

## Improvement of Juvenile Pacific Salmon Production in a Regional Ecosystem after the 1998 Climatic Regime Shift

R. J. BEAMISH,\* R. M. SWEETING, AND C. M. NEVILLE

Pacific Biological Station,  
3190 Hammond Bay Road, Nanaimo, British Columbia V9T 6N7, Canada

**Abstract.**—Beginning in 2000, juvenile Pacific salmon *Oncorhynchus* spp. in the Strait of Georgia, British Columbia, fed more frequently, contained greater volumes of prey in their stomachs compared with the previous 3 years, and increased in size. Abundances in July also increased in 2000 and 2001. Marine survival increased, as indicated by the early marine survival of coho salmon *O. kisutch* in 2000 and 2001, which improved to more than twice the annual survival estimates for 1997–1999. Other indicators of improved marine survival included exceptional returns of pink salmon *O. gorbuscha* to the Fraser River in 2001 and sockeye salmon *O. nerka* in 2002. The change to a more productive regime for juvenile Pacific salmon was a lagged response to an abrupt change in climate in 1998, as shown by regional, basin-scale, and planetary indices.

The fishery for Pacific salmon *Oncorhynchus* spp. in the Pacific Northwest was in the midst of a crisis in the 1990s, as stock abundances declined to such low levels that some stocks were listed as endangered (McElhany et al. 2000). Fisheries were closed or diminished, resulting in devastating economic consequences for a number of small, coastal communities. The declines were generally believed to result from overfishing, mismanagement, and the loss of freshwater spawning habitat (Lichatowich 1999). However, there was evidence that climate and climate change also played key roles in the declining abundance trends observed for Pacific salmon (Beamish and Bouillon 1993; Francis and Hare 1994).

The impacts of climate and climate change were particularly profound for Canada's Pacific salmon fishery. The total Pacific salmon catch averaged 65,000 metric tons from 1920 to 2001. Catch abruptly increased in the early 1980s, and the highest annual catch on record (107,430 metric tons) occurred in 1985 (Beamish and Noakes, in press). Catch subsequently declined just as abruptly in the 1990s, falling to a record low of 17,020 metric tons in 1999. The unexpected increase in the mid-1980s (Ricker 1973) and the decline in the 1990s were attributed primarily to changes in productivity resulting from changes in climate (Beamish and Noakes, in press).

Beginning in the mid-1990s, we conducted a study of the mechanisms that linked climate and Pacific salmon production. Our study area was in the Strait of Georgia, located between Vancouver

Island and the British Columbia mainland on Canada's west coast (Figure 1). The Strait of Georgia is a major rearing area for Pacific salmon, as well as one of the important coastal marine ecosystems in the North Pacific Ocean. Pacific salmon that enter the strait as juveniles can account for approximately 40% of Canada's total Pacific salmon catch in some years (Beamish et al. 1994). We were fortunate to be able to conduct this study before and after a major climate shift. In this paper, we demonstrate that the large-scale change in climate over the subarctic Pacific basin in 1998 was linked to the physical and biological changes observed in the Strait of Georgia. Although a modest budget prevented us from conducting detailed examinations of all of the possible mechanisms involved, we were able to demonstrate that a climate shift in mid-1998 changed the Strait of Georgia from a relatively unproductive environment to a productive one for Pacific salmon in 2000.

### Oceanography of the Strait of Georgia

The Strait of Georgia is a semi-enclosed marine ecosystem that is connected to the Pacific Ocean in the north by Johnstone Strait and in the south by the Juan de Fuca Strait (Figure 1). The Fraser River (Figure 1) provides approximately 80% of the freshwater that enters the Strait of Georgia, and most of this water flows out through Juan de Fuca Strait as surface water (Waldichuck 1957). As it exits Juan de Fuca Strait, the less-dense surface water entrains denser, saltier water, thereby creating an estuarine circulation (Thomson 1981). The estuarine circulation results in the transport of deep, nutrient-rich, offshore water into the Strait of Georgia via Juan de Fuca Strait. Inflowing bot-

\* Corresponding author: beamishr@pac.dfo-mpo.gc.ca

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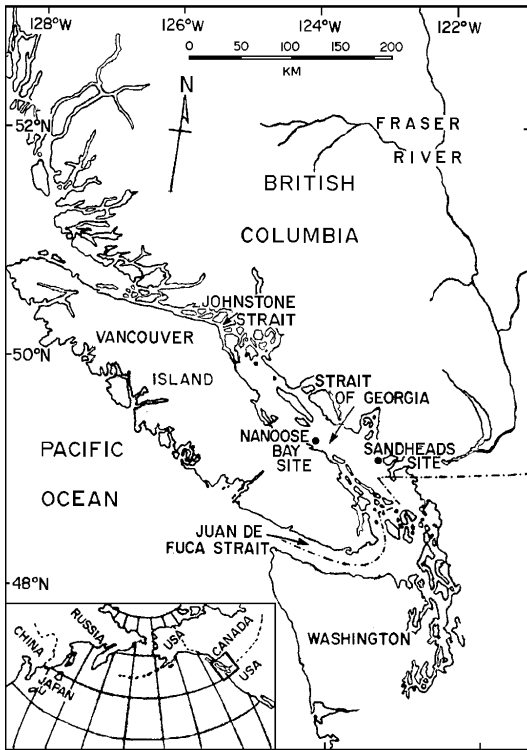


FIGURE 1.—Map of the Strait of Georgia and the west coast of British Columbia.

tom water from Juan de Fuca Strait is upwelled within the Strait of Georgia, providing a nitrate level approximately six times greater than that received from all internal sources, including the atmosphere (Mackas and Harrison 1997). Nutrients supplied from the entrained offshore water are critical to the primary production in the Strait of Georgia (Yin et al. 1996).

