

Abstract.—Rearing experiments have shown that instantaneous growth rate, G (d^{-1}), of juvenile salmonids scales with body weight, W (g), as $G = \alpha W^{-b}$, where b has an average value of 0.37. Research on nonsalmonid fishes has shown that instantaneous natural marine mortality rate, M (d^{-1}), also scales with body weight as $M = cW^{-x}$, where x has an average value of 0.37. Therefore, if $b - x \sim 0$, then $c < \alpha$. These two hypotheses were tested for Pacific salmon with data on smolt-adult survival, s , smolt weight, W_0 (g), and adult weight, W (g), taken from the scientific literature. A nonlinear regression of survival on weight was developed, on the basis of allometric marine growth: $\log_e(s) = -(\alpha/\beta)(W^\beta - W_0^\beta)$, where $\alpha = c/\alpha$ and $\beta = b - x$. The regression model explained 33% of the variance in mean $\log_e(s)$ of sockeye salmon (*Oncorhynchus nerka*) with parameter values ($\pm 1SD$) of $\alpha = 0.226 \pm 1.171$ and $\beta = 0.120 \pm 0.990$. The model explained 68% of the variance in the pooled mean $\log_e(s)$ of pink (*O. gorbuscha*), chum (*O. keta*), coho (*O. kisutch*), and sockeye salmon, as well as steelhead trout (*O. mykiss*), with parameter values ($\pm 1SD$) of $\alpha = 0.528 \pm 0.490$ and $\beta = -0.053 \pm 0.221$. The near-zero estimates of β and the fractional estimates of α support the hypothesis that $x \sim 0.37$ and $c < \alpha$. Therefore, the best estimate of M for Pacific salmon is $M = 0.528\alpha W^{-0.37}$, or, since $\alpha = G/W^{-0.37}$, $M = 0.528G$. These survival-size and mortality-size relationships may be used to make preliminary estimates of survival and mortality for wild populations of Pacific salmon.

Allometry of marine mortality of Pacific salmon

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There are few accurate estimates of instantaneous natural marine mortality rate, M (d^{-1}), for the seven species of Pacific salmon (genus *Oncorhynchus*), despite the importance of this information for reconstructing stock histories (Pacific Salmon Commission, 1992) and for modeling the dynamics of salmon populations (Ricker, 1962, 1976; Walters et al., 1978). For example, Ricker's (1976) review of marine mortality of Pacific salmon identified only three estimates of monthly M for the last year of sea life, which had no known bias and small sampling errors. No new estimates of marine M of Pacific salmon have been added to the primary scientific literature in the last 15 years (Groot and Margolis, 1991), although many estimates of smolt-adult survival have been reported (Table 1).

The lack of new estimates of M is probably due to the difficulty of calculating it. Current methods of population enumeration provide, at most, an estimate of the number of smolts that go to sea and an estimate of the total number of adults that return 1–5 years later. They do not cover the 1–5 years of sea life during which marine mortality occurs. It is possible to calculate an average marine M for a brood year by dividing the natural logarithm of smolt-adult survival by the average duration of sea life. However, such estimates of average M cannot accurately predict the decrease in abundance of a salmon population for time periods shorter than a

salmon's entire sea life, as is required by cohort analysis and by simulation models with time steps of days or weeks. This is because M of fishes is not constant over a life stage but decreases with increasing body size. Average marine M underestimates M of smolts and overestimates M of adults. The degree of bias is proportional to the duration of sea life and can be significant for salmon that spend more than one year at sea.

To model the marine dynamics of a salmon population, a model of the way in which M varies with body size is required. Following Ursin (1967), Peterson and Wroblewski (1984), Dickie et al. (1987), McGurk (1993), and others, I assume that M follows the allometric rule: $M = cW^{-x}$, where W = body weight (g), $c = M$ (d^{-1}) at a weight of 1 g, and x is a dimensionless exponent. In this paper, I provide the first empirically derived estimate of the weight exponent x for the marine life stages of five of the nine species of the genus *Oncorhynchus*: pink (*O. gorbuscha*), chum (*O. keta*), coho (*O. kisutch*), and sockeye (*O. nerka*) salmon, and steelhead trout (*O. mykiss*). The estimates are based on an analysis of the weight dependency of published estimates of smolt-adult survival for wild populations. I also provide a method for estimating the coefficient c for Pacific salmon from the instantaneous marine growth rate of salmon.

Before describing the methods used to estimate x and c , it is useful

Table 1

Mean \log_e -transformed smolt-adult survival, s , for wild populations of five species of Pacific salmon (genus *Oncorhynchus*). s is the total number of adult salmon from a single brood year that returned to their natal stream to spawn divided by the total number of smolts from that stream and brood year that went to sea 1–5 years earlier. The number of returning adults was the sum of all commercial and sport catch plus escapement. SD is the standard deviation of mean $\log_e(s)$, and "no." is the number of brood years used to calculate mean $\log_e(s)$. W_0 is mean smolt weight and W is mean adult weight at return. Data were taken from the scientific literature.

