Available online at www.sciencedirect.com
SCIENCE DIRECT
Fisheries Research 63 (2003) 379–392
FISHERIES RESEARCH
www.elsevier.com/locate/fishres

Multi-year effects of high densities of sockeye salmon spawners on juvenile salmon growth and survival: a case study from the *Exxon Valdez* oil spill

Gregory T. Ruggerone*, Donald E. Rogers

Fisheries Research Institute, School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195, USA

Received 2 August 2002; received in revised form 11 February 2003; accepted 27 February 2003

Abstract

Reduced fishing after the 1989 *Exxon Valdez* oil spill in Prince William Sound, Alaska, contributed to exceptionally large numbers of sockeye salmon spawners up to 860 km from the spill site. We measured annual scale growth of adult sockeye salmon from four affected populations, 1970–1997, in order to test the hypothesis that large spawner densities can have multi-year effects on juvenile size and subsequent adult abundances as a result of intraspecific competition among juveniles in the nursery lake. Sockeye salmon scale growth in fresh water was significantly reduced by the large 1989 spawner densities in the Kenai River system, Red Lake, Akalura Lake, but not Chignik Lake. Scale growth in the three affected systems recovered to previous levels 2–4 years after the oil spill, but subsequent moderately high spawner densities led to exceptionally low growth. Juvenile salmon growth was negatively related to parent spawners, spawners from the next brood year (second season in lake), and spawners from the previous brood year. Multi-variate time series analyses indicated adult sockeye salmon abundance increased with greater numbers of parent spawners, but decreased as a result of either large numbers of spawners in the previous year or small juvenile salmon size. These results indicate sockeye salmon spawners can affect juvenile growth and adult production of adjacent year classes. Implications for stock-recruitment modeling and spawner density management are discussed.

Keywords: Alaska; Competition; *Exxon Valdez*; Growth; Management; Oil spill; *Oncorhynchus nerka*; Salmon; Sockeye; Stock-recruitment

1. Introduction

The *Exxon Valdez* oil tanker ran aground in Prince William Sound on March 24, 1989, spilling approximately 258,000 barrels (42 million liters) of crude oil. During the following month, approximately 25% of the oil exited Prince William Sound (Wolfe et al., 1993) and interfered with Pacific salmon fisheries in Prince William Sound, Cook Inlet, Kodiak and Chignik (Fig. 1). Oil on the water surface led to reduced fishing that allowed large numbers of sockeye salmon (*Oncorhynchus nerka* Walbaum) to reach freshwater spawning grounds. In the Kodiak Island area, about 768,000 sockeye salmon entered into Red Lake (Ayakulik), approximately three times the management goal of 200,000–300,000 fish. At Akalura Lake, Kodiak Island, the 1989 spawner density of 116,000 sockeye was about twice the management goal of 40,000–60,000 sockeye salmon. In Upper Cook Inlet,

* Corresponding author. Present address: Natural Resources Consultants Inc., 1900 West Nickerson Street, Suite 207, Seattle, WA 98119, USA. Tel.: +1-206-285-3480; fax: +1-206-283-8263.
E-mail address: GRuggerone@nrccorp.com (G.T. Ruggerone).

0165-7836/03/$ – see front matter © 2003 Elsevier Science B.V. All rights reserved.
doi:10.1016/S0165-7836(03)00099-7

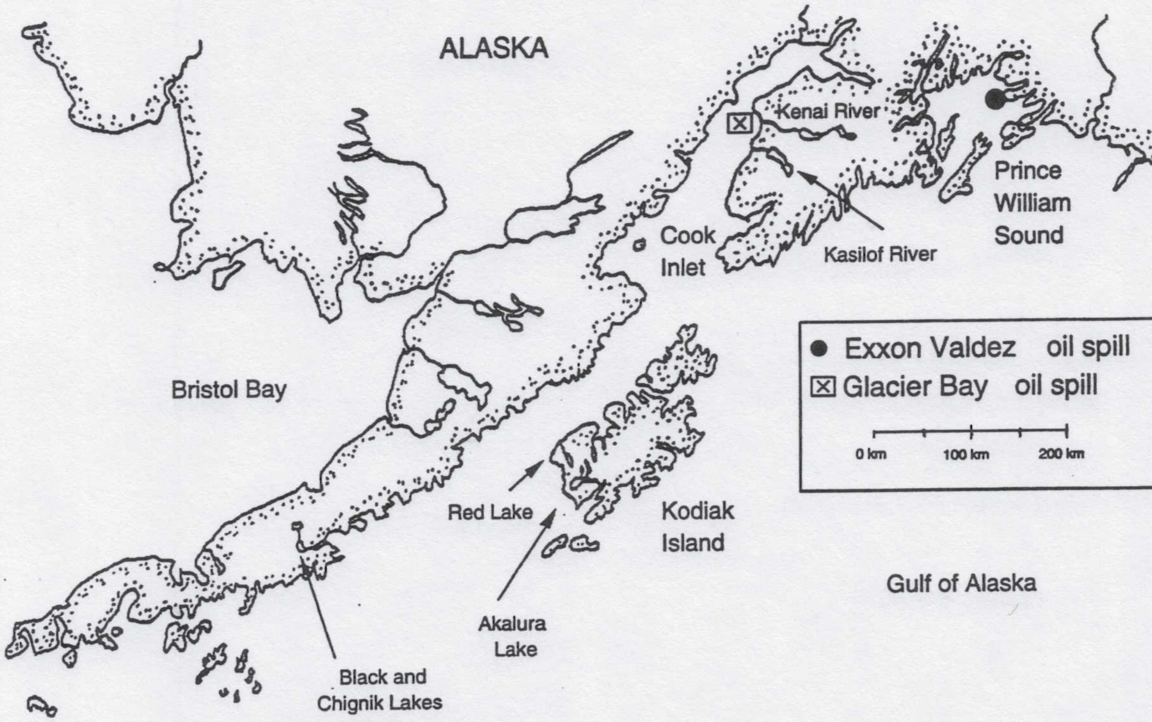

Fig. 1. Map of the study area showing locations of *Exxon Valdez* oil spill in Prince William Sound, *Glacier Bay* oil spill in Cook Inlet and the sockeye salmon populations described in this investigation.

an estimated 1.33 million sockeye salmon entered into the Kenai River system, approximately 2.5 times the management goal of 400,000–700,000 fish. The great numbers of salmon entering the Kenai system in 1989 followed large spawner densities during 1987 (1.3 million fish) and 1988 (0.84 million fish). On the Alaska Peninsula, about 860 km from Prince William Sound, the presence of oil in and near Chignik Lagoon led to a density of 557,000 sockeye salmon in Chignik Lake, more than twice the management goal of 250,000 fish.

