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[Article]

Early Marine Survival of Coho Salmon in the Strait of Georgia Declines to Very Low Levels

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Abstract.—The marine survival of juvenile coho salmon *Oncorhynchus kisutch* from the time they enter the Strait of Georgia in mid-May to the time of our trawl survey in mid-September declined from an average of about 15% in 1998 to approximately 1% in 2007. Early marine survival rates for juvenile coho salmon have been consistently low (<5%) since 2002, and the rate of decline in early marine survival was greater for hatchery fish than for wild fish. This suggests that hatchery coho salmon are perhaps less able to survive than wild fish in the current marine ecosystem. The steady decline in total marine survival for coho salmon over the past four decades coincided with a warming of the Strait of Georgia, where both sea surface and sea bottom temperatures have increased by approximately 1°C since 1970. Another factor that appears to have contributed to the decline in early marine survival since the late 1990s is an increase in the number of days with an average sustained wind strength greater than 25 km/h. The linkage between wind strength and marine survival requires further study, but wind strength is known to affect the timing and level of primary productivity. The processes that caused the declining marine survival remain to be identified and may include factors associated with disease originating in both freshwater and salt water, metabolic stress, competition, and predation. The data suggest that coho salmon brood year strength is now mostly determined during the first 4 months spent in the Strait of Georgia. If the current low levels of marine survival continue, management initiatives to protect wild coho salmon will be urgently required, and it will be timely to critically evaluate the hatchery programs and policies.

In the 1970s, the number of coho salmon *Oncorhynchus kisutch* available for fisheries was considered to be limited mainly by the number of juveniles entering the Strait of Georgia and not by the capacity of the strait to produce coho salmon. Consequently, hatcheries were used to release more juvenile coho salmon into the Strait of Georgia (Fisheries and Environment Canada 1978). Beginning in the late 1970s, hatcheries annually produced an increasing number of coho salmon that ranged between approximately 6 million and 12 million smolts from the late 1980s to 2007 (Figure 1). The largest production of 12 million coho salmon smolts occurred in 1985 as part of an effort to provide better fishing opportunities for visitors to the 1986 World Exposition on Transportation and Communication in Vancouver, British Columbia. Despite the addition of these hatchery fish in the 1980s, the thriving recreational and commercial fisheries in the Strait of Georgia had virtually collapsed by the mid-1990s (Beamish et al. 1999, 2000, 2008; Figure 2). There were two main reasons for the collapse of these fisheries. One was the decline in total marine survival from about 10% in the late 1970s to less than 1% in recent years (Beamish et al. 2008; Figure 1). The other was a change in behavior that resulted in coho salmon leaving the Strait of Georgia late in their first marine year (Beamish et al. 1999, 2008; Chittenden et al. 2009) and not returning until shortly before they spawned in their natal rivers. This behavior virtually eliminated opportunities for a recreational fishery in the strait.

Coho salmon enter the Strait of Georgia in late May and remain in the strait until late in the year (Chittenden et al. 2009), after which they migrate offshore. A large number of these fish originates from

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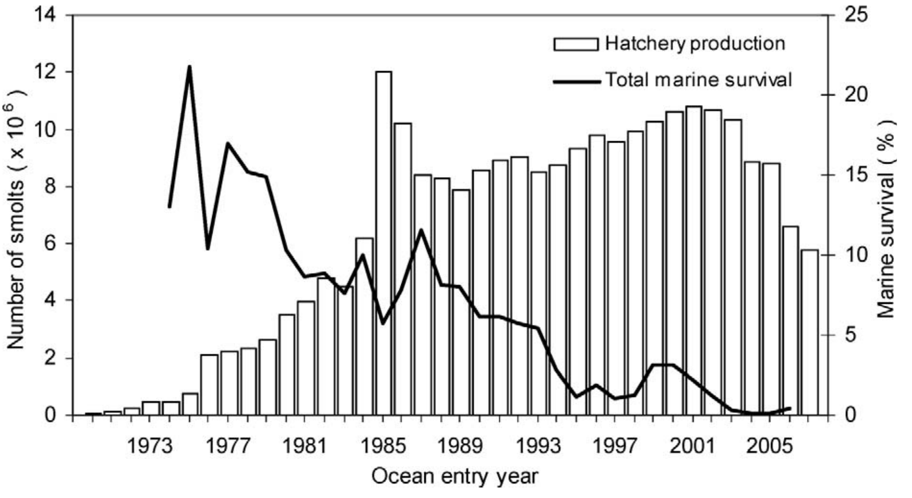

FIGURE 1.—Number of coho salmon smolts produced from hatcheries (1970–2007) and total marine survival (1974–2006) of coho salmon that enter the Strait of Georgia. The ocean entry year is the year in which the smolts entered the strait. The brood year would be 2 years earlier, and the adult return year would be 1 year later.

hatcheries, and a large percentage (67–89%) of hatchery fish received adipose fin clips starting in 1998. The existence of these marked hatchery fish enabled us to use trawl surveys to study the population dynamics of the juvenile fish during the early marine period. Unexpectedly, during the 10-year study described here, we observed a large decline in marine survival from mid-May (the time of coho salmon entry into the strait) to mid-September. Our estimate of survival through mid-September is closely related to total marine survival, indicating that coho salmon brood year strength is now mostly determined during the first 4 months spent in the Strait of Georgia. Our study shows that if these low levels of early marine survival continue, strategic approaches for wild coho salmon management in the Strait of Georgia that recognize the potential impacts of climate well into the future will be urgently needed.

