Effect of Short-Duration Seawater Exposure on Plasma Ion Concentrations and Swimming Performance in Coho Salmon (*Oncorhynchus kisutch*) Parr

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The effect of seawater (sw) on plasma ion concentrations and critical swimming velocity (U_{crit}) was investigated in hatchery-reared coho salmon (*Oncorhynchus kisutch*) parr exposed to one of four treatments: 24 h of seawater exposure (SW1), 5–7 d of seawater (SW5), 24 h in seawater followed by 24 h in fresh water (SW-FW), and a freshwater control (FWC). Only the SW1 fish demonstrated a reduced U_{crit} and, at rest, elevated plasma [Na^+], [Cl^-], and [SO_4^{2-}]. With exercise, SW1 fish were characterized by an increase in plasma ion concentrations and a decrease in both hematocrit (Hct) and muscle moisture content. There is a strong relationship between plasma [Na^+] at rest and U_{crit}, where an optimal swimming velocity is obtained in animals with resting levels of approximately 147 mEq·L^{-1}. Traditionally, the 24-h seawater challenge is used to test the hypoosmoregulatory ability in smolting salmonids, however, our data suggest that it may also predict the aerobic swimming potential of salmonids following seawater transfer. We suggest that the reduction in Hct and increase in plasma [Na^+] result in reduced oxygen delivery to the muscle and that decrease in muscle moisture content impairs the contractile process.

L'effet de l'eau de mer sur les concentrations plasmatiques d'ions et la vitesse natatoire critique (U_{crit}) a été étudié chez des tacons de saumon coho (*Oncorhynchus kisutch*) élevés en écloserie et exposés à l'un des quatre traitements suivants : exposition de 24 h à l'eau de mer (SW1), exposition de 5 à 7 jours à l'eau de mer (SW5), 24 h dans l'eau de mer puis 24 h dans l'eau douce (SW-FW), et un traitement témoin dans l'eau douce (FWC). Chez les poissons SW1, on a observé une réduction de U_{crit} et, au repos, des concentrations plasmatiques élevées de Na^+, de Cl^- et de SO_4^{2-}. Lorsqu'ils étaient en mouvement, les poissons SW1 étaient caractérisés par une augmentation des concentrations plasmatiques d'ions et une diminution de l'hématocrite (Hct) et de la teneur musculaire en eau. Il existe une forte relation entre la concentration plasmatique de Na^+ au repos et U_{crit}, où la vitesse natatoire optimale est atteinte chez les animaux ayant des niveaux au repos d'environ 147 mEq·L^{-1}. Traditionnellement, l'épreuve de 24 h dans l'eau de mer est utilisée pour mettre à l'essai la faculté hypo-osmorégulatrice des salmonidés en cours de smoltification; toutefois, nos données semblent indiquer qu'elle peut également prédire le potentiel natatoire aérobie des salmonidés après transfert dans l'eau salée. Nous pensons que la réduction de l'hématocrite et l'augmentation de la concentration plasmatique de Na^+ se traduisent par une diminution de l'apport d'oxygène dans les muscles et que la diminution de la teneur en eau des muscles altère le processus contractile.

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Salmon smolts moving from fresh water into an estuary are prone to extremely high mortality rates (Parker 1962; Durkin 1982; Healy 1982). Although the factors responsible for these high death rates are unknown, mortality could result from a variety of factors such as osmoregulatory stress, low food availability (Clarke 1982), predation (Larsson 1985), and other forms of competition. Individual survivorship is dependent on the ability of the challenged smolt to outperform inter- and intraspecific opponents. Migration into an estuary requires a dramatic change in osmoregulatory strategy (Eddy 1982), the success of which is dependent on the physiological status of the smolt.

The 24-h seawater challenge has frequently been used as a means to objectively quantify the hypoosmoregulatory condition of smolting salmonids before they are transferred to seawater net pens or released from hatcheries (Clarke and Blackburn 1977; Wedemeyer et al. 1980; Clarke 1982; Hogstrand and Haux 1985; Blackburn and Clarke 1987). Smolting salmonids that exhibit large increases in plasma [Na^+] following 24 h in full-strength seawater generally experience high mortality or survival with stunted growth following transfer to seawater net pens (Clarke and Shelbourn 1982). Clarke and Blackburn (1977) demonstrated in the laboratory that the greatest growth rates in salmonids transferred to seawater were achieved by those performing well in the seawater challenge. These data indicate that in a controlled environment, this test can be a reliable indicator of survival and growth potential following seawater transfer in salmonids. Little is known, however, about the effects of elevated ion levels on physical activities such as swimming ability which is fundamental to survival.

