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# Advanced Photoperiod and Water Temperature Effects on Gill $\text{Na}^+ - \text{K}^+$ Adenosine Triphosphatase Activity and Migration of Juvenile Steelhead (*Salmo gairdneri*)

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Under raceway conditions, an advanced photoperiod schedule caused migratory movements and elevation in gill  $\text{Na}^+ - \text{K}^+$  adenosine triphosphatase activity ( $\text{Na}^+ - \text{K}^+$  ATPase) to occur about 1 mo earlier than normal in yearling summer steelhead (*Salmo gairdneri*) from Dworshak National Fish Hatchery (Idaho). Exposure of migrants to 13°C for 20 d resulted in serious impairment of continued migratory behavior and a reduction of gill  $\text{Na}^+ - \text{K}^+$  ATPase activity. Migrants outnumbered nonmigrants at fork lengths of 16 cm and longer. It is proposed that the potentially detrimental effects of warming river temperatures during the normal migratory season and delayed migration caused by dams and impoundments might be partially overcome by inducing early smolt transformation and migration with the use of advanced photoperiods.

*Key words:* ATPase, steelhead, migration, temperature, photoperiod, smolts

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Chez des truites steelhead (*Salmo gairdneri*) d'été d'un an maintenues dans des canaux à l'établissement de pisciculture nationale de Dworshak (idaho), une régime de photopériodes avancées résulte en des mouvements migratoires et en une élévation de l'activité de la  $\text{Na}^+ - \text{K}^+$  adénosine triphosphatase ( $\text{Na}^+ - \text{K}^+$  ATPase) branchiale à peu près 1 mois avant la date normale. Une exposition à 13°C pendant 20 jours des poissons qui émigrent dérange notablement le comportement migratoire et cause une diminution de la  $\text{Na}^+ - \text{K}^+$  ATPase branchiale. À des longueurs à la fourche de 16 cm et plus, les poissons qui émigrent dépassent en nombre les non migrants. Nous sommes d'avis que les effets potentiellement nuisibles de l'élévation de la température dans les rivières durant les saisons normales de migration et le retard à la migration dû aux barrages et à la retenue des eaux peuvent être partiellement compensés en provoquant une transformation et une migration hâtives des smolts par des photopériodes avancées.

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HATCHERY programs for rearing anadromous salmonids can be successful only if the juvenile fish are able to complete seaward migration and fully acclimate to the seawater environment. However, this is not always possible for steelhead (*Salmo gairdneri*) from regions of the upper Columbia and Snake River drainages. In their attempt to reach the ocean, these fish must pass through hundreds of kilometres of a nearly continuous chain of dam reservoirs at rates greatly reduced from those in free-flowing streams (Raymond 1968,

1969). At these reduced rates of travel, their ability to reach the estuary prior to reverting to a nonmigratory stage, which normally occurs in late June (Conte and Wagner 1965; Zaugg et al. 1972), is placed in jeopardy. Raymond et al. (1974, 1975) observed that more steelhead remained in Snake and Columbia River reservoirs and did not complete their seaward migration in the low-flow year of 1973 than in 1974, a year of relatively high spring flows. Likewise, Sims et al. (1978) reported that large numbers of steelhead did not migrate from reservoirs in 1977, another record low-flow year.

Rising river temperatures, especially manifested in years of low water flow, impose additional threats to successful seaward migration. Under laboratory conditions temperatures of 12.7 and 15°C inhibited the development of elevated gill  $\text{Na}^+ - \text{K}^+$  ATPase activity and increased mortality due to salt-

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water exposure of steelhead (Zaugg et al. 1972; Adams et al. 1973, 1975). Zaugg and Wagner (1973) found that elevated water temperature not only decreased gill  $\text{Na}^+-\text{K}^+$  ATPase enzyme activity but also inhibited downstream migration of winter steelhead.

