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Effects of 70 Years of Freshwater Residency on Survival, Growth, Early Maturation, and Smolting in a Stock of Anadromous Rainbow Trout from Southeast Alaska

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Abstract.—Progeny of wild, freshwater sequestered (resident) rainbow trout *Oncorhynchus mykiss*, descendants of a stocking of steelhead (anadromous rainbow trout) in 1926, and progeny of the wild, ancestral steelhead lineage and their reciprocal crosses were compared for two brood years in a hatchery environment to determine the effects of 70 years of freshwater residency on growth, survival, early maturity, and smolting proportion. Resulting smolts were tagged, released, and recovered as maturing adults to evaluate marine survival. For the 1996 brood, 75 families were maintained in separate freshwater raceways for 10 months. Approximately 100 fish from each family were tagged with passive integrated transponder tags, pooled by type, and cultured until age 2. An additional group was tagged with coded-wire tags and reared in the same manner. For the 1997 brood, 80 families were coded-wire-tagged, separated by breeding type, and cultured at different densities. Size-at-age and survival were reduced significantly in progeny of resident females when compared with progeny from anadromous females during the first 2 months after first feeding. No significant differences were observed in subsequent growth or survival through age 2. A higher proportion of smolting at age 2 and a lower proportion of early male maturity was observed in families from anadromous parents. Smolts produced by anadromous parents had four to five times higher marine survival than those from resident parents. While smolting proportions and smolt survival were lower for the progeny of freshwater resident fish, the results indicate that significant numbers of smolts and adults can still be produced by populations landlocked for up to 70 years and 20 generations. The results have substantial implications for the use of natural freshwater environments for the preservation of endangered anadromous stocks of rainbow trout, the rehabilitation of anadromous stocks, and the actual effective breeding size of anadromous rainbow trout populations.

Introduction

In the past 100 years, habitat destruction from logging, hydropower development, urbanization, farming, and ranching combined with overfishing on the West Coast of the United States has resulted in serious declines in most salmonid stocks, including anadromous rainbow trout (steelhead *Oncorhynchus mykiss*). Status reviews of West Coast steelhead stocks sponsored by the National Marine Fisheries Service (NMFS) have resulted in the classification of 15 evolutionarily significant units or ESUs (Busby et al. 1996). These ESUs are the lowest classification within a species that can be authorized for protection under the Endangered Species Act (ESA). Of the 15 ESUs recognized, 67% are currently listed as threatened or endangered under the act.

Because of this coastwide decline and official protection under the ESA, plans are being developed for stock and habitat preservation, rehabilitation, and restoration. While many stocks have reached critically low levels, and their continued survival relies on cooperation of virtually all levels of society, preservation and restoration must be conducted with comprehensive scientific information on the potential effects of proposed actions or inaction. In the most serious cases, it may be decided that the probability of continued survival of an endangered stock in its native habitat is

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unlikely and the only reasonable chance for future restoration efforts would be to remove the remaining individuals, or a portion thereof, to some form of protective custody as has been done with a number of species, notably, the California condor.

For fish which spend their entire lives in freshwater, protective custody generally involves moving the individuals or their progeny into a hatchery or other intensive culture environment using artificial incubation and rearing containers and/or grow-out ponds in which each life stage is carefully regulated through human intervention. For anadromous fishes, which normally spend a significant portion of their lives in seawater, the seawater portion of the life cycle has been reproduced by using marine net-pens or land-based rearing containers with pumped seawater as in the case of the Snake River sockeye (Flagg et al. 1995).

Questions have been raised by many researchers as to the potential negative impacts of intentional or inadvertent adaptive and genetic changes to captive and manipulated populations resulting from captivity and hatchery influence (Doyle and Talbot 1986; Leider et al. 1990; Doyle et al. 1995; Reisenbichler and Brown 1995; Berejikian et al. 1996; Heath et al. 2003). It is currently unknown if adaptation to an artificial environment, for possibly decades until the native habitat is restored, will significantly alter important life history characteristics. Also unknown are the impacts these changes might have on attempts at future restoration in the former native habitat or on the interactions of the preserved fish with a possible remnant population.

In an attempt to counter some of these unknown effects, a technique that attempts to minimize human influence has been to move the population of concern into another natural environment where they can be protected, as in the case of the desert pupfish (Dunham and Minckley 1998). While the potential negative consequences of adapting to a different natural environment could also be severe, it does reduce human influence and potential associated maladaptations throughout the life cycle. While this technique may be possible with fish that spend their entire lives in freshwater, to date, there do not exist any "natural" marine environments where endangered anadromous populations can be protected through that portion of the life cycle. It may be possible, however, to sequester a normally anadromous population in freshwater, bypassing the marine portion of the life cycle, and still retain adaptations necessary for successful future rehabilitation efforts. Long-term efforts of this nature have not been tried to date, and their potential for success is unknown.

Another important issue is whether the resident portion of a population that has an anadromous component should be considered part of the breeding population for the anadromous fish. Recent genetic evidence (Docker and Heath 2003) and otolith evidence (Zimmerman and Reeves 2000) indicates that the relationship between resident and anadromous forms is complex and varies between systems.

