Aquaculture, 51 (1985) 33—47
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

IMPORTANCE OF RIVER MIGRATION TO THE DEVELOPMENT OF SEAWATER TOLERANCE IN COLUMBIA RIVER ANADROMOUS SALMONIDS

W.S. ZAUGG, E.F. PRENTICE and F.W. WAKNITZ

Coastal Zone and Estuarine Studies Division, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, WA 98112 (U.S.A.)

(Accepted 14 August 1985)

ABSTRACT

Zaugg, W.S., Prentice, E.F. and Waknitz, F.W., 1985. Importance of river migration to the development of seawater tolerance in Columbia River anadromous salmonids. *Aquaculture*, 51: 33—47.

Gradually increasing levels of gill Na^+-K^+ ATPase activity were observed in juvenile chinook, *Oncorhynchus tshawytscha*, and coho, *Oncorhynchus kisutch*, salmon and steelhead trout, *Salmo gairdneri*, undergoing parr—smolt transformation in artificial rearing facilities on the Columbia River. Portions of the same populations released to migrate seaward, however, generally showed much greater increases in enzyme activity with time and distance from the release point. After migrating 714 km to the Columbia River estuary, spring chinook salmon had a mean gill Na^+-K^+ ATPase activity 2.5 times greater than fish retained at the hatchery and 1.9 times greater than fish adapted to 28 ppt seawater for 208 days. Similar observations were made on coho salmon.

INTRODUCTION

Anadromous fishery programs on the Columbia River system in the northwestern United States provide excellent opportunities to study nearly all aspects of freshwater development in resident wild and hatchery-reared salmonid populations. Numerous hatcheries throughout the river system annually produce millions of fish reared under widely varying environmental conditions. Several hydroelectric dams are equipped with facilities to collect downstream migrants that can be marked and released or transported by barge or truck to lower regions of the river (Basham et al., 1983; Sims et al., 1983). Migrating smolts have also been captured by purse and beach seines near the Columbia River estuary. Many of these migrants have been tagged or branded to evaluate river survival, migration rates, behavior, smolt condition, food, and disease incidence (Dawley et al., 1982).

0044-8486/85/$03.30

Completely developed smolts suffer less stress during seawater adaptation than do juveniles that are less well developed (Clarke and Blackburn, 1978; Eddy, 1981; Wedemeyer and McLeay, 1981). It is assumed that chances for survival are increased if a migrant is capable of maintaining homeostasis through complete development of systemic hypo-osmoregulatory mechanisms. In the gill, hypo-osmoregulatory development can be measured biochemically as Na^+-K^+ ATPase, or sodium pump, activity. Gill Na^+-K^+ ATPase activity is elevated by seawater exposure (Utida et al., 1966; Epstein et al., 1967; Kamiya and Utida, 1968, 1969; Folmar and Dickhoff, 1980). Enzyme activity also increases during parr—smolt transformation in fresh water as a preparatory step for subsequent seawater exposure (Zaugg and McLain, 1970; Folmar and Dickhoff, 1980; Wedemeyer et al., 1980; Johnston and Saunders, 1981; Zaugg, 1982a; Sullivan et al., 1983).

Suboptimal rearing conditions, poor release timing, or other factors may contribute to the release of marginally-smolted salmonid juveniles from hatcheries. When this occurs, the interval between release and ocean entry may be especially important to provide the time and environment necessary for full development of hypo-osmoregulatory capability as suggested by increases in gill Na^+-K^+ ATPase activity observed in seaward migrating salmonids (Zaugg and Wagner, 1973; Bjornn et al., 1978; Schreck et al., 1980; Hart et al., 1981; Buckman and Ewing, 1982; Zaugg, 1982a).

Data presented here support the hypothesis that a period of time free from hatchery influence, where seaward migration occurs concurrently with development of hypo-osmoregulatory capacity (measured by gill Na^+-K^+ ATPase activity), may be important for successful seawater adaptation of most populations of hatchery-reared juvenile salmonids in the Columbia River system.

TABLE 1

Information on facilities supplying fish for this study

Hatchery	Location	R km
Leavenworth NFH[a]	Icicle Creek (Washington)	789
Dworshak NFH	Clearwater R. (Idaho)	809
Spring Creek NFH	Mainstem Columbia R. (Washington)	269
Toutle (WDF)[b]	Green R. (Washington)	160
Kalama Falls (WDF)	Kalama R. (Washington)	141
Big Creek (ODFW)[c]	Big Creek (Oregon)	49
Jones Beach[d]	Mainstem Columbia R. (Oregon)	75

[a] National Fish Hatchery.
[b] Washington Department of Fisheries.
[c] Oregon Department of Fish and Wildlife.
[d] National Marine Fisheries Service.

