The Importance of Smolt Development to Successful Marine Ranching of Pacific Salmon

W.S. ZAUGG AND C.V.W. MAHNKEN

Northwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East
Seattle, Washington 98112

ABSTRACT

Fall run, underyearling chinook salmon (*Oncorhynchus tshawytscha*) released from four different hatcheries into the Columbia River system migrated faster as distance from the point of release to the estuary increased. Also, migrants traveling greater distances were more inclined to move to midriver by the time they reached the estuary. Fish released in various stages of smolt development, as measured by gill Na^+-K^+ ATPase activity, exhibited differences in migratory behavior and survival to adulthood. Those with more complete prerelease development a) migrated seaward more rapidly and were recovered at the upper entrance to the estuary in greater numbers than fish showing little or no smolting tendency at release, b) were recovered more frequently in midriver locations as opposed to nearshore areas for fish less well developed at release, and c) survived to adulthood in greater numbers. This study indicates that the degree of prerelease smolt development affects postrelease behavior and survival and is an important facet of the hatchery rearing period.

Introduction

Ultimately, the measure of success in the marine ranching of hatchery-reared salmonids is how many juveniles survive and contribute as adults. Although there are many environmental and developmental factors involved in determining survival or contribution, none of these can be designated most important all of the time. For example, one year a specific ocean condition may play a predominant role in determining survival, whereas another year the primary regulator of survival may be predation in the estuary, disease in the hatchery population, malnutrition, or any other of many factors. Investigators have proposed that survival of hatchery coho salmon (*Oncorhynchus kisutch*) in the northeastern Pacific Ocean off the coasts of northwestern United States and Canada is much better in years of strong upwelling (Gunsolus 1978; Nickelson 1986). Others have suggested that survival is density dependent (McGie 1981; McCarl and Rettig 1983) especially in years of low upwelling (McGie 1984; Peterman and Routledge 1983). Fisher and Pearcy (1988) found that high mortality of coho salmon juveniles occcurred within one month of ocean entry and that poor survival was not associated with starvation or low growth rates. They suggested that high predation may be responsible for low survivals and that this condition may be intensified in years of low upwelling. Hvidsten and Hansen (1988) reported increased numbers of adult Atlantic salmon (*Salmo salar* L.) recovered from hatchery smolts released during high water discharge and also concluded that predation during low discharge was responsible for decreased survival.

General health or condition of hatchery fish is known to influence ocean survival. High rearing densities adversely affected survival of coho salmon (Fagerlund et al. 1983; Sandercock and Stone 1982) and yearling spring chinook salmon (*O. tshawytscha*) (J.L. Banks, Abernathy Salmon Culture Technology Center, Longview, WA 98623, pers. commun., Nov. 1989). High rearing densities appear to affect smolt physiology by retarding development of increased plasma thyroxine levels, gill Na^+-K^+ ATPase activity and blood sodium regulatory ability (Schreck et al. 1985; Patino et al. 1986). Other hatchery conditions that create stress also affect the ability of the juvenile salmon to develop and function normally (Schreck 1982; Wedemeyer et al. 1984).

Few studies have looked at the relationship between smolt development in the hatchery and postrelease performance (e.g., seaward migration and survival to adulthood).

In Marine ranching: proceedings of the seventeenth U.S.-Japan meeting on aquaculture; Ise, Mie Prefecture, Japan, October 16, 17, and 18, 1988 (Ralph S. Svrjcek, editor). NOAA Technical Report NMFS 102 (1991).

Among other changes, active seaward migration of smolts is accompanied by elevated levels of gill Na^+-K^+ ATPase activity (Zaugg and Wagner 1973; Bjornn et al. 1978; Schreck et al. 1980; Hart et al. 1981; Buckman and Ewing 1982; Zaugg 1982a; Weitkamp and Loeppke 1983; Rondorf et al. 1985, 1988; Zaugg et al. 1985; Rodgers et al. 1987), gill succinic dehydrogenase activity (Langdon and Thorpe 1985; Chernitsky 1986), and skin guanine content (Rodgers et al. 1987).

Greater adult contributions have been compared to higher gill Na^+-K^+ ATPase activity at release in coho salmon (Wahle and Zaugg 1982). Soivio and Virtanen (1985) reported that adult recapture rates were higher in hatchery-reared Atlantic salmon that had been

Table 1

Release dates and mean weights of underyearling fall chinook salmon from 15 Columbia River hatcheries (Vreeland 1990).