### Climate Indicators

A climatic regime is defined as a persistent trend in an index of climate and the ocean environment; an abrupt change to a new trend is referred to as a regime shift. There is general agreement that regime shifts occurred in 1925, 1947, 1977, and 1989 (Mantua et al. 1997; Minobe 2000; Yasunaka and Hanawa 2002). A recent climatic regime shift in the subarctic Pacific Ocean in 1998 was detectable in the Atmospheric Forcing Index (AFI; McFarlane et al. 2000; Figure 2). The AFI is a composite of the Pacific Decadal Oscillation (PDO; Hare and Mantua 2000), the Aleutian Low Pressure Index (Beamish et al. 1997), and the Pacific Circulation Index (McFarlane et al. 2000). We identified the timing of the 1998 regime shift

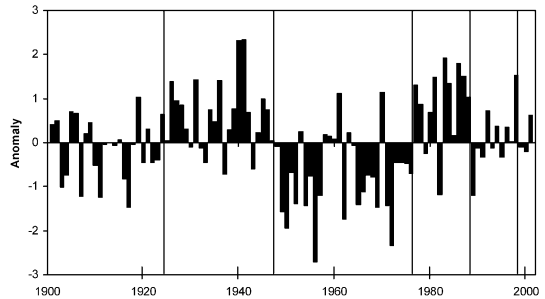


FIGURE 2.—Pacific Ocean climatic regimes based on the Atmospheric Forcing Index (AFI) from 1901 to 2002. Vertical lines denote regime shifts in 1925, 1947, 1977, 1989, and 1998; regimes encompass the years between the vertical lines.

as approximately mid-year, based on data relating to the length of day (LOD). The rotation of the solid Earth (crust and mantle) is not constant (Hide and Dickey 1991). Changes in the rotation rate of the solid Earth are identified as changes in the LOD, which represent millisecond deviations from the standard day length of 86,400 s. We obtained LOD determinations from the International Earth Rotation Service (<http://hpiers.obspm.fr/iers/eop>). A number of studies have identified the factors that affect LOD; the summary by Hide and Dickey (1991) provides an excellent introduction into this area of climate-related research. Deviations greater than 2 ms occur on a decadal scale and are generally believed to be related to exchanges of angular momentum between the solid Earth and the liquid core (Jault et al. 1988; Jault and Le Mouél 1990). Changes less than 2 ms are seasonal and are closely associated with changes in the atmospheric angular momentum (Eubanks et al. 1985; Rosen and Salstein 1985). The observed seasonal pattern (Figure 3) of a deceleration in the Northern Hemisphere during fall and winter and an acceleration during the spring and summer relates to various torques that connect the solid Earth to its atmosphere (Rosen 1993). Beginning in May 1998, there was an abrupt decrease in LOD (Figure 3) that has persisted to the present.

### Assessment of 1998 Regime Shift Impacts in the Strait of Georgia

We used sea surface temperature from a site in Nanoose Bay (Figure 1) and wind direction from the Sandheads Lighthouse (Figure 1) as indicators of climatic and oceanic changes in the Strait of Georgia. Sea surface temperatures increased after the 1977 regime shift (Figure 4A). The warmest period was from 1989 to 1998, after which there

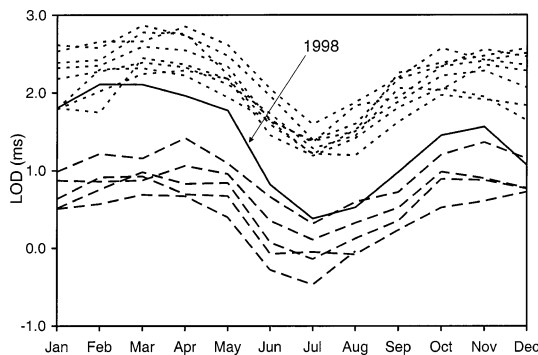


FIGURE 3.—Seasonal patterns in the length of day (LOD) anomaly. The LOD anomaly is the deviation from the standard day length of 86,400 s. Dotted lines represent the LOD anomaly values from 1990 to 1997. The solid line represents the pattern observed in 1998, showing the change to a new trend in mid-year. The dashed lines represent the LOD anomaly trends from 1999 to 2003 (the 2003 trend line shows January–August values only).

was a cooling trend to temperatures characteristic of the 1977–1988 regime. The change in trend after the 1998 regime shift is evident in the pattern of residuals from a linear regression of sea surface temperatures (Figure 4B).

Wind direction data at Sandheads Lighthouse for October to December were obtained from Environment Canada. The data were summarized as the total number of hours in a day that wind blew to a particular direction, based on four compass vectors: northeast (10–90°), southeast (100–180°), southwest (190–270°), and northwest (280–360°) (Figure 5). These directions were selected to conform to the orientation of the Strait of Georgia to allow inclusion of winds blowing up and down the strait. The months from October to December were selected to correspond with the period that many juvenile salmon leave the strait. In the 1990s, there was a large increase in the percentage of hours that the wind blew to the northwest (directly up the Strait of Georgia). The pattern changed in 1998, resulting in an increase in the number of hours that the wind blew to the southeast and a slight decrease in the number of hours that the wind blew to the northwest. Thus, more wind blew down the Strait of Georgia late in the year after the 1998 regime shift. Wind blowing up and down the strait affects the position of the Fraser River plume and the amount of upwelling, thereby affecting primary productivity (Yin et al. 1997).