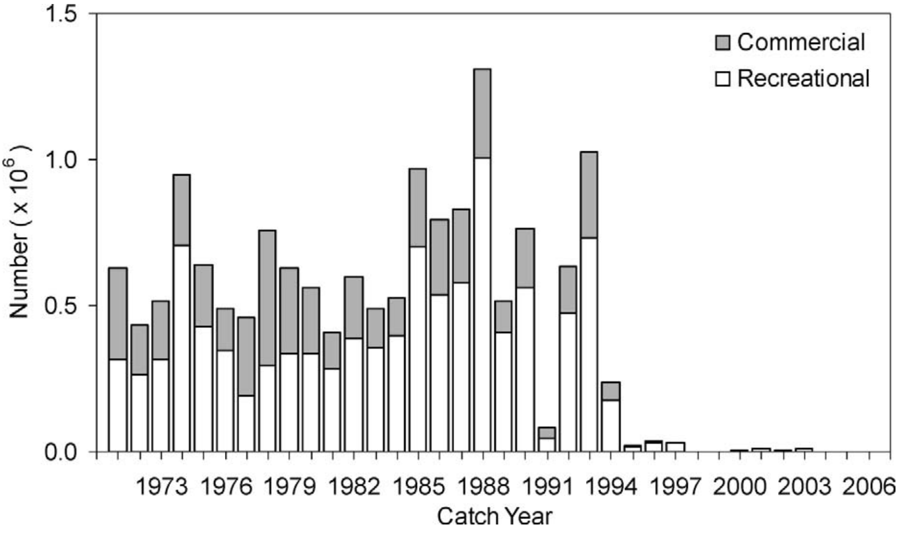

FIGURE 2.—Commercial and recreational catches (numbers of fish) of coho salmon in the Strait of Georgia (1971–2006). The catch year is the second ocean year and the year in which they would return to spawn. The ocean entry year is 1 year earlier.

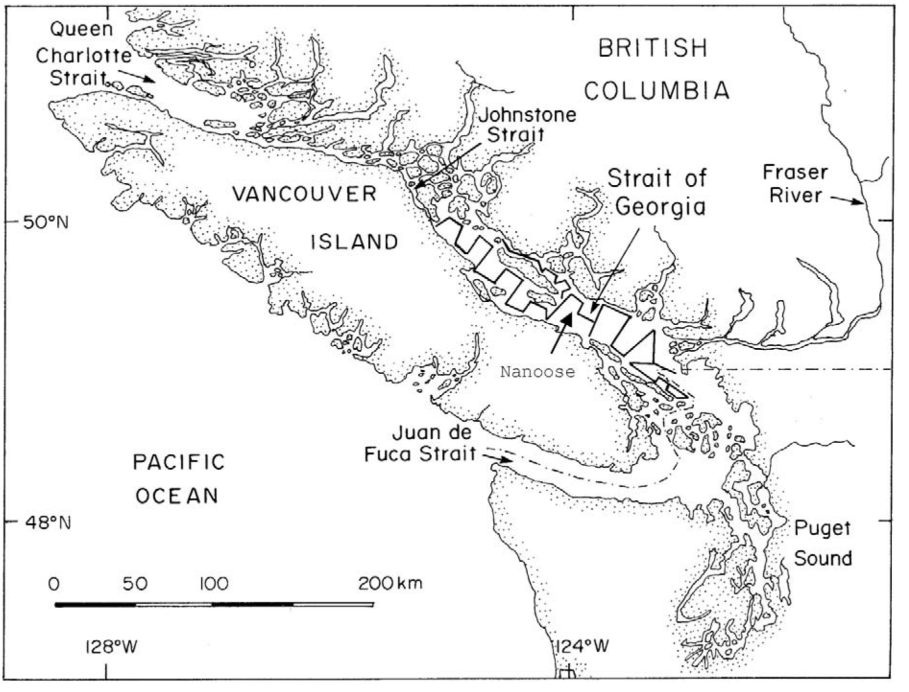

FIGURE 3.—Map of the Strait of Georgia and surrounding areas, showing the location of the trawl survey track lines (bold solid lines) from 1998 to 2007.

Methods

Survey.—Annual trawl surveys were conducted in the Strait of Georgia in July and September from 1998 to 2007. Survey dates varied slightly depending on ship availability, and there was no survey in July 2003. The net design and survey methodology have been reported by Beamish et al. (2000) and Sweeting et al. (2003). The modified midwater trawl net (approximate opening depth = 15 m; opening width = 30 m) was fished for 30 min at a speed of about 2.6 m/s (5 knots). All catches were standardized to catch per unit effort (CPUE), which was the catch that would occur in 1 h of fishing. All surveys followed a standardized track line (Figure 3), with the headrope positioned at the surface (0–4 m), 15 m, or 30 m. Some deeper sets were made, but 99% of coho salmon were captured above 45 m. All coho salmon were counted, checked for coded wire tags (CWTs) using a detection wand, and examined for clipped fins. Stomach contents were also analyzed, although the results are not reported in this paper. In addition, fork length was measured to the nearest millimeter.

