

Influence of Time and Size at Release of Juvenile Coho Salmon (*Oncorhynchus kisutch*) on Returns at Maturity

H. T. BILTON, D. F. ALDERDICE, AND J. T. SCHNUTE

Department of Fisheries and Oceans, Resource Services Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

BILTON, H. T., D. F. ALDERDICE, AND J. T. SCHNUTE. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Can. J. Fish. Aquat. Sci. 39: 426-447.

Juvenile coho salmon (*Oncorhynchus kisutch*) were raised in six ponds at Rosewall Creek, Vancouver Island, British Columbia, from which releases were made at four times: April 14, May 12, June 10 and July 8, 1975. Prior to each release a portion of the juveniles in each pond were graded into three size groups (small, medium, large) based on size distributions in each pond. The juveniles were nose-tagged according to size group, pond, and release date, and marked by adipose fin removal. A total of 57 groups were released. Returns of adults and precocious males (jacks) to the weir and to the fishery (commercial, sport) were subjected to response surface analysis. Maximum adult returns of 43.5%, to the weir and fishery, were predicted for release of 25.1-g coho juveniles on the 173rd (Julian) day from January 1 (June 22, 1975). A significant interaction was noted between release time and size: maximum returns from early (April 14) releases would be expected from release of 16- to 17-g juveniles. Returns of jacks from the six ponds ranged from 0.0 to 4.65%. Predicted returns of jacks would be maximized from early release of large juveniles (>~20 g in April). The benefit-cost ratio at the center of the time and size of release surface for maximum adult returns was estimated as 12.2:1. Maximum benefit-cost ratios were calculated for release of smaller juveniles between June 17 and 22, 1975. Benefit-costs associated with releases on the path of joint optimality between the two response centers rose from 12.2:1 (maximum adult returns) to a calculated 16.5:1 for release of 7.5-g juveniles on June 17, 1975. Size and time at juvenile release and success of adult returns are viewed as initial and final aspects of a biological system whose central components as yet are imperfectly understood. Some parts of the system are discussed in relation to possible ways of increasing the efficiency and cost-effectiveness of salmonid hatchery technology, as well as in predicting the success of returns in relation to conditions influencing survival and growth of juvenile migrants from natural stocks.

Key words: coho salmon, juvenile salmon, release time and size, response surface analysis and optimization, survival, biomass, benefit-costs

BILTON, H. T., D. F. ALDERDICE, AND J. T. SCHNUTE. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Can. J. Fish. Aquat. Sci. 39: 426-427.

Des jeunes saumons coho (*Oncorhynchus kisutch*) ont été élevés dans six étangs à Rosewall Creek, île Vancouver (Colombie-Britannique). Ils furent libérés à cet endroit à quatre occasions : 14 avril, 12 mai, 10 juin et 8 juillet 1975. Avant chaque mise en liberté, un certain nombre de chaque étang furent classés en trois groupes (petits, moyens et grands) selon la distribution des tailles dans chaque étang. On fixa une étiquette sur le nez selon la taille, l'étang et la date de mise en liberté, et on les marqua par ablation de la nageoire adipeuse. Un total de 57 groupes furent ainsi libérés. Les retours d'adultes et de mâles précoces (« jacks ») dans les parcs et les pêches (commerciale, sportive) furent soumis à une analyse de surface de réponse. Le plus haut pourcentage de retours d'adultes, soit 43,5 %, devait se produire, d'après les prédictions applicables aux poissons de 25,1 g, au 173^e jour (julien) à partir du 1^{er} janvier (le 22 juin 1975). Nous avons observé une interaction significative entre le moment de mise en liberté et la taille : on pourrait s'attendre que les retours les plus nombreux de poissons mis en liberté de bonne heure (14 avril) se produiraient avec les jeunes de 16-17 g. Les retours de « jacks » des six étangs ont varié de 0,0 à 4,65 %. En libérant tôt des juvéniles de plus grande taille (>~20 g en avril) on maximiserait les retours prédits des « jacks ». On a estimé à 12,2:1 le rapport coûts-bénéfices au point médian du

temps et de la taille de la surface de mise en liberté pour des retours d'adultes maxima. Les rapports coûts-bénéfices maxima ont été calculés dans le cas de mise en liberté de juvéniles de petite taille entre les 17 et 22 juin 1975. Les coûts-bénéfices associés avec les mises en liberté sur la voie d'une optimalité conjointe entre les deux centres de réponse passa de 12,2:1 (retours d'adultes maxima) à un rapport calculé de 16,5:1 avec la libération de jeunes de 7,5 g le 17 juin 1975. Nous envisageons la taille et le moment de mise en liberté des juvéniles et la réussite des retours d'adultes comme les aspects initial et final d'un système biologique dont les éléments centraux sont encore mal compris. Nous analysons certaines parties du système en relation avec des méthodes susceptibles d'accroître le rendement et le coût-efficacité de la technologie des établissements d'élevage des saumons et permettant de prédire le succès des retours par rapport aux conditions influençant la survie et la croissance des migrants juvéniles de stocks naturels.

Received May 7, 1981
Accepted November 16, 1981

Reçu le 7 mai 1981
Accepté le 16 novembre 1981

UNDER a federal-provincial Salmonid Enhancement Program, efforts are being made to increase British Columbia salmonid stocks. One strategy being employed is to seek ways for improving the biological effectiveness of existing and proposed salmonid hatcheries. An associated tactical approach to this objective has involved examination of the influence of size of juvenile salmon and the time of their release on their subsequent return as mature fish. Evidence obtained by American salmonid hatcheries on the Pacific Coast indicates that survival of juvenile coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon can be influenced by the size of smolts at release (Wallis 1968; Johnson 1970; Hopley and Mathews 1975; Hager and Noble 1976). The study by Hopley and Mathews (1975) indicated that both time and size at release of yearling coho influenced the survival and the size of returning adults, those fish maturing in their 3rd yr of life.

The objective of the experiment reported here was to determine the simultaneous effects of both time and size at release of juvenile coho salmon on their subsequent survival, growth, and age at maturity. A number of supporting details of the study, including escapement and catch data, have been reported elsewhere (Bilton 1978, 1980). This paper, based on the data from the earlier reports, uses response surface analysis to compute those conditions of release that maximize the numbers and biomass of returning adults. In doing so, it examines the contribution of the various experimental release groups in terms of percent survival and biomass of returning adults and jacks (precocious males maturing as 2-yr-olds). It also examines benefit-cost ratios for returning fish in relation to time and size at juvenile release. Because the response surface centers associated with percent return, biomass, or benefit-cost ratios would not necessarily coincide, a further analysis describes alternative time and size of release conditions in terms of efficiency of return and associated benefit-cost ratios. These conditions are described on a path of joint optimality lying between the response centers for maximum percent return and maximum benefit-costs.

Experimental Methods

LOCATION, STOCK, AND REARING

The experiment was carried out at Rosewall Creek hatchery, Vancouver Island, B.C., which is operated by the Pacific

Biological Station, Nanaimo, B.C. (Fig. 1). Rosewall Creek is located ~80 km north of Nanaimo on the east coast of Vancouver Island, and flows into Georgia Strait.

The coho eggs used were from the Big Qualicum River, ~24 km south of Rosewall Creek. A total of 200 thousand eggs were taken, fertilized, and incubated to the "eyed" stage at the Big Qualicum hatchery. The eyed eggs were transferred to the Rosewall Creek hatchery and incubated in well water at temperatures of 6–7°C.

The resulting fry were divided equally into six groups and moved into six Burrows ponds. Throughout rearing, the fish were fed Oregon Moist Pellets (OMP) from automatic feeders every 15 min daily during daylight hours. Water temperatures were partially controlled using Rosewall Creek water or groundwater, separately or mixed.

EXPERIMENTAL DESIGN

Initially it was planned (1) to rear three populations of juvenile coho to three successively larger mean sizes by manipulating water temperature; (2) to replicate each of the three populations once, making a total of six populations; (3) to release one-third of each of the six populations at three different times, in April, May, and June; and (4) to compare the returns from each release. However, this plan was not achieved; temperature differences in the two available water supplies were not sufficient to provide the required differences in growth rate. The six ponds in Table 1 refer to the six original experimental populations. Average water temperature of ponds 1 and 4, set up to provide "small" fish, was only 2.3°C lower than that of ponds 2 and 5, set up to provide "medium-sized" fish. Average water temperature of the latter ponds was 0.2°C lower than that of ponds 3 and 6, set up to provide "large" fish. By the time of the first proposed release, only a small difference (1.2 g) was evident between the average weights of the medium (ponds 2, 5) and large (ponds 3, 6) fish. Therefore, to achieve larger differences in size among the groups of juveniles, we graded the fish in each of the six pond populations into three size groups (S, small; M, medium; L, large) prior to tagging (Table 1). Hence the original design, involving populations of fish of different sizes replicated between ponds, was abandoned in favor of providing graded size groups in the populations within ponds. The size groups selected were based on preliminary sampling for length distribution of fish in each population. The middle

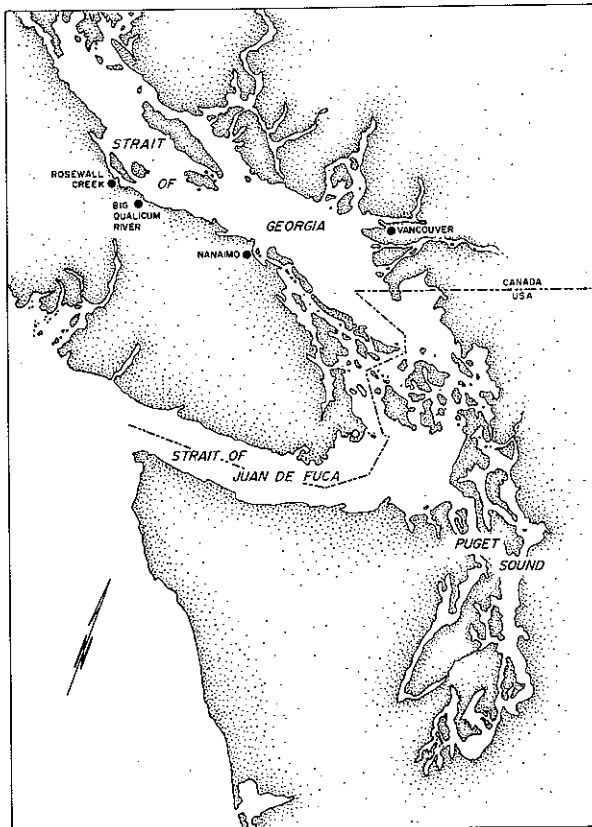


FIG. 1. Locations and geographic features mentioned in the text.

portion of the distributions, constituting 50% of the sample, provided the range for medium-sized fish. Those below and above the midrange, comprising 25% of the sample in each group, were classed as small and large, respectively. The potential genetic bias introduced by grading is considered later in the analysis.

A fourth release of juveniles was made in July using the combined excess fish from the six ponds. In this instance, three size groups were tagged and released from the single population. These and the groups previously released provided a total of 57 individually tagged groups. That is, three size groups were liberated from each of the six ponds in each of the first three releases plus the three groups making up the last release (Table 1).

The number of smolts making up each of the three size groups from the six populations at each release time ranged as follows:

Release	Small	Medium	Large
April 14	1243-1788	3585-3867	1657-1787
May 12	1830-1888	3639-3784	1839-1909
June 10	878-1642	1853-3937	1172-1898
July 8	1432	3704	1801

Fish in each of the 57 groups released were tagged several weeks prior to release using coded wire nose tags. A specific tag code identified each release group, and all tagged fish

were marked, for later recognition, by removal of the adipose fin. At the time of each release a sample of fish was obtained. These fish were sacrificed and individuals were sampled for length, weight, scales, and percent nose tag retention. These data provided estimates of size distribution and sex ratio in each release group.

RECOVERY OF JACKS AND ADULTS

Jack coho salmon (age 1.0¹) were recovered from Rosewall Creek in the fall of 1975, and adults (age 1.1¹) in the fall of 1976. Marked fish, those with a missing adipose fin, were captured in a trap adjacent to the release ponds, located immediately downstream from an electric fence. Approximately 200 unmarked fish, assumed to be wild fish or fish that had escaped from the hatchery, were transferred alive upstream above the fence. All marked jacks and adults were sacrificed and sampled (fork length (cm), weight (g), sex, scale samples). The heads were removed, frozen, and retained for subsequent recovery of the nose tags. The returning fish were assigned to their appropriate release groups after inspection of the recovered tags.

Nose-tagged coho also were recovered from the commercial net and troll fisheries by random sampling of catches at a target intensity of 20% (Heizer et al. 1978). Estimates of numbers of fish caught from each tag group were obtained on the basis of the actual number of tagged fish recovered from the fisheries, the sampling effort, and the marked-to-unmarked ratio in the catches (Bilton 1980).

In addition, returns of tagged coho from sport catches were obtained through the Georgia Strait head recovery program (Argue et al. 1977). This program depends on voluntary return of heads from marked chinook and coho salmon by Georgia Strait and Strait of Juan de Fuca sport fishermen. To estimate the total number of tagged Rosewall Creek coho that contributed to the sport fishery we assumed that 28% of tagged fish caught would be recognized and reported. This "awareness factor," based on a number of values not directly measured, was assigned a value on the basis of area-by-area comparison with Puget Sound fisheries (Argue et al. 1977), and use of Puget Sound awareness factors for 1974 (Kimura 1976). Assumed Georgia Strait values can be referred to as Puget Sound equivalent awareness factors.