Nursery system	Lat. (°N)	W_0 (g)	W (g)	$\log_e(s)$			Sources ¹
				mean	SD	no.	
Pink (<i>O. gorbuscha</i>)							
Hooknose Creek, B.C.	52.1	0.25	2289	-3.139	0.938	7	1, 16, 23
Fraser River, B.C.	49.1	0.25	2597	-3.571	0.545	12	1, 18, 23
Lakelse River, B.C.	54.4	0.25	2208	-3.969	0.555	8	1, 11, 23
Jones Creek, B.C.	49.3	0.23	2644	-4.255	0.632	12	8, 23
Chum (<i>O. keta</i>)							
Inches Creek, B.C.	49.1	0.35	5073	-4.397	0.272	6	6, 23
Fraser River, B.C.	49.1	0.38	5217	-4.591	0.606	14	1, 2, 23
Big Qualicum River, B.C.	49.4	0.36	5015	-5.243	0.756	14	9, 23
Coho (<i>O. kisutch</i>)							
Vedder-Chilliwack River, B.C.	49.1	11.00	3301	-1.424	0.088	4	7, 23, 24
Black Creek, B.C.	49.8	15.08	3160	-1.487	0.078	2	4, 23
Campbell River, B.C.	49.0	11.00	3301	-1.814		1	23, 25
Salwein Creek, B.C.	49.1	11.00	3301	-1.839		1	7, 23, 25
Carnation Creek, B.C.	48.9	8.44	3133	-1.860	0.385	17	13, 14
Salmon River, B.C.	49.1	8.90	3301	-1.895	0.185	3	23, 25
Carnation Creek, B.C.	48.9	4.91	3133	-2.093	0.514	17	13, 14
Salmon River, (Langley) B.C.	49.1	8.90	3301	-2.117	0.384	6	23, 26
Big Qualicum River, B.C.	49.4	11.18	3859	-2.273	0.335	15	9, 23
Oregon Production Area	44.0	11.15	4131	-2.487	0.408	26	5, 10
Upper Pitt River, B.C.	49.4	6.70	3301	-2.830	0.000	2	23, 24, 24
Birkenhead River, B.C.	50.4	11.00	3301	-3.194		1	23, 25
Steelhead (<i>O. mykiss</i>)							
Keogh River, B.C.	50.6	49.00	3794	-1.918	0.485	7	15, 28
Sockeye (<i>O. nerka</i>)							
Karluk Lake, AK	57.4	27.04	1679	-1.081	0.145	6	22
Big Lake, AK	61.5	19.46	1747	-1.179	0.449	4	19, 20
Karluk Lake, AK	57.4	31.71	1679	-1.211		1	22
Karluk Lake, AK	57.4	21.02	1679	-1.301	0.079	6	22
Egegik River, AK	58.2	15.10	2771	-1.380	0.353	5	29, 30
Hidden Lake, AK	60.5	44.48	2146	-1.473	1.156	17	19, 20
Leisure Lake, AK	59.5	5.81	2000	-1.491	0.598	8	19, 20
Hugh Smith Lake, AK	55.1	3.83	2934	-1.685	0.326	8	19, 20
Karluk Lake, AK	57.4	11.26	1679	-1.726		1	22
McDonald Lake, AK	56.0	3.13	3376	-1.775	0.345	8	19, 20
Tustumena Lake, AK	60.3	3.95	1700	-1.856	0.501	9	19, 20
Egegik River, AK	58.2	9.90	2771	-1.927	0.943	5	29, 30
Egegik River, AK	58.2	21.00	2771	-2.103	1.031	3	29, 30
Ugashik River, AK	57.5	17.90	2719	-2.307		1	29, 30
Crescent Lake, AK	60.4	2.96	2450	-2.345	1.465	2	19, 20
Kvichak River, AK	59.5	10.60	2498	-2.376	0.801	16	29, 30
Washington Lake, WA	47.3	18.50	2720	-2.466	0.478	11	3, 23, 27
Ugashik River, AK	57.5	11.90	2719	-2.477	0.940	4	29, 30
Chilko Lake, B.C.	51.4	4.62	2767	-2.502	0.596	34	12, 23
Hobiton Lake, B.C.	48.8	3.60	2152	-2.575	0.313	2	17, 23
Kvichak River, AK	59.5	5.90	2498	-2.615	1.131	16	29, 30
Wood River, AK	59.5	6.00	2550	-2.703	0.282	13	29, 30
Henderson Lake, B.C.	49.0	3.60	2152	-2.703	0.386	2	17, 23

Table 1 (continued)

Nursery system	Lat. (°N)	W_0 (g)	W (g)	$\text{Log}_e(s)$			Sources
				mean	SD	no.	
Great Central Lake, B.C.	49.4	3.57	2155	-2.783	0.205	3	17, 23
Babine Lake, B.C.	54.7	4.45	2784	-2.801	0.319	3	21, 23
Cultus Lake, B.C.	49.0	6.10	3074	-2.884	0.808	18	22, 23
Nuyakuk River, AK	60.0	6.60	2902	-2.917	1.662	4	29, 30
Bare Lake, AK	57.4	4.49	1847	-2.997	0.359	4	23
Ugashik River, AK	57.5	6.90	2719	-3.088	0.986	4	29, 30
Wood River, AK	59.5	8.60	2550	-3.163	0.949	14	29, 30
Babine Lake, B.C.	54.7	5.07	2715	-3.356	0.711	21	21, 23
Nuyakuk River, AK	60.0	4.60	2902	-3.474	1.374	4	29, 30