Abundance of hatchery and wild coho salmon.—Abundance estimates were used to determine early marine survival. We estimated the abundance of juvenile coho salmon separately for each depth stratum (0–15 m, >15 to 30 m, and >30 to 45 m). Volumes for each stratum were estimated using the procedures of Thomson and Foreman (1998). The abundance of coho salmon was then estimated by expanding the catches in the volume of water fished to the volume in each stratum using the procedures of Beamish et al. (2000). An assumption in the calculation was that all fish in front of the net opening were caught or that the catchability of the net was 1.0 (Beamish et al. 2000). The true catchability of the net is not known, but it may be less than 1.0. Thus, the abundance estimates are comparable among years but may be consistently low.

Abundance was determined for Canadian-origin coho salmon by removing coho salmon originating from Puget Sound, USA (Figure 3). The number of coho salmon of U.S. origin was estimated using the CWTs in our catch and the known percentage of coho salmon that received a CWT in the USA (Beamish et al. 2008). We used the value of 24% wild coho salmon in Puget Sound (Packer et al. 2005) to estimate the number of wild coho salmon from the USA. The abundance of Canadian-origin coho salmon was then separated into hatchery and wild abundance. Beginning in 1998, approximately 80% of all coho salmon released from hatcheries had their adipose fins removed, allowing the fish in our catches to be readily

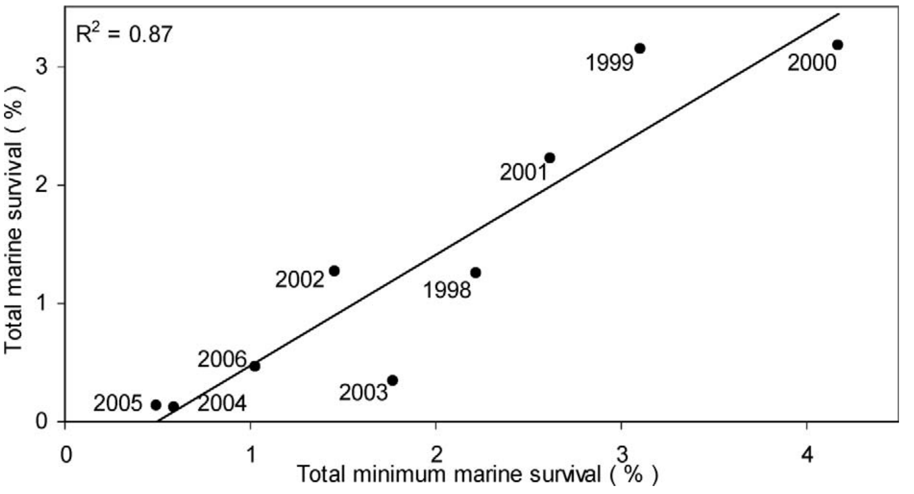

FIGURE 4.—Relationship between the minimum total marine survival (calculated from escapements only) of coho salmon returning to the eight major hatcheries that release fish into the Strait of Georgia and total marine survival (calculated from coded wire tags).

identified as hatchery fish (missing an adipose fin) and wild fish (with an adipose fin); the methods of Beamish et al. (2008) were used to correct for the hatchery fish that were not fin-clipped. We estimated the rate of decline in abundance of hatchery and wild coho salmon from ocean entry in mid-May to September to compare the marine survival of the two rearing types (i.e., hatchery and wild). Because there was a reduction in the number of hatchery salmon released beginning in 2004, we adjusted the September hatchery abundance estimates to remove the effect of release numbers. The number of fish released from all hatcheries was standardized by making the largest release equal to 1.0 and the smaller releases a proportion of the largest release. The standardized abundance was then calculated as the abundance of hatchery coho salmon observed in September divided by the standardized release number.

Marine survival.—Total marine survival is the survival from ocean entry in about mid-May until the fish either are caught or return to freshwater to spawn. In this study, hatchery fish were used to estimate total marine survival since very few wild coho salmon stocks are monitored for stock-specific catch, spawning escapement, or the number of wild juvenile salmon that migrate from freshwater to the ocean (out-migration). Total marine survival was calculated as the number of coho salmon with CWTs that were recovered as adults when they returned to rivers or hatcheries to spawn or when they were captured in fisheries divided by the number of coho salmon smolts with CWTs that were released from hatcheries. The actual number of CWTs counted each year was expanded to estimate the total number of recovered adult coho salmon with CWTs (catch in all fisheries plus spawning escapement) using expansion factors determined by the Mark Recapture Program (Kuhn et al. 1988). Although there are many hatcheries and salmon enhancement projects (large and small) that release coho salmon into the Strait of Georgia, eight major salmon hatcheries produced an average of 81% of the hatchery coho salmon that entered the strait from 1998 to 2007. Total marine survival for fish from these eight major hatcheries was used to assess the accuracy of the total marine survival estimate for all hatcheries. We also compared the estimate of total marine survival to an estimate of "minimum" total marine survival, which accounts for fish that return to spawn in freshwater but does not account for catch and thus would be expected to underestimate total marine survival. The minimum total marine survival of coho salmon returning as adults to the eight major hatcheries was closely (and linearly) related to the estimated total marine survival ($R^2 = 0.87$, $P < 0.05$; Figure 4). Because the minimum total marine survival estimates and the total marine survival estimates were highly correlated, we considered the estimate of total marine survival to be a reliable index.

