 | 206-361 | 0.018-0.026 | 0.09-0.95 | | | | |
| Steelhead | Mean ± SE | 719 ± 105.6 | 2.41 ± 0.270 | 18.6 ± 4.14 | 354 ± 36.2 | 0.050 ± 0.0068 | 1.64 ± 0.348 | | | | |
| | No. of fish | 7 | 7 | 6 | 7 | 7 | 7 | | | | |
| | Range | 344-1000 | 1.56-3.62 | 8.4-34.7 | 251-545 | 0.021-0.074 | 0.45-2.48 | | | | |
| 1:8-slope | Mean ± SE | 616 ± 110.5 | 2.46 ± 0.228 | 15.0 ± 2.29 | 407 ± 21.0 | 0.040 ± 0.0044 | 1.48 ± 0.366 | | | | |
| | No. of fish | 6 | 6 | 6 | 6 | 6 | 6 | | | | |
| | Range | 216-1000 | 1.81-3.26 | 5.6-20.6 | 330-475 | 0.027-0.059 | 0.54-3.07 | | | | |

than the average in control chinook, but did not differ significantly from the values for 104-pool terminated fish in the same fishway or long-run fish in the 1:16 fishway. The mean muscle glycogen in long-run chinook in the steeper fishway was 0.068% and represented a significant decrease from the control level ($0.005 > P > 0.001$). Like the blood lactate, the muscle glycogen of long-run fish in the 1:8 fishway was not significantly different from either the 104-pool or the 1:16 long-run levels.

The small size of the long-run sample groups ($n = 7$ in each fishway) probably contributed to the fact that more of the differences recorded were not statistically significant.

Chinook salmon apparently can accomplish extended ascents of up to 1000 pools in either fishway without showing evidence of more than a moderate degree of activity as judged by the blood lactate changes. In the 1:16 fishway muscle glycogen levels are not diminished during either moderate or long ascents. In the 1:8 fishway, the utilization of muscle glycogen is significant with respect to the control value in both 104-pool and long ascents, and although statistically unproven, appears to be progressive. At the end of 104 pools, the average glycogen level of chinook was about $\frac{3}{4}$ of the control value. In long-run fish it had diminished to $\frac{3}{4}$ of the 104-pool level, or $\frac{1}{2}$ the control level.

The average times taken to accomplish each 100-pool section of the prolonged ascents are shown in Fig. 5. A progressive increase in rate of ascent occurred in chinook during the first 300–500 pools of both fishways. Between the 500th and 800th pools, a marked reduction in rate appears which coincides with the volitional interruptions in progress mentioned earlier. This phenomenon of stopping in the fishways is similar to that seen in volitional fish.

SOCKEYE. Sockeye salmon ascended an average of 839 pools (range, 648–1000) before termination in the 1:16 fishway, and 772 pools (range, 536–1000) in the 1:8 fishway. In both fishways the ascents were considerably longer than those of chinook salmon.

The average blood lactate level of long-run sockeye in the 1:16 fishway was 19.7 mg% (Table VIII). This value was not significantly different from the control level (Table III) and was significantly lower ($0.05 > P > 0.025$) than the level for 104-pool terminated sockeye in the same fishway (Table VI). The average blood lactate of long-run sockeye in the 1:8 fishway was 30.6 mg% which represents a significant increase ($0.01 > P > 0.005$) over the control level. In the steeper fishway the blood lactate level of long-run fish was again lower than that of 104-pool terminated fish, but the difference was not significant. The difference in blood lactates of long-run sockeye between the fishways was not significant, probably because of the small size of the sample groups.

The average muscle glycogen level of 0.028% in the 1:16 fishway (Table VIII) was significantly lower ($P < 0.001$) than both the control level (Table III) and the level in 104-pool terminated sockeye in the same fishway (Table VI). The average muscle glycogen level for long-run sockeye in the 1:8 fishway (0.024%) was slightly, but not significantly lower than the 1:16 level. It was, however,

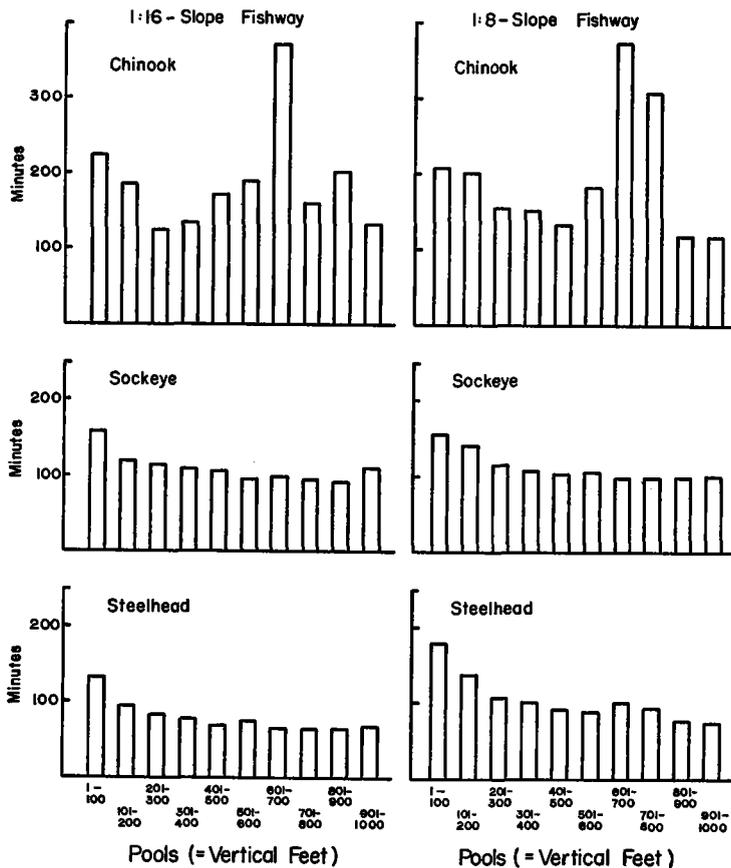


FIG. 5. Average ascent times in minutes per 100 pools for long-run terminated chinook salmon (*Oncorhynchus tshawytscha*), sockeye salmon (*O. nerka*) and steelhead trout (*Salmo gairdneri*) in the 1:16- and 1:8-slope experimental "endless" fishways. Bonneville, 1959.

significantly below both the control level ($P < 0.001$) and the 104-pool terminated level ($0.005 > P > 0.001$) in that fishway.

