

CHANGES IN SWIMMING BEHAVIOR AND STAMINA DURING SMOLTING OF COHO SALMON

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Abstract

In 1978 and 1979, coho salmon, *Oncorhynchus kisutch*, were tested in a modified Blazka respirometer for swimming performance and stamina during parr, smolt, and post-smolt stages of their life cycle in fresh and saltwater. The smolts characteristically showed an increase in tailbeat frequency compared to parr and post-smolt stages for any given swimming velocity (body lengths per second). The relative velocity at which fish fatigued generally decreased after direct entry into seawater (29‰). Only one group showed no decrease in stamina, perhaps the only group to enter seawater exactly at the physiologically optimum time. Recovery to levels of swimming stamina comparable to the pre-entry (freshwater) level required up to 3 weeks. During the first few days in seawater, fish which swam until fatigued suffered significant mortality 3 to 7 days after fatigue. Survival following fatigue tests in seawater correlated with the freshwater developmental peaks of thyroxine (T₄) and gill Na⁺-K⁺ ATPase.

Introduction

One of the benefits of rearing coho salmon, *Oncorhynchus kisutch*, in seawater net pens is the opportunity to document detailed data on the marine survival of smolts. Such data is normally unobtainable when fish are released from the hatchery. The sometimes low survival of coho salmon smolts upon entry into seawater prompted a multidisciplinary study of smolting indicators which could serve as predictors of hatchery release time for smolts to ensure maximum survival and subsequent growth.

Our study of changes in swimming performance was a part of a larger project in which groups of coho salmon smolts were transferred into seawater net-pens every 2 weeks from April through July in 1978 and 1979. We also had some data from preliminary studies in 1977. The objective of our study was to correlate changes in swimming behavior with other indicators of smolting and the subsequent survival of the smolts in seawater. This paper presents a summary of our findings (Flagg and Smith, in preparation; Flagg et al., in preparation).

Methods

The coho salmon used in these tests were reared at the National Marine Fisheries Service (NMFS), Northwest and Alaska Fisheries Center (NWAFC), Seattle, Washington. Fish were reared at ambient temperatures to produce yearling smolts or growth was accelerated at 15°C to produce 0-age smolts. Swimming tests were conducted in a Blazka type respirometer, similar to, but smaller than that described by Smith and Newcomb (1970). Four or eight fish were tested at a time. Initial chamber velocities were 1.0 or 1.5 body length per second (l/s) and were increased by 0.5 l/s every 15 minutes until the fish reached fatigue. The critical fatigue level was determined for the swimming speed at which the fish could no longer hold position against the current and remained impinged against an electrified screen. Swimming stamina measurements generally followed Brett's (Beamish, 1978) procedures and are fully detailed in Flagg (1981). For entry into seawater (29‰), fish traveled by tank truck to NMFS Marine Experimental Station near Manchester, Washington, and were transferred into floating net-pens without any acclimation period at intermediate salinities. Stamina testing of fish in freshwater was done at the NWAFC in Seattle; whereas testing in seawater was conducted at Manchester.

During the last half of the 15-minute velocity interval, we made one or more estimates of the tail beat frequency (TBF). One tailbeat consisted of a complete oscillation - the caudal fin traveling from one side to the other and back again. Either we counted tailbeats for 30 seconds or timed 40 tailbeats; then converted the data to tailbeats per minute. Swimming proficiency was evaluated by determining the number of tailbeats/minute required to maintain position against a known water velocity. This is analogous to a runner's stride length and any change in tailbeat frequency most probably reflects a change in tailbeat amplitude. Fish were considered to be more proficient in their swimming when fewer tailbeats were required to maintain position against the same flow.

Results and Discussion

Coho salmon smolts showed two kinds of changes in swimming behavior - an increase in TBF during smolting and, typically, a decrease in swimming stamina when transferred directly into seawater. It appears that these two changes in swimming behavior are distinct, unrelated events, both of which have the potential to be used as indicators of smoltification status and thus, migratory readiness.