Rapid seawater transfer results in a reduction in sustained swimming performance in coho (*Oncorhynchus kisutch*) (Flagg et al. 1983; Smith 1987; Glova and McInerney 1977) and chum salmon (*O. keta*) (Houston 1959). The basis for this impairment has been speculated to be an osmoregulatory disturbance;

however, the only evidence to substantiate this is the work of Houston (1959) who found that the physical impairment following rapid seawater transfer in chum salmon was correlated with total body chloride and water levels. If the reduction in swimming performance is induced by an ionic imbalance detectable by ion analysis of the plasma, information obtained from a 24-h seawater challenge test may be used to estimate the degree to which swimming performance will be impaired in salmonids following transfer to seawater. Thus, the 24-h seawater challenge traditionally used to determine the hypoosmoregulatory status of a smolt may also be used as an indication of the animal's physical status and, therefore, chances for survival upon entry into a seawater environment such as an estuary.

This experiment was designed to test the hypothesis that elevated plasma ion concentrations, in particular Na^+, result in a reduced ability for aerobic swimming in coho salmon. The parr–smolt transition is characterized by massive physiological adjustments, predisposing salmonids for marine survival while living in a freshwater medium (McCormick and Saunders 1987; Hoar 1988). Correlated with these changes is a large, transient reduction in swimming stamina in animals still in fresh water (Smith 1987) which is exacerbated by the seawater transfer. To examine the direct effect of elevated plasma ion concentrations on swimming performance independent of the reduction in swimming performance associated with smolting, the experiment was performed using presmolt coho salmon rapidly transferred to seawater. The physiological changes associated with this anticipated reduction in swimming performance were also determined.

Materials and Methods

Fish Acquisition and Care

Hatchery-reared coho salmon parr were obtained and transported from Spius Creek Hatchery, B.C., to the University of British Columbia. They were fed daily and held in dechlorinated fresh water at 10°C for 3 mo prior to experimentation. Mean length and weight were 10.1 ± 0.1 cm and 8.9 ± 0.2 g, respectively, during the test which was conducted between November 1989 and January 1990. Based on the visible parr marks and the season of the study, the fish used in the experiments are referred to as parr.

Experimental Procedure

Groups of 15 fish were randomly subjected to one of four treatments at 10°C : 24 h in natural seawater (26.5 ± 0.7 ppt) (SW1), 5–7 d in natural seawater (SW5) following 24 h in 50% seawater, 24 h in natural seawater followed by 24 h in fresh water (SW-FW), and a fresh water control (FWC). In all treatments, fish were rapidly transferred by dip net to the respective static water baths kept at constant temperature by placement in cooling troughs. The treatments were replicated six times over the duration of this study. Care was taken to ensure that fish densities during the various exposure regimes did not exceed 3.0 $g \cdot L^{-1}$ as is recommended by Blackburn and Clarke (1987). In this study, all parr survived the transfer to seawater.

Following each exposure regime, 10 of the 15 fish were placed in a modified Brett-type respirometer (Gehrke et al. 1990) filled with seawater (SW1 and SW5) or fresh water (SW-FW and FWC) and forced to swim for 2 h at a velocity of 3 body lengths $(Bl) \cdot s^{-1}$. Subsequently, the critical swimming velocity (U_{crit}) was determined for each fish by subjecting the group to hourly 1-$Bl \cdot s^{-1}$ increases in water velocity until all animals had fatigued. Fish were removed as they fatigued and individual U_{crit}s were calculated by adding the velocity of the most recently completed increment and the product of the proportion of the fatigue increment completed and the increase in velocity of that increment (Brett 1964). The proportion of the fatigue increment refers to the length of time the fish swam at the final velocity divided by 1 h, and the increase in velocity of the fatigue increment was 1 $Bl \cdot s^{-1}$. No correction for the solid blocking effect of the fish was included in this calculation, as the total cross-sectional area of the fish did not exceed 5% of that of the swim tube. In these experiments, fatigue was defined as that point at which a fish could no longer remove itself from the posterior screen despite repeated prodding.

