PERSPECTIVE

Cycles of abundance among Fraser River sockeye salmon (*Oncorhynchus nerka*)

W.E. Ricker

Abstract: In some but not all populations of sockeye salmon (*Oncorhynchus nerka*) that mature mainly at age 4, there has been a persistently "dominant" line, a "subdominant" line about 10–25% as large, and two weak lines having less than 1% as many fish as the dominant one. Suggested causes of this phenomenon that have been shown to be wrong or inadequate are the presence of a few sockeye of ages 3 and 5 in the spawning stocks and a somewhat larger rate of harvest of the nondominant lines. The only plausible type of explanation that has been suggested so far involves interaction between the dominant line and the others, and the only specific example involves a 4-year cycle of abundance of a predacious fish at Shuswap Lake, described by F.J. Ward and P.A. Larkin. Other types of interaction are possible, but have not been documented. The magnitudes of the instantaneous interaction mortality rates at Shuswap Lake are estimated as about 0.78 per generation for the subdominant line out of a 7.65 total, and 1.11 out of 7.94 for the weak line 3, line 4 being similar.

Résumé : Dans certaines populations, mais non dans toutes, de saumon sockeye (*Oncorhynchus nerka*) dont la maturité est atteinte principalement à l'âge de 4 ans, on a observé une lignée « dominante » de manière persistante, une lignée « subdominante » qui compte environ 10–25% du nombre de poissons de la lignée dominante et deux lignées faibles comptant moins de 1%. Les causes proposées de ce phénomène que l'on a démontré erronées ou inappropriées sont la présence de quelques saumons d'âge 3 et 5 ans dans les stocks de reproducteurs, et un taux de récolte légèrement plus élevé dans les lignées non dominantes. Le seul type d'explication plausible proposé jusqu'ici fait intervenir l'interaction entre la lignée dominante et les autres, et le seul exemple spécifique fait intervenir un cycle d'abondance de 4 ans d'un poisson prédateur du lac Shuswap décrit par F.J. Ward et P.A. Larkin. D'autres types d'interactions sont possibles, mais n'ont pas été documentées. L'importance des taux instantanés de mortalité par interaction dans le lac Shuswap est estimée à environ 0,78 par génération pour la lignée subdominante sur un total de 7,65 et à 1,11 sur 7,94 pour la lignée 3 faible, la lignée 4 étant semblable.
[Traduit par la Rédaction]

1. Introduction

Among Fraser River sockeye salmon (*Oncorhynchus nerka*) the principal age of maturity is 4 years, so that most of the populations have been treated as though divided into four lines of descent. Also, both in the past and at present, there have been large differences in abundance between these four lines in some populations. When Earle Foerster and I were working at Cultus Lake during the 1930s, we came to the conclusion that the only reasonable kinds of explanation for this would involve some type of interaction between the lines. One possibility was a buildup of populations of predacious fishes, or of parasites, in a year when young sockeye were abundant, which would put pressure on the young fish of succeeding generations. Or even without any change in predator abundance, if one generation, by chance, became much more numerous than the others, it might saturate the appetites of the predators, perhaps at a life-history stage like downstream migration, when for a short time the smolts are assembled in large numbers. Two other possibilities were cannibalism among the sockeye

themselves, or some kind of interaction with the lake's production of plankton crustaceans, but there was evidence against both of these. These observations and conjectures were put forward in 1942 and elaborated in 1950 (Foerster and Ricker 1942; Ricker 1950).

Maps of the Fraser watershed are available in the annual reports of the Fraser River Panel of the Pacific Salmon Commission and in many of their special reports, most recently that by Gilhousen (1992).

Since 1950, much has been learned about sockeye, including a direct attack on the problem of dominance at Shuswap Lake by Ward and Larkin (1964). Recently there have been a dozen or more pertinent publications, whose titles are listed in the References and which will be mentioned in what follows.

Terminology

Population or stock: Sockeye that spawn in a particular stream or lake, at a particular time of year, or in a series of similar streams from which the fry move into the same lake. The name given to a population is either that of the lake in which its members make their freshwater growth, that of the principal river in which they spawn, or both.

Run: The spawners of, and the catch taken from, a given population or populations in a given year.

W.E. Ricker. Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, BC V9R 5K6, Canada.

Year-class: Sockeye produced from eggs laid in a particular year (in summer or autumn).

Adult sockeye: Sockeye that have spent all or part of at least 3 years in the ocean and are of age 4 or older when spawning (counting from the fertilized egg), or are nearing that age during their return migration toward or in fresh water.

Jack sockeye: Sockeye that have made 2 years of ocean growth and are usually of age 3 when spawning. They are much smaller than the adults and are excluded from some statistical tables.

Recruits: Anadromous sockeye (catch plus escapement) produced by a given year-class; often only adults are considered.

Line or cycle line: A sequence of runs separated by an interval that is the principal age of maturity of the population in question. On the Fraser River, successive spawnings of a line are 4 years apart, except possibly at Pitt Lake where age 5 fish are common. Lines are identified by the year in which each occurred at the start of this century, i.e., 1901–1904, and also (where dominance exists) by their position in the cycle (see below).

Cycle: A sequence of x lines in successive calendar years, where x is the principal age of maturity in the population ($x = 4$ on the Fraser). Any individual cycle is identified by the year-classes included, e.g., 1984–1987. (Some authors, including myself in 1950, use cycle in the sense of line as defined above).

Dominance and cycle position: A line whose average abundance is considerably greater than that of other lines in the population is called dominant. Those of the 1901 line up to 1913 are called the old big years. The dominant line is assigned the first position in the cycle and is called line 1. The other lines follow in order regardless of their relative abundance. Line 2 is usually next to line 1 in abundance, and has been called subdominant when that is so. Lines 3 and 4 are usually quite scarce, and are here called weak or small lines; some authors use the term offcycle for them. Lines 2, 3, and 4 collectively are referred to as nondominant. Figure 1 shows the trends in abundance of the four lines at the Lower Adams River, where the 1902 line has been dominant since 1926.

Life-history type: Defined by the number of years a sockeye spends in fresh water and in the ocean, respectively. The code used here is the one proposed by Ricker (1995), which has two numbers separated by a slant. For example, 1/3 indicates that the fish had 1 year of freshwater growth and almost 3 years of growth in the ocean (the last growing season in the sea is curtailed by the spawning migration). The sum of the two numbers is the age of the fish at maturity, starting from the fertilized egg. For brevity, the total symbol is often referred to as the age of the fish. Age 1/3 corresponds to 4_2 of the Gilbert system and to 1.2 of the "European" system. Sockeye of age 1/2, the jacks, are predominantly male.

AR: Annual reports of the International Pacific Salmon Fisheries Commission (IPSFC) and the Fraser River Panel of the Pacific Salmon Commission (FRP), which provide much of the information to be used.

P: Adult sockeye, of both sexes, that are present on the spawning grounds of any stock, here called parents.

Q: Effective female parents, as estimated by the commissions cited above.

R: Recruits of both sexes (often excluding age 3) that are produced by a year-class of parents.

Recruitment curve: A plot of R against P, and any line fitted to such points.

Principal sources of data

Early information concerning the abundance of sockeye on the Fraser spawning areas is available in the annual reports of the Canadian and British Columbia departments of fisheries. These include estimates of the runs to the Lower Adams River, Scotch Creek, and Chilko, Seton, and Quesnel lakes and the take of eggs at several hatcheries. Later, there were counts of adults at Cultus Lake. Estimates of the natural spawnings elsewhere continued to be made, but most were not published. Packs of canned sockeye from the Fraser region were published each year, and a useful compilation was put together by Rounsefell and Kelez (1938). From 1911, information on the age and sex composition, lengths, and weights of the fish was obtained from samples taken from the catch. The data from 1915 through 1960 were tabulated by Killick and Clemens (1963); data for earlier years are in Table 18 and Fig. 31 of Gilhousen (1992).

The annual reports of the IPSFC include estimates of sockeye, from 1938 onward, on all important spawning areas, including separate figures for adult males, adult females, and jacks. From 1952 the IPSFC has also estimated the catch taken from each of the important stocks or groups of stocks. Those from 1969 to 1980 are in Table 2 of the review by Vernon (1982), and similar data were used, but not published, by Walters and Staley (1987). Cass (1989) published the complete series of data for brood years from 1948 to 1982 and parent populations for 1983–1985. Roos (1991) has the spawning populations from 1938 to 1985. In all of the above except the IPSFC annual reports the age 3 fish are included in both the spawner and recruit estimates. Since then, a new compilation has been prepared by the Pacific Salmon Commission (here called the 1994 tables), which includes the adult fish only: jacks are excluded from both parents and recruits.

In addition, one of the referees of this paper, Dr. J.C. Woodey of the Pacific Salmon Commission (600 Robson Street, Vancouver, B.C.), has contributed new or additional information at several points.

In Fig. 1 and several later figures, estimates of parent populations are shown. These are the best available indications of the size of a line over a period of years, but they are only a part of each year's total adult stock. The rest, usually 70–85%, are captured by the subsistence and commercial fisheries, mostly the latter. This fraction has been varied, from year to year, by adjusting times of fishing permitted by different gears in order that adequate numbers of spawners would be available. For example, following a greatly reduced recruitment from the 1958 year-class at the Lower Adams River, rates of harvest in two or three subsequent generations of that line were reduced. Of course, such individual attention has usually been feasible only for the larger lines. On the whole, however, the Fraser ecosystem has been remarkably productive of sockeye. Partly this is because of natural advantages such as the absence of several parasites that occur in more northern watersheds, but mainly it is because international cooperation has been able to control potentially disastrous overfishing.

2. Recruitment curves

Much of the recent literature about dominance makes use of recruitment curves. Usually, it is a "Ricker" curve, probably because that curve has two features that conform to available observations about salmon reproduction: it can have a "dome" to the left of the replacement point, and there is always *some* recruitment from any finite level of spawning. In a simple form, it is represented by

(1) $\ln(R/P) = a - bP$

where P is the number of adult parents of both sexes and R is the number of adult recruits they produce.

The statistics a and b of eq. 1 describe the following stock characteristics (Ricker 1975, Appendix 3). The unit of time is a generation (4 years).

|	
a	The instantaneous rate of increase of the stock when $P \rightarrow 0$
e^a	The actual rate of increase at that point (R_0/P_0)
$1/b$	The number of parents at maximum recruitment (P_m)
e^{a-1}/b	The maximum number of recruits (R_m)
$1 - e^{1-a}$	The rate of harvest needed to maintain maximum recruitment
a/b	The replacement number of parents and recruits (P_r)
b	The compensatory mortality coeffcient
bP	The instantaneous compensatory mortality rate at any abundance P of parents
$Z - a$	The instantaneous density-independent mortality rate, where Y is the average number of eggs available per parent (both sexes), and $Z = \ln(Y)$
$1/a$	P_m/P_r

The rationale of these relationships is as follows. Let the average number of eggs produced by a sockeye (including both sexes) be a family of eggs, and let it be equal to Y. Then the average potential rate of increase per parent is Y, when all of the eggs survive to become recruits, and the potential instantaneous rate of increase is $\ln(Y) = Z$. Now when $P \rightarrow 0$ the actual average maximum instantaneous rate of increase of the families is $\ln(R_0/P_0) = a$; hence the difference between Z and a is the instantaneous mortality rate of an average family at that point. Thus, $Z - a$ is a density-independent mortality rate because there is no competition between families when $P \rightarrow 0$.

In eq. 1 the instantaneous density-dependent or compensatory mortality rate, owing to competition (in the broadest sense) among the families of a year-class at any level P of parent abundance, is assumed to be proportional to P and is put equal to bP. Adding the two types of mortality, the instantaneous total mortality rate of an average family at parental abundance P is $Z - a + bP$.

At replacement abundance, when $R = P$ and only one egg of an average family survives to become a recruit, the average familial survival rate is $1/Y$. The corresponding instantaneous mortality rate is $-\ln(1/Y) = \ln(Y) = Z$, which is the same as the potential rate of increase, as is necessary when a stock is neither increasing nor decreasing. Consequently, at replacement, $bP - a$ must be zero, and replacement abundance = $P_r = a/b$.

At maximum recruitment the rate of harvest needed to maintain abundance at that level is $(R_m - P_m)/R_m = (e^{a-1}/b - 1/b)/(e^{a-1}/b) = 1 - e^{1-a}$. The rate of harvest that provides the maximum sustainable harvest is somewhat greater than this. It

Fig. 1. Estimates of the male and female sockeye of ages 4 and 5 that arrived at the spawning beds of the Lower Adams and adjacent streams, 1922–1992. The four lines are labelled by their spawning years at the beginning of this century. Data are from the ARs.
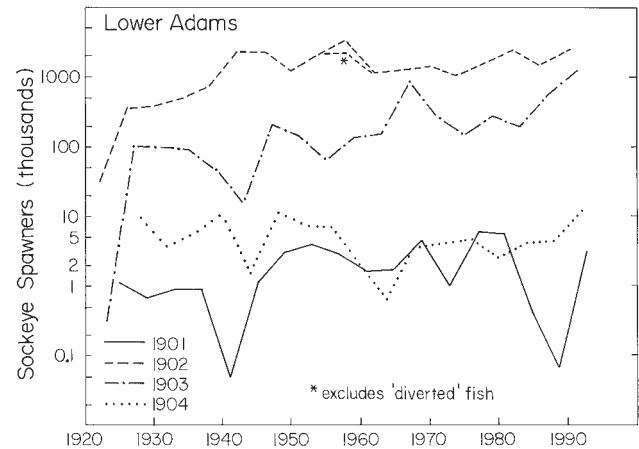
can be computed from $(R_s - P_s)/R_s$, where P_s is found by solving $(1 - bP_s)e^{a-bP_s} = 1$ by successive approximations (Ricker 1975, p. 285), and R_s follows from eq. 1.