In 1926, on southern Baranof Island in southeast Alaska, juvenile rainbow trout were collected by cannery workers from the lower portion of Sashin Creek, which contained a population of steelhead, and transported above two natural barriers that completely blocked fish passage to the upper reaches of the watershed where they were planted in Sashin Lake (Anonymous 1939.). During the intervening 70 years, no subsequent transplants of fish have been made into the lake and the watershed has remained in a virtually pristine state. Surveys done in the 1930s indicated that the lake population numbered in the thousands and continues so to this day. Because of the geography of the system, all fish in the lake that underwent the normal smolting process associated with the downstream migration characteristic of steelhead, migrated over the barrier falls and were lost to the breeding population of the lake.

Because this system represented a "worst case" scenario for long-term intensive genetic selection against a critical life history trait (smolting) for an anadromous fish, and to improve our ability to assess the potential success of future recovery efforts on endangered stocks of steelhead, the National Marine Fisheries Service funded a study in 1996 to determine how this period of freshwater residency had altered smolting and other important life history characteristics in this stock of steelhead. Our hypothesis was that because of the complete selection against downstream migration in this population, the production of smolts from the resident fish would be negligible when compared with the production from the ancestral steelhead lineage in the lower reaches. We also wanted to determine if differences existed between the two populations in other important life history characteristics such as survival, growth, and early sexual maturity. To evaluate differences between populations, we made within-line matings and between-line matings of resident fish in the upper watershed and anadromous fish in the lower watershed in 1996 and 1997 and cultured the fish under hatchery conditions until age 2. We released coded-wire-tagged smolts from all four groups for both brood years and evaluated marine survival and size for returning adults.

Methods

We captured mature fish from both the anadromous and resident populations and artificially spawned them to produce pure stock families from each population, and also performed reciprocal crosses between populations to produce a total of 90 families in 1996 and 83 families in 1997. Seventy-five of these families of the 1996 brood year and 80 families of the 1997 brood year were raised in separate containers until large enough to tag with passive integrated transponder (PIT) tags (1996 brood) or sequentially coded-wire tags (SCWT) (1997 brood) at age 1 and then combined by breeding type and raised until age 2. The additional families and individual fish surplus to the PIT-tagged portion in the 1996 brood were combined by type, and the smolts were tagged with coded- wire tags for anadromous release at age 2. The populations were regularly sampled during incubation and rearing for growth and survival information and sampled at age 2 for early maturity and smolting.

In late May and early June of 1996 and 1997, mature resident rainbow trout were captured at the outlet of Sashin Lake using a 1.3-m-diameter baited hoop trap, and anadromous adults (steelhead) were captured at the Sashin Creek weir (Figure 1). Resident fish were killed prior to spawning, and anadromous fish were live spawned, retained in freshwater containers, and used once to several times. The gametes were stored in plastic bags on ice until mixed in the laboratory, usually within several hours of spawning.

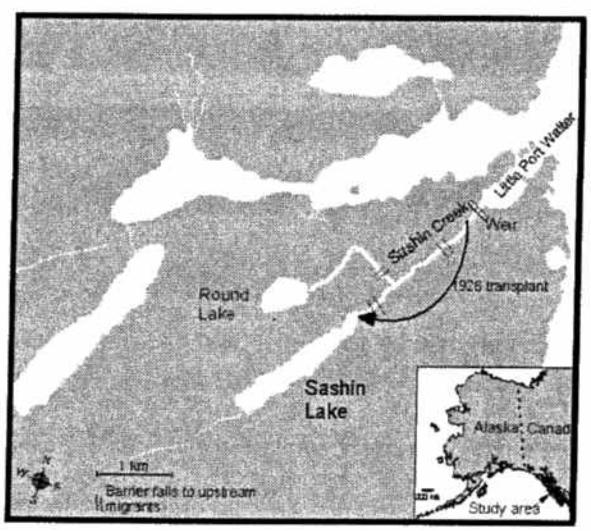

Figure 1. Map of the Sashin Creek drainage showing the initial transplant (1926) from the anadromous portion of the stream to Sashin Lake, located above two barriers to upstream migration.

For the 1996 brood, 90 families were produced from 5 anadromous males, 18 anadromous females, 32 resident males, and 49 resident females. From these, 80 families were reared in individual containers (Heintz and Joyce 1992) for 10 months, and then approximately 100 fish were randomly chosen from each of 75 of those families and tagged with PIT tags. These tagged fish were combined by type (anadromous female × anadromous male [A × A]-type; anadromous female × resident male [A × R]-type; resident female × resident male [R × R]-type; resident female × anadromous male [R × A]-type) and reared in freshwater vertical raceways (Martin and Heard 1987) until age 2. Fish from the nonPIT-tagged families were combined by type in other vertical raceways. Surplus fish from the 75 family groups were added to these 2 months after ponding, when densities in the individual containers were reduced to a maximum of 300 fish each, and again at PIT tagging at age 1. These fish were tagged with coded-wire tags prior to release at age 2.

For the 1997 brood, 83 families were produced from 8 anadromous males and 10 anadromous females, 28 resident males, and 28 resident females. From these, 80 families were grown in individual containers for 1 year (as above) and then tagged with SCWTs, pooled by type, and then split into high density (177 fish/m^3), low density (106 fish/m^3), and variable density (45–141 fish/m^3) groups.