Many investigators feel that summer run steelhead, which migrate great distances, may not respond physiologically to photoperiod changes and temperature differences in the same manner as the coastal, or winter run, species which migrate only short distances. Experiments reported in this paper demonstrate that summer run steelhead do respond in a similar way to these environmental stimuli and that temperature conditions presently existing in the Columbia River pose a real threat to successful migration of smolts from distant upriver locations.

### Materials and Methods

Yearling juvenile steelhead were brought to the Willard National Fish Hatchery, Washington, from Dworshak National Fish Hatchery, Idaho, on January 7, 1976. On January 8, two groups of ~400 fish were placed in the upper pool of separate  $3 \times 25$  m production raceways which had been modified for testing migration. This modification consisted of placing one dam about 7.7 m from the upper end of the raceway and a second lower dam at the midpoint of the raceway (about 4.3 m from the first). A screen was placed across the first dam for 1 mo to prevent escapement of fish until they had accustomed themselves to the new surroundings. A plywood covering was placed over the lower portion of the first pool (just above the first dam) to provide cover for the fish. Water below the second dam was kept at a low level (about 15 cm) to prevent return of fish to the upper pools once migration over both dams had been accomplished. Migrating fish were netted from the lower pond and, until April 8, were returned to the upper pond.

One of the two modified raceways was equipped with electric lighting to extend daily photoperiods during the evening hours. Light from this raceway had no influence on the natural lighting of the control group. Lights consisted of three equidistantly spaced clusters of three 300-W outdoor flood lamps 1.7 m above the water surface of the upper pond. The lights were turned on at 15:00 each day and were left on each evening according to the following schedule:

| Dates (1976)    | Lights off |
|-----------------|------------|
| Jan. 9–Jan. 19  | 21:00      |
| Jan. 20–Jan. 29 | 21:15      |
| Jan. 30–Feb. 8  | 21:30      |
| Feb. 9–Feb. 17  | 21:45      |
| Feb. 18–Feb. 26 | 22:00      |
| Feb. 27–Mar. 7  | 22:15      |
| Mar. 8–Mar. 17  | 22:30      |
| Mar. 18–Mar. 28 | 22:45      |
| Mar. 29–Apr. 7  | 23:00      |
| Apr. 8–Apr. 19  | 23:15      |

On April 19, after good migration had developed in fish under the advanced photoperiod schedule (AP), lights were turned off. From April 8 to May 5 all migrants that received

AP and natural light (NL) were captured from their respective last pools in the raceways and, with the exception of a few abnormally small fish, were marked with finclips and placed in Fibreglas tanks, indoors, under normal photoperiod conditions, and in water at 6°C. The NL migrants were divided into two groups. Individual fish in one group were marked with an adipose and a right ventral finclip and fish in the other group were marked with an adipose and left ventral clip. The AP migrants were also divided, one group receiving right ventral and the other left ventral clips. All fish having the same ventral clip, both NL and AP, were placed in a common tank so that on May 5, one tank contained 45 fish with adipose–left ventral clips (NL) and 89 fish with left ventral clips only (AP) while another tank contained 44 fish with adipose–right ventral clips (NL) and 92 fish with right ventral clips only (AP).

On May 5, water temperature in the tank containing fish with left ventral clips was raised to 13°C. Water in the other tank, containing fish with right ventral clips, remained at 6°C. After 20 d under these conditions, both groups of fish were placed together in the upper pool of a raceway modified for migration testing. A screen preventing downstream movement was left in place on the upper dam for 2 d. Fish migrating to the lower pool were then collected, measured, and tested for gill  $\text{Na}^+-\text{K}^+$  ATPase activities until June 16, at which time all migration had ceased. Those fish remaining in the upper pond were retrieved and measured and several were tested for  $\text{Na}^+-\text{K}^+$  ATPase activity. Water temperatures in the raceways had ranged from 4 to 7°C during these studies.