The statistics a and b are usually estimated by regressing $\ln(R/P)$ against P, so that b is the slope of the line obtained and a is the ordinate intercept. Values of R computed from such a line are geometric mean (GM) estimates of R at each P. They can be converted to arithmetic mean (AM) estimates by multiplying by $\exp(s^2/2)$, where s is the standard deviation of observed values of $\ln(R/P)$ from the regression line of $\ln(R/P)$ against P.

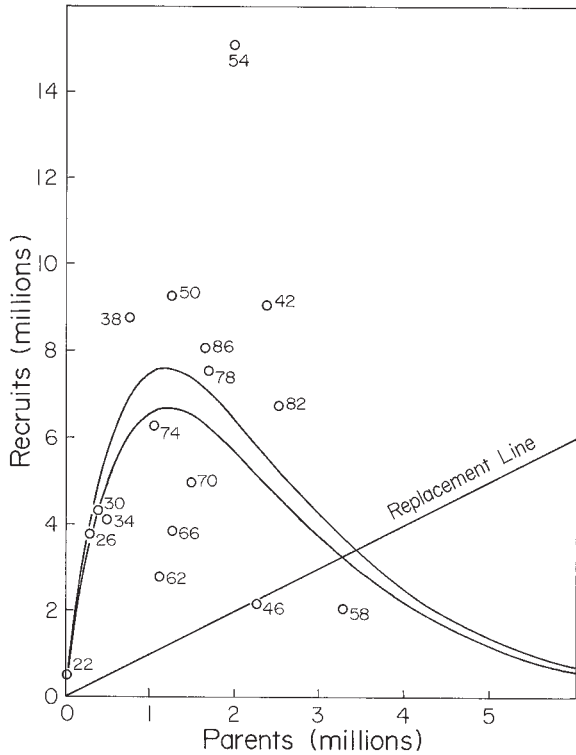A Ricker curve for the Lower Adams dominant line is shown in Figs. 2 and 3. The curve fitted has the equation

(2) $\ln(R/P) = 2.71 - 0.832P \times 10^{-6}$

The standard deviation of the regression coefficient b is 0.144×10^{-6}, and that of the intercept a is 0.24. However, the variability of the data is not uniform; it increases with increase in P (Fig. 3). For fewer than a million parents, it is quite small, so that the statistical reliability of the estimate $a = 2.71$ is greater than what is indicated by a standard deviation of 0.24. The standard deviation of the observations from the line in Fig. 3 is 0.511, which gives the factor $\exp(0.511^2/2) = 1.139$ that is used to compute the upper or AM curve in Fig. 2.

The Ricker curve has been widely used and has been called "the most parsimonious functional form" (Collie et al. 1990), but it has two principal rigidities. One is that compensatory mortality is assumed to be a *linear* function of parental abundance, and the other is that survival rate at maximum absolute recruitment is always $1/e = 37\%$ as large as at minimum absolute recruitment (when $P \rightarrow 0$ and R/P is a maximum). If either condition seems unreasonable, a three-parameter curve can be used, or even a nonparametric curve of some sort, but the ascending limbs of all such curves tend to be similar (Schnute and Kronlund 1996).

Walters and Staley (1987) and Cass (1989) have fitted Ricker curves to data for Fraser sockeye on a somewhat different basis. They use effective female parents (Q) instead of all adult parents of both sexes (P), but their recruits (R) include both sexes. Their expression can be written

Fig. 2. Relationship between parents and recruits of ages 4 and 5 for the dominant (1902) line of the Lower Adams sockeye population. The lower curve is the GM relationship, and the upper curve is the AM relationship. In this and later figures, numbers by the points represent the year-class of sockeye involved.

Fig. 3. Plot of $\ln(R/P)$ against P for the 1902 line at Lower Adams River, as listed in Appendix 1. The solid line is fitted to all of the points, and the broken line is for the 1950–1986 year-classes. See also Table 2.
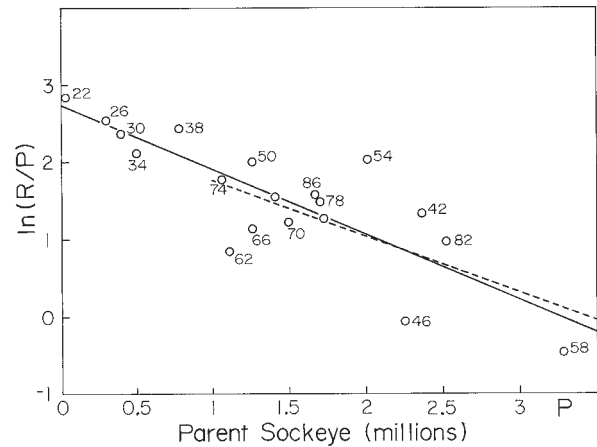

(3) $\ln(R/Q) = a' - b'Q$

If k represents the ratio of total parents (male and female, effective and ineffective) to effective female parents, the statistics a and b of eq. 1 are related to a' and b' as follows: $e^a = e^{a'}/k$, so $a = a' - \ln(k)$; $b = b'/k$.

Collie and Walters (1987, p. 1556) estimated k at the Lower Adams from the fraction of females in the adult spawning stock (0.594) and the fraction of them that are effective (0.966), so that $k = 1/(0.594 \times 0.966) = 1.7427$. Thus, $P = 1.7427Q$, $b = b'/1.7427$, and $a = a' - \ln(1.7427) = a' - 0.555$. In Table 1, these transformations are used for all stocks to make an approximate conversion of parts of Table 2 of Cass (1989) to the basis of total parents.

The statistics in Cass's (1989) Table 2 are somewhat different from Walters and Staley's (1987) Table 1 because they included a few more year-classes. Cass listed the values of a' and b' of eq. 3 here whereas Walters and Staley listed "Ricker productivity" (=a') and "equilibrium stock size." The latter is apparently equal to a'/b', although the true estimate of equilibrium or replacement stock is $a/b = k(a' - \ln(k))/b'$ in terms of total parents, or $(a' - \ln(k))/b'$ in terms of effective females, which is the unit they used. Also, it is somewhat misleading to use a' (or $e^{a'} = R_0/Q_0$) as a general or overall estimate of a stock's productivity, for this index applies only when a stock is very small and is producing few recruits in absolute terms. (Schnute and Kronlund (1996) suggested that R/P at maximum sustainable yield would be a more appropriate index.)

The Lower Adams value of R_0/P_0 that corresponds to the a

of eq. 2 is $e^{2.71} = 15.0$ recruits per parent. Its value for a in Table 1 is almost the same: 2.70. Among the other four dominant lines in Table 1, a varies from 2.50 to 2.86; their average is again 2.70, corresponding to 14.9 recruits per parent.

There is also direct evidence that 15 is a reasonable figure for R/P when a population is small. During 1942–1946 the Early Stuart spawning populations were small, and during 1946–1950, their progeny were almost completely protected from commercial fishing by postponement of the season's opening date, so that the spawning populations of those years included all of the recruits except a few taken by the subsistence fishery along the river. Estimates of parents are summarized in Appendix 11 of Ricker (1987). Summing the parents of the years 1942–1946 and dividing this value into the sum of their spawning progeny 4 years later gives $R/P = 14.3$. R/P ratios for the individual years vary from 1.2 to 30.2, with an average of 12.9. These figures would of course be a little smaller than R/P at the point of origin (where $P \to 0$).

3. Differences between the four lines in a cycle

Of the eight stocks whose statistics are tabulated in Walters and Staley (1987, Table 1), those that have experienced sustained dominance of a single line are Late Stuart, Horsefly, Lower Adams, and Portage. Early Stuart is similar but is anomalous in that it is a mixture of two major groups of spawning populations, only one of which has a dominant line (Driftwood River region). Consequently the Early Stuart parents of lines 3 and 4 are more numerous, relative to line 1, than in the other populations mentioned.

The definition of dominance given earlier and used above is based on numerical differences between lines, without implying any particular cause of those differences. Large differences between lines can in fact be accidental, particularly when a population is increasing after a period of low abundance. However, when lines have ceased to increase, and at least one of them has reached a high level of abundance about which it fluctuates without a sustained trend, it becomes appropriate to suspect that any marked imbalance is a result of

954

Can. J. Fish. Aquat. Sci. Vol. 54, 1997

Table 1. Estimates of the average number of adult parents ($\overline{P}$) and adult recruits ($\overline{R}$) for each of nine stocks during 1948–1988, from the 1994 tables, estimates of the eq. 1 statistics, converted from a' and b' (his a and b) of Table 2 of Cass (1989), which are based on effective female parents and on total recruits (including jacks) 4 years later, and computed maximum (GM) number of recruits (R_m) for each line, from e^{a-1}/b.

Stock	Line	Position in cycle	$\overline{P}$ (1000s)	$\overline{R}$ (1000s)	a	$b \times 10^6$	R_m (1000s)
Early Stuart	1901	1	224	848	2.68	5.55	967
	1902	2	38	121	2.10	22.52	134
	1903	3	60	213	2.67	21.46	298
	1904	4	32	109	2.28	35.74	101
Late Stuart	1901	1	300	1509	2.86	4.65	1381
	1902	2	31	137	3.20	117.7	77
	1903	3	14	62	2.98	139.4	52
	1904	4	2.5	21	3.70	675.2	11
Horsefly (Quesnel L.)	1901	1	495	3105	2.50	1.57	2855
	1902	2	59	253	2.15	3.03	1042
	1903	3	5.3	13	2.60	859	6
	1904	4	0.9	3	3.25	5969	2
Lower Adams (Shuswap L.)	1901	4	3.2	28	3.77	468	34
	1902	1	1735	6646	2.70	0.88	6220
	1903	2	288	1708	1.98	1.08	2467
	1904	3	4.3	25	2.15	140	23
Portage Creek (Seton L.)	1901	4	2.9	19.7	2.60	80.7	61
	1902	1	13.0	70.5	2.77	97.9	60
	1903	2	3.7	26.7	3.63	578	24
	1904	3	0.8	9.7	3.82	1169	14
Gates Creek (Anderson L.)	1901	2	3.3	16.9	—	—	—
	1902	3	1.1	3.2	—	—	—
	1903	4	3.8	13.0	—	—	—
	1904	1	17.4	104.7	—	—	—
Chi1ko River (Chilko L.)	1901	—	73	320	1.94	7.20	356
	1902	—	200	1135	3.04	9.24	832
	1903	—	368	1549	2.40	2.29	1771
	1904	—	453	2053	2.47	2.01	2164
Stellako River (Fraser L.)	1901	—	44	193	2.38	20.55	193
	1902	—	92	528	1.71		
	1903	—	126	764	2.79	7.16	837
	1904	—	80	379	2.44	14.24	296
	1901	—	35	277	2.64	14.41	358
Birkenhead River (Lilloet, Tenas, and Harrison lakes)	1902	—	92	546	2.47	5.59	778
	1903	—	73	411	3.02	20.57	366
	1904	—	67	284	2.29	10.87	334

some kind of influence of the dominant line upon the others. It is this situation that Walters and Staley (1987) had in mind when they suggested that "if dominance is a real phenomenon (in the sense of depensation and interaction between cycle years) . . . there should be clear differences in stock–recruitment parameters between cycle years."

The information in their Table 1 evidently convinced Walters and Staley (1987) that they had failed to find differences of this sort, and in fact the statistics a' (or a) do not differ greatly among the four lines of each stock (Table 1). The b statistics do differ, being very large for lines 3 and 4 as compared with lines 1 and 2 (Tables 1 and 2). This implies that their maximum recruitment is small and occurs at a very small stock size. However, it is unreasonable to expect the data for lines 3 and 4 to tell us anything about what those lines would do if their spawners were to become abundant. If plotted on

Fig. 2, their data would occupy only a few square millimetres in the lower left corner (see Fig. 4 of Collie et al. 1990). Moreover, there is much uncertainty about the estimates of recruits for the small lines (Appendix 2). Actually, their estimated adult catches are probably somewhat too large, and if so, their rates of harvest in Table 3 are also too large. For the late-running stocks to the Lower Adams and Portage, another indication of this is that the estimated rates of harvest in lines 3 and 4 (1904 and 1901 lines in Table 3) are greater than those of Weaver Creek, a large downriver stock that occurs in the fishery at the same time. For this reason, in later tables the Weaver rates of harvest are substituted for those of lines 3 and 4 at the Lower Adams.