Individual U_{crit}s were determined for fish that swam in a group. The validity of this method has been criticized (Lindsey 1978) because schooling behaviour may result in nonfatigued fish drifting to the rear of the swim tunnel with other fatigued fish resulting in premature termination of the test by the researcher. In this study the choice was made to exercise fish in groups of 10, as Bams (1964) found no effect of schooling on fatigue in sockeye salmon (*Oncorhynchus nerka*) fry exercised in groups of 10–12 animals or less. An opaque plastic cover was placed at the anterior portion of the swim tunnel, enticing the salmon to remain there until the velocity could no longer be maintained and fatigue ensued. This prevented interactions with the posterior screen prior to exhaustion and ensured that animals were truly fatigued when they were removed. In all tests, the coho parr fatigued independently of one another and in an approximately normal distribution, suggesting that schooling behaviour has little influence on fatigue in this protocol. In addition, there was no apparent change in U_{crit} over the duration of the experiment in any of the treatment replications.

Sampling Procedure

Measurements in resting fish (rest) were obtained by terminal anaesthetization with MS 222 (200 $mg \cdot L^{-1}$) by injecting a highly concentrated solution of the anaesthetic into a tank containing five animals isolated from their respective group at least 12 h prior to the U_{crit} determination. Anaesthetization prior to sampling has been demonstrated to have no effect on plasma ion concentrations (Blackburn and Clarke 1987). Exercised fish were killed either by concussion immediately following fatigue (U_{crit}) or by terminal anaesthetization after a 2-h recovery period (recovery). The latter technique was used in resting and recovering fish to minimize struggling associated with sampling and thus changes in muscle lactate concentration that would occur without anaesthesia. Terminal anaesthesia was not deemed necessary in fatigued fish because at this time, they were completely exhausted and could easily be removed and killed without the problems associated with struggling. Sampling consisted of recording fork length and weight, severing the caudal peduncle, and collecting blood in 60-μL microhematocrit tubes. The tubes were centrifuged at 11 500 rpm for 5 min in a Damon IEC MB microhematocrit centrifuge and the hematocrit (Hct) was measured in quadruplicate. Fish carcasses were frozen in liquid nitrogen within 2 min of death and the plasma and fish carcasses were stored at −80°C for later analyses.

Analytical Techniques

Muscle lactate concentrations were determined from 0.5 g of dorsal epaxial muscle. The muscle was homogenized in 3 mL

of ice-cold 0.6 N perchloric acid (PCA) for 15 s using a Kinematica GmbH polytron. The homogenate was then centrifuged in a Sorvall Instruments RC5C refrigerated centrifuge at 13 000 rpm for 10 min at 2°C. One millilitre of the supernatant was placed in a 1.5-mL polypropylene Eppendorf micro test tube and neutralized with 0.1 mL of 3 M $KHCO_3$ and 0.5 M triethanolamine. This mixture was vortexed and placed in an Eppendorf centrifuge 3200 for 5 min. The supernatant was analyzed for lactate using a Sigma lactate assay kit (826-UV) and a Shimadzu UV-160 visible recording spectrophotometer.

Plasma ion concentrations were determined on a Shimadzu ion chromatograph (model HIC-6A) (IC) except in two of the six treatment replications where plasma sodium concentrations were determined on a Perkin-Elmer model 2380 atomic absorption spectrophotometer (aa). The plasma in microhematocrit tubes was thawed and in the case of the aa analyses diluted to within the linear range of the machine's detection. Preparation of plasma for the IC analysis consisted of adding 20 μL of plasma to 20 μL of methanol, for the purpose of deproteination, and 60-μL of distilled deionized water in a 0.5-mL centrifuge tube. The contents were vortexed and spun in an Eppendorf centrifuge 3200 for 5 min. To measure monovalent cation concentrations, a 20-μL aliquot of the supernatant was injected into the IC equipped with a Shodex Y521 cation column and a 5 mM nitric acid mobile phase. A separate injection was required for anionic analysis which warranted the installation of a Shim-pak IC-A1 anion column to the IC and the use of a 6 mM boric acid, 18 mM mannitol, and 7.5 mM Tris (tris(hydroxymethyl)aminomethane) mobile phase.

Muscle moisture was determined on 0.5–1.0 g of dorsal epaxial muscle by expressing weight loss following desiccation as a function of initial wet weight of the tissue. Muscle was dried at 75–80°C to constant weight, approximately 96 h.