#### Juvenile Pacific Salmon Studies

In this paper, we use the term “juvenile salmon” in collective reference to Pacific salmon in their

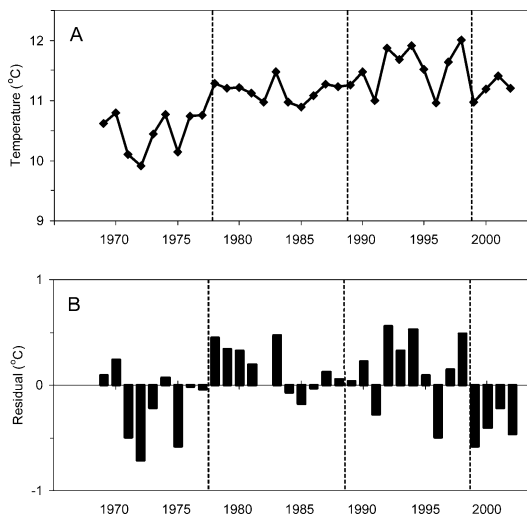


FIGURE 4.—Panel (A) shows average annual sea surface temperatures at the Nanoose Bay sampling site in the Strait of Georgia (Figure 1) from 1970 to 2002. Each point represents the mean annual temperature, calculated as the average of 12 monthly means of 3–12 observations per month. The vertical dashed lines indicate the regime shifts in 1977, 1989, and 1998. Panel (B) shows residual values from a straight-line fit to the sea surface temperature data, which highlight the abrupt cooling trend after 1998.

first ocean year. The survey design, the type of net, and the method of fishing we used enabled us to catch all Pacific salmon at any depth and during virtually all weather conditions in the Strait of Georgia (Beamish et al. 2000). We used a mid-water rope trawl with an opening approximately 15 m deep by 30 m wide. The front end of the net was 54 m long and was equipped with mesh that

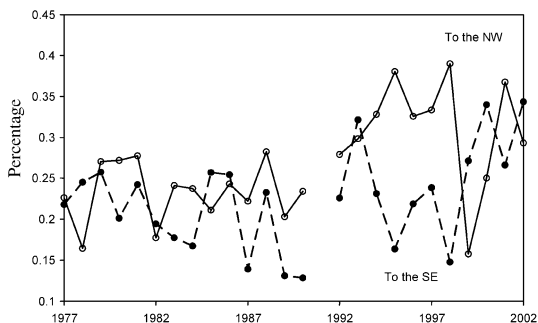


FIGURE 5.—Percentage of total hours that the wind at Sandheads Lighthouse in the Strait of Georgia (Figure 1), blew to the northwest (NW; solid line) or the southeast (SE; dashed line) during October–December 1977–2002. Only NW and SE are shown. The 1991 data were incomplete and are not shown on the figure.

ranged from 20.0 to 3.8 m square measure. The intermediate section of the net had mesh ranging from 1.6 m to 20 cm. The cod-end mesh was 10 cm with a 7.6-m-long liner of 1-cm mesh. The net filtered approximately  $2.08 \times 10^6 \text{ m}^3$  of water during an average 30-min tow at a speed of approximately 5 knots/h. Systematic surveys (Beamish et al. 2000) were used to determine the abundance of juvenile salmon. We assumed that all fish in front of the net were captured, although it was probable that catchability was less than 1.0. The estimated abundances probably were low but would be relative among years. The catches and abundance estimates, therefore, measured the population dynamics of juvenile salmon in the same way that catches in standardized research surveys are commonly used in stock assessment (Double-day and Rivard 1981). Abundance was estimated with the method given by Beamish et al. (2000). The habitat for each salmon species was determined based on the catch per unit effort (CPUE) for each depth stratum fished. The depth strata were defined by the net opening; the headrope depth was varied in increments of approximately 15 m. Strata were excluded when the CPUE was less than 10% of the total catch for each salmon species for each cruise. The habitat depths used for each species were 0–30 m for coho salmon *Oncorhynchus kisutch*, 0–45 m for Chinook salmon *O. tshawytscha*, 0–15 m for chum salmon *O. keta*, and 0–15 m for pink salmon *O. gorbuscha*. Abundance was estimated as the total volume of the habitat times the catch in numbers, divided by the total volume of water that passed through the net.

Survival of juvenile coho salmon to July of each year was estimated as July abundance divided by the number of juveniles that entered the Strait of Georgia. The total number of coho salmon (wild and hatchery fish) that entered the strait was determined by dividing the total hatchery production by the percentage of hatchery coho salmon in the July catches (Sweeting et al. 2003). The estimate of the percentage of hatchery coho salmon in the catches was adjusted by Sweeting et al. (2003) to account for fin-clip marking percentages in hatcheries and for hatchery fish produced in the United States.

Catches of juvenile salmon were processed immediately after each tow. All juvenile salmon were identified based on a combination of standard taxonomic characters. Identification of juvenile Pacific salmon is not a trivial task, and it occasionally required an examination of gill raker length and

spacing, body color patterns, scale size, gut length, and otolith size and shape. The fork length of each fish was measured to the nearest millimeter.

Stomach contents were determined at sea from all collected fish or, when necessary, from randomly selected samples of approximately 30 fish. The contents of the fundic and cardiac portions of the stomach were removed and placed in a petri dish. The volume of the contents was estimated to the nearest  $0.1 \text{ cm}^3$ . Visual estimates were calibrated volumetrically on occasion, and a set of standard plastic volumes was placed on the sampling table for reference. Estimating volumes rather than measuring them requires training and skill, and is a qualitative rather than quantitative measure. The volumes of all stomach contents were estimated by one individual, who also identified all diet items. This individual was experienced at identifying plankton and was able to reliably identify the major diet items at the reported taxonomic level. The stomach contents in the petri dish were diluted with seawater sprayed from a wash bottle with enough force to separate items. Diet items were then identified under a  $4\times$  magnifying glass. An advantage of identifying stomach contents from recently captured fish was the ability to quantify the relative volumes of soft-bodied items, such as ctenophores and jellyfish, and to process large numbers of specimens. A disadvantage was that some smaller or less numerous items might have been missed. However, we preferred to have a large number of biomass observations for the major prey taxa in order to study diet overlaps among species (King and Beamish 2000). The relative contribution of each prey group was estimated as a percentage of the total volume (to the nearest 10%). For this paper, prey items were combined into major categories, which were then reported as percentages of the total volume.