The data for the subdominant or No. 2 line at the Lower Adams are based on samples containing reasonably large numbers of spawners and recruits, although the line has been much

less abundant than line 1 (Fig. 1). Its values of *a* and *b* in Table 2 and Fig. 4 are likely to be reasonably representative, even if they do not differ from those of line 1 with 95% certainty. A reason for the poorer performance of line 2 is discussed later, in section 6.

4. Effect of rate of harvest

The very large values of *b* for the weak lines in Tables 1 and 2 could be a result of a large compensatory mortality rate, and a possible source for this might be that they were being fished more heavily than the dominant line. In fact, rate of harvest estimates for lines 2–4 at the Lower Adams did prove to be larger, on the average, than those for line 1 (Collie and Walters 1987, Fig. 3). The rates of harvest corresponding to the average values of the rate of fishing, from the 1994 tables, are shown in Table 3. The pattern of somewhat larger estimates of rate of harvest of the weaker lines is also evident at Late Stuart and Portage Creek, but not at Early Stuart, Gates, or Horsefly, although they too exhibit moderate to strong dominance.

Quantitatively, however, none of these rates of harvest of the nondominant lines is large enough to account for the small populations present in these lines, or for the larger values of *b* in Table 1. To illustrate, suppose that the nondominant lines at the Lower Adams do conform to the same recruitment curve as the dominant line, but are held at their observed low levels by a large rate of harvest. For example, in the No. 2 or subdominant line, 288 000 was the average number of parents from 1951 to 1987. Inserting this in eq. 2, $R = 3\,406\,000$ (GM) or 3 879 000 (AM), and the equilibrium rate of harvest is $(3879 – 288)/3879 = 0.926$, corresponding to a rate of fishing of 2.60. The complete series is shown in Table 4, where the Weaver Creek rates of harvest and fishing are substituted for the unreliable figures for lines 3 and 4.

Only in line 1 has the average rate of fishing been close to what maintains the line at its present average level of abundance. For the other three lines, these rates are not nearly large enough to keep the parent populations as small as they are; hence, it is impossible that the scarcity of sockeye in the nondominant years at the Lower Adams can be mainly a result of their being fished more heavily than the dominant line. This conclusion does not depend critically on what exact recruitment curve is used. For example, with the statistics for the shorter series of line 1 spawnings shown in Table 2, the subdominant line would have an average (AM) equilibrium rate of harvest of 2937/3255 = 91%, which only one of its yearclasses equalled or exceeded; the 21 weak year-classes would need an average rate of harvest of 93% to maintain their low level of abundance by this means.

Cass and Wood (1994) examined this question in more detail and concluded that depensatory fishing is not an important cause of the sockeye cycle at Shuswap Lake.

5. Age structure of the four lines in a cycle

In 1992, a new candidate for a possible cause of dominance was proposed by Walters and Woodey, namely the age structure of the different lines in a population. Differences in age of maturity in Pacific salmon are determined partly by environmental conditions such as temperature and partly by heredity (Ricker 1972, 19.2 and 19.3; Hankin et al. 1993). The hereditary

Table 2. Statistics of Ricker curves fitted to the Lower Adams parents (*P*) and recruits (*R*) shown in Appendix 1.

	Line 1	Line 1	Line 2	Line 3	Line 4
1. Number of observations	17	10*	10	11	10
2. *a*	2.71	2.49	1.97	2.64	2.57
3. SD of *a*	0.24	0.50	0.40	0.48	0.85
4. e^a (recruits per parent)	15.0	12.2	7.2	14.0	13.1
5. $b \times 10^6$	0.832	0.710	0.746	231	245
6. SD of *b* ($\times 10^6$)	0.144	0.268	1.085	96	228
7. $1/b$ (thousands)	1202	1409	1340	4.33	4.08
8. e^{a-1}/b (thousands)	6645	6250	3536	22.4	19.7
9. SD from regression	0.511	0.565	0.797	0.806	1.443

Note: Row 7 is the computed (AM) number of parents needed for maximum recruitment, row 8 is the computed (GM) maximum number of recruits, and row 9 is the standard deviation of the observations of ln(*R*/*P*) from the regression line of ln(*R*/*P*) against *P*.

*Omits year-classes 1922–1946.

mechanism is almost certainly multifactorial, similar to the inheritance of meristic characters in herring as described by Fisher (1930). Hankin et al. (1993) computed heritabilities (h^2) of 0.39–0.41 for male chinook salmon (*Oncorhynchus tshawytscha*) and 0.49–0.57 for females. An important feature is that a large fraction of the progeny of parents having peripheral ages (either younger or older than the population median) regress toward the median age for the sex in question. For both sexes of Fraser sockeye, this is from age 3 to age 4 and from age 5 to age 4. The latter shift is demonstrated in Fig. 3 of Walters and Woodey (1992): on average, about two thirds of the progeny of age 5 parents were of age 4.

In fitting recruitment curves to individual sockeye lines, there is an implication that the four lines are independent entities consisting solely of age 4 fish, but this is of course only approximately true. To consider age 3 first, it has always been obvious that males of that age produced by the dominant line play a role in the spawning of line 4. At the Lower Adams, they must have made a large contribution to the fertilization of the eggs in most years of that line (Fig. 5).

Another aspect of the line 4 spawnings at the Lower Adams is that the jacks include a small fraction of females. Estimates in the early ARs are summarized in Table 14 of Ricker (1972). In 1945 and 1949, these were 1.43 and 1.26%, respectively (average 1.34%), and in 1945, jack females were estimated to exceed the number of adult females on the redds. However, the small size and reduced egg production of the jack females mean that they make much less than a proportional contribution to reproduction. One effect of their activities is to make estimates of line 4 recruitment per adult female somewhat too large. Because of regression to the median age, many or most of the progeny, especially the female progeny, of the jack females that spawn in line 4 will be of age 4, thus adding to the number of adult sockeye in that line. Those that mature at age 3 will of course add to the number of jacks in line 3.

The average percentage of jack sockeye of both sexes that are produced by each of the four lines at the Lower Adams (based on spawning ground estimates) can be computed from the ARs for 11 or 12 cycles as follows: line 1, 4.0%; line 2, 5.2%; line 3, 11.2%; line 4, 19.2%. (These figures are of course larger than the total percentage productions of age 3 because jacks are fished less heavily than the older sockeye.) As expected, line 4 produced the largest percentage of jacks.

956

Can. J. Fish. Aquat. Sci. Vol. 54, 1997

Table 3. Average instantaneous rate of fishing (F) and corresponding rate of harvest (u) for each of the four lines of 11 Fraser sockeye stocks, based on the harvest years 1952–1986.

	1901 line		1902 line		1903 line		1904 line	
	F	u	F	u	F	u	F	u
Early Stuart	1.554*	0.789	1.311	0.730	1.682	0.814	1.505	0.778
Late Stuart	1.548*	0.787	1.433	0.761	1.573	0.793	1.793	0.834
Horsefly	1.533*	0.784	1.450	0.765	1.315	0.732	1.360	0.743
Lower Adams	2.185	0.888	1.183*	0.694	1.529	0.783	1.625	0.803
Portage	1.768	0.829	1.617*	0.802	1.859	0.844	2.107	0.878
Gates	1.643	0.807	1.200	0.700	1.492	0.775	1.595*	0.797
Chilko	1.385	0.750	1.675	0.813	1.547	0.787	1.458	0.766
Stellako	1.611	0.800	1.777	0.831	1.884	0.848	1.558	0.789
Birkenhead	2.035	0.869	1.839	0.841	1.868	0.846	1.364	0.744
Weaver	1.710	0.819	1.573	0.793	1.642	0.806	1.599	0.798
Cultus	1.692	0.816	1.765	0.829	1.740	0.824	1.365	0.745

Note: Data were computed from the 1994 tables. $u = 1 - e^{-F}$.
*Dominant lines.

Fig. 4. (A) Plot of $\ln(R/P)$ against P for the subdominant (1903) line of sockeye at the Lower Adams River. (B) Relationship between parents (P) and recruits (R) of ages 4 and 5, with a fitted Ricker curve (AM and GM).
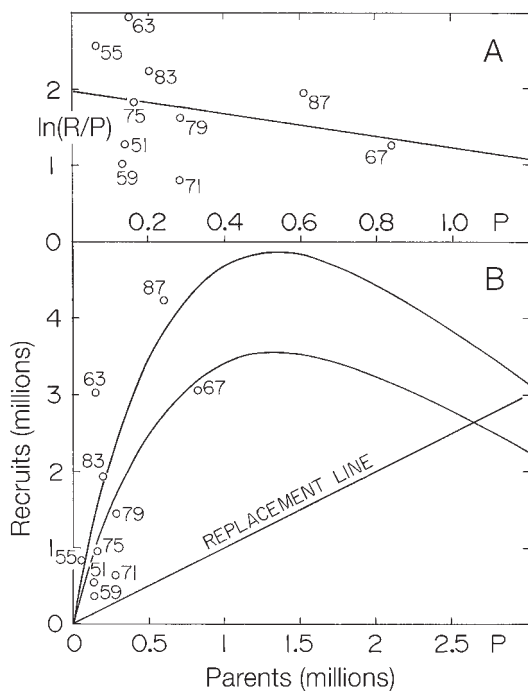
The next largest percentage, 11.2% for line 3, indicates significant inheritance of genes favouring age 3, from line 4 to line 3.

Fraser sockeye of age 5 consist of 81% of life-history type 1/4 and 19% of type 2/3 (Killick and Clemens 1963, Table 11). On the average, both types have slower growth rates than fish of age 1/3. However, the 2/3 type, which spend the extra year in fresh water, are smaller at maturity than the 1/4s, which have their extra year of growth in the ocean. During 1915–1960, female Fraser sockeye of age 2/3 were on average only 17 g (0.65%) larger than the 1/3s whereas 1/4 females were 668 g (26.0%) larger (Killick and Clemens 1963, Table 18).

Table 4. Average observed number of adult parents in the four sockeye lines at the Lower Adams during 1948–1988 and the corresponding number of adult recruits computed from eq. 2 for all lines (rows 1–3); rates of harvest and of fishing that would reduce the recruits of row 3 to the level of parental abundance shown in row 1 (rows 4 and 5; rate of fishing is approximately proportional to the amount of gear in use); and observed rates of fishing from Table 3, the figures for lines 3 and 4 being those of the Weaver Creek population (row 6) (see text).

	Line 1	Line 2	Line 3	Line 4
1. Parents (AM) (thousands)	1735	288	4.35	3.16
2. Recruits (GM) (thousands)	6156	3406	65.1	47.4
3. Recruits (AM) (thousands)	7012	3879	74.1	54.0
4. Rate of harvest that would reduce recruits to the level in row 1	0.753	0.926	0.941	0.941
5. Corresponding rate of fishing	1.40	2.60	2.83	2.83
6. Observed rate of fishing	1.18	1.53	1.60	1.71

Age 5 sockeye must have a smaller overall survival rate than those of age 4. The principal reason is simply that they are exposed to predators and other hazards for a year longer. Ricker (1976) concluded that the best estimate of the average instantaneous mortality rate for sockeye during their final year in the ocean is 0.18, which means a survival rate of 83.5%. However, this probably represents only part of the disadvantage of maturing at age 1/4 rather than at age 1/3. The other disadvantage stems from the slower rate of growth of age 5 sockeye of both types. From the time of Gilbert's (1918) study, it has been known that sockeye of age 1/4 have grown less in fresh water than age 1/3 sockeye of the same stock and year-class. Henry (1961, p. 14) noted that smolts having larger numbers of 1st-year circuli on the scales return from the sea more frequently than those with fewer circuli, and Henderson and Cass (1991) found that among three year-classes of sockeye at Chilko Lake, the largest smolts produced 2.3–2.8 times as many adults as the smallest ones. Walters and Woodey (1992) estimated that overall survival of age 5 sockeye (both types) is 70% of that of age 4; this seems reasonable, although its source is not described.

Offsetting this loss is the fact that females of age 1/4 produce more eggs than the 1/3 type do. If egg production is

Fig. 5. Estimates of the number of jack (age 3) and adult (ages 4 + 5) parents of both sexes on the spawning grounds of the Lower Adams stock in the weak 1901 line (line 4 of the cycle). Data are from the ARs.
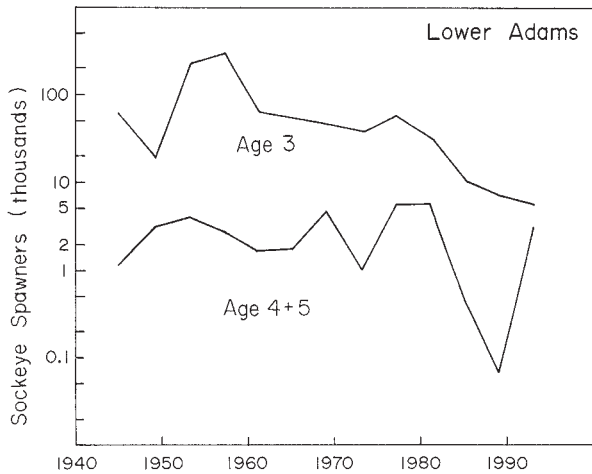
proportional to weight, the 1/4 females should produce 26% more eggs than those of age 1/3. (Within each of the British Columbia sockeye stocks in Fig. 22 of Foerster (1968) the average number of eggs is approximately proportional to the cube of average length.) Thus, there is competition between the greater egg production of age 1/4 and their lower survival rate, but for almost all Fraser sockeye populations the latter effect has been the stronger one, as shown by the fact that natural selection has determined that 1/3 would be the predominant type of life history. No similar estimate can be made of the disadvantage of living an extra year in a lake, and on the basis of body weight the 2/3 sockeye produce less than 1% more eggs than the 1/3s. However, they comprise only a fifth of the age 5 total.