Growth and survival data were obtained by periodically weighing all fish in a container and counting all by hand to determine an average weight and survival by period. After PIT tagging in June 1997, all fish were individually weighed using an electronic balance accurate to 0.1 g and measured using a digitizing board accurate to 1 mm. Individual PIT tag numbers were electronically recorded using a Biomark PIT tag station.

In early June 1998 and 1999 (for 1996 and 1997 broods respectively), all fish (both PIT- and coded-wire-tagged) were anesthetized in MS-222, inventoried, and graded into three groups depending on physiological condition: mature, smolt, or resident (nonmaturing, nonsmolting). A fish was considered mature only if gametes could be obtained with gentle pressure on the abdomen. Questionable fish (<5% of the total) were classified as resident. Resident fish were inventoried a second time in mid-June to determine if any additional maturation or smoltification had taken place.

Survival by period, length, weight, and condition factor by life stage were analyzed using one-way analysis of variance (ANOVA). Grouping by physiological condition was analyzed using a log likelihood ratio test for goodness of fit (G-test). The results of all tests were evaluated using a significance level of 0.05%.

Results

Average size of the wild resident rainbow spawners was substantially smaller in both years than the steelhead spawners (Table 1). While the anadromous fish were not significantly different between years, the resident fish, both males and females, were significantly larger in 1997.

Freshwater Survival

1996 Brood

Survival was variable by period and between types (Figure 2). Incubation survival (from eyed egg to emergent fry) was not different between pure parental types (92% average) but was significantly lower for the anadromous female by resident male type (80%). First summer survival was significantly lower for the fry derived from resident females regardless of male parental type (62%) versus fry derived from anadromous females (82%). First winter survival (October 1996 to May 1997) was not significantly different between types and averaged 97%. Second summer survival (May 1997 to October 1997) was not significantly different between types; however, survival of coded-wire-tagged groups was higher (99% average) than PIT-tagged groups (96% average). Subsequent survival to June 1998 was high (99% average) and not different for all groups.

1997 Brood

Survival was variable by period and between types (Figure 3). Incubation survival was generally high (96.1% average) and not significantly different between pure types; however, progeny of matings between resident females and anadromous males survived significantly better (97.8%) than those of the pure anadromous type (92.9%). First summer survival was significantly lower for progeny of resident females crossed with anadromous males (84.8%) when compared with progeny of all other mating types. No differences in survival of progeny between types was detected for the first winter period (93.5% average) or throughout the second year of rearing (98.1% average).

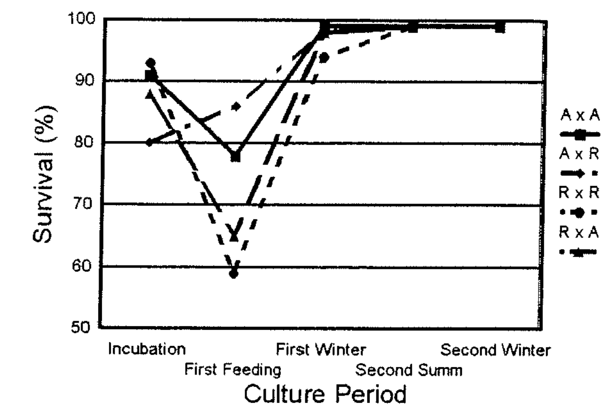

Figure 2. Survival of juvenile rainbow trout (1996 brood year) of pure anadromous, pure resident, or reciprocal cross origin during freshwater residence to age 2, indicating poor early survival of juveniles originating from resident females.

Growth

1996 Brood

Size at emergence (August 1996) was significantly smaller for progeny of resident females (0.14 g average weight) than those of anadromous females (0.24 g average weight). By June 1997, only the pure resident type remained significantly smaller (3.7 g average weight) than the other three types, which were

Table 1. Average size of wild, sequestered resident (Sashin Lake) and anadromous (Sashin Creek) *O. mykiss* spawners used to produce the 1996 and 1997 broods.

		1996					1997				
Spawners	Sex	*n*	Mean length (mm)	SE	Mean weight (g)	SE	*n*	Mean length (mm)	SE	Mean weight (g)	SE
Resident	male	26	190.9	17.5	128.2	36.8	28	277.7	12.4	269.3	33.2
	female	27	320.7	12.7	426.7	47.6	28	363.6	6.9	574.0	27.9
Anadromous	male	5	665.4	15.6	3128	186.3	8	683.8	12.4	3032	180.5
	female	15	706.8	21.0	3964	340.8	10	725.5	17.6	4006	291.7

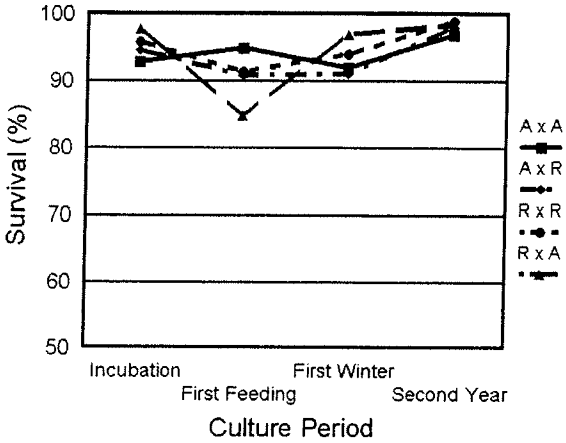

Figure 3. Survival of juvenile rainbow trout (1997 brood year) of pure anadromous, pure resident, or reciprocal cross origin during freshwater residence to age 2, indicating very similar survival trajectories for all types.

not significantly different from each other (4.6 g average weight) (Figure 4).