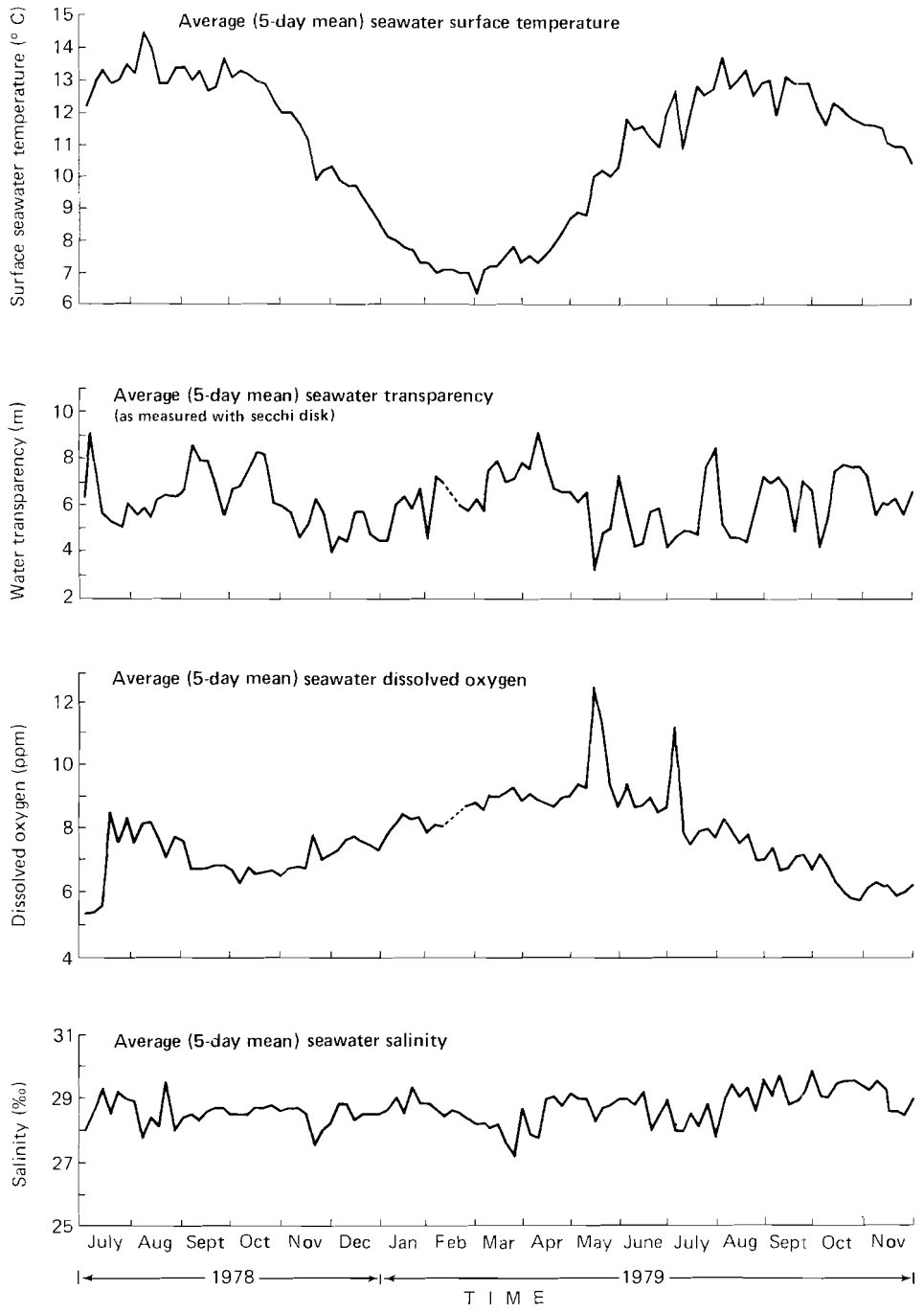

Fig. 1. Environmental data at Clam Bay, Washington, for July 1978 to November 1979.

MATERIALS AND METHODS

Random samples of fish were collected by dip net from production ponds at state and national fish hatcheries (Table 1). Fish were weighed and measured (fork length) and used in experiments of seawater adaptation and/or gill Na^+-K^+ ATPase measurements. With the exceptions noted in Table 3, gill Na^+-K^+ ATPase analyses (as described in Zaugg, 1982b) were performed on 10 groups of three fish each from hatcheries or on individual migrants. Enzyme activities are reported as μmoles ATP hydrolyzed · mg protein^{-1} · h^{-1}. Juvenile spring chinook and coho salmon were transported from the participating hatcheries to Manchester, Washington, and held in fresh water 1—4 days prior to direct transfer into seawater. Seawater exposure tests were conducted using floating net-pens in Clam Bay in Puget Sound at the Manchester Marine Experimental Station of the National Marine Fisheries Service (Prentice et al., 1980). Seawater environmental data are presented in Fig. 1. Migrating juveniles were captured