Walters and Woodey (1992) suggest that the age 5 fish may contribute to the phenomenon of line dominance because a large fraction of a small line's production "may be 'lost' to the cycle line, in the form of age 5 recruits to other cycle lines." However, age 5 recruits lost from one line are added to the next, so this mechanism, by itself, would not keep the nondominant lines small. Their only losses would be their contribution of jacks, nearly all males, from line 2 to line 1 and of a few age 5 fish from line 4 to line 1.

On p. 288 of their paper Walters and Woodey (1992) estimated the proportion of age 5 sockeye in the Lower Adams dominant line as 0.1%, but a check on scale reading has shown this figure to be too large (J.C. Woodey, personal communication). This is suggested also by the fact that the parents of line 4, which produce the age 5 fish of line 1, included an average of only 1600 adult females, of which only 2% were of age 5. These few females could not produce 1800 (0.1% of 1.8 million) age 5 recruits when the larger line 3 population, containing 25% of age 5, produced only 60 (Table 5). Accordingly, I have estimated that the average number of age 5 fish present among the line 1 parents could not exceed 30, half as many as in line 4, and was probably less.

Row 5 of Table 5 shows the rate of accretion of age 5 sockeye to each line. In line 3, for example, 1090 fish of age 5 are added to 3260 fish of age 4 in an average generation, so the

Table 5. Number of age 5 spawning sockeye (both sexes) produced by the parent populations at the Lower Adams River.

	Line 1	Line 2	Line 3	Line 4
1. Average number of parents, 1948–1988	1 735 000	288 000	4350	3160
2. Proportion of age 5 (%)	—	4	25	2
3. Average number of age 5	<30*	11 500	1090	60
4. Number of age 5 produced	11 500	1 090	60	<30*
5. Rate of accretion	<0.000 02	0.04	0.29	0.02

Note: Numbers in row 1 are age 4 + 5 averages from the 1994 tables. Percentages in row 2 are from p. 288 of Walters and Woodey (1992). Numbers in row 3 are the product of the two preceding rows, except in line 1. In row 4 the numbers in row 3 are shifted to the line that contains the parents that produced them. See the text regarding row 5.

*Estimated by comparison with line 3.

instantaneous rate of accretion is ln(4350/3260) = 0.29, a figure that will be used later.

Table 5 shows that line 3 receives 1090 age 5 parents from line 2 and contributes 60 to line 4. Line 4 accepts the 60 and passes on less than 30 to line 1. Thus, the age 5 fish cannot be a cause of the scarcity of the weak lines, and hence of the dominance phenomenon. On the contrary, they tend to increase the abundance of adult sockeye in the nondominant lines, and so do the age 4 progeny of the female jacks produced by the dominant line.

6. Ecological interaction between lines

Ward–Larkin predation cycle

If one line of a sockeye cycle can start from small beginnings and become abundant, why cannot the others? Even more puzzling is the fact that after a dominant line appears, other lines may even decrease. This is what impressed Foerster and me back in the 1930s and made us propose the interaction hypothesis (Foerster and Ricker 1942; Ricker 1950). But what kind of interaction would it be? It was natural to suspect some aspect of the food chain in the lake. Foerster (1925) had shown that pelagic plankton crustaceans were the principal food of sockeye in Cultus and other lakes and that the sockeye were eaten in large numbers by various larger fishes. Year-round studies during the 1930s confirmed that sockeye were part of a "key industry" in Cultus Lake, and this was put on a quantitative basis by Foerster (1938), Ricker (1937, 1941), and Ricker and Foerster (1948). Unfortunately, Cultus Lake's dominant 1903 line of sockeye had been reduced to mediocrity by 1935, so it was no longer possible to relate natural dominance to the food chain there.

However, this was done at Shuswap Lake by Ward (1957) and Ward and Larkin (1964). They reported cyclical changes in the abundance and "condition" of a major consumer of sockeye, the rainbow trout (*Oncorhynchus mykiss*). The additional information about the Shuswap fauna published by Goodlad et al. (1974) and Williams et al. (1989a) confirmed the earlier studies. For example, both Ward and Larkin (1964) and Gilhousen and Williams (1989) found that in dominant years, trout consume a great many sockeye eggs on and downstream from the spawning grounds, thus starting the quadrennial increase in size and condition of trout even before the young sockeye leave the gravel.

Other interaction models have been proposed, but Ward and

958

Can. J. Fish. Aquat. Sci. Vol. 54, 1997

Larkin's (1964) is the only one for which a specific mechanism has been identified. For example, Peterman (1977) showed that a sinuous recruitment curve can describe the existence of two (possibly even three) levels of abundance of a salmon stock, but did not indicate what ecological conditions could make this possible. Similarly, Larkin (1971) developed equations that imply an influence, on a given sockeye line, of all the other lines in the habitat, but again their mode of action is not apparent.

In addition to being based on an observed cycle of foraging and nutrition, the Ward–Larkin scenario has the great merit of accounting for the fact that line 2 is usually much more abundant than line 3 or 4. They pointed out that in the spring of their 1st year the fingerlings of line 2 are buffered from the increasing predation potential by the presence of abundant line 1 smolts, and later in the year by the line 1 yearlings (age 1) that did not leave the lake. The latter are only a small percentage of their own year-class, but their absolute numbers are considerable, and individually they are much larger than the line 2 fingerlings (age 0) that they live with. Thus, line 2 escapes the full brunt of the attack of the increased numbers and size of the fish eaters, while its eggs and fingerlings, together with the yearlings from line 1, contribute to a further increase in the size and condition of those predators (Ward and Larkin 1964, Figs. 14 and 15). Next year the full force of the piscivores' attack falls upon the scarce fingerlings of line 3, so the survival rate drops abruptly. The predators also have a hard time of it that year, living on very short rations as far as sockeye are concerned. They do have other foods, but apparently there is nothing to match the quantity and suitability of what a big brood of sockeye provides. The rainbow trout, at least, turn mainly to insects to help them stay alive (Ward and Larkin 1964, Fig. 12). The following year is no better for the would-be fish eaters, and many of those that had prospered during lines 1 and 2 of the cycle are nearing the end of their life-span. By the close of the 4th year, many will have died, leaving a reduced battalion of mainly small survivors to enjoy the feast when the eggs, fry, and fingerlings of the next dominant sockeye spawning make their appearance.

This pattern of dominant, subdominant, and two weak lines is not just a modern phenomenon. The Province of British Columbia's hatchery on Seton Creek started operation in 1903. Their counts or estimates of the sockeye that arrived in that creek were tabulated by Ricker (1987, p. 7). To obtain order-of-magnitude estimates of the total abundance of the Seton–Anderson stocks during the first 4 years, before operation of the hatchery could have had any effect on recruitment, the escapements can be divided by their rate of survival from the commercial fishery. Estimating this as 15% for the nondominant years, the total runs become 107 000 in 1906 (line 2), 6500 in 1903 (line 3), and 7000 in 1904 (line 4). For the dominant line at that time, recent estimates of escapement range from about 20% (Gilhousen 1992) to 65% (Ricker 1987), and applying these to the "more than 200 000" spawners of 1905, that year's total run was from 1 000 000+ to 310 000+. Either figure indicates strong dominance in the big year, with a moderate subdominant run and two very small weak lines.

Change in abundance of predators during the cycle
An objection to the Ward–Larkin predation cycle has been that it seems to require too great a fluctuation in predator abundance over the short span of 4 years. (Predator abundance will be used as a convenient short term for predation potential, which is a combination of the abundance of the fish, their size, activity, and possibly other characteristics.) However, the average number of fish in a sockeye line is a very poor indicator of the average abundance of the predators that attack them. Ricker (1952, 1954) showed that, in the situation where a kill occurs at a fixed fraction of random encounters between predator and prey, the instantaneous rate of predation mortality (K) is directly proportional to predator abundance, and the relationship between the prey's survival rate (S) and K is of course $S = e^{-K}$. This means that a rather small increase in predators will cause a large decrease in S, provided the survival rate from predation is already fairly small. For example, to decrease S from 10 to 1% requires only a doubling of the number of predators.

For a more realistic illustration, Williams et al. (1989b, Table C9) estimated an instantaneous mortality rate of 1.978 for fingerlings of the subdominant 1975 year-class in Shuswap Lake between May 5, 1976, and March 8, 1977. By the time of smolting, this would be increased to about 2.3, corresponding to a 10% survival rate during lake life. Cutting this survival rate to 5% would be more than enough to start a line toward extinction. Survival of 5% means an instantaneous mortality rate of 3.0, so if all of the lacustrine mortality were from predation, the predators would have to increase by only (3.0 – 2.3)/2.3 = 30%. If predation were causing only two thirds of the sockeye mortality in the lake, the necessary increase in predators would be by 46%. Although the mechanics of predation on sockeye are probably not strictly random, it is clear that the changes in predator abundance during the course of the Ward–Larkin cycle need not be unusually large.

In addition to predacious fishes, there are a number of species of birds that consume young sockeye, including loons, grebes, and especially mergansers. Although these can, to some extent, shift to other species or to other localities in years when sockeye are scarce, they too must play some role as intermediaries in the sockeye abundance cycle.

Shuswap Lake synchrony
A phenomenon for which I have seen no explanation except on the basis of interaction between lines is the fact that all the sockeye populations of Shuswap Lake have now conformed to the 1902 line dominance that became established for the Lower Adams stock in 1926. Up to 1913, they had all been dominant in the 1901 line, but that line's dominance was destroyed by massive mortality from rock dumped into the canyon in 1913 and from overfishing in 1917. Conformity with the new 1902 line dominance could be expected of the other autumn runs, of which the Lower Shuswap River's is now the largest (Fig. 6A), because they are in the fishery at the same time. But in addition the Shuswap summer runs (Anstey, Eagle, Scotch, and Seymour) are now all dominant in the 1902 line. This agreement cannot be a result of common harvesting policies over the years because the summer runs go through the fishery at least a month earlier than the late runs. Nor did this happen without a struggle. No Seymour line had a clear advantage during the late 1940s and early 1950s, and later, its 1902 and 1903 lines seesawed up and down until the 1902 line leaped ahead in the 1980s (Fig. 6B). At Scotch Creek the 1901 1ine was largest from 1945 to 1981. Its 1902 line was a late starter, first

Fig. 6. Estimates of adult parent sockeye for seven stocks tributary to Shuswap Lake. Data are from the ARs.
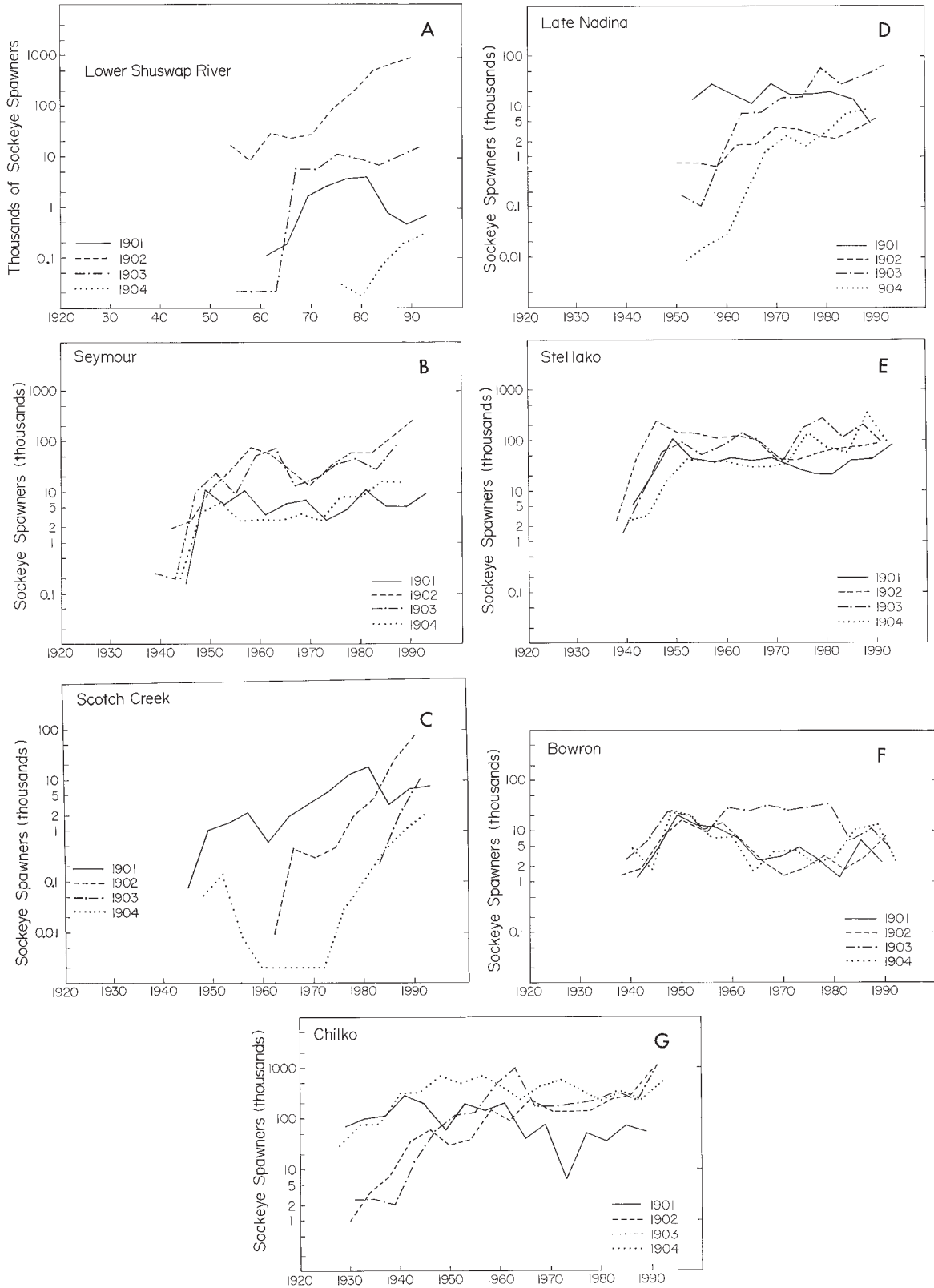
recorded in 1962, yet it rose rapidly to dominance in 1986 and 1990 (Fig. 6C). At Anstev and Eagle rivers the progression was easier; the 1902 line started out largest and has remained