¹ Sources: 1 = Beachum and Murray (1990), 2 = Beachum and Starr (1982), 3 = Burgner (1991), 4 = Clark and Irvine (1989), 5 = Emlen et al. (1990), 6 = Federenko and Bailey (1980), 7 = Federenko and Cook (1982), 8 = Fraser and Federenko (1983), 9 = Fraser et al. (1983), 10 = Gunsolus (1978), 11 = Harding (1970), 12 = Henderson and Cass (1991), 13 = Holtby et al. (1990), 14 = Holtby and Healey (1986), 15 = Hooton et al. (1987), 16 = Hunter (1959), 17 = Hyatt and Stockner (1985), 18 = International Pacific Salmon Fisheries Commission (1986), 19 = Koenings et al. (1993), 20 = G. Kyle, Alaska Dep. Fish and Game, Soldatna, Alaska 99669, personal commun., 21 = Macdonald et al. (1987), 22 = Ricker (1962), 23 = Ricker (1981), 24 = Schubert and Federenko (1985), 25 = Schubert and Zallen (1990), 26 = Schubert et al. (1974), 27 = Thorne and Ames (1987), 28 = Ward and Slaney (1988), 29 = Woolington et al. (1991), 30 = Yuen et al. (1981).

to review briefly the history of research on the weight dependency of marine mortality in fishes in order to establish testable hypotheses about the probable values of x and c .

Previous research on allometry of M

It has been known for at least 40 years that smolt-adult survival of Pacific salmon is positively correlated with smolt size (Foerster, 1954; Ricker, 1962). Positive and significant correlations have been reported within single populations of coho salmon (Holtby et al., 1990) and steelhead trout (Ward and Slaney, 1988), and among populations of sockeye salmon (Ricker, 1962; Koenings et al., 1993). To date, the relationship between smolt-adult survival and adult size of Pacific salmon has not been examined, nor have the interrelationships between smolt-adult survival, smolt size, and adult size.

Mathews and Buckley (1976) were the first to model the functional relationship between M of Pacific salmon and body size. They assumed that marine M of hatchery-reared coho salmon released into Puget Sound, Washington, was proportional to W^{-1} . In his comprehensive review of marine M of salmon, Ricker (1976) judged their assumption to be intuitively reasonable but unproven. Furnell and Brett (1986, a and b) used the inverse-weight hypothesis to model the marine population dynamics of Babine Lake sockeye salmon, despite the lack of empirical support for the hypothesis (McGurk, 1986b).

In the nearly two decades since the inverse-weight hypothesis was presented, much literature has been

published showing that the weight-exponent of mortality for fishes actually falls within the range of 0.25 to 0.40. Ursin (1967) was the first to measure the mortality-size relationship of fish; his review of published reports showed that natural mortality scaled with $W^{-0.33}$. Fenchel (1974) and Blueweiss et al. (1978) reported that the intrinsic rate of natural increase of animals, which is equal to M under equilibrium conditions, decreased with $M^{-0.25}$. Banse and Mosher (1980) showed that the weight exponent of the production-biomass ratio of animal populations, which is also equivalent to M under equilibrium conditions, was -0.37 . Peterson and Wroblewski (1984) derived a size-dependent equation for the mortality rate of marine pelagic organisms, including invertebrates and fishes, from biomass spectrum theory and concluded that M scaled with $W^{-0.25}$. I reported a similar conclusion from a review of natural mortality of marine organisms that included invertebrates, fishes, and marine mammals (McGurk, 1986a) and later showed that M for larval and adult stages of both Atlantic herring (*Clupea harengus*) and Pacific herring (*C. pallasii*) scaled with dry weight to the power of -0.4 (McGurk, 1993).

These studies showed that data sets incorporating a wide variety of distantly related groups of animals tend to have weight exponents of M close to -0.25 , whereas data sets restricted to a single species or a group of closely related species tend to have weight exponents close to -0.40 . In an attempt to explain this observation, Dickie et al. (1987) proposed that there are two size-dependent processes: 1) over an entire ecosystem the slope of mortality versus

weight is about -0.18 and is due mainly to metabolic processes, but 2) within individual species the slope is about -0.37 and is related to ecological factors such as the relative sizes and distributions of predators and prey.

Therefore, the primary hypothesis to be tested in this study is that M scales as $W^{-0.37}$ for Pacific salmon.

Much less is known of the probable numerical value of the parameter c . However, an upper limit can be placed on c if some assumptions are made about the value of the weight exponent of growth rate in Pacific salmon. The instantaneous rate of growth of salmonid fishes, G (d^{-1}), decreases with body weight according to the allometric relationship $G = aW^{-b}$, where a is the instantaneous growth rate (d^{-1}) at a weight of 1 g, and b is a dimensionless exponent (Brett and Shelbourne, 1975; Elliott, 1975; Jobling, 1983). The biomass of a brood year of salmon is usually assumed to increase continuously with age, at least until the brood year is old enough to be fished. Therefore, if $b \sim x$, then c must have an absolute value that is lower than a . Otherwise, the biomass of a brood year would not increase with age, and may even decrease with age, thereby extinguishing the brood year before it was able to reproduce. To assess the validity of the assumption that $b \sim x$, I briefly reviewed the history of growth experiments with salmonid fishes.

Previous research on allometry of G

Estimates of b have been published for seven species of salmonid fishes: five species of Pacific salmon (pink, coho, and sockeye salmon, as well as chinook salmon [*O. tshawytscha*] and steelhead trout), brook trout [*Salvelinus fontinalis*], and brown trout (*Salmo trutta*). Reported values of b have ranged from 0.20 to 0.50 with a mean of 0.37 (SD=0.08, $n=19$) (Iwama and Tautz, 1981). With one exception, all values were estimated from juvenile salmonids weighing 0.3 to 350 g that were reared in hatcheries or laboratory aquaria. The exception was Parker and Larkin (1959) who reported that b ranged from 0.20 to 0.33 for sexually mature steelhead captured from the Chilliwack River, B.C., and from 0.37 to 0.44 for chinook salmon captured in their final year of sea life off southeast Alaska.