Hatchery	Dates of release				Weight (g)			
	1979	1980	1981	1982	1979	1980	1981	1982
Abernathy	4/17–5/18	4/09–5/14	4/15–5/26	4/20–6/01	4.8	7.7	6.6	8.9
Big Creek	5/21	5/13	5/07–5/18	5/17	5.6	5.8	5.9	6.1
Bonneville	5/01–5/29	5/20	4/24	4/23	6.1	6.1	6.2	5.7
Cowlitz	6/27–10/16	6/03–7/11	6/27–6/28	6/24–7/08	5.3	3.5	5.3	5.0
Elokomin	6/15	6/19	6/01	6/15	4.6	5.7	4.5	5.7
Grays River	6/09–6/12	6/01–6/24	6/01–6/08	6/01	4.9	5.3	5.3	5.2
Kalama Falls	6/22–7/13	6/13–6/24	5/22–5/28	6/10–7/02	2.6	3.7	4.4	4.5
Klaskanine	5/29	6/04	5/10	6/07	6.4	5.7	5.3	5.3
Klickitat	5/14–6/13	5/27	6/05	6/04	5.7	5.3	5.8	5.5
Little White	6/22	6/10	6/04–6/05	6/02–6/03	4.1	4.5	4.8	4.9
Priest Rapids	5/23	5/20–6/24	6/23–6/24	5/24–6/16	6.1	6.6	5.1	5.2
Sea Resources	5/01–5/31	5/20	4/16–4/29	4/01–5/07	4.1	5.0	4.6	4.5
Stayton Pond	5/07–5/21	4/20–5/21	4/27–6/16	5/03–5/21	6.8	5.2	6.1	5.2
Washougal	6/14–9/02	6/30	6/30–7/06	6/30–7/06	5.8	4.6	6.1	5.0
Spring Creek	3/20–5/18	3/10–5/09	3/25–5/05	3/25–5/21	5.7	6.0	5.2	6.2

Table 2

Percent adult recovery (Vreeland 1990) and between-year rank order for fall chinook salmon released as underyearlings from 15 Columbia River hatcheries. Years are ranked 1 to 4 in descending order of percent recovery of adults (commercial and sport fishery, and hatchery returns) from juveniles released in the year shown.

Hatchery	Percent recovery					Rank order (year of release)			
	1979	1980	1981	1982		1979	1980	1981	1982
Abernathy	0.56	0.58	1.00	0.20		3	2	1	4
Big Creek	0.38	1.04	0.27	0.54		3	1	4	2
Bonneville	0.38	0.14	0.27	0.31		1	4	3	2
Cowlitz	0.28	0.23	0.40	0.17		2	3	1	4
Elokomin	0.01	0.08	0.11	0.03		4	2	1	3
Grays River	0.06	0.20	0.23	0.04		3	2	1	4
Kalama Falls	0.06	0.29	0.16	0.18		4	1	3	2
Klaskanine	0.13	0.14	0.07	0.05		2	1	3	4
Klickitat	0.11	0.16	0.04	0.10		2	1	4	3
Little White	0.20	0.30	0.27	0.019		3	1	2	4
Priest Rapids	0.17	0.42	0.54	0.57		4	3	2	1
Sea Resources	0.10	0.40	0.14	0.70		4	2	3	1
Stayton Pond	0.75	0.74	0.32	0.45		1	2	4	3
Washougal	0.13	0.33	0.21	0.19		4	1	2	3
Spring Creek	1.01	1.47	0.40	0.43		2	1	4	3
			Total numbers for each rank order:		1's:	2	7	4	2
					2's:	4	5	3	3
					3's:	4	2	4	5
					4's:	5	1	4	5

judged to be better smolts using a series of physiological indices.

This report 1) examines in- and between-year variations in adult survival of fall chinook salmon released as underyearlings from fifteen Columbia River Basin hatcheries, 2) looks at the influence of migration distance on rate of migration and horizontal position of juvenile migrants as they approach the estuary and, 3) reports adult returns from juveniles released during five successive years at one specific hatchery in comparison to degree of smolt development as measured by pre-release gill Na^+-K^+ ATPase activity and by post-release migratory behavior.

Materials and Methods

All fish used for gill ATPase determinations were underyearling fall chinook salmon. Fish were taken randomly from production ponds (biweekly) by dip net, killed by a blow to the head, weighed (g), and measured (fork length, mm). Gill filaments were trimmed from the arches, placed in buffered sucrose, and stored at −25° C until analysis of Na^+-K^+ ATPase activity (μmoles $P_i \cdot$ mg protein$^{-1} \cdot h^{-1}$) as described by Zaugg (1982b). On each sampling date during the period 1978–80, samples of gill filaments were taken from 30 fish. These were divided into 10 assay samples, each containing gill filaments from 3 fish. In 1981 and 1982, 10 to 40 fish were taken on each sampling date and used for individual ATPase analysis.

Migrants were captured daily in the Columbia River at Jones Beach, Oregon, 75 km upriver from the mouth and identified from coded wire tags. Captures were accomplished nearshore by seining from the beach with a 95-m seine and in deep-water, midriver channels using a purse seine (Dawley et al. 1985). Numbers of migrants caught were adjusted to a standard fishing effort. Migration rates were estimated by dividing the distance from release points to the recovery point at Jones Beach by the number of days from the first day of release to the date of median fish recovery. In 1979 underyearling chinook salmon with coded wire tags (some groups in replicate) were released at approximately the same time in June from four hatcheries located at varying distances from Jones Beach. Migrants were captured at Jones Beach with purse and beach seines as described earlier. Adult recovery information was obtained from the Pacific Marine Fishery Commission, Portland, Oregon, and from Vreeland (1990). Adult recoveries were estimated from samples of the commercial and sport fishery catches and hatchery returns.