Early marine survival was defined as the survival from ocean entry (about mid-May) to mid-September, when our trawl surveys were conducted. Early marine survival was calculated by determining the abundance of Canadian hatchery and wild coho salmon in the Strait of Georgia in September and dividing this abundance by the total number of hatchery and wild

TABLE 1.—Variables used in the regression models and other analyses of coho salmon survival in the Strait of Georgia.

Year		Early marine survival		
Biological coho salmon data	Catch per unit effort from trawl surveys	Fraser River flow	Average sea surface temperature for each month	Wind speed
Early marine survival	Coho salmon	Average flow for each month	Chrome Island	<25 km/h (Feb–Apr; May–Jul)
Total marine survival	Chinook salmon *Oncorhynchus tshawytscha*		Departure Bay	
Hatchery smolt releases	Chum salmon *O. keta*		Entrance Island	Average wind speed (Feb–Apr; May–Jul)
Percentage of hatchery fish in September			Sisters Island	
	Pink salmon *O. gorbuscha*		West Vancouver	
	Sockeye salmon *O. nerka*		Nanoose Bay	

coho salmon smolts that entered the Strait of Georgia. Ocean entry dates vary, but mid-May is a common release time for many hatcheries and we therefore used mid-May as an average ocean entry date (Beamish et al. 2008). The number of hatchery fish produced and the percentage of marked fish were provided through hatchery statistics. The number of wild coho salmon entering the Strait of Georgia in May was calculated using the estimated percentage of hatchery and wild coho salmon in the September survey and assuming equal marine survival for both hatchery and wild fish during the mid-May to mid-September period. The number of wild coho salmon entering the strait in May was then estimated by back-calculation (Beamish et al. 2008). We discuss the validity of the assumption of equal early marine survival of hatchery and wild coho salmon and consider the consequences of this assumption in the Discussion.

The number of released fish reported by hatcheries would be larger than the number of fish entering the Strait of Georgia because of postrelease mortality in freshwater. It was not possible to provide an average estimate of mortality for all hatchery coho salmon in freshwater using published data. Thus, we consider a scenario in which 20% of the hatchery fish die in freshwater before they reach the Strait of Georgia. This scenario provides an assessment of the impact of freshwater mortalities on our estimates of early marine survival.

Environmental data.—A range of environmental data was examined to determine potential linkages with both total and early marine survival. Water temperature data were available from the Nanoose Bay Station, Department of National Defence Canada (Figure 3). The station is within the Nanoose Bay Naval Underwater Weapons Test Range located in the Strait of Georgia east of Nanoose Bay, British Columbia. In addition, we considered the average monthly sea surface temperatures from five lighthouse locations within the Strait of Georgia (Fisheries and Oceans Canada 2009; Table 1). Flow data from the Fraser River at Hope (station number 08MF005) are available from Environment Canada through the Water Survey of Canada, National Water Quantity Survey Program (Environment Canada 2009a). Wind speed data measured at the Vancouver International Airport were also obtained from Environment Canada (Environment Canada 2009b). Hourly measurements were examined on a 24-h clock to determine daily average wind velocities, which were then used to examine changes in average monthly wind speed. The number of days with wind speeds below 25 km/h for the entire day was also determined. The value of 25 km/h was based on the observations of Yin et al. (1996) that mixing layer stability was disturbed in the Strait of Georgia when winds over 21.6 km/h were sustained for a 36-h period. A day was counted as having wind speeds below 25 km/h if no winds exceeded this value in 24 h. Daily and average wind speeds for the February–July period were examined in this study.

A variety of models, including regression models, tree regression (Breiman et al. 1984), and principal components analysis, was employed to examine the relationship between total and early marine survival of coho salmon and biological and environmental variables for the period 1998–2007. The variables in the analysis included the number of hatchery coho salmon entering the Strait of Georgia, the CPUE of four other species of juvenile Pacific salmon in our September surveys, the average monthly sea surface temperature at six locations (Chrome Island, Departure Bay, Entrance Island, Sisters Island, West Vancouver, and Nanoose Bay), the total number of days in February–April and May–July with wind speeds less than 25 km/h, and the average wind speed for these months (Table 1).

Estimates of abundance, hatchery percentage, and marine survival in this paper may differ slightly from those published in previous papers (Sweeting et al. 2003; Beamish et al. 2008). We use estimates of hatchery production, including the number of fish with adipose fins removed, that are available from databases in Canada and the United States. Numbers in these databases change slightly, and we revised our estimates accordingly.

Results

Coho Salmon Abundance

The September abundance of juvenile coho salmon in the Strait of Georgia from all sources ranged from approximately 0.45 million in 2007 to 3.33 million in 1999 (Table 2, column I). The percentage of coho salmon captured in the Strait of Georgia and produced (spawned) in Puget Sound (i.e., U.S. origin) ranged from 5% in 2000 to 41% in 2007 (Table 2, column III). When coho salmon of U.S. origin were removed, the September abundance of Canadian-origin juvenile coho salmon averaged 1.42 million and ranged from 0.27 million in 2007 to 2.93 million in 1999 (Table 2, column IV).