We used analysis of variance (ANOVA) to conduct statistical analyses; the Student–Newman–Keuls multiple range test was used to compare multiple groups. Significance was accepted at the 0.05 level. We compared average lengths of coho salmon, Chinook salmon, chum salmon, and pink salmon for each cruise. As cruise dates varied according to the availability of ship time, we also used standard sampling dates of July 1–15 and September 12–26 for comparison of lengths.

We completed 12 surveys from 1997 to 2002: six in the July period and six in the September period (Table 1). The total number of 30-min sets was 1,142; the number of sets per individual survey ranged from 69 to 128. The number of sets

TABLE 1.—The number of trawl sets made within each depth stratum for July and September surveys of juvenile Pacific salmon in the Strait of Georgia, British Columbia, from 1997 to 2002.

Survey	Depth stratum (m)					Total
	0–15	16–30	31–45	46–60	61+	
July surveys						
Jun 17–20 and Jul 6–8, 1997	31	14	8	10	6	69
Jun 30–Jul 9, 1998	27	21	15	15	17	95
Jun 30–Jul 8, 1999	41	24	12	9	10	96
Jul 13–20, 2000	50	19	19	7	7	102
Jul 7–15, 2001	44	18	14	10	3	89
Jul 2–11, 2002	56	22	15	5	3	101
September surveys						
Sep 8–14 and 19–27, 1997	60	31	19	6	12	128
Sep 8–16, 1998	45	33	11	6	11	106
Aug 31–Sep 8, 1999	36	22	15	6	6	85
Sep 14–24, 2000	43	23	16	5	4	91
Sep 16–26, 2001	60	18	15	4	5	102
Sep 20–28, 2002	43	19	12	3	1	78
Total	536	264	171	86	85	1,142

varied according to the amount of ship time that was available and the number of complications, which are typical of marine surveys of Pacific salmon. We caught 26,770 juvenile coho salmon, 23,810 juvenile Chinook salmon, 52,830 juvenile chum salmon, and 14,161 juvenile pink salmon.

Of these, 19,460 coho salmon, 20,900 Chinook salmon, 21,130 chum salmon, and 9,090 pink salmon were sampled (Tables 2, 3). We also caught juvenile sockeye salmon *O. nerka*. We did not include sockeye salmon in this report because comparisons among years are complicated by the in-

TABLE 2.—Average lengths of juvenile Pacific salmon captured by trawl in the Strait of Georgia, British Columbia, in July and September 1997–2002. See Table 1 for exact dates of sampling.

Species and year	Jul			Sep		
	Length (mm)	SD	N	Length (mm)	SD	N
Coho salmon						
1997	159	22.5	520	246	21.9	911
1998	173	23.3	1,220	250	31.2	1,453
1999	168	22.3	1,639	229	22.1	1,598
2000	200	23.4	3,360	248	23.8	1,543
2001	185	21.0	2,957	255	24.9	1,799
2002	169	22.7	1,895	246	23.1	567
Chinook salmon						
1997	140	33.8	1,585	142	45.3	3,655
1998	121	36.9	1,411	169	41.5	1,447
1999	139	37.4	1,664	174	42.5	1,312
2000	144	36.9	1,994	184	40.8	1,168
2001	146	32.3	2,211	188	43.3	1,098
2002	136	28.8	1,987	152	42.2	1,369
Chum salmon						
1997	122	25.6	907	192	22.4	2,931
1998	123	15.0	1,206	190	13.3	1,880
1999	116	19.4	1,227	191	24.5	1,402
2000	128	18.0	2,609	203	18.4	2,273
2001	130	17.5	2,192	195	18.2	2,624
2002	115	15.2	1,067	191	17.7	809
Pink salmon						
1998	119	13.6	1,432	178	11.3	1,751
2000	118	12.6	1,985	182	14.7	946
2002	111	15.5	2,188	176	16.4	642

TABLE 3.—Average lengths of juvenile Pacific salmon captured by trawl in the Strait of Georgia, British Columbia, for the 14-d reference periods in July and September 1997–2002

Species and year	Jul 1–15			Sep 12–26		
	Length (mm)	SD	N	Length (mm)	SD	N
Coho salmon						
1997	177	1.77	115	245	0.69	863
1998	171	0.74	1,011	242	0.91	886
1999	172	0.54	1,361			
2000	201	0.55	1,867	250	0.62	1,320
2001	185	0.39	2,957	255	0.56	1,709
2002	169	0.52	1,895	248	1.00	495
Chinook salmon						
1997	135	1.82	641	149	1.06	1,947
1998	121	1.08	1,246	176	1.34	986
1999	141	0.80	1,348			
2000	145	1.17	725	182	1.25	1,076
2001	145	0.63	2,205	187	1.35	1,010
2002	136	0.54	1,987	158	1.61	698
Chum salmon						
1997	143	1.12	350	194	0.54	1,666
1998	122	0.43	1,080	193	0.36	1,389
1999	116	0.57	1,184			
2000	125	0.47	1,359	202	0.40	2,094
2001	131	0.37	2,192	193	0.40	2,110
2002	115	0.47	1,067	199	0.79	383
Pink salmon						
1998	120	0.39	1,183	181	0.38	990
2000	115	0.36	1,149	182	0.50	807
2002	111	0.33	2,188	179	0.66	515