Results

In a 4-year study described by Vreeland (1990), fall chinook salmon released as underyearlings from 15 Columbia River hatcheries weighed less than 10 g (Table 1). Although annual differences in weight were not great at any given hatchery there were significant differences between hatcheries. Usually, each hatchery released about the same time of the year for each year of the study. Percent total adult recoveries and between-year rank orders for each hatchery are shown in Table 2. Most rank orders were ones and twos, and fewest were threes and fours observed for adult recoveries of fish released in 1980. Nevertheless, the general random order of rank indicates that there is much between-year variability in total adult recoveries among the groups of fish released from the 15 hatcheries during the four-year period.

Underyearling chinook salmon were released from four Columbia River Basin hatcheries in 1979, presumably in about the same stage of development, prior to any increase in gill Na^+-K^+ ATPase activity (Table 3). Migrants captured at Jones Beach showed that those fish released at greater distances traveled downstream at higher rates

Table 3

Changes in migrations rates with distance from point of release for tagged underyearling chinook salmon released from hatcheries and caught at Jones Beach.

	At release					Caught at Jones Beach	
Hatchery	Date: June1979	Wt. (g)	Number tagged	Gill ATPase	Migration distance (km)	Beach seine	Purse seine
Kalama Falls	30	2.5	214,500	7	66	2,799	206
Toutle	17	2.8	12,000	7	85	85	11
Toutle	17	2.8	132,000	7	85	973	108
Washougal	14	4.8	93,700	9	138	318	43
Washougal	14	4.8	154,500	9	138	634	104
Little White	22	4.3	177,800	10	186	221	131
Little White	22	3.7	264,800	10	186	400	161

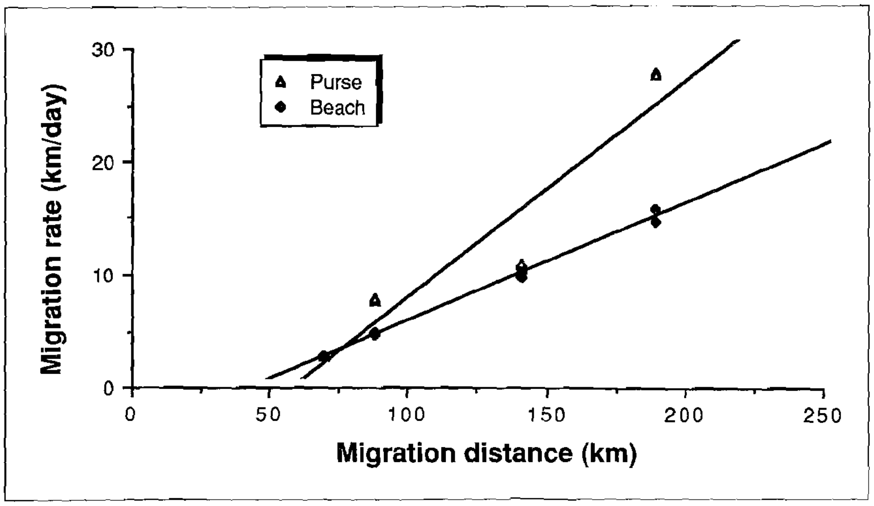

Figure 1
Increase of median migration rate with distance traveled by underyearling chinook salmon. Seven tagged groups were released from 4 hatcheries during 14–30 June 1979 (Table 3) and migrants were captured at Jones Beach with a beach or purse seine. Correlation coefficients for migration rates vs. distance are purse, 0.94 ($P<0.01$); beach, 0.99 ($P<0.01$). Data from Dawley et al. 1985.

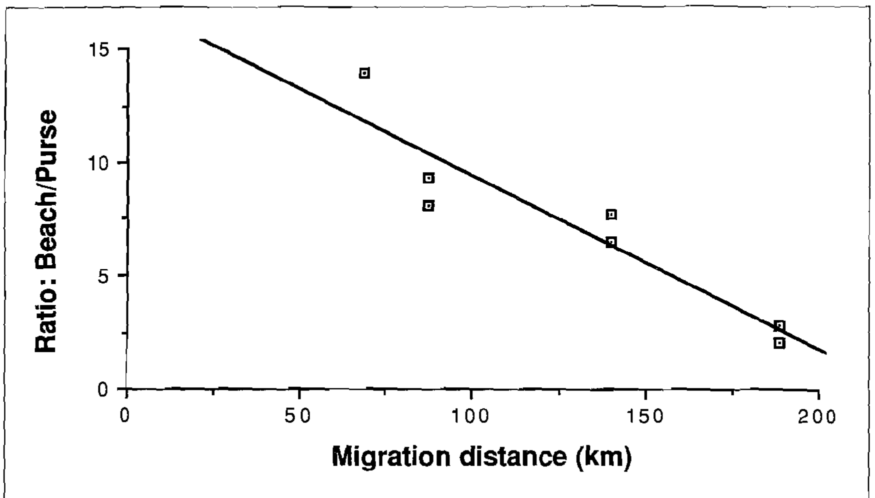

Figure 2
Ratio of the number of underyearling chinook salmon caught in the beach seine to the number of those caught in the purse seine at Jones Beach vs. distance migrated, 14–30 June 1979. Correlation coefficient 0.93 ($P<0.01$).