Hatchery Coho Salmon Abundance and Survival

The percentage of hatchery coho salmon in the trawl catch that were produced in Canadian hatcheries started to decline in about 2002 and reached the lowest level of 25% in 2006 (Table 2, column V). Between 2005 and 2007, this percentage varied between 25% and 35% (Table 2, column V). The estimate for 2008 is 25%, but this value is preliminary and is not included in Table 2. The abundance of Canadian hatchery coho salmon in September ranged between 0.96 million and 2.02 million from 1998 to 2001 and then declined to between 0.09 million (2007) and 0.53 million (2003; Table 2, column VI).

The estimated abundance of hatchery fish in September (Table 2, column VI) divided by the estimated production (Table 2, column X) indicated that the early marine survival of hatchery coho salmon declined at an average rate of 1.5% per year (Figure 5A). The trend was statistically significant ($R^2 = 0.68$, $P < 0.05$), although the decline could also represent a step change in 2002 that resulted in a shift between the two periods. The linear trend represents an average decline from an estimated early marine survival of 15% in 1998 to an estimate of 1% in 2007, or about a 93% decline in early marine survival. In the scenario that considered an average mortality of 20% in freshwater (Table 2, column XI), the average early marine survival decreased from 19% in 1998 to 2% in 2007, which translates to an approximate 91% decline in early marine survival (Figure 5B).

Hatchery and Wild Coho Salmon Abundance and Survival

Abundance estimates of wild coho salmon in September ranged from 0.18 million in 2007 to 1.24 million in 2001 (Table 2, column VII). The estimates of early marine survival of wild coho salmon are the abundance determined from the September surveys (Table 2, column VII) divided by the total number of wild coho salmon that enter the Strait of Georgia (Table 2, column XII). The estimated total number of wild coho salmon entering the Strait of Georgia is based on the percentages of hatchery fish in the catch (Table 2, column V) and an assumption of equal early marine mortality of hatchery and wild coho salmon. Thus, the numbers of wild coho salmon entering the strait ranged from 4.59 million to 25.75 million (Table 2, column XII), and the estimated total number of hatchery and wild smolts entering the Strait of Georgia from all Canadian sources varied from 14.80 million to 34.80 million (Table 2, column XIV).

The abundance of Canadian juvenile coho salmon in the September survey was positively and significantly related to total marine survival ($R^2 = 0.72$, $P < 0.001$; Figure 6). The adult returns in 2008 are not finalized but are small, consistent with the position of the arrow (Figure 6) indicating abundance for September 2007. The abundance of hatchery coho salmon in September (Table 2, column VI) declined at a rate of 150,000 fish/year (Figure 7A), or 130,000 fish/year when adjusted for differences in release numbers among years (standardized abundance; Figure 7B). The abundance of wild coho salmon from ocean entry to September (Table 2, column VII) declined at a rate of 60,000 fish/year (Figure 7C). The more rapid decline of Canadian-origin hatchery fish standardized for release abundance resulted in an increasing proportion of wild coho salmon in September even though the abundance of wild coho salmon continued to decrease (Table 2, column VII). There was more variability in the decline of wild coho salmon as indicated by the smaller R^2 of 0.41 compared with an R^2 of 0.67 for hatchery coho salmon.

Changing Trends in the Environment of the Strait of Georgia

The average annual water temperature measured at the surface, 10 m, and bottom (395 m) at the Nanoose Bay site (Figure 8A) increased by an average of 1.1, 0.8, and 0.8°C, respectively, since 1970. The average trend (rise) in surface water temperature was greater during the early marine period for coho salmon from

TABLE 2.—Data used to estimate the early marine survival (May–September) of hatchery and wild coho salmon of Canadian origin in the Strait of Georgia. Roman numerals are used to refer to columns in presenting Results.

Year	Sep abundance (I)	2 SDs (II)	% US coho salmon (III)	Canadian abundance (IV)	% Canadian hatchery coho salmon in Sep (V)	Abundance of Canadian hatchery fish in Sep (VI)	Abundance of Canadian wild fish in Sep (VII)	Smolts released from Canadian hatcheries (VIII)
1998	2,075,000	821,000	9	1,888,000	60	1,133,000	755,000	9,622,000
1999	3,325,000	1,506,000	12	2,926,000	69	2,019,000	907,000	9,857,000
2000	1,982,000	560,000	5	1,882,000	51	960,000	922,000	10,224,000
2001	2,816,000	1,169,000	8	2,591,000	52	1,347,000	1,244,000	10,939,000
2002	873,000	427,000	10	786,000	39	307,000	479,000	10,489,000
2003	1,177,000	480,000	8	1,083,000	49	531,000	552,000	10,177,000
2004	718,000	412,000	11	639,000	26	166,000	473,000	8,772,000
2005	856,000	460,000	17	710,000	35	249,000	461,000	8,571,000
2006	1,096,000	542,000	6	1,030,000	25	258,000	772,000	7,744,000
2007	452,000	387,000	41	267,000	34	91,000	176,000	6,419,000