Brett and Shelbourne (1975) were the first to identify a universal value of b ; they concluded that the average value for salmonids was 0.41 (SD=0.06, $n=10$). Elliott (1975) reported exponents ranging from 0.28 to 0.33 for juvenile brown trout, which led Brett (1979) to suggest that the range of exponents for salmonids may be wider than that reported by Brett

and Shelbourne (1975). Iwama and Tautz (1981) argued that the best value of b for the purpose of modeling growth of hatchery-reared salmonids was closer to 0.33 than 0.41 because the line of $W^{1/3}$ versus time was linear with temperature over the temperature range commonly found in fish hatcheries and because $W^{1/3}$ is easily converted to length. Jobling (1983) reported that b for Atlantic cod (*Gadus morhua*) and seven other nonsalmonid fishes weighing 0.9 to 150 g ranged from 0.33 to 0.63 with a mean of 0.41 (SD=0.06, $n=52$) and argued that a universal slope of 0.4 was applicable to all species of fish. Wangila and Dick (1988) found that the average value of b for two strains of rainbow trout, the freshwater form of steelhead trout, was 0.31 but that slopes varied significantly among strains and rearing temperatures, suggesting that a universal value of b must be employed with caution.

In summary, the best estimate of b for salmonids is the grand mean of all exponents or 0.37 (Iwama and Tautz, 1981). The value of b for sockeye salmon, the species of salmon on which the most experimental work has been conducted, ranges from 0.39 to 0.49 with a mean of 0.41 (SD=0.05, $n=4$). This shows that b is indeed close to the most probable value of x , which in turn supports the hypothesis that c is a constant fraction of a , i.e. $c = \alpha a$.

Therefore, the second hypothesis to be tested by this study is that α has a value greater than zero but less than one.

Allometry of survival

To test the hypotheses that $x = 0.37$ and $c = \alpha a$, a mathematical model that relates smolt-adult survival to smolt weight and adult weight is required. Such a model can be created by using size as an index of age in the simple allometric model of natural mortality. The first step in developing the model is the adoption of a growth model that can be easily integrated over time so that age and size can be interchanged.

Over periods of days, growth in weight of salmon can be accurately modeled with the well-known exponential model:

$$dW/dt = GW. \quad (1)$$

However, over longer periods of time, G decreases with increasing weight. Substituting $G = aW^{-b}$ into Equation 1 leads to

$$dW/dt = aW^{1-b}, \quad (2)$$

which can be integrated over time to give the growth model:

$$W = (W_0^b + abt)^{1/b}, \quad (3)$$

where W_0 = initial weight (g). Equation 3 was first introduced by Parker and Larkin (1959) to describe marine growth of chinook salmon and steelhead trout. Elliott (1975) and Iwama and Tautz (1981) used the model to describe successfully the freshwater growth of several species of salmonids. Apart from being based on an allometric growth argument, this model has the important advantage of easier integration over time in comparison with other three-parameter growth models that have been applied to fish.

Mortality of Pacific salmon can also be modeled as a power function of body weight:

$$dN/dt = -MN = -cW^{-x}N, \quad (4)$$

where N is the population number and c has units of d^{-1} (Ursin, 1967; Peterson and Wroblewski, 1984; McGurk, 1993). Substituting Equation 3 into Equation 4 and integrating over the duration of sea life gives an expression for smolt–adult survival, s , in terms of body weight:

$$\log_e(s) = \log_e(N/N_0) = -\left(c/(a(b-x))\right)(W^{b-x} - W_0^{b-x}), \quad (5)$$

where N = the total number of adults that return to their natal stream (the sum of catches in all commercial and recreational fisheries plus the number of fish that escaped the fisheries and were counted on the spawning grounds); N_0 = the number of smolts; W = adult weight (g); and W_0 = smolt weight (g). Aggregating parameters in Equation 5 gives a simple expression that is suitable for nonlinear regression:

$$\log_e(s) = -(\alpha/\beta)(W^\beta - W_0^\beta), \quad (6)$$

where $\alpha = c/a$ and $\beta = b - x$. Both α and β are dimensionless numbers.

In this paper, Equation 6 was used to regress $\log_e(s)$ on W and W_0 and thereby estimate values of α and β . I tested two hypotheses about the values of α and β : 1) β is a small number that is not significantly different from zero because $b \sim x \sim 0.37$, so $\beta = b - x = 0$; and 2) α has a value significantly lower than 1.0 but greater than zero because $\alpha = c/a$ and $c < a$.

In fitting Equation 6 to the available smolt–adult survival data, it was necessary to pool survival and size information from five species of Pacific salmon because, with the exception of sockeye salmon, the range of mean survivals and mean sizes within a single species was too narrow to estimate reliable

values of α and β for particular species. Therefore, I assumed that there are average values of c and x for *Oncorhynchus* species which have practical utility over different time and space scales (species, population, and brood year) and that overlaid on this average allometry is species-specific, population-specific, and brood-year specific variability which cannot as yet be estimated given the information available in the primary literature.

Materials and methods

Sources of data

Survival I searched the primary scientific literature for well-documented records of smolt–adult survival for wild populations of *Oncorhynchus*. Records derived entirely from secondary sources were not included because of difficulties in obtaining information on body sizes. A few records reported in primary sources were also excluded for the same reason. Populations of pink, chum, and coho salmon that were composed predominately of hatchery production were excluded because of controversy over whether hatchery fish have the same smolt–adult survival as wild fish of the same body size. The exceptions to this rule were estimates of smolt–adult survival calculated from populations of sockeye enhanced by stocking of young fry into nursery lakes (e.g. Leisure Lake, Alaska: Koenings and Burkett, 1987; Koenings et al., 1993). These fish spent a minimum of one year after release in a natural nursery system before migrating to sea.