A typical representation of the changes in swimming proficiency associated with smoltification of coho salmon is presented in Fig. 1. This data shows the decrease in swimming proficiency coinciding with smoltification and the subsequent recovery after the fish have smolted. This recovery occurred whether the fish were transferred to seawater or held in freshwater past smolting. The magnitude of the decrease in swimming proficiency is shown in Fig. 1. At the constant swimming velocity of 4.0 l/s, a parr requires approximately 275 tailbeats/min to maintain position, whereas a maximally inefficient smolt requires up to 390 tailbeats/min to maintain position against the same flow. This represents a maximal decrease in swimming proficiency of over 40%.

Our studies of TBF over the range of swimming velocities show that there are dramatic decreases in swimming proficiency associated with the smoltification of coho salmon. Examination of both 0-age and yearling fish indicate this is a normally occurring phenomenon of smolting coho salmon, and this phenomenon occurs throughout a range of swimming speeds. The decrease in swimming proficiency was larger at increased swimming speeds since TBF increases linearly as swimming velocity is increased (Bainbridge, 1958).

We originally described this increased TBF as representing decreased swimming efficiency and that the fish were working harder at the higher TBFs. However, we obtained some preliminary data on oxygen consumption and were not convinced that the higher TBF mode of swimming was accompanied by increased oxygen consumption. Therefore, we are now describing the high TBF mode as decreased performance or decreased proficiency (Dickhoff et al., 1981) to avoid making a premature value judgment concerning efficiency.

The function of this decrease in swimming proficiency is unclear, and we have no indication it is detrimental. However, events during the parr-smolt transformation cause a bottom dwelling parr to become a pelagic migrating smolt. The decrease in swimming proficiency may render the fish behaviorally unable to maintain its normal position in the stream and, thus, may be the impetus for downstream migration.

Further experiments have shown this decrease in swimming proficiency is concurrent with the springtime thyroxine (T_4) surge that accompanies smoltification (Dickhoff et al., 1981). Increases in thyroid activity have been correlated with increased migratory restlessness in salmon smolts (Hoar, 1976; Folmar, 1979). Whereas we have no data from migrating wild fish, it seems possible they also experience hormonally induced TBF changes and that these are associated with migratory restlessness. We believe this decrease in swimming proficiency may be useful as an indicator of smoltification status and migratory readiness in coho salmon.

Direct entry into seawater can cause immediate ionic, hormonal, and enzymatic imbalances that reequilibrate as salmon smolts adapt to seawater (Conte et al., 1966; Miles and Smith, 1968; Clarke and Blackburn, 1978; Folmar and Dickhoff, 1979). In addition, seawater transfer may initially reduce muscular efficiency (swimming stamina) and overall behavioral activity (Huntsman and Hoar, 1939; Houston, 1957, 1959). Ten of the eleven groups of coho salmon transferred directly into seawater during our studies had depressions in stamina representing an average decrease in swimming ability of over 35% (range 15-75%). This compromise in muscular activity probably occurred through an increase in plasma magnesium concentration causing inhibition of the presynaptic transmitter substance acetylcholine (Houston, 1957; Miles, 1971; Wedemeyer¹, personal communication) and/or increased metabolic energy demands during the adjustive phase of seawater adaptation leaving less available energy for locomotion (Houston, 1959).

The initial reductions in swimming stamina were followed by a progressive return to the freshwater level. In all cases, the return to the freshwater swimming stamina level required from 2 to 3 weeks. Fig. 2 shows the typical depression in swimming stamina at direct seawater entry, and the subsequent recovery to the freshwater level exhibited by the test groups.