mid-May to mid-September, increasing by 1.5°C from 1970 to the present (Figure 8B). Sea surface temperatures in June were more strongly related to early marine survival than sea surface temperatures for any other single month ($R^2 = 0.36$, $P < 0.05$; Figure 9A). The average sea surface temperatures from March to June were weakly related to early marine survival ($R^2 = 0.24$, $P \approx 0.08$; Figure 9B). Total marine survival from 1998 to 2006 was negatively related to the average annual sea surface temperature ($R^2 = 0.67$, $P < 0.05$; Figure 9C). Early marine survival of coho salmon exhibited a significant positive correlation with the cumulative number of days in May–July with hourly wind speeds less than 25 km/h ($R^2 = 0.71$, $P < 0.01$; Figure 10A). Early marine survival also appeared to be significantly higher during 1998–2001 than during 2002–2007 (Figure 10A). The boundary between the two periods (at 58.5 d with hourly wind speeds less than 25 km/h; Figure 10A) was identified using a regression tree, with early marine survival rates of approximately 13% during 1998–2001 and 3% during 2002–2007. A similar relationship was found for total marine survival, although there was more overlap in survival rates between the two groups and the linear relationship was considerably weaker ($R^2 = 0.31$, $P \approx 0.09$; Figure 10B). Despite the negative relationship between total marine survival and sea surface temperature (Figure 8), the knowledge of sea surface temperature did not allow us to predict into which of the two periods (1998–2001 or 2002–2007) total marine survival would fall; the best predictor was perhaps the previous year's marine survival rate (Figure 10C). Principal components analysis also found that the May–July wind speed data constituted the most significant environmental factor, with the first principal component explaining nearly 90% of the variability in early marine survival.

Discussion

There was a declining trend in the early marine survival of hatchery and wild juvenile coho salmon during the study period from 1998 to 2007. The decline of approximately 93% over 10 years (with no adjustment made for freshwater mortality of smolts) was a substantial reduction in the survival of juvenile coho salmon. The decline was similar when estimates were adjusted to reflect 20% freshwater mortality. The rate of decline in September abundance for hatchery fish was also larger than that for wild coho salmon, which suggests that wild coho salmon may currently have a higher marine survival rate than hatchery fish. If the early marine survival of wild coho salmon is indeed higher than that of hatchery fish, then the estimated abundance of wild coho salmon entering the strait may be smaller than we calculated. There is some indication that the escapements of wild coho salmon have not increased in recent years, and there is a possibility of declines in some populations (DFO 2005a). Reduced early marine survival of hatchery coho salmon compared with wild fish is an important possibility as it may indicate that in a stressful environment, hatchery fish will exhibit lower survival than wild fish. More importantly, wild coho salmon may be better adapted to a Strait of Georgia ecosystem that is now quite different from the 1970s ecosystem, which was assumed to be able to produce more coho salmon, thus prompting the establishment of large hatchery programs.

Canada's wild salmon policy (DFO 2005b) clearly places a priority on protecting wild salmon, and current hatchery programs and policies also need to be reviewed in that context. The relatively stable levels and timing of hatchery releases make it difficult to evaluate potential interactions between hatchery and wild coho salmon and their environment. Large-scale,

TABLE 2.—Extended.

Year	Smolts resulting from fry released from Canadian hatcheries (IX)	Total Canadian hatchery smolt production (X)	Total Canadian hatchery smolt production if 20% freshwater mortality (XI)	Total Canadian wild smolt production (XII)	Total Canadian wild smolt production if 20% freshwater mortality (XIII)	Total Canadian hatchery and wild fish entering the Strait of Georgia (XIV)	Total Canadian hatchery and wild smolt production if 20% freshwater mortality (XV)
1998	259,000	9,881,000	7,905,000	6,587,000	5,270,000	16,468,000	13,175,000
1999	354,000	10,211,000	8,169,000	4,588,000	3,670,000	14,799,000	11,839,000
2000	390,000	10,614,000	8,491,000	10,198,000	8,158,000	20,812,000	16,649,000
2001	421,000	11,360,000	9,088,000	10,487,000	8,389,000	21,846,000	17,477,000
2002	319,000	10,808,000	8,646,000	16,905,000	13,523,000	27,713,000	22,169,000
2003	261,000	10,438,000	8,350,000	10,864,000	8,691,000	21,303,000	17,041,000
2004	275,000	9,047,000	7,238,000	25,749,000	20,600,000	34,796,000	27,838,000
2005	252,000	8,823,000	7,058,000	16,386,000	13,108,000	25,209,000	20,166,000
2006	186,000	7,930,000	6,344,000	23,790,000	19,032,000	31,720,000	25,376,000
2007	159,000	6,578,000	5,262,000	12,676,000	10,140,000	19,264,000	15,402,000

