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SWIMMING STAMINA AND SURVIVAL FOLLOWING DIRECT SEAWATER ENTRY DURING PARR—SMOLT TRANSFORMATION OF COHO SALMON (*ONCORHYNCHUS KISUTCH*)

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ABSTRACT

Flagg, T.A., Prentice, E.F. and Smith, L.S., 1983. Swimming stamina and survival following direct seawater entry during parr—smolt transformation of coho salmon (*Oncorhynchus kisutch*). *Aquaculture*, 32: 383—396.

Swimming stamina and survival in relation to severe stress (swimming fatigue) were assessed in fresh water and seawater during various stages of the parr—smolt transformation for both 0-age and yearling coho salmon (*Oncorhynchus kisutch*). It was determined that coho salmon normally experience transient reductions in stamina when transferred directly to seawater. Coho salmon also experience transient reductions in their ability to survive severe physical stress (swimming fatigue) at direct seawater entry. Stress survival during the first week of seawater residence was significantly correlated to the status of smoltification, with the maximum ability to survive stress coinciding with the freshwater developmental peaks of both plasma thyroxine (T_4) and gill Na^+-K^+ ATPase.

INTRODUCTION

In recent years, the research and development of marine salmonid culture has been largely focused on coho salmon, *Oncorhynchus kisutch* (Novotny, 1975). Present net-pen culture techniques often require the transfer of fish directly from fresh water to seawater. In many instances these transfers are not entirely successful; unacceptable mortality rates, poor growth, and long term smoltification problems are often encountered (Clarke and Nagahama, 1977; Clarke and Blackburn, 1977, 1978; Woo et al., 1978). A thorough understanding of the physiological and behavioral interactions accompanying direct seawater entry is essential to maximize the success of marine husbandry.

The direct transfer of salmonids from a freshwater to a seawater environment can have an initial debilitating effect. The sudden change in salinity can

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cause immediate ionic, hormonal, and enzymatic imbalances that re-equilibrate as the fish adapts to seawater (Conte et al., 1966; Miles and Smith, 1968; Clarke and Blackburn, 1978; Folmar and Dickhoff, 1979). In addition, direct seawater transfer may initially reduce both muscular efficiency (swimming stamina) and overall behavioral activity of salmonids (Huntsman and Hoar, 1939; Houston, 1957, 1959).

Coho salmon undergo a distinct parr—smolt transformation which physiologically pre-adapts them for seawater residence. Several investigators have emphasized the importance of this transformation to overall seawater adaptability and survival (Hoar, 1976; Clarke and Nagahama, 1977; Woo et al., 1978; Folmar and Dickhoff, 1980; Wedemeyer et al., 1980). Glova and McInerney (1977) noted an overall decrease in critical swimming speed during the freshwater transition from parr to smolt. However, little is known concerning the influence of smoltification on swimming stamina at seawater entry or the ability of fish to cope with severe physical stress, such as swimming fatigue.

The present study investigated the relationship between swimming stamina and smoltification status in both 0-age and yearling coho salmon. The goals were to: (1) investigate changes in swimming stamina of both 0-age and yearling coho salmon in fresh water and seawater during various stages of the parr—smolt transformation and (2) determine if the ability of yearling coho salmon to survive severe physical stress (swimming fatigue) varies with various stages of smoltification.

METHODS AND MATERIALS

The present investigation was conducted over a 3-year period (1977–1979). Several stocks of coho salmon were tested during the study: 1977, yearling Issaquah Creek and Toutle River stock; 1978, accelerated growth (0-age) Toutle River stock; and 1979, eight entries of yearling Toutle River stock (Table I). All fish were reared from eggs at the National Marine Fisheries Service's (NMFS) Seattle Laboratory and subsequently transferred to seawater net-pens (salinity ~29‰) at the NMFS Marine Experimental Station near Manchester, Washington (Table I).