(Fig. 1). Those captured in midriver with the purse seine traveled faster than those captured near shore with the beach seine (Fig. 1). In addition, fish traveling farther were caught in increasing numbers in the midriver purse seine (Fig. 2), indicating movement from shoreline to midriver migration with time and with distance from release. These observations are summarized in Figure 3.

Figure 4 presents an idealized profile for gill Na^+-K^+ ATPase activity generally observed in hatchery populations of anadromous salmonids during smolt development, when fish are either held for extended periods in the hatchery environment or released to migrate seaward. The shaded portion under the profile represents that percent of the total area under the curve that is completed by the time of a hypothetical release. We have used this percent as a basis to evaluate the relationship between gill Na^+-K^+ ATPase activity in groups of underyearling chinook salmon released from the Spring Creek National Fish hatchery during 1978 through 1982, and post release performance, as reflected in migratory behavior and survival to adulthood (Fig. 5).

This percentage was compared to the numbers of smolts captured at Jones Beach (migration distance = 194 km) and to adult recoveries from fish released in each of those years (Table 4). Correlations and significance of the data collected during the study are also shown in Table 4.

Discussion

The four-year study of underyearling fall chinook salmon released from hatcheries in the Columbia River Basin reported by Vreeland (1990) illustrates that considerable variability in adult recoveries exists from year to year among the several production facilities. Rank order information suggests that fish released from most of the hatcheries in 1980 performed better than fish released in other years. It would appear, therefore, that conditions in the estuary and ocean were more favorable for fish released in 1980 than those for fish released in the other three years of the study. Fisher and Pearcy (1988) have shown that

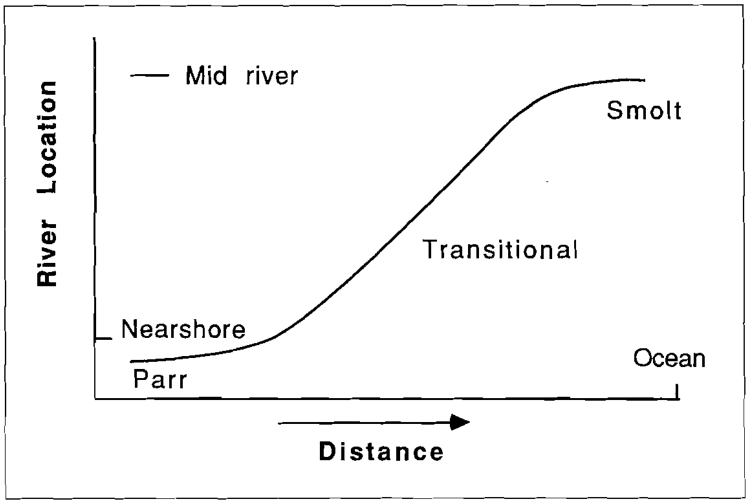

Figure 3
Summary of expected migratory behavior for underyearling fall chinook salmon released into the Columbia River system and completing smolt transformation during migration.

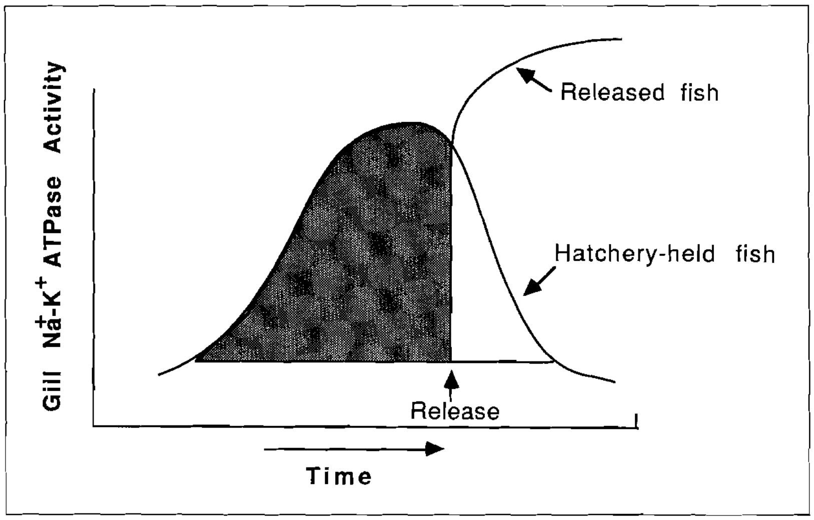

Figure 4
Illustration of a typical gill Na^+-K^+ ATPase activity profile for hatchery-reared anadromous salmonids undergoing parr-smolt transformation and either retained at the hatchery or released to migrate seaward. The shaded area represents that portion of the total area under the curve completed by the time of a hypothetical release.

the success of any year class of coho salmon may be determined soon after ocean entry, and this may also be the critical time for juvenile chinook salmon. If so, the degree of smolt development at that time may be a significant contributing factor to survival.