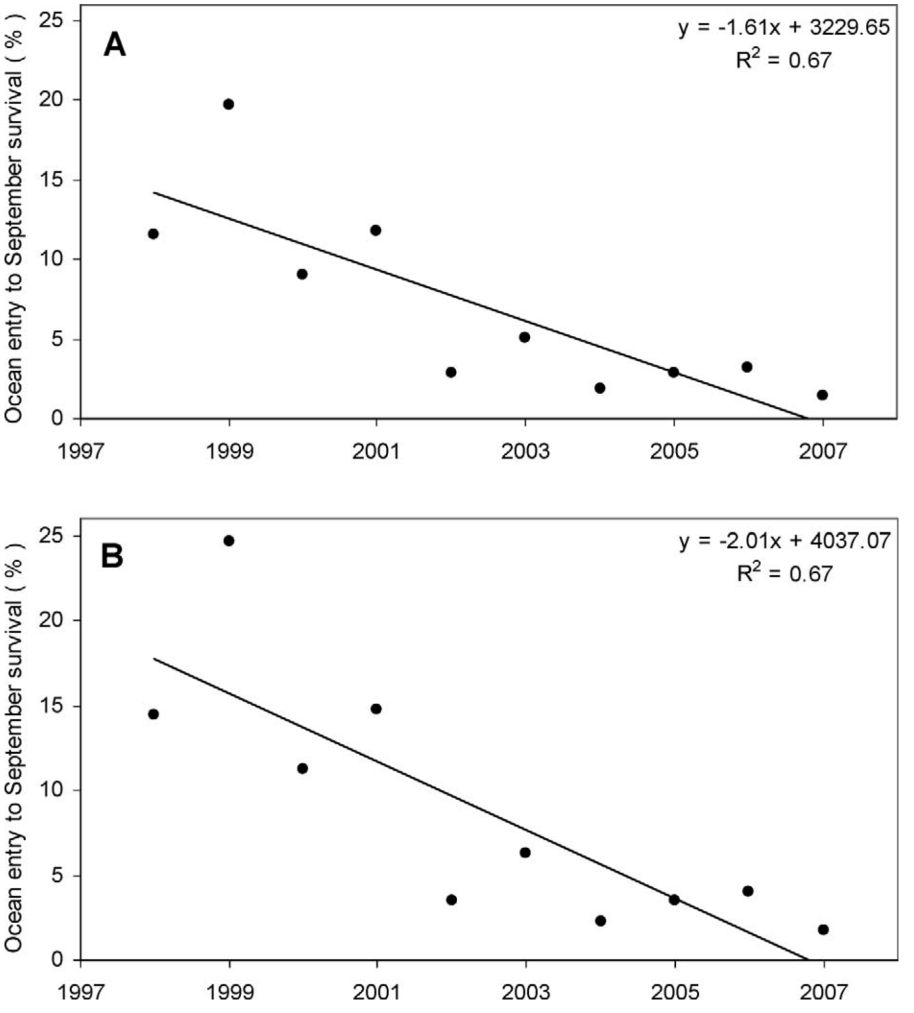

FIGURE 5.—Early marine survival from ocean entry to September for **(A)** hatchery coho salmon and **(B)** hatchery coho salmon under an assumption of 20% freshwater mortality.

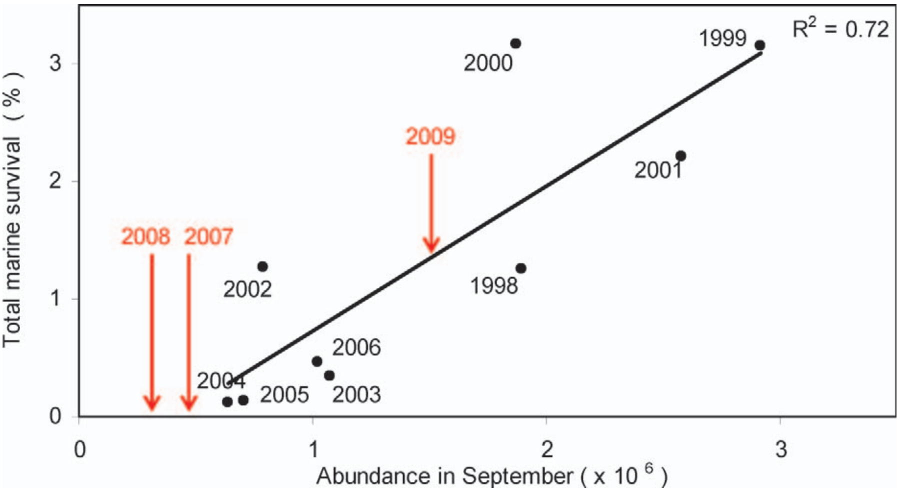

FIGURE 6.—Relationship between September abundance of Canadian-origin hatchery and wild coho salmon in the Strait of Georgia and total marine survival (1997–2006). The years shown in the plot are survey years. Adults would return 1 year later.

multiyear experimental manipulations of release numbers and changes in release timing need to be planned and implemented in order to test for interactions.

The reliability of our early marine mortality estimates is dependent on being able to show that most coho salmon remain in the Strait of Georgia through to the end of the September survey. An acoustic tagging study by Chittenden et al. (2009) and an analysis of CWT recoveries (Beamish et al. 2008) showed that in recent years, most juvenile coho salmon have remained in the Strait of Georgia through October or November of their first marine year. These studies also showed that when juvenile coho salmon left the Strait of Georgia, most migrated through the Strait of Juan de Fuca. After the Chittenden et al. (2009) study in 2006, we captured 954 coho salmon in the combined September catches from the Strait of Juan de Fuca in 2007–2009. Only one fish had a CWT of Canadian origin. In the Strait of Georgia during the same period, we caught 1,269 coho salmon and 22 contained CWTs from populations around the Strait of Georgia. Thus, although there may be some movement out of the Strait of Georgia prior to the end of September, the acoustic tagging study and the recaptures of fish with CWTs indicate that most coho salmon remain within the Strait of Georgia during the September survey. Also, the average decline in the percentage of hatchery coho salmon between the July and September surveys was about 11%, indicating that selective movement of either rearing type out of the strait is unlikely. If wild coho salmon survive better than hatchery coho salmon, this observation of a small decline in the percentages of hatchery and wild coho salmon between July and September would indicate that much of the difference in wild and hatchery fish survival occurs between mid-May, when the wild and hatchery fish enter the strait, and mid-July.