Throughout the study  $\text{Na}^+-\text{K}^+$  ATPase activities were determined on microsomal fractions of gill homogenates from individual fish or from groups by combining approximately equal quantities of gill filaments from the individual fish. Procedures were similar to those used and reported previously (Zaugg and McLain 1970), differing primarily by a 50% reduction in centrifuging times. Activities are reported as micromoles ATP hydrolyzed per milligram protein per hour.

### Results

Elevation of gill  $\text{Na}^+-\text{K}^+$  ATPase activity was first detected on May 7 in migrants receiving NL collected from the lower pool of the modified raceway (Table 1) and on April 2 in migrants under AP (Table 2). Upper ponds (nonmigrants, Tables 1 and 2), from which several samples were taken during the experiment, were not sampled at times of peak migration in order to avoid possible downstream movement due to fright.

From February 23 to March 22 straying over the dams was about the same for both NL and AP groups and averaged less than one fish per day. Beginning on March 22, there was much more downstream movement in the AP raceway, but until April 6 all fish that migrated (except those tested for ATPase activity) were returned to the upper pools (102 AP and 12 NL fish). On April 7 and thereafter, all migrants were removed from the system. Figure 1 records the daily movement of fish after April 6 and therefore indicates only about a 2-wk difference in timing between AP and NL migrations. In reality, however, the type of migratory activity observed in AP fish beginning about March 22 was not observed in NL fish until early May, thus making a difference of more than

TABLE 1. Gill  $\text{Na}^+-\text{K}^+$  ATPase activities and fork lengths of yearling steelhead under natural light. Asterisks indicate values significantly greater than those prior to May 7 (\* $P < 0.05$ ,  $t$ -test).

| Group and date           | Mean ATPase activities <sup>a</sup> | Standard error | Mean length (cm) | Range of lengths (cm) | No. of fish |
|--------------------------|-------------------------------------|----------------|------------------|-----------------------|-------------|
| Migrants (lower pond)    |                                     |                |                  |                       |             |
| Feb. 23                  | 20.5                                | 1.5            | 14.5             | 13.6–17.1             | 6           |
| Mar. 10                  | 15.7                                | 0.5            | 14.8             | 14.1–15.3             | 5           |
| Apr. 6                   | 21.0                                | 0.8            | 16.5             | 16.1–16.9             | 3           |
| May 7                    | 32.0*                               | 4.0            | 16.5             | 16.2–16.7             | 4           |
| May 14                   | 32.0*                               | —              | 16.2             | 16.0–16.4             | 3           |
| May 24                   | 37.3*                               | 4.4            | 16.3             | 13.5–19.3             | 6           |
| June 3                   | 37.1*                               | 2.9            | 15.6             | 15.1–16.5             | 7           |
| June 7                   | 33.3*                               | 1.7            | 17.1             | 15.3–18.6             | 9           |
| June 18 <sup>b</sup>     | 39.3*                               | 0.8            | 18.7             | 17.5–19.6             | 8           |
| Nonmigrants (upper pond) |                                     |                |                  |                       |             |
| Feb. 10                  | 19.0                                | 2.0            | 13.7             | 11.9–13.9             | 6           |
| Mar. 23                  | 15.5                                | 0.5            | 17.0             | 15.8–18.4             | 12          |
| Apr. 19                  | 20.8                                | 0.7            | 16.9             | 15.2–18.9             | 11          |
| June 16                  | 19.8                                | 1.5            | 16.5             | 13.7–19.1             | 12          |

<sup>a</sup>Micromoles ATP hydrolyzed per milligram protein per hour.

<sup>b</sup>Migrated from May 5 to May 25, 1976 and held inside at 6°C until this date.