so. However, even for them, it is unlikely that it was pure chance that got them started in the 1902 line. These rivers were presumably repopulated by strays from the other two summer

populations on Shuswap Lake, and at the time this occurred the 1901 line was dominant at Scotch Creek, while at Seymour the 1903 and 1902 lines were equally abundant.

However, the fact that all of the tributaries of Shuswap Lake are now dominant in the 1902 line does not necessarily mean that the causative interaction takes place throughout the whole lake, although that is possible. It may merely be that in dominant years the smolts from the various tributaries all benefit from assembling in great schools as they move down the west arm of the lake toward its outlet. At this time, members of large schools should be less exposed to predation than those in smaller ones, especially if predator stomachs in dominant years quickly become filled to capacity. Hvidsten and Johnsen (1993) found that when hatchery-reared Atlantic salmon (*Salmo salar*) were released into a large school of migrating wild smolts, their survival rate was 3.4 times as large as the average for those released into small schools.

The protection of large numbers would presumably continue during downstream migration, at least as far as Lytton where clear water ends and hunting by sight becomes impractical. However, it has not been sufficient to swing the stocks from Adams Lake and the North Thompson River into the same dominance pattern as Shuswap's. This is not really surprising, considering that many generations passed before the Seymour and Scotch Creek populations fell into line, although their young were reared in Shuswap Lake itself.

Interaction without sustained dominance

There are several Fraser sockeye populations that have not had any consistently dominant line, yet show signs of the presence of interaction. For the Late Nadina River stock, dominance has shifted from one line to another (Fig. 6D). At Stellako, dominance of the 1902 line disappeared after 1960 (Fig. 6E). Bowron maintained dominance of the 1903 line for six cycles before it was overtaken by the 1904 line, although the latter has not maintained its position (Fig. 6F). What suggests interaction in these situations is that when a new line became the most numerous one, as can happen by the accident of an unusually favourable survival year, the previous leader decreased in abundance (Fig. 6D); or, when a dominant line decreased, the other lines were able to increase (Fig. 6F). Both events suggest that interaction is at work.

At Chilko, there is a different pattern (Fig. 6G). This was the first midseason upriver run to regain substantial spawning populations subsequent to 1913, which it did in 1928 and 1929. Throughout the 1930s, these two lines (1904 and 1901) increased gradually but remained not very different in abundance. Since then the 1901 line decreased and up to 1989 was the smallest of the four. In 1950, I predicted that the 1904 line would prevail over the 1901 line and become dominant, simply because the earlier of two adjacent nearly equal lines is in a better position to exert pressure on the other, and the 1904 line did in fact become the larger by far. What I did not predict was that the 1902 and 1903 lines, then very small, would increase and finally surpass the 1904 line. Chilko Lake has been fertilized since 1990, and the 1989 spawning of the 1901 line produced the exceptionally good return of 2.4 million recruits from 63 000 parents (*R/P* = 38; J.C. Woodey, personal communication).

7. Magnitude of interaction mortality

We have distinguished between compensatory mortality, a result of competition between members of the same line and year-class, and interaction mortality, which is an indirect consequence of the presence of another line or lines of sockeye in the same environment. Whatever biological processes may be involved, the result of interaction mortality will be a reduced production of recruits per parent by nondominant lines, as compared with the dominant one, and this can be used to estimate the magnitude of interaction. From data in Appendix 1 the schedule below has been computed. The first row is the average number of adult parents, in thousands, for each line at the Lower Adams during 1948–1988, the second row is the average number of recruits that would be produced by the parents of each line if they were as productive as line 1, computed for each year-class from eq. 2 and converted to arithmetic mean values, and the third row is the average observed number of adult recruits:

	Line 1	Line 2	Line 3	Line 4
Mean number of parents	1735	288	4.35	3.16
AM of computed AM recruits	6722	3414	73	52
AM of observed recruits	6646	1708	25	28
Ratio	0.99	0.50	0.34	0.54

The productivity of line 2 has been about half of that of line 1, and that of the weak lines must be considerably less, considering that their recruit estimates are probably too large.

Table 6 has similar but more approximate computations made from the *mean* adult parental abundances of all the stocks in Table 1 that exhibit dominance. In all cases the estimates of the productivity of the nondominant lines have been been less than that of the dominant line. Productivity estimates for lines 3 and 4 have been, on the average, less than for line 2, even though their catches may have been overestimated.

An analysis using the statistics described in section 2 can be made for any stock whose lines have reached a steady level of abundance, approximately at least. The Lower Adams stock comes close to this condition because its lines 1, 3, and 4 have settled into a fluctuating pattern relative to natural conditions and rate of fishing, without any sustained trend in abundance upward or downward since 1950 (Fig. 1). In this quasi-equilibrium situation the sockeye of all such lines, however numerous or scarce, must have the same average total mortality rate. As described in the section on recruitment curves, this instantaneous rate is the natural logarithm of the average number of eggs per parent (including both sexes). At the Lower Adams, it is $Z = 7.65$ (J.C. Woodey, personal communication). For any line, the interaction mortality rate (I) will be equal to Z less the sum of its other three component mortality rates: the line's compensatory mortality (bP), the line's rate of fishing (F), and the density-independent mortality ($Z - a$). Hence,

$$(4) \quad I = Z - (bP + F + (Z - a)) = a - F - bP$$

That is, interaction mortality takes over as compensatory mortality decreases, if rate of fishing and total mortality rate remain unchanged.

Table 7 illustrates this relationship for the Lower Adams

Table 6. Numbers (thousands) of recruits (R_c) for all lines of the first five stocks of Table 1, computed from the mean number of adult parents (P) using the a and b statistics for the dominant line of each stock and converted to AM values by multiplying by 1.139, compared with the observed average number (thousands) of adult recruits (R) for each stock.

Stock		Line 1	Line 2	Line 3	Line 4
Early Stuart	P	224	38	60	32
	R_c	1073	511	714	445
	R	848	121	213	109
	Ratio	0.79	0.24	0.30	0.24
Late Stuart	P	300	31	14	2.5
	R_c	1478	534	261	49
	R	1509	137	62	21
	Ratio	1.02	0.26	0.24	0.43
Horsefly	P	495	59	5.3	0.7
	R_c	3157	746	73	13
	R	3105	253	13	3
	Ratio	0.98	0.34	0.18	0.24
Lower Adams	P	1735	288	4.3	3.2
	R_c	6451	3826	73	55
	R	6646	1708	25	28
	Ratio	1.03	0.45	0.34	0.51
Portage	P	13.0	3.7	0.8	2.9
	R_c	66.2	46.8	13.4	39.7
	R	70.5	26.7	9.7	19.7
	Ratio	1.07	0.57	0.72	0.50

population using the statistics of eq. 2 for a small selection of parental abundances. The several sources of mortality are listed down the columns. Compensatory mortality rates are computed from $b = 0.832 \times 10^{-6}$ in row 4. Row 5 has the density-independent mortality rate estimated from the dominant line: $Z - a = 7.65 - 2.71 = 4.94$. Row 6 lists instantaneous rates of fishing, except that there is no fishing in the natural replacement situation of column 2. Columns 3–5 use $F = 1.18$, obtained for the dominant line in Table 3. In column 6, line 2 uses its own estimate of $F = 1.53$ from Table 3, but lines 3 and 4 use the Weaver Creek figures, as described earlier. The sums of these three types of mortalities in row 7 are less than 7.65 for all parental stocks smaller than 1 839 000. The differences are the interaction mortality rates, shown in row 9, which are necessary if an equilibrium situation is to be maintained.

The 0.78 mortality for line 2 may seem large; it corresponds to 54% actual mortality, or 46% survival, from interaction. However, this agrees fairly well with the survival ratio 0.50 shown in the schedule in the first paragraph of this section, and with the ratio of 0.45 shown in Table 6.

There are two interesting aspects of this computation. First, the interaction mortality is independent of the total mortality rate, Z, which disappears in eq. 4 and cancels out in Table 7. Second, in column 4 of Table 7 the number of parents required to produce recruits that will maintain a line in equilibrium at instantaneous rate of fishing F is simply

$$(5) \quad \frac{a - F}{b}$$

Table 7 describes the situation when all parents and recruits of a line are of age 4. Actually, lines 3 and 4 receive enough

additional parents from adjacent lines to modify the picture somewhat. Table 5 suggests that 1090 of the estimated average number (4350) of adult parents of line 3 are of age 5. Line 4 also obtains part of its adult parents from outside, although there is no available estimate of their number. These are of age 4, and are the progeny of the numerous age 3 or jack spawners that it receives from line 1 (Fig. 5). Of course, the jacks include less than 2% of females, and weigh only one quarter to one third as much as the older sockeye, but their progeny would be mainly of age 4 because of regression to the median age (cf. section 5).

These outside contributions enable the weak lines to sustain a greater total mortality rate than they otherwise would. For line 3 the average instantaneous rate of accretion of adult spawners of age 5 was estimated as 0.29 in Table 5, and this must be opposed by an equal average mortality rate, additional to the 7.65 of Table 7, for a total of 7.94, to maintain the line's equilibrium status. But however great their mortality rates might become, the weak lines will not disappear entirely as long as they are getting contributions from their neighbours.

Unlike the other three lines at the Lower Adams, line 2 has increased gradually since 1951 (Fig. 1), at an average instantaneous rate of about 0.16 per generation. This is subtracted from the equilibrium figure 7.65 in Table 7 to estimate line 2's average total mortality rate. Yet although it has been able to increase in numbers, line 2's production of recruits has been only about half of the dominant line's at equal parental abundances, as described earlier. If this is so, why is it line 2, rather than line 1, that has been able to increase recently? The reason is simply that its parent spawnings have been much smaller. Most of them are situated on the steep part of their recruitment curve (Fig. 4), so they have produced more recruits per parent than the line 1 parents, which surround the dome of their curve (Fig. 2). Since 1950 the line 2 parents have produced 7.8 recruits each, on the average, whereas those of line 1 have produced only 4.2 (Appendix 1).

In 1991 the line 2 parents were estimated to have reached 1.2 million, equal to the number that, in line 1, has produced the maximum number of recruits on the average. It might, in future, even displace the 1902 line from the dominant position, although that seems unlikely. For anyone who cares to risk predicting the future of the Adams River sockeye lines, there is another possible complication. Most of the Shuswap Lake sockeye populations have increased greatly since 1950, especially in the dominant 1902 line. The Seymour and Scotch Creek runs are shown in Figs. 6B and 6C. The strongly dominant Lower Shuswap River's autumn run has done even better, perhaps because part of the foraging of its fingerlings is done in Mara Lake (Fig. 6A). There are also substantial kokanee populations (Levy and Wood 1992), especially those of the Eagle and Lower Shuswap rivers. These compete with young sockeye for food, and may even consume a few of them. Thus, the lake's capacity to produce sockeye is already being strained (Hume et al. 1994). Smolts of the dominant line average only about 3 g in weight, among the smallest anywhere, and any further reduction might quickly reach a critical limit. Although the increased number of smolts now leaving the lake probably tends to increase survival rate owing to predator satiation (section 6), their small size must be a handicap during ocean life.