In sockeye salmon, muscle glycogen is apparently utilized during long ascents of either fishway, in contrast to chinook in which utilization was observed only in the 1:8 fishway. Evidence of a progressive decrease in muscle glycogen stores, related to the total number of pools ascended, is more definite in sockeye salmon in both fishways than in the chinook in the 1:8 fishway. Of great interest is the reduction in blood lactate levels which appears in sockeye when the ascent is prolonged beyond the 104th pool. This reduction may possibly be related to the increased rate of ascent observed during the first 400-500 pools (Fig. 5) and may indicate some form of "learning" or adaptation in the experimental situation. None of the long-run sockeye stopped moving during the later stages as did the chinook.

STEELHEAD. The long-run steelhead trout were terminated at an average number of pools intermediate between the chinook and sockeye salmon. As shown in Table VIII, the average number of pools completed in the 1:16 fishway (mean, 719; range, 344–1000) was somewhat greater than the number in the 1:8 fishway (mean, 616; range, 216–1000).

The slight increases in mean blood lactate levels of long-run steelhead (Table VIII) in both fishways were not significant when compared with the control fish (Table III). Nor was the difference between the blood lactate level of 104-pool terminated steelhead (Table VII) and that of long-run fish in the 1:16 fishway. In the 1:8 fishway however the average blood lactate value of 15.0 mg% in the long-run steelhead was significantly lower than the average of 20.5 mg% in the 104-pool terminated fish ($0.05 > P > 0.025$). There was no significant difference in blood lactate levels of long-run steelhead between the 1:16 and 1:8 fishways.

The average muscle glycogen level in long-run steelhead in the 1:16 fishway was 0.050% (Table VIII) which value was significantly lower ($0.025 > P > 0.01$) than the control level of 0.079% (Table III). Muscle glycogen in long-run steelhead in the 1:8 fishway (0.040%) was also significantly lower than the control level ($P < 0.001$) and the level of 0.065% (Table VII) in 104-pool terminated steelhead ($0.01 > P > 0.005$) in the same fishway. The difference in muscle glycogen levels between the two fishways was not significant for long-run steelhead.

Steelhead appear to be more like sockeye than chinook in their response to prolonged ascents. The moderate accumulation of lactate seen during the early stages (i.e. the first 104 pools) is reduced in long-run fish especially in the 1:8 fishway. Muscle glycogen is utilized during long ascents in both fishways, although no significant reduction had been observed after 104 pools in the 1:16 fishway. In the steeper fishway, the breakdown of muscle glycogen is definitely progressive as was the case with sockeye. Steelhead also showed a consistent increase in rate of ascent during the first 400–500 pools in both fishways (Fig. 5) and showed no tendency to stop moving as did the chinook.

1000-POOL TERMINATED FISH

Lactate and glycogen levels of individual fish of all three species which were terminated after 1000 pools in both fishways are given in Table IX, together with body weights, sex, total duration of the ascent, and total duration of inactive periods which exceeded 60 min in those chinook which stopped. These data were included in the averages for long-run terminated fish discussed above, but are presented separately here in order to give some indication of the biochemical status of fish which have completed a prolonged ascent of a uniform specified length. The number of fish in any given group was not sufficient to permit comparison of mean lactate and glycogen levels. The individual blood lactate and muscle glycogen levels appear to follow the patterns discussed above for the mean levels in long-run terminated fish. The performance data and blood lactate levels of these fish have been discussed fully by Collins *et al.* (1962).

TABLE IX. Body weights, sex, blood and muscle lactate levels, and muscle and liver glycogen levels of individual migrating Columbia river chinook salmon (*O. tshawytscha*), sockeye salmon (*O. nerka*) and steelhead trout (*S. gairdneri*) at the completion of ascents of 1000 pools (1000 ft) in the experimental fishways. The times taken to complete 1000 pools are given in column 4. The number (column 5) and the total length (column 6) of inactive periods which exceeded 60 min are presented. Bonneville, 1959.

| | 1 Fishway slope | 2 Body weight | 3 Sex | 4 Duration of ascent | 5 Number of stops | 6 Total length of inactive periods | 7 Lactate | | 9 Glycogen | |
|-----------|-----------------------|---------------------|----------|----------------------------|-------------------------|---|-----------|----------|------------|-------|
| | | | | | | | Blood | Muscle | Muscle | Liver |
| | | kg | | hr:min | | hr:min | mg% | mg/100 g | % | % |
| Chinook | 1:16 | 9.65 | F | 28:46 | 1 | 1:29 | 30.3 | 477 | 0.291 | 1.01 |
| | 1:8 | 9.88 | F | 31:26 | 2 | 5:59 | 28.7 | 380 | 0.101 | 0.57 |
| | 1:8 | 10.19 | F | 31:17 | 2 | 7:39 | 26.6 | 407 | 0.042 | 0.23 |
| Sockeye | 1:16 | 1.44 | F | 15:24 | 0 | 0 | 20.7 | 397 | 0.022 | 0.40 |
| | 1:16 | 1.33 | M | 22:01 | 0 | 0 | 7.9 | 257 | 0.015 | 0.31 |
| | 1:8 | 1.44 | M | 20:11 | 0 | 0 | 21.9 | 350 | 0.026 | 0.66 |
| | 1:8 | 1.16 | F | 17:18 | 0 | 0 | 28.9 | 206 | 0.022 | 0.09 |
| Steelhead | 1:16 | 1.78 | M | 11:34 | 0 | 0 | 8.4 | 324 | 0.074 | 1.63 |
| | 1:16 | 2.27 | M | 9:19 | 0 | 0 | 19.7 | 387 | 0.021 | 0.45 |
| | 1:16 | 3.05 | F | 12:37 | 0 | 0 | 9.8 | 368 | 0.057 | 0.46 |
| | 1:8 | 1.81 | F | 15:22 | 0 | 0 | 13.4 | 441 | 0.059 | 0.85 |