Swimming stamina was evaluated for random samples of these fish at: (1) 1 to 8 weeks prior to seawater transfer (depending on year tested); (2) during the first week of seawater residence (normally at days 1, 2, and 3); (3) at the end of the second week of seawater residence (normally at days 12, 13, and 14); (4) at the end of the third week of seawater residence (normally at days 19, 20, and 21); and (5) fish in 1977 and 1978 were also tested during weeks 4—16 in seawater (Tables II and III). During the study, fish were held and tested at ambient temperatures which were within accepted limits for coho salmon (Table I). At the time of testing, the predominant stage of smoltification was determined for each fish using external (visual) criteria developed by NMFS personnel (Prentice et al., 1980).

TABLE I

Sampling periods, stocks, and water temperature during coho salmon (*Oncorhynchus kisutch*) stamina tests (1977—1979)

Test year[a] and stock	Sampling period	Seawater entry date	Mean length (mm)	Water temperature range[b] (°C)	
				Fresh water	Seawater
1977					
Issaquah yearlings	April to September	17 May	108 to 200	10.4 to 13.4	10.0 to 13.0
Toutle yearlings	April to September	17 May	133 to 223	10.4 to 13.4	10.0 to 13.0
1978					
Toutle 0-age	May to September	11 July	81 to 144	13.3 to 16.3	12.9 to 13.9
1979					
Toutle yearlings	March to August	eight serial entries[c]	137 to 182	7.2 to 13.5	7.8 to 15.5

[a] Yearling fish reared under ambient conditions, allowing them to smolt in their second year; 0-age fish reared in heated water, allowing them to smolt in their first year.
[b] Values indicated are from beginning of sampling period to end of sampling period.
[c] Seven bi-weekly entries from 20 March to 12 June and a final entry on 24 July.

Swimming stamina tests were conducted in a modified (27.4 l) version of the Blaska respirometer-stamina chamber described by Smith and Newcomb (1970). A single chamber was used during the 1977 study in tests on individual fish, whereas during the 1978 and 1979 studies, two chambers were used and divided into four equal compartments each containing a single fish. Each test chamber was equipped with an intermittingly used electrified screen at the downstream end assuring maximum fish performance.

Fish were individually anesthetized (tricaine methane sulfonate at 1:20 000), fork length determined, and then placed into a test compartment. After a 1-h recovery period, the initial swimming speed was set at 1.5 body lengths per second (l/s), i.e., for a 100 mm fish, 1.5 l/s = 150 mm/s water flow. Thereafter, the water velocity was increased 0.5 l/s every 15 min until the fish were fatigued, i.e., could no longer hold position in the current and remained impinged against the electrified screen. A swimming stamina rating (U-critical) was established for each fish, using the swimming speed at fatigue and the time of fatigue, by the methods first described by Brett (1964, in Beamish, 1978).

In the 1979 study, mortalities were monitored for 7 days following fatigue

TABLE II

Swimming stamina levels, sample size, and smoltification status for yearling Issaquah Creek and Toutle River stock coho salmon (*Oncorhynchus kisutch*) (1977 study) and accelerated underyearling (0-age) Toutle River stock coho salmon (1978 study)

Test group	Test period[a] (U-critical (body lengths/second))[b]												
	8-FW	6-FW	5-FW	4-FW	3-FW	1-FW	1-SW	2-SW	3-SW	4-SW	7-SW	10-SW	18-SW
Issaquah, 1-year old	—	3.5 ±0.6 (8,t)	3.8 ±0.5 (18,s)	—	4.0 ±0.3 (14,s)	4.0 ±0.3 (5,s)	1.1 ±1.7 (9,a)	2.5 ±1.7 (8,sa)	4.2 ±0.2 (18,sa)	—	—	—	4.1 ±0.5 (13,sa)
Toutle, 1-year old	—	—	3.3 ±0.1 (10,t)	3.5 ±0.3 (14,s)	—	3.5 ±0.2 (6,s)	3.7 ±0.2 (6,sa)	3.5 ±0.6 (6,sa)	—	3.1 ±0.3 (7,sa)	—	—	4.1 ±0.5 (13,sa)
Toutle, 0-age	6.2 ±0.6 (7,p)	6.1 ±0.9 (19,t)	—	5.3 ±0.6 (9,s)	—	4.7 ±0.6 (12,s)	2.8 ±1.4 (21,a)	3.5 ±1.2 (15,sa)	4.5 ±0.2 (12,sa)	—	4.1 ±0.3 (9,sa)	4.1 ±0.4 (15,sa)	—