Alaska Department of Fish and Game (ADFG) biologists expressed concern that exceptionally large 1989 spawner populations would lead to low returns of adult salmon. Large spawner abundances can lead to overcrowding of the spawning grounds or to reduced growth in the nursery lakes if spawning grounds are not limiting juvenile abundance (Ricker, 1954). Field studies after the oil spill indicated that large numbers of subyearlings were produced by the spawners and the investigators hypothesized that intense competition for prey in the nursery lakes may have a prolonged adverse effect on sockeye growth and survival (Schmidt et al., 1994, 1996; Swanton et al., 1996).

Observations of density-dependent growth of sockeye salmon in lakes (Burgner, 1987; Bugaev et al., 1994) are important because larger juvenile salmon typically experience higher survival at sea (Koenings et al., 1993). Past studies of density-dependent growth focused on effects within the large year class of progeny produced by parent spawners, although Eggers and Rogers (1987) reported that peak-cycle year abundances of sockeye salmon in Iliamna Lake, Alaska, affected first year growth of juveniles from the post-cycle year class. The concept of a large spawner density having an effect on multiple year classes of sockeye salmon has not been investigated except for field studies initiated after the *Exxon Valdez* oil spill.

The objective of this investigation was to test whether the large sockeye salmon spawning populations in 1989 led to reduced growth of their progeny, the progeny of subsequent spawning populations, and yearlings of the previous brood year that co-inhabited the lakes. Additionally, the effect of these interactions on adult sockeye salmon returns was examined. To test the concept of interaction between broods, we developed a long-term index of annual sockeye salmon growth in selected watersheds using measurements of sockeye salmon scales. Length of juvenile sockeye salmon is correlated with scale radius (Clutter and Whitesel, 1956; Fukuwaka and Kaeriyama, 1997; Ruggerone and Rogers, 1998) and scales have been used to describe sockeye salmon growth in lakes (Henderson and Cass, 1991; Bugaev et al., 1994).

2. Methods

Historical collections of adult sockeye salmon scale impressions were obtained from ADFG for the four stocks receiving large spawner densities during 1989 and two stocks receiving average spawner densities (Table 1). The latter two stocks were used to observe whether stocks receiving average spawner densities experienced similar scale growth during and after 1989. Both of the control stocks were within the oil spill area but the runs were small and harvest management was able to control spawner densities. Scales from sockeye runs during 1970–1997 were measured when available. Only scales from the dominant age group of each stock were selected for measurement.

Scales were collected from adult sockeye salmon that recently entered fresh water or were near the natal stream in order to minimize potential mixing with other stocks. Chignik and Black Lake sockeye salmon scales were collected in Chignik Lagoon. Chignik Lake sockeye were sampled during August when no Black Lake sockeye salmon are present, whereas Black Lake sockeye were sampled prior to June 20 when relatively few age 1.3 Chignik Lake sockeye salmon are present (Dahlberg, 1968). Age 1.3 refers to sockeye salmon that spent one winter in the lake and three winters in the ocean. Sockeye salmon typically spend one or two winters rearing in freshwater nursery lakes, followed by two or three winters rearing in the North Pacific Ocean. Growth rate may affect freshwater and marine age, i.e., smaller sockeye salmon will tend to spend an additional year in the lake or ocean but will smoltify or mature at a larger body size (Rogers, 1987; Burgner, 1987).

Scales were selected for measurement only when: (1) we agreed with the age determination previously made by ADFG; (2) the scale shape indicated the scale was removed from the "preferred area"; (3) circuli were clearly visible and not affected by scale regeneration. Up to 100 scales per year, representing equal numbers of male and female salmon were measured from each stock.

Scale measurements followed procedures described by Davis et al. (1990). Scales were measured with the Optical Pattern Recognition System (Model OPRS-512, BioSonics Inc., Seattle) at a magnification of 113× (freshwater growth) or 56× (marine growth). These magnifications allowed for minimum distances between adjacent measurements of 4.7 μ (<1 mm juvenile fish length) for freshwater growth and 9.5 μ for marine growth. The measurement axis was determined by a perpendicular line drawn from each end of the first salt water annulus. Scales were measured from the scale focus to the outer edge of each

Table 1
Characteristics of investigated sockeye salmon populations, including the percentage change in spawner density associated with the 1989 oil spill

Sockeye stock	Age	Years sampled	Spawning density, 1989 (1000 s)	Mean spawners prior to large escapement (1000 s)	Change (%)	Management goal (1000 s)
Kenai River system	Age 1.3	1972–1997, excluding 1975	1333	368	262	400–700
Akalura Lake	Age 2.2	1986–1997	116	18	539	40–60
Red Lake	Age 2.2	1970–1997, excluding 1972	768	220	226	200–300
Chignik Lake	Age 2.3	1970–1997	583	309	89	250
Kasilof River system	Age 1.3	1971–1997	150	178	−16	150–250
Black Lake	Age 1.3	1970–1997	384	469	−18	400

freshwater annulus (FW1, FW2), spring plus growth (FWPL), each ocean annulus (SW1, SW2, SW3), and to the edge of the scale (SWPL) if resorption was not significant.

Scale measurements were compared with spawner and adult salmon return statistics (brood tables) maintained by ADFG (Tobias and Tarbox, 1999; Swanton, C., Owen, D., ADFG Kodiak, pers. commun.), and seasonal air temperature data recorded at King Salmon and Cold Bay weather stations operated by the National Weather Service. Air temperature is important to juvenile sockeye salmon rearing in lakes because it influences date at which ice leaves the lakes, the length of the growing season, and it is correlated with water temperature during ice-free months (Rogers, 1973; Edmundson and Mazumder, 2001). Adult salmon returns described here are the sum of all age groups produced by spawners in a given year.

2.1. Data analysis

Multi-variate time series analysis (Liu and Hudak, 1992) was used to test for significant relationships between freshwater scale growth and factors that might influence growth such as abundance of parent spawners, abundance of spawners during the previous year, and air temperature during spring and summer. Time series analysis was also used to test for factors influencing adult returns such as scale growth, spawner density, air temperature, and precipitation. Models reported here were not significantly affected by autocorrelation or collinearity.

Partial residual analysis (Larsen and McCleary, 1972) was used to graphically show the partial effect of each independent variable on the dependent variable in the multi-variate model. The mean partial residual was equal to the mean of the dependent variable values of each plot. Normalized *Z*-values (standard deviations above and below the mean) of annual scale measurements were plotted, based on mean and standard deviation prior to the 1989 *Exxon Valdez* oil spill, so that post-spill salmon growth and spawner abundances could be compared with previous values. However, in the Kenai River system, post-spill values were compared with years prior to 1987 because exceptionally large spawner densities began in 1987 as a result of the large run and the *Glacier Bay* oil spill.