Statistics

Statistical differences between the treatment groups and physiological states were determined by a split plot, randomized complete block design ANOVA, followed by a Tukey test, with a probability level of 0.05 chosen as the limit of statistical significance. Correlation analyses were computed by least squares regression and tested for significance. All data are presented as mean ± standard error.

Results

Aerobic swimming performance, as indicated by U_{crit}, was significantly reduced in the SW1 group, while all other treatments had no effect on swimming performance (Fig. 1). The reduction in U_{crit} seen in SW1 is not solely a result of the seawater exposure at the time of U_{crit} as no effect on U_{crit} was seen in the 5-d acclimated animals that also swam in seawater. In the SW1 group, extracellular $[Na^+]$, $[Cl^-]$, and $[SO_4^{2-}]$ were significantly elevated relative to control (FWC) values at all sampling times (rest, fatigue, and recovery). In the SW1 group, ion concentrations at fatigue and recovery were all significantly elevated relative to the SW1 resting levels, with the exception of $[SO_4^{2-}]$ at fatigue (Fig. 2). Thus, the greatest deviations in extracellular ion concentrations within and between treatments are seen in fish with the lowest U_{crit} (SW1). In the SW5 group, the extracellular ions do not differ significantly from the FWC values until fatigue and recovery.

There is a reduction in U_{crit} as the plasma $[Na^+]$ increases in resting animals. This relationship is best represented by a second-order regression ($r^2 = 0.68$) that indicates that an optimal U_{crit} is attained in coho with a resting plasma $[Na^+]$ of 147.4 $mEq \cdot L^{-1}$ (Fig. 3). There is a strong positive correlation ($r^2 = 0.89$) between the plasma $[Na^+]$ and $(Cl^-]$ measured in these animals at different activity levels following the various exposure regimes. For this reason, only the relationship between plasma $[Na^+]$ and U_{crit} is presented (Fig. 3) but a similar relationship also exists for $[Cl^-]$.

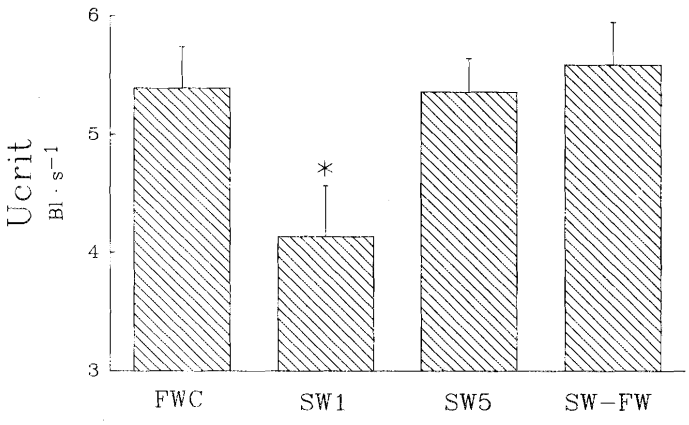

FIG. 1. Effect of salinity exposure regimes on critical swimming velocity (U_{crit}) of coho salmon parr. Treatments were as follows: FWC, freshwater control; SW1 and SW5, fish exposed to seawater for 1 and 5 d, respectively, prior to swimming in seawater; SW-FW, fish exposed to seawater for 1 d followed by 1 d in freshwater and U_{crit} determined in fresh water. The asterisk indicates a significant difference from the FWC group. In each treatment, six trials were performed, each consisting of 10 fish.

There are changes in both Hct and dorsal epaxial muscle moisture content, in addition to fluctuations in the concentrations of plasma ions following seawater exposure. At rest, there was no significant difference in Hct between treatments; however, at fatigue and following recovery, Hct in both groups that swam in seawater (SW1 and SW5) was significantly reduced relative to that measured at the same activity level in control (FWC) fish (Fig. 4). At recovery, Hct was significantly lower than the initial resting values in both seawater groups (SW1 and SW5).

The moisture content of the dorsal epaxial muscle was not significantly different between treatments in resting fish (Fig. 5). At fatigue, the only significant reduction in moisture content relative to that in control animals was in SW1 animals. Moisture content in the SW5 animals that swam in seawater does not differ significantly from control values at fatigue; however, during recovery, there is a significant reduction in content approaching that seen in SW1 animals. Thus, initially, SW5 animals are able to cope with the perturbation of elevated external salinity; however, this is not the case during recovery from exercise.