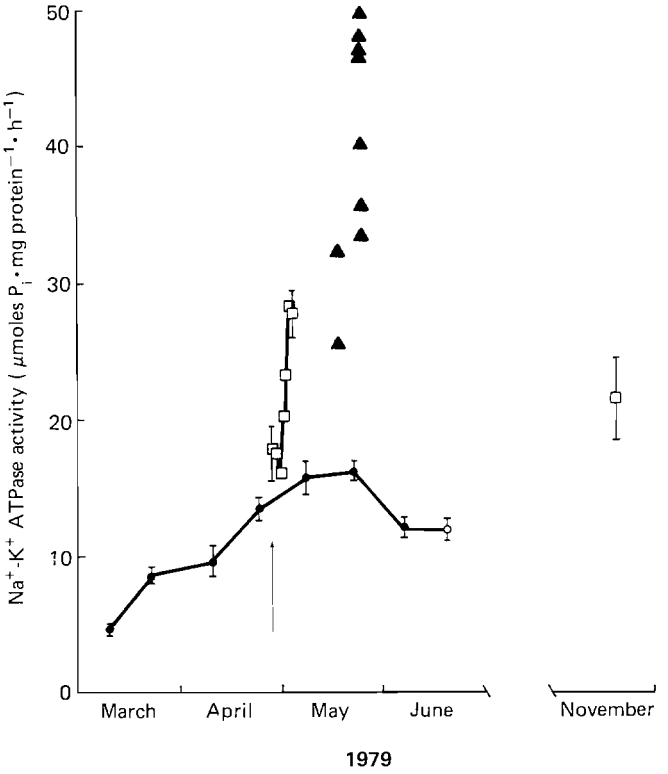

Fig. 2. Gill Na^+-K^+ ATPase activities in spring chinook salmon from Leavenworth NFH, (± SEM). Mean Na^+-K^+ ATPase activities with standard error were determined at the hatchery (•) and for fish placed in seawater (□) on the release date (26 April, arrow) and for seven consecutive days and on 20 November (208 d). Individual enzyme activities (▲) were determined for migrants captured at Jones Beach after migrating 714 km.

by purse and beach seines at Jones Beach (Oregon), 75 km from the mouth of the Columbia River, and identified from coded wire tags (Dawley et al., 1980). In addition, samples of migrating steelhead were obtained in 1976 at Lower Granite Dam on the Snake River and John Day Dam on the Columbia River (Bjornn et al., 1978). All hatchery fish and migrants appeared to be in good health with no overt signs of disease.

RESULTS

Yearling spring chinook salmon

Gill Na^+-K^+ ATPase activities in spring chinook salmon at the Leavenworth NFH (Washington) increased from March to release on 26 April 1979 (Fig. 2). Activities continued to rise until the latter part of May in fish retained in a small raceway for extended sampling. Fish transferred directly to seawater at release time (mean fork length, 122 mm) experienced rapid elevation in activity after the third day. Since no samples were taken in seawater between days 7 and 208, the time or level of maximal activity was not determined. However, by day 208 gill Na^+-K^+ ATPase activity had declined. Smolts that had migrated 714 km in 3—4 weeks to Jones Beach (mean fork length of seven fish, 144 mm) had the highest enzyme activities (Fig. 2, Table 2).

TABLE 2

Mean fork lengths (FL, mm, ± SE) and mean gill Na^+-K^+ ATPase activities (± SE) of chinook and coho salmon, either released from hatcheries, captured at Jones Beach, or held in seawater

Experimental group	Release data			Capture data			Seawater Na^+-K^+ ATPase	
	No.	FL	Na^+-K^+ ATPase[a]	No.	FL	Na^+-K^+ ATPase	Short term	Long term[b]
Leavenworth spring chinook	30	123(2)	13.5(0.8)	9	144(2)	39.9(2.9)	27.4(1.8)[c]	21.7(3.0)
Toutle coho	30	132(2)	10.8(0.6)	5	133(4)	22.5(2.0)	42.7(1.7)[d]	29.8(2.1)
Big Creek coho	30	129(1)	17.8(0.6)	—	—	—	48.5(1.8)[d]	21.1(1.8)
Spring Creek fall chinook[e]								
Release 1	30	67(1)	9.1(0.6)	5	77(1)	16.1(2.3)	—	—
Release 2	30	75(1)	8.6(0.6)	5	79(3)	20.7(2.7)	—	—
Release 3	30	95(1)	14.6(0.9)	3	95(2)	23.8(2.0)	—	—
Release 4	30	121(1)	24.8(1.8)	17	123(2)	44.0(1.8)	—	—
Kalama Falls fall chinook[f]								
Release 1	30	68(1)	6.3(0.4)	3	72(3)	16.8(1.2)	—	—
Release 2	30	70(1)	7.8(0.7)	24	76(2)	24.5(1.6)	—	—

[a] Na^+-K^+ ATPase activity: μmoles P_i·mg protein^{-1}·h^{-1}.
[b] 188—208 days.
[c] Day 7.
[d] Day 35.
[e] Release 1, 20 March; Release 2, 20 April; Release 3, 18 May; Release 4, 13 August 1979.
[f] Release 1, 22 June; Release 2, 12 July 1979.

Age-0 fall chinook salmon

Fall chinook salmon, released with low gill Na^+-K^+ ATPase activities as age-0 fish on 21 March (release 1) from Spring Creek NFH on the Columbia River (Fig. 3), moved seaward relatively slowly at a median rate of about 10 km/day (captured from 26 March to 9 June) and appeared to migrate near the shore (88% of fish captured at Jones Beach were taken in beach seine sets, 12% with mid-river purse seine) (Dawley et al., 1980;