3. Results

3.1. Kenai River, Cook Inlet

Approximately 71% of Kenai sockeye salmon migrated to sea after one winter in the lakes. Freshwater scale growth (FW1) of subyearling Kenai sockeye salmon was relatively high during brood years 1967–1986 (average 388 μ) when spawner density was relatively low (average 368,000 fish), then growth declined approximately 21%, on average, during 1987–1992 following the exceptionally large spawner densities beginning in 1987 (average 905,000 fish) (Fig. 2). Sockeye salmon scale growth resulting from the 1987 spawner density (1.3 million fish) declined abruptly from the long-term average of 388 to 324 μ, the lowest growth recorded up to that year. In 1988, spawner density declined to 840,000 fish, but it was still high relative to most years and sockeye scale growth remained exceptionally low. In 1989, the year of the *Exxon Valdez* oil spill and the third exceptional spawner density (1.3 million fish), scale growth declined to its lowest recorded level (308 μ). In 1990, spawner density (440,000 fish) decreased 60% compared with the previous 3 years, but scale growth declined again (297 μ). In 1991, spawner density was small again (378,000 fish) and scale growth increase to a level (353 μ) that approached the pre-1987 average (388 μ). However, in 1992, spawner density increased again to 753,000 sockeye salmon and the corresponding scale growth declined to the lowest level (240 μ) of the 21-year period and was approximately 38% below average growth prior to the large spawner densities. Spring and summer air temperatures corresponding to the 1992 brood year were above average, thus temperature did not explain the low growth.

A key factor leading to the first exceptionally large spawner density in 1987, in addition to the presence of oil in the harvest areas, was the record large run to the Kenai system. The total Kenai run in 1987 was 8.6 million sockeye, approximately 3.6 times greater than the previous 5-year average. Freshwater scale growth of age 1.3 sockeye salmon (481.5 μ) that produced 84% of this large run was significantly greater than all other years (Bonferronni/Dunn multiple contrast test, $P < 0.001$), indicating large size in fresh water contributed to the large adult return.

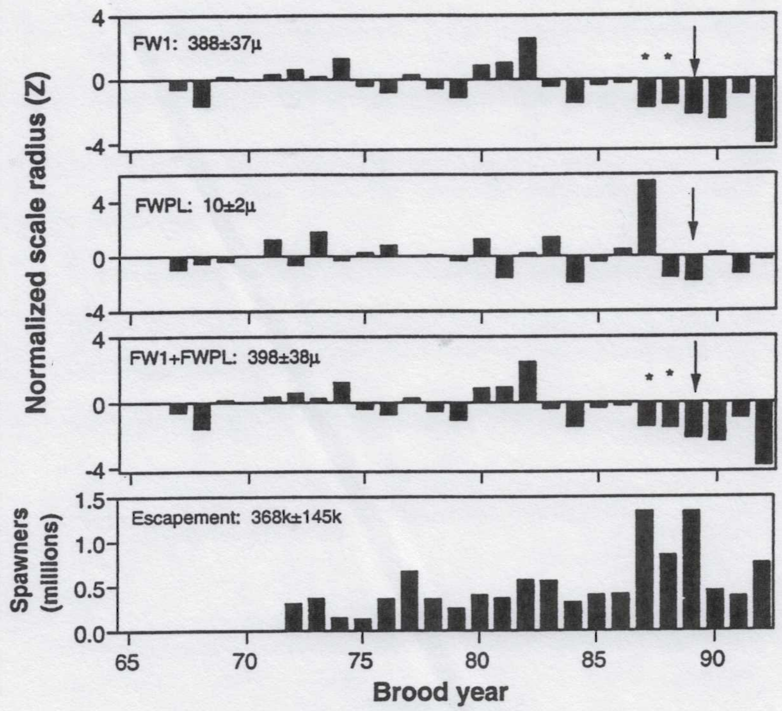

Fig. 2. Relative scale growth of Kenai River sockeye salmon, brood years 1967–1992. Arrows identify the 1989 *Exxon Valdez* oil spill. All normalized values are relative to mean (±S.D.) values prior to the 1987 oil spill. Asterisks identify previous years when exceptionally large spawner densities occurred. Spawner density is shown in the bottom of the figure. No scales were available in 1970.

A single factor ANOVA indicated that mean Kenai sockeye scale growth in fresh water during years following the large spawner density in 1987 (309 µ) was significantly smaller than scale growth prior to the large spawner density (388 µ) (d.f. $= 1, 2472$, $P < 0.001$). Sockeye salmon scale growth significantly decreased when greater numbers of parent sockeye escaped to the spawning grounds ($n = 21$, $P = 0.033$, $r^2 = 0.22$), indicating increased competition for prey in the rearing lakes at high juvenile salmon densities. However, the effect on scale growth was best explained by average spawner density of the parents and the three previous broods ($n = 21$, $P < 0.001$, $r^2 = 0.48$), indicating spawner abundance can have a prolonged effect on salmon growth in the lakes. Potential factors such as spring and summer air temperatures did not contribute significant new information.

No evidence of rearing an additional year in the Kenai lakes as a result of slow growth was detected (except for the 1983 brood year as discussed below). For example, the percentage of the total brood return represented by sockeye salmon spending 2 years in fresh water (average 29%) was not correlated with freshwater scale growth, abundance of parent spawners, nor spawners during previous years ($n = 20$, $P > 0.05$), suggesting either no effect on age at seaward migration or high mortality of those that remain in the lakes for a second year.

An important question was whether numerous small sockeye salmon led to large or small returns of adult salmon. Multi-variate time series analysis indicated total sockeye return to the Kenai River was positively correlated with both parent spawners (partial $P < 0.001$) and scale growth (FW1 + FWPL) at the time of seaward migration (partial $P < 0.05$, $n = 21$) (Table 2). Model coefficients indicated the effect of spawners on adult return was greater than the effect of scale growth. This model identified an outlier associated with brood year 1983, where below average growth in the lakes and the exceptionally cold spring in 1985 led to an unusually

Table 2
Multi-variate time series models describing factors affecting sockeye salmon growth in fresh water and adult returns[a]

Stock	Dependent variable	Independent variable	Parameter	S.E.	*n*	*T*-value	*P*
Kenai River system	Adult return (millions)	Constant	−6.4020	3.0957	21	−2.07	
		Parent spawner density	0.0055	0.0012		4.63	<0.001
		Total freshwater scale growth (FW1, FWPL)	0.0174	0.0073		2.38	<0.05
Kenai River system	Adult return (millions)	Constant	−10.496	3.8449	21	−2.73	
		Parent spawner density	0.0059	0.0010		5.61	<0.001
		Spawners, year-1	−0.0027	0.0010		−2.60	<0.02
		Ocean scale growth (SW3)	0.0188	0.0060		3.13	<0.01
Red Lake	ArcSin % ocean age 2 and 3	Constant	2.3497	0.3320	24	7.08	
		Freshwater scale growth (FW1)	−0.0052	0.0011		−4.60	<0.001
		November–March air temperature prior to FW2	−0.0821	0.0301		−2.72	<0.02
Red Lake	Adult return (1000 s)	Constant	−1307.5841	479.5725	26	−2.73	
		Parent spawner density	1.5762	0.3595		4.38	<0.001
		Freshwater scale growth (FW1)	5.2319	1.5846		3.30	<0.005
Akalura Lake	Freshwater scale growth end age 2 (cFW2)	Constant	444.287	12.8734	7	34.51	
		Parent spawner density	−0.5369	0.1736		−3.09	<0.05
		Spawners, year + 1	−0.8171	0.1874		−4.36	<0.02

[a] Spawner density values are reported in 1000 s of fish. Statistical significance tests based on two-tail tests.

large return of freshwater age 2 sockeye salmon in 1989.