962

Can. J. Fish. Aquat. Sci. Vol. 54, 1997

Table 7. Computation of GM recruitments and interaction mortality rates for three arbitrary and four observed levels of parental stock, using the *a* and *b* statistics of eq. 2 and rates of fishing described in the text.

		1	2	3	4	5	6	7	8
1. Position in the cycle		—	—	—	—	Line 1	Line 2	Line 3	Line 4
2. Parents (thousands)	P	3257	2500	1839	1735	288	4.35	3.16
3. Recruits (thousands)	R	3257	4694	5985	6156	3406	65	47
4. Compensatory mortality	bP	2.71	2.08	1.53	1.44	0.24	0.00	0.00
5. Density-independent mortality	$Z - a$	4.94	4.94	4.94	4.94	4.94	4.94	4.94
6. Fishing mortality	F	0	1.18	1.18	1.18	1.53	1.60	1.71
7. Mortality subtotal (rows 4–6)	—		7.65	8.20	7.65	7.56	6.71	6.54	6.65
8. Total mortality	Z	7.65	8.20	7.65	7.65	7.49*	7.65	7.65
9. Interaction mortality	I	0	—	0	0.09	0.78	1.11	1.00

Note: Column 2 shows the replacement recruitment in the absence of fishing. Column 4 has replacement recruitment when the rate of fishing is 1.18. Columns 5–8 use the average number of parents for the lines indicated, at the Lower Adams River. Column 3 is not an equilibrium situation, so interaction mortality cannot be computed. All mortalities are on the instantaneous basis, with the 4-year generation as the unit of time.

*Equal to 7.65 – 0.16, 0.16 being the average rate of increase of line 2.

8. Discussion

Causes of interaction mortality

The evidence for the Ward–Larkin predation cycle should not blind us to other possible contributions to interaction mortality, and Levy and Wood (1992) listed several possibilities. At the time their paper was in preparation, Scotch Creek was still dominant in the 1901 line, so they postulated that interaction must occur in each spawning tributary separately. Although Scotch Creek now has the same dominant line as the other Shuswap tributaries, the fact that it remained out of step for so long supports the idea of spawning-stream interaction. This could involve stream insects such as carnivorous stoneflies, whose laciniae might be capable of piercing a salmon egg, and would certainly be able to kill newly emerged fry.

For almost any kind of animal, reproduction at a single age sets the stage for major fluctuations in abundance caused either by predation of one brood upon a later one or by interaction between them that involves other organisms, either food, predators, parasites, or parasitoids. This occurs most frequently and most conspicuously among insects, the 17-year cicadas being an extreme example. Thus, the existence of line dominance in some Fraser sockeye populations is not surprising. It may well be caused by different types of interactions in different lakes, or by more than one kind of interaction in the same lake. Nor is it surprising that in some lakes, dominance is unstable enough that it can be shifted from one line to another by the vagaries of environmental conditions for survival, or that in some lakes, it is absent or too weak to be identified.

Line dominance among Fraser pink salmon (*Oncorhynchus gorbuscha*) is even more marked than among sockeye and has the same fundamental basis: reproduction at a single age (age 2). As with sockeye, there are other pink populations in which dominance does not occur, or where it has shifted from one line to the other (Ricker 1962). For pinks, several kinds of interaction seem possible, but these have yet to be quantitatively assessed.

Recruitments during the old big years

If the old big years of the 1901 line had a recruitment curve anything like Fig. 2, there are interesting historical implications. For one thing, before the commercial fishery started, the dominant line would tend to vary in abundance between large and very large in successive generations, over an extreme range of about 1–17, in the irregular cycle that can be computed from eq. 2. Scaled down to the abundance of that single stock, the largest year-classes of the old big years would then contain 6.1–6.6 million, followed 4 years later by the smallest (0.4–0.6 million), and then by 4.3–5.4 million and finally 0.9–1.8 million, but fluctuations from environmental causes could easily obscure this pattern.

Any line of a population's cycle that has a recruitment curve with a dome to the left of the replacement line will oscillate in abundance, given an initial displacement from the equilibrium position. These oscillations are self-propagating and are permanent if the curve crosses the replacement line at a slope steeper than –1 (Ricker 1954). The curve of eq. 2 has a slope of $1 - a = -1.71$ at replacement, which means that it will generate permanent oscillations in the natural condition, as described above. If the angle at replacement is steeper yet, the line 1 sequence of spawning populations becomes "chaotic".

Introducing a fishery moderates such swings, but they do not disappear completely until the point of maximum recruitment is reached. In Fig. 2, this means a harvest rate of $1 - e^{1-a} = 82\%$, and a parent stock $1/a = 37\%$ as large as at the natural replacement point.

The populations of the old 1901 line, up to 1913, may well have had flatter recruitment curves, on the average, than the recent 1902 line shown in Fig. 2, and hence less extreme natural oscillations. In the statistics the amplitude of oscillations would be reduced by the inclusion of catches from downriver stocks that apparently had no intrinsic cycles with dominance in the 1901 line. Nevertheless, there is a suggestion of oscillation in descriptions of the fishery during the early years of the century. Sockeye were evidently less abundant in 1909 than in either 1905 or 1913. Both in 1905 and in 1913, but not in 1909, the Fraser River canneries imposed a limit of 200 fish per day that they would accept from each gill-net boat, for a few days at the height of the run (Babcock 1914 and earlier reports).

Even with a flatter curve and only small or moderate oscillations, starting a commercial fishery would at first have *increased* average recruitment in the old big years by reducing the spawning stock: moving it toward the point (P_m) where it produces maximum recruits. The 1913 run may well have been the largest ever, as indeed was the opinion of observers at the time.

Distribution of dominance

The distribution of dominance in the various lakes of the Fraser watershed indicates that, today at least, it is a phenomenon that develops in each lake separately. How, then, did dominance become synchronized in the whole of the Upper Fraser watershed during the old big years of the 1901 line? One possibility is that the lakes were all first colonized in that line when the melting glaciers opened their basins (Ricker 1950). Another and more likely sequence of events is that the old big year dominance developed gradually during prehistoric times. It may have been related to, or assisted by, intensive fishing by the large indigenous human populations that existed in the region before western contacts brought a succession of virulent epidemic diseases, starting with smallpox in the 1790s. Another possibility is some effect of predation by river lamprey (*Lampetra ayresi*) in the lower Fraser and in its plume in the Strait of Georgia (Beamish and Neville 1995). These have poor eyesight and must locate their prey in the muddy water by smell, vibrations, or electrical impulses. The only dominant line that is attested for downriver stocks is the 1903 line at Cultus Lake, whose smolts go to sea a month earlier than those from the upper river.

Mathematical models of sockeye cycles

Models of sockeye cycles have been developed by Ward and Larkin (1964), Larkin (1971), and Collie and Walters (1987). Welch and Noakes (1990) reviewed these efforts and presented their own version. A weakness of all of these models, pointed out by referee J.C. Collie (University of Rhode Island, Narragansett Bay Campus, R.I.), is that none of them will continue to cycle in the absence of a fairly substantial rate of harvest. By contrast, the old big years maintained their cycle throughout the 19th century before any commercial fishery began and when aboriginal populations were at a low ebb.

Leaving that aside, all of the models suggest that a more even distribution of parents among the four lines would result in greater overall sockeye production from a lake. Moreover, the work of Ricker (1937) at Cultus Lake and of Ward (1957) at Shuswap Lake showed that during years of low sockeye abundance, plankton production was sufficient to support many additional sockeye. On the other hand, when two big spawnings occurred in succession at Cultus Lake (the 1939 and 1940 year-classes) the smolts in 1941 were numerous but very small (2.7 g), while those of 1942 were scarcer and larger (5.3 g)[1] but not up to the lake's average (about 6.5 g). The result was that the adult returns from both spawnings were very poor; only 17–19% of their parents' numbers appeared at the lake (Foerster and Ricker 1953, Tables 6 and 7).

Even if four sockeye lines equal to a dominant line are too much to ask of a lake, half of that number in all 4 years of the cycle would represent a substantial increase in average smolt production and subsequent adult harvest. Another possible advantage of having a fairly large number of parents in all 4 years would be greater fertilization of the lake and increased primary production.

However, the possible ecological ramifications of such a change cannot be forecast: the models are not that prescient. For example, if the great abundance of the dominant years depends on the saturation of predators' appetites at some stage of sockeye life history, and if lean years are necessary to keep the predators in check, equalization could destroy both of these conditions, so that production of really large numbers of smolts would not be possible. Hence the outcome of a move toward equalization of the sockeye lines can be determined only by experiment, and this of course has been discussed (Woodey 1987; Collie et al. 1990; Welch and Noakes 1991). However, the very real danger of ending up with a worse situation rather than an improved one has prevented any attempt along those lines.

Larkin (1971) suggested reduction of predacious fishes as a concomitant of any equalization experiment. It might be possible to direct this mainly at such unpopular species as squawfish (*Ptychocheilus oregonensis*), thus deflecting anglers' objections to the destruction of trout by means other than their own activities. However, such a program has its own ecological uncertainties. If the fish in question has a recruitment curve that is domed to the left of the replacement line (as in Fig. 2), a moderate removal of adults will increase the production of recruits. The work at Cultus Lake suggested that natural regulation of the abundance of squawfish, and possibly trout, was by way of cannibalism of adults on young (Foerster and Ricker 1942, 1953). This is a situation that tends to generate steep recruitment curves (Ricker 1954). Thus, greater removals of adult piscivores, unless very intensive, could easily increase their subsequent abundance in a lake. Certainly, an 80% reduction of large squawfish in Cultus Lake seemed not to reduce the recruitment of their young to the sockeye-eating size; if anything, it was increased (Foerster and Ricker 1953, Fig. 3). However, because the young squawfish took 3 years to reach the minimum sockeye-eating size of about 200 mm fork length (Ricker 1938), the *immediate* effect of the removal of the adults was a major increase in survival rate of the young sockeye.

9. Summary

Fraser sockeye mature predominantly at age 4, so they are divided into a series of 4-year cycles of largely self-reproducing lines of descent. In some populations, one of these (line 1) has been persistently the most numerous (dominant) for many generations. In such populations, line 2 usually contains 10–25% as many fish as line 1, but lines 3 and 4 may be less than 1% as numerous. Up to 1913, sockeye stocks of the upper river, above Hell's Gate, were dominant in the 1901 line. Although there is uncertainty about the actual size of the dominant line at that time, in the one region (Seton–Anderson) where estimates of spawners are available in all 4 years of the cycle, the relative abundances of the four lines conform to the pattern described above. After destruction of most of the spawners that returned in 1913 and 1914, new dominant lines gradually developed in several upriver lakes, the first and still the largest being the late run to the Lower Adams River, a tributary of Shuswap Lake, where the 1902 line is now dominant.

The ecological mechanism that sustains this cycle was described in 1964 by Ward and Larkin. Nevertheless, questions about such cycles have been raised in recent decades, suggesting either that they are accidental rather than ecologically supported,

---

[1] The age 1 smolts produced by the 1940 spawning may have had an average size considerably less than 5.3 g because in 1942, there was difficulty in distinguishing the smaller of the numerous age 2 smolts from those of age 1. The poor return in 1944 from the 1940 year-class was partly because its numerous 2nd-year smolts would return at age 2/3 in 1945.

964

Can. J. Fish. Aquat. Sci. Vol. 54, 1997

that they result from overharvesting of the nondominant lines, or that they are in some way related to the fact that Fraser River sockeye produce a small minority of fish of ages 3 and 5.

In Figs. 1 and 6 are shown estimates of the spawners in a number of cyclical and noncyclical sockeye populations from as far back as any kind of estimates are available. The best data are from the International Salmon Commission's surveys, starting in 1938, but Department of Fisheries and Oceans estimates for earlier years are available for important stocks. Estimates of catch from the larger stocks or groups of stocks are available starting in 1948. To these, a series of recruitment curves has been fitted by Cass (1989) and others. The parameters of a number of these are shown in Table 1 here, adjusted (approximately) to terms of total parents (the originals are in terms of effective females). From these curves the estimates of production at very small population abundance have averaged about 15 recruits per parent for dominant lines, and not much less or more for the other three lines. Also from the curve parameters, estimates of maximum recruitment for weak lines have usually been extremely small, but much of this may be a result of occasional misidentification of the origin of fish in samples from a catch in which a weak line is mixed with a much more numerous strong line. In any event the range of abundances of a weak line is so small that its parameters cannot be usefully projected to greater abundances.

The nondominant lines at the Lower Adams River and some other cyclical populations have been harvested somewhat more heavily than the dominant line, but the differences are much too small to maintain those lines at their observed low level of abundance. Hence, this makes only a minor contribution to the dominance phenomenon. Also, the sockeye of age 3 and age 5 that are produced by a dominant line increase the numbers of sockeye of age 4 in the other lines because most of the progeny of spawners of those ages tend to regress toward the median age in the population; hence, they are not a cause of scarcity of the nondominant lines.