During the second year of culture (June 1997 to June 1998), the fish that had been PIT-tagged and combined by type (four types, four raceways) grew uniformly, and there were no significant differences in weight between types by June 1998 (80.7 g average weight) (Figure 4). The remaining fish, which were also combined by type and later coded-wire-tagged, displayed significant differences in average weight by June 1998 (Figure 4). The resident female × anadromous male type was significantly larger (83.9 g average weight) than the other three types, which were not significantly different from each other (60.8 g average weight).

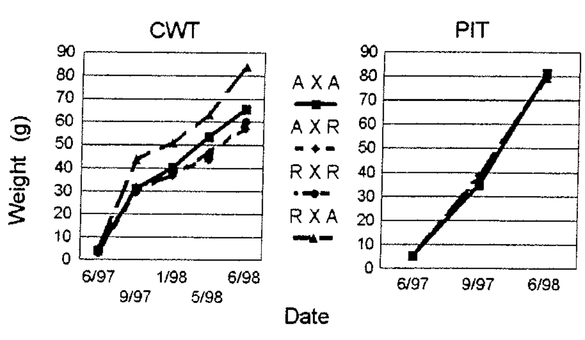

Figure 4. Growth of juvenile rainbow trout (1996 brood year) of pure anadromous, pure resident, or reciprocal cross origin during freshwater residence to age 2, for two treatment groups indicating significantly greater growth in the resident female × anadromous male reciprocal cross type in one group (Coded-wire-tagged) and similar growth for all types in the other (PIT-tagged).

1997 Brood

Progeny of resident females (0.19 g average weight) were significantly smaller at emergence (late July 1997) than those of anadromous females (0.23 g average weight) (Figure 5). By October 1997, there were no significant differences between types in average weight (3.31 g average weight); however, by the end of June 1998, progeny of resident females were significantly larger (13.3 g average weight) than those of anadromous females (12.3 g average weight).

During the second year of growth, from July 1998 to mid-June 1999, growth varied between types and between densities. In all densities, the resident female × anadromous male type grew to a significantly larger size than the other three types (Figure 5). In the high and low density groups, the other three types were not significantly different from each other; however, in the variable density group, the pure anadromous type was significantly larger than either the pure resident or anadromous female × resident male types.

Life History Type

1996 Brood

Individual examination of each fish in the coded-wire-tagged (n = 8,968) and PIT-tagged (n = 6,653) populations in June 1998 revealed significant differences between proportions of the four breeding types that matured as males, transformed into smolts for a ma-

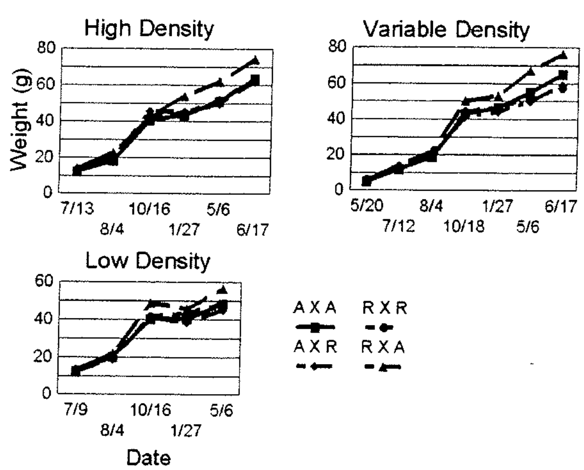

Figure 5. Growth of juvenile rainbow trout (1997 brood year) of pure anadromous, pure resident, or reciprocal cross origin during freshwater residence to age 2, for three treatment groups, indicating significantly greater growth in the resident female × anadromous male reciprocal cross type.

rine existence, or remained unchanged (Figure 6). Within both populations, the pure anadromous type produced significantly more smolts (67.8% and 65.4%, respectively) than the pure resident type (55.6% and 46.5%). The resident female × anadromous male type produced the highest proportion of smolts (79.4% and 72.3%), while the anadromous female × resident male type produced proportions (50.0% and 50.0%) similar to the pure resident type. Averaging both PIT-tagged and coded-wire-tagged populations, matings using anadromous males produced 1.4 times more smolts than those using resident males.

Early male maturity averaged 11.8% and was not significantly different between types. The proportion of fish that did not undergo significant physiological change (remained as residents) varied roughly inversely with smolt proportion.

Examination 1 year later at age 3 of all of the remaining PIT-tagged fish in freshwater that had not smolted in 1998 (n = 2573) revealed only 77 age-3 smolts representing all four breeding types. Of the pure anadromous type remaining, 32 fish or 4.3% smolted. Of the pure resident type remaining, only 5 fish or 0.8% smolted. The reciprocal crosses had intermediate levels of smolting.