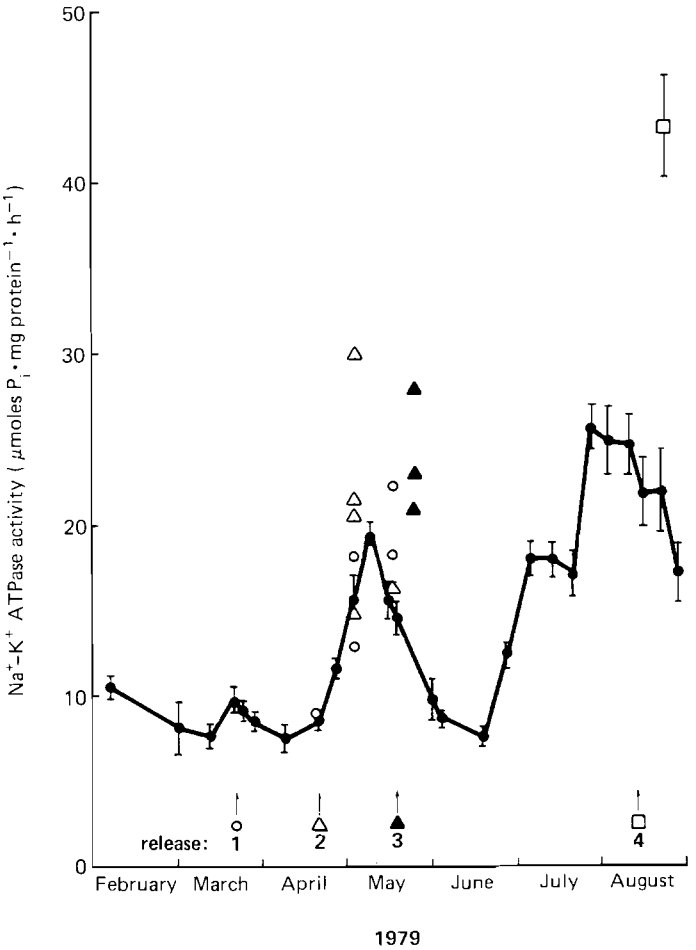

Fig. 3. Mean gill Na^+-K^+ ATPase activities (•) in fall chinook salmon from Spring Creek NFH (± SEM) and individual migrants recovered at Jones Beach, 194 km from point of release. Migrants were released (arrow) on 20 March, 20 April, 18 May, and 13 August (releases 1, 2, 3, and 4). Enzyme activities of individual migrants from the first three releases, captured at Jones Beach (194 km from release point), are shown with symbols (○, △, and ▲). A mean activity (□) with standard error is shown for the examined August migrants (see Table 2).

Zaugg, 1982a). However, after the 194-km migration to Jones Beach, enzyme activities were generally higher than at release. Fish retained at the hatchery experienced a rapid April and May increase in ATPase activity that kept pace with migrants from the March release. Fish released on 20 April (release 2) migrated more rapidly (median rate about 14 km/day, Dawley et al., 1980) than fish released in March, and again were captured near shore (92% with beach seine, 8% with mid-river purse seine). Migrants generally had higher enzyme activities than fish held at the hatchery. After 9 May fish held at the hatchery showed a rapid decline in enzyme activity

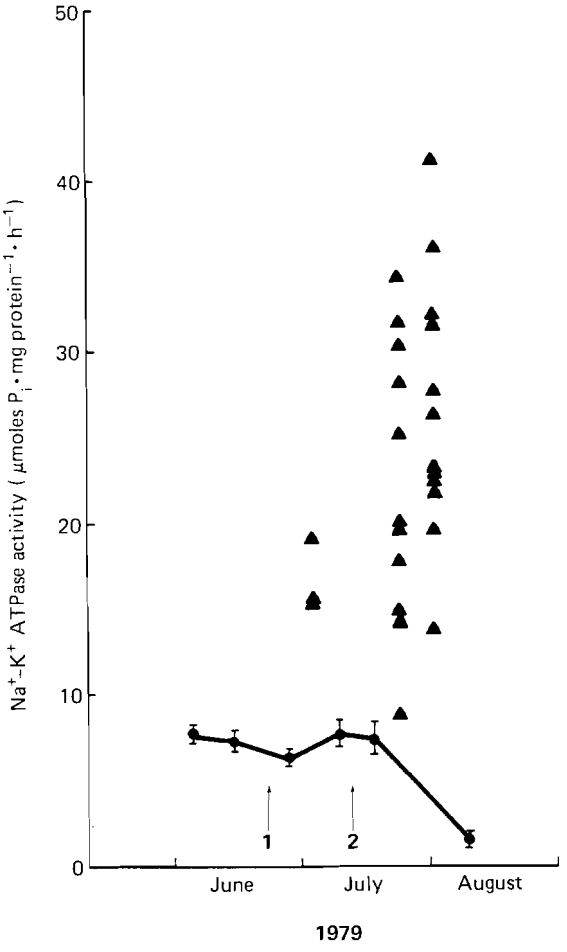

Fig. 4. Mean gill Na^+-K^+ ATPase activities in fall chinook salmon from Kalama Falls hatchery (WDF) (± SEM). Mean gill Na^+-K^+ ATPase activities (•) are shown for fish held in hatchery raceways up to release times of 22 June and 12 July (arrows). Both release groups carried the same tag code. After 12 July, fish were held in a raceway live trap for further sampling. Points (▲) are for individual migrants caught at Jones Beach after migrating 66 km (see Table 2).

although migrants from the third release (18 May) experienced further increases. Most migrants from this release were captured at Jones Beach in mid-river purse seine sets (77%) and had migrated at a median rate of about 48 km/day. This is consistent with observations that larger fish tend to migrate in the river channel and smaller fish near shore (Dawley et al., 1980). Gill Na^+-K^+ ATPase activities increased again in July and August in hatchery-held fish but were still much lower than activites observed in migrants from the 13 August release (release 4), which migrated rapidly to Jones Beach (38 km/day, Dawley et al., 1980).