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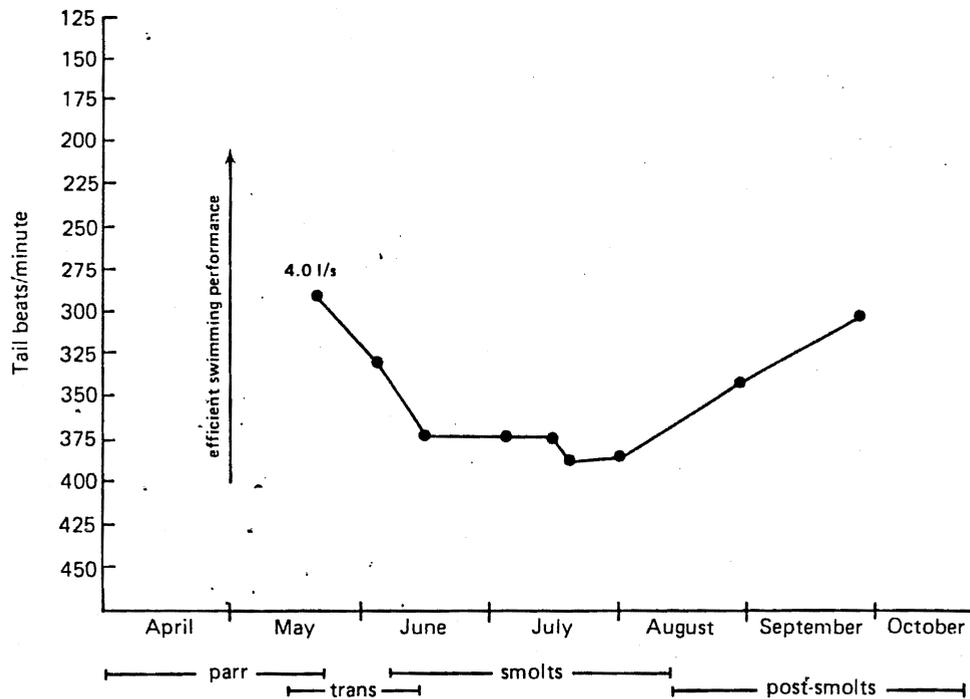


Fig. 1. Typical changes in swimming proficiency (tailbeats/minute required to maintain position against a constant water flow) associated with smoltification of coho salmon.

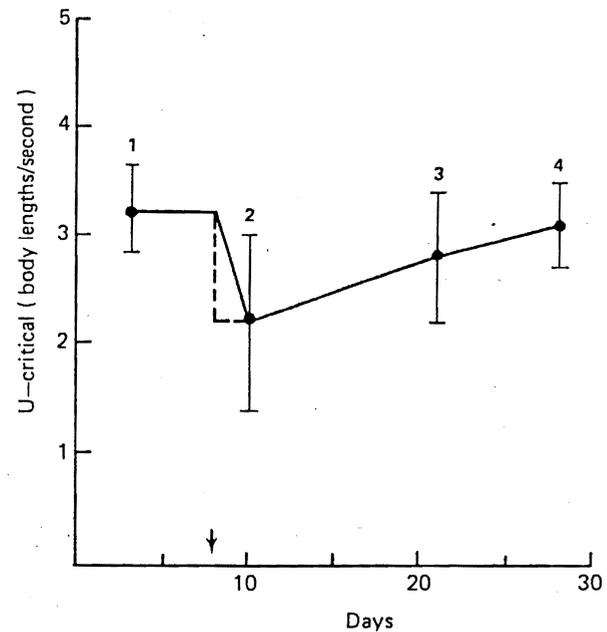


Fig. 2. Typical depression in swimming stamina (U-critical) normally associated with direct seawater entry, and the recovery to the pre-entry (freshwater) level, for coho salmon smolts. Figure shows: (1) freshwater swimming stamina, (2) swimming stamina at the end of the second week of seawater residence, (3) swimming stamina at the end of the second week of seawater residence, (4) swimming stamina at the end of the third week of seawater residence. Arrow indicates seawater entry. Dashes indicate decrease in swimming stamina coinciding with seawater transfer. Brackets indicate \pm one standard deviation.