Smolt–adult survivals were collected only for brood years, defined as the production of adult fish of all ages from a single year's spawning in a single nursery system. To account for multiple ages of return, the number of returning adults of the i th brood year, N_i , was summed over all ages as

$$N_i = \sum^t (C_{it} + E_{it}), \quad (7)$$

where C_{it} = the catch of the i th brood year at an age of return of t years; and E_{it} = the escapement of the i th brood year at an age of return of t years. To account for multiple ages of smolting, the number of smolts was summed over all smolt ages. For all populations of pink and chum salmon, there was only one smolt age because the newly emergent fry immediately went to sea. The same situation applied to some coho and sockeye populations that were predominantly of a single smolt age. For example, 95% of Chilko Lake sockeye smolts migrate to sea at an age of 1+ yr (Henderson and Cass, 1991). The exception

to the rule of combining smolt ages were those populations of coho and sockeye salmon for which the number of returning adults could be assigned an age at smolting based on scale patterns. In those cases, each age class of smolts was treated as a separate "brood year" and separate smolt-adult survivals calculated for each smolt age class.

Smolt-adult survival is log normally distributed (Peterman, 1981), so the best estimate of the central tendency of smolt-adult survival for a system is the geometric mean survival or the arithmetic mean of the \log_e -transformed survivals for each brood year for a particular system. Only $\log_e(s)$ was used to estimate the parameters of Equation 6 because only in a few cases was each brood year's survival accompanied by a mean smolt weight or a mean adult weight, or both. In almost all cases, all that was available from the literature was a mean smolt weight and a mean adult weight for each system. The exceptions were those systems for which mean smolt weights and mean smolt-adult survivals were available for each of several age classes of smolts (i.e. sockeye salmon from rivers entering Bristol Bay, Alaska; Yuen et al., 1981; Woolington et al., 1991).

Weight In the absence of direct reports, mean smolt weights of pink and chum salmon were assumed to be the midpoints of the ranges of emergent fry weights reported by Beachum and Murray (1990) for eggs incubated at a constant 8°C (0.25 g for pink and 0.35 g for chum). For studies that did not report mean smolt weight for coho and sockeye salmon, and for which there were no accompanying reports that included smolt weights, mean smolt weight was estimated from mean smolt length by using weight-length equations reported by Chapman (1965) and Koenings and Burkett (1987).

Mean adult weight of coho salmon from Carnation Creek was calculated from mean length of returning adults by using the weight-length relationship reported by Holtby and Healey (1986). Mean adult weight of steelhead trout from the Keogh River was calculated from mean length of returning spawners with the weight-length regression reported by Hooton et al. (1987). Mean adult weights for other systems were taken from records of commercial fisheries because there was no published information on their mean size at re-entry to freshwater (Gunsolus, 1978; Ricker, 1981; Yuen et al., 1981; Kyle¹). I converted mean lengths (L , mm) of Bristol Bay sockeye to mean weights (W , g) using a functional regression of $\log_e(W)$

on $\log_e(L)$ calculated from mean weights and lengths for separate age groups of Bristol Bay sockeye for the years 1963–77: $W = 1.713 \times 10^{-5}L^{3.00}$ ($n=61$, $r^2=0.94$, $P<0.001$). Mean adult weight for each nursery system was the mean weight for the ocean statistical area adjacent to the stream for which smolt-adult survivals were available. This procedure assumes that the majority of the catch from a population is taken by marine salmon fisheries near the mouth of the population's natal stream.

In most systems in British Columbia, mean adult weight was calculated from the years for which smolt-adult survivals were reported. This is important because mean weight of pink, chum, coho, and sockeye salmon in British Columbia has decreased over the last 30 years (Ricker, 1981). However, this was not possible for all systems, particularly those with smolt-adult survivals reported after 1981. In those cases, mean adult weight was taken from the latest catch data available. Thus, the accuracy and reliability of mean adult weights is variable, being relatively high for most systems in British Columbia but lower for most systems in Alaska. The exceptions are the sockeye rivers of Bristol Bay where a 20-yr time series of adult sockeye weights was reported by Yuen et al. (1981).

Mean adult weight for nursery systems with more than one age group of smolts was assumed to be the same for all smolt ages. This assumption was necessary because adult weights were rarely reported for separate smolt ages.

Fitting the model

Equation 6 was fitted with nonlinear regression (NLR) by using the Levenberg-Marquardt algorithm contained in the NLR procedure of the computer program SPSS (SPSS Inc., 1993). The mean $\log_e(s)$ for each system was first regressed on mean W and W_0 for sockeye salmon and then for all species combined. Mean $\log_e(s)$ was weighted by sample size under the assumption that the accuracy of mean $\log_e(s)$ is directly proportional to the number of brood years used to calculate it. The coefficients of determination (r^2) of the regression models were adjusted for the number of degrees of freedom in the model. Standard errors of regression parameters were based on asymptotic or large-sample approximations. It was not possible to test the statistical significance of a nonlinear regression using the usual F -test applied to linear regressions, because the residual mean square of a nonlinear regression is not an unbiased estimate of the error variance (SPSS Inc., 1993). The significance level, P , for linear correlations was set at 5%, i.e. $P = 0.05$.

¹ Kyle, G. 1994. Alaska Dep. of Fish and Game, 34828 Kalifornsky Beach Road, Soldatna, AK 99669-3150. Personal commun.