In contrast to the pattern of Na^+-K^+ ATPase activity observed at the Spring Creek NFH, fall chinook salmon at the Washington Department of Fisheries (WDF) Kalama Falls Hatchery gave no indication of elevated activity while confined in rearing ponds (Fig. 4, Table 2). Once liberated (arrows 1 and 2, Fig. 4), however, high gill Na^+-K^+ ATPase activities developed while fish slowly migrated 66 km to Jones Beach (median rate 2 km/day, captures from 24 June to 14 September, Dawley et al., 1980).

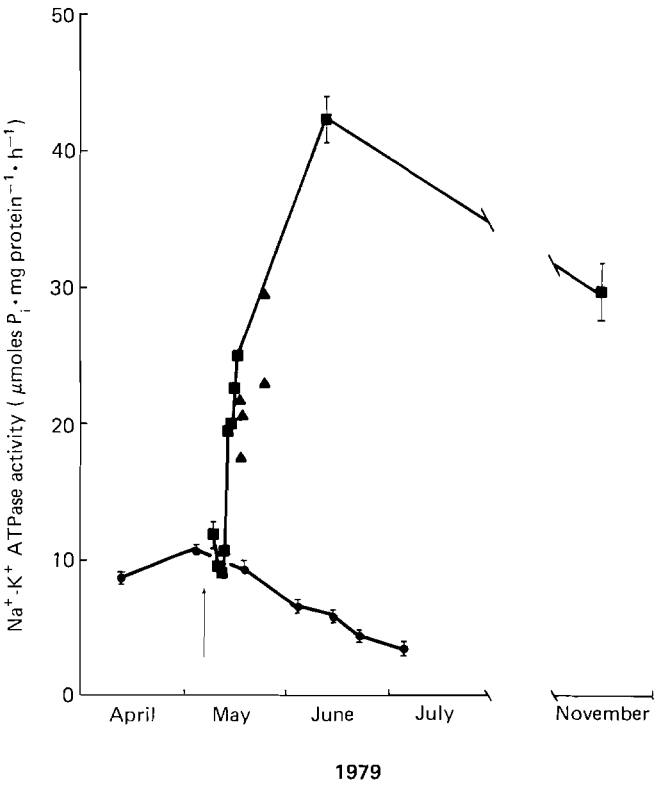

Fig. 5. Gill Na^+-K^+ ATPase activities in coho salmon from Toutle Hatchery (WDF). Mean Na^+-K^+ ATPase activities (with standard error) were determined at the hatchery (•) and in fish held in seawater (▪) at Clam Bay after release (7 May, arrow). Enzyme activities were determined on five individual migrants captured at Jones Beach (▲) 85 km from release site (see Table 2).

Yearling coho salmon

Yearling coho salmon were sampled for gill Na^+-K^+ ATPase activities at the WDF Toutle Hatchery from April to July 1979 (Fig. 5). A subsample of the May release was transferred directly to seawater, and gill Na^+-K^+ ATPase activities were determined at various time intervals thereafter. Activities at 190 days (November) were lower than at 35 days (June) (Fig. 5, Table 2). Five migrants, sampled at Jones Beach after traveling 85 km, had higher enzyme activities than fish held in fresh water at the hatchery but not higher than those held in seawater. In another study, yearling coho salmon at the Oregon Department of Fish and Wildlife Big Creek Hatchery showed a similar decline in enzyme activity after extended seawater residence (Table 2).

Steelhead

Migrating steelhead from Dworshak NFH in Idaho developed higher gill Na^+-K^+ ATPase activities than fish held in laboratory troughs, and the enzyme levels increased with time and migration distance (Table 3). Wild migrants (determined visually by fin condition) also showed higher enzyme activity at more downstream collection localities (Table 3). Increases in enzyme activities observed as hatchery fish migrated from Lower Granite Dam to John Day Dam suggest that values equivalent to those of wild fish may have been reached eventually.

DISCUSSION

Hypo-osmoregulatory ability develops during parr—smolt transformation and is essential to survival and growth of juvenile salmonids in seawater. Progress in development of this ability can be determined by blood sodium levels following seawater challenge, by survival in seawater, and by gill Na^+-K^+ ATPase activity (see review by Wedemeyer et al., 1980). In most instances these tests are administered to populations that are reared in laboratory tanks or hatchery ponds and raceways, and although hypo-osmoregulation develops to a greater or lesser degree under these conditions, it is becoming apparent that environmental influences can have major effects on the extent of development (Wedemeyer et al., 1980; Zaugg, 1982c). Therefore, when hatchery rearing conditions compromise hypo-osmoregulatory development, the period after liberation becomes a critical time for completion of this development, permitting fish to enter the ocean with maximal tolerance to seawater (Buckman and Ewing, 1982).