DATA COMPILATION

Percent return of mature fish — Total returns from the 57 groups of juveniles released were determined, as indicated, from the number of returning jacks and adults in the escapement and the numbers estimated to have been caught in the commercial and sport fisheries. Percent return, for each release group, was derived from the number of jacks and adults recovered in relation to the number of juveniles released (Table 1). The numbers of jacks and adults recovered

¹The European system of age designation (Koo 1962) is used in this report. The first digit indicates the number of annuli formed in fresh water and the second digit the number of annuli formed in the ocean. Hence a 1.0-fish returns in its 2nd yr (from hatching) after spending 1 yr in freshwater and part of 1 yr in the ocean. A 1.1-fish returns in its 3rd yr after spending 1+ yr in the ocean.

TABLE 1. Release and return data for tagged juvenile coho liberated from the original six pond populations, each population graded into three size groups: S, small; M, medium; L, large (see text). The four entries under each pond and size group represent, respectively: average juvenile weight (g) at release, percent return of adults, of jacks, and total return (adults plus jacks). Release dates, in Julian days, refer to the number of days elapsed from January 1, 1975.

Release date 1975	Size group	Pond populations					
		Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6
April 14 (Julian day 104)	S	5.1 g	9.0 g	9.2 g	7.0 g	9.6 g	10.6 g
		11.58	3.13	7.44	10.00	8.76	9.46
		0.08	0.12	0.00	0.00	0.21	0.11
		11.66	3.25	7.44	10.00	8.97	9.57
	M	8.1 g	11.6 g	12.9 g	9.6 g	12.6 g	14.2 g
		8.40	7.16	9.49	9.02	5.08	6.23
		0.08	0.21	0.25	0.19	0.08	0.14
		8.48	7.37	9.74	9.21	5.16	6.37
	L	10.9 g	15.4 g	16.1 g	13.3 g	16.7 g	18.8 g
		8.47	7.66	4.42	5.99	4.43	3.94
		0.34	0.30	0.62	0.17	0.96	0.62
		8.81	7.96	5.04	6.16	5.39	4.56
May 12 (day 132)	S	8.3 g	12.5 g	11.7 g	7.7 g	13.8 g	14.0 g
		15.91	15.98	13.83	16.00	12.39	19.02
		0.16	0.32	0.32	0.00	0.70	0.87
		16.07	16.30	14.15	16.00	13.09	19.89
	M	11.9 g	15.7 g	15.1 g	11.0 g	18.1 g	18.5 g
		14.65	18.67	17.62	16.65	15.54	16.47
		0.55	1.49	0.75	0.42	2.42	2.42
		15.20	20.16	18.37	17.07	17.96	18.89
	L	15.1 g	20.8 g	19.2 g	15.3 g	23.9 g	25.8 g
		13.61	15.77	12.48	17.28	13.72	15.66
		1.49	4.19	3.55	1.17	3.66	5.00
		15.10	19.96	16.03	18.45	17.38	20.66
June 10 (day 161)	S	12.3 g	15.6 g	14.4 g	12.3 g	17.3 g	17.6 g
		32.71	34.53	24.74	32.69	29.99	36.44
		0.00	0.24	0.07	0.11	0.07	0.25
		32.71	34.77	24.81	32.80	30.06	36.69
	M	16.0 g	20.1 g	18.9 g	16.3 g	22.1 g	23.6 g
		37.63	41.40	39.77	40.26	38.57	42.03
		0.54	0.89	0.83	0.49	1.36	1.26
		38.17	42.29	40.60	40.75	39.93	43.29
	L	20.2 g	28.3 g	25.1 g	19.9 g	28.7 g	31.8 g
		38.21	31.80	38.36	43.34	30.30	30.80
		2.67	4.48	5.00	2.15	6.16	7.42
		40.88	36.36	43.36	45.49	36.46	38.22
July 8 (day 189)	S	14.9 g					
		4.82					
		0.00					
		4.82					
	M	24.8 g					
		20.17					
		0.97					
		21.14					
	L	33.1 g					
		13.71					
		3.05					
		16.76					

in the escapement are highly reliable as it was possible to examine all fish in the escapement. Estimates of numbers of fish caught by the commercial fishery are considered reasonable but less certain. They arise from a consistent sampling effort carried out routinely in most commercial fishing areas over the fishing season, from which good estimates of the catches and marked-to-unmarked ratios were obtained. How-

ever, estimates of numbers of fish caught by the sport fishery (Bilton 1980) are considered lower in reliability. More recent evidence suggests the awareness factor for northern Georgia Strait (Fig. 1), an area adjoining the release location, may have been substantially lower than the equivalent Puget Sound awareness factor we used. Hence estimates of numbers of tagged coho caught by the sport fishery, as used herein,

TABLE 2. Release and return data for tagged juvenile coho liberated from six pond populations, each population graded into three size groups: S, small; M, medium; L, large (see text). The four entries under each pond and size group represent, respectively: average juvenile weight (g) at release, and biomass of adults, of jacks, and total biomass (adults plus jacks). Biomass (thousands of pounds) is based on pounds of returning fish per 100 000 juveniles released. Release dates, in Julian days, refer to the number of days elapsed from January 1, 1975.

Release date 1975	Size group	Pond populations						
		Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6	
April 14 (Julian day 104)	S	5.1 g	9.0 g	9.2 g	7.0 g	9.6 g	10.6 g	
		55.71	23.17	43.09	54.77	45.82	53.79	
		0.08	0.13	0.00	0.00	0.30	0.16	
	M	55.79	23.30	43.09	54.77	46.12	53.95	
		8.1 g	11.6 g	12.9 g	9.6 g	12.6 g	14.2 g	
		49.33	42.89	50.61	47.23	28.81	44.81	
	L	0.08	0.22	0.28	0.16	0.12	0.19	
		49.41	43.11	50.89	47.39	28.93	45.00	
		10.9 g	15.4 g	16.1 g	13.3 g	16.7 g	18.8 g	
	May 12 (day 132)	S	57.31	49.45	21.33	32.36	30.73	28.24
			0.36	0.32	0.70	0.14	1.34	0.85
			57.67	49.77	22.03	32.50	32.07	29.09
M		8.3 g	12.5 g	11.7 g	7.7 g	13.8 g	14.0 g	
		88.41	100.90	84.65	84.97	78.52	117.33	
		0.14	0.37	0.37	0.00	0.88	0.98	
L		88.55	101.27	85.02	84.97	79.40	118.31	
		11.9 g	15.7 g	15.1 g	11.0 g	18.1 g	18.5 g	
		88.24	120.70	106.93	94.36	101.36	110.50	
June 10 (day 161)		M	0.49	1.70	0.87	0.37	2.88	3.01
			88.73	122.40	107.80	94.73	104.24	113.51
			15.1 g	20.8 g	19.2 g	15.3 g	23.9 g	25.8 g
	L	78.65	113.50	81.12	102.55	97.01	107.06	
		1.51	5.05	4.61	1.11	4.71	6.36	
		80.16	118.55	85.73	103.66	101.72	113.42	
	July 8 (day 189)	S	12.3 g	15.6 g	14.4 g	12.3 g	17.3 g	17.6 g
			161.82	173.45	131.19	151.78	147.40	199.50
			0.00	0.20	0.06	0.08	0.06	0.20
		M	161.82	173.65	131.25	151.86	147.46	199.70
			16.0 g	20.1 g	18.9 g	16.3 g	22.1 g	23.6 g
			185.71	214.06	205.79	201.51	206.58	226.38
L		0.42	0.72	0.72	0.34	1.16	1.04	
		186.13	214.78	206.51	201.85	207.74	227.42	
		20.2 g	28.3 g	25.1 g	19.9 g	28.7 g	31.8 g	
S		199.75	179.00	211.77	216.11	163.43	169.42	
		1.93	3.67	4.25	1.65	5.30	6.19	
		201.68	182.67	216.02	217.76	168.73	175.61	
	14.9 g							
	21.0							
	0.00							
M	21.10							
	24.8 g							
	88.32							
	0.55							
	88.87							
	33.1 g							
L	61.38							
	1.79							
	63.17							

probably are conservative.

Biomass of mature fish returns — Estimates of biomass of returning fish from each of the 57 release groups (Table 2) were computed as thousands of pounds (1 kg = 2.2 lb) per 100 000 juveniles released. These estimates are based on (1) rate of return of jacks and adults from the 57 release groups (Table 1); (2) proportionally, the numbers that would have

returned if 100 000 juveniles had been released in each of the 57 groups; and (3) the final average weight of jacks and of adults for each of the release groups sampled in the escapement. The latter calculation uses the weight of fish returning to the fence as a standard. It would be unbiased if none of the fish were caught in the fishery, and all were free to return to the hatchery. The estimated biomass of jacks originating from

TABLE 3. Release and return data for tagged juvenile coho liberated from six pond populations, each population graded into three size groups: S, small; M, medium; L, large (see text). The four entries under each pond and size group represent, respectively: average juvenile weight (g) at release, and benefit-cost ratios for returns of adults, of jacks, and for total returns (adults plus jacks). Benefit-cost ratios are based on the value of returns (\$Can/lb) relative to production costs (\$Can/100 000 juveniles) to time of release. Release dates, in Julian days, refer to the number of days elapsed from January 1, 1975.

Release date 1975	Size group	Pond populations					
		Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6
April 14 (Julian day 104)	S	5.1 g	9.0 g	9.2 g	7.0 g	9.6 g	10.6 g
		9.569	2.255	4.103	6.854	4.181	4.446
		0.014	0.013	0.000	0.000	0.027	0.013
		9.583	2.268	4.103	6.854	4.208	4.459
	M	8.1 g	11.6 g	12.9 g	9.6 g	12.6 g	14.2 g
		5.336	3.239	3.437	4.310	2.003	2.765
		0.009	0.016	0.019	0.015	0.008	0.012
		5.345	3.255	3.456	4.325	2.011	2.777
	L	10.9 g	15.4 g	16.1 g	13.3 g	16.7 g	18.8 g
		4.606	2.813	1.161	2.131	1.612	1.316
		0.029	0.018	0.038	0.009	0.070	0.040
		4.635	2.831	1.199	2.140	1.682	1.356
May 12 (day 132)	S	8.3 g	12.5 g	11.7 g	7.7 g	13.8 g	14.0 g
		11.383	8.627	7.732	11.793	6.081	8.956
		0.019	0.031	0.034	0.000	0.068	0.075
		11.402	8.658	7.766	11.793	6.149	9.031
	M	11.9 g	15.7 g	15.1 g	11.0 g	18.1 g	18.5 g
		7.925	8.216	7.568	9.168	5.985	6.383
		0.044	0.116	0.061	0.036	0.170	0.174
		7.969	8.332	7.629	9.204	6.155	6.557
	L	15.1 g	20.8 g	19.2 g	15.3 g	23.9 g	25.8 g
		5.566	5.832	4.515	7.163	4.334	4.435
		0.107	0.259	0.256	0.078	0.211	0.264
		5.673	6.091	4.771	7.241	4.545	4.699
June 10 (day 161)	S	12.3 g	15.6 g	14.4 g	12.3 g	17.3 g	17.6 g
		17.325	14.642	11.998	16.250	11.220	14.927
		0.000	0.016	0.006	0.009	0.004	0.015
		17.325	14.658	12.004	16.259	11.224	14.942
	M	16.0 g	20.1 g	18.9 g	16.3 g	22.1 g	23.6 g
		15.285	14.024	14.339	16.280	12.309	12.632
		0.035	0.047	0.050	0.028	0.069	0.058
		15.320	14.071	14.389	16.308	12.378	12.690
	L	20.2 g	28.3 g	25.1 g	19.9 g	28.7 g	31.8 g
		13.022	8.329	11.110	14.301	7.499	7.016
		0.126	0.171	0.223	0.109	0.243	0.256
		13.148	8.500	11.333	14.410	7.742	7.272
July 8 (day 189)	S	14.9 g					
		2.165					
		0.000					
		2.165					
	M	24.8 g					
		5.445					
		0.034					
		5.479					
	L	33.1 g					
		2.835					
		0.083					
		2.918					

each release group is considered highly reliable as virtually all are considered to have been recovered. Only small numbers of jacks were estimated to have been taken by the fishery in the year of release; estimates ranged from 4 to 83 fish for the various release groups (Bilton 1980). On the other hand, final average weight of the adults escaping to the fence likely

overestimates the biomass of adults actually produced from each release group. Weights of adults taken in the fishery would have been lower, particularly for those fish caught early in the season when the fish would be smaller.

Benefit-cost ratios — Estimated benefit-cost ratios for returning jacks and adult coho were calculated for the value

of returns relative to the costs incurred in rearing the fish at the experimental hatchery (Table 3). A simplified benefit-cost relation is used; its main function is to provide a relative comparison of returns among the 57 tagged groups released. Estimates of benefit or value were derived as follows: (1) from the escapement, estimates were obtained of the expected biomass (per 100 000 juveniles released) of returning adults and jacks from each release group (Table 2); (2) the returning poundage of adults and jacks was assigned a single value of \$0.90 Can./lb at the hatchery weir. Hence, benefits were calculated by multiplying the poundage of adults or jacks by the single rate of \$0.90/lb. These estimates of benefit are conservative, underestimating the true value of returns taken by the commercial and sport fisheries.

Estimates of production costs at the experimental hatchery were derived as follows: (1) costs per pound of juveniles reared, excluding capital costs, were accumulated to each release date; (2) the estimated weight per 100 000 juveniles was computed from the mean juvenile weights for each release group. From these figures the noncapital operating costs of production were estimated (Bilton and Jenkinson 1976) to be \$4.66 Can. (per pound) for the April release, \$3.82 for May, \$3.10 for June, and \$2.67 for July. Over the total period of culture there was an increase per fish in the cost of rearing. However, this increase was offset by higher food conversion efficiency in the latter months of culture so that the cost of production per pound of juveniles declined between the first and final releases. The estimates of cost, based on releases from an experimental hatchery, may not truly represent the costs incurred in a production hatchery. However, discussions with production hatchery personnel suggest the estimates presented here are not unreasonable.