[a] Test period indicates weeks before and after seawater entry, FW = fresh water, SW = seawater, seawater entry dates: Issaquah 1-year old, 17 May 1977; Toutle 1-year old, 17 May 1977; Toutle 0-age, 11 July 1978.
[b] U-critical = mean swimming speed ± one standard deviation; number in parenthesis indicates sample size; letter(s) in parenthesis indicate: in freshwater, status of smoltification, p = parr, t = transitional, s = smolt, ps = post-smolt; in seawater, degree of adjustment to the saline environment as defined by statistical ($\alpha \leqslant 0.05$) return of U-critical to the pre-entry (freshwater) level, a = adjusting, sa = seawater adjusted.

TABLE III

Swimming stamina levels, sample size, and smoltification status for the yearling Toutle River coho salmon (*Oncorhynchus kisutch*) serial entry test groups (1979 study)

Test period[b]	Serial entry group (U-critical (body lengths/second)[a])							
	1	2	3	4	5	6	7	8
1-FW	3.3 ±0.3 (20,t)	3.3 ±0.3 (34,t)	3.2 ±0.2 (24,s)	3.5 ±0.4 (24,s)	3.5 ±0.3 (23,s)	3.5 ±0.3 (24,s)	3.3 ±0.5 (24,s)	2.3 ±1.0 (23,ps)
1-SW	2.5 ±0.8 (40,a)	2.6 ±0.3 (24,a)	2.2 ±0.5 (24,a)	2.2 ±1.0 (24,a)	1.9 ±1.0 (24,a)	2.1 ±1.0 (24,a)	2.0 ±1.1 (24,a)	1.9 ±1.0 (24,a)
2-SW	2.7 ±0.4 (24,a)	3.0 ±0.2 (24,a)	3.1 ±0.4 (24,sa)	2.6 ±1.1 (24,a)	2.5 ±0.4 (24,a)	2.7 ±0.7 (23,a)	2.8 ±0.6 (24,sa)	2.8 ±0.7 (24,sa)
3-SW	3.1 ±0.3 (24,sa)	3.3 ±0.4 (24,sa)	3.1 ±0.3 (24,sa)	3.2 ±0.3 (24,sa)	3.5 ±0.5 (24,sa)	3.0 ±0.5 (23,sa)	2.8 ±0.5 (24,sa)	2.7 ±0.6 (24,sa)

[a] U-critical = mean swimming speed ± one standard deviation; number in parenthesis indicates sample size; letter(s) in parenthesis indicate: in fresh water, status of smoltification, p = parr, t = transitional, s = smolt, ps = post-smolt; in seawater, degree of adjustment to the saline environment as defined by statistical ($\alpha \leqslant 0.05$) return of U-critical to the pre-entry (freshwater) level, a = adjusting, sa = seawater adjusted.
[b] Test period indicates weeks before and after seawater entry, FW = fresh water, SW = seawater, seawater entry dates: entry 1, 29 March 1979; entry 2, 3 April 1979; entry 3, 17 April 1979; entry 4, 1 May 1979; entry 5, 15 May 1979; entry 6, 30 May 1979; entry 7, 12 June 1979; entry 8, 24 July 1979.

tests and compared to nontested controls. These mortalities were periodically necropsied for pathogens to determine cause of death.

The results of the 1979 study were compared to two of the presently accepted freshwater biochemical indicators of smoltification [gill sodium-potassium activated adenosine triphosphatase (Na^+-K^+ ATPase) and plasma thyroxine (T4) concentrations] (Folmar et al., 1980). Data from all 3 years were subjected to one-way analysis of variance and Scheffe's multiple comparison procedure. Data from the 1979 study were also subjected to Pearson's Product Moment Test of Correlation. For all data analyses, significance was determined for $\alpha \leqslant 0.05$ using the methods of Sokal and Rohlf (1969).