The one test group which exhibited no decrease in swimming stamina at entry to seawater was the only one which we had determined (at the pre-entry inspection of their visual status of smoltification) to be optimally suited for seawater entry. In subsequent experiments of 1979, the depressions in swimming stamina at seawater entry were not related to the test groups' status of smoltification as determined by the freshwater smolting profiles (Folmar et al., 1980) of gill $\text{Na}^+\text{-K}^+$ ATPase and plasma thyroxine (T_4). It is possible there is a narrow time frame coinciding with the optimal period of smoltification that enables coho salmon to enter seawater without experiencing reductions in swimming stamina. Even so, the present study indicates that in most cases direct seawater transfer will have an initial debilitating effect on coho salmon.

Test groups that exhibited depressions in swimming stamina at seawater entry also were lethargic and easy to capture in the seawater net-pens. In cases where the test groups exhibited an extreme depression in fatigue level (usually greater than 40%), the fish often displayed a concomitant change in body coloration, with the parr marks returning and showing clearly through the otherwise silvery appearance of the smolt. As the fish's swimming stamina recovered, the parr marks progressively faded, and the fish returned to the normal silvery appearance of a smolt. We believe this change in body coloration (return of parr marks) to be stress related and, further, that the return to the normal silvery smolt appearance is an indication of adjustment to the saline environment.

In migratory release situations, it is believed that fish that move rapidly through the river system and enter seawater during some naturally optimal period have a better chance to survive in the ocean. Muscular inefficiency at the time of seawater entry may impede ocean migration and feeding and increase susceptibility to predation. Therefore, proper assessment of optimum release timing is essential to attain maximum survival. We believe that an indexing system, utilizing measurements of swimming stamina and/or return of parr marks at seawater transfer, would be useful in assessing proper migratory release timing.

During the 1979 studies, mortality related to swimming fatigue was also investigated. In these studies, mortality was documented to 7 days post-test since our research has consistently shown that non-acute stress related mortality often occurs 3 or more days post-test. No immediate deaths could be attributed to swimming fatigue in either freshwater or seawater. Delayed mortalities occurred after the seawater swimming fatigue tests. During the first week of seawater residence, swimming fatigue caused significant (8.3-50.0%) mortalities in all test groups; thereafter, swimming fatigue was usually not a lethal stress. Most necropsied fish showed no pathogens; therefore, it is assumed that osmoregulatory dysfunction was the major contributing factor.

The seasonal increase in gill $\text{Na}^+\text{-K}^+$ ATPase activity and plasma thyroxine concentrations are generally considered to be important components in the preparatory mechanisms that enable adequate osmoregulation at seawater entry (Folmar and Dickhoff, 1980). We found both of these measures of smoltification to be significantly related to the fish's ability to survive swimming fatigue at entry to seawater. The ability to survive fatigue increased as the test groups approached the peak of smoltification and declined thereafter - suggesting that adequate osmoregulatory preadaptation is a major factor in coping with stress during adjustment to seawater. These relationships further enforce the need for proper assessment of optimum release timing if maximum seawater survival is to be attained.

Conclusions

1. During smoltification, coho salmon undergo a hormonally induced decrease in swimming proficiency which may be an important component in downstream migration.
2. Coho salmon smolts may experience a transient depression in swimming stamina at direct entry to seawater. Our research indicates there may be a period during the peak of smoltification that enables cultured fish to enter seawater without experiencing depressions in stamina.
3. Reappearance of parr marks at seawater transfer (with the parr marks returning and showing clearly through the otherwise silvery appearance of the smolt) is indicative of coho salmon smolts that are experiencing severe depressions in swimming stamina.
4. Coho salmon smolts experience transient depressions in their ability to survive severe physical stress when transferred directly to seawater. This survival ability is related to the fish's status of smoltification. Our research shows that the maximum ability to survive physical stress at seawater entry is attained in conjunction with the freshwater (smolting) developmental peaks of plasma thyroxine (T_4) and gill $\text{Na}^+\text{-K}^+$ ATPase.

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