1997 Brood

Individual examination of each fish in the controlled (n = 18,353) and variable (n = 15,148) density populations in June 1999 revealed significant differences between proportions of the four breeding types that matured as males, transformed into smolts for a marine existence, or remained unchanged (Figure 7). Within both controlled and variable density populations, the pure anadromous type produced significantly more smolts (64.9% and 63.9%, respectively) than the pure resident type (36.3% and 32.2%, respectively). The resident female × anadromous male type produced the highest proportion of smolts (75.3% and 73.1%, respectively), while the anadromous female × resident male type produced proportions of smolts (39.5% and 39.3%) similar to the pure resident type. Combining results of both densities, matings using anadromous males produced 1.9 times more smolts than those using resident males (69.3% and 36.8%, respectively).

Unlike the 1996 brood, early male maturity was significantly different between types in the 1997 brood. The pure anadromous type had a significantly lower proportion of early male maturity for both controlled and variable densities (15.5% and 18.0%, respectively) than either the pure resident type (30.5% and 33.0%, respectively) or the anadromous female × resident male type (27.3% and 31.2%, respectively), which were not different from each other. The lowest maturation proportion for either density and all types was observed in the resident female and anadromous male type (9.0% and 7.9%, respectively). Combining results of both densities, matings using anadromous males produced 2.4 times fewer maturing males than those using resident males (12.6% and 30.5%, respectively).

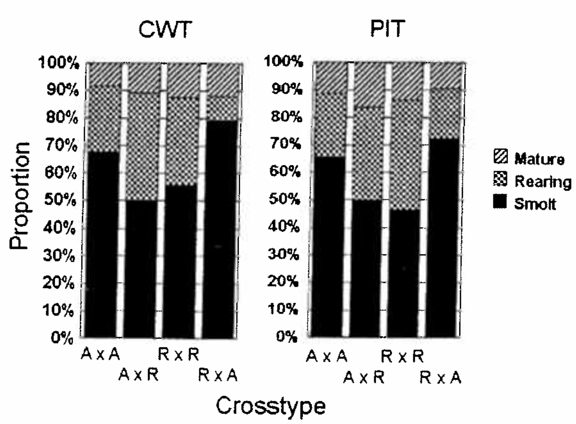

Figure 6. Proportion of smolts, residents, and mature fish for pure anadromous, pure resident or reciprocal cross types (1996 brood) at age 2 for two treatments, indicating a higher proportion of smolts produced by the pure anadromous type in both treatments and the lowest proportion of smolts in the pure resident type.

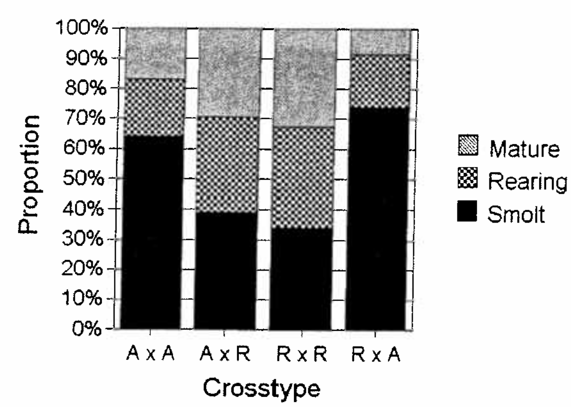

Figure 7. Proportion of smolts, residents, and mature fish for pure anadromous, pure resident, or reciprocal cross types (1997 brood) at age 2 for two treatments, indicating a higher proportion of smolts produced by the pure anadromous type and the lowest proportion of smolts in the pure resident type in both treatments.

Size by Life History Type

Mean length and weight varied substantially between smolts, residents, and mature fish at age 2 (Tables 2 and 3). In both brood years and all groups, smolts were significantly larger (both length and weight) than either residents or mature fish. Residents typically displayed a bimodal size distribution, however, with the larger mode similar to the smolts in length but heavier. The small size mode was significantly smaller than the mature fish. In general, smolts also had the lowest condition factor and mature fish had the highest.

1996 Brood

Coded-wire-tagged and PIT-tagged groups varied significantly in length and weight except for R × A type

Table 2. Comparison of length, weight and condition factor between type (A × A, A × R, R × R ,or R × A) within lifestage (smolt, resident or mature) for coded-wire-tagged or PIT-tagged groups of the 1996 brood of rainbow/steelhead at Little Port Walter. Breeding types within cells (e.g. smolt length, resident weight) with the same lower case letter are not significantly different.

1996 brood coded-wire-tagged groups

		Length				Weight				Condition factor			
Smolts	Type	Mean	SE	*n*		Mean	SE	*n*		Mean	SE	*n*	
	A × A	193.27	1.05	113	a	72.41	1.24	113	a	0.9927	0.0058	113	a
	A × R	191.51	1.36	84	a	70.85	1.70	84	a	0.9936	0.0079	84	a
	R × R	191.42	1.35	93	a	71.88	1.55	93	a	1.0122	0.0072	93	ab
	R × A	203.92	0.95	73	b	88.13	1.41	73	b	1.0345	0.0083	73	b
Residents													
	A × A	160.34	4.40	61	ab	51.51	4.01	61	ab	1.096	0.0134	61	a
	A × R	152.33	2.67	108	a	43.86	2.28	108	a	1.1216	0.0087	108	ab
	R × R	154.79	2.55	89	ab	44.62	2.08	89	a	1.1364	0.0099	89	bc
	R × A	164.69	3.96	71	b	58.93	4.19	71	b	1.1611	0.0095	71	c
Mature													
	A × A	158.28	2.43	46	a	49.02	2.29	46	a	1.196	0.0123	46	a
	A × R	153.71	2.42	52	a	44.57	2.09	52	a	1.1815	0.0130	52	a
	R × R	157.65	2.06	46	a	47.87	2.07	46	a	1.1893	0.0144	46	a
	R × A	180.56	7.99	9	b	74.57	8.60	9	b	1.2167	0.0166	9	a