Multi-variate time series analysis indicated total sockeye salmon returning to the Kenai River was positively correlated with parent spawners (partial $P < 0.001$) and scale growth during the third year at sea (partial $P < 0.01$), but negatively correlated with spawners during the previous year (Table 2) (partial $P < 0.02$; $n = 21$). Partial residual plots show that the effect of parent spawners on adult returns was nearly double the effect of spawners during the previous year (Fig. 3). This relationship indicates large spawner densities can reduce sockeye returns of future broods.

3.2. *Red Lake, Kodiak Island*

On average, approximately 68% of sockeye salmon returning to Red Lake spent 2 years in the lake. Scale growth of the 1989 year class during the first year in the lake (236 μ) was third lowest of the time series, averaging 81% of the previous 23-year mean (Fig. 4). Growth of the 1989 year class was markedly lower compared to the consistently high growth during the previous 5 years (average 324 μ), even though Kodiak air temperature during spring and summer was above average. Incremental growth during the second year (FW2) in the lake was 76% of the long-term average (Fig. 4). Cumulative growth (420 μ) at the end of the second year (FW1 + FW2) was 80% of long-term average and 73% of the previous 6-year average (average 572 μ), indicating the large spawner density led to reduced sockeye salmon growth.

Although spawner densities significantly declined after 1989, scale growth of sockeye salmon inhabiting Red Lake for 1 and 2 years remained low until the 1992 rearing year, when growth of both subyearlings and yearlings increased (Fig. 4). However, growth declined during the 1993 rearing year, a period when spring and summer air temperatures were above average. In spite of above average growing conditions in 1992, cumulative sockeye salmon scale growth (FW1 + FW2 + FWPL) remained below average from 1989 to 1993 brood year.

In contrast to the apparent effects of large spawner density in 1989, growth of sockeye in fresh water was not noticeably reduced by large spawner density in 1980. The effect of large 1980 spawner density on juvenile sockeye salmon growth may have been compensated, in part, by exceptionally warm spring air temperature (46% above average) that occurred in 1981.

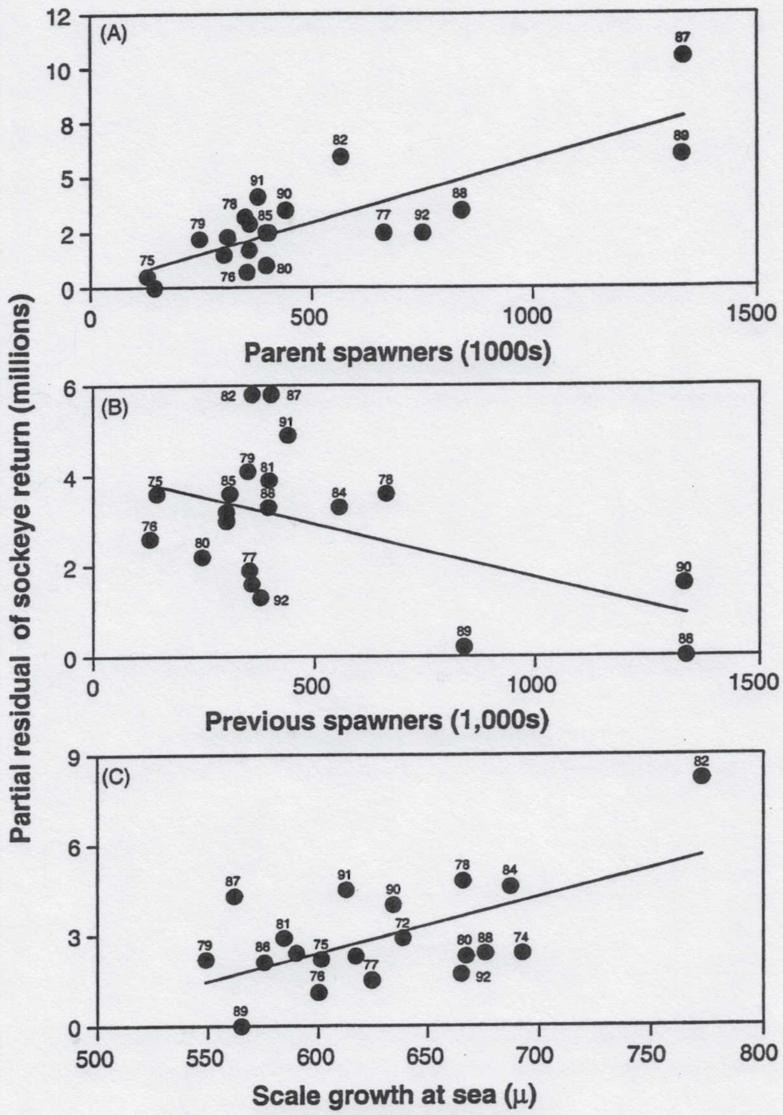

Fig. 3. Multi-variate partial residual plots showing the effect of parent spawners (A), spawners during the previous year (B), and sockeye salmon scale growth during the third year at sea (C) on adult return of sockeye salmon to the Kenai River system, brood years 1972–1992. Parent spawning year is shown next to filled circles. Multi-variate equation is shown in Table 2.

Scale growth of subyearlings in Red Lake was positively correlated with annual scale growth of yearling sockeye that co-inhabited the lake (Fig. 5). For example, growth of sockeye salmon from the 1988 brood year, which inhabited the lake as yearlings (FW2) with the 1989 subyearlings, was below average (Fig. 4). This relationship indicated that factors influencing growth in the lake, such as food availability and temperature, acted on both year classes that co-inhabited the lake.