Gill Na^+-K^+ ATPase activity, one of several possible ion regulatory systems, is instrumental in maintaining proper body salt balance (Folmar and Dickhoff, 1980). Anticipatory increases of this enzyme activity observed during smolt development in hatchery ponds and seaward migra-

TABLE 3

Mean fork lengths (FL, mm, ± SE) and mean gill Na^+-K^+ ATPase activities (± SE) of steelhead in releases from Dworshak National Fish Hatchery and of wild migrants (1976)

Group	Date of gill Na^+-K^+ ATPase determination														
	14 April			27 April			10—17 May			20—21 May			8—14 June		
	n[a]	FL	Na^+-K^+ ATPase[b]	n	FL	Na^+-K^+ ATPase	n	FL	Na^+-K^+ ATPase	n	FL	Na^+-K^+ ATPase	n	FL	Na^+-K^+ ATPase
Release of 14 April:															
Laboratory held[c]	84	176(2)	17(1)	24	184(3)	21(1)	33	165(2)	24(3)	18	168(3)	29(3)	—	—	—
Migrants:															
Lower Granite[d]	—	—	—	8	186(5)	27(2)	—	—	—	—	—	—	—	—	—
John Day[e]	—	—	—	—	—	—	15	190(2)	50(2)	—	—	—	—	—	—
Release of 5 May:															
Laboratory held	—	—	—	48[f]	183(3)	20(1)	45	180(3)	26(2)	24	179(3)	28(2)	25	183(3)	24(2)
Migrants:															
Lower Granite	—	—	—	—	—	—	14	180(4)	33(1)	—	—	—	—	—	—
John Day	—	—	—	—	—	—	—	—	—	17	179(4)	51(2)	—	—	—
Wild migrants:															
Lower Granite	—	—	—	14	172(4)	35(3)	9	168(6)	55(1)	6[g]	171(4)	54(1)	—	—	—
John Day	—	—	—	—	—	—	8	185(12)	61(8)	4[h]	194(3)	65(1)	—	—	—

[a] Number of fish used in assay.

[b] Activities (μmoles $P_i \cdot mg\ protein^{-1} \cdot h^{-1}$) were determined in duplicate on individuals or groups of up to six fish using microsomal preparations (Zaugg, 1981).

[c] Fish in release group were transported to the Western Fish Nutrition Laboratory (Cook, WA) and held in wooden trough at 6°C.

[d] Hatchery migrants captured at Lower Granite Dam on the Snake River (Idaho), 116 km from release site.

[e] Hatchery migrants captured at John Day Dam on the Columbia River, 462 km from release site.

[f] Date of determination for this group is 6 May.

[g] Brought to laboratory on 12 May and held to this date.

[h] Brought to laboratory on 13 May and held to this date.

tion, and rapid increases during seawater challenge tests, suggest an essential role of this enzyme in seawater survival. It is interesting that levels of activity in yearling spring chinook salmon migrating from Leavenworth NFH, 714 km upstream, exceeded those of a companion group acclimated to seawater for 208 days (Fig. 2). It is also of interest that gill Na^+-K^+ ATPase activities in seawater-adapted spring chinook and coho salmon decreased during long-term residence (Figs. 2 and 5; Table 2). These observations suggest that development of gill Na^+-K^+ ATPase activity during migration exceeded that required for a fully-adapted animal. In the freshwater migrant, development of this "excess" ability might be an inherent protective mechanism to minimize the stress of seawater acclimation. Further, when placed in seawater, an animal with poor hypo-osmoregulatory capacity may overcompensate in response to sudden osmotic stress. In either case, once the initial adaptation period is completed, the level of enzyme activity appears to adjust to that required for proper osmoregulation in accordance with salt concentration, temperature, and other environmental factors, and the activation of other osmoregulatory systems that may develop with time, resulting in decreased need for gill participation in overall homeostasis. Fish that have shown only moderate freshwater increases in gill Na^+-K^+ ATPase activity while held in the hatchery have successfully adapted to seawater in controlled experiments; however, it is possible that stresses of a natural environment require a more completely developed system to ensure survival of the fish.

Studies (unpublished) have shown high enzyme levels in some hatchery-held fish, especially 0-age fall chinook salmon. One predominant feature at hatcheries where this occurs is warmer than usual water temperatures (11—15°C) which promote rapid growth. This may be an important key to the stimulation of more rapid and complete smolt transformation in fall chinook salmon. Temperature—growth relationships are certainly also important in smolt development of other anadromous species under conditions of hatchery confinement. The lack of high, migrant-like Na^+-K^+ ATPase activities in the gills of most hatchery "smolts" coincident with rapidly elevating activities in liberated fish from the same groups indicates that conditions in hatcheries generally do not favor maximal development. In some cases the hatchery influence may be seen for some time after release, as observed in Kalama Falls fall chinook salmon released in July 1979 (Fig. 4) where a large portion of the population did not migrate for several weeks (Dawley et al., 1980; Prentice et al., 1980). Sub-optimal hypo-osmoregulatory development under hatchery conditions may have serious implications in direct transfers of salmonids from rearing ponds to seawater (net-pen and ocean-ranching programs) and releases from hatcheries near the ocean. These fish may not be optimally prepared for seawater and consequently may be subject to stress and/or high mortality. Further information on the importance of migration to successful seawater adaptation might be obtained by comparing stocks of juvenile salmonids from

coastal hatcheries with those stocks that have migrated from farther upstream. Criteria for such a comparison might be hypo-osmoregulatory development, migration, ocean entry, and salinity-related mortality. In enhancement programs such as those of the Columbia River where juvenile salmonids are transported from upriver locations to points nearer the ocean, it may be important to allow sufficient distance from the point of release to the point of seawater entry for hypo-osmoregulatory development during migration.