Nevertheless, among the 15 hatcheries shown here, the patterns of adult recovery varied widely in an inconsistent manner. For example, adult recoveries from the Little White Salmon hatchery (river km 261) ranged from only 0.02 to 0.03 percent during the four years of the study whereas recoveries from the Spring Creek hatchery (located only 9 km further upstream) were 50-fold greater. Fish released from the Bonneville hatchery (31 km downstream) had adult recoveries that were intermediate between the other two hatcheries during the initial two years (1979–80) and similar to Spring Creek for the final two years (1981–82). These observations strongly suggest that hatchery rearing methods and practices greatly influence survival to adulthood.

Variability in gill Na^+-K^+ ATPase activity profiles in chinook salmon reared at the Spring Creek hatchery from 1978 to 1982 is further evidence that physiological development in hatchery-held salmon can differ from one year to the next. Important, but subtle differences in rearing methods and diets may have greater influences on juvenile development and survival than is commonly thought.

Dawley et al. (1986) reported that migration rates of underyearling chinook salmon in the Columbia River increased with distance traveled. However, these investigators did not assess possible differences in degree of smolt development in the fish used for their study. The degree of smolt development reached in steelhead (*O. mykiss*) at the time of release affected rates of migration (Zaugg and Wagner 1973). As the act of migration proceeds, smolt development is intensified (Zaugg 1982a; Zaugg et al. 1985; Rondorf et al. 1985, 1988). In the present study fish released 186 km from Jones Beach (Little White Salmon hatchery) probably underwent more extensive