The benefit-cost ratios were derived through division of the calculated benefits by the estimated production costs. For example, for every dollar spent in producing 5.1-g juveniles for release in April there was a yield of \$9.57 Can. in terms of adult flesh produced (Table 3). The estimates of value per pound of adult flesh produced are considerably lower than the true value realized by the fisheries. Hence the benefit-cost ratios, calculated from these data, must be viewed as conservative in absolute value.

Analytical Methods

RESPONSE SURFACE METHODS

The design and results of the entire experiment are summarized in Tables 1-3. For each of the 57 releases, the (Julian) release date, x_1 , is shown along with mean juvenile weight at release, x_2 , in grams. These two variables are considered control variables; potentially they may be controlled, at least to some extent, in the hatchery. Nine possible responses to these controls are listed (Table 4), as measured in this experiment.

Sophisticated analysis hardly is necessary to prove that manipulating time and size at release (x_1, x_2) has an effect on the responses y_j ($j = 1, 2, \dots, 9$). For example consider y_1 , the percentage of smolts returning as adults. Table 1 shows that the April release resulted in returns of 3.13-11.58%, the May release gave increased returns of 12.39-19.02%, and the June release led to still greater returns of 24.74-43.34%.

Finally, the July release gave reduced returns in the range of 4.82-20.17%. Obviously, release time affects adult returns and an analysis of the variance of y_1 , in relation to the four release dates (analysis not given here), would easily prove the point.

Although the experiment was designed with analysis of variance in mind, conventional ANOVA is insufficient to capture the structure that the data suggest. Not only do differences in time of juvenile release appear to affect the outcome, they also appear to have a *systematic* effect. As the release data is delayed into June, the results increase steadily; yet further delay into July appears detrimental. Similarly, although perhaps less clearly, there appears to be a size effect. In June, for example, the juveniles most productive of adults come from the middle of the size range, whereas both smaller and larger juveniles give somewhat smaller returns.

The standard method for modeling such consistent effects of the control variables x_1 and x_2 on a response y is to fit a suitable response function to the data

$$(1) \quad y = f(x_1, x_2).$$

In the present context, an increase in x_1 or x_2 typically is beneficial to the response at first, but eventually further increase becomes detrimental. The modified quadratic surface

$$(2) \quad y = b_0 + b_1x_1^{\alpha_1} + b_2x_2^{\alpha_2} + b_{11}x_1^{2\alpha_1} + b_{12}x_1^{\alpha_1}x_2^{\alpha_2} + b_{22}x_2^{2\alpha_2}$$

can exhibit just such behavior, so it is reasonable to choose model (2) as a model for the data at hand. There is extensive literature on this particular function (reviewed in Lindsey et al. 1970).

In practice, model (2) commonly is viewed as the final possibility in a hierarchy of models. These include, for example, the quadratic surface

$$(3) \quad y = b_0 + b_1x_1 + b_2x_2 + b_{11}x_1^2 + b_{12}x_1x_2 + b_{22}x_2^2$$

with $\alpha_1 = \alpha_2 = 1$, and the constant surface

$$(4) \quad y = b_0.$$

where all b 's except b_0 are equal to zero. An analysis of variance (given later) can be used to determine which of the models within the hierarchy should be adopted. Because the final model (4) is independent of x_1 and x_2 , it can be taken as a null hypothesis to be rejected if, in fact, the control variables influence the response y .

To estimate the parameters in models (2), (3), or (4) and to complete the variance analysis just described, it is necessary to introduce an assumption on the nature of statistical error in the response. The most common assumption is that errors enter additively, so that model (2) is replaced by

$$(5) \quad y_i = b_0 + b_1x_{1i}^{\alpha_1} + b_2x_{2i}^{\alpha_2} + b_{11}x_{1i}^{2\alpha_1} + b_{12}x_{1i}^{\alpha_1}x_{2i}^{\alpha_2} + b_{22}x_{2i}^{2\alpha_2} + \epsilon_i$$

where i (from 1 to 57) indexes the observations and ϵ_i is the random deviation of the response from the model. (The index j from 1 to 9, corresponding to different responses, is sup-

TABLE 4. Responses investigated, and their notations (y_1, \dots, y_9), in relation to the control variables of time (x_1 , Julian days) and size (x_2 , g) at juvenile release. Table numbers in the third column refer to the tables in which the original data are tabulated.

Notation	Response	Table
y_1	Adult returns (%)	1
y_2	Jack returns (%)	1
y_3	Total returns (adults and jacks) (%)	1
y_4	Adult biomass (lb/100 000 juveniles)	2
y_5	Jack returns (lb/100 000 juveniles)	2
y_6	Total biomass (adults and jacks) (lb/100 000 juveniles)	2
y_7	Benefit-cost ratio, adult returns	3
y_8	Benefit-cost ratio, jack returns	3
y_9	Benefit-cost ratio, total (adult and jack) returns	3

pressed here.) The ϵ 's are assumed to be independently normally distributed with mean 0 and standard deviation σ . This error model at best is only approximately correct for the present data. For example, Table 1 shows instances in which y_2 (% returning jacks) is 0%. If the errors were truly additive, then y_2 with finite probability could take negative values, but such values are impossible. Because of this problem, model (5) should be regarded as an appropriate description of error structure only where the response is significantly different from zero. For the practitioner this is not a troublesome restriction, as only significantly nonzero responses are of real interest.

The maximum likelihood criterion applied to model (5) leads to a least squares regression to estimate the eight unknown parameters $b_0, b_1, b_2, b_{11}, b_{12}, b_{22}, \alpha_1$, and α_2 . This regression is linear for the first six parameters, but nonlinear in the exponents α_1 and α_2 . Appendix A describes the method used for solving the nonlinear regression problem whereby estimates are obtained for all eight parameters. There, problems with nonunique solutions are also discussed, and an estimate is provided for σ , the standard deviation of responses from the model.

SURFACE OPTIMA

Once a response function is found that fits the data, it can be used to assess the nature of the system's response to control. In the present context, a key feature is the locus at which a maximum response y is achieved. At such a point the slope is zero; that is, the two equations.

$$(6) \quad \frac{\partial y}{\partial x_1} = 0, \quad \frac{\partial y}{\partial x_2} = 0$$

are satisfied. The criteria (6) characterize not only maxima, but also minima and saddle points of the surface. The latter, saddle point or minimax, is a stationary point lying on a col between ascending ridges and descending valleys of a surface. The response function (4) almost always has a critical point (x_{1s}, x_{2s}) where (6) is satisfied. Its coordinates can be determined by the formulas

$$(7) \quad \begin{aligned} x_{1s}^{\alpha_1} &= (b_2 b_{12} - 2b_1 b_{22})/c, \\ x_{2s}^{\alpha_2} &= (b_1 b_{12} - 2b_2 b_{11})/c, \end{aligned}$$

where

$$c = 4b_{11}b_{22} - b_{12}^2.$$

This point corresponds to a maximum if $c > 0$ and $b_{11} < 0$, a minimum if $c > 0$ and $b_{11} > 0$, and a saddle point if $c < 0$. Proofs for these relations are given in Appendix B.

Theoretically it is possible that $c = 0$, whence formulas (7) are undefined. In practice this does not happen because c is a statistic (computed from estimates for b_{11}, b_{12} , and b_{22}), which takes the precise value 0 with probability 0. More realistically c may be small and, as a result, the estimates for x_{1s} and x_{2s} are large and outside the range of the observed data. The correct interpretation for this outcome is simply that the data indicate a trend in response but do not suggest that a critical point will be found within the observed range. A related difficulty is that the right-hand sides of (7) may be negative. In that instance we adopt the convention, used throughout, that " x^{α} " simply means " x^{α} " when $x > 0$, but " $-|x|^{\alpha}$ " when $x < 0$.² This allows (7) to have negative solutions for x_{1s} or x_{2s} . Again, the correct interpretation is that the data indicate trends with no critical point located within the observed range.

JOINT OPTIMALITY

In this paper we are concerned with nine possible responses y . The critical points (7) in fact are different for each response. It happens, for example, that the optimum conditions of time and size at release for adult survival are not the same as those maximizing the benefit-cost ratio. In such instances, sometimes it is appropriate to consider points of joint optimality for two objective functions y_a and y_b . Any such point (x_1, x_2) is determined by maximizing (or minimizing) y_b on a fixed (suboptimal) contour for y_a . In other words the joint optimality point (x_1, x_2) makes the response y_b as high as possible for a given suboptimal locus associated with y_a . We call the collection of all such points a *path of joint optimality*.

²However the expression $x^{2\alpha}$ in (2) is interpreted as $(x^{\alpha}) \cdot (x^{\alpha})$, and therefore it is always positive. This interpretation comes from viewing (2) as a variation of (3) in which x_1 and x_2 have been transformed exponentially, utilizing the convention given. Hence the convention, standard when α is an odd integer but not otherwise, extends the response function (2) to unrealistic values $x_1 < 0$ and $x_2 < 0$ in such a way that (i) the function (2) is consistent with (1), and (ii) the equations (7) always have real solutions (x_{1s}, x_{2s}) consistent with global trends in the function (2).

TABLE 5. Least squares estimates for the power parameters (α_1, α_2) and coefficients (b_0, \dots, b_{22}) of the second-order polynomial (text equation 5) used to model nine responses (y_1 to y_9) of coho salmon with respect to time (x_1) and size (x_2) at juvenile release. The estimated critical point (x_{1c}, x_{2c}) is shown for each surface, along with the estimate of critical response, y_c , at that point. Bracketed critical points lie outside the observed range of the data.

Parameter estimates	y_1 , returns, adults only (%)	y_2 , returns, jacks only (%)	y_3 , returns, all fish (%)	y_4 , biomass, adults only (lb)	y_5 , biomass, jacks only (lb)	y_6 , biomass, all fish (lb)	y_7 , benefit-cost, adults only	y_8 , benefit-cost, jacks only	y_9 , benefit-cost, all fish
α_1	6.6890	1	6.4175	5.5270	1	5.4981	4.9443	1	4.8655
α_2	2.7113	4.0875	3.1129	2.8412	3.4257	2.9310	0.8876	2.9875	0.8129
b_0	4.0329	-9.7089	3.5769	1.2971 $\times 10^4$	-1.0021 $\times 10^4$	1.2845 $\times 10^4$	6.6998	-7.0353 $\times 10^{-1}$	6.966
b_1	7.7068 $\times 10^{-14}$	1.5024 $\times 10^{-1}$	3.1742 $\times 10^{-13}$	1.6297 $\times 10^{-7}$	1.5270 $\times 10^2$	1.8941 $\times 10^{-7}$	2.7016 $\times 10^{-10}$	1.0917 $\times 10^{-2}$	4.0476 $\times 10^{-10}$
b_2	1.0322 $\times 10^{-3}$	1.9425 $\times 10^{-5}$	4.5079 $\times 10^{-4}$	5.6882	2.1770 $\times 10^{-1}$	4.6135	-5.0750 $\times 10^{-1}$	3.1404 $\times 10^{-5}$	-6.3297 $\times 10^{-1}$
b_{11}	-4.712 $\times 10^{-29}$	-5.5988 $\times 10^{-4}$	-7.9545 $\times 10^{-28}$	-4.4500 $\times 10^{-20}$	5.7216 $\times 10^{-1}$	-5.9997 $\times 10^{-20}$	-1.6592 $\times 10^{-21}$	-4.1234 $\times 10^{-5}$	-3.7877 $\times 10^{-21}$
b_{12}	1.8568 $\times 10^{-18}$	-7.3261 $\times 10^{-8}$	1.5437 $\times 10^{-18}$	2.6329 $\times 10^{-12}$	-9.5931 $\times 10^{-4}$	2.1286 $\times 10^{-12}$	5.0259 $\times 10^{-12}$	-1.0231 $\times 10^{-7}$	9.8326 $\times 10^{-12}$
b_{22}	-2.2183 $\times 10^{-7}$	-1.7372 $\times 10^{-12}$	-1.3883 $\times 10^{-8}$	-5.6159 $\times 10^{-4}$	-1.0655 $\times 10^{-7}$	-3.0442 $\times 10^{-4}$	-1.5611 $\times 10^{-2}$	-1.9205 $\times 10^{-10}$	-2.6990 $\times 10^{-2}$
$x_{1c}(d)$	173.2	(610.2)	172.7	170.0	(260.6)	169.9	(158.4)	(46.2)	(158.1)
$x_{2c}(g)$	25.1	(-47.7)	27.1	25.6	(-32.5)	26.0	(-5.0)	(41.7)	(-3.2)
y_c	43.5 ^a	(-34.5) ^b	46.2 ^a	215.0 $\times 10^3$ ^a	(-6.637 $\times 10^3$) ^b	218.0 $\times 10^3$ ^a	(17.90) ^a	(0.64) ^a	(17.92) ^a

^aMaximum point.
^bSaddle point.

for y_a and y_b . Geometrically, it turns out that points on this path correspond to points where the respective contours for y_a and y_b are tangent to one another.

In practice, the path of joint optimality can be useful in resolving the conflict where the critical points (x_{1c}, x_{2c}) differ for two responses y_a and y_b . As both optima cannot be achieved simultaneously, it is reasonable to select points that optimize the trade-off between them. Given that the responses y_a and y_b are of primary importance, the control variables (x_1, x_2) should at least be restricted to the path of joint optimality between them. Where a particular point is chosen on this path, and whether it is closer to the critical point or optimum y_a or y_b , depends on a decision regarding the relative importance of y_a or y_b .

Unfortunately, points of joint optimality cannot be expressed by simple formulas similar to (7). They must be determined by a recursive nonlinear estimation process (Appendix C).