TABLE 2. Gill  $\text{Na}^+-\text{K}^+$  ATPase activities and fork lengths of yearling steelhead on an advanced photoperiod schedule. Asterisks indicate values significantly greater than those prior to April 2 (\* $P = 0.1$ , \*\* $P < 0.05$ ).

| Group and date           | Mean ATPase activities <sup>a</sup> | Standard error | Mean length (cm) | Range of lengths (cm) | No. of fish |
|--------------------------|-------------------------------------|----------------|------------------|-----------------------|-------------|
| Migrants (lower pond)    |                                     |                |                  |                       |             |
| Feb. 10                  | 17.7                                | 0.3            | 14.7             | 13.2–16.9             | 9           |
| Feb. 13                  | 20.5                                | 0.5            | 14.3             | 12.9–16.3             | 6           |
| Feb. 26                  | 18.5                                | 1.1            | 15.3             | 13.8–16.5             | 6           |
| Mar. 10                  | 18.4                                | 1.7            | 16.1             | 14.4–18.0             | 5           |
| Mar. 24                  | 21.5                                | 1.5            | 16.8             | 16.7–16.9             | 2           |
| Apr. 2                   | 27.8*                               | 1.9            | 16.1             | 12.5–18.3             | 5           |
| Apr. 6                   | 26.7*                               | 1.1            | 17.2             | 15.7–18.5             | 7           |
| Apr. 12                  | 23.7                                | 1.6            | 16.4             | 15.2–18.0             | 3           |
| Apr. 16                  | 25.9*                               | 1.2            | 15.9             | 14.7–17.1             | 8           |
| May 7                    | 37.3**                              | 1.0            | 16.6             | 14.3–18.7             | 9           |
| May 17                   | 32.5**                              | 6.1            | 17.4             | 15.3–19.9             | 4           |
| June 18 <sup>b</sup>     | 28.6**                              | 2.9            | 19.3             | 18.5–20.4             | 7           |
| Nonmigrants (upper pond) |                                     |                |                  |                       |             |
| Feb. 10                  | 14.3                                | 1.9            | 15.0             | 13.3–16.5             | 9           |
| Mar. 23                  | 18.8                                | 2.1            | 16.2             | 15.2–17.7             | 10          |
| June 3                   | 26.0                                | 2.1            | 16.7             | 14.2–19.8             | 13          |
| June 15                  | 21.0                                | 2.6            | 18.0             | 15.2–19.6             | 8           |

<sup>a</sup>Micromoles ATP hydrolyzed per milligram protein per hour.

<sup>b</sup>Migrated from May 5 to May 25, 1976 and held inside at 6°C until this date.

4 wk between the two groups in the initiation of strong migratory behavior.

Steelhead exposed to 13°C water for 20 d had a reduced tendency to migrate (Fig. 2 and 3). The effect was greater on AP fish than on NL fish and also resulted in depressed gill  $\text{Na}^+-\text{K}^+$  ATPase activities (Table 3).

Comparing numbers of migrants with numbers of nonmigrants in fork length increments of 0.5 cm shows that migrants began to outnumber nonmigrants noticeably at 16.0–16.5 cm for both NL (Fig. 4) and AP (Fig. 5) fish. Nevertheless, several fish (22) in the fork length range of 12.5–15.7 cm migrated and had elevated gill  $\text{Na}^+-\text{K}^+$

ATPase activities ( $28 \pm 2$  (SE)) which compares with seven nonmigrants, 13.9–15.9 cm fork length, with lower ATPase activities ( $17 \pm 2$  (SE)). These data suggest a minimum fork length of about 16 cm for a high percentage of migrants.