RESULTS

1977 study

Swimming stamina testing of the yearling Issaquah Creek and Toutle River stocks of coho salmon was begun during the late transitional stage of the parr—

smolt transformation. There was no significant change in swimming stamina (U-critical) for the 1-year-old Issaquah coho salmon during the freshwater portion of this study (Table II and Fig. 1). These fish were transferred to seawater after their apparent optimal entry period as defined by visual smoltification criteria. At seawater entry there was a significant ($\alpha = 0.01$) depression in swimming stamina, representing a 72.5% decrease from freshwater ability. The swimming stamina of this group had statistically ($\alpha = 0.01$) returned to the pre-entry (freshwater) level by the second week of seawater residence. This group exhibited a further increase in swimming stamina between the second and third weeks of seawater residence and remained at this level throughout the study. The 1-year-old Toutle coho salmon entered seawater at their apparent optimal entry period as defined by visual smoltification criteria. The swimming stamina of these fish did not change significantly throughout the freshwater portion of this study nor during the first 4 weeks of seawater residence. This group had a significant ($\alpha = 0.01$), unexplained, increase in swimming stamina between the fourth week of seawater residence and the termination of the study.

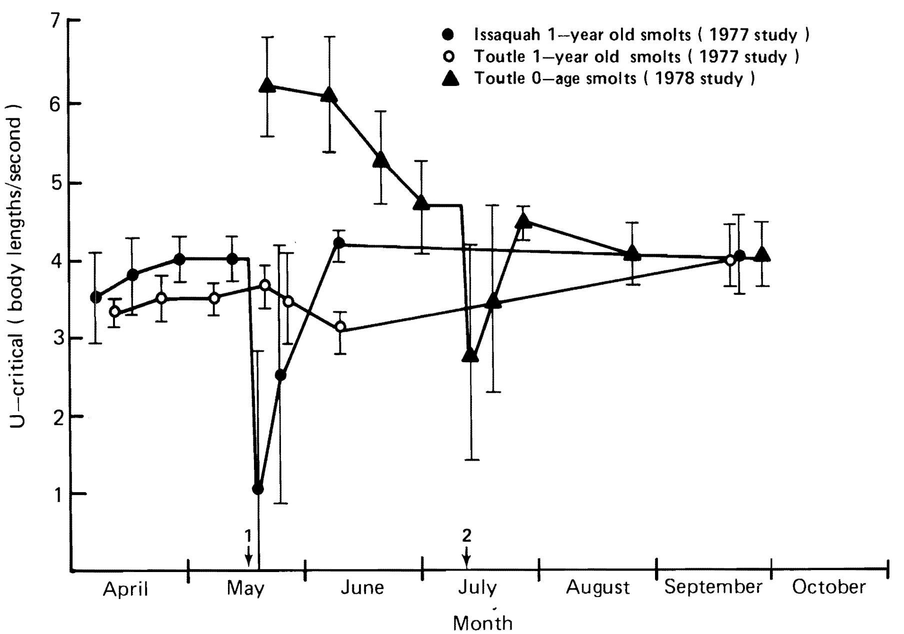


Fig. 1. Changes in swimming stamina levels (U-critical) associated with smoltification and direct seawater transfer for 1-year-old Issaquah Creek and Toutle River stock coho salmon (*Oncorhynchus kisutch*), 1977 study, and accelerated underyearling (0-age) Toutle River stock coho salmon, 1978 study. Arrows indicate: (1) 1977 seawater entry date (17 May) and (2) 1978 seawater entry date (11 July). Brackets indicate ± one standard deviation.