Annual scale growth during each year in Red Lake was compared with parent spawners, previous spawners, subsequent spawners and spring, summer and winter air temperature at Kodiak. Annual scale growth during the first and second years was not correlated with these variables ($P > 0.05$), even though

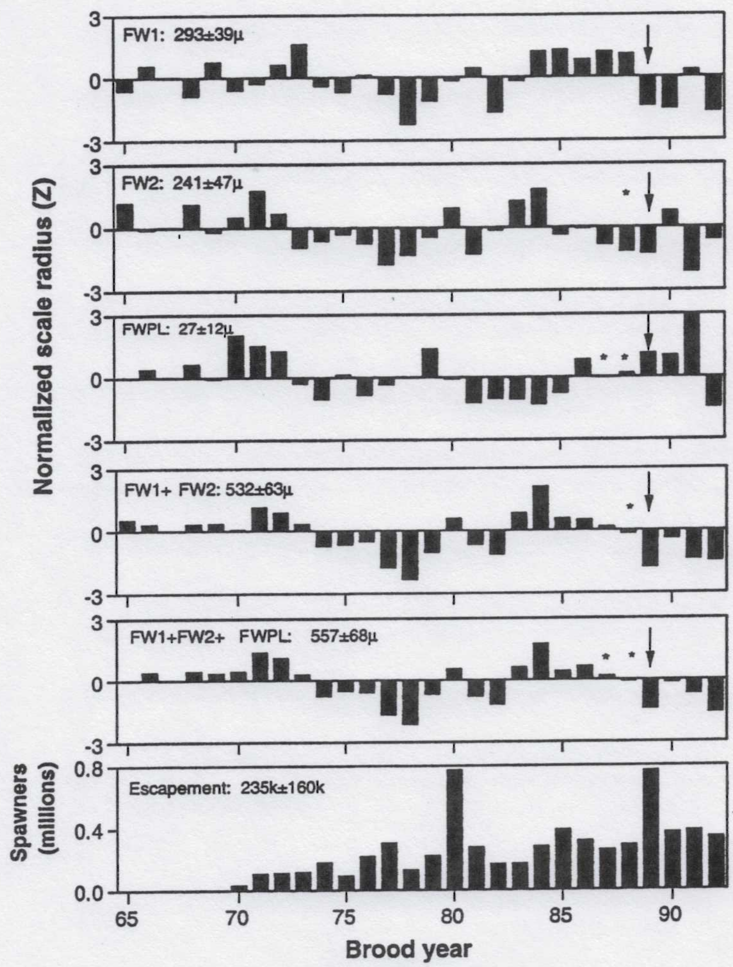

Fig. 4. Relative scale growth of Red Lake sockeye salmon, brood years 1965–1992. Arrows identify the 1989 *Exxon Valdez* oil spill. All normalized values are relative to mean (±S.D.) values prior to the oil spill. Asterisks identify life stages of previous brood years co-inhabiting the lake with the 1989 brood year. Spawner densities are shown in the bottom of the figure. No scales were available in 1967.

sockeye growth appeared to be reduced by the large 1989 spawner density. Lack of correlation between spawner density and age-specific scale growth may be related to the propensity for slow growing Red Lake fish to spend three winters in the lake, as discussed below.

In Red Lake, the large 1989 spawner density resulted in the greatest percentage of adult sockeye salmon spending 3 years in the lake (14.1%) compared to other brood years (average 1.6%). The 1988 brood year, which co-inhabited the lake with the 1989 brood year during its second year, also produced an exceptionally large percentage of sockeye spending 3 years in the lake (5.8% of adult return). Multi-variate time series analysis indicated that the percentage of adult sockeye salmon spending 2 or more years in Red Lake as juveniles was negatively correlated with scale growth during the first year in the lake (partial $P < 0.001$) and negatively correlated with winter air temperature (Kodiak, November–March) prior to the second year in the lake (Table 2, partial $P < 0.02$). Thus, Red Lake sockeye salmon delayed seaward migration when growth during the first year was slow and when conditions influencing growth during their second spring, such as temperature, were less conducive to growth.

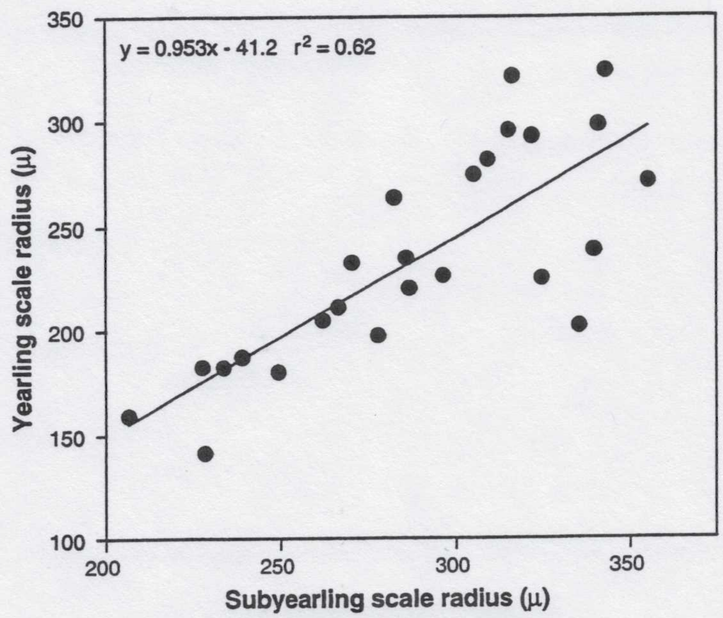

Fig. 5. Relationship between annual scale growth of subyearling and yearling sockeye salmon co-inhabiting Red Lake during rearing years 1967–1993.

Multi-variate analysis indicated the number of adult sockeye salmon returning to Red Lake during brood years 1966–1992 was positively correlated with both parent spawners (partial $P < 0.001$) and growth during the first year in fresh water (partial $P < 0.005$) (Table 2 and Fig. 6). This suggests that more sockeye salmon returned from numerous, relatively large juveniles. Temperature did not add significant information to this model.

3.3. *Akalura Lake, Kodiak Island*

Most sockeye salmon emigrated from Akalura Lake after two winters. Scale growth of offspring produced by the 1989 brood was exceptionally small during the first year in the lake, averaging 76% of the previous 8-year mean (Fig. 7). Growth during the second year remained below average and cumulative growth at the end of the second year was 80% of the previous 8-year mean.

Second year scale growth of sockeye from the previous brood year (1988), which inhabited the lake when the 1989 fry emerged, was exceptionally low, averaging 71% of the previous 7-year mean (Fig. 7). Scale growth during the second year in the lake was highly correlated with scale growth of first year sockeye that co-inhabited the lake ($n = 11$, $P < 0.001$, $r^2 = 0.83$), indicating both yearling and subyearling sockeye salmon responded similarly to growing conditions in the lake.

Cumulative freshwater scale growth of Akalura sockeye salmon (FW1 + FW2 + FWPL) was exceptionally low following the 1988 and 1989 broods, which were directly influenced by the large 1989 spawner density (Fig. 7). Spawner density in 1990 and 1991 was 60% lower and cumulative growth of sockeye salmon produced by these parents increased slightly, but still remained below growth prior to the *Exxon Valdez* oil spill even though Kodiak air temperatures during spring and summer were above average. Cumulative growth of the 1992 brood (411 μ) was similar to growth prior to the oil spill (average 418 μ), indicating that sockeye salmon growth returned to average levels 4 years after the oil spill.