INTERPRETATION OF THE ANALYSES

Use of response surface analysis leads to two further questions: (i) interpretation of the resulting surfaces, and (ii) assessment of their credibility. The first question pertains to surface shape or topology; the second involves analysis of variance. These aspects of the analysis are considered in relation to specific problems posed by the present data.

Surface shapes — Table 5 lists the complete set of estimates computed for the parameters in model (5). Estimates of the response functions y_1 to y_9 , along with the critical point for each surface obtained from (7), were calculated from the data in Tables 1–3 (for computational detail, see Appendix A). The critical points (Table 5) are of four types: (i) a maximum within the observed range of the data (y_1, y_3, y_4, y_6), (ii) a maximum below the observed range in the x_1, x_2 -plane (y_7, y_9), (iii) a saddle to the lower right of the observed range (y_2, y_5), and (iv) a maximum to the upper left (y_8).

These results can be interpreted in light of the contour plots shown in Fig. 2. There, three types of surface shape may be identified: (a) a surface with a peak within the observed x_1, x_2 -range (Fig. 2) (y_1, y_3, y_4, y_6); (b) a ridge ascending toward the bottom of the figure (y_7, y_9); and (c) a ridge ascending to the upper left from a flat area with response near zero at the bottom of the figure (y_2, y_5, y_8). The peaks in (a) obviously match the maxima (i) just described. Similarly the ridges (b) match (ii) in the sense that the ridges appear to rise toward theoretical maxima below the x_1, x_2 -range. Finally, the ridges (c) match (iii) and (iv); the ridges appear to rise toward a theoretical maximum in the upper left or they may rise from

FIG. 2. Influence of time of release (Julian days) and mean size at release (g) of juvenile coho salmon on returns at maturity (to the fence and commercial and sport fisheries): percent return of (a) y_1 , adults, (b) y_2 , jacks, (c) y_3 , adults plus jacks; biomass of returns in thousands of lb per 100 000 juveniles released for (d) y_4 , adults, (e) y_5 , jacks (f) y_6 , adults plus jacks; benefit-cost ratios for returns of (g) y_7 , adults, (h) y_8 , jacks, (i) y_9 , adults plus jacks. Contours in each panel are based on equation (5) (see text) for which estimates of the parameters are listed in Table 5. In (a) the ridge of optimum release weight refers to sizes (g) at release predicted to give maximum returns for given release times; in (a), (c), (d), and (f) maximum response on the surface (y_c) is at the critical point (x_{1c}, x_{2c}).

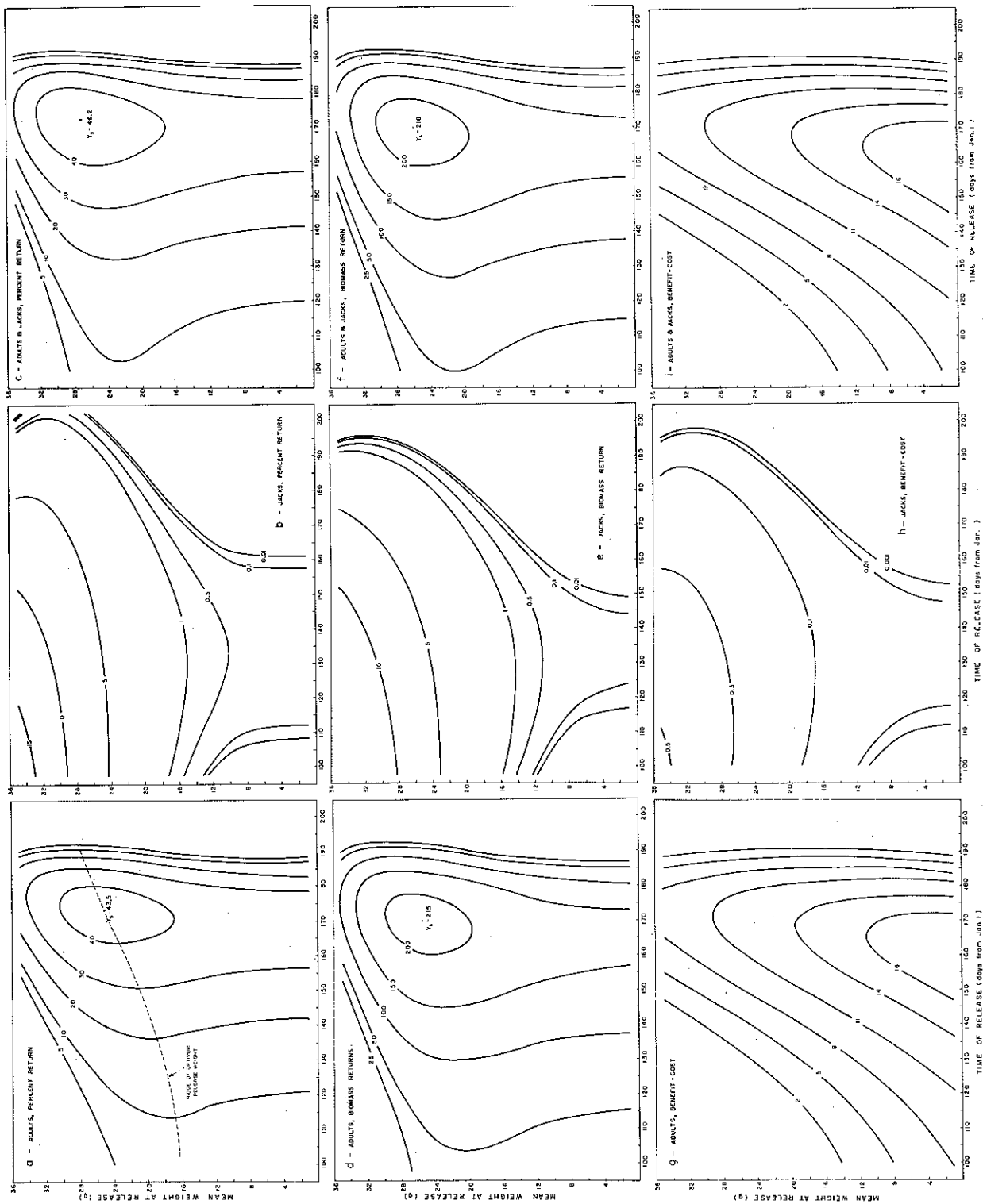


TABLE 6. Unexplained variances for three models of the general form of equation (5) used to describe the responses of coho salmon to time and size at juvenile release. The first model assumes no direct time-size effect ($b_1, \dots, b_{22} = 0$); b_0 is the mean of y for all observations. The second model assumes a time-size effect with $\alpha_1 = \alpha_2 = 1$; the third assumes an effect with α_1, α_2 as given in Table 5. Standard deviations (σ) refer to deviations between observed and predicted values. Variance refers to total sums of squares of deviations from the data points.

Model	Estimate	y_1	y_2	y_3	y_4	y_5	y_6	y_7	y_8	y_9
Only $b_0 \neq 0$; remaining b 's set to zero (56 df)	b_0 (mean)	19.20	1.26	20.46	105.8×10^3	1249	107.1×10^3	7.73	0.0690	7.80
	$\hat{\sigma}$	12.36	1.72	12.96	62.2×10^3	1705	62.7×10^3	4.53	0.0792	4.53
$\alpha_1 = \alpha_2 = 1$ (51 df)	Variance	8559.2	165.69	9409.8	216.78×10^6	162.86×10^6	220.25×10^6	1151.3	0.35155	1148.4
	$\hat{\sigma}$	6.95	0.70	6.95	32.5×10^3	739	32.4×10^3	2.48	0.0413	2.47
α_1, α_2 as shown in Table 5 (49 or 50 df)	Variance	2461.3	24.76	2463.1	53.95×10^6	30.65×10^6	53.57×10^6	314.2	0.08681	310.8
	$\hat{\sigma}$	3.21	0.63	3.29	16.9×10^3	708	16.9×10^3	1.38	0.0394	1.38
	Variance	506.2	19.87	531.2	13.93×10^6	25.09×10^6	13.92×10^6	93.1	0.0778	93.1

a saddle in the lower part of the figure. For any of these surface shapes, the data indicate either a maximum response or a trend in response within the tested x_1, x_2 -range. Maxima outside the tested range have no valid interpretation except as indicators of trend.

Variance — Table 6 presents variance information that can be used to assess how well the response functions estimated in Table 5 explain the experimental observations of Tables 1-3. Three possible response models are considered. The first assumes that the observed response (57 observations for each function) bears no relation to time and size at juvenile release. Such a model would be given by equation (5) with $b_1, b_2, b_{11}, b_{12},$ and b_{22} all taken to be zero. In this case, b_0 simply corresponds to the mean observed response. The second model (Table 6) is the special case of (5) obtained with $\alpha_1 = \alpha_2 = 1$. This model corresponds to a response dependent on time and size at juvenile release with elliptical (or hyperbolic) contours. Finally, the third model is (5) with α_1 and α_2 values as in Table 5. This model is characterized by distorted elliptical (or hyperbolic) contours as in Fig. 2.

Each of the models has an associated number of degrees of freedom (df). In the first model there are 57 observations with one parameter (b_0) estimated, leaving 56 df. In the second model all six b 's are estimated, leaving 51 df. In the third model one or both α 's also are estimated, leaving 50 or 49 df. The unexplained variances in Table 5 all represent the total sum of squares (for 57 points) of deviations between observations and model predictions. The square root of the ratio of variance to df-number gives the estimated standard deviation $\hat{\sigma}$ in each case (see equation A6, Appendix A).

As an example of the use of these variances for assessing model validity, consider the percentage of juveniles that survive as adults (y_1). Mean survival is 19.20%, with a standard deviation of 12.36% and total variance of 8559.2 (units of percent squared). With model (5), assuming $\alpha_1 = \alpha_2 = 1$, the unexplained variance is reduced to 2461.2. With $\alpha_1 = 6.6890$ and $\alpha_2 = 2.7113$ (Table 5, column 2), the unexplained variance is reduced further to 506.3. The F -statistic used to reject the first model (Table 6) in favor of the final one is

$$((8559.2 - 506.2)/506.2) \times (49/(56 - 49)) = 111.4$$

with 7 and 49 df. Given these degrees of freedom, the upper limit of tabled F -values at the 5% level is 2.21; at the 1% level it is 3.01 and at the 0.1% level it is 4.24. Because the observed F -value is very much larger than any of these, there is almost no possibility that so large a difference could have occurred by chance. Intuitively, because the third model (Table 6) explains so much of the original variance with only seven additional parameters, it must be accepted. This confirms statistically not only that both time and size at juvenile release influence survival, but also that the model (5) expresses the survival response rather well.

The estimated standard deviation, $\hat{\sigma} = 3.21\%$ in this instance, suggests that points on the response surface are known to within about

$$\pm 1.96 \times 3.21\% = \pm 6.3\%$$

at the 95% confidence level. This result can be used to assess

the precision of the contours in Fig. 2 (y_1 , panel 1). For example, an observed response of 30% might be expected when the predicted response lies between 23.7% and 36.3%. Hence, the contours themselves provide approximate confidence limits for each other. (This statistical approximation is valid only within the range of the observed data.) In the vicinity of the response maximum (y_s) at the critical point, only one-sided confidence limits are appropriate. Thus an observed response of 40% might be expected anywhere within the predicted 33.7% contour; consequently that contour may be used to define an approximate confidence region for the predicted maximum response on the surface. Incidentally, the highest observed adult survival (Table 1) is 43.34% on day 161, with a mean weight of 19.9 g at juvenile release. Predicted adult survival y_1 for these conditions is 37.37%.

In Table 6 the response functions y_3 , y_4 , y_6 , y_7 , and y_9 all lead to variance analyses similar to that described for y_1 . The version of model (5) with $\alpha_1 = \alpha_2 = 1$ explains about 75% of the original variance. If α_1 and α_2 are allowed to move to their estimated values in Table 5, ~75% of the remaining variance again can be explained. The final model explains over 90% of the original variance.

By contrast, the functions y_2 , y_5 , and y_8 , all pertaining to response of the jacks, give somewhat different results. Model (5) with $\alpha_1 = \alpha_2 = 1$ still explains over 75% of the original variance; however, the improvement possible by allowing arbitrary values of α_1 and α_2 is not so great as before. In all instances there is some advantage to be gained in allowing free values for α_2 , but almost no improvement is obtained by freeing α_1 . For y_2 this situation is summarized as follows:

α_1	α_2	Unexplained variance of y_2
1	1	24.76
1	4.0875	19.87
0.55293	4.2521	19.74

The third entry, although a slight improvement on the second, does not represent enough variance reduction to justify freeing the parameters α_1 . For that reason, the second entry is used and not the third, as shown in Tables 5 and 6. In practice the nonlinear search algorithm employed had difficulty locating the result shown in the third entry as the sum of squares changed only slightly for rather large changes in α_1 .

Results

PERCENT RETURN OF MATURE FISH

For adult returns (Fig. 2a), the predicted maximum return at the center of the surface (y_s) is 43.5%, corresponding to release on day 173.2 (June 22, 1975) at a mean juvenile weight of 25.1 g (Table 5). The standard deviation for percent return of adults (y_1) over the surface is $\pm 3.21\%$ (Table 6) and the contours are known with a precision of about $\pm 6.3\%$ ($P = 0.05$). The surface also shows an interaction between time of release and size at release with respect to the magnitude of adult returns. In Fig. 2a this can be illustrated as follows. A curve drawn to connect the points at which tangents to the surface contours are parallel to the axis of mean weight ($\partial y_1 / \partial x_2 = 0$, equation (5)) provides estimates of release weights for which percent return of adults is maximized

maximized for specified release times. Hence, from the figure, maximum returns are predicted to occur from early release of smaller juveniles and later release of larger juveniles. For the four Julian days of Table 1 (day 104, 132, 161, 189), these approximate weights are, respectively, 16–17, 18–19, 22–23, and 27–28 g. The surface also indicates that returns from releases made after approximately day 180 (June 29, 1975) can be expected to drop sharply whatever the mean size at release may be. From a practical viewpoint, a fish culturist might enquire about the width of the time "window" through which juveniles might be released with high expectation of adult returns. It is assumed that one would wish to avoid the portion of the surface to the right of y_s , where predicted returns drop sharply at later release dates. One also might define the 40% contour as the boundary for acceptable returns. Recognizing that this contour is known with a precision of about $\pm 6.3\%$, one might find in some trials aimed at a 40% return that the actual returns would be as low as 34%. Interpolating, this contour could be associated with a release time at about day 163. Hence, one would conclude that fish of 22–25 g mean weight could be released between days 163 and 173 with expectations of high (40% or greater) adult returns.