1978 study

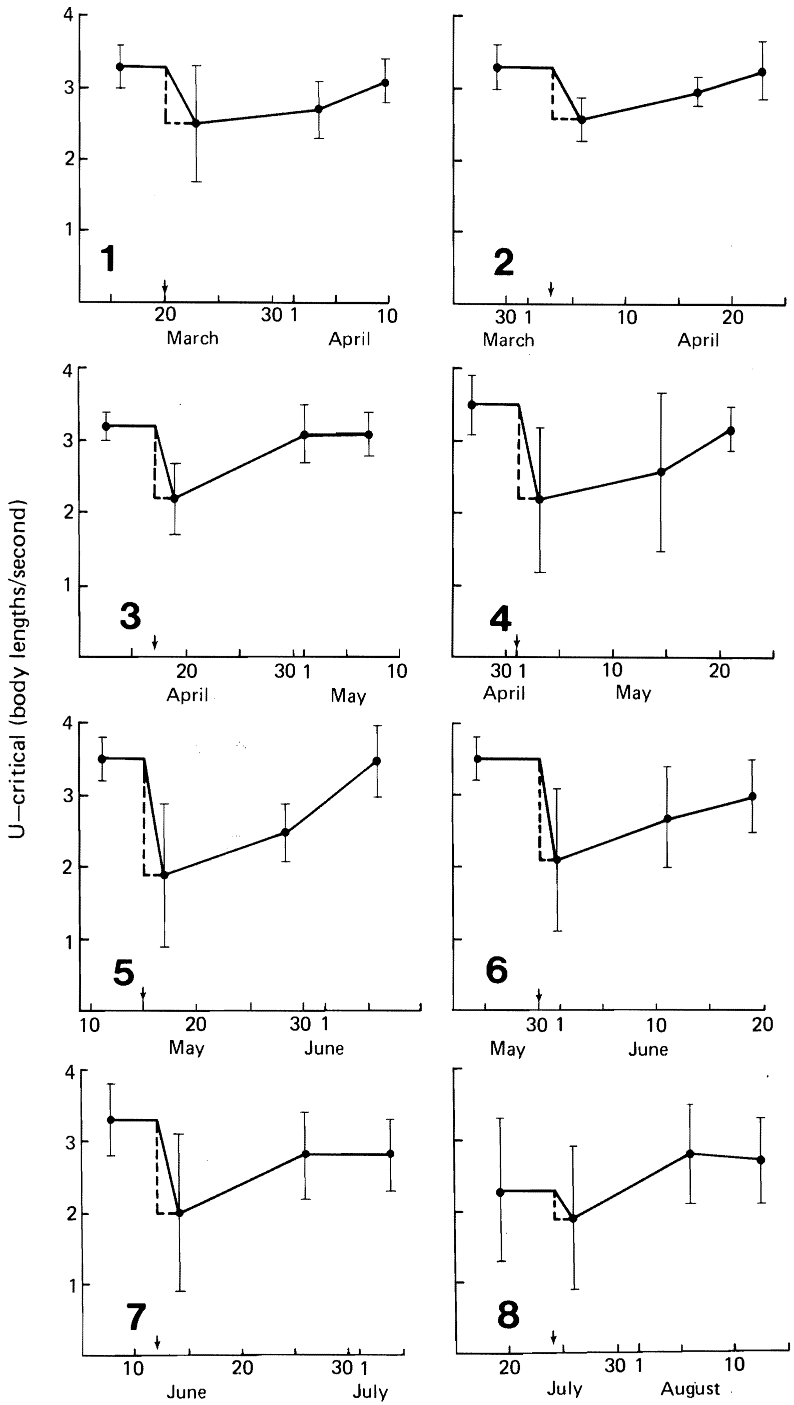
Swimming stamina testing of the 0-age Toutle River stock of coho salmon was begun during the parr stage of the parr—smolt transformation. Although there was an overall reduction in swimming stamina (U-critical) during the freshwater portion of this study, the accelerated growth (0-age) Toutle River coho salmon did not show a significant change between the successive freshwater testing periods (Table II and Fig. 1). These 0-age fish were transferred to seawater after their apparent optimal entry point, as defined by visual smoltification criteria. When this group was transferred directly to seawater, a significant ($\alpha = 0.01$) decrease (40.4%) in swimming stamina was observed, compared to the freshwater level. Swimming stamina had statistically ($\alpha = 0.01$) returned to the pre-entry (freshwater) level by the second week of seawater residence. The Toutle 0-age fish exhibited a further increase in U-critical between the second and third week of seawater residence and their swimming stamina remained at this level throughout the study.