Multi-variate time series analysis indicated cumulative scale growth at the end of the second year in the lake was negatively correlated with parent spawner density (partial $P < 0.05$) and negatively correlated with spawners from the following year class, which produced subyearlings that co-inhabited the lake with

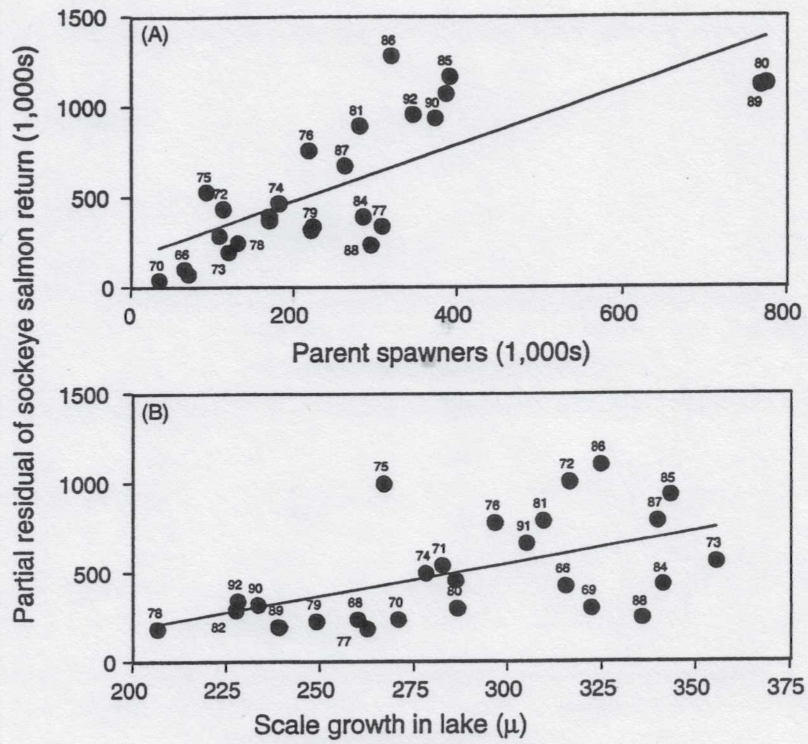

Fig. 6. Multi-variate partial residual plots showing the effect of parent spawners (A) and sockeye salmon scale growth during the first year in the lake (B) on adult return of sockeye salmon to Red Lake, brood years 1966–1992. Multi-variate equation is shown in Table 2.

yearling sockeye salmon (partial $P < 0.02$) (Table 2). Thus, growth of Akalura sockeye salmon that inhabited the lake for 2 years was directly influenced by both parent spawners and spawners that produced the next year class.

Too few data were available to statistically test the effects of scale growth on abundance of adult sockeye salmon returning to Akalura Lake. However, average run size produced by spawners during 1989–1991 (approximately 25,000 sockeye salmon per year) was only 22% of previous 8 years (average 110,000 sockeye salmon), suggesting that large spawner density and reduced growth may have contributed to the small returns.

3.4. Chignik Lake, South Alaska Peninsula

Approximately 75% of adult returns to Chignik Lake spent two winters in the lake. Moderately large spawner density in Chignik Lake during 1989 did not significantly affect the observed size of subyearlings and yearlings, and the corresponding adult return was 40% above the recent 10-year average. First year scale growth of sockeye salmon produced by the 1989 brood (232 μ) was slightly above average (208 μ). Second year scale growth (139 μ) was slightly below average (146 μ), leading to cumulative growth (FW1 + FW2) in fresh water (371 μ) that was slightly above average (354 μ). No correlation was observed between spawner density and salmon growth in the lake, but spawner densities varied relatively little during the study period. Chignik scale growth during the first year in the lake was not correlated with second year scale growth of yearling sockeye salmon that co-inhabited the lake ($P = 0.24$, $n = 28$), suggesting that growth of Chignik subyearlings and yearlings may be influenced by different factors in the lake.

3.5. Stocks receiving average spawner density

Freshwater scale growth of sockeye salmon populations not influenced by large spawner densities

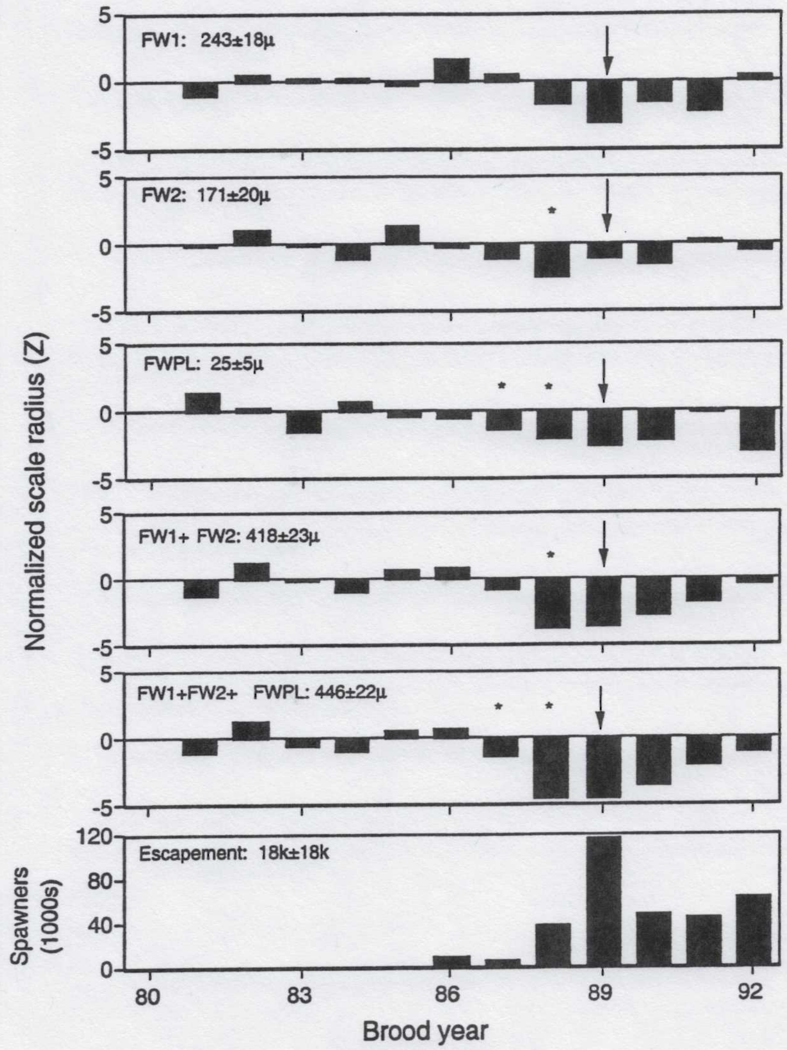

Fig. 7. Relative scale growth of Akalura Lake sockeye salmon, brood years 1981–1992. Arrows identify the 1989 *Exxon Valdez* oil spill. All normalized values are relative to mean (±S.D.) values prior to the oil spill. Asterisks identify life stages of previous brood years co-inhabiting the lake with the 1989 brood year. Spawner densities are shown in the bottom of the figure. No scales were available prior to 1981.

in 1989 were examined to see if these stocks experienced below average growth during and after the *Exxon Valdez* oil spill. Black Lake (Chignik system) sockeye salmon scale growth corresponding to the 1989–1991 brood years was equal to or above the long-term mean. No salmon originating from Chignik Lake, which received many spawners, migrate upstream to Black Lake. Kasilof River (Cook Inlet) sockeye salmon scale growth corresponding to the 1989 brood year was 9% below the long-term mean, but growth during the next three seasons was within 2% of the mean. Spring and summer air temperature during 1990–1993 rearing seasons was above average. These data suggest that there was not a region-wide decline in growth that might otherwise explain reduced growth among populations receiving large spawner densities in 1989.