1996 brood PIT-tagged groups

		Length				Weight				Condition factor			
Smolts	Type	Mean	SE	*n*		Mean	SE	*n*		Mean	SE	*n*	
	A × A	207.74	0.35	1423	a	87.38	0.46	1423	a	0.9636	0.0019	1416	a
	A × R	208.91	0.70	675	a	96.08	0.97	675	b	1.0308	0.0027	676	b
	R × R	203.64	0.54	555	b	90.38	0.78	555	c	1.0634	0.0030	539	c
	R × A	205.53	0.31	1363	c	85.59	0.39	1364	d	0.9781	0.0017	1388	d
Residents													
	A × A	182.57	1.35	498	a	70.61	1.46	497	a	1.0749	0.0033	497	a
	A × R	170.7	1.39	462	b	63.11	1.50	464	b	1.1685	0.0034	462	b
	R × R	175.61	1.27	459	c	69.41	1.38	458	a	1.2082	0.0041	457	c
	R × A	176.78	1.51	344	c	65.88	1.56	344	ab	1.1086	0.0036	344	d
Mature													
	A × A	181.63	1.24	246	a	71.09	1.42	246	ab	1.1455	0.0042	245	a
	A × R	174.91	1.27	220	b	67.56	1.45	221	b	1.2206	0.0048	221	b
	R × R	176.93	1.36	159	b	73.22	1.61	159	ac	1.2878	0.0062	159	c
	R × A	182.43	1.18	181	a	74.65	1.39	182	ac	1.2011	0.0052	181	d

A × A - Anadromous female crossed with anadromous male
A × R - Anadromous female crossed with resident male
R × R - Resident female crossed with resident male
R × A - Resident female crossed with anadromous male

Table 3. Comparison of length, weight and condition factor between type (A × A, A × R, R × R, or R × A) within lifestage (smolt, resident or mature) for controlled density or variable density groups of the 1997 brood of rainbow/steelhead at Little Port Walter. Breeding types within cells (e.g. smolt length, resident weight) with the same lower case letter are not significantly different.

1997 brood controlled density

		Length				Weight				Condition factor			
Smolts	Type	Mean	SE	*n*		Mean	SE	*n*		Mean	SE	*n*	
	A × A	191.1	0.95	149	a	70.69	1.05	149	a	1.004	0.0036	149	a
	A × R	191.3	1.30	80	a	73.81	1.51	80	ab	1.045	0.0045	80	b
	R × R	192.3	1.40	57	a	77.2	1.74	57	bc	1.076	0.0088	57	c
	R × A	197.5	0.92	155	b	79.37	1.20	155	c	1.021	0.0048	155	d
Residents													
	A × A	167.1	2.28	86	a	52.52	1.97	86	a	1.078	0.0046	86	a
	A × R	170.1	2.00	145	a	57.25	1.85	145	ab	1.1	0.0043	145	b
	R × R	172.5	2.00	136	a	62.22	1.95	136	bc	1.159	0.0057	136	c
	R × A	180.1	2.53	96	b	67.03	2.48	96	d	1.097	0.0075	96	b
Mature													
	A × A	165.3	2.10	47	a	53.57	2.12	47	a	1.162	0.0089	47	a
	A × R	164.8	2.03	77	a	54.68	2.04	77	a	1.183	0.0054	77	a
	R × R	162.2	1.96	83	a	54.69	1.97	83	a	1.236	0.0071	83	b
	R × A	166.7	3.46	21	a	56.08	3.65	21	a	1.181	0.0141	21	a

1997 brood uncontrolled density

		Length				Weight				Condition factor			
Smolts	Type	Mean	SE	*n*		Mean	SE	*n*		Mean	SE	*n*	
	A × A	190.8	0.82	260	a	71.2	0.98	260	a	1.009	0.0029	260	a
	A × R	189.6	1.12	113	a	70.79	1.19	113	a	1.03	0.0052	113	b
	R × R	192.8	1.23	95	a	77.23	1.59	95	b	1.065	0.0051	95	c
	R × A	198.6	1.37	103	b	80.92	1.97	103	b	1.015	0.0053	103	ab
Residents													
	A × A	174	1.97	145	a	58.7	1.76	145	a	1.062	0.0048	145	a
	A × R	168.4	1.68	192	b	54.37	1.51	192	ab	1.08	0.0040	192	b
	R × R	164.3	1.68	209	b	52.27	1.42	209	bc	1.114	0.0045	209	c
	R × A	185.5	2.18	85	c	70.92	2.38	85	d	1.071	0.0073	85	ab
Mature													
	A × A	163.4	3.25	49	ab	54.27	3.06	49	ab	1.184	0.0093	49	ab
	A × R	167	1.87	91	a	56.65	1.79	91	a	1.179	0.0062	91	a
	R × R	157.4	1.62	97	b	48.35	1.52	97	b	1.203	0.0052	97	b
	R × A	169.2	5.84	14	ab	60.71	5.74	14	a	1.202	0.0141	14	ab

A × A - Anadromous female crossed with anadromous male
A ×R - Anadromous female crossed with resident male
R × R - Resident female crossed with resident male
R × A - Resident female crossed with anadromous male

smolts and R × A mature fish, which were not different between groups (Table 2).