Lactate analysis of dorsal epaxial muscle was determined to quantify the relative contribution of anaerobiosis during the U_{crit}; however, no significant differences between treatment conditions were detected (Fig. 5).

The SW-FW treatment was incorporated into the experimental design as an additional control for the FWC treatment. Due to the transfer into seawater, these animals experienced the same osmoregulatory perturbations and handling stresses as the SW1 animals and an additional transfer back into fresh water prior to swimming. In all parameters reported in this study, there were no significant differences between SW-FW and FWC treatments.

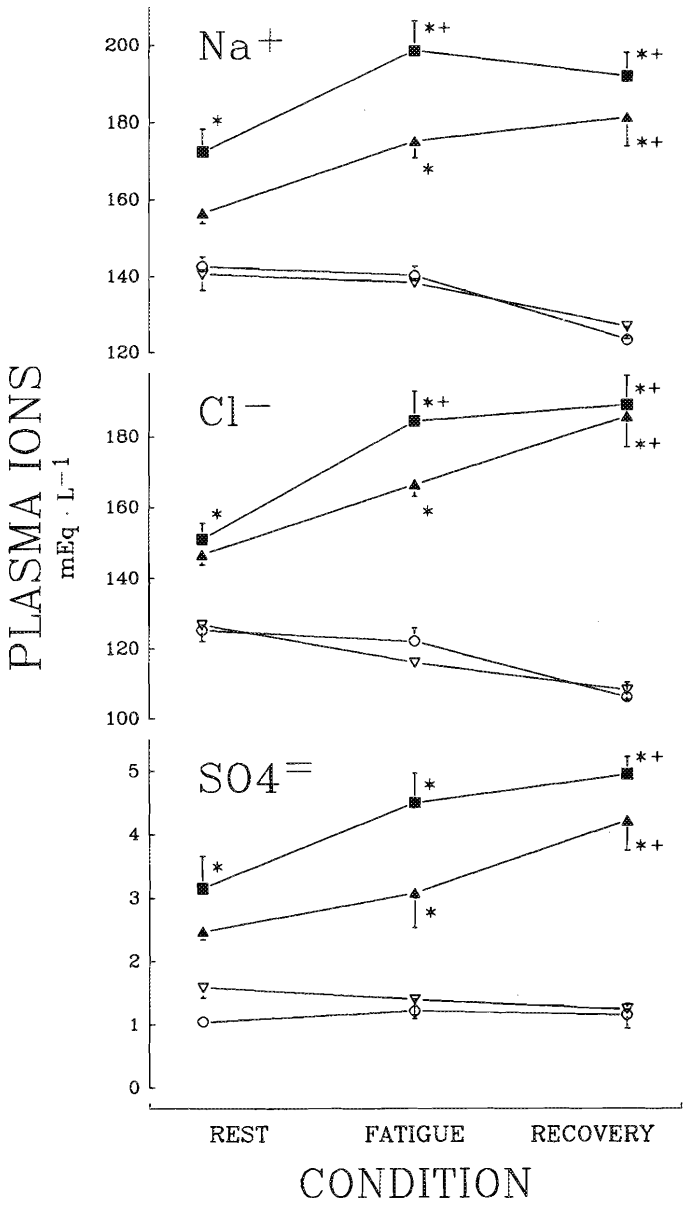

FIG. 2. Effect of treatment condition on plasma $[Na^+]$, $[Cl^-]$, and $[SO_4^{2-}]$ for four salinity exposure regimes: FWC (○), SW1 (■), SW5 (▲), and SW-FW (▽) (see Fig. 1 for further description). Rest, fatigue, and recovery refer to measurements taken before the fish began swimming, at U_{crit}, and 2 h following the U_{crit} determination, respectively. Asterisks indicate a significant difference relative to the same level of activity in FWC. Plus signs indicate a significant difference from the respective treatment resting value. In each treatment, six trials were performed, each consisting of five fish at each level of activity.