For returns of jacks (Fig. 2b), predicted values on the surface increase from low mean weights over a broad range of release times toward higher mean weights at early release dates. The ridge associated with this trend ($\partial y_2 / \partial x_1 = 0$) is of particular interest; it implies that *greater returns of jacks may be expected from early release of larger juveniles*. Overlaying the surface for jack returns (Fig. 2b) on that for adult returns (Fig. 2a) indicates that jack returns of about 1–5% would be expected in association with maximum and near-maximum (40% or greater) returns of adults. The standard deviation over the surface for jack returns is about $\pm 0.63\%$ (Table 6). Hence the contours are known with a precision of about $\pm 1.2\%$ ($P = 0.05$).

For the return of all fish, adults and jacks combined (Fig. 2c), the predicted maximum return at the center of the response surface (y_s) is 46.2%, corresponding to release on day 172.7 (June 22, 1975) at a mean juvenile weight of 27.1 g. The standard deviation for percent return of all fish (y_3) over the surface is $\pm 3.3\%$ (Table 6). Hence, the contours are known with a precision of about $\pm 6.5\%$ ($P = 0.05$). Comparison of the surface for percent return of all fish with that for adults only shows them to be very similar in shape. The predicted maximum response in both instances is achieved on about the same date of juvenile release, but expected maximum returns of all fish are realized from release of juveniles of a slightly larger predicted mean size of 27.1 g (Table 5). For returns of all fish there also is an interaction between time and size at juvenile release similar to that seen on the surface for adult returns (Fig. 2a).

BIOMASS OF RETURNS

For returns in terms of adult biomass (Fig. 2d) the predicted maximum response at the center of the surface (y_s) is 215 thousand lb per release of 100 000 juveniles. The center (y_s) corresponds to release of juveniles on day 170.0 (June 19, 1975) at a mean weight of 25.6 g. The standard deviation of adult biomass (y_4) over the surface is ± 16.9 thousand lb

(Table 6), and the surface contours are known with a precision of about ± 33.1 thousand lb ($P = 0.05$). The shape of the surface and the interaction between time of release and mean juvenile weight at release again are similar to those for y_1 and y_3 (Fig. 2a, 2c). The shape of the surface for y_4 indicates that maximum adult biomass is expected from early release of smaller juveniles and later release of larger juveniles, the interaction involved being similar to that for percent return of adults.

For biomass of returning jacks (Fig. 2c), predicted values on the surface increase from low mean release weights over a range of release times toward higher mean weights at early release dates. The shape of the surface and the interaction between release times and mean release weights are similar to those for percent return of jacks (Fig. 2b). Hence the conditions at release associated with higher percent return of jacks are those leading to greater biomass of returning jacks, as might be expected. The standard deviation over the surface for biomass of jack returns is about ± 708 lb (Table 6). Hence the contours are known with a precision of about ± 1.39 thousand lb ($P = 0.05$).

For the biomass of returns of all fish, combining adults and jacks (Fig. 2f), the predicted maximum (y_6) at the center of the response surface is 218 thousand lb per 100 000 juveniles released. The surface center corresponds to a release of juveniles on day 169.9 (June 19, 1975) at a mean weight of 26.0 g. The standard deviation for total biomass of returns (adults plus jacks) (y_6) over the surface is ± 16.9 thousand lb (Table 6); the surface contours are known with a precision of about ± 33.1 thousand lb ($P = 0.05$). Predicted maximum biomass of all fish is very similar to that for adult biomass, and is achieved on the same date of release of juveniles of approximately the same size.

BENEFIT-COST RATIOS

The benefit-cost surfaces, relating production costs to the value of returning biomass for given times and mean sizes at juvenile release, are similar for adults (y_7) and for adults and jacks combined (y_8) (Fig. 2g, 2i). In both figures there is a rising ridge showing a trend toward increasing benefit-cost ratios extending from later release of larger juveniles toward earlier release of smaller fish. In both instances the presumed maximum response on the surface lies outside the range of the data at negative release weights near day 158 (Table 5). Obviously the estimates of the surface centers are extrapolated values, and should be viewed only as indicative of trends. A biological interpretation of the location of the surface centers would suggest that maximum benefit-cost ratios might be obtained from release of small (< 12 g) fish near day 160, as the mean size of the smallest release groups on day 161 (Table 1) was 12.3 g.

For benefit-cost ratios for jacks (Fig. 2h), predicted values on the surface increase from low mean release weights over a range of release times toward higher mean weights at early release dates. The presumed surface center (Table 5) is located beyond the range of the data in the direction of the rising ridge. Again, the surface center has no exact biological meaning. It may be interpreted as an estimate of the limit of the ridge describing the interaction between time and size at juvenile release. More significantly, the ridge indicates that

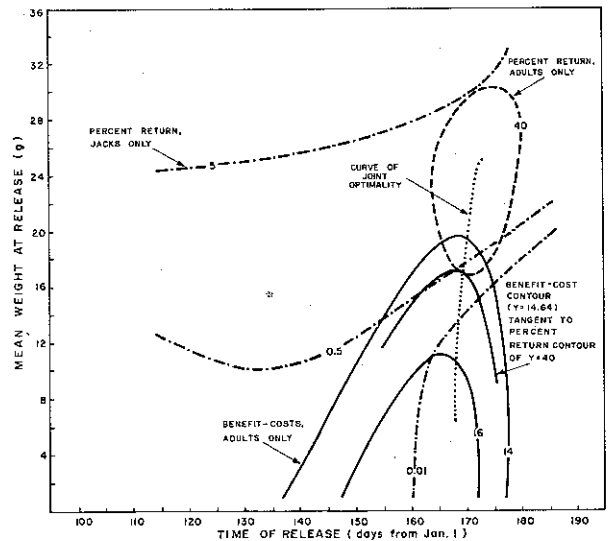


FIG. 3. Composite of portions of three of the response surfaces examined (Fig. 2) showing interrelations between percent return of adults (y_1), of jacks (y_2), and benefit-cost ratios associated with percent return of adults (y_7). The path of joint optimality runs from the center of the surface for y_1 toward the center for y_2 (located outside the factor space examined). On the path, benefit-cost ratios decrease with increasing returns of adults and jacks. Maximum adult returns are associated with less than maximum benefit-costs; conversely, higher benefit-cost ratios are associated with less than maximum adult returns. On the path, these relations between adult returns and associated benefit-costs are seen to be more sensitive to differences in mean release weights than release times.

maximum benefit-cost ratios for jacks may be expected from early releases of large juveniles. Noted also is the fact that the benefit-cost ratios for jacks (Fig. 2h) are substantially smaller than those for adults (Fig. 2g). Hence in practice one would opt to maximize benefit-cost ratios for adult returns while minimizing those for jacks. From the surfaces (Fig. 2g, 2h) both results would be achieved through later release of smaller juveniles.

JOINT OPTIMALITY

An overlay of contours for three responses evaluated from the data is shown in Fig. 3. A central contour (40%) of the surface for percent return of adults (y_1 ; Fig. 2a) is shown in the upper right of the figure. Several contours (0.01, 0.5, 5%) of the response surface for percent return of jacks (y_2 ; Fig. 2b) also are shown. In addition, several contours (14, 14.64, 16) of the benefit-cost ratio surface for adult returns (y_7 ; Fig. 2g) are shown in the lower right. Also shown is the path of joint optimality running from the center of the surface (y_6) for percent return of adults (y_1) toward the center of the surface for benefit-cost based on percent return of adults (y_7). The center of the latter surface is outside the release time-release weight factor space considered; hence, benefit-cost estimates at low mean release weights (e.g. < 6 g) presumably have doubtful value.

The composite of surface contours (Fig. 3) indicates, in general, that maximum and near-maximum predicted return

TABLE 7. Selected points on the path of joint optimality between the center of the surface for percent return of adult coho, and that for benefit-costs associated with adult returns. Each locus is defined in terms of a time of release and mean weight at release at which the adult returns and benefit-costs are jointly determined.

Coordinates of surface		Response	
Release time (d)	Mean weight (g)	Adult returns (%)	Benefit-costs (\$/\$)
173.1 ^a	25.1 ^a	43.5	12.2
172.9	24.7	43.5	12.4
172.3	24.0	43.4	12.6
171.7	23.0	43.1	13.0
171.0	21.1	42.4	13.5
169.6	16.9	40.0	14.6
169.1	15.2	39.0	15.1
168.7	13.3	38.0	15.5
168.3	11.0	37.0	16.0
168.0	7.5	36.0	16.5

^aLocus of center of surface for percentage adult returns.

of adults is associated with percent returns of jacks ranging from about 0.5 to 5%. Furthermore, maximum and near-maximum adult returns are obtained at less than maximum benefit-costs. As one moves upward toward higher mean release weights on the path of joint optimality, adult and jack returns increase and benefit-cost ratios decrease. With movement upward on the path of joint optimality the time to release, for maximum adult returns, increases slightly. By comparison, however, the relation between adult returns and benefit-costs related to adult returns is more sensitive to differences in mean release weight than time of release. The relations between release time, mean weight at release, adult returns, and associated benefit-cost ratios are shown for selected points on the path of joint optimality in Table 7. The following observations are summarized from the table. (1) At the center of the surface for adult returns (y_{1s} , 43.5%) a benefit-cost ratio of 12.2:1 is predicted. (2) The optimum time of release of juveniles is relatively constant (days 168.0–173.1) on the path of joint optimality. (3) Release of smaller juveniles on or near day 170 should increase monetary benefits relative to production costs, while at the same time maximizing yield of adults with respect to suboptimum mean release weight of juveniles. (4) Conversely, higher adult returns are coupled with increased returns of jacks, presumably a major reason for the concomitant reduction in benefit-costs in moving on the path of joint optimality toward the center of the surface for adult returns.

Discussion

ASSESSMENT OF EXPERIMENTAL DATA

One important potential source of error, among those that could influence the results, lies in the uncertainty of recovery of tagged individuals caught by the commercial and sport fisheries. As mentioned previously, the proportion of juveniles from each release group recovered in the commercial fishery as adults was estimated by sampling the commercial catch at an intensity of 20%. Size selectivity of commercial gear against capture of jacks resulted in the likelihood that

virtually all of the jacks were recovered at the hatchery fence. In addition, estimates of the number of fish in each release group captured by the sport fishery were based on the recognition and reporting of marked fish. The awareness factor (0.28), used to adjust for the incomplete recognition of marked fish in the sport fishery, itself is subject to considerable uncertainty. Only counts of fish returning to the hatchery weir can be considered to be without error; all fish returning to the weir were a product of the experiment and all were sampled.

A further potential source of error arose from the fact that all of the original experimental fish in each pond were graded into three size groups (small, medium, large) prior to tagging. It could be argued that this method of setting up size groups to determine the influence of juvenile size on success of return might be biased, for the following reasons. There is accumulating evidence (Ricker 1972) suggesting that hereditary factors are at least partly involved in rate of growth and age of return at maturity. Although the available evidence as yet is not at all clear, it appears that predisposition toward early maturity may be genetically induced, finding its full expression when favorable environmental circumstances, such as abundant food supply, favor rapid growth. If this proposition were true, then some proportion of the faster growing, larger male juveniles in a population would show a greater propensity to mature earlier and return as jacks. Hence, it could be argued that selection of "large" juveniles in the current study would result in an inflated proportion of jacks originating from the "large" juveniles, a proportion that more properly should apply to the population as a whole from which the "small, medium, and large" groups were drawn. In view of this potential difficulty, there is an alternative to grading a population into size groups, i.e., to grow three populations, in this instance, at different rates (temperatures) and to divide the three populations among the various release times. Yet theoretically even this alternative might bias the results. It is possible that growth at different temperatures may lead to differences in biochemical composition or fish "quality," which itself may influence survival potential. In addition, although temperature manipulation of growth rate seems a very plausible alternative, it often may be difficult to put into practice. Most hatcheries do not have the temperature control and space required for growing a substantial array of fish groups under experimental conditions.

The question of grading fish into size groups subsequently led to further inspection and analysis of the original data (Bilton 1978). These data indicate that the proportions of jacks returning from the graded groups released in April, May, and June were not demonstrably different, for a given size, than the proportion returning to a combined population of small, medium, and large release groups having the same mean size. There was one exception among the groups compared: a higher proportion of jacks than expected returned from the June release of large juveniles. In the language of analysis of variance there are two sources of variance that refer to size effects: the mean weight in grams of juveniles in a release group, and the designation of the group size (small, medium, large) at release. With the exception of the June release of large fish just noted, analysis of variance showed that information on groups did not add significantly to that provided by mean release weight in explaining jack returns.