The only plausible causes of cyclic dominance involve interaction between the dominant line and the weaker lines, and the distribution of dominance indicates that this interaction occurs in each sockeye nursery lake separately. In addition to lines that have been consistently dominant over a long period of years, there are examples of a shift of dominance from one line to another, or where dominance has disappeared, perhaps only temporarily. It seems likely that interaction between the sockeye lines in a lake occurs quite generally, but develops into dominance only under special circumstances.

Among the recent cyclic populations the only cause of interaction mortality that has support from observations in nature is the Ward–Larkin cycle of abundance of piscivorous fishes, especially rainbow trout, at Shuswap Lake. This subjects nondominant lines, and particularly lines 3 and 4, to a greater freshwater mortality rate than the dominant line. Identified first in 1926 at the Lower Adams River, a common pattern of dominance has gradually developed among sockeye of all major tributaries of Shuswap Lake, so that its four summer and two autumn runs are now all dominant in the 1902 line sequence. A likely cause is that young sockeye from all of these tributaries benefit from predator satiation during their migratory concentration as they proceed down the west arm of the lake to its outlet. The same may occur in the river and two lakes downstream from the outlet, but its effect there has not been strong enough to swing the stocks from Adams Lake and the North Thompson River into the 1902 line of dominance.

Among stocks that have a dominant line and whose lines are not increasing or decreasing in abundance, the number of recruits (R) produced by any given abundance of parents (P) is less for nondominant lines than for dominant ones, the difference being an estimate of the interaction mortality rate. At the Lower Adams River, this instantaneous rate is about 0.78 for line 2, 1.11 for line 3, and 1.00 for line 4, the corresponding actual mortalities being 54, 67, and 63% per generation.

The basic condition that permits the development of a 4-year cycle among Fraser sockeye, and a 2-year cycle among pink salmon, as well as similar cycles among insects, is that the members of a population should mature only once, and predominantly at the same age. The ecological mechanism involved may be of various kinds, including cannibalism, exhaustion of food supply, predation by other organisms, or incidence of parasitism.

Acknowledgements

References

Babcock, J.P. 1914. The spawning beds of the Fraser. Report of the Commissioner of Fisheries for British Columbia for 1913. British Columbia Provincial Department of Fisheries, Victoria, B.C. pp. 17–38.

Beamish, R.J., and Neville, C.E.M. 1995. Pacific salmon and Pacific herring mortalities in the Fraser plume caused by river lamprey *Lampetra ayersi*. Can. J. Fish. Aquat. Sci. **52**: 644–650.

Cass, A.J. 1989. Stock status of Fraser River sockeye. Can. Tech. Rep. Fish. Aquat. Sci. No. 1674.

Cass, A.J., and Wood, C.C. 1994. An evaluation of the depensatory fishing hypothesis as an explanation for population cycles in Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **51**: 1839–1854.

Collie, J.S., and Walters, C.J. 1987. Alternative recruitment models of Adams River sockeye salmon, *Oncorhynchus nerka.* Can. J. Fish. Aquat. Sci. **44**: 1551–1561.

Collie, J.S., Peterman, R.M., and Walters, C.J. 1990. Experimental harvest policies for a mixed stock fishery: Fraser River sockeye salmon, *Oncorhynchus nerka.* Can. J. Fish. Aquat. Sci. **47**: 145–155.

Fisher, R.A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.

Foerster, R.E. 1925. Studies in the ecology of sockeye salmon (*Oncorhynchus nerka*). Contrib. Can. Biol. (N.S.), **2**: 335–422.

Foerster, R.E. 1938. Mortality trend among young sockeye salmon (*Oncorhynchus nerka*) during various stages of lake residence. J. Fish. Res. Board Can. **4**: 184–191.

Foerster, R.E. 1968. The sockeye salmon, *Oncorhynchus nerka.* Bull. Fish. Res. Board Can. No. 162.

Foerster, R.E., and Ricker, W.E. 1942. The effect of reduction of

predacious fish on survival of young sockeye salmon at Cultus Lake. J. Fish. Res. Board Can. **5**: 315–336.

Foerster, R.E., and Ricker, W.E. 1953. Predator control and sockeye salmon production. Fish. Res. Board Can. Manuscr. Rep. No. 478.

Gilbert, C.H. 1918. Contributions to the life-history of the sockeye salmon. No. 4. Report of the Commissioner of Fisheries for British Columbia for 1917. British Columbia Provincial Department of Fisheries, Victoria, B.C. pp. 33–80.

Gilhousen, P. 1992. Estimation of Fraser River sockeye escapements from commercial harvest data, 1892–1944. Int. Pac. Salmon Fish. Comm. Bull. No. 27.

Gilhousen, P., and Williams, I.V. 1989. Fish predation on juvenile Adams River sockeye in the Shuswap lakes in 1975 and 1976. Int. Pac. Salmon Fish. Comm. Bull. No. 24. pp. 83–100.

Goodlad, J.C., Gjernes, T.W., and Brannon, E.L. 1974. Factors affecting sockeye salmon (*Oncorhynchus nerka*) growth in four lakes of the Fraser River system. J. Fish. Res. Board Can. **31**: 871–892.

Hankin, D.G., Nicholas, J.W., and Downey, T.W. 1993. Evidence for inheritance of age of maturity in chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **50**: 347–358.

Henderson, M.A., and Cass, A.J. 1991. Effect of smolt size on smolt to adult survival for Chilko Lake sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **48**: 988–994.

Henry, K.A. 1961. Racial identification of Fraser River sockeye and pink salmon by means of scales and its application to salmon management. Int. Pac. Salmon Fish. Comm. Bull. No. 12.

Hume, J.M.B., Williams, I.V., and Morton, K.F. 1994. Factors affecting the production of juvenile sockeye salmon (*Oncorhynchus nerka*) in Shuswap and Quesnel lakes, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. No. 1190.

Hvidsten, N.A., and Johnsen, B.O. 1993. Increased recapture rate of adult Atlantic salmon released as smolts into large shoals of wild smolts in the River Orkla, Norway. N. Am. J. Fish. Manage. **13**: 272–276.

Killick, S.R., and Clemens, W.A. 1963. The age, sex ratio and size of Fraser River sockeye salmon 1915 to 1960. Int. Pac. Salmon Fish. Comm. Bull. No. 14.

Larkin, P.A. 1971. Simulation studies of the Adams River sockeye salmon, *Oncorhynchus nerka*. J. Fish. Res. Board Can. **28**: 1493–1502.

Levy, D.A., and Wood, C.C. 1992. Review of proposed mechanisms for sockeye salmon population cycles in the Fraser River. Bull. Math. Biol. **54**: 241–261

Ludwig, D., and Walters, C.J. 1981. Measurement errors and uncertainty in parameter estimates for stock and recruitment. Can. J. Fish. Aquat. Sci. **38**: 711–720.

Peterman, R.M. 1977. A simple mechanism that causes collapsing stability regions in exploited salmonid populations. J. Fish. Res. Board Can. **34**: 1130–1142.

Ricker, W.E. 1937. The food and the food supply of sockeye salmon (*Oncorhynchus nerka* Walbaum) in Cultus Lake, British Columbia. J. Biol. Board Can. **3**: 450–468.

Ricker, W.E. 1938. A comparison of seasonal growth rates of young sockeye salmon and young squawfish in Cultus Lake. Fish. Res. Board Can. Progr. Rep. Pac. Coast Stn. **36**: 3–5.

Ricker, W.E. 1941. The consumption of young sockeye salmon by predacious fish. J. Fish. Res. Board Can. **5**: 293–313.

Ricker, W.E. 1950. Cycle dominance among the Fraser sockeye. Ecology, **31**: 6–26.

Ricker, W.E. 1952. Numerical relations between abundance of predators and survival of prey. Can. Fish Cult. **13**: 5–9.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. **11**: 559–623.

Ricker, W.E. 1962. Regulation of the abundance of pink salmon populations. *In* Symposium on Pink Salmon. *Edited by* N.J. Wilimovsky. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, B.C. pp. 155–201.

Ricker, W.E. 1972. Hereditary and environmental factors affecting certain salmonid populations. *In* The stock concept in Pacific salmon. *Edited by* R. Simon and P.A. Larkin. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, B.C. pp. 19–160.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Ricker, W.E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. J. Fish. Res. Board Can. **33**: 1483–1524.

Ricker, W.E. 1987. Effects of the fishery and of obstacles to migration on the abundance of Fraser River sockeye (*Oncorhynchus nerka*). Can. Tech. Rep. Fish. Aquat. Sci. No. 1522.

Ricker, W.E. 1995. Trends in the average size of Pacific salmon in Canadian catches. *In* Climate change and northern fish populations. *Edited by* R.J. Beamish. Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 593–602.

Ricker, W.E., and Foerster, R.E. 1948. Computation of fish production. Bull. Bingham Oceanogr. Coll. **11**: 173–211.

Roos, J.F. 1991. Restoring Fraser River salmon. The Pacific Salmon Commission, Vancouver, B.C.

Rounsefell, G.A., and Kelez, G.B. 1938. The salmon and salmon fisheries of Swiftsure Bank, Puget Sound, and the Fraser River. Bull. U.S. Bur. Fish. **49**(27): 693–823.

Schnute, J.T., and Kronlund, A.R. 1996. A management oriented approach to stock recruitment analysis. Can. J. Fish. Aquat. Sci. **53**: 1281–1293.

Vernon, E.H. 1982. Fraser River sockeye: the stocks and their enhancement. Department of Fisheries and Oceans, Vancouver, B.C.

Walters, C.J. 1985. Bias in the estimation of functional relationships from time series data. Can. J. Fish. Aquat. Sci. **42**: 147–149.

Walters, C.J., and Ludwig, D. 1981. Effect of measurement errors on the assessment of stock–recruitment relationships. Can. J. Fish. Aquat. Sci. **38**: 704–710.

Walters, C.J., and Staley, M.J. 1987. Evidence against the existence of cyclic dominance in Fraser River sockeye (*Oncorhynchus nerka*). *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 375–384.

Walters, C.J., and Woodey, J.C. 1992. Genetic models for cyclic dominance in sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **49**: 281–292.

Ward, F.J. 1957. Seasonal and annual changes in availability of the adult crustacean plankters of Shuswap Lake. Int. Pac. Salmon Fish. Comm. Prog. Rep. No. 3.

Ward, F.J., and Larkin, P.A. 1964. Cyclic dominance in Adams River sockeye salmon. Int. Pac. Salmon Fish. Comm. Prog. Rep. No. 11.

Welch, D.W., and Noakes, D.J. 1990. Cyclic dominance and the optimal escapement of Adams River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **47**: 838–849.

Welch, D.W., and Noakes, D.J. 1991. Optimal harvest rate policies for rebuilding the Adams River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **48**: 526–535.

Williams, I.V., and Saito, W. 1989. Studies of Adams River sockeye from spawning to emergent fry. Int. Pac. Salmon Fish. Comm. Bull. No. 24. pp. 11–27.

Williams, I.V., Gilhousen, P., Saito, W., Gjernes, T., Morton, K., Johnson, R., and Brock, D. 1989*a*. Studies of the lacustrine biology of sockeye salmon (*Oncorhynchus nerka*) in the Shuswap system. Int. Pac. Salmon Fish. Comm. Bull. No. 24.

Williams, I.V., Gjernes, T., Johnson, R., and Saito, W. 1989*b*. Juvenile sockeye lacustrine population dynamics. Int. Pac. Salmon Fish. Comm. Bull. No. 24. pp. 29–57.

Woodey, J.C. 1987. In-season management of Fraser River sockeye (*Oncorhynchus nerka*): meeting multiple objectives. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 367–374.

966

Can. J. Fish. Aquat. Sci. Vol. 54, 1997

Appendix 1

Estimates of parents (*P*), and the recruits (*R*) that they produced, for ages 4 and 5 at the Lower Adams (note the scale difference between lines 1 + 2 and 3 + 4).

Line 1			Line 2			Line 3			Line 4		
Year-class	*P* (1000s)	*R* (1000s)	Year-class	*P* (1000s)	*R* (1000s)	Year-class	*P* (pieces)	*R* (pieces)	Year-class	*P* (pieces)	*R* (pieces)
1922	28	480	1923	0.3	—	1924		—	1925	1050	—
1926	300	3 790	1927	100	—	1928	10 000	—	1929	660	—
1930	400	4 320	1931	100	—	1932	4 000	—	1933	900	—
1934	500	4 110	1935	90	—	1936	6 000	—	1937	900	—
1938	775	8 780	1939	50	—	1940	11 700	—	1941	50	—
1942	2368	9 040	1943	15	—	1944	1 567	—	1945	1152	—
1946	2254	2 190	1947	198	—	1948	10 356	22 876	1949	3593	29 456
1950	1259	9 220	1951	144	522	1952	7 317	16 451	1953	3472	29 548
1954	2009	15 072	1955	64	852	1956	3 521	7 672	1957	2807	21 365
1958	3288	2 013	1959	134	371	1960	1 907	2 412	1961	1118	6 215
1962	1113	2 778	1963	156	3033	1964	604	17 132	1965	1795	50 353
1966	1256	3 852	1967	839	3055	1968	3 686	20 551	1969	4986	11 834
1970	1496	4 991	1971	284	635	1972	4 153	38 519	1973	1014	72 378
1974	1062	6 264	1975	162	986	1976	4 750	12 994	1977	6151	56 378
1978	1699	7 547	1979	289	1462	1980	2 480	21 378	1981	6218	3 427
1982	2506	6 712	1983	204	1942	1984	4 260	35 058	1985	471	432
1986	1663	8 016	1987	606	4218	1988	4 813	81 587	1989	75	—
1990	2636	—	1991	1242	—	1992	12 560	—	—	—	—

Note: Figures from 1948 onward are from the 1994 tables. Parents from 1938 to 1947 are from the ARs. Earlier parents are from Department of Fisheries and Oceans annual reports, in a few cases projected from qualitative statements (Ricker 1950). The Line 4 parents for 1925–1937 are 6% of the total sockeye, the remainder being of age 3 (6% is the average figure for 1945, 1949, and 1953). Line 1 recruits from year-classes 1926–1942 are the spawning ecapements plus the total catch in IPSFC Convention waters (Table 11 of the 1982 AR), less an estimate of 1.2 million produced by stocks other than the Lower Adams. Recruits from the 1922 year-class are the 300 000 spawners of 1926 plus 180 000 estimated caught by the Canadian late fishery that year (few were caught late in the season in United States waters).