### Discussion and Conclusions

The studies reported here have shown that migratory behavior and elevation in gill  $\text{Na}^+-\text{K}^+$  ATPase activity in summer run steelhead from Dworshak National Fish Hatchery can be advanced at least 1 mo under conditions similar to those existing in a production facility by advancing photoperiods

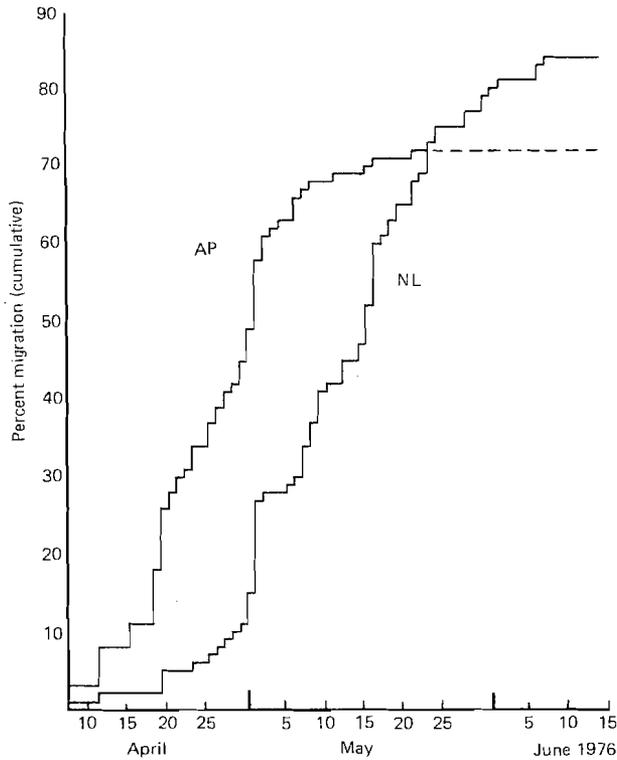


FIG. 1. Migration of yearling steelhead subjected to natural light (NL) or to advanced photoperiods (AP).

through the use of electric lighting. Thus, steelhead from the upper river drainages appear to respond to photoperiod adjustment much as winter run steelhead (Wagner 1974; Zaugg and Wagner 1973) with respect to these indicators of smolt transformation (Hoar 1976). Fish receiving advanced photoperiods migrated initially nearly as well as those on natural light (Fig. 1). However, after being held (at 6°C) under natural light conditions from 3 to 6 wk, while other fish were being collected, migration was much less than NL fish (Fig. 2 and 3). Apparently, in addition to an advance in the manifestation of these smolt indicators, the AP group must have experienced an accelerated reversion to a nonmigratory parr, or postsmolt state, an event that normally occurs from early to late June, depending on water temperatures. This reversion may have resulted from response to either an advance in the biological clock or to the abrupt change from an advanced (long) to a normal, shorter photoperiod. What effect this might have on animals liberated into a natural environment after experiencing early development of smolting indicators by advanced photoperiods is unknown. Recent studies (W. S. Zaugg, National Oceanic and Atmospheric Administration, Northwest and Alaska Fisheries Center, Coastal Zone and Estuarine Studies Division, 2725 Montlake Boulevard East, Seattle, WA 98112, USA, unpublished results) have shown that coho salmon (*Oncorhynchus kisutch*) released in June and July, after having experienced an increase then a decrease in gill  $\text{Na}^+ - \text{K}^+$  ATPase activity while in the hatchery environment, rapidly migrated seaward with elevating ATPase levels. It is quite possible that, in spite of the abrupt change in photo-