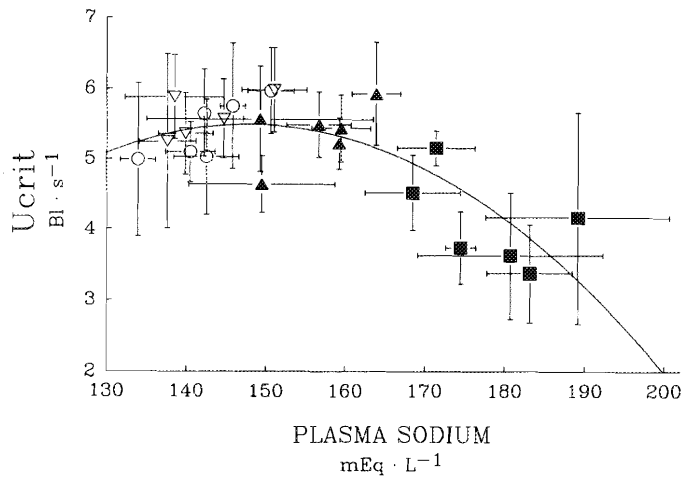

FIG. 3. Correlation between plasma $[Na^+]$ at rest and U_{crit} ($r^2 = 0.68$) (see Fig. 2 for symbol explanations).

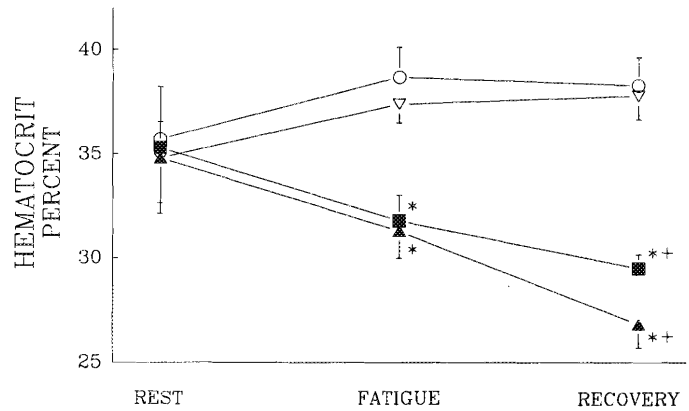

FIG. 4. Effect of treatment condition on Hct for four salinity exposure regimes (see Fig. 2 for other details).

Discussion

The only condition to significantly reduce U_{crit} was exposure to seawater for 24 h (SW1) prior to exercise (Fig. 1). Transfer to seawater has been shown by others to impair swimming performance in coho smolts (Glova and McInerney 1977; Flagg et al. 1983; Smith 1987) and juvenile chum (Houston 1959). The SW1 group was characterized by significantly elevated plasma $[Na^+]$, $[Cl^-]$, and $[SO_4^{2-}]$ at all sample times relative to the FWC group (Fig. 2), indicating an ionic basis for the impairment in swimming performance.

The U_{crit} determination is predominantly an aerobic test. As a fish approaches fatigue, however, there is a sequential recruitment of the anaerobic muscle fibres (Bone 1978; Bone et al. 1978) such that when the animal finally collapses, it is both aerobically and anaerobically exhausted. Anaerobic metabolism was unaffected by the various treatments as indicated by the similarity in muscle lactate concentrations following the various seawater exposure regimes (Fig. 5). Tang and Boutilier (1991) found rainbow trout (*Oncorhynchus mykiss*) acclimated to seawater to have higher muscle lactate at exhaustion and reduced lactate following recovery compared with fish exercised in fresh water, due to a greater clearance rate of lactate in the seawater animals. This was not found with seawater exposure in this study but these coho were only subjected to seawater for 5 d, while the rainbow trout used by Tang and Boutilier (1991) were acclimated for over 2 mo.

U_{crit} is strongly correlated with the plasma $[Na^+]$ of the resting animal (Fig. 3). The best-fit second-order regression suggests that an optimal swimming performance is achieved in aminals with resting extracellular $[Na^+]$ levels of 147.4 mEq·L^{-1}. As $[Na^+]$ increases above this value, there is a reduction in U_{crit}. There is also a trend towards a reduction in U_{crit} as the $[Na^+]$ decreases below this value; however, ion levels were not depressed sufficiently in this study to show the effect unequivocally. The relationship between resting ion concentration and U_{crit} also exists for extracellular $[Cl^-]$, as there is a strong correlation between extracellular $[Cl^-]$ and $[Na^+]$.