TABLE X. Body weights, blood and muscle lactate levels, and muscle and liver glycogen levels in migrating Columbia river chinook salmon (*O. tshawytscha*), sockeye salmon (*O. nerka*) and steelhead trout (*S. gairdneri*) sampled at the end of a 60-min volitional stop during ascent of the experimental fishways. The average numbers of pools completed before stopping are given in column 2. Bonneville, 1959.

| 1 | | 2 | 3 | 4 | | 5 | | 6 | | 7 | | |
|-----------|------------|-----------------------------------|----------------------------|----------------------------------|----------------------------------|-------------------------------|-------------------------------------|-------------------------------------|---------------------------------|---|--|--|
| | | | | Lactate | | Glycogen | | | | | | |
| | | No. of pools completed | Body weight | Blood | Muscle | Muscle | Liver | | | | | |
| | | | | kg | mg% | mg/100 g | % | % | | | | |
| Chinook | 1:16-slope | Mean ± SE No. of fish Range | 65 ± 21.7 10 3-242 | | 8.54 ± 1.113 10 2.60-12.71 | 20.8 ± 3.42 10 5.4-40.8 | 439 ± 35.4 10 260-590 | 0.111 ± 0.0217 10 0.045-0.243 | 0.66 ± 0.197 10 0.23-1.94 | | | |
| | 1:8-slope | Mean ± SE No. of fish Range | 189 ± 89.0 11 4-964 | 5.66 ± 1.126 11 1.78-12.14 | 20.1 ± 3.54 11 8.7-48.1 | 434 ± 29.4 11 242-562 | 0.097 ± 0.0127 11 0.042-0.203 | 0.54 ± 0.175 11 0.10-2.18 | | | | |
| Sockeye | 1:16-slope | Mean ± SE No. of fish Range | 263 ± 83.3 8 35-632 | 1.42 ± 0.063 8 1.19-1.70 | 10.3 ± 1.44 8 5.2-16.9 | 408 ± 42.7 8 224-583 | 0.064 ± 0.0110 8 0.028-0.132 | 1.05 ± 0.363 8 0.18-3.37 | | | | |
| | 1:8-slope | Mean ± SE No. of fish Range | 232 ± 70.0 8 46-577 | 1.46 ± 0.097 8 1.21-2.09 | 15.3 ± 3.48 8 5.5-34.0 | 361 ± 20.8 8 268-441 | 0.053 ± 0.0086 8 0.019-0.088 | 0.83 ± 0.188 8 0.01-1.61 | | | | |
| Steelhead | 1:16-slope | Mean ± SE No. of fish Range | 244 ± 97.8 10 26-985 | 2.21 ± 0.102 10 1.81-2.60 | 12.9 ± 3.25 10 4.1-39.0 | 454 ± 29.8 10 261-576 | 0.047 ± 0.0057 9 0.015-0.075 | 1.00 ± 0.285 9 0.23-2.83 | | | | |
| | 1:8-slope | Mean ± SE No. of fish Range | 229 ± 76.6 10 9-679 | 3.28 ± 0.421 10 1.70-5.55 | 10.7 ± 1.56 10 3.6-20.6 | 407 ± 13.8 10 357-513 | 0.063 ± 0.0117 10 0.012-0.141 | 1.21 ± 0.129 10 0.74-1.87 | | | | |

TABLE XI. Body weights, blood and muscle lactate levels, and muscle and liver glycogen levels in individual migrating Columbia river chinook salmon (*O. tshawytscha*) and sockeye salmon (*O. nerka*) sampled after a 30-min volitional stop, and in individual chinook salmon and steelhead trout (*S. gairdneri*) which stopped for 60 min in the 1st pool during ascents of the experimental fishways. Bonneville, 1959.

| Species | Fishway slope | Condition | | Body weight | Lactate | | Glycogen | |
|-----------|---------------|------------------|------------------------|-------------|------------|-----------------|----------|----------|
| | | Duration of stop | No. of pools completed | | Blood | Muscle | Muscle | Liver |
| | | <i>min</i> | | <i>kg</i> | <i>mg%</i> | <i>mg/100 g</i> | <i>%</i> | <i>%</i> |
| Chinook | 1:16 | 30 | 47 | 6.43 | 21.6 | 405 | 0.155 | 0.25 |
| | 1:16 | 30 | 18 | 9.03 | 49.7 | 412 | 0.031 | 0.30 |
| | 1:16 | 30 | 22 | 14.72 | 50.0 | 315 | 0.107 | 1.06 |
| | 1:16 | 30 | 214 | 6.45 | 27.7 | 554 | 0.170 | 0.29 |
| | 1:8 | 30 | 97 | 3.71 | 15.7 | 384 | 0.105 | 1.01 |
| | 1:8 | 30 | 17 | 7.93 | 75.4 | 513 | 0.091 | 1.17 |
| Sockeye | 1:16 | 30 | 93 | 1.19 | 34.6 | 417 | 0.027 | 0.36 |
| | 1:8 | 30 | 43 | 1.42 | 18.1 | 314 | 0.080 | 0.31 |
| Chinook | 1:16 | 60 | 1 | 1.61 | 15.8 | 359 | 0.081 | 0.30 |
| | 1:16 | 60 | 1 | 3.62 | 10.4 | 353 | 0.044 | 0.33 |
| | 1:16 | 60 | 1 | 5.07 | 18.1 | 455 | 0.111 | 0.06 |
| Steelhead | 1:16 | 60 | 1 | 3.82 | 9.8 | 331 | 0.077 | 2.06 |
| | 1:16 | 60 | 1 | 1.81 | 21.0 | 372 | 0.072 | 0.64 |