On this basis we assume a small bias occurs in relation to the June release of large juveniles; however, we also presume this bias would have only a minor influence on the production equation relative to the total variance associated with treatment effects. Hence, returns of jacks can be explained on the basis of mean release weight, and designated release groups did not add significantly to the explanation of variance. For the adults a similar analysis showed that the extra information provided by grouping did not explain any significant portion of the variance associated with adult returns. Hence, for both jacks and adults, there was little evidence to support the possibility that genetic factors influenced the returns through the grading technique used. Yet, the evidence from other sources suggests that hereditary factors are at least partly involved in expression of growth rate and age of return. Therefore the inference that genetic factors could influence adult and jack returns would appear to remain valid. We conclude that grading could produce minor alterations in the curvature of a response surface for adult or jack returns, while not altering the general configuration of the surface itself. Given these uncertainties we conclude that different size groups should be obtained, where possible, through temperature-controlled growth rate rather than grading of populations into size groups.

In the current study, marking and nose tagging of all fish groups occurred several weeks prior to each release (Bilton and Jenkinson 1976). The period between tagging and release, used to evaluate tagging mortality and tag retention, was short. In some instances in similar studies it may not be possible to mark and tag the fish close to the time of release. In some hatchery situations, if water temperatures are higher than desirable, the stress imposed from crowding and handling during marking and tagging may trigger outbreaks of disease. To avoid such problems may require that grading and tagging occur several months (even the previous fall) prior to release, when water temperatures are lower. In the ensuing interval between tagging and release, significant growth may occur. Also, with a more prolonged period between tagging and release, an exact inventory of numbers released may be more difficult to obtain. Under such circumstances, sampling the groups for estimates of mean size and sex ratio just prior to release is of paramount importance.

In addition to the factors outlined that could influence the design and interpretation of the experimental results are those that would apply on a larger scale at various production hatcheries. There are two general variables that could influence the interpretation of the effects of time and size at release on the success of returns of mature fish. These are the influences of (1) site-specific variation and (2) annual variation on the biological system examined. A number of site-specific factors unique to the Rosewall Creek experiment could have influenced the release—return relations obtained. These could include the diet provided the cultured fish, the feeding rate, the temperature regime, the characteristics of the water supply, the genetic nature of the fish stock used, rearing density and associated water quality, diseases endemic to the water system used in culture, and the type of estuary that the fish would enter upon release. In effect, the background variables of the experimental system, their levels, and combined effects might produce different release—return relations if the current experiment were to be repeated at other sites. Therefore

general application of the results for coho from the present experiment could be modified by site-specific factors, which together could form sets of unique background conditions in similar studies repeated elsewhere. The situation might be stated as follows. A specific hatchery may require "tuning" to optimize time and size at release, where the processes involved are influenced by an unrecognized and uncontrolled set of background variables associated with a given culture site.

The second source of variability is that associated with annual variation in factors influencing survival of juveniles following release. Juvenile coho emigrating into the near-shore and coastal ecosystem, and their growth and survival therein, may be influenced by annual variations in meteorological and oceanographic events that in turn could affect the food web in which the juveniles act both as foragers and as prey for other species. Thus annual variability in the timing and magnitude of cyclic events in the nearshore and coastal ecosystem could act as a further source of error in the prediction of optimum conditions of time and size at release, not only for cultured fish but also for wild progeny subjected to the same postmigration conditions. In general, further examination of the influence of time and size at release of juveniles on returns of mature fish would seem to require recognition of sources of variation within and between sites and between different brood years.

COMPARISON OF EXPERIMENTAL AND PRODUCTION HATCHERY RETURNS

Some appreciation of the potential variability in returns, associated with different sites and brood years, may be obtained from an overlay of the response surface generated from the Rosewall Creek experiment in relation to 1971–74 production hatchery returns in British Columbia (E. A. Perry, Vancouver, B.C., personal communication) (Fig. 4), and to Washington State (USA) (R.C. Hager, Olympia, WA, personal communication) hatchery returns for the 1971–73 brood years (Fig. 5). The British Columbia production hatchery data conform in general with the predicted surface for percent adult returns generated from the Rosewall Creek data, assuming that the surface contours describing the latter are known with a precision of $\pm 6.3\%$. However, the data are insufficient to indicate whether the differences between the returns to the three British Columbia production hatcheries and the Rosewall Creek site (Fig. 4) could be ascribed to site-specific or annual differences in potential for return. Of the points on the surface, six represent "accelerated" or zero-age juveniles (Bilton and Jenkinson 1980a, b) released in the year of hatching (Fig. 4; site C, 1973 brood year). Three of these, describing releases on day 162 (June 10, 1974) at average weights of 6, 8, and 14 g, are shown in the figure. Also shown are three releases of normal-age juveniles (1-yr-old, site C, 1972 brood year) released on the same day at average weights of 11, 17, and 23 g. Percentage returns from the former (0.7, 2.5, 7.4%) are considerably lower than those from the normal-age migrants (42.1, 48.3, 46.5%). The fact that both groups were released on the same day, and that the ranges of average release weights of the three releases in each of the two groups overlap, strongly suggests that factors other than time and size at release are important in deter-

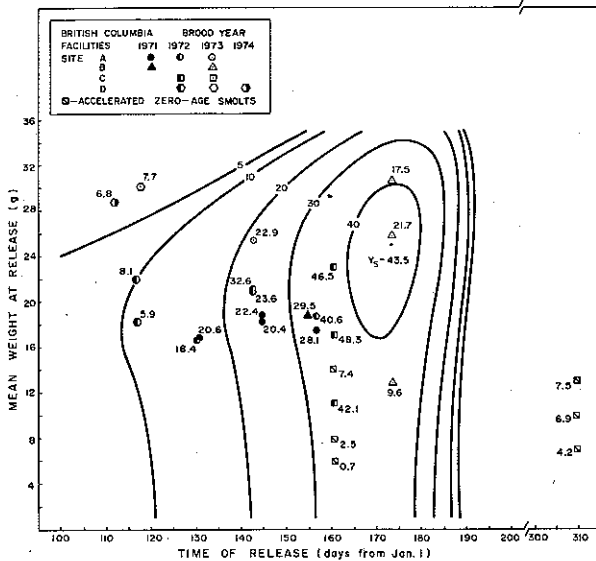


FIG. 4. Release (time, Julian days; size, mean weight, g) and return (adults, percentage) data for coho salmon from three southern British Columbia production hatcheries (sites A, B, D) overlaid on the contours for percentage adult return generated from the Rosewall Creek (site C) experimental data. Six zero-age (accelerated) releases shown are not strictly comparable with the remaining estimates (see text). Attention is drawn to the six (site C) estimates for releases on day 162; these compare returns for zero-age and normal-age migrants released at different mean weights (see text). y_s , predicted response at the surface center; contours, percent return of adults (Rosewall Creek data).

mining the success of return. The differences in returns cannot be attributed to different lengths of sea life prior to return; both the zero-age and 1-yr-old migrants returned as jacks and adults, respectively, in the fall of 1974 and 1975. It could be inferred that the accelerated fish may not have been physiologically ready to migrate, even when released at the same time and (by interpolation) at similar sizes. The data are minimal but suggestive that zero-age smolts, as currently produced, may prove ineffective as a means of building up stocks of coho salmon through hatchery manipulation.

The British Columbia production hatchery data (Fig. 4) portray a pattern of releases presumably influenced in the freshwater phase by site conditions as well as operator decision on the timing of release. In the figure there is a cluster of releases between days 130 and 160 approximately, and at mean release weights of 16–23 g. This cluster reflects, in part, attainable weight in relation to available growing conditions, as well as operator decision that better returns may be obtained from May to early June releases. In comparison, the Rosewall Creek data and their estimated precision suggest that high adult returns ($\geq 40\%$) should be obtained from releases between days 163 and 173 at mean release weights of 22–25 g. Thus the operator appears to promote releases several weeks earlier than the Rosewall Creek data would suggest for optimizing adult returns. In addition, the production hatchery data illustrated (Fig. 4) show an average return of about 25%, whereas returns of 38–50% appear attainable based on the Rosewall Creek experiment. The po-

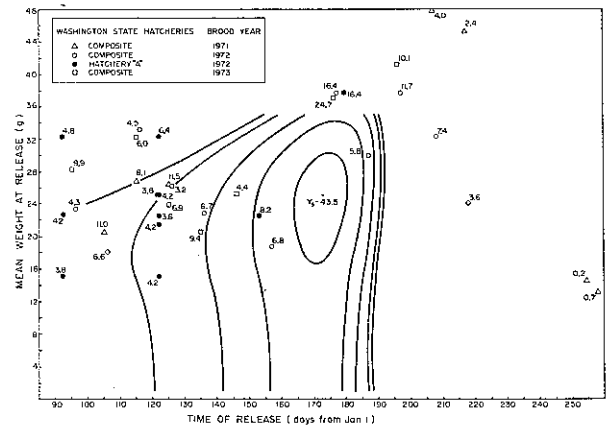


FIG. 5. Release (time, Julian days; size, mean weight, g) and return (adults, percent) data for coho salmon from representative Washington State (USA) hatcheries overlaid on the contours for percent return of adults generated from Rosewall Creek (British Columbia) data. Symbols represent data from four hatcheries; for three of these, "composite" estimates represent averaged returns for numerous release groups having identical or nearly identical release times and mean weights within the brood years indicated. y_s , predicted response at the surface center; contours, percent return of adults (Rosewall Creek data).

tential twofold increase in returns suggested provides a target for improvement of production hatchery efficiency, achievable through optimization of time and size at juvenile release. However, confirmation of this potential will require a substantial accumulation of production hatchery data, particularly in areas of the surface for time and size at juvenile release that remain inadequately or only modestly sampled.

In comparison with British Columbia hatchery returns, those for the Washington State hatcheries (Fig. 5) show a rather different pattern of returns in relation to data on juvenile release. An average of the estimates of percent adult return from the figure is about 7%, between one-third and one-quarter of the average for British Columbia facilities. Ultimately it may be found that conditions of time and size at juvenile release, maximizing Washington State hatchery returns, may differ from those suggested by the British Columbia data. The assumed poor correspondence between the Rosewall Creek and Washington State results may arise through the influence of other factors as yet unrecognized. Nevertheless, the Rosewall Creek data provide the basis for a comparison that otherwise could not be made. Accepting the Rosewall Creek response surface patterns in this manner, the following observations can be made. Many of the points for Washington State hatchery releases (Fig. 5) represent returns for juveniles released early (before day 130) at a relatively large mean weight (> 20 g). The Rosewall Creek contours for percent return predict poor returns associated with those release conditions. In addition, no releases appear to have been made in the region of the surface where maximum returns might be anticipated (163–173 d, 22–25 g). However, in the earlier period between days 150 and 163 there are two estimates of returns (Fig. 5) from the American hatcheries, 6.8 and 8.2%. These values are much lower than the range of Canadian hatchery returns for the same time period

(28.1–48.3%), suggesting that optimum conditions of time and size at juvenile release may differ in Washington State hatcheries. The highest returns obtained from Washington State releases in the figure appear to occur for large (e.g. 36–37 g) juveniles released between days 175 and 180 (16.4–24.7%).

In these comparisons of American and Canadian production hatchery returns it must be remembered that assumptions and conclusions are based on the available data. Areas of the time–size release surface for which there are few or no data could alter preliminary conclusions if data were available for those poorly sampled areas. Obviously, two-factor designs involving a grid of juvenile release times and sizes are required to provide, efficiently, the type of data leading to the optimization of release conditions that will maximize hatchery returns. Practically speaking, a completely orthogonal grid design, in which the small, medium, and large release sizes are identical at each release time, probably is impossible to achieve due to growth of the cultured fish between releases. However, we suspect that biases introduced through lack of design orthogonality will not interfere seriously with ultimate interpretation of the results of such tests. On the other hand, if production hatcheries were to accept the Rosewall Creek results without question and make the majority of future releases near the presumed center of the surface for adult returns, then returns could improve, yet the assumptions underlying the relations between time and size at release and adult returns could remain much at their current level of understanding. Therefore, we recommend that the Rosewall Creek model be viewed as the best current representation of the data, and that multifactor designs be employed to investigate further the influence of time and size at release on the success of adult returns.

RATIONALE FOR OPTIMIZING TIME AND SIZE AT RELEASE

Optimum release "windows" — The nature of the surfaces relating release conditions to success of adult returns suggests that some underlying biological phenomenon must be operating on the migrating juveniles. Many factors may influence the life cycle of salmonids from seaward migrants to returning spawners, including migration to the sea, nearshore and coastal ecology, offshore migration, conditions on the high seas, returning migration at maturity, and ascent into fresh waters to spawn. We suspect that time and size at release may have a dominant influence on success of returns through conditions the juvenile migrants experience in the several months following migration to salt water. The major factors suspected to be operating on juvenile survival, as outlined earlier, are food supply and predation. For example, optimum conditions of time and size at release may be those providing for entry of juveniles into the nearshore and coastal ecosystems at a time and size when maximum advantage can be obtained from the available food supply in terms of growth rate and survival. The attainment of such an advantage may itself be dependent on the injection of juveniles into the ecosystem at a time when the presence and abundance or density of forage organisms of a particular type and size allow for maximum food intake relative to the cost of energy expended in foraging. Conditions that maximize the food supply, such as the onset of the spring plankton pulse, in turn may vary geographically and temporally in relation to meteorological and oceanographic

events in the nearshore and coastal marine environments. Regional and annual variations in the timing of these events could influence the food supply and feeding opportunities, and hence the growth and survival of the new migrants in salt water. We assume that rapid growth is advantageous; susceptibility of juveniles to size-dependent predation could be foreshortened by more rapid growth through the intervals of higher vulnerability assumed to be associated with smaller size. Japanese experience suggests that release of chum salmon (*O. keta*) fry may require the avoidance of coastal migrations of predator fishes (Iioka 1976; Iioka et al. 1977). Therefore, maximized adult returns may result from injection of juveniles into the marine environment through specific release windows where time and size at release maximize feeding and growth potential through episodes of vulnerability to predation whose impact on survival declines with growth and increasing juvenile size. This hypothesis could apply to the survival potential of both hatchery stocks and natural migrants.