4. Discussion

Analysis of sockeye salmon scales indicated juvenile sockeye salmon growth was reduced in three of four populations that received exceptionally large spawner densities as a result of the 1989 *Exxon Valdez* oil spill. In the Kenai River system, juvenile growth was also influenced by high spawner densities that occurred during the 2 years prior to the *Exxon Valdez* oil spill. In these lakes, juvenile growth recovered to historical levels 2 or 4 years after the high spawner densities. Chignik Lake sockeye salmon did not experience reduced growth, but the increase in spawner density to this system was not as pronounced as the other systems. Growth in Chignik Lake was influenced by significant but variable annual immigrations of sockeye salmon from Black Lake that have a relatively great effect on yearling compared with subyearling sockeye salmon in Chignik Lake (Ruggerone et al., 1993).

One year following the return to average growth in the Kenai and Red Lake populations, juvenile salmon growth from the 1992 brood year of both stocks declined to low levels. In the Kenai River system, exceptionally low scale growth corresponded with a moderate increase of spawners in 1992, whereas reduced juvenile growth in Red Lake followed moderate spawner densities during 1990–1992. Spring and summer air temperatures in Kodiak were above average, thus this low growth cannot be explained by temperature. Adult returns to Red Lake from the 1992 spawning year were below average, whereas the return to the Kenai system was above average. These data suggested that the large spawner densities in 1989 and other years may have destabilized the relationship between salmon growth and abundance in the lakes, possibly owing to changes in the zooplankton community.

Schmidt et al. (1994, 1996) conducted field studies in the Kenai River system and suggested that large spawner densities produced numerous juvenile salmon that overgrazed zooplankton, leading to low overwinter survival of the salmon. The authors provided evidence that high grazing rates of salmon may have altered diel vertical migration of zooplankton, thereby reducing zooplankton availability to foraging salmon. Field data indicated exceptionally low numbers of salmon migrating to sea during 1992 and 1993, suggesting that large spawner densities during 1987–1989 may have had a prolonged adverse effect on juvenile sockeye salmon production. The authors conjectured that recovery of salmon growth may occur soon after spawner densities recovered to average levels if the zooplankton response was behaviorally induced, or salmon recovery may be delayed if high predation rates led to long-term changes in diel vertical migration of zooplankton. Our study of salmon scale growth in the Kenai system indicated growth approached average levels relatively fast (i.e., after 2 years of low spawner density), but growth declined sharply following the moderately large spawner density in 1992.

Scale growth in the Kenai River system, Red and Akalura Lakes indicated sockeye salmon growth may be influenced by progeny produced by parent spawners, progeny from the next brood year, and progeny from the previous brood year. In the Kenai system, where most sockeye salmon emigrate to sea after one winter in the lakes, subyearling growth was influenced by both the parent and previous spawners. In Akalura Lake, where most sockeye salmon emigrate to sea after two winters in the lake, growth was influenced by parent abundance, previous spawners, and spawners that produced subyearlings that co-inhabited the lake with yearlings. In Red Lake, salmon growth from the 1988 and 1990 brood years appeared to be affected by progeny from the 1989 brood year, but the high spawner density in 1980 did not affect growth of progeny, apparently because air temperature was exceptionally high and the growing season was long. Growth of subyearling and yearling salmon co-inhabiting Red and Akalura Lakes were correlated, indicating these two age groups responded similarly to environmental conditions, including density-dependent factors. Low juvenile growth in some years, such as the 1979 and 1983 rearing years in Red Lake was not explained by spawner density or air temperature. Possibly, zooplankton biomass, which is known to be highly correlated with smolt size (Edmundson and Mazumder, 2001), was low in these years.

Sockeye salmon can delay seaward migration when growth in lakes is relatively low (Burgner, 1987). The large spawner densities in 1989 resulted in greater percentages of returning adult salmon that had spent three rather than two winters in both Red and Akalura Lakes. In contrast, reduced growth in the Kenai system, where most juveniles emigrate after one winter, did not lead to delayed migration except for the 1983 brood year. In the glacial Kenai system, it is possible that spending two rather than one winter in the lakes may lead to relatively high mortality. In Akalura Lake, adult returns from the 1989 and 1990 brood years, which produced relatively high percentages of salmon spending three winters were relatively small (Swanton et al., 1996). The likelihood of delaying seaward migration and overwintering in the lake for an additional year in response to reduced growth is presumably related to the long-term probability of survival and genetic control of the relationship between growth and age at smoltification (Burgner, 1987; Rogers, 1987).

An important question in the management of sockeye salmon nursery lakes is whether adult returns are most dependent on numbers or size of juvenile sockeye salmon. Analysis of adult returns, spawner densities, and juvenile scale growth of Kenai River and Red Lake sockeye salmon suggests that adult returns are relatively great when both parent spawner density and juvenile growth are great. This relationship reflects the adverse effect of successive large spawner densities on juvenile sockeye growth in both systems. However, it was apparent from the multi-variate model coefficients that the positive effect of parent spawner density on adult returns was greater than negative effect of reduced juvenile growth in the lakes. These relationships suggest that greater adult salmon returns were produced by numerous relatively small juvenile salmon rather than small numbers of large fish. Other factors in fresh water and the ocean, such as predation, competition and climate, influence salmon survival (Beamish and Bouillon, 1993; Ruggerone et al., 2003) and introduce considerable variability in the relationship between adult salmon returns and juvenile abundance and size in the lakes.

When interpreting the results of this scale growth study it is important to consider effects of size-dependent mortality on scale growth patterns observed from adult sockeye salmon. Data from numerous watersheds indicate smaller juvenile salmon have lower smolt to adult survival rates (Koenings et al., 1993). Lower survival of smaller individuals may have weakened relationships between juvenile salmon scale growth and spawner density or adult return because scale growth measurements were made from survivors. Preliminary analyses based on small sample sizes indicated size of juvenile sockeye salmon measured in the lakes or during smolt migration was correlated with adult salmon scales (Ruggerone and Rogers, 1998). These data and the results of this investigation indicate size-dependent mortality was typically not sufficient to mask relationships between freshwater scale growth and spawner densities or adult returns. Nevertheless, high spawner densities likely affected juvenile growth more than indicated by scales growth measurements because smaller individuals likely experienced greater mortality.