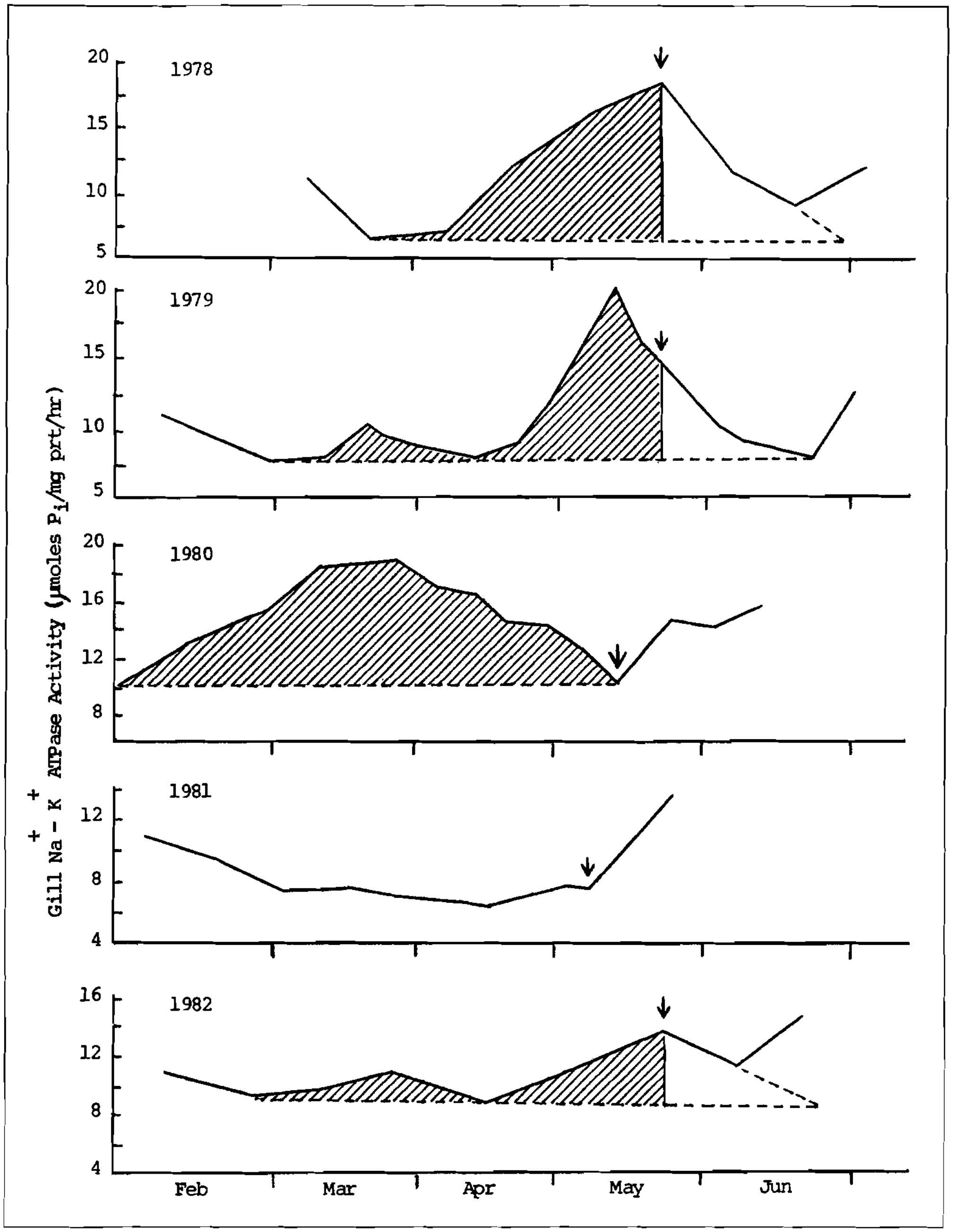

Figure 5
Gill Na^+-K^+ ATPase activity profiles for underyearling fall chinook salmon at Spring Creek National Fish Hatchery, 1978–82. Arrows indicate the date of final release (groups were also released in March and April). The shaded areas represent that portion of the total area under the curve (dashed lines) completed by the final release dates. Spring Creek hatchery is located at river km 269 on the Washington shore of the Columbia River. prt = protein.

smolt development during migration and thus exhibited more rapid downstream movement over the total distance traveled than did fish released closer to the capture site (Kalama Falls, Toutle, and Washougal hatcheries). It appears that more completely smolted fish move offshore to faster-moving midriver waters as indicated by both faster migration rates and higher percentages of migrants being caught in the midriver purse seine. The ratio of numbers caught in the beach seine to numbers caught in the purse seine decreased as the distance traveled increased.

Generally, underyearling chinook salmon, as well as yearling coho salmon, migrate more rapidly when released while gill Na^+-K^+ ATPase activity is declining (following a previous increase and peak) than when the activity is on the increase (before peaking, Zaugg 1982a). When releases are made during the period of decline, however, ATPase activities are rapidly re-elevated as migrants move downriver. Ewing et al. (1984) showed that underyearling spring chinook salmon released later (mid-June vs. mid-May) migrated faster and in equal numbers. However, when released in August these

Table 4

Comparisons of shaded areas under ATPase profiles (expressed as percent of the total area under the curve, Fig. 5) to various measurements of post-release performance of all fall chinook salmon released (March, April, and May each year) from Spring Creek National Fish Hatchery[a].

Year of release[b]	Percent ATPase curve[c]	Percent caught at Jones Beach[d]	Percent caught in purse seine[e]	Ratio beach/purse seine[f]	Percent adult recovery[g]
1978	65	0.14	0.018	6.9	0.87
1979	80	0.17	0.036	3.6	1.01
1980	100	0.20	0.031	5.3	1.47
1981	0	0.12	0.006	18.1	0.40
1982	66	0.14	0.009	14.1	0.43
Correlation coefficients and significance					
% ATPase	—	0.86 $P<0.1$	0.77 $P<0.2$	0.84 $P<0.1$	0.83 $P<0.1$
% Caught (total)	—	—	0.86 $P<0.1$	0.78 $P<0.1$	0.93 $P<0.2$
% Caught (purse)	—	—	—	0.93 $P<0.02$	0.87 $P<0.05$
Ratio	—	—	—	—	0.85 $P<0.05$

[a]Spring Creek National Fish Hatchery is located at river km 269 on the Columbia River.
[b]Three releases were made each year, in March, April, and May.
[c]Percent of the total area under profiles in Figure 5, depicted by shading.
[d]Percent of all fish released (March, April, and May) caught at Jones Beach (rkm 75) with both beach and purse seines. Numbers adjusted to a standard fishing effort (Dawley et al. 1985).
[e]Percent of all fish released (March, April, and May) caught at Jones Beach (rkm 75) in the mid-river purse seine. Numbers adjusted to a standard fishing effort (Dawley et al. 1985).
[f]Ratio of numbers of migrants caught at Jones Beach in the beach seine to numbers caught in the purse seine for all fish released each year (March, April, and May).
[g]Includes adults caught in the commercial and sport fishery, and returns to the Spring Creek hatchery from all three releases each year. Data from Pacific Marine Fishery Commission, Portland, OR and Vreeland (1990).

salmon showed reduced migration and an increase in stream residence.

The importance of elevated gill Na^+-K^+ ATPase activity for successful adaptation to seawater has been demonstrated in hatchery- and laboratory-reared steelhead (Adams et al. 1975), coho salmon (Harache et al. 1980), and Atlantic salmon (McCormick et al. 1987; Besner and Audet 1988). Observations suggest that smolts actively migrating seaward in the natural environment also require high gill Na^+-K^+ ATPase activities for successful transition to seawater.

We have attempted to determine whether smolting-associated pre-release increases in gill Na^+-K^+ ATPase activity are related to post-release behavior and survival of underyearling chinook salmon. In order to relate the enzyme activity quantitatively to post-release behavior and survival we have used as a measurement that portion of the total area under the ATPase profile curve which is completed by release time. This method takes into account post-release migrational characteristics that appear to be more influenced by the time-dependent development pattern of the enzyme activity than by the absolute value at the highest point. By applying this analysis to the gill Na^+-K^+ ATPase activity profiles observed for five successive years in underyearling fall chinook salmon at the Spring Creek hatchery, we obtained results which support assumptions that the degree of smolt development is related to the numbers of migrants reaching the estuary, their location in the river, and to percent adult recovery. Although the percent ATPase completed by the May release of 1982 is similar to the percent in 1978 (66 and 65), other observations for that year (migrants caught in the purse seine, beach/purse seine ratios, and adult recovery) more closely resemble the values obtained in 1981. The total area under the 1982 profile is small compared with the years of better survival (1978–80) and it appears that this may also indicate poor smolt development during the hatchery rearing period.