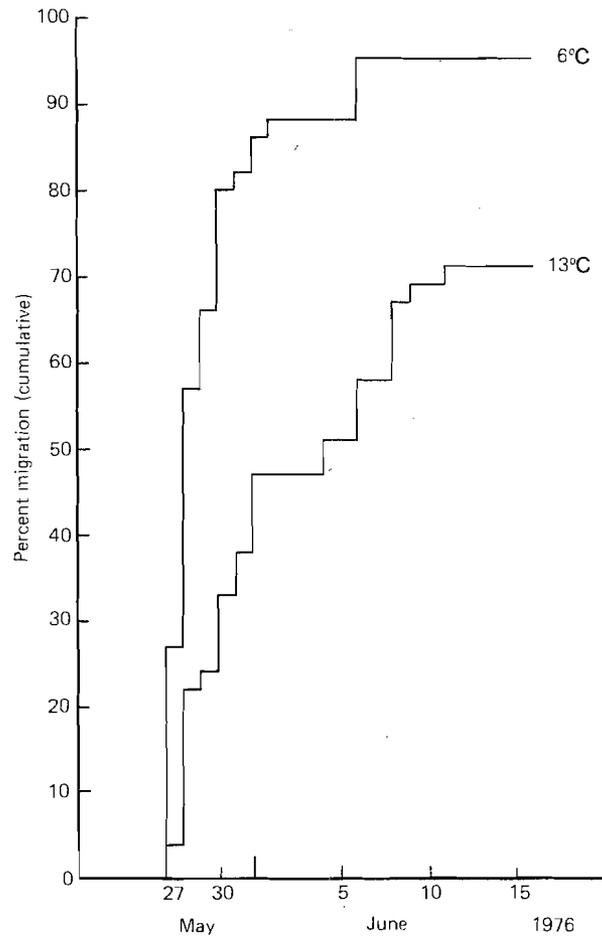


FIG. 2. Migration of yearling steelhead smolts from natural light which had been exposed for 20 d to either 6 or 13°C water.

period, steelhead induced to initiate the smolting process early would be less likely to revert prematurely while actively migrating in a natural river than while being confined under the conditions of this experiment. However, this supposition is necessarily subject to experimental verification.

Presently, peak steelhead migration from the upper Columbia and Snake rivers occurs from early to mid-May, with some movement being observed during the latter half of April and into June (Bjornn et al. 1978; Chrisp and Bjornn 1978; Ebel et al. 1975; Raymond et al. 1975). Using migration rates for moderate flows determined by Raymond et al. (1975), Chrisp and Bjornn (1978) calculated the travel time for steelhead from the Pahsimeroi and Lemhi rivers in Idaho to the Columbia River estuary at 57 d. Migrants leaving these streams on the first of May would theoretically arrive at the estuary near the end of June, at a time when normal reversion occurs. Therefore, even in years of moderate water flow many steelhead smolts may not be able to reach the estuary from upper river regions before some loss of smolt condition. Consider, then, the potential loss of smolts in years of low water flow, when the calculated migrating time is 94 d (Chrisp and Bjornn 1978).

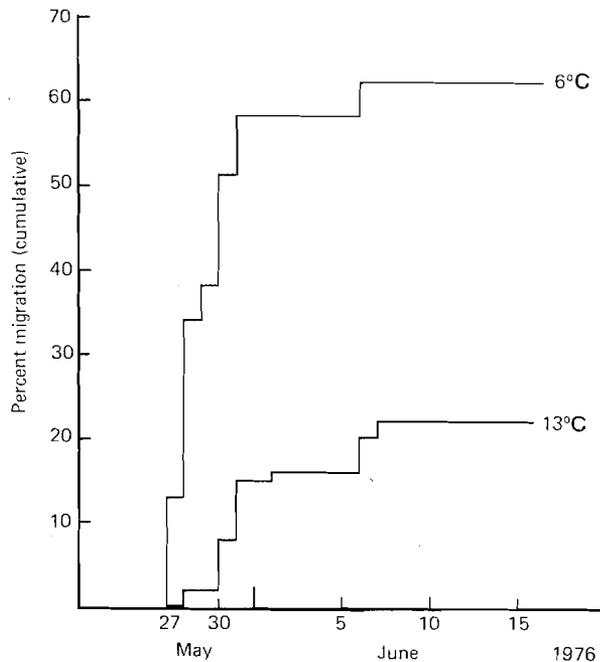


FIG. 3. Migration of yearling steelhead smolts from advanced photoperiods which had been exposed for 20 d to either 6 or 13°C water.