The observation of interactions between adjacent year classes of sockeye salmon has implication for stock-recruitment modeling. Presently, sockeye salmon spawning goals are often established using recruitment models such as the Ricker or Beverton–Holt models (Hilborn and Walters, 1992). These models assume recruitment is primarily related to spawner density and that no interaction occurs between year classes of juveniles inhabiting the lakes. Analyses presented here suggest that variability in the relationship between spawners and adult returns may be reduced if abundance of adjacent year classes is incorporated into the model. This effect is apparent when an unusually large spawner density results from an oil spill like the *Exxon Valdez*, a strike by fishermen, or a surprisingly large adult return. It is apparent from this study that the primary factor affecting salmon growth and adult return is the abundance of parent spawners rather than the abundance of adjacent year classes. However, a slight reduction in spawner density might be beneficial during the year following an unusually large spawner density.

Acknowledgements

This study was funded by the *Exxon Valdez* Trustees Council (Restoration Project 96048-BAA) and the Biological Resources Division of the US Geological Survey. We appreciate support of ADFG staff for contributing sockeye scales and associated data for use in this project, including C. Swanton, P. Nelson, L. Coggins Jr., D. Owen, K. Tarbox, and T. Tobias. We thank K. Myers, J. Condiotty, K. Ramstad, M. Ferguson and A. Reichauer for assistance with data collection. D. Alverson and J. Hardy provided helpful comments on the manuscript.

References

Beamish, R.J., Bouillon, D.R., 1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. 50, 1002–1016.

Bugaev, V.F., Bazarkina, L.A., Dubynin, V.A., 1994. Annual variation in scale growth in groups of sockeye salmon, *Oncorhynchus nerka*, in relation to feeding and temperature conditions. J. Ichthyol. 34, 117–131.

Burgner, R.L., 1987. Factors influencing age and growth of juvenile sockeye salmon (*Oncorhynchus nerka*) in lakes. Can. Spec. Publ. Fish. Aq. Sci. 96, 129–142.

Clutter, R.I., Whitesel, L.E., 1956. Collection and interpretation of sockeye salmon scales. Int. Pac. Salmon Fish. Commun. Bull. 9, 159.

Dahlberg, M.L., 1968. Analysis of the dynamics of sockeye salmon returns to the Chignik Lakes, Alaska. Ph.D. Thesis. University of Washington, Seattle, WA, 337 pp.

Davis, N.D., Myers, K.W., Walker, R.V., Harris, C.K., 1990. The Fishery Research Institute's high-seas salmonid tagging program and methodology for scale pattern analysis. Am. Fish. Soc. Symp. 7, 863–879.

Edmundson, J.A., Mazumder, A., 2001. Linking growth of juvenile sockeye salmon to habitat temperature in Alaskan Lakes. Trans. Am. Fish. Soc. 130, 644–662.

Eggers, D.M., Rogers, D.E., 1987. The cycle of runs of sockeye salmon (*Oncorhynchus nerka*) to the Kvichak River, Bristol Bay, Alaska: cyclic dominance or depensatory fishing? Can. Spec. Publ. Fish. Aquat. Sci. 96, 343–366.

Fukuwaka, M., Kaeriyama, M., 1997. Scale analyses to estimate somatic growth in sockeye salmon, *Oncorhynchus nerka*. Can. J. Fish. Aquat. Sci. 54, 631–636.

Henderson, M.A., Cass, A.J., 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon. Can. J. Fish. Aquat. Sci. 48, 988–994.

Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman & Hall, New York.

Koenings, J.P., Geiger, H.J., Hasbrouck, J.J., 1993. Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*): effects of smolt length and geographic latitude when entering the sea. Can. J. Fish. Aquat. Sci. 50, 600–611.

Larsen, W.A., McCleary, S.J., 1972. The use of partial residual plots in regression analysis. Technometrics 14, 781–790.

Liu, L., Hudak, G.B., 1992. Forecasting and Time Series Analysis Using the SCA Statistical System. Scientific Computing Associates Corporation, Illinois.

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

Rogers, D.E., 1973. Abundance and size of juvenile sockeye salmon (*Oncorhynchus nerka*) and associated species in Lake Aleknagik, Alaska, in relation to their environment. Fish. Bull. 71, 1061–1075.

Rogers, D.E., 1987. The regulation of age at maturity in Wood River sockeye salmon (*Oncorhynchus nerka*). Can. Spec. Publ. Fish. Aquat. Sci. 96, 78–89.

Ruggerone, G.T., Rogers, D.E., 1998. Historical analysis of sockeye salmon growth among populations affected by large escapements associated with the *Exxon Valdez* oil spill. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 96048-BAA). Natural Resources Consultants, Seattle, WA.

Ruggerone, G.T., Harvey, C., Bumgarner, J., Rogers, D.E., 1993. Investigations of salmon populations, hydrology, and limnology of the Chignik Lakes, Alaska, during 1992. FRI-UW-9302. University of Washington, Seattle.

Ruggerone, G.T., Zimmermann, M., Myers, K.W., Nielsen, J.L., Rogers, D.E., 2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. Fish. Oceanogr. 12, 209–219.

Schmidt, D.C., Koenings, J.P., Kyle, G.B., 1994. Predator-induced changes in copepod vertical migration: explanations for decreased overwinter survival of sockeye salmon. In: Stouder, D.J., Fresh, K.L., Feller, R.J. (Eds.), Theory and Applications in Fish Feeding Ecology. University of South Carolina Press, Columbia, pp. 187–210.

Schmidt, D.C., Tarbox, K.E., King, B.E., Brannian, L.K., Kyle, G.B., Carlson, S.R., 1996. Kenai River sockeye salmon: an assessment of overescapements as a cause of decline. Am. Fish. Soc. Symp. 18, 628–638.

Swanton, C.O., Nelson, P.A., Coggins, L.G., 1996. Sockeye smolt population estimates, outmigration timing, and size at age characteristics for Red, Akalura, and Frazer Lakes, 1995. Reg. Info. Rep. No. 4K96-16. Alaska Department of Fish and Game, Kodiak, AK.

Tobias, T., Tarbox, K.E., 1999. An estimate of total return of sockeye salmon to upper Cook Inlet, Alaska, 1976–1998. Reg. Info. Rep. No. 2A99-11. Alaska Department of Fish and Game, Anchorage, AK.

Wolfe, D.A., Hameedi, M.J., Galt, J.A., Watabayashi, G., Short, J., O'Clair, C., Rice, S., Michel, J., Payne, J.R., Braddock, J., Hanna, S., Sale, D., 1993. Fate of the oil spilled from the *T/V Exxon Valdez* in Prince William Sound, Alaska. In: Proceedings of the *Exxon Valdez* Oil Spill Symposium, *Exxon Valdez* Oil Spill Trustee Council, Anchorage, AK, pp. 6–9.