If the degree of smolt development reached by the time of release is important to survival, and that degree of development is inconsistent from one year to the next, as seen at the Spring Creek hatchery, then it becomes important to identify and control as many of the variables involved as possible. Although factors causing variable smolt development in the Spring Creek fish during the five-year study remain unidentified, there are known culture practices and conditions that are candidates. Ogata and Konno (1986) demonstrated that additional dietary lipid may promote smolt development in cherry salmon (*O. masou*). Other dietary ingredients undoubtedly influence smolt development and may need closer scrutiny to insure more uniform smolting patterns. Growth rate, temperature, and size are interdependent and can affect the rate and extent of smolt development. Although better adult returns are generally associated with larger juveniles there was no significant relationship between size at or time of release and adult recovery in the Spring Creek study (Zaugg 1989). Disease and disease treatments, pond densities, and stresses accompanying normal and abnormal hatchery operations must certainly cause year-to-year variablility in the ability of hatchery-reared fish to develop properly. These and other, perhaps yet undetermined factors, must surely be important to the success of a hatchery program.

Acknowledgments

We thank W. Dickhoff for preparation of figures and hatchery personnel for their help and cooperation.

Citations

Adams, B.L., W.S. Zaugg, and L.R. McLain.
1975. Inhibition of saltwater survival and Na-K-ATPase elevation in steelhead trout (*Salmo gairdneri*) by moderate water temperatures. Trans. Am. Fish. Soc. 104:766–769.

Besner, M., and C. Audet.
1988. Smoltification and ability of Atlantic salmon smolts to acclimate to seawater transfers. *In* Aquaculture Assoc. Can. Bulletin 88-4, September (S.L. Waddy, ed.), p. 7–9.

Bjornn, T.C., R.R. Ringe, and P. Hiebert.
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 R.D. Ewing.
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.

Chernitsky, A.G.
1986. Quantitative evaluation of the degree of parr-smolt transformation in wild smolts and hatchery juveniles of Atlantic salmon (*Salmo salar* L.) by SDH activity of chloride cells. Aquaculture 59:287–279.

Dawley, E.M., R.D. Ledgerwood, and A.L. Jensen.
1985. Beach and purse seine sampling of juvenile salmonids in the Columbia River estuary and ocean plume, 1977–1983. Vol. II: Data on marked fish recoveries. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-75, 397 p.

Dawley, E.M., R.D. Ledgerwood, T.H. Blahm, C.W. Sims, J.T. Durkin, J.T. Kirn, A.E. Rankis, G.E. Monan, and F.J. Ossiander.
1986. Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary 1966–1983. Final report to Bonneville Power Adm., Portland, OR, April, 250 p.

Ewing, R.D., C.E. Hart, C.A. Fustish, and G. Concannon.
1984. Effects of size and time of release on seaward migration of spring chinook salmon, *Oncorhynchus tshawytscha*. Fish. Bull., U.S. 82:157–164.

Fagerlund, U.H.M., J.R. McBride, B.S. Dosanjh, E.T. Stone, and F.K. Sandercock.
1983. Influence of culture density on juvenile coho salmon production and ocean survival. Smolt releases in 1979 and 1980 from Capilano hatchery. Canadian Technical Report of Fisheries and Aquatic Sciences 1229.

Fisher, J.P., and W.G. Pearcy.
1988. Growth of juvenile coho salmon *Oncorhynchus kisutch* off Oregon and Washington, USA, in years of differing coastal upwelling. Can. J. Fish. Aquat. Sci. 45:1036–1044.

Gunsolus, R.T.
1978. The status of Oregon coho and recommendations for managing the production, harvest, and escapement of wild and hatchery-reared stocks. Oreg. Dep. Fish Wildl. Proc. Rep., Portland, OR, 59 p.

Harache, Y., G. Boeuf, and P. Lasserre.
1980. Osmotic adaptation of *Oncorhynchus kisutch* Walbaum. III: Survival and growth of juvenile coho salmon transferred to seawater at various times of the year. Aquaculture 19:253–273.

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

Hvidsten, N.A., and L.D. Hansen.
1988. Increased recapture rate of adult Atlantic salmon, *Salmo salar* L., stocked as smolts at high water discharge. J. Fish Biol. 32:153–154.

Langdon, J.S., and J.E. Thorpe.
1985. The ontogeny of smoltification: developmental patterns of gill Na^+/K^+-ATPase. SDH, and chloride cells in juvenile Atlantic salmon, *Salmo salar* L. Aquaculture 45:83–90.