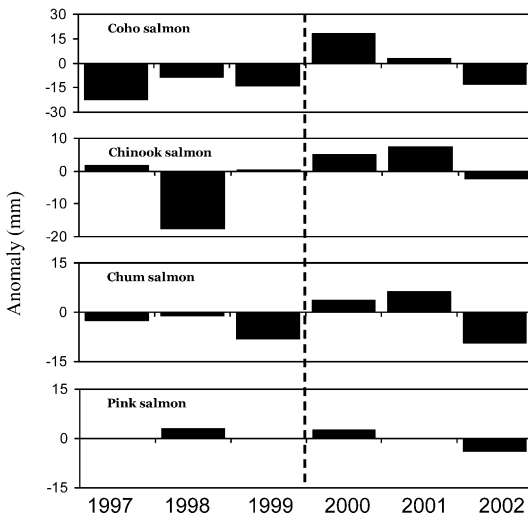


FIGURE 6.—Annual anomalies from the 1997–2002 average lengths of juvenile Pacific salmon captured during July surveys in the Strait of Georgia. Pink salmon juveniles are virtually absent from the strait during odd-numbered years. The vertical dashed line indicates that the 1998 regime shift lagged to the beginning of 2000.

fluence of the 4-year cyclic dominance phenomenon (Ricker 1997) and by the tendency for sockeye salmon juveniles to spend less time in the Strait of Georgia than the other Pacific salmon.

## Results

Synchronous and significant (ANOVA,  $P < 0.05$ ) increases in the average lengths of coho salmon, Chinook salmon, and chum salmon occurred in July 2000 and 2001 (Table 2, Figure 6). The increases were also significant when lengths were compared for the July standard reference period (Table 3), although there was a small change in average lengths. The increases in size remained significant for Chinook salmon and chum salmon in September 2000 and for coho salmon and Chinook salmon in September 2001 (Table 2, Figure 7; ANOVA,  $P < 0.05$ ). The significance of the increases was the same when the September standard reference period was used (Table 3). Unfortunately, the September 1999 survey started on August 31, and the data collection did not overlap with any other survey times. Thus, the September standard reference period was not available for that year. In general, we did not observe significant changes in the length of pink salmon, except for

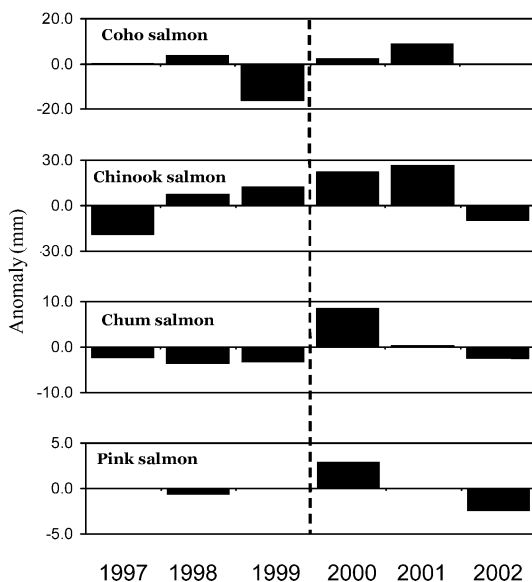


FIGURE 7.—Annual anomalies from the 1997–2002 average lengths of juvenile Pacific salmon captured during September surveys in the Strait of Georgia. Pink salmon juveniles are virtually absent from the strait during odd-numbered years. The vertical dashed line indicates that the 1998 regime shift lagged to the beginning of 2000.

a significant increase in the September 2000 sample. The mean lengths of coho salmon, Chinook salmon, and chum salmon concurrently experienced significant decreases in July 2002 (Table 2; ANOVA,  $P < 0.05$ ); the decrease persisted for Chinook salmon in the September 2002 sample (Figures 6, 7; Tables 2, 3). The significance of length changes was the same when the standard reference periods were used (Table 3).

#### Relative Abundance and Survival

In 2000 and 2001, the July abundance estimates of all juvenile salmon in the Strait of Georgia increased relative to the 1997, 1998, and 1999 estimates (Table 4). Average abundance of juvenile coho salmon in 2000 and 2001 was approximately fourfold higher than the average estimates of the

previous 3 years. Pink salmon and Chinook salmon abundance approximately doubled and chum salmon abundance approximately tripled relative to the earlier estimates. The highest total juvenile salmonid abundance (51.57 million fish) occurred in July 2000, a cycle year for pink salmon juveniles to enter the Strait of Georgia (virtually all Fraser River pink salmon spawn in odd-numbered years and juveniles enter the ocean in even-numbered years). The second-highest abundance (29.40 million fish) occurred in 2001, when juvenile pink salmon were naturally absent from the strait. Abundance estimates in 2002 were lower than the 2000 and 2001 estimates and similar to pre-2000 estimates. The estimates of survival of juvenile coho salmon to July in 2000 and 2001 were over two times greater than any of the 1997–1999 estimates (Table 5). Early marine survival declined in 2002, but the average for 2000–2002 was 49.6%, compared to an average of 19.6% for the years 1997–1999.

#### Diet Analysis

The number of stomachs examined in the July and September surveys was 11,677 and 12,529, respectively. In July of 2000 and 2001, the percentage of empty stomachs synchronously declined in all four salmonid species compared to the estimates in 1997, 1998, and 1999. The average volume of stomach contents synchronously increased among all four species in 2000 and 2001 (Table 6). In all cases, the changes in 2000 and 2001 represented significant increases from the average estimates for 1997, 1998, and 1999 (ANOVA,  $P < 0.05$ ). In July 2002, the percentages of empty stomachs for Chinook salmon and chum salmon declined significantly, whereas percentages for coho salmon and pink salmon were comparable to prior estimates. In the September surveys (Table 6), the percentages of empty stomachs in 2000, 2001, and 2002 were either smaller than or similar to the mean for all years, except for juvenile chum salmon. Average stomach volumes in September were significantly larger than the pre-2000 esti-

TABLE 4.—Estimates of juvenile salmon average abundance (millions; 2 SDs shown in parentheses) from July trawl surveys in the Strait of Georgia, British Columbia, 1997–2002.