1979 study

The yearling Toutle River stock coho salmon used in the 1979 study were transferred to seawater on a serial entry schedule throughout the parr—smolt transformation (Table I). These serial entries encompassed the range of smoltification status from freshwater transitional to freshwater post-smolt. The direct transfer from fresh water to seawater induced significant ($\alpha = 0.01$) depressions in swimming stamina (U-critical) for the first seven of the eight serial entry groups (Fig. 2). These groups had statistically ($\alpha = 0.01$) the same freshwater swimming stamina level and the same degree of stamina depression at seawater entry — an average decrease in ability of 33%. The freshwater swimming stamina of the fish in the eighth test group was significantly ($\alpha = 0.01$) reduced from that of the previous groups. This group had a slight, but not significant, depression in U-critical at seawater entry.

All eight groups had statistically ($\alpha = 0.01$) similar swimming stamina levels during the first week of seawater residence. Initial reductions in swimming stamina at seawater entry were followed by progressive increases in ability, with swimming stamina eventually returning to the freshwater (pre-entry) level. In all cases the return to a freshwater swimming stamina level required from 2 to 3 weeks (Table III and Fig. 2).

In the 1979 study, no deaths could be attributed to swimming fatigue during or immediately after testing. However, during the first week of seawater residence swimming to fatigue induced significant delayed mortalities (8.3—50.0%) in all eight test groups as compared to controls (Table IV). The majority of these mortalities usually occurred between days 4 and 7 post-test. Death presumably was a result of osmoregulatory dysfunction, since most necropsied fish showed no pathogens. By the second week of seawater residence, and thereafter, swimming to fatigue was usually not a lethal stress.


U–critical (body lengths/second)
1
March
April
2
March
April
3
April
May
4
April
May
5
May
June
6
May
June
7
June
July
8
July
August

At transfer to seawater, the ability of the fish to survive swimming fatigue was significantly correlated to both freshwater gill Na^+-K^+ ATPase activity ($\alpha = 0.02$) and freshwater plasma thyroxine (T_4) concentrations ($\alpha = 0.01$) (Fig. 3 and Table IV). There were no significant correlations between the swimming stamina levels of the serial entry groups (in fresh water or at the 1-, 2-, or 3-week seawater testing periods) and either their ability to survive swimming fatigue or their status of smoltification (as determined by the freshwater profiles of gill Na^+-K^+ ATPase and plasma thyroxine concentrations). Additionally, there were no significant relationships between the mean length of the fish or the mean water temperature during testing and either the swimming stamina of the fish or their ability to survive swimming fatigue.

TABLE IV

Seven-day post-test survival from swimming fatigue tests during the first week of seawater residence and freshwater biochemical information pertaining to smoltification for the yearling Toutle coho salmon serial entry test groups used in the 1979 study.

Test[a] group	Fatigue survival (%) $n = 24$	Control survival (%) $n = 150$	$\overline{X}$ FW[b,c,d] ATPase	$\overline{X}$ FW[b,d,e] plasma T_4
1	50.0	92.6	9.3 ± 2.3	11.7 ± 1.5
2	70.8	95.3	11.5 ± 3.0	23.7 ± 1.1
3	87.5	97.3	18.0 ± 3.5	31.9 ± 2.1
4	91.7	100.0	27.0 ± 5.6	39.2 ± 2.1
5	83.3	98.7	17.0 ± 2.5	22.4 ± 1.1
6	70.8	100.0	8.9 ± 1.2	25.5 ± 1.1
7	66.6	98.6	5.6 ± 1.8	17.9 ± 1.7
8	66.6	99.3	4.9 ± 1.6	21.9 ± 2.3

[a] 1—8 indicates successive serial entry group.
[b] Samples taken in fresh water, about 1 week before seawater entry.
[c] $\overline{X}$ FW ATPase = mean freshwater gill Na^+-K^+ ATPase activity (μmoles Pi mg Prot.$^{-1}$ h^{-1}) ± one standard deviation.
[d] Biochemical data from Folmar et al. (1980).
[e] $\overline{X}$ FW plasma T_4 = mean plasma thyroxine concentration (ng/ml) ± one standard deviation.

DISCUSSION

The direct transfer from a hypo-osmotic environment (fresh water) to a hyper-osmotic environment (seawater) can severely compromise the swimming

Fig. 2. Changes in swimming stamina (U-critical) between fresh water and 1, 2, and 3 weeks of seawater residence for the eight (graphs 1—8 sequentially) yearling Toutle River stock coho salmon (*Oncorhynchus kisutch*) serial entry test groups (1979 study). Arrow indicates seawater entry. Dashes indicate probable decrease in U-critical coinciding with seawater transfer. Brackets indicate ± one standard deviation.