Appendix 2

Sources of bias in the data

Walters (1985) described an unusual statistical source of bias that tends to overestimate both *a* and *b* of eq. 1. However, figures adjusted for this in Table 2 of Walters and Staley (1987) are on the whole not greatly different from the unadjusted values. In any event the bias tends to disappear as the number of observations increases, which is one of the reasons that data back to 1922 were included in eq. 2 and Fig. 2. Cass (1989, p. 7) discussed this and two kinds of correlation bias, all tending to make estimates of *a* and *b* too large, but it was seldom that these overestimates were serious.

In Figs. 3 and 4 the ordinary regression of $\ln(R/P)$ against *P* is used to describe the relationship between the two. This is appropriate when *P* is known without error and all of the variability in the data lies in the values of $\ln(R/P)$. However, *P* is usually estimated by mark and recapture, and the number of recaptures (*C*), which is proportional to $1/P$, is a member of a Poisson series; when large, it has a standard deviation approximately equal to its own square root (see also Appendix 2 of Ricker 1975). Walters and Ludwig (1981) and Ludwig and Walters (1981) considered some effects of variability of *P* in the Ricker model. Here, it is only necessary to point out that because it is a logarithm, the term $\ln(R/P)$ has much less absolute variance than *R*, *P*, or *R/P*, so when regressed against values of *P* that are not wildly inaccurate, reasonable estimates

of *a* and *b* are possible. In any event, variability in *P* makes an ordinary regression's estimate of *b* too small, thus opposing the positive biases mentioned above.

A possible source of bias in estimates of recruitment is misidentification. Henry (1961) described the methods used to estimate the abundance of stocks in the commercial catches. Most important are differences in migration times and, among stocks that occur in the fishery at the same time, counts of the 1st-year circuli on the scales. Because of overlapping of the frequency distributions of these counts for different stocks, it is clear that there will be some misidentification, and this of course was recognized. Levy and Wood (1992) pointed out that "errors in identifying the origin of fish caught in mixed-stock fisheries always cause the catch of minor stocks (that contribute little to the mixed-stock catch) to be overestimated, and the catch of major stocks to be underestimated."

Table 8 is a numerical model of this effect. A weak line, designated A, has true population parameters equal to those of the dominant line at the Lower Adams shown in eq. 2. This weak line fluctuates from year to year between 2000 and 16 000 parents, much like lines 3 and 4 at the Lower Adams. The first seven rows of the table describe the unbiased situation. Parents (*P*) are assumed to be known without error, and recruitments are computed from eq. 2, but over the small range of stock sizes considered, *R/P* practically does not vary with *P* and is equal to 15. The average rate of harvest is set at 80%.

In the catches that are to be sampled, the type A recruits are

mixed with much more numerous sockeye of another stock or stocks (type B). The type As vary from 2 to 16% (row 1). Rows 8–10 describe the composition of a sample of 200 recruits from each year-class. The true type A fish are given their most probable number in row 8, and five misidentified false type As are added to obtain the total in row 10. (More accurately, five is the difference between the type Bs misidentified as type A and the type As misidentified as type B.) The biased estimate of catch in row 11 and column 2 is equal to 9/4 times the true figure in row 4, and similarly for the C' in the other columns. In row 12 the escapement of row 5 is added to C' to obtain the biased estimate of recruitment (R'), and the other biased statistics follow in rows 13–15.[2]

Figure 7A shows how the percentage of misidentification varies with change in the percentage of type A fish in the catch sampled, for three different levels of misidentification. For example, if the catch sampled contained 6% of true type As, and the sample contained five more false type As than false type Bs, and also the most probable number (12) of true type As, the estimate of type A recruits is $(17 - 12)/12 = 42\%$ greater than it should be, as indicated at the circled point in Fig. 7A. Clearly, the smaller the percentage of true type A fish in the sample, the greater will be the misclassification bias that increases the estimate of the recruits, and this bias increases steeply if true type As become really scarce.

The effects of the bias on estimates of stock parameters are shown in Fig. 7B. The natural logarithms of R'/P in row 15 of Table 8 are plotted against P (the circled points). The straight line fitted to these points has a slope of 35×10^{-6}. This is 42 times larger than the true value of b, which is 0.832×10^{-6}, which indicates the order of magnitude of the bias to be expected. It could be considerably larger, or smaller. For example, if the data of Table 8 and Fig. 7 had contained no year-class larger than 10 000, the estimate of b is increased to 60×10^{-6}. If there were no year-class as small as 2000, it is reduced to 22×10^{-6}; but even much smaller biases cannot be ignored. For example, using only the data from $P = 10\,000$ to $P = 16\,000$ along the curve of two misclassifications in Fig. 7, b is about 5×10^{-6}, or six times the true value.

The biases in estimates of a are not as spectacular as those for b, but they are large enough to be important. The straight line in Fig. 7B estimates a as 3.29, or 0.58 greater than the true value 2.71. For the 2000 – 10 000 series, it is 0.72 greater.

Although the relationship between $\ln(R/P)$ and P is a curved line when there is any misidentification, this is rarely apparent on actual graphs of $\ln(R/P)$ plotted against P. The distribution of the points is very scattered, as shown by their large standard deviations in Table 2. There are four reasons for this. The true type A fish in each sample, which are given their most probable value in Fig. 7, have something close to a Poisson distribution, with corresponding sampling error. The number of misclassifications is subject to random variability and might also vary from cycle to cycle if the difficulty of separating stocks also varies. Estimates of parents and of recruits are both

Fig. 7. (A) Overestimation of the number of sockeye in a weak line (type A) present in a catch where they are mixed with a much more abundant stock or stocks (type B), in relation to the percentage of type A in the catch sampled, for three levels of misidentification. (B) Estimation of a and b of eq. 1 for a weak line, as described in the text.
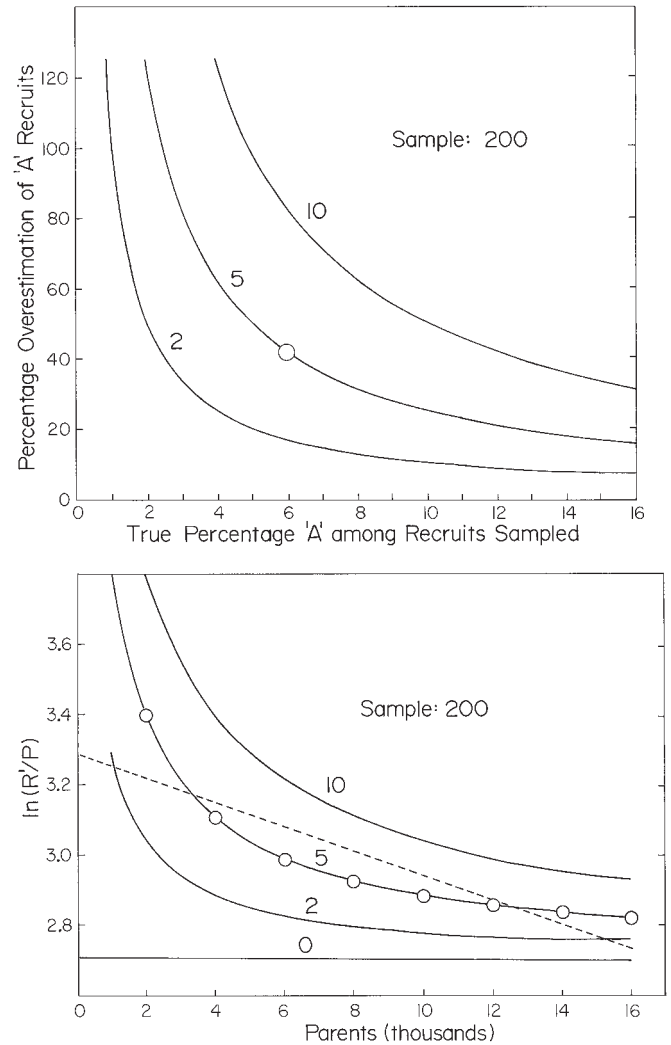
usually subject to the variability of a random sampling procedure. Finally, there will be much real natural variability between cycles in the number of recruits produced by any given number of parents of a particular stock and line. Thus, it is not surprising that straight lines have been fitted to such graphs by earlier authors, with the results shown in Table 2 here. Accordingly, all the estimates of a and b for small lines, if made by this method, are of little value.

To summarize, the effects of misidentification on small lines of sockeye will be as follows. (*i*) Catches and rates of harvest are somewhat overestimated, and the smaller the number of recruits in a line, the greater is the percentage overestimation. This is independent of any recruitment curve that may be fitted. (*ii*) When a Ricker curve is fitted by the method of Fig. 3, the value of a is somewhat overestimated, hence, so is e^a, the initial slope of a plot of R against P, which is the rate of recruitment at small stock sizes. (*iii*) Using the same

---

[2] Table 8 does not describe a line that is in numerical balance because the escapements (E) are three times as numerous as the parents (P) that produce them. However, a small line in any real population is held in check by the interaction mortality described in section 6. Without this, C/R would have to be $14/15 = 0.933$, on average, to prevent the line from increasing in numbers (cf. section 4).

Table 8. Model of a weak line of sockeye (type A) for which the catch is estimated from a sample of 200 fish containing 5 that are incorrectly identified (explanation in the text).

		1	2	3	4	5	6	7	8	9
	True statistics									
1. Proportion of type A in the catch sampled (%)		—	2	4	6	8	10	12	14	16
2. Number of parents (thousands)	P	2	4	6	8	10	12	14	16	
3. Recruits (thousands)	R	30	60	90	120	150	180	210	240	
4. Catch (thousands)	C	24	48	72	96	120	144	168	192	
5. Ecapement (thousands)	E	6	12	18	24	30	36	42	48	
6. Rate of recruitment	R/P	15	15	15	15	15	15	15	15	
7. Rate of harvest	C/R	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	
	In sample of 200									
8. Type A correctly identified		—	4	8	12	16	20	24	28	32
9. False type As		—	5	5	5	5	5	5	5	5
10. True and false type As		—	9	13	17	21	25	29	33	37
	Biased statistics									
11. Catch (thousands)	C'	54	78	102	126	150	174	198	222	
12. Recruits (thousands)	$R' = C' + E$	60	90	120	150	180	210	240	270	
13. Rate of recruitment	R'/P	30.0	22.5	20.0	18.8	18.0	17.5	17.1	16.9	
14. Rate of harvest	C'/R'	0.90	0.87	0.85	0.84	0.83	0.83	0.82	0.82	
15. Natural logarithm of R'/P		—	3.40	3.11	3.00	2.93	2.89	2.86	2.84	2.83

Note: An average parent (both sexes) produces 15 recruits.

method, the value of b in eq. 1 can be estimated as at least 5–50 times its true value, so that both the maximum number of recruits (e^{a-1}/b) and the parent stock that produces them ($1/b$) will be grossly underestimated.

Thus, this source of bias could account for two peculiarities of Table 2. One is that lines 3 and 4 both have a somewhat larger value of a than line 2 does whereas their scarcity suggests that it should be smaller. The other is that the very large values of b for lines 3 and 4 may arise simply from the exaggerated slope of the regression line of $\ln(R/P)$ against P, similar to what is illustrated in Fig. 7. In combination, this means that an unbiased Ricker curve for a weak line would have somewhat less initial slope (smaller a), and a much larger maximum recruitment at much larger parental abundance (from a greatly reduced b).

However, bias on the scale suggested above has usually been reduced or avoided. The catches of two or more small lines have been estimated together, or in combination with a larger line, after which the individual catches are separated in proportion to each line's spawning ground estimate (J.C. Woodey, personal communication).

In any event, none of the above applies to abundant lines. The fish that weak lines gain by misclassification are lost to the large lines that contribute them, but this reduces their estimates of R by only a few percent at most. Consequently, their estimates of a and b are only slightly altered. A subdominant line is in an intermediate position, but will probably be affected by misidentification to only a minor degree.