Estimation of x and c from β and α

An estimate of x was obtained by subtracting an estimate of β from the weight exponent of growth rate, b , i.e. $x = b - \beta$. Estimates of β were obtained by fitting regression Equation 6 to survival and weight data. The appropriate value of b was obtained from a review of the scientific literature on salmonid growth experiments (see introductory section). Estimates of c could not be obtained directly. Instead, c was expressed as a fraction of the initial growth rate, i.e. $c = \alpha a$. Estimates of α were obtained from regression Equation 6.

Results

I found 20 studies that reported 52 mean smolt–adult survivals for five species of Pacific salmon (Table 1). The means were calculated from 432 brood years released from 38 nursery systems ranging over more than 15° of latitude from the Oregon coast (44.0°N) to southcentral Alaska (61.5°N). Over 60% of the mean survivals were reported for sockeye salmon.

Sockeye salmon

The regression of $\log_e(s)$ on W and W_0 for sockeye salmon explained 33% of the variance in mean $\log_e(s)$, with parameter values (± 1 SD) of $\alpha = 0.226 \pm 1.171$ and $\beta = 0.120 \pm 0.990$ (Fig. 1). The estimate of α indicated that c had a value that was only 22.6% of the value of a . The estimate of β indicated that x has a value of 0.29, if b for sockeye salmon is assumed to be closer to 0.41 than to 0.37 (Brett and Shelbourne, 1975).

There were no significant correlations between residual mean $\log_e(s)$ and W_0 , W , latitude of the nursery system, or the predominant smolt age, indicating that body weight was the single most important variable affecting smolt–adult survival. The sensitivity of α and β to possible underestimation or overestimation of adult sockeye weight was examined by fitting Equation 6 after altering W by -25 to $+25\%$ at 5% intervals: α decreased by 8% for a 25% decrease in W and increased by 6% for a 25% increase in W , indicating that α was relatively insensitive to bias in estimation of W (Table 2); β increased 26% for a 25% decrease in W and decreased 17% for a 25% increase in W , indicating that β was about three times more sensitive to bias in estimation of W than was α . The adult weights of sockeye salmon shown in Table 1 are more likely to be underestimates of the true weight at return than overestimates because they were calculated from mean weights of commer-