Species	1997	1998	1999	2000	2001	2002
Coho salmon	1.65 (1.89)	2.81 (1.30)	3.42 (1.16)	9.23 (1.10)	9.27 (1.25)	2.55 (0.84)
Chinook salmon	4.74 (2.43)	2.42 (1.51)	4.41 (1.53)	7.94 (1.39)	5.89 (1.68)	3.91 (1.12)
Chum salmon	1.98 (1.12)	11.00 (0.78)	7.28 (0.65)	27.00 (0.63)	14.24 (0.70)	1.45 (0.45)
Pink salmon		3.70 (2.07)		7.40 (3.01)		3.59 (1.38)
Total	8.37	19.93	15.11	51.57	29.40	11.50

TABLE 5.—Abundance and survival of juvenile coho salmon from the time of seawater entry to July. No data were available for two items in 1994–1996.

Year	Abundance (millions)			Survival (%)
	Hatchery fish in July	Hatchery and wild fish in July	Hatchery and wild fish in July <sup>a</sup>	
1994	8.7	17.3		
1995	9.5	17.3		
1996	9.6	15.5		
1997	9.3	13.7	1.65	12.0
1998	10.0	13.9	2.81	20.2
1999	10.2	12.9	3.42	26.5
2000	10.4	15.2	9.23	60.7
2001	9.7	13.1	9.27	70.8
2002	9.3	14.8	2.55	17.2

<sup>a</sup> From Table 4.

mates for coho salmon in 2001 and 2002, for Chinook salmon in 2000, 2001, and 2002, and for pink salmon in 2002 (ANOVA,  $P < 0.05$ ; Table 6).

The prey taxa depicted in Figure 8 accounted for at least 90% of the stomach contents observed in the July surveys. All remaining items, including those which could not be identified (primarily due to condition or degree of digestion) were classified as “other.” There were differences in prey taxonomic composition among the four salmon species, but there was no indication of a major change

in prey composition throughout the study. Coho salmon stomachs contained teleosts, amphipods (gammarids and hyperiids), decapods (mostly crab zoeae and megalopae), and euphausiids. For juvenile Chinook salmon, the largest prey volume was contributed by teleosts (Pacific herring *Clupea pallasii*), accounting for 58% of the combined July and September samples. Chum salmon stomachs contained chaetognaths, calanoid copepods, hyperiids, decapods, euphausiids, and ctenophores; these taxa collectively accounted for 26% of the

TABLE 6.—Number of fish examined ( $N$ ), percentage of empty stomachs (volume  $< 0.1 \text{ cm}^3$ ), and average stomach volume ( $\text{cm}^3$ ; includes fish with empty stomachs) for juvenile Pacific salmon collected during July and September midwater trawl surveys in the Strait of Georgia, British Columbia, from 1997 to 2002.

Species	Variable	1997	1998	1999	2000	2001	2002	Average
<b>July</b>								
Coho salmon	$N$	272	573	776	813	826	668	655
	% empty	11	12	7	5	4	8	7.8
	Volume	0.98	0.98	0.58	1.4	1.51	1.43	1.15
Chinook salmon	$N$	631	677	930	772	667	821	750
	% empty	30	45	21	12	13	14	22.5
	Volume	0.87	0.54	0.50	0.96	0.91	0.83	0.77
Chum salmon	$N$	191	408	379	460	412	281	355
	% empty	71	42	25	11	4	15	28.0
	Volume	0.16	0.28	0.16	0.52	0.51	0.34	0.33
Pink salmon	$N$		427		327		366	373
	% empty		54		13		32	33.0
	Volume		0.14		0.39		0.30	0.28
<b>September</b>								
Coho salmon	$N$	718	738	848	810	641	405	693
	% empty	35	36	31	25	20	29	29.3
	Volume	0.96	1.49	1.13	1.05	1.84	1.97	1.41
Chinook salmon	$N$	645	840	909	815	541	747	750
	% empty	42	26	28	22	27	14	26.7
	Volume	0.47	0.99	0.98	1.21	1.13	1.33	1.02
Chum salmon	$N$	259	739	544	513	514	316	481
	% empty	32	21	5	23	21	11	17.0
	Volume	0.37	0.71	0.94	0.58	0.69	0.96	0.71
Pink Salmon	$N$		507		250		230	329
	% empty		24		26		15	25.0
	Volume		0.59		0.62		0.83	0.68