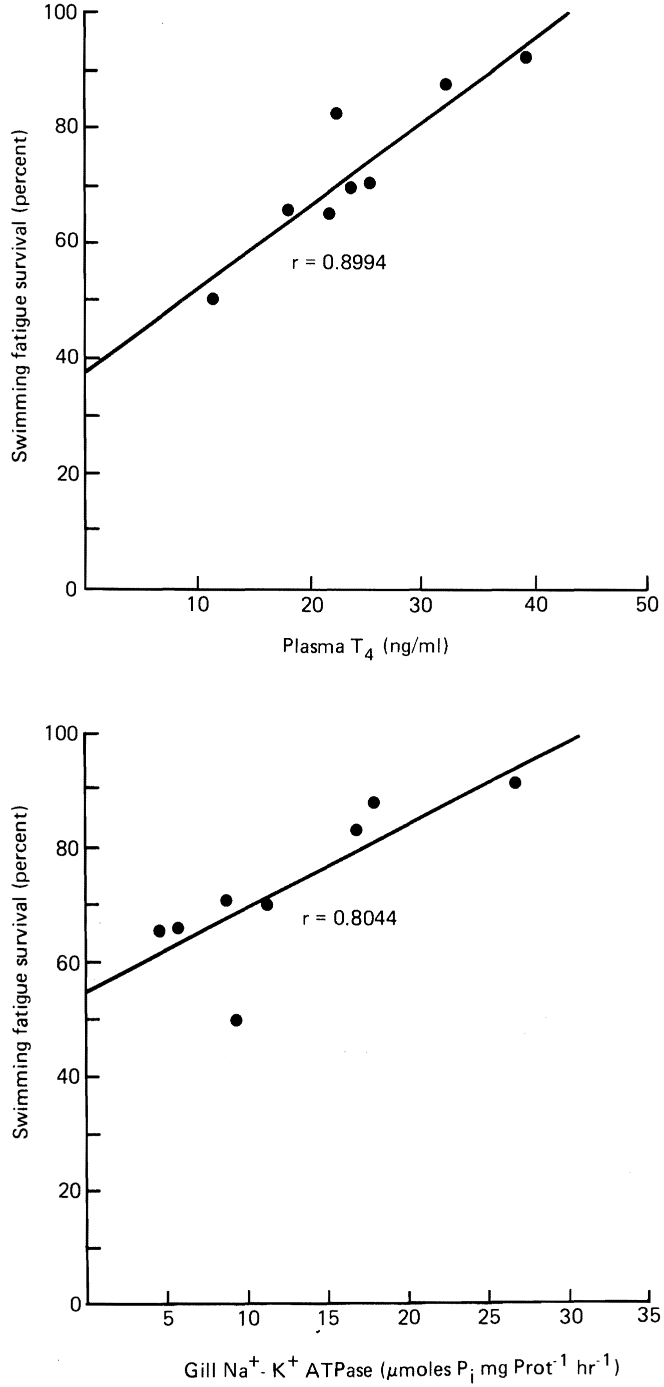


Fig. 3. Percentage swimming fatigue survival (7 day) for the yearling Toutle River stock coho salmon (*Oncorhynchus kisutch*) serial entry test groups fatigued during their first week of seawater residence vs their mean freshwater (pre-saltwater entry) plasma thyroxine concentrations and gill Na^{+}-K^{+} ATPase activity.

ability of both 0-age and yearling coho salmon. Ten of the 11 groups of coho salmon transferred to seawater throughout this study had reductions in swimming stamina which required up to 3 weeks to return to normal freshwater levels. These compromises in swimming stamina are believed to be physiologically motivated. Houston (1959) postulated that muscular inefficiency associated with seawater transfer is primarily due to ionic imbalances which cause inhibitions of the neuromuscular system. He also suggested that biochemical imbalances at seawater entry may result in increased metabolic energy demands during the adjustive phase of seawater adaptation; thus, these imbalances could also contribute to the depression of locomotory performance. Reductions in swimming stamina at seawater entry are apparently associated with these physiological imbalances, and recovery to the freshwater swimming stamina level is believed indicative of adjustment to the saline environment.