VOLITIONAL-STOP FISH

CHINOOK. The chinook salmon which were sampled after they had stopped for 60 min in one pool during ascent of the experimental fishways (Table X) had completed an average of 65 pools (range, 3–242) in the 1:16 fishway and 189 pools (range, 4–964) in the 1:8 fishway. The large difference is due to the fact that two fish in the 1:8 fishway had ascended 529 and 964 pools, respectively, before sampling, as compared with the maximum ascent of 242 pools in the 1:16 fishway. When these two fish are eliminated, the average number of pools completed in the 1:8 fishway becomes 63 (range, 4–121). However, when the individual lactate and glycogen levels for these two fish were considered, they were found to be within the range of all volitional chinook in the 1:8 fishway, therefore they are included with this group.

A small group of fish which did not proceed beyond the first pool in the 1:16 fishway within 60 min is considered to be a special case and is presented in Table XI. Salmon which were sampled after stopping for 30 min in one pool are also considered separately.

The percentage of chinook salmon which stopped volitionally before reaching the 104th pool was 23.6% in the 1:16 fishway and 21.5% in the 1:8 fishway (Table XII). These figures do not include volitional stops of 30 min, nor volitional stops after ascents longer than 104 pools.

TABLE XII. Percentage of migrating Columbia river chinook salmon (*O. tshawytscha*), sockeye salmon (*O. nerka*) and steelhead trout (*S. gairdneri*) which completed 104 pool (104 ft) ascents of the experimental fishways without stopping volitionally for 60 min. These figures do not include fish which were sampled after a 30-min volitional stop. Bonneville, 1959.

| | 1:16-slope | | | 1:8-slope | | |
|----------------------------------|------------|---------|-----------|-----------|---------|-----------|
| | Chinook | Sockeye | Steelhead | Chinook | Sockeye | Steelhead |
| No. of fish completing 104 pools | 84 | 26 | 49 | 84 | 26 | 49 |
| No. of volitional stops | 26 | 4 | 9 | 23 | 4 | 6 |
| Total no. of fish | 110 | 30 | 58 | 107 | 30 | 55 |
| Percentage completing 104 pools | 76.4 | 86.7 | 84.5 | 78.5 | 86.7 | 89.1 |
| Percentage stopping volitionally | 23.6 | 13.3 | 15.5 | 21.5 | 13.3 | 10.9 |

The blood lactate levels in volitional chinook of 20.8 mg% for the 1:16 fishway and 20.1 mg% for the 1:8 fishway (Table X) were not significantly higher than the control value of 17.8 mg% (Table III) nor were they significantly different from each other. They were however significantly lower than the levels in 104-pool terminated chinook (Table IV) in both the 1:16 fishway ($0.025 > P > 0.01$) and the 1:8 fishway ($0.005 > P > 0.001$).

Muscle glycogen levels in volitional chinook were 0.111% in the 1:16 fishway and 0.097% in the 1:8 fishway (Table X). These values are slightly lower than the control level of 0.127% (Table III), but the differences are not significant. Nor were there any significant differences between muscle glycogen levels in volitional chinook and those in 104-pool terminated fish in the corresponding fishways (Table IV). The difference between muscle glycogen levels of volitional chinook in the two fishways was not significant.

Although the blood lactate levels of volitional chinook are significantly lower than the 104-pool terminated levels, the true degree of recovery during the 60 min they remained in one pool cannot be estimated, since the actual lactate levels at the time of stopping are not known. However some degree of recovery seems probable. Similarly, the extent of muscle glycogen recovery is unknown, but appears to be slight.

It should be noted that although these volitional fish stopped moving up the fishways, they were not completely inactive during the 60-min period. They maintained their position against the flow of water, and swam about the pool. Chinook salmon which had been exhausted by extremely rapid ascents in one of the unsuccessful design modifications of the 1:8 fishway in 1958 were studied by Collins *et al.* (1963). These fish were obviously fatigued, drifted back down the fishway to the lowermost pool and showed an average blood lactate of 123 mg%. The volitional fish under consideration in the present paper showed none of these signs of fatigue. It is most probable that unassessed factors such as sexual maturity, water temperature and different behavioural patterns are involved in this tendency to stop moving. In the case of chinook salmon, volitional stops were observed mainly in the spring-run. In fact a tendency to balkiness was characteristic of these fish in both the experimental and the regular fishways at Bonneville dam. Tests in 1958 (Collins *et al.*, 1963) indicated that approximately 40% of the spring chinooks stopped for 60 min or more in a fishway pool. By contrast, virtually all of the fall-run passed through the fishway without making a 60-min stop.

SOCKEYE. The average number of pools ascended by volitional sockeye salmon (Table X) before stopping was 263 pools (range, 35–632) in the 1:16 fishway and 232 (range, 46–577) in the 1:8 fishway. Half of the volitional sockeye in each fishway were from the long-run group (i.e. had ascended more than 104 pools). The percentage of sockeye which stopped of their own volition for 60 min before reaching the 104th pool was 13.3% in both fishways (Table XII).