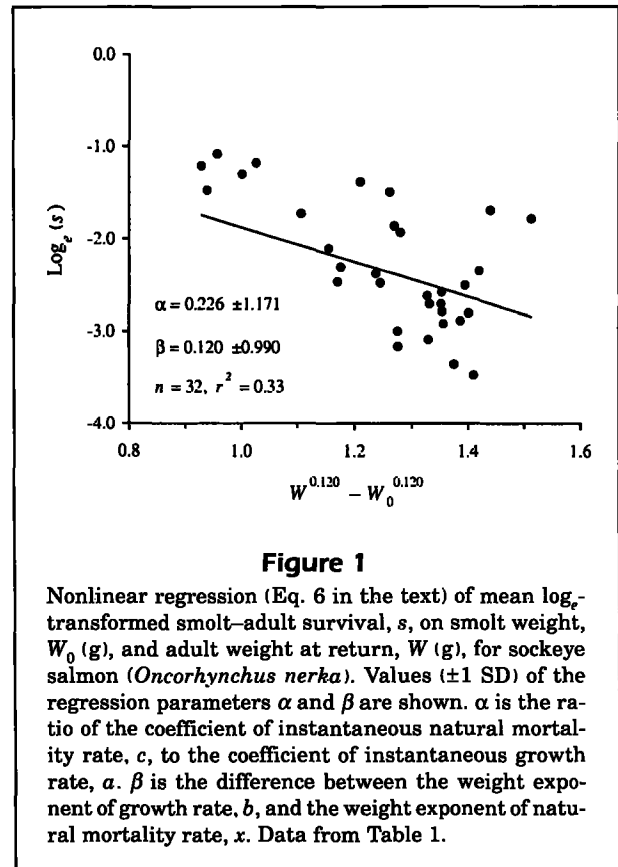


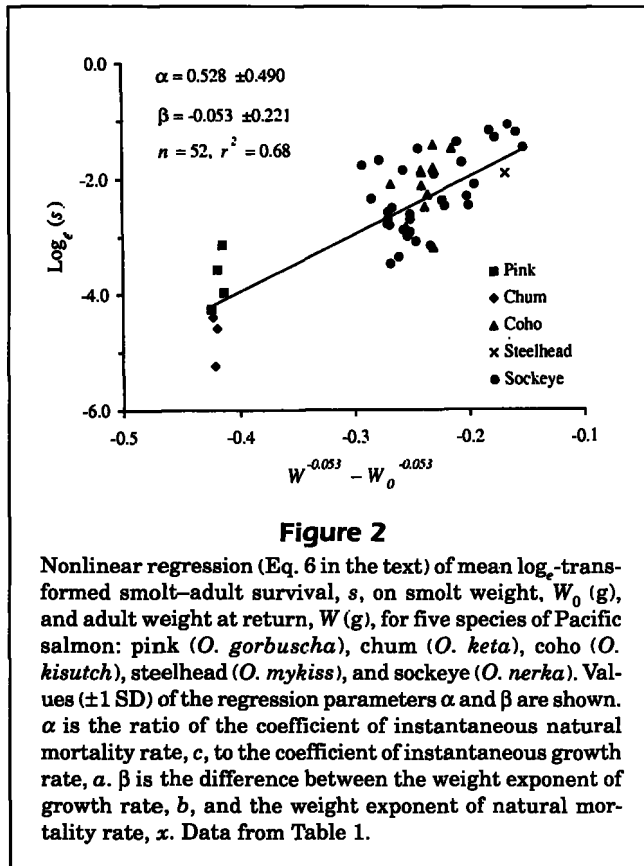
Figure 1

Nonlinear regression (Eq. 6 in the text) of mean \log_e -transformed smolt–adult survival, s , on smolt weight, W_0 (g), and adult weight at return, W (g), for sockeye salmon (*Oncorhynchus nerka*). Values (± 1 SD) of the regression parameters α and β are shown. α is the ratio of the coefficient of instantaneous natural mortality rate, c , to the coefficient of instantaneous growth rate, a . β is the difference between the weight exponent of growth rate, b , and the weight exponent of natural mortality rate, x . Data from Table 1.

cial catches rather than mean weights of spawners in their natal stream. The last few months of growth may not be included in adult weights from commercial catches. Because underestimation of W tends to inflate β , the true value of β for sockeye salmon is lower than 0.120 and, therefore, the true value of x for sockeye salmon is greater than 0.29.

Combined species

A regression of mean $\log_e(s)$ on W and W_0 for the five species of salmon combined explained 68% of the variance in mean $\log_e(s)$ with parameter values (± 1 SD) of $\alpha = 0.528 \pm 0.490$ and $\beta = -0.053 \pm 0.221$ (Fig. 2). The estimate of α indicated that c had a value that was 52.8% of the average value of a . The estimate of β indicated that x had a value of 0.38 to 0.42 for an average b of 0.33 or 0.37, respectively. The doubling of the r^2 statistic over that measured for the sockeye regression was accompanied by a substantial decrease in the variance of α and β . The coefficient of variance of α , $CV_\alpha (=SD_\alpha \cdot 100/\alpha)$, decreased from 518% for the sockeye regression to 93% for the combined regression. CV_β decreased from 825% for the sockeye regression to 417% for the combined regression.



There were no significant correlations between residual mean $\log_e(s)$ and W_0 , W and latitude of nursery system. Residual mean $\log_e(s)$ did not vary significantly among species (ANOVA: $F_{4,47}=1.995$, $P=0.111$), indicating that body weight was the most important variable affecting mean smolt-adult survival. A sensitivity analysis showed that α changed by 1% or less for a $\pm 25\%$ change in W , indicating that its value was essentially independent of bias in estimation of W (Table 2). β increased by 21% for a 25% decrease in W and decreased by 15% for a 25% increase in W . However, the maximum change in the absolute numerical value of β caused by $\pm 25\%$ changes in W was only 0.008, indicating that the near-zero value of β was essentially independent of bias in estimation of W .

Discussion

Parameters α and β

The estimates of α and β derived in this study are consistent with the original hypotheses. The small, near-zero value of β estimated for sockeye salmon alone and for five species of *Oncorhynchus* combined

supports the hypothesis that the weight exponents of growth and mortality for *Oncorhynchus* species are virtually identical. There is no consensus on the exact value of the weight exponent of growth rate of Pacific salmon. However, the average of all reported values of salmonid b is 0.37 (Iwama and Tautz, 1981), which is identical to the weight-exponent of natural mortality for single species that was proposed by Dickie et al. (1987). Thus, the cumulative evidence supports the hypothesis that, on average, marine M of Pacific salmon scales with $W^{-0.37}$. Although the average value of x is close to 0.37, it may also vary among populations and species, and among year classes within populations and species. For example, this study found that x varied from a low of 0.29 for sockeye salmon to a high of 0.42 for the data from five species.

The second important feature of the regression parameters is that α is significantly lower than 1.0 which supports the hypothesis that initial mortality rate, c , is a fraction of initial growth rate a . The combined regression indicates that c has a value equal to 52.8% of the value of a at any body weight. Therefore, the best estimate of M for all species of Pacific salmon combined can be predicted as: $M = 0.528aW^{-0.37}$. Estimates of M can be obtained if one has an independent estimate of the parameter a , perhaps through scale analysis. Alternatively, if one assumes that $a = G/W^{-0.37}$, then $M = 0.528G$. In other words, average marine M for a short time period can be estimated if one has an independent estimate of average G over the same short period.

Third, the absence of significant differences in residual mean $\log_e(s)$ among species suggests that a single survival-weight relationship may be applicable to all five species of *Oncorhynchus*. This finding supports the basic assumption of this paper—that species within the genus *Oncorhynchus* share similar allometries of growth and mortality but differ in smolt and adult body sizes. However, it is clearly inappropriate to assume that the survival-weight and mortality-weight relationships developed in this study can be applied without qualification to every salmon population or to every brood year within each population. Accurate brood-year-specific prediction of salmonid survival will depend on information collected from that brood year.

Sources of error

This paper presents preliminary numerical estimates of α and β for Pacific salmon. Improved estimates will undoubtedly be calculated in the future as more information on smolt-adult survival and smolt and adult weights become available in the primary literature.

Table 2

Analysis of the sensitivity of the regression parameters α and β of text Equation 6 to changes in the mean adult body weights, W , of Pacific salmon (genus *Oncorhynchus*) shown in Table 1. Mean weights were changed by -25% to $+25\%$ at 5% increments and α and β were recalculated at each increment. The 95% confidence limits (CL) of α and β are also shown. Analyses were performed for sockeye salmon alone and for five species of salmon combined: pink (*O. gorbuscha*), chum (*O. keta*), coho (*O. kisutch*), steelhead (*O. mykiss*), and sockeye (*O. nerka*).