Exploring the biological rationale suggested as underlying the observed phenomenon of time and size at release could provide a more precise technology for hatchery operations. Examination of oceanographic and meteorological events in association with structured releases of juveniles over a period of years should provide insight into correlations between success of return of spawners and ecosystem parameters in the initial juvenile marine phase. The concept of course is related to that of the Japanese "plankton watch" of recent years. From such associations simple "flags" might be recognized, such as threshold temperatures in the nearshore environment, signaling the beginning of improved options regarding time of release. Sea surface temperature appears to be used to determine time of release in some Japanese chum salmon hatchery operations (Hokkaido Salmon Hatchery 1976; Iioka et al. 1977). It is conceivable that the hypothesis outlined regarding entry of juvenile migrants into the nearshore and coastal marine environment may apply to all of the Pacific Coast anadromous salmonids. A knowledge of correlative factors in the initial marine phase and their use as flags with respect to time and size at release could serve to "tune" hatchery sites to minimize both site-specific and annual variations in return of spawners.

Conditions influencing juvenile growth and development — The release of cultured juveniles from hatchery facilities at specific times and sizes requires a consideration of growth rates needed to achieve target sizes at time of release. Two options are presented: (1) to manipulate growth rate to utilize release windows, or (2) to locate hatchery facilities on water systems affording easy achievement of appropriate size at optimum time of release. Temperature is the dominant factor influencing growth rates, and the two options differ mainly in the amount of temperature control available to the fish culturist. In terms of temperature control the latter option would be simpler and less expensive. In "warm-water" hatcheries, where ambient temperatures over the winter period may be 8–10°C, growth would be more rapid than in "cold-water" hatcheries, averaging 2–5°C over the winter period. Recent evidence (C. Clarke, Nanaimo, B.C., personal communication; D. Higgs, Vancouver, B.C., personal communication) also indicates that the effects of dietary protein–fat ratios on

growth rates of salmonids are temperature dependent. In addition, evidence suggests that withholding of food can be deleterious to fish quality and possibly survival in warm-water hatcheries but not in cold-water hatcheries (Bilton and Robins 1971; K. Sandercock, Vancouver, B.C. personal communication). In general, control over growth may be achieved by temperature manipulation, by reduced feeding in cold-water hatcheries, or by alteration of protein-fat ratios in warm-water or cold-water culture. Pond loading or fish density also can influence growth rate. However, controlling growth through manipulation of pond loading should be regarded with caution; Sandercock and Stone (1979) have found an inverse relationship between pond loading rate in the juvenile stage and subsequent survival and return of adults.

Clarke and Blackburn (1978) have found that migration readiness can be judged in terms of clearance rates of sodium from the blood of juveniles transferred to salt water. The rate at which adjustment of sodium level occurs appears to be maximized in relation to the presumed normal migration period. Clarke and Shelbourn (1981), working with zero-age accelerated coho juveniles of Big Qualicum River origin, found that rates of sodium clearance were maximized at a temperature of 14°C near June 30. Submaximum clearance rates occurred at supra- and sub-optimal temperatures. Their data also suggest that submaximum clearance rates may remain at peak levels for shorter periods at colder (<10°C) than at warmer (>14°C) temperatures. Hence for accelerated fish, clearance rates relative to migration readiness appear to be temperature dependent. Also, the period of maximum clearance rate, relative to the size of the release window, may be shorter in colder culture waters. Similar studies would be most useful in relating sodium clearance rates to optimum conditions of time and size at release using normal-age juveniles.

Conditions influencing benefit-costs — The relations between success of adult returns and benefit-costs of hatchery production were described on the basis of simplified costs and dollar returns. The criteria for describing such relations could be modified to fit more closely the benefits and costs of production hatchery activities. In general, however, the Rosewall Creek experiment indicates that one could optimize the culture system either for maximum adult production or for maximum benefit-costs. The path of joint optimality (Fig. 3) shows that maximum or near-maximum benefit-costs are achieved from releases of smaller juveniles at the expense of some loss in potential returns of adults. Conversely, maximum adult returns are achieved through release of larger smolts at less than maximum benefit-costs. As one moves upward on the path of joint optimality, adult and jack returns increase and benefit-cost ratios diminish. In all of these options (Table 7) the calculated release times, maximizing adult returns and benefit-costs jointly, occurred within a rather narrow computed range of ~168–173 Julian days.

Rearing strategies and optimization — Heretofore, the problem of optimization has been approached as if the time of release (x_1) and mean weight at release (x_2) were mutually independent variables. For example, the center (x_{1s} , x_{2s}) on the surface for percent adult returns (Fig. 2a) gives conditions for optimal adult returns if indeed juvenile coho can be reared to mean weight x_{2s} at the time x_{1s} . The ridge of optimum

release weight (Fig. 2a) represents a variation on this idea. If the release time (x_1) is prescribed by hatchery requirements, then the corresponding weight x_2 on this ridge is optimal for adult returns. Again, this presupposes that a particular juvenile mean weight x_2 is exactly achieved at a particular time x_1 . Further, if two responses, such as percentage adult returns (Fig. 2a) and benefit-costs (Fig. 2g), are to be considered simultaneously, then the path of joint optimality represents optimal release conditions for various levels of trade-off. Once more, to achieve a specific point on this path, juvenile coho must be reared to a particular weight at a particular time.

When the question is raised as to how the surfaces should be "climbed" to achieve optimum conditions it is obvious that growth ($\Delta x_2/\Delta x_1$) is involved and the variables no longer can be considered independent. Growth, to achieve a target size at a given time, would be subject to constraints such as (1) initial weight, (2) conditions influencing growth rate, and (3) the range of growth rates attainable by the species in question. Temperature is a dominant factor influencing growth. Hence temperature could require the most attention, particularly in hatchery culture where temperature control, if available, might be modest at best. Recently, McLean (1979) examined a number of variables associated with growth of salmonids in culture. His generalized growth and rearing model would allow prediction of growth, in a manner similar to that of Stauffer (1973), under variable environmental conditions including temperature, aspects of water quality, ration level, water exchange rate, and fish density in culture. Given that some prior knowledge of expected ambient temperatures and possible feeding rates was available, growth rates could be backcalculated from the locus of optimum release conditions on a response surface to explore growth rates and initial weights required to achieve those conditions.

Estimates of growth that might be attained in practice are suggested in Fig. 6. There, surfaces for percent adult returns (Fig. 2a) and benefit-costs associated with adult returns (Fig. 2g) are superimposed and overlaid with three growth lines (G1, G2, G3). The lines G2 and G3 are constructed, as reasonable examples, from the data for small and large juveniles, respectively, in Table 1 (pond 1). The line G1 is hypothetical and has been added to complete the argument. Loci at which the growth lines are tangent to surface contours estimate release conditions that maximize response for juveniles growing at the rates indicated. These loci are shown for the benefit-cost and percent adult return surfaces, respectively, by points *a* and *b* in the figure. For each growth line it is seen that size attained, relative to attendant growth circumstances, forces a decision governing release time at which either benefit-costs or percent adult returns would be maximized. For maximum benefit-costs these release times occur between days 163 and 168 (tangents *a*); maximum percent adult returns occur later between days 171 and 173 (tangents *b*).

The growth line examples in Fig. 6 are indicative of the importance of culture temperature and feeding rate and their potential for manipulation in attempts to optimize time and size at release. The benefits of optimizing release conditions suggest the need for substantial exploration of growth control as a means of achieving that objective. Such trials presumably would consider restricted feeding or withdrawal of food during the winter period of low ambient water temperatures, and growth potential at higher temperatures in relation to feeding

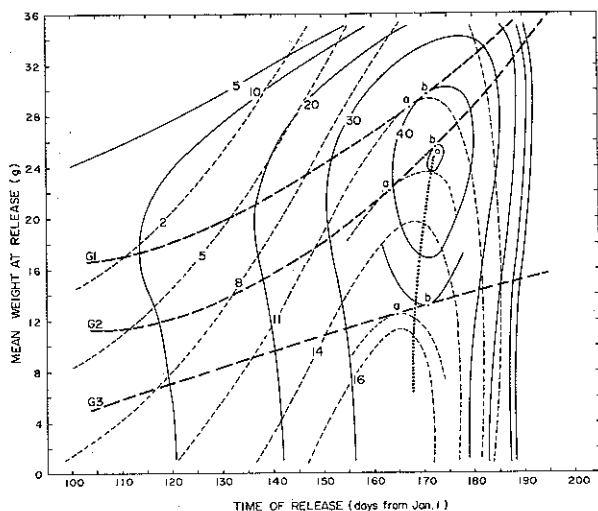


FIG. 6. Potential for optimization of release conditions for coho juveniles cultured under sets of suggested environmental constraints. Two surfaces are superimposed, that for percent adult returns (solid contours 5, 10, 20, 30, 40%) and that for benefit-costs associated with these returns (broken contour lines 2, 5, 8, 11, 14, 16). The path of joint optimality also is shown. Potential growth lines (G1, G2, G3) illustrate how the surfaces may be "climbed" under the constraints of possible conditions influencing growth; these are tangent to contours of the benefit-cost surface at points *a*, and to contours of the percent adult return surface at points *b*. Rapid growth (G1) or slow growth (G3) could prevent the attainment of ultimate optimum release conditions for adult returns, which are nearly reached on line G2 at *b*.

rates and food conversion efficiency. Information on growth potential and growth control should provide further insight into the relative effectiveness of ambient temperature regimes (cold-water vs. warm-water conditions) at various hatchery sites, and the possible advantages of temperature control. For example, if growth line G3 were representative of a cold-water hatchery, that system would be unable to reach its full biological potential for culture of coho with respect to adult returns. If the G1 line were representative of a warm-water hatchery, optimum release conditions for coho might not be attainable because of too rapid growth. In contrast, the line G2 represents the situation where near-optimum conditions of time and size at release are achieved, leading to near-maximum adult returns. It is possible that further knowledge of growth potential and growth control for a given species also might assist in determining the optimal use and placement of new hatcheries relative to the constraints imposed by ambient temperature regimes or the need for temperature control.

Rearing other salmonid species — We assume that response surfaces analogous to those for coho salmon juveniles will be found to apply in other species of Pacific salmon and steelhead (*Salmo gairdneri*) in their North Pacific Ocean range. Until more evidence is available, it is presumed that response surfaces based on time and size at juvenile release may be fairly specific with reference to (1) genetic differences between stocks, (2) local geographic, climatic, and ecological conditions, (3) gross geographic, climatic, and ecological

differences (e.g. Alaska vs. California), (4) differences between species, including those associated with variation in freshwater residence and years of marine life before maturity, and (5) annual differences in climatic and oceanographic events.

Response surface configuration in the chum (*O. keta*) and pink (*O. gorbuscha*) salmon may differ from that of the coho, as both species migrate to sea as fry. The response surfaces for chum and pink salmon also may vary because of differences between them in years of sea life prior to maturation. Benefit-cost surfaces of seagoing chum and pink fry should differ markedly from those of coho, chinook (*O. tshawytscha*), and steelhead; perhaps they would show major benefits from warm-water incubation and rearing, with release occurring at the appropriate time but at a larger size. Examination of the relations between time and size at release that maximize returns and benefit-cost ratios in hatchery production of chinook salmon and steelhead should be instructive; populations of both salmonids currently show substantial decreases compared with historical levels, and both are subject to increasing artificial culture in British Columbia waters.

For the coho salmon, influence of time and size at release, and their effects on adult returns, are seen as inputs and outputs of an ecological system whose central components are not yet well understood. We suspect that nearshore and coastal ecological dynamics may be particularly involved. Events in early marine life of salmonids are likely to have a major impact on the survival potential of individuals and stocks in a manner similar to that of the "critical theory" of survival of year classes of marine fishes (May 1974). As food preference varies among the species, the ecological dynamics associated with food supply, growth, and survival in nearshore and coastal waters may vary accordingly. We suspect that investigation of the ecological dynamics of entry, feeding, and growth of juvenile salmonid populations in such waters would provide a better understanding of the biological nature of the time and size at release phenomenon, leading not only to improved hatchery production strategies but also to improved management of natural populations. Toward this goal, the Rosewall Creek data show that the returns of hatchery-produced coho adults may be raised from a current average of 25% to a maximum near 50% in southern British Columbia waters. In addition, site-specific and annual variability in returns of hatchery-produced coho salmon currently are being investigated through the release of similar arrays of juvenile groups at two southern British Columbia hatcheries.

Acknowledgments

The major portion of this study was undertaken by one of us (H. T. B.) between 1974 and 1979, and the collaborative efforts of D. W. Jenkinson, R. M. Humphreys, and G. E. Johnston during the incubation, culture, tagging, release, and recovery operations contributed much to the project. One of us (D. F. A.) suggested the application of response surface analysis to the compiled data and undertook the preliminary calculations; in this, the assistance of Marilyn R. Marshall is gratefully acknowledged. As a result of difficulties with this analysis, J.T.S. applied more robust analytical technique aimed at finding optima and identifying variance. The authors are indebted to Messrs R. C. Hager, Olympia, WA, and E. A. Perry, Vancouver, B.C., respectively, for their information on State of Washington and British Columbia hatchery returns.