Identification of environmental factors responsible for stimulating development of the high gill Na^+-K^+ ATPase activity observed in migrants and in some hatchery populations may be especially important to net-pen and ocean-ranching programs as well as to salmon rearing facilities located near the ocean. If hypo-osmoregulatory development could be stimulated by proper manipulation of the hatchery environment, seawater transition would likely be more successful, resulting in higher survival. Some factors other than temperature and growth rate that may influence overall smolt development include pond density, water flow, exercise, disease incidence and treatment, and perhaps diet (composition as well as amount). Attempts to induce sustained elevated gill Na^+-K^+ ATPase activity in steelhead, coho and chinook salmon by altering water sources, changing holding environments and water flow rates have been unsuccessful thus far (unpublished).

Horizontal distribution of migrating fall chinook salmon may not only be dependent upon size but also upon degree of smolt development. Fish released from Spring Creek NFH in March and April, having shown little change in gill Na^+-K^+ ATPase activity prior to release (Fig. 3), were caught at Jones Beach primarily near shore in beach seines. Fish that were released in May, after elevated enzyme activities had developed, migrated more rapidly and were caught primarily in mid-river purse seines. A 5-year study (unpublished) at Spring Creek NFH has shown that mid-river location of migrating fall chinook salmon is related to the occurrence of pre-release changes in gill Na^+-K^+ ATPase activity. Thus, the degree of hypo-osmoregulatory development prior to release appears to affect river distribution and rate of migration, and perhaps, survival.

There was no increased enzyme activity in 0-age fall chinook salmon held at the Kalama Falls hatchery (Fig. 4), yet migrants developed elevated levels during the same time period. Many of the released fish did not migrate rapidly and therefore had sufficient time to develop seawater tolerance before ocean entry. Some 0-age chinook salmon fry appear to require a period of estuarine rearing for development of the osmoregulatory system (Reimers, 1973; Healey, 1980; Levy and Northcote, 1982).

Results from tests commonly used to estimate seawater tolerance and degree of smolt transformation in hatchery populations must be evaluated with caution. Certain populations such as the Kalama Falls fall chinook salmon that give no indication of hypo-osmoregulatory development in the hatchery may be capable of doing so after liberation. Thus, the absence

of positive signs of smolting may not categorically mean that the group will perform poorly. In these instances, some measure of performance after release (e.g., rate and percent of migration) is essential to the evaluation, realizing that slow migrants may be subjected to extensive predation.

Advantage might be taken of increased dietary salt to stimulate enzyme activity in situations where seawater entry might occur prior to full hypo-osmoregulatory development. Experiments have shown that sodium chloride added to diets (7—8%) for 6 weeks prior to release has increased survival of fall chinook salmon from hatchery releases and from direct transfers to seawater net-pens (Zaugg et al., 1983).

Results reported in this communication and from observations of many other hatchery populations suggest that most anadromous salmonids in the Columbia River system, and probably elsewhere, do not develop maximum hypo-osmoregulatory capability while confined to the hatchery environment, but appear to require a period of active downstream migration. How important this migratory experience is to overall survival is a question for further investigation. However, careful evaluations of hypo-osmoregulatory development during hatchery rearing, and a measure of migratory performance after release, can provide useful information in the management of Columbia River anadromous fish production.

ACKNOWLEDGEMENTS

The authors are grateful to hatchery personnel for their cooperation and assistance, and to Earl Dawley, Dick Ledgerwood, and others at Jones Beach for their assistance.

REFERENCES

Basham, L.R., Delarm, M.R., Pettit, S.W., Athearn, J.B. and Barker, J.V., 1983. Fish transportation oversight team annual report — FY82 transportation operations on the Snake and Columbia Rivers. NMFS, NWAFC, Seattle, WA, 34 pp.

Bjornn, T.C., Ringe, R.R. and Hiebert, P., 1978. Seaward migration of Dworshak Hatchery steelhead trout in 1976. Univ. Idaho, Forest, Wildl. Range Exp. Stn., Tech. Rep., 6: 1—45.

Buckman, M. and Ewing, R.D., 1982. Relationship between size and time of entry into the sea and gill (Na+K)-ATPase activity for juvenile spring chinook salmon. Trans. Am. Fish. Soc., 111: 681—687.

Clarke, W.C. and Blackburn, J., 1978. Seawater challenge tests performed on hatchery stocks of chinook and coho salmon in 1977. Can. Fish. Mar. Serv., Resour. Dev. Tech. Rep., 76: 1—19.

Dawley, E.M., Sims, C.W., Ledgerwood, R.D., Miller, D.R. and Thrower, F.P., 1980. A study to define the migration characteristics of chinook and coho salmon and steelhead in the Columbia River estuary. Annual Report, 1979. NMFS, NWAFC, Seattle, WA, 53 pp.

Dawley, E.M., Ledgerwood, R.D., Blahm, T.H. and Jensen, A.L., 1982. Migrational characteristics and survival of juvenile salmonids entering the Columbia River estuary in 1981. Processed Report. NMFS, NWAFC, Seattle, WA, 43 pp.

Eddy, F.B., 1981. Effects of stress on osmotic and ionic regulation in fish. In: A.D. Pickering (Editor), Stress and Fish. Academic Press, London and New York, NY, pp. 77—102.

Epstein, F.H., Katz, A.I. and Pickford, G.E., 1967. Sodium and potassium activated adenosine triphosphatase of gills: role in adaptation of teleosts to seawater. Science (Wash., D.C.), 156: 1245—1247.

Folmar, L.C. and Dickhoff, W.W., 1980. The parr—smolt transformation (smoltification) and seawater adaptation in salmonids. A review of selected literature. Aquaculture, 21: 1—37.