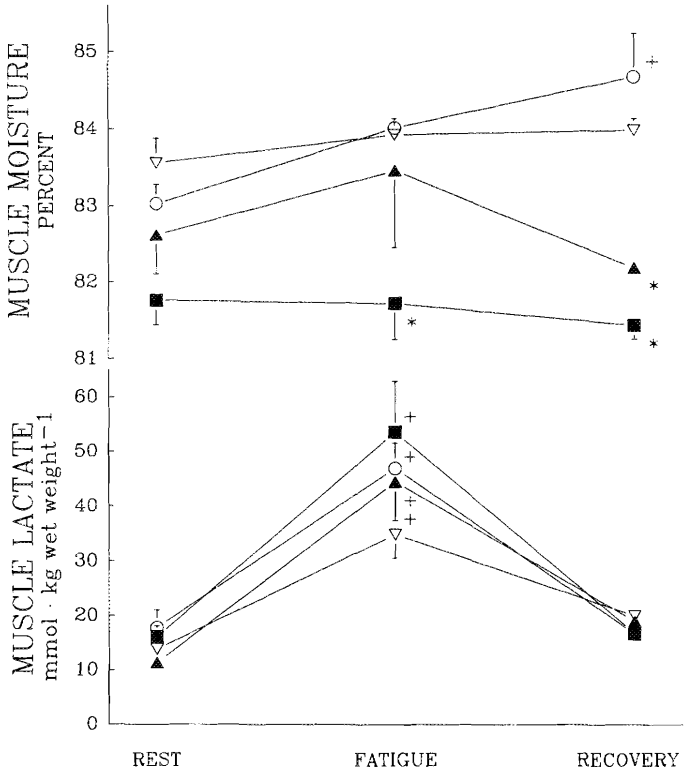

FIG. 5. Effect of treatment condition on percent muscle moisture and muscle lactate concentration for four treatment regimes (see Fig. 2 for other details).

This is in agreement with the work of Houston (1959) who found that sustained swimming performance was correlated with the total body [Cl^-] at fatigue. These results imply that data acquired from a 24-h seawater challenge are of value in estimating a salmonid's ability to exercise, which has been used as an indicator of the overall condition of the animal.

Initially, 5 d appeared sufficient for the parr to compensate for the osmoregulatory stress associated with seawater transfer, as extracellular ion concentrations at rest in the SW5 group did not differ significantly from those in the FWC fish (Fig. 2) and U_{crit} was not affected by this treatment (Fig. 1). During recovery, however, the extracellular ion disturbance in the SW5 group was as severe as that observed in the SW1 group. This would indicate that in a second U_{crit} determination, the aerobic swimming ability may be equally impaired in both groups, if ion levels during recovery are indicative of exercise potential. Thus, SW5 animals were capable of initial compensation for the increased environmental salinity at rest and consequently were able to exploit their full aerobic capacity; however, during recovery the cost became apparent. Full adaptation to seawater in coho parr takes up to 30–35 d based on gill Na^+, K^+-ATPase activity (Zaugg and McLain 1970).

The reduced U_{crit} in group SW1 may be due to the poor hypoosmoregulatory ability; however, limitations to exercise may also exist at the level of the circulatory system or the muscle. In the circulatory system, the sites of impairment may be in the transfer of oxygen across the respiratory surface or in the transport and delivery of oxygen to the muscle by the blood. In the gills of rainbow trout immersed in 67% seawater in vitro, Bath and Eddy (1979a) demonstrated considerable dehydration of the secondary lamellae which could potentially explain the reduction in arterial Po_2 (Pa_{O_2}) seen in salmonids at rest during seawater transfer. In rainbow trout resting in 67% seawater, this reduction in Pa_{O_2} lasts for over 10 d (Bath and Eddy 1979a), and in resting Atlantic salmon (*Salmo salar*) parr exposed to full-strength seawater, 48 h was not sufficient for recovery (Stagg et al. 1989). The degree to which Pa_{O_2} is reduced during exercise following seawater exposure, and the impact it will have on aerobic swimming performance, is questionable, as both groups SW1 and SW5 were exercised in seawater, while only the former experienced an impairment in locomotor activity; however, it may be that 5 d is sufficient for the coho parr to rehydrate the lamellae in seawater and restore blood oxygenation.

The transport and delivery of oxygen to the active tissues is also affected by seawater transfer. The Hct in the SW1 group decreased significantly with exercise relative to the freshwater groups, but the same trend was seen in the SW5 group (Fig. 4), demonstrating that the reduction in U_{crit} is not simply related to the reduction in Hct. A reduction in Hct in salmonids following seawater transfer has been attributed to dehydration of the erythrocytes (Bath and Eddy 1979a; Blackburn and Clarke 1987); however, it could also be due to an increased plasma volume, as rainbow trout have been demonstrated to greatly increase drinking rate (Eddy and Bath 1979) and reduce urination rate (Bath and Eddy 1979b) almost immediately following rapid transfer to 67% seawater. In smolting coho salmon, the reduction in Hct seen following seawater transfer is due to an increased plasma volume which results in a reduction in oxygen carrying capacity of the blood (C. J. Brauner, J. M. Shrimpton, and D. J. Randall, unpubl. data).