- ARGUE, A. W., J. COURSELY, AND G. D. HARRIS. 1977. Preliminary revision of Georgia Strait and Juan de Fuca Strait tidal salmon sport catch statistics, 1972 to 1976, based on Georgia Strait head recovery program data. Can. Dep. Environ. Fish. Mar. Serv. Pac. Reg. Tech. Rep. Ser. PAC/T-77-16. 68 p.
- BILTON, H. T. 1978. Returns of adult coho salmon in relation to mean size and time at release of juveniles. Fish. Mar. Serv. Tech. Rep. 832: 73 p.
1980. Returns of adult coho salmon in relation to mean size at release of juveniles to the catch and the escapement. Can. Tech. Rep. Fish. Aquat. Sci. 941: 41 p.
- BILTON, H. T., AND D. W. JENKINSON. 1976. Time and size at release experiment: three releases of three major size categories of juvenile coho salmon from Rosewall Creek in the spring of 1975. Fish. Mar. Serv. Data Rec. 7: 16 p.
- 1980a. Returns to the fishery and escapement of adult coho salmon from accelerated and normally reared juveniles. Can. Tech. Rep. Fish. Aquat. Sci. 925: 11 p.
- 1980b. Return to the fishery and escapement of adult coho salmon from accelerated juveniles released in the fall of 1974. Can. Tech. Rep. Fish. Squat. Sci. 943: 11 p.
- BILTON, H. T., AND G. L. ROBINS. 1971. Response of young sockeye salmon (*Oncorhynchus nerka*) to prolonged periods of starvation. J. Fish. Res. Board Can. 28: 1757-1761.
- CLARKE, W. C., AND J. BLACKBURN. 1978. Seawater challenge tests performed on hatchery stocks of chinook and coho salmon in 1977. Fish. Mar. Serv. Tech. Rep. 761: 19 p.
- CLARKE, W. C., AND J. E. SHELBOURN. 1981. Growth and smolting of underyearling coho salmon in relations to photoperiod and temperature. N. Pac. Aquaculture Symp., Anchorage, Alaska, 1980. (In press)
- HAGER, R. C., AND R. E. NOBLE. 1976. Relation of size at release of hatchery-reared coho salmon to age, size and sex composition of returning adults. Prog. Fish Cult. 38: 144-47.
- HEIZER, S. R., R. J. COOK, AND A. W. ARGUE. 1978. Basic data for the 1975 Canadian chinook and coho catch sampling and mark recovery program. Fish. Mar. Serv. Data Rep. 57: 479 p.
- HOKKAIDO SALMON HATCHERY FISHING AGENCY OF JAPAN. 1976. An outline of the management of salmon hatching and rearing. Vol. 9. p. 1-43. (Fish. Mar. Serv. Transl. Ser. 4320, Vancouver, B.C., 1978)
- HOPLEY, C. W., AND S. B. MATHEWS. 1975. The effects of experimentally varying the size and time of release of hatchery-reared coho salmon (*Oncorhynchus kisutch*). Unpubl. MS, Salmon Culture Division, Wash. Dep. Fish. 15 p. (R. Hager, Olympia, WA, personal communication.)
- IIOKA, C. 1976. Report on hatchery returns: summary of results of surveys in coastal waters. Iwate Ken Suisan Shikenjo Hokoku, Sept. 1976. (Fish. Mar. Serv. Transl. Ser. 4338, Vancouver, B.C., 1978)
- IIOKA, C., J. TERAJIMA, K. YAMAMOTO, S. OGAWA, S. SATO, AND Y. NAKAMURA. 1977. An examination of the release of seawater-reared fingerlings. Iwate Ken Suisan Shikenjo Hokoku-sho, 1977. (Fish. Mar. Serv. Transl. Ser. 4384, Vancouver, B.C., 1978)
- JOHNSON, K. A. 1970. The effect of size at release on the contribution of 1964 brood Big Creek Hatchery coho salmon to the Pacific Coast sport and commercial fisheries. Oregon Fish. Comm. Res. Rep. 2: 12 p.
- KIMURA, D. K. 1976. Estimating the total number of marked fish present in a catch. Trans. Am. Fish. Soc. 105: 664-668.
- KOO, T. S. Y. 1962. Age designation in salmon, p. 37-38. In T. S. Y. Koo [ed.] Studies of Alaska red salmon. Univ. Washington Press, Seattle, WA.
- LINDSEY, J. K., D. F. ALDERDICE, AND L. V. PIENAAR. 1970. Analysis of nonlinear models — the nonlinear response surface. J. Fish. Res. Board Can. 27: 765-791.
- MAY, R. C. 1974. Larval mortality in marine fishes and the critical period concept, p. 3-19. In J. H. S. Blaxter [ed.] The early life history of fish. Springer-Verlag, New York.
- MCLEAN, W. E. 1979. A rearing model for salmonids. M.Sc. thesis, Dep. Interdisciplinary Studies, Univ. British Columbia, Vancouver, B.C. 134 p.
- NELDER, J. A., AND R. MEAD. 1965. A simplex method for function minimization. Computer J. 7: 308-313.
- O'NEILL, R. 1971. Algorithm AS47, Function minimization using a simplex procedure. Appl. Statist. 20: 338-345.
- RICKER, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations, p. 19-160. In R. C. Simon and P. A. Larkin [ed.] The stock concept in Pacific salmon. H. R. MacMillan Lectures in Fisheries. Mitchell Press Ltd., Vancouver, B.C.
- SANDERCOCK, F. K., AND E. T. STONE. 1979. The effect of rearing density on subsequent survival of Capilano coho, p. 136-143. Proceedings of the N.W. Fish Culture Conf., Portland, OR.
- STAUFFER, G. D. 1973. A growth model for salmonids reared in hatchery environments. Ph.D. thesis, Univ. Washington, Seattle, WA. (University Microfilms International, Ann Arbor, MI, 1978).
- WALLIS, J. 1968. Recommended time, size and age for release of hatchery-reared salmon and steelhead trout. Fish. Comm. Oregon Processed Rep. 61 p.

Appendix A. Estimating Parameters in (5)

Define the two parameter vectors

$$\theta_1 = (b_0, b_1, b_2, b_{11}, b_{12}, b_{22}),$$

$$\theta_2 = (\alpha_1, \alpha_2).$$

The problem is to find estimates $\hat{\theta}_1$ and $\hat{\theta}_2$ that minimize the sum of squares

$$(A1) \quad S(\theta_1, \theta_2) = \sum_{i=1}^n [y_i - b_0 - b_1 x_{1i}^{\alpha_1} - b_2 x_{2i}^{\alpha_2} - b_{11} x_{1i}^{2\alpha_1} - b_{12} x_{1i}^{\alpha_1} x_{2i}^{\alpha_2} - b_{22} x_{2i}^{2\alpha_2}]^2,$$

given the observations (x_{1i}, x_{2i}, y_i) , $i = 1, \dots, n$ (where $n = 57$ here), that is, to find θ_1, θ_2 so that

$$(A2) \quad S(\hat{\theta}_1, \hat{\theta}_2) = \min_{\theta_1, \theta_2} S(\theta_1, \theta_2).$$

As a first step, notice that for a prescribed parameter vector θ_2 (i.e. prescribed α 's) the quantity

$$(A3) \quad S_1(\theta_2) = \min_{\theta_1} S(\theta_1, \theta_2)$$

can be found explicitly. This can be done by regarding the minimization problem as a six-variable linear regression for θ_1 from the data $(x_{1i}^{\alpha_1}, x_{2i}^{\alpha_2}, y_i)$, $i = 1, \dots, n$.

In this way, estimates $\hat{\theta}_1(\theta_2)$, which depend on the given value of θ_2 , are obtained. These estimates solve the least-squares problem (A3), that is,

$$(A4) \quad S_1(\theta_2) = S(\hat{\theta}_1[\theta_2], \theta_2).$$

The function $S_1(\theta_2)$ is a well-defined, though complicated, function of the two variables α_1 and α_2 . The problem of minimizing S in (A1), a function of eight variables, is thus

reduced to the more manageable problem of minimizing S_1 in (A4), a function of two variables. In other words if $\hat{\theta}_2$ minimizes S_1 , then it also minimizes S with

$$\hat{\theta}_1 = \bar{\theta}_1(\hat{\theta}_2).$$

With these ideas in mind, a computer was used to solve the problem (A2). It employed the simplex method of searching for a function minimum, as conceived by Nelder and Mead (1965) and implemented by O'Neill (1971). This method works quite well with only two variables, and it was applied to the function S_1 , given by (A4). Notice that the actual calculation of $S_1(\theta_2)$ involves first performing the six-variable linear regression (A3).

Interestingly, the problem (A1) may not have a unique solution. Sometimes there are four local minima for S in which the signs of (α_1, α_2) are, respectively, $(+, +)$, $(+, -)$, $(-, +)$, and $(-, -)$. This fact is not too surprising when one realizes that the values $\alpha_1 = 0$, or $\alpha_2 = 0$ are singularities. For example, if $\alpha_1 = 0$, then the response function (4) no longer depends on x_1 . One can reasonably take the point of view that four distinct models are available corresponding to the four choices of sign for (α_1, α_2) . In this paper, the model with both α 's positive was always selected. Other possibilities (including the log transformation as a counterpart to the possibilities $\alpha_1 = 0$ or $\alpha_2 = 0$) did not give better results.

Once $(\hat{\theta}_1, \hat{\theta}_2)$ is found, the maximum likelihood estimate for the variance σ^2 turns out to be

$$(A5) \quad \hat{\sigma}^2 = \frac{1}{n} S(\hat{\theta}_1, \hat{\theta}_2).$$

This is known to be biased (especially for small n), and a preferred estimator is

$$(A6) \quad \sigma^2 = \frac{1}{n-k} S(\hat{\theta}_1, \hat{\theta}_2),$$

where k is the number of parameters estimated. Here $k = 8$ ordinarily, but k might be 7 or 6 if α_1 , α_2 , or both are fixed at 1. The usual argument in going from (A5) to (A6) depends on linear approximations when some parameters, such as α_1 and α_2 , enter nonlinearly. All estimates cited in this paper were obtained from (A6).

Appendix B. Technicalities of Locating Optima

For the particular response function (4), the equations (6) become

$$(B1) \quad \begin{aligned} b_1 + 2b_{11}x_{1s}^2 + b_{12}x_{2s}^2 &= 0, \\ b_2 + b_{12}x_{1s}^2 + 2b_{22}x_{2s}^2 &= 0. \end{aligned}$$

These are a pair of linear equations in the two unknowns x_{1s}^2 and x_{2s}^2 . Their solution is given by (7).

Equations (B1) also can be used to obtain alternative expressions for b_1 and b_2 in (4). After some algebraic manipulation, (4) becomes

$$(B2) \quad y = y_s + b_{11}(x_{1s}^{\alpha_1} - x_{1s}^{\alpha_1})^2 + b_{12}(x_{1s}^{\alpha_1} - x_{1s}^{\alpha_1})(x_{2s}^{\alpha_2} - x_{2s}^{\alpha_2}) + b_{22}(x_{2s}^{\alpha_2} - x_{2s}^{\alpha_2})^2,$$

where y_s is the value of y at (x_{1s}, x_{2s}) . When $b_{11} \neq 0$, (B2) is algebraically equivalent to

$$(B3) \quad y = y_s + \frac{1}{b_{11}} \left[b_{11}^2 \left(z_1 + \frac{b_{12}}{2b_{11}} z_2 \right)^2 + cz_2^2 \right],$$

where $z_i = x_i^{\alpha_i} - x_{is}^{\alpha_i}$ (for $i = 1$ or 2). This shows that when $c > 0$, y takes a value which is (i) y_s or larger when $b_{11} > 0$, or else (ii) y_s or smaller when $b_{11} < 0$. Consequently the critical point is a minimum when $c > 0$ and $b_{11} > 0$ and a maximum when $c > 0$ and $b_{11} < 0$. When $c < 0$, the bracketed expression in (B3) is zero at (x_{1s}, x_{2s}) , positive on the line $z_2 = 0$ (i.e. $x_2 = x_{2s}$), and negative on the curve

$$z_1 + \frac{b_{12}}{2b_{11}} z_2 = 0.$$

This alternation between positive and negative values characterizes a saddle point. When $b_{11} = 0$, (B3) no longer applies, but a simpler proof from (B2) shows that (x_{1s}, x_{2s}) is a saddle point. (In this case $c < 0$; we still disallow $c = 0$.)

Appendix C. Path of Joint Optimality

The problem of joint optimality, in principle, can be solved by derivative methods using Lagrange multipliers, and a system similar to (B1) can be obtained. Unfortunately, it involves two distinct sets of exponents (α_1, α_2) , and, consequently, cannot be regarded as a linear system like (B1). However, the nonlinear search methods described in Appendix A can be used to maximize the two-variable function $y_a(x_1, x_2)$ subject to the constraint

$$(C1) \quad y_b(x_1, x_2) = C,$$

for some prescribed constant C .

To apply the search algorithm, it is necessary to replace the exact constraint (C1) by the inequality

$$(C2) \quad y_b(x_1, x_2) \geq C.$$

For examples in this paper, the constraints (C1) and (C2) always give the same result because, in the region of interest, y_a decreases as y_b increases, so that a maximum for y_a is achieved on the boundary of the region (C2). The constrained problem thus can be solved by maximizing the composite function

$$Y(x_1, x_2) = \begin{cases} y_a(x_1, x_2), & \text{if } y_b(x_1, x_2) \leq C, \\ y_a(x_1, x_2) - P[y_b(x_1, x_2) - C]^2, & \text{otherwise,} \end{cases}$$

where P is a larger penalty constant. All joint optima reported here were obtained in this way, using the Nelder-Mead simplex search described in Appendix A. Because the algorithm actually finds minima, Y was maximized by minimizing $-Y$.

Theoretically, points of joint optimality also could be found by maximizing the linear combination

$$Z(x_1, x_2) = w_a y_c(x_1, x_2) + w_b y_b(x_1, x_2),$$

with prescribed constant weights w_a and w_b . This method was

tried also, but it led to serious numerical instabilities that could be avoided by use of the function Y .