For smolting coho salmon it is generally assumed that the major stress at seawater entry is associated with the plasma ion imbalances which stabilize within the first few days (Conte et al., 1966; Miles and Smith, 1968; Clarke and Blackburn, 1977, 1978). In the present study, the 2- to 3-week period for total swimming stamina recovery after seawater entry suggests a much longer seawater adjustive phase than was previously recognized. These data invite further investigation of the biochemical imbalances that occur with transfer to seawater.

It is widely accepted that for salmonids an important relationship exists between smoltification status and successful seawater adaptation (Hoar, 1976; Folmar and Dickhoff, 1980; Wedemeyer et al., 1980). Early in this study, we believed we had evidence that smoltification status also influenced the degree of muscular inefficiency associated with direct seawater transfer. The 1977 yearling Toutle River stock did not experience reductions in swimming stamina when transferred to seawater. These fish were judged (by visual smoltification criteria) to be optimally suited for seawater entry. Whereas, the 1977 yearling Issaquah Creek stock and the 1978 0-age Toutle River stock experienced significant reductions in swimming stamina at seawater entry. Both of these latter groups were transferred to seawater after their apparent optimal entry point.

The 1979 study was designed to investigate further the influence of smoltification status on the reductions in swimming stamina associated with direct seawater entry. In addition to visual smoltification criteria, the 1979 study also documented smolt status utilizing presently accepted freshwater biochemical indicators of smoltification (e.g., gill Na^+-K^+ ATPase and plasma thyroxine). In this portion of the study, all eight entry groups experienced reductions in swimming stamina at seawater entry regardless of smoltification status. There were no statistical relationships between the swimming stamina of these fish and the entry groups status of smoltification, as determined by visual or biochemical measures. Peak smoltification may have been missed, however, due to the serial nature of the entry schedule. It still seems possible that an optimal transfer period, probably coinciding with peak smoltification, enables coho salmon to enter seawater without experiencing reductions in swimming stamina. Even so, it appears that most direct seawater transfers will have an initial debilitating effect on coho salmon, resulting in a transient depression in swimming stamina.

The 1979 study did reveal an important relationship between smoltification status and survival in relation to severe stress (swimming to fatigue). During the first week of seawater residence, survival after swimming to fatigue progressively increased as the entry groups approached the peak of smoltification (based on visual and biochemical indicators), but this ability declined thereafter. Moribund fish from these tests were necropsied. Most fish showed no pathogens, and therefore we assume that osmoregulatory dysfunction was a contributing factor to these mortalities.

The seasonal freshwater (smolting) increases in gill Na^+-K^+ ATPase activity and plasma thyroxine (T_4) concentrations are considered to be important components in the preparatory mechanisms that enable adequate osmoregulation at the time of seawater entry (Zaugg and McLain, 1972; Zaugg and Wagner, 1973; Hoar, 1976; Lasserre et al., 1978; Dickhoff et al., 1978; Folmar and Dickhoff, 1980). In the 1979 study, the ability of the fish to survive swimming fatigue at transfer to seawater was significantly related to these measures of smoltification status. Our data suggest that adequate osmoregulatory preadaptation is a major factor in coping with stress during adjustment to seawater. Evidence indicates that, for coho salmon, the maximum ability to survive stress (such as swimming fatigue) at seawater entry is attained in conjunction with the freshwater developmental peaks of both plasma throxine (T_4) and gill Na^+-K^+ ATPase.

The relationships documented in the present study are believed important to seawater adjustment and survival. Muscular inefficiency at the time of direct seawater entry may impede ocean migration and feeding and increase susceptibility to predation for those fish released to the natural environment, whereas in marine net-pen culture this lethargy may most markedly effect feeding behavior and initial growth. The correlation between the parr—smolt transformation and the ability of the fish to survive stress at transfer to seawater is important to those involved in both marine net-pen culture and enhancement of migratory runs. In either situation, minimizing stress during and after seawater transfer is recommended.

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