Although the decrease in Hct is not directly responsible for the reduction in U_{crit}, it may have exacerbated the effects of the increased plasma ion levels on the binding of oxygen to haemoglobin. Sauer and Harrington (1988) found that hyperchloremia in vitro reduced the haemoglobin's affinity for oxygen in sockeye salmon. The oxygen content of whole blood from white sucker (*Catostomus commersoni*) was significantly reduced in vitro following the addition of NaOH and HCl to approximate the strong ion difference seen in animals exposed to saline water (Walker et al. 1989); however, this reduction in oxygen content could have been induced partly by changes in pH. Thus, elevated plasma ions and a reduced Hct in concert may have limited oxygen delivery during exercise in the SW1 group.

An increased ionic composition of the blood may also influence oxygen delivery to the tissues through a reduction in cardiac output. Following NaCl injections in the toad *Bufo marinus* and the bullfrog *Rana catesbeiana*, Hillman (1984) observed that hypernatremia in excess of 170 $mEq \cdot L^{-1}$ reduced maximal cardiac output through a reduction in heart rate and stroke volume. In the toad, peak systolic pressure and cardiac contractility have also been shown to decrease following NaCl injections (Hillman and Withers 1988). The authors attributed the latter to a direct negative inotropic effect of hypernatremia and hyperchloremia on the cardiac muscle. If the salmonid cardiovascular system responds similarly to elevated extracellular ions, cardiac output and consequently the rate of oxygen delivery to the working muscles could be compromised in the SW1 group reducing U_{crit}.

The limitation to aerobic exercise in the SW1 group may also lie at the level of the muscle. Muscle moisture content of the SW1 group was significantly lower at fatigue and recovery than that of the groups exercised in fresh water (Fig. 5). This has been demonstrated in resting rainbow trout (Finstad et al. 1988) and chum fry exercising (Houston 1959) in seawater. Hyper-

osmotic infusions in dogs results in a reduction in muscle moisture content and an intracellular alkalosis (Makoff et al. 1970). Intracellular changes in pH will have an effect on muscular contraction through direct actions on enzyme activity, and a reduction in intracellular moisture content may affect ion and metabolite concentrations resulting in a deviation from optimal conditions for contractility.

Within each treatment, only the FWC group showed a significant change in muscle moisture from rest to recovery, increasing slightly in agreement with the observations of Wood and Randall (1973). U_{crit} was not affected in the SW5 group and muscle moisture did not differ significantly from the control group until recovery, furthur indicating that impairment in swimming performance would be seen in this group in a subsequent bout of aerobic exercise.

The elevated ionic composition of the plasma may have a direct effect on muscular contractility. Houston (1959) theorized that the reduced locomotory activity in chum salmon rapidly transferred to seawater was a direct result of altered electrolyte concentration on the neuromuscular apparatus. Homsher et al. (1974) observed a reduction in contractility following stimulation in frog sartorius muscle bathed in various hypertonic solutions. The authors attributed this to ionic disruption of contractile proteins. Thus, the direct action of elevated extracellular ions and the induced muscle water movements may also contribute to the locomotory impairment seen in the SW1 coho.

In conclusion, there is a reduction in swimming performance with an increased plasma $[Na^+]$ in response to a 24-h exposure to seawater (SW1) (Fig. 1). There is a strong correlation between the plasma $[Na^+]$ and $[Cl^-]$ measured at rest and the subsequent maximal aerobic swimming velocity. This implies that the seawater challenge test used as an indicator of seawater adaptability in smolting salmonids (Blackburn and Clarke 1987) may also be used as an indicator of the exercise potential of salmonids entering a seawater environment. The impairment in swimming performance seen in the SW1 group is related to the hypoosmoregulatory ability of the coho. The ionic composition of the plasma increases and there is a reduction in Hct and muscle moisture. The limitation to aerobic activity is postulated to exist at the level of the circulatory system, affecting oxygen delivery to the muscles, and at the cellular level of the muscle where a reduced moisture content leads to an impairment of contractility.

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