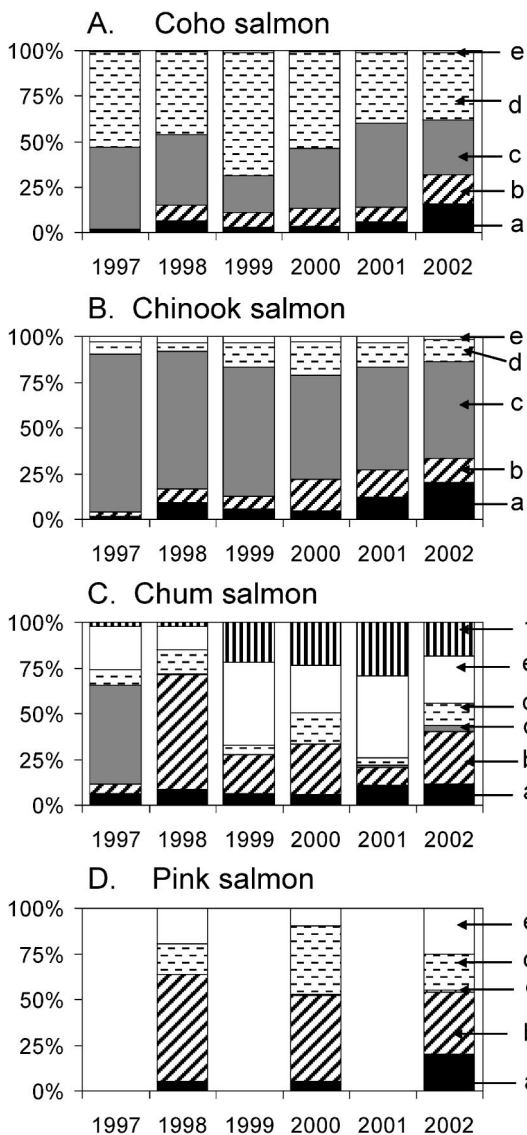


FIGURE 8.—Stomach contents of juvenile (A) coho salmon, (B) Chinook salmon, (C) chum salmon, and (D) pink salmon captured in July surveys in the Strait of Georgia during 1997–2002. Starting from the bottom of each column, diet groups are (a) euphausiids (solid black), (b) amphipods (diagonal hatched lines), (c) tel-eosts (solid gray), (d) decapods (horizontal dashed lines), (e) other (solid white), and (f) ctenophores (vertical lines; chum salmon only).

stomach contents in the combined July and September samples. Pink salmon consumed mainly amphipods and decapods, but euphausiids, calanoid copepods, and ostracods also made up substantial proportions of the diet (Figures 8, 9). Unidentified digested matter was the dominant item

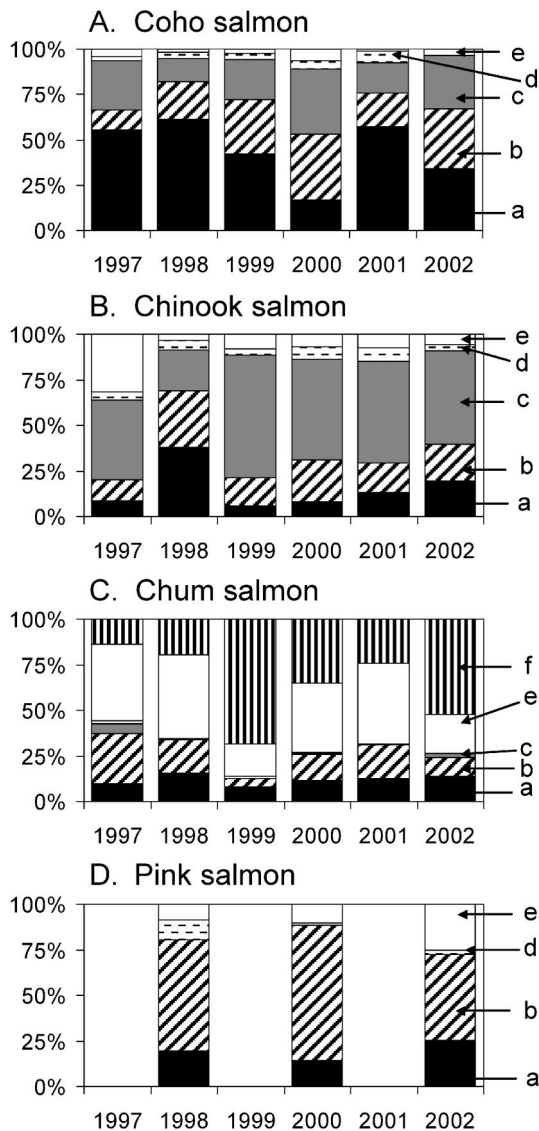


FIGURE 9.—Stomach contents of juvenile (A) coho salmon, (B) Chinook salmon, (C) chum salmon, and (D) pink salmon captured in September surveys in the Strait of Georgia during 1997–2002. Starting from the bottom of each column, diet groups are (a) euphausiids (solid black), (b) amphipods (diagonal hatched lines), (c) tel-eosts (solid gray), (d) decapods (horizontal dashed lines), (e) other (solid white), and (f) ctenophores (vertical lines; chum salmon only).

in the “other” category for pink salmon and chum salmon.

In the July samples, some changes occurred in the percentages of the major diet items after 1999, but there was no indication of a major shift in diet composition, such as a dramatic increase in the

consumption of euphausiids. Over the 6 years of the study, the diet of chum salmon was the most variable. In 1997 only, juvenile Pacific herring were the dominant food item. Ctenophores were not common in the chum salmon diet in 1997 or 1998, but were common prey in all years after 1998. For the September surveys (Figure 9), few major changes occurred in the percentages of prey items after 1999. One major change was a reduction in the consumption of euphausiids by coho salmon in 2000. We observed some anomalies, such as reduced consumption of teleosts by Chinook salmon in 1998, but in general, the relative importance of the various prey taxa did not vary extensively.

### Discussion

Feeding, growth, and survival changed concurrently among juveniles of the four salmonid species in the Strait of Georgia during 2000 and 2001. Juveniles of all four species grew to larger sizes during those 2 years. They consumed more prey, as indicated by larger average stomach volumes and reduced percentages of empty stomachs. Major switching of prey taxa was not observed; rather, each salmon species ate more of its preferred prey taxa. In another paper, we showed that euphausiid biomass approximately doubled in 2000 compared to 1999 and 1998 (Beamish et al. 2001). The increase in euphausiid biomass indicated an associated increase in biomass of the prey taxa selected by euphausiids (Beamish et al. 2001). Thus, beginning in 2000, evidence indicated that the Strait of Georgia underwent a productivity increase that resulted in increased growth of juvenile salmon during early marine residence. Improved growth would result in improved early marine survival, consistent with the findings of a relationship between early marine growth and the survival of coho salmon during their first marine winter (Beamish et al. 2004).