In this study steelhead which had previously migrated to the lower end of the raceway and then were exposed to a 13°C temperature for 20 d showed a reduced tendency to move down a second time (Fig. 2 and 3). Even those fish that migrated had lower gill  $\text{Na}^+\text{-K}^+$  ATPase activities than control fish which had been held at 6°C (Table 3). Lower enzyme activity indicates that these fish were in the process of reverting and would not be capable of a sustained downstream migration in this state. This conclusion is supported by observations from several studies that all active, seaward, migrating steelhead examined have had elevated gill  $\text{Na}^+\text{-K}^+$  ATPase levels.

Temperatures of the Columbia River at Bonneville Dam

generally reach 12°C by mid-May. However, this can occur much earlier in years of low water flow, for example on May 5 in 1973 and on April 28 in 1977. If seaward migrants are affected by river temperatures above 12°C as are test fish in laboratory situations (Adams et al. 1975), then present river conditions pose a very serious threat. Temperature-induced reversion may have been an important factor in the failure of large numbers of steelhead smolts to complete seaward migration and to hold over in 1973 and again in 1977 in Lower Monumental, Little Goose, Lower Granite, and John Day reservoirs (Raymond et al. 1974; Sims et al. 1978). Such reversions may, and probably do, also occur in years of moderate flow.

An optimum length of 20 cm has been suggested for summer steelhead reared 1 yr in hatcheries (Chrisp and Bjornn 1978). However, the present study shows that fish as small as 16 cm are capable of good smolt development where factors such as pond density, water temperature, and water quality do not interfere with this development. Under the right conditions then, size should not be limiting in the ability of steelhead at Dworshak to undergo early smolt transformation induced by advanced photoperiods.

If steelhead which initiate smolt transformation early as a result of advanced photoperiods (and consequently begin seaward migration up to 1 mo earlier than normal) could successfully complete migration, then the potentially disastrous effects of warming river water might be avoided. Early migrating steelhead would likely reach the estuary at a time corresponding more closely to historic arrivals, which were not delayed by reservoirs and dams, and would be exposed to fewer disease organisms than might be encountered later in warmer water.

It is proposed that early migrating steelhead should be able to overcome in some measure the adverse conditions of dam-delayed migration and warm river temperatures, and that further studies should be undertaken to explore the potential for success of such an approach.

### Acknowledgments

I express sincere appreciation to Lynn McLain and Bonnie Ternahan for their technical assistance and to personnel at Dworshak

TABLE 3. Gill  $\text{Na}^+\text{-K}^+$  ATPase activities in yearling steelhead under natural light (NL) and advanced photoperiods (AP) exposed to 6 and 13°C water. Enzyme activities determined on May 28–June 7 were on fish retrieved from the lower ponds whereas fish used on June 17 were from the upper ponds.

| Date    | Light | Temperature (°C) | No. of fish | Mean fork length (cm) | Length range (cm) | Mean ATPase <sup>a</sup> | Standard error |
|---------|-------|------------------|-------------|-----------------------|-------------------|--------------------------|----------------|
| May 28– |       |                  |             |                       |                   |                          |                |
| June 7  | NL    | 6                | 8           | 18.2                  | 16.1–20.6         | 34.8                     | 1.3            |
|         | NL    | 13               | 10          | 18.4                  | 17.0–20.1         | 19.0                     | 1.7            |
|         | AP    | 6                | 10          | 17.5                  | 15.8–19.0         | 34.8                     | 3.1            |
|         | AP    | 13               | 6           | 17.5                  | 16.0–20.0         | 19.7                     | 1.4            |
| June 17 | NL    | 6                | 1           | 19.5                  | —                 | 37.0                     | —              |
|         | NL    | 13               | 6           | 17.7                  | 16.7–19.0         | 19.7                     | 0.6            |
|         | AP    | 6                | 6           | 17.2                  | 15.6–19.3         | 21.7                     | 2.7            |
|         | AP    | 13               | 6           | 18.1                  | 16.8–18.8         | 19.0                     | 1.1            |

<sup>a</sup> $\text{Na}^+\text{-K}^+$  ATPase activity expressed as micromoles ATP hydrolyzed per milligram protein per hour. All differences in activities between temperature treatments were significant ( $P < 0.05$ ) except for AP on June 13 which showed no significant difference.