Coded-wire-tagged groups.—Mean length of smolts was similar for all types except the resident female × anadromous male type, which was significantly larger than the others (Table 2). Mean weight was also similar for all types except the R × A type, which was significantly larger. Condition factor was similar for the A × A and A × R types, which was significantly lower than the R × A type. Condition factor of the R × R type was not different from any of the other types.

Mean length of residents was similar between types with the exception of the R × A type being significantly larger than the A × R type. Mean weight was similar except that the R × A type was significantly larger than either the A × R or the R × R types. Condition factor was lowest (1.096) for the A × A type and highest for the R × A type (1.1611).

Mean length and weight of mature males was significantly greater for the R × A type than all other types, which were not significantly different from each other. No difference in condition factor was detected between any of the types.

PIT-tagged groups.—Smolts produced by anadromous females were significantly longer than those produced by resident females (208 and 204 mm respectively); however, the difference was small. Mean weights were significantly different for all types with the A × R type the largest (96.1 g) and the R × A the smallest (85.6 g). Condition factor was also significantly different between all types, with the lowest mean observed in the A × A type (0.9636) and the highest (1.0634) in the R × R type.

Pure anadromous type residents were significantly larger on average (182.6 mm) and A × R type residents were significantly smaller on average (170.7 mm) than the other types. Mean weights ranged from 63.1 to 70.6 g, with the A × R type significantly smaller than the A × A or R × R types. All types had significantly different condition factors, with the lowest factor (1.075) in the A × A type and the highest factor (1.208) in the R × R type.

Mature fish of the A × A and R × A types were significantly longer than those in the A × R and R × R types. Mean weight for the A × R type was significantly lower than either R × R or R × A types. Condition factor for mature fish maintained the pattern observed for the residents and smolts, with the A × A type having a significantly lower mean condition factor (1.146) and the R × R type having a significantly higher factor (1.288) than the reciprocal cross types.

1997 Brood

Smolts in both densities were significantly longer, heavier, and had a lower condition factor than either residents or mature fish (Table 3). Mature fish were shorter on average and had significantly higher condition factors than the smolts or residents. Sample size for mature fish in both densities was low, however. Smolt size by type was similar in both densities, with the R × A type significantly larger in both. The R × A type residents were also larger than the other types in both densities. Patterns of differences in sizes of mature fish between and within densities were not apparent.

Controlled density.—Smolts of the R × A type were significantly longer than any of the other types, which were not different from each other. The R × A type smolts were also significantly heavier than either the A × A or A × R types. All types had significantly different condition factors, with the A × A type having the lowest (1.004) and the R × R type the highest (1.076).

The R × A type residents were significantly longer and heavier than the other types. Condition factor was lower in the A × A type and highest in the R × R type.

No differences in length or weight between types of mature fish was detected; however, condition factor was significantly higher in the R × R type.

Variable density.—The R × A type smolts were significantly longer than the other types, which were not different from each other. Smolts produced from resident females were significantly heavier than those produced from anadromous females. Condition factor was significantly higher in the R × R type. The R × A type residents were significantly longer and heavier than the other types. Condition factor was significantly higher in the R × R type.

The R × A type residents were significantly longer and heavier than the other types. The R × R type residents had a significantly higher condition factor than the other types.

While mean length, weight, and condition factor were not the same for mature fish across types, there was considerable overlap in means, with no clear pattern of differences.

Marine Survival

1996 Brood

Marine survival of tagged smolts was significantly higher in the two groups sired by anadromous males (pure anadromous 2.8% and resident female × anadromous male 2.7%) than in the groups sired by resident males (pure resident 0.7% and anadromous female × resident male 1.1%) (Figure 8).

1997 Brood

Marine survival of tagged smolts was lower for the 1997 brood overall than the 1996 brood (Figure 8). The pattern of survival between groups was similar between broods, however, with groups sired by anadromous males (pure anadromous 1.9%, and resident females × anadromous males 1.3%) surviving better than those sired by resident males (pure resident 0.4%, and anadromous females × resident males 1.1%).

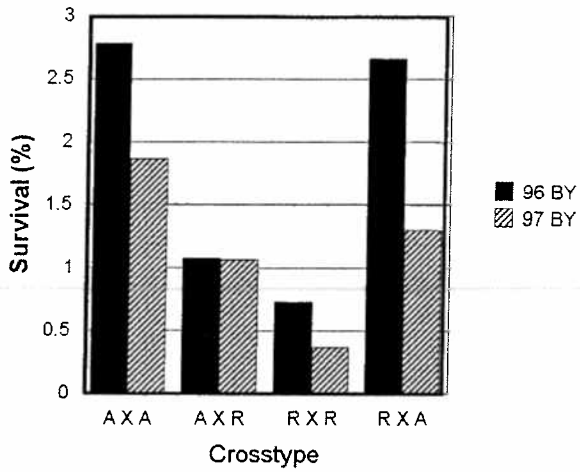

Figure 8. Marine survival of smolts, as measured by recovery of tagged fish at the weir upon return, for pure anadromous, pure resident, or reciprocal cross types (1996 and 1997 broods), indicating fourfold to fivefold higher survival of pure anadromous type compared to pure resident type.