Hart, C.E., Concannon, G., Fustish, C.A. and Ewing, R.D., 1981. Seaward migration and gill (Na+K)-ATPase activity of spring chinook salmon in an artificial stream. Trans. Am. Fish. Soc., 110: 44—50.

Healey, M.C., 1980. Utilization of the Nanaimo River estuary by juvenile chinook salmon, *Oncorhynchus tshawytscha*. U.S. Natl. Mar. Fish. Serv., Fish. Bull., 77: 653—668.

Johnston, C.E. and Saunders, R.L., 1981. Parr—smolt transformation of yearling Atlantic salmon (*Salmo salar*) at several rearing temperatures. Can. J. Fish. Aquat, Sci., 38: 1189—1198.

Kamiya, M. and Utida, S., 1968. Changes in activity of sodium-potassium activated adenosine triphosphatase in gills during adaptation of the Japanese eel to seawater. Comp. Biochem. Physiol., 26: 675—685.

Kamiya, M. and Utida, S., 1969. Sodium-potassium activated adenosine triphosphatase activity in gills of freshwater, marine, and euryhaline teleosts. Comp. Biochem. Physiol., 31: 671—674.

Levy, D.A. and Northcote, T.G., 1982. Juvenile salmon residency in a marsh area of the Fraser River estuary. Can. J. Fish. Aquat. Sci., 39: 270—276.

Prentice, E.F., Mahnken, C., Gores, K., Waknitz, W., Zaugg, W., Folmar, L., King, R., Mighell, J., Dickhoff, W., Flagg, W., Harrell, L., Novotny, A., Damkaer, D., Wold, E. and Vreeland, R., 1980. A study to assess status of smoltification and fitness for ocean survival of chinook and coho salmon and steelhead. Summary Report Project 10990060. NMFS, NWAFC, Seattle, WA, 408 pp.

Reimers, P., 1973. The length of residence of juvenile fall chinook salmon in Sixes River, Oregon. Res. Rep. Fish Comm. Oreg., 4: 1—43.

Schreck, C.B., Jacobs, S.E., Specker, J.L. and Sandoval, W.A., 1980. Effects of transportation on outmigration and fitness for marine survival of Columbia River salmon. Completion Report. Oregon Coop. Fish. Res. Unit, Oregon State University, Corvallis, OR, 108 pp.

Sims, C.W., Giorgi, A.E., Johnsen, R.C. and Brege, D.A., 1983. Migrational characteristics of juvenile salmon and steelhead in the Columbia River basin — 1982. Processed Report. NMFS, NWAFC, Seattle, WA, 35 pp.

Sullivan, C.V., Dickhoff, W.W., Brewer, S.D. and Johnston, G.P., 1983. Plasma thyroid-hormone concentrations and gill (Na+K)-ATPase activities in postemergent pink salmon. Trans. Am. Fish. Soc., 112: 825—829.

Utida, S., Hirano, T., Oide, W., Kamiya, M., Saishu, S. and Oide, H., 1966. Na^+-K^+ activated adenosine triphosphatase in gills and Cl^- activated alkaline phosphatase in the intestinal mucosa with special reference to salt adaptation of eels. Proc. 11th Pac. Sci. Congr., Tokyo, 7: 5—7.

Wedemeyer, G.A. and McLeay, D.J., 1981. Methods for determining the tolerance of fishes to environmental stressors. In: A.D. Pickering (Editor), Stress and Fish. Academic Press, London and New York, NY, pp. 247—275.

Wedemeyer, G.A., Saunders, R.L. and Clarke, W.C., 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. U.S. Natl. Mar. Fish. Serv., Mar. Fish. Rev., 42(6): 1—14.

Zaugg, W.S., 1981. Advanced photoperiod and water temperature effects on gill Na—K adenosine triphosphatase activity and migration of juvenile steelhead (*Salmo gairneri*). Can. J. Fish. Aquat. Sci., 38(7): 758—764.

Zaugg, W.S., 1982a. Relationships between smolt indices and migration in controlled and natural environments. In: E.L. Brannon and E.O. Salo (Editors), Proc. Salmon and Trout Migratory Behavior Symposium. Univ. Washington, Seattle, WA, pp. 173—183.

Zaugg, W.S., 1982b. A simplified preparation for adenosine triphosphatase determination in gill tissue. Can. J. Fish. Aquat. Sci., 39: 215—217.

Zaugg, W.S., 1982c. Some changes in smoltification and seawater adaptability of salmonids resulting from environmental and other factors. Aquaculture, 28: 955—965.

Zaugg, W.S. and McLain, L.R., 1970. Adenosine triphosphatase activity in gills of salmonids: seasonal variations and salt water influence in coho salmon, *Oncorhynchus kisutch*. Comp. Biochem. Physiol., 35: 587—596.

Zaugg, W.S. and Wagner, H.H., 1973. Gill ATPase activity related to parr—smolt transformation and migration in steelhead trout (*Salmo gairdneri*): influence of photoperiod and temperature. Comp. Biochem. Physiol. B, 45: 955—965.

Zaugg, W.S., Roley, D.D., Prentice, E.F., Gores, K.X. and Waknitz, F.W., 1983. Increased seawater survival and contribution to the fishery of chinook salmon (*Oncorhynchus tshawytscha*) by supplemental dietary salt. Aquaculture, 32: 183—188.