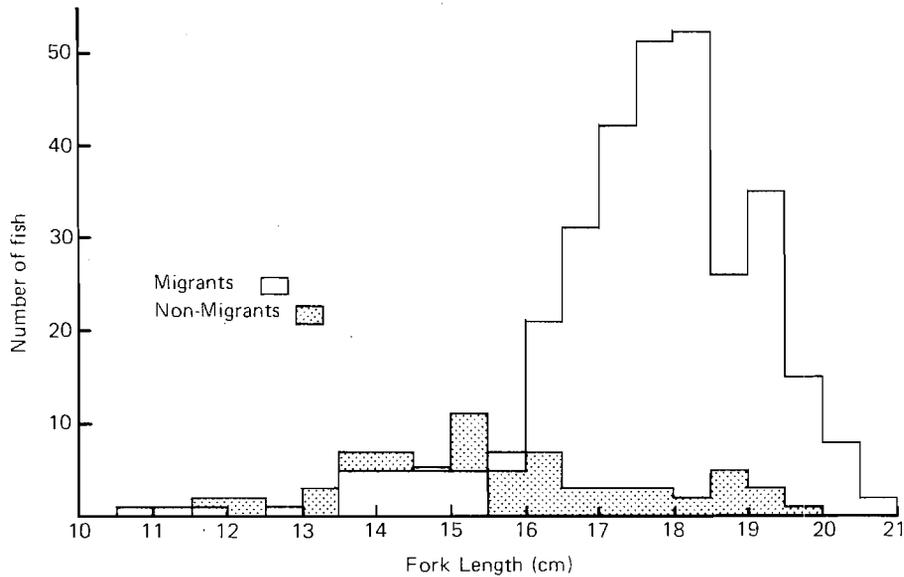


FIG. 4. Relationship of fork length to migration of steelhead under natural light.

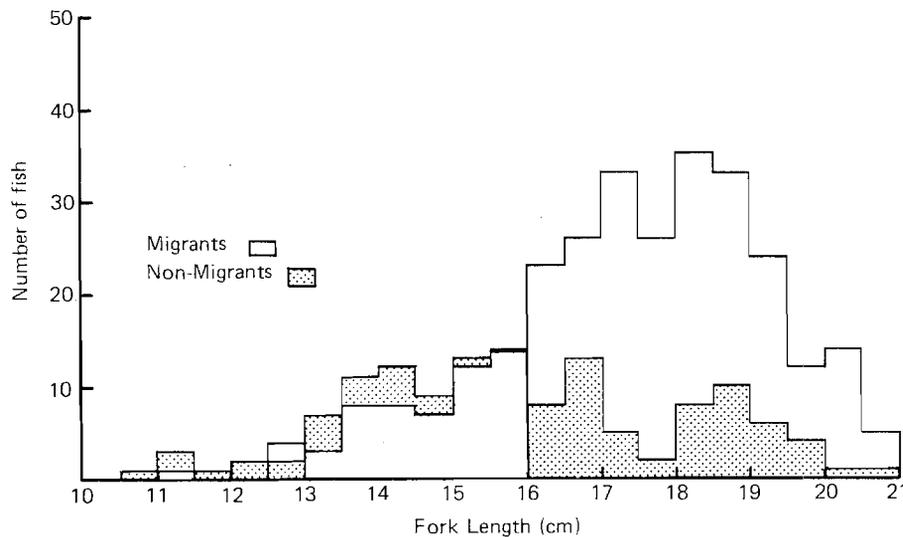


FIG. 5. Relationship of fork length to migration of steelhead under advanced photoperiods.

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