Average blood lactate level of volitional sockeye in the 1:16 fishway (10.3 mg%, Table X) was significantly lower ($0.01 > P > 0.005$) than the control level of 17.4 mg% (Table III). It was also significantly lower ($P < 0.001$) than the level in 104-pool terminated sockeye in the same fishway (31.2 mg%, Table VI). The blood lactate level of volitional sockeye in the 1:8 fishway was 15.3 mg% (Table X) which is very close to the control level and significantly lower ($P < 0.001$) than the level in 104-pool terminated sockeye in the 1:8 fishway. The difference between the blood lactate levels of volitional sockeye in the 1:16 and 1:8 fishways was not significant.

The average muscle glycogen level in volitional sockeye salmon in the 1:16 fishway was 0.064% (Table X), a value which is lower than both the control level of 0.086% (Table III) and the 104-pool terminated level of 0.074% (Table VI). The differences however were not significant. In the 1:8 fishway, the muscle glycogen level of volitional sockeye averaged 0.053% (Table X) which is identical with the level in 104-pool terminated sockeye in the same fishway (Table VI), and significantly lower than the control level ($0.01 > P > 0.005$). There was no significant difference between the muscle glycogen levels of volitional sockeye in the 1:16 and 1:8 fishways.

The very low blood lactate level in volitional sockeye in the 1:16 fishway is similar to that observed in control sockeye which had been held overnight (Table III). Probably this level more nearly represents the true unexercised state than the average of 17.4 mg% recorded for all sockeye controls. Evidently sockeye either were less active or experienced less stress when isolated in one pool of the 1:16 fishway than when kept in the holding pool for 1-6 hr. Although, as in the case of chinook salmon, the true extent of recovery as judged by the blood lactate level is not known, it appears to be quite marked in sockeye within 60 min of the cessation of exercise in both fishways. Muscle glycogen values in volitional sockeye showed no real evidence of recovery from levels for actively ascending fish during the 60-min stop.

STEELHEAD. The average number of pools completed by volitional steelhead trout in the 1:16 fishway was 244 (range, 26-985), with four out of ten fish in the long-run category. In the 1:8 fishway, the average was 229 pools (range, 9-679) with one-half of the fish from the long-run group.

In the 1:16 fishway, 15.5% of the steelhead stopped of their own volition before reaching the 104th pool. In the 1:8 fishway the percentage was 10.9% (Table XII)

Average blood lactate levels of volitional steelhead were 12.9 mg% in the 1:16 fishway and 10.7 mg% in the 1:8 fishway (Table X). These values were not significantly different, nor did either of them differ significantly from the control level of 12.2 mg% (Table III). The blood lactate level of volitional steelhead in the 1:16 fishway did not differ significantly from the level for 104-pool terminated fish in the same fishway (Table VII). The level in volitional steelhead in the 1:8 fishway was however significantly lower ($P < 0.001$) than the level for 104-pool terminated fish.

In the 1:16 fishway, the average muscle glycogen level was 0.047% (Table X) which was significantly lower than both the control level of 0.079% ($0.005 > P > 0.001$), and the 104-pool terminated level of 0.070% ($0.025 > P > 0.01$). In the 1:8 fishway, the average muscle glycogen level of volitional steelhead was 0.063% (Table X) which was similar to the 104-pool terminated level (Table VII), but not significantly different from either the control (Table III) or the 1:16 volitional levels.

The volitional steelhead, like the chinook and sockeye, gave some indication of recovery during the 60 min stop on the basis of lowered lactate levels, although

the extent to which this represents true recovery is not known. Muscle glycogen levels did not appear to be restored to the control level during this time.

Steelhead, like the spring-run chinook discussed earlier, have been known to linger in fishways for lengthy periods during certain times of the year. Each winter during draining of the fishways at Bonneville for repair purposes, large numbers of steelhead are found in the pools. Since only a token migration of steelhead passes the Bonneville dam during winter, the fish found in the fishways are presumably previous summer and fall migrants that have taken up residence in the pools. These apparently stay in the fishway for several months before moving upstream in the spring for spawning. It is quite possible that these fish have found the hydraulic conditions in the fishway pools to their liking and are merely spending the time in the process of maturation. It is equally probable that the volitional fish in this study stopped for similar reasons and not because of fatigue.

VOLITIONAL FISH—SPECIAL CONDITIONS

Data for individual fish which were sampled after a 30-min volitional stop and for fish which did not proceed beyond the first pool within 60 min (i.e. 1-pool volitional fish) are presented in Table XI. The data are too few to permit statistical treatment.

The 30-min volitional chinook salmon showed rather high blood lactate levels (1:16 fishway mean, 37.3 mg%; 1:8 mean, 45.6 mg%) as compared with the 60-min volitional (Table X) and control chinook (Table III). These 30-min volitional mean values were, in fact, higher than the corresponding levels in the 104-pool terminated chinook (Table IV), although the ranges of values coincide, for the 1:16 fishway at least. The high blood lactate values after a 30-min stop may be some indication of the degree of recovery taking place in the 60-min volitional chinook. However, the data are not complete nor consistent enough to permit an unequivocal interpretation. The muscle glycogen levels in 30-min volitional chinook do not appear to be markedly depleted. In the 30-min volitional chinook, in the 1:16 fishway only, the liver glycogen levels were quite low (mean, 0.48%). It is also interesting to note that the only obvious biochemical alteration in the chinook which stopped for 60-min in the first pool of the 1:16 fishway was the low liver glycogen level (mean, 0.23%). However, because of the wide range of liver glycogen values in control chinook (0.04–2.62%, Table III), it is not possible to attach any real significance to these findings.