Discussion

Freshwater Survival

The primary difference in juvenile survival observed between types was the reduced survival of progeny of resident females in the 1996 brood. Resident females used for spawning in 1996 were very small compared to anadromous females and had substantially smaller eggs (0.10 g versus 0.16 g mean eyed weight, respectively), which produced substantially smaller fry. While care was taken to provide small food sizes for these fry, it is quite possible that a significant portion of the disparate mortality shortly after first feeding was due to mechanics of the fish culture system. In 1997, we were able to obtain larger resident females, which resulted in larger eggs and fry and less of a disparity in size between resident and anadromous types (0.13 g versus 0.16 g mean eyed weight, respectively). In this brood, survival exceeded 90% (for all but the R × A type) which was significantly better than survival during the same period for all types of the 1996 brood. Survival during all other culture periods was generally very high and not different between types. In natural environments, early life stages typically have high mortality rates and larger fry tend to survive better than smaller fry.

Growth

Perhaps the most interesting outcome of the comparisons of growth in freshwater was the consistently higher growth rate of the resident female by anadromous male type. This occurred in both brood years under a range of culture conditions, which indicates a strong, heritable genetic component (heterosis). This increased growth rate may be linked to the higher smolting rate also seen in this type. The larger mean size of all types within the PIT-tagged groups at age 2, while retaining similar proportions of smolts when compared to the coded-wire-tagged groups, indicates that the linkage between smoltification and size is not necessarily an incremental process, at least after a certain size has been reached, but is probably one that incorporates size and growth rate at specific times, presumably in concert with other factors.

Life History Type

Smolting Rate

We expected the smolting rate in the resident type to be negligible after 70 years of complete counter-selection. The mean smolting rate was lower for the resident type than for the anadromous type in both brood years; however, substantial numbers of smolts were produced from the resident type in both years. The lower rate does imply a heritable component to smolting. The continued production of large numbers of smolts indicates that a suite of genes may be involved and/or environmental conditions are important for activation of smolting genes. There is a substantial body of scientific literature on the importance of factors such as size, growth rate, and temperature on smoltification in salmonids. It is also probable that anadromy, as a life history strategy, is numerically a relatively minor component of the rainbow trout metapopulation associated with rivers that have the potential for anadromous runs. The anadromous portion may represent a distinct, reproductively isolated portion in some rivers, while in others it simply represents a form that freely interbreeds with the resident fish (Zimmerman and Reeves 2000). Reduced proportions of the anadromous form are more evident as one nears the geographic maximums of range for *O. mykiss* in North America. In the Bristol Bay region of Alaska, there are large populations of *O. mykiss* inhabiting the large river systems that are home to huge runs of other salmonids; however, the anadromous form of *O. mykiss* is not found there. In Southern California and northern Mexico, *O. mykiss* populations are prevented from developing anadromy by thermal limits to successful migration or physical blockage of river mouths. This is not to say that anadromy is not important to metapopulation survival; in fact, some researchers (Nielsen et al. 1994b) believe that anadromy and the associated straying of maturing adults is a crucial mechanism for the exchange of genetic information between river systems and the establishment of new populations.

It is important to note that the use of resident females in conjunction with anadromous males did not lower the smolting rate, as occurred when resident males were used. This result could have specific application in re-establishing anadromous runs when resident females and anadromous males are available for recovery efforts and resident males or anadromous females are in short supply.

Early Maturation

The tendency of progeny of resident males to mature at a higher rate than those of anadromous males is an expected outcome given the severe selection constraints imposed for 70 years on the population. However, the differences between brood years indicates that substantial genetic variation for this trait still exists in the resident population.

Marine Survival

Because of the substantial reduction in genetic variation found in the resident population by Thrower et al. (2004), it is impossible to determine if the reduction in marine survival of the pure resident type is related to low genetic diversity or counterselection for survival in a freshwater lake. It is possible that a larger founder population that preserved more of the genetic variation might also have survived better in the current marine environment.

Conclusion

The success of any recovery program that utilizes some form of captive broodstock ultimately relies on the production and survival of the juveniles produced. Sequestered populations in refugia have many potential problems such as lack of control of breeding population size, uncontrolled disease outbreaks or other sources of mortality, and adaptation to an environment dissimilar to the one they will be returned to. However, many of the known problems with domestication selection in completely captive populations might be avoided by utilizing natural refugia. This study indicates that anadromous *O. mykiss* can be maintained for decades in freshwater residency and still produce smolts and adults that survive the natural marine environment. Careful attention to initial breeding population size and monitoring to avoid genetic bottlenecks (Schonhuth et al. 2003) might result in improved smolt and adult production over that seen in this study. The results also imply that resident populations of *O. mykiss* may contribute significantly to the maintenance of anadromous populations. Further evidence of this has recently been added by Docker and Heath (2003) in a genetic analysis of sympatric resident and anadromous populations. This evidence indicates that important genetic resources of anadromous *O. mykiss* probably still exist in many water storage and power generation reservoirs on the West Coast of North America. These populations need to be studied to assess their potential use in rebuilding depressed populations, and protected where warranted.

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