McCarl, B.A., and R.B. Rettig.
1983. Influence of hatchery smolt releases on adult salmon production and its variability. Can. J. Fish. Aquat. Sci. 40: 1880–1886.

McCormick, S.D., R.L. Saunders, E.B. Henderson, and P.R. Harmon.
1987. Photoperiod control of parr-smolt transformation in Atlantic salmon (*Salmo salar*): changes in salinity tolerance, gill Na^+-K^+-ATPase activity, and plasma thyroid hormones. Can. J. Fish. Aquat. Sci. 44:1462–1468.

McGie, A.M.
1981. Trends in escapement and production of fall chinook and coho salmon in Oregon. Oreg. Dep. Fish Wildl., Fish Div. Info. Rep. 81-7, 44 p.
1984. Commentary: evidence for density dependence among coho salmon stocks in the Oregon Production Index area. *In* The influence of ocean conditions on the production of salmonids in the North Pacific: a workshop (W.G. Pearcy, ed.), p. 37–49. Oregon State Univ., Sea Grant Coll. Prog., ORESU-W-83.

Nickelson, T.E.
1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production Area. Can. J. Fish. Aquat. Sci. 43: 527–535.

Ogata, H., and S. Konno.
1986. Growth response and smolt production of 1 year cherry salmon fed with diets having different protein and lipid levels. Bull. Jpn. Soc. Sci. Fish. 52:313-318.

Patino, R., C.B. Schreck, J.L. Banks, and W.S. Zaugg.
1986. Effects of rearing conditions on the developmental physiology of smolting coho salmon. Trans. Am. Fish. Soc. 115: 828-837.

Peterman, R.M., and R.D. Routledge.
1983. Experimental management of Oregon coho salmon (*Oncorhynchus kisutch*): designing for yield of information. Can. J. Fish. Aquat. Sci. 40:1212-1223.

Rodgers, J.D., R.D. Ewing, and J.D. Hull.
1987. Physiological changes during seaward migration of wild juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 44:452-457.

Rondorf, D.W., M.S. Dutchuk, A.S. Kolok, and M.L. Gross.
1985. Bioenergetics of juvenile salmon during the spring outmigration. Annual Rep. (1983) to Bonneville Power Administration, Portland, OR, 78 p.

Rondorf, D.W., J.W. Beeman, M.E. Free, and D.E. Liljegren.
1988. Correlation of biological characteristics of smolts with survival and travel time. Annual Rep. (1987) to Bonneville Power Administration, Portland, OR, 96 p.

Sandercock, F.K., and E.J. Stone.
1982. A progress report on the effect of rearing density of subsequent survival of Capilano coho. *In* Proc. North Pacific Aquacult. Symp.; Aug. 1980, Anchorage, AK (B.R. Melteff and R.A. Neve, ed.), p. 151. Alaska Sea Grant Rep. 82-2.

Schreck, C.B.
1982. Stress and rearing of salmonids. Aquaculture 28:241-249.

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

Schreck, C.B., R. Patino, C.K. Pring, J.R. Winton, and J.E. Holway.
1985. Effects of rearing density on indices of smoltification and performance of coho salmon, *Oncorhynchus kisutch*. Aquaculture 45: 345-358.

Soivio, A., and E. Virtanen.
1985. The quality and condition of reared *Salmo salar* smolts in relation to their adult recapture rate. Aquaculture 45:335-343.

Vreeland, R.R.
1990. Evaluation of the contribution of fall chinook salmon reared at Columbia River hatcheries to the Pacific salmon fisheries. Final Report (1989) to Bonneville Power Administration, Portland, Oregon, 113 p.

Wahle, R.J., and W.S. Zaugg.
1982. Adult coho salmon recoveries and their Na^+-K^+-ATPase activity at release. Mar. Fish. Rev. 44(11):11-13.

Wedemeyer, G.A., D.J. McLeay, and C.P. Goodyear.
1984. Assessing the tolerance of fish and fish populations to environmental stress: the problems and methods of monitoring. *In* Contaminant effects on fisheries (V.W. Cairns, P.V. Hodson, and J.O. Nriagu, eds.), p. 164-195. John Wiley & Sons, Inc., New York.

Weitkamp, D.E., and R.R. Loeppke.
1983. Physiological monitoring of smoltification and stress in mid-Columbia chinook and steelhead, 1983. Report, Document no. 83-1130-0110, Parametrix, Inc., Bellevue, WA, 54 p.

Zaugg, W.S.
1982a. Relationship between smolt indices and migration in controlled and natural environments. *In* Proc. Salmon and Trout Migratory Behavior Symposium (E.L. Brannon and E.O. Salo, eds.), p. 173-183. Univ. Washington, Seattle, WA.
1982b. A simplified preparation for adenosine triphosphatase determination in gill tissue. Can. J. Fish. Aquat. Sci. 39:215-217.
1989. Migratory behavior of underyearling *Oncorhynchus tshawytscha* and survival to adulthood as related to prerelease gill Na^+-K^+ ATPase development. Aquaculture 82:339-353.

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