DISCUSSION

The results of the 1959 experiments at Bonneville are, in general, similar to those reported by Collins *et al.* (1963) for the previous year's work. However, the additional data collected in 1959, in particular the muscle glycogen values, make clear several aspects of fishway passage which were not obvious from the earlier studies.

Fish of all three species tested (chinook and sockeye salmon and steelhead trout) appeared equally willing to enter, and capable of ascending, either the 1:16- or the steeper 1:8-slope fishway under favourable hydraulic conditions.

The percentage of fish completing a moderate ascent of 104 ft without stopping for 60 min or more was actually greater in the 1:8 fishway for chinook and steelhead, and was at no time less than 76% of those starting. Although the rate of ascent of all species was less in the steeper fishway, and significantly so for sockeye and steelhead, the slower passage may have been due to the creation of blind pockets on the downstream side of each weir by the installation of vertical stabilizers in the 1:8 fishway. When the ascents were extended beyond 104 ft, the difference in passage times between the fishways was reduced. All fish showed the ability to increase their rates of ascent during the first half of long passages in both fishways. After this initial increase, sockeye and steelhead maintained the faster rate up to 1000 ft. Chinook, particularly the spring-run, occasionally stopped voluntarily in the latter half of long ascents in both fishways. Steelhead showed the fastest passage times in both fishways, closely followed by sockeye, while the larger chinook salmon were slowest.

The biochemical data, especially blood lactate and muscle glycogen levels, indicate that the degree of effort involved even in prolonged ascents of either fishway was of the order of magnitude associated with moderate sustained exercise. Muscle lactate values were consistently high in both control and experimental fish, probably because of struggling and delay in sampling. No significant changes in muscle lactate levels were observed in response to exercise in either fishway. The liver glycogen levels in these experiments did not appear to be related to the amount of muscular exercise performed. This lack of change in liver glycogen levels may have been due to the high degree of individual variation between samples. However, it is more likely that the amounts of work performed by these fish were not sufficient to influence the liver glycogen levels.

The blood lactate levels indicate that the greatest degree of anaerobic metabolism occurs during the first approximately 100 ft of ascent in both fishways. All species exhibited a significant $1\frac{1}{2}$ - to $2\frac{1}{2}$ -fold increase in blood lactate over the rather high control levels during ascent of the first 104 pools of either fishway. Presumably this may have been due either to the stress of a new environment, together with a possible delay in readjustment of circulation and respiration and/or to an increased rate of turnover of glycogen. The magnitude of the lactate increase is very similar to that observed in moderately exercised $1\frac{1}{2}$ -year-old rainbow and Kamloops trout (Black, 1957a; Black *et al.*, 1960, 1962), and in no way approaches the large increases found by these and other workers (Secondat and Diaz, 1942; Nakatani, 1957; Black 1957b,c; Leivestad *et al.*, 1957; Parker and Black, 1959; Parker *et al.*, 1959; Tomlinson *et al.*, 1961; Barrett and Connor, 1962; Heath and Pritchard, 1962) in fishes following severe exercise or handling procedures. Only the sockeye salmon in the present study showed a significantly higher blood lactate level after 104 pools in the 1:8 than in the 1:16 fishway.

During ascent of the first 104 pools of the 1:16 fishway, the muscle glycogen levels of all species tested were not significantly decreased below the control levels. Evidently, the utilization of muscle glycogen is so slight at this level of

exercise that the rate of replacement is not exceeded. It is possible that energy for this mild form of exercise could be supplied from direct metabolism of protein and/or fat (Greene, 1921; Pentegoff *et al.*, 1928; Fontaine and Hatey, 1953; Idler and Clemens, 1959; Blažka, 1962, personal communication) or other carbohydrate substrates (Tarr and Leroux, 1962), in which case it seems that a moderately long ascent of the 1:16 fishway does not exceed the energy-producing capabilities of these alternate metabolic pathways. In the 1:8 fishway, however, the muscle glycogen levels of all species after an ascent of 104 pools were significantly below the control levels. The reduction ranged from 18–38% of the control value. In chinook and sockeye salmon, the muscle glycogen levels following 104-pool ascents in the 1:8 fishway were significantly lower than following similar ascents in the 1:16 fishway. It appears that an ascent of moderate height (104 ft) in the steeper 1:8 fishway cannot be accomplished without the utilization of muscle glycogen. The decreases in muscle glycogen, like the increases in blood lactate were not nearly as great as those found following 15 min strenuous exercise in immature trout (Black *et al.*, 1960, 1962).

When the ascents were prolonged up to 1000 pools, the blood lactate levels tended to be lower than those found after 104-pool ascents, especially in sockeye and steelhead. It is probable that lactate is disposed of by excretion and/or by conversion to pyruvate with eventual oxidation. An improvement in circulation at later stages of prolonged ascents would provide more efficient operation of the excretory organs and more adequate tissue oxygenation. It is also possible that the reduction in lactate levels resulted from a lessening of initial stress or a "learning" process, such as that noted by McLeod and Nemenyi (1941) for trout in experimental fishways, which would enable the fish to negotiate the overfalls with less muscular effort. The increasing rate of ascent seen during the first 400–500 pools in long-run fish may be interpreted either as evidence of "learning" or as a result of improved circulatory function.

Despite the fact that lactate levels were reduced in long-run terminated fish, muscle glycogen levels were significantly lower than the control levels in all long-run fish except chinook salmon in the 1:16 fishway. The reduction in muscle glycogen appeared to be progressive, and to depend on the total amount of work accomplished. The apparently continuous expenditure of muscle glycogen makes it doubtful that the low lactate levels in long-run fish were due to the use of alternate pathways of energy production (fat or protein breakdown) to the exclusion of glycolysis. It is equally unlikely that the low lactate levels resulted from exhaustion of muscle glycogen stores in the long-run fish. The muscle glycogen values upon termination (Table VIII) do not seem to be low enough to limit glycolysis. Levels as low as 0.001% have been recorded in young rainbow trout following 2–9 min of strenuous exercise (Black *et al.*, 1962). These trout showed changes in behaviour which suggested severe fatigue. Such evidence of fatigue was not observed in the long-run fish in the present experiments.