We recorded large increases in the abundance of individual juvenile salmon species in July 2000 and 2001. The total abundance of all species of juvenile salmon also increased substantially in 2000 and 2001. These increases occurred at the same time that the juveniles increased in size and consumed more prey, indicating that a substantially greater number of prey was available to juvenile salmon in these years. The reasons for the increased abundance of juvenile salmon are difficult to establish, as it was not possible to determine the total number of salmon juveniles that enter the Strait of Georgia each year. However, we

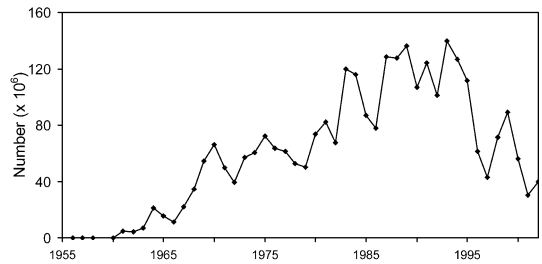


FIGURE 10.—Total releases of chum salmon from Canadian hatcheries into the Strait of Georgia from 1956 to 2002.

were able to estimate the number of coho salmon that entered the strait based on the information given by Sweeting et al. (2003). These estimates showed that the numbers of juvenile coho salmon entering the strait were relatively stable from 1994 to 2002, varying by about 25% over this period. We estimated that the early marine survival of juvenile coho salmon from the time of seawater entry to July more than doubled in 2000 and 2001 compared to 1997–1999. The total number of returning coho salmon adults was difficult to estimate because this species was produced in a large number of rivers. However, hatcheries produced about 75% of all coho salmon during this period (Sweeting et al. 2003), and four major hatcheries produced about 55% of the hatchery-reared coho salmon. Data from these hatcheries and from one monitored wild stock indicated that the marine survival of adult coho salmon increased from 1.9% in 2000 (coho salmon that entered the ocean in 1999) to 4.4% in 2001 (coho salmon that entered the ocean in 2000) (Simpson et al. 2002). Although the evidence is incomplete, marine survival of coho salmon probably improved beginning in 2000.

Improved production of other Pacific salmon species was evident in the Strait of Georgia after the 1998 regime shift. Chum salmon raised in hatcheries are released into freshwater flowing into the strait each year (Figure 10). However, in 2000 and 2001, fewer juveniles were released than in the previous 3 years (Figure 10), indicating that the increased abundances of chum salmon in July of 2000 and 2001 may have resulted from improved early marine survival. Returns of pink salmon to the Fraser River reached record-high levels in 2001 (Beamish 2002). The estimated total return of pink salmon adults in 2001 was 22 million, the second highest estimate on record. This exceptional return was produced by the third-lowest abundance of spawners (3.6 million) since 1957, when reliable records started. The record-

high returns of pink salmon must have resulted from the improved marine survival of juveniles in the Strait of Georgia in 2000 and throughout their range in 2000 and 2001. Sockeye salmon that entered the Strait of Georgia in 2000 also had high marine survival, as evidenced by the return of more than double the 2002 forecast, as well as the largest recorded return of the dominant stock (A. Cass, Pacific Biological Station, Nanaimo, British Columbia, personal communication).

Pacific salmon productivity collectively improved beginning in 2000. This indicates that there was a lag between the regime shift in mid-1998 and the increased productivity in the Strait of Georgia in 2000. Productivity in the strait is strongly influenced by the transport of deep, nitrogen-rich, offshore water, as described previously. The mid-1998 regime shift improved production offshore in 1999, as reported by Peterson and Schwing (2003). The productivity increase in the Strait of Georgia in the spring of 2000 probably occurred after water was transported from deeper areas into the strait during 1999. The estuarine circulation is closely related to the flow of Fraser River water through Juan de Fuca Strait, and Fraser River flows are largest in the summer (Thomson 1981); therefore, the productivity of the Strait of Georgia was likely first affected by nutrient changes in offshore water during the spring of 2000.

In 2002, the trend in juvenile salmon growth was reversed, as there was a synchronous reduction in growth and stomach volumes in all species relative to 2000 and 2001. Estimates of relative abundance for all four species were also lower in 2002. There is little doubt that the ecosystem changed in 2002, as the responses were similar among all Pacific salmon species. We propose that the change in 2002 was part of the natural variability that would occur during any regime.

We linked the increased production of Pacific salmon in the Strait of Georgia to a rapid change in atmospheric circulation in the subarctic Pacific. The shifts in both temperature and wind pattern trends in the strait were synchronous with changes in the basin-scale index of climate and ocean conditions in the subarctic Pacific, indicating a linkage between basin-scale and regional-scale changes. Other studies have reported a major shift in the climatic and oceanic environment occurring in approximately 1998 in the subarctic Pacific. Bond et al. (2003) used the second principal component of the North Pacific Ocean winter sea surface temperature fields to show a strong and persistent shift beginning in 1999. They concluded that the shift

was to a new regime rather than an oscillation of the PDO. They also reported that a single indicator, such as the PDO, does not provide complete characterization of North Pacific Ocean climate. Peterson and Schwing (2003) reported an abrupt change in the climate of the North Pacific Ocean in late 1998. They identified both a switch from warmwater to coldwater copepod species and a doubling of copepod biomass off the coast of Oregon in 1999. Thus, evidence from our study and from other studies indicates that a climatic regime shift in 1998 affected the oceanography and biology of marine ecosystems beginning in 1999 and 2000.

Our study demonstrated that large-scale climate patterns and climate change can have sudden and major impacts on the production of Pacific salmon in a regional marine ecosystem. It is possible that the temporal limits to the new Strait of Georgia ecosystem state can be defined by the seasonal pattern of deviations from LOD. Seasonal and interannual changes in LOD are accepted as being almost entirely due to variations in the zonal wind component of the atmospheric angular momentum (Munk and MacDonald 1960; Hide et al. 1980; Lambeck 1980; Barnes et al. 1983; Eubanks et al. 1985; Rosen and Salstein 1985; Hide and Dickey 1991; Rosen 1993). As the AFI and other major climate-change indices are also related to large-scale atmospheric circulation patterns, a persistent change in the seasonal pattern of LOD may provide a simple method for detecting regime shifts.

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