Percent change in W	α -95%CL	α	α +95%CL	β -95%CL	β	β +95%CL
Sockeye (<i>O. nerka</i>)						
-25	-0.190	0.207	0.605	-0.222	0.151	0.523
-20	-0.192	0.211	0.614	-0.225	0.144	0.513
-15	-0.193	0.215	0.624	-0.228	0.137	0.503
-10	-0.194	0.219	0.632	-0.231	0.131	0.494
-5	-0.195	0.222	0.640	-0.234	0.126	0.485
0	-0.197	0.226	0.648	-0.236	0.120	0.477
5	-0.197	0.229	0.655	-0.239	0.116	0.470
10	-0.198	0.232	0.662	-0.241	0.111	0.463
15	-0.199	0.235	0.669	-0.243	0.107	0.456
20	-0.200	0.238	0.675	-0.244	0.103	0.450
25	-0.200	0.240	0.681	-0.246	0.099	0.444
Pacific salmon combined						
-25	0.386	0.522	0.659	-0.105	-0.042	0.021
-20	0.387	0.524	0.661	-0.107	-0.045	0.018
-15	0.388	0.525	0.662	-0.109	-0.047	0.015
-10	0.389	0.526	0.663	-0.111	-0.049	0.013
-5	0.390	0.527	0.664	-0.113	-0.051	0.010
0	0.391	0.528	0.665	-0.115	-0.053	0.008
5	0.392	0.529	0.666	-0.116	-0.055	0.006
10	0.392	0.530	0.667	-0.118	-0.057	0.004
15	0.393	0.530	0.668	-0.119	-0.058	0.002
20	0.394	0.531	0.669	-0.120	-0.060	0.001
25	0.394	0.532	0.669	-0.122	-0.061	-0.001

The most important source of error in this analysis was associated with estimating mean body weights of smolts and adults. The methods of estimating mean adult weights were less than optimal mainly because of a lack of information on this subject in the primary literature. Part of the problem in obtaining adult weights is that salmon fisheries are rarely located at the ocean terminus of the salmon's spawning migration. Rather, fishing pressure on a single stock is often distributed over thousands of square kilometers and over several separate management jurisdictions. For those studies that did not report mean adult weight, it was necessary to assume that all fisheries were terminal in order to estimate adult weight from catch records. The assumption was undoubtedly violated for many stocks that are subjected to fishing mortality for a considerable portion of their last year of sea life. For those populations, mean weight at sea will tend to underestimate weight at re-entry.

A second source of error was the inability to adjust mean adult weight for the presence of jacks, those

male salmon that mature at an early age and small size. The effect of a significant number of jacks in a population is to underestimate adult weight at return, thereby increasing the bias introduced by assuming that adult weight can be estimated from commercial catches. However, sensitivity analyses showed that adult weight would have to be consistently over- or under-estimated by more than 25% before these two sources of error would seriously affect the conclusions of this study.

A third source of error was the use of weights predicted from length rather than observed weights, because weight-length relationships may vary among populations and among brood years within populations. However, Koenings and Burkett (1987) reported that known weight-length relationships for sockeye smolts in Alaska were virtually identical. Further, this source of error would not bias the analysis in a specific direction.

The lack of smolt and adult weights derived from the same brood years resulted in the within-population variation in survival being confounded with

among-population variation in survival. This does not invalidate the model as long as one assumes that within a single species or group of closely related species, the weight exponents of growth and mortality are stable parameters with similar ranges and little variation.

The second most important source of error was the choice of an appropriate value of b for the growth model. Most estimates of b were available from experiments with young salmonids grown in enclosures at constant temperatures and fed to satiation or ad libitum. These are not conditions commonly faced by wild salmonids, and thus making use of these estimates in estimating marine mortality for wild salmonids is suspect. There is clearly a need for more research on the weight-, ration- and temperature-dependence of growth of large, sea-going salmonids derived from wild stocks and grown in marine enclosures.

Effect of latitude on smolt–adult survival

Koenings et al. (1993) demonstrated that smolt–adult survival of sockeye salmon increased with latitude of nursery systems as well as with smolt length, a finding that was not confirmed by this study for sockeye salmon or for any other species of *Oncorhynchus*. There are at least two possible reasons for the lack of a latitude effect in this study. First, within-system variation in smolt–adult survival was ignored because adult weights were not available for each brood year for each system. In contrast, Koenings et al. (1993) were able to compare smolt–adult survivals and smolt lengths for individual brood years within each system. Second, this study regressed smolt–adult survival on both adult weight and smolt weight rather than on smolt weight alone. This allowed variation in survival to be adjusted for variation in adult size between nursery systems as well as for variation in smolt size. The latitude effect observed by Koenings et al. (1993) may have resulted from restricting analysis of survival-weight relations to smolt size.

Applications of allometry of mortality for Pacific salmon

The equations reported in this study may be useful for making preliminary estimates of survival and mortality for wild populations of *Oncorhynchus* species for which information is limited. For example, the results of this study imply that smolt–adult survival of wild chinook salmon should be similar to other species of salmon with similar smolt and adult weights. There are at present no published estimates of wild chinook smolt–adult survival in the primary

literature. The allometry of M reported in this study may also be useful for modeling survival and mortality of Pacific salmon in spatially explicit simulation models (i.e. Walters et al., 1978). Not only may it provide more realistic daily mortality rates than could be calculated from fry-smolt and smolt–adult survivals, but by relating mortality with body size it links survival to trophic dynamics and to density-dependent growth.

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