Fish of all three species which stopped moving of their own volition were able to maintain position for 60 min or more in either slope fishway. When these

fish were sampled at the end of 60 min in one pool, the blood lactate levels were similar to, or even lower than, the control levels. Although the true degree of recovery is not known since the levels of lactate and glycogen at the time the fish stopped moving were not measured, it is very likely that some reduction in blood lactate occurred. Despite the 60 min of relative inactivity, muscle glycogen levels of most volitional fish remained indistinguishable from or significantly lower than those in corresponding groups terminated at the end of 104 pools. Although the volitional muscle glycogen levels were not significantly different from the control levels in most cases, it seems probable that little, if any, restoration took place during the 60 min.

From the data obtained, it does not seem likely that the volitional fish stopped moving because of glycolytic fatigue. It is possible that exhaustion of other essential metabolites such as ATP or creatine-PO₄, or inactivation of any of the enzyme systems involved in intermediary metabolism might be the limiting factor. These factors were not studied in the present experiments. However, subjective observations and data on fish passage collected for both the experimental "endless" fishways and the regular operating fishways at Bonneville dam make it appear more probable that the tendency to stop moving for lengthy periods is a behavioural phenomenon. Such factors as water temperature, state of maturity and favourable hydraulic conditions probably affect the movement of migrating fish. The relationship of these factors to the pattern of movement of volitional fish in the experimental fishways has not been fully investigated.

Since the feasibility of using the steeper 1:8-slope fishway for the passage of salmonid fishes has been demonstrated by the performance records in the experimental "endless" fishways, the problem of immediate practical importance is the effect of ascending such fishways on the ultimate well-being of migrating fish. As has been stated repeatedly, the degree of effort, as judged by analysis of the primary carbohydrate energy cycle, is only moderate in either the 1:8- or the 1:16-slope fishway provided the proper hydraulic conditions are attained. However, there is evidence that moderately long ascents (approximately 100 ft) of the steeper fishway require a small but significant expenditure of muscle glycogen which is not required during a similar ascent in a 1:16-slope fishway. The effect of such reduction in muscle glycogen upon the fish after they leave the fishway is not known and needs investigation.

According to Black *et al.* (1962), muscle glycogen is probably the primary fuel for rapid evasive or strenuous activity since it provides the most readily mobilized source of energy. Furthermore, when utilized in severe exercise its restoration to normal levels in immature trout is remarkably slow if the fish are not fed. However, Fontaine and Hatey (1953) in examining mature, migrating Atlantic salmon found no depletion of muscle glycogen upon completion of the upstream migration. These latter authors were of the opinion that migrating salmon must have a well-adapted ability to regulate gluconeogenesis (i.e. formation of carbohydrate from protein and fat stores) in accordance with the energy demand. It is possible that the hormonal changes accompanying maturation

in migrating salmonids may considerably alter the pattern of carbohydrate metabolism normally seen in young trout. In view of the fact that migrating salmonids are in a non-feeding condition and are faced with a situation where sustained demands may be made upon energy-producing mechanisms, it indeed seems probable that rapid replenishment of muscle glycogen can occur in these fish even without feeding.

Thus until experiments are carried out to establish the prime source of energy in mature migrating fish, and the rate and means by which muscle glycogen is restored following exercise in these fish, the significance of the increased utilization of muscle glycogen in the steeper fishway cannot be ascertained. It should be noted that fish counts at the Rock Island dam on the Columbia river indicate no decline in population after 30 years of operation of a 1:10-slope fishway. The recently constructed Ice Harbour dam, which includes both a 1:16- and a 1:10-slope fishway, should provide the opportunity for direct physiological comparison under actual operating conditions.

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REFERENCES

- BARKER, S. B., AND WILLIAM H. SUMMERSON. 1941. The colorimetric determination of lactic acid in biological material. *J. Biol. Chem.*, **138**(2): 535-554.
- BARRETT, IZADORE, AND ANNE ROBERTSON CONNOR. 1962. Blood lactate in yellowfin tuna, *Neothunnus macropterus*, and skipjack, *Katsuwonus pelamis*, following capture and tagging. *Inter-Amer. Trop. Tuna Comm., Bull.*, **6**(6): 233-280.

- BLACK, EDGAR C. 1957a. Alterations in the blood level of lactic acid in certain salmonoid fishes following muscular activity. I. Kamloops trout, *Salmo gairdneri*. *J. Fish. Res. Bd. Canada*, **14**(2): 117-134.
- 1957b. Alterations in the blood level of lactic acid in certain salmonoid fishes following muscular activity. II. Lake trout, *Salvelinus namaycush*. *Ibid.*, **14**(4): 645-649.
- 1957c. Alterations in the blood level of lactic acid in certain salmonoid fishes following muscular activity. III. Sockeye salmon, *Oncorhynchus nerka*. *Ibid.*, **14**(6): 807-814.
- BLACK, EDGAR C., WING-GAY CHIU, FRANCIS D. FORBES AND ARTHUR HANSLIP. 1959. Changes in pH, carbonate and lactate of the blood of yearling Kamloops trout, *Salmo gairdneri*, during and following severe muscular activity. *J. Fish. Res. Bd. Canada*, **16**(4): 391-402.
- BLACK, EDGAR C., ANNE ROBERTSON CONNOR, KWOK-CHEUNG LAM AND WING-GAY CHIU. 1962. Changes in glycogen, pyruvate and lactate in rainbow trout (*Salmo gairdneri*) during and following muscular activity. *J. Fish. Res. Bd. Canada*, **19**(3): 409-436.
- BLACK, EDGAR C., ANNE C. ROBERTSON, ARTHUR R. HANSLIP AND WING-GAY CHIU. 1960. Alterations in glycogen, glucose and lactate in rainbow and Kamloops trout, *Salmo gairdneri*, following muscular activity. *J. Fish. Res. Bd. Canada*, **17**(4): 487-500.
- BLACK, EDGAR C., ANNE C. ROBERTSON AND ROBERT R. PARKER. 1961. Some aspects of carbohydrate metabolism in fish. Pages 89-124 in *Comparative physiology of carbohydrate metabolism in heterothermic animals*. Edited by Arthur W. Martin. Univ. Washington Press, Seattle, 168 pp.
- CARROLL, NICHOLAS V., ROBERT W. LONGLEY AND JOSEPH H. ROE. 1956. The determination of glycogen in liver and muscle by use of anthrone reagent. *J. Biol. Chem.*, **220**: 583-593.
- CHANG, VIOLET M., AND D. R. IDLER. 1960. Biochemical studies on sockeye salmon during spawning migration. XII. Liver glycogen. *Canadian J. Biochem. Physiol.*, **38**: 553-558.
- COLLINS, GERALD B., CARL H. ELLING, JOSEPH R. GAULEY AND CLARK S. THOMPSON. 1963. Effect of fishway slope on performance and biochemistry of salmonids. *U.S. Fish and Wildlife Service, Fishery Bull.*, **63**(1): 221-253.
- COLLINS, GERALD B., JOSEPH R. GAULEY AND CARL H. ELLING. 1962. Ability of salmonids to ascend high fishways. *Trans. Am. Fish. Soc.*, **91** (1): 1-7.
- FONTAINE, M., AND J. HATEY. 1953. Contribution à l'étude du métabolisme glucidique du saumon (*Salmo salar* L.) à diverses étapes de son développement et de ses migrations. *Physiol. Comp. et Oecologia*, **3**(1): 37-52.
- FRASER, DORIS I., SOMSEE PUNJAMAPIROM AND W. J. DYER. 1961. Temperature and the biochemical processes occurring during rigor mortis in cod muscle. *J. Fish. Res. Bd. Canada*, **18**(4): 641-644.
- GREENE, CHARLES W. 1921. Carbohydrate content of the king salmon tissues during the spawning migration. *J. Biol. Chem.*, **48**: 429-436.
- HEATH, ALAN G., AND AUSTIN W. PRITCHARD. 1962. Changes in the metabolic rate and blood lactic acid of bluegill sunfish, *Lepomis macrochirus*, Raf., following severe muscular activity. *Physiol. Zool.*, **35**(4): 323-329.
- IDLER, D. R., AND W. A. CLEMENS. 1959. The energy expenditures of Fraser river sockeye salmon during the spawning migration to Chilko and Stuart lakes. *Internat. Pacific Salmon Fish. Comm., Progress Report*, 80 pp.
- LEIVESTAD, H., H. ANDERSEN AND P. F. SCHOLANDER. 1957. Physiological response to air exposure in codfish. *Science*, **126**(3272): 505.
- MCLEOD, A. M., AND PAUL NEMENYI. 1941. An investigation of fishways. *Univ. Iowa Studies in Engineering, Bull.*, No. 24, 64 pp.

- MONTGOMERY, REX. 1957. Determination of glycogen. *Arch. Biochem. Biophys.*, **67**(2): 378-386.
- NAKATANI, ROY E. 1957. Changes in the inorganic phosphate and lactate levels in blood plasma and muscle tissue of adult steelhead trout after strenuous swimming. *Univ. Washington School of Fisheries, Techn. Rep.*, No. 30, Seattle, 14 pp.
- PARKER, ROBERT R., AND EDGAR C. BLACK. 1959. Muscular fatigue and mortality in troll-caught chinook salmon (*Oncorhynchus tshawytscha*). *J. Fish. Res. Bd. Canada*, **16**(1): 95-106.
- PARKER, R. R., E. C. BLACK AND P. A. LARKIN. 1959. Fatigue and mortality in troll-caught Pacific salmon (*Oncorhynchus*). *J. Fish. Res. Bd. Canada*, **16**(4): 429-448.
- PENT-GOFF, B. P., U. N. MENTOFF AND E. F. KURNAEFF. 1928. Physico-chemical characteristics of breeding migration fast of keta. (R.S.F.S.R.) *Pacific Scient. Fish. Stn., Bull.*, **2**(1), Vladivostock, 65 pp. (English translation by Mrs N. B. Notkin, 1942.)
- SECONDAT, MARCEL, AND DIÉGO DIAZ. 1942. Recherches sur la lactacidémie chez le poisson d'eau douce. *Compt. rend. acad. sci. (Paris)*, **215**: 71-73.
- SNEDECOR, GEORGE W. 1956. Statistical methods applied to experiments in agriculture and biology. 5th ed. Iowa State College Press, Ames, 534 pp.
- TARR, H. L. A., AND M. LEROUX. 1962. Acid-soluble phosphorous compounds and free sugars in fish muscle and their origin. *Canadian J. Biochem. Physiol.*, **40**: 571-589.
- TOMLINSON, N., E. S. ARNOLD, EVE ROBERTS AND S. E. GEIGER. 1961. Observations on *post mortem* biochemical changes in fish muscle in relation to *rigor mortis*. *J. Fish. Res. Bd. Canada*, **18**(3): 321-336.
- TOMLINSON N., AND S. E. GEIGER. 1962. Glycogen concentration and post mortem loss of adenosine triphosphate in fish and mammalian skeletal muscle. A review. *J. Fish. Res. Bd. Canada*, **19**(6): 997-1003.