The Chittenden et al. (2009) acoustic tagging study can also be used to measure the marine survival between July and September, which can be compared with the survival determined from our abundance estimates for the same period. Chittenden et al. (2009) fitted coho salmon with acoustic tags in the Strait of Georgia during July ($n = 94$) and September ($n = 79$) 2006. Eighteen (19%) of the fish tagged in July and 41 (52%) of the fish tagged in September left the Strait of Georgia; most of these fish (88%) left the strait from October to December 2006. For the 18 fish tagged in July that survived to leave the strait, survival can be partitioned into survival from tagging until September and survival from September until the fish left the strait. The survival experienced by the fish tagged in September was 52%. Thus, fish that were tagged in July and survived until September may have also experienced 52% survival after September. Thirty-five of the 94 fish tagged in July would have had to survive until September to result in 52% survival after September (i.e., for 18 fish to survive to leave the strait after September). This indicates that the mortality between July and September for fish that were tagged in July was approximately 63%. In 2006, our abundance estimate of coho salmon was 3.86 million in July and 1.03 million in September. The mortality between July and September would be about 74% and similar to the mortality estimated from the acoustic tagging study. These estimates are approximate, but

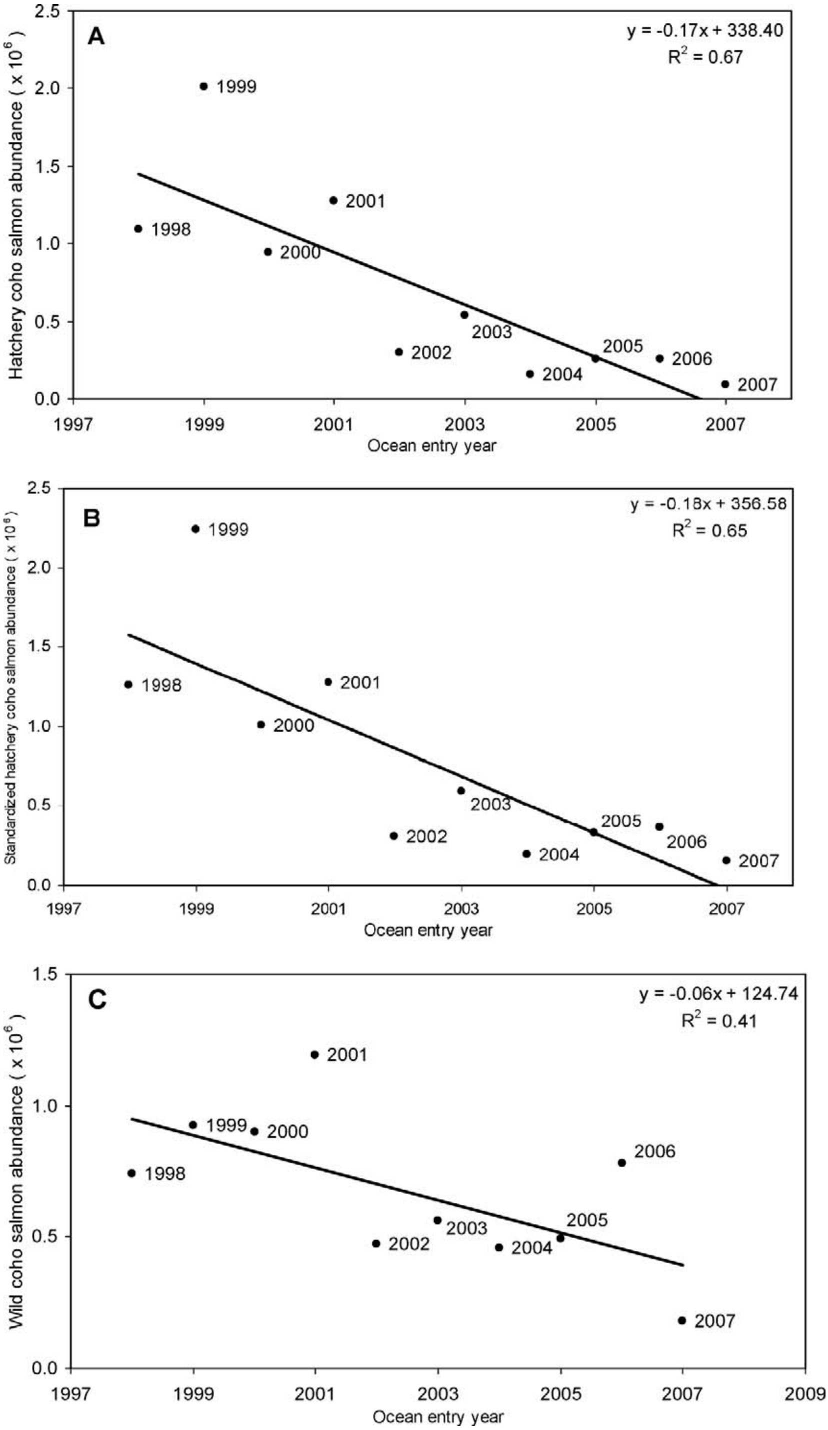

FIGURE 7.—September abundance of Canadian-origin coho salmon in the Strait of Georgia: **(A)** hatchery fish abundance, **(B)** standardized hatchery fish abundance, and **(C)** wild fish abundance. The ocean entry year is the year in which smolts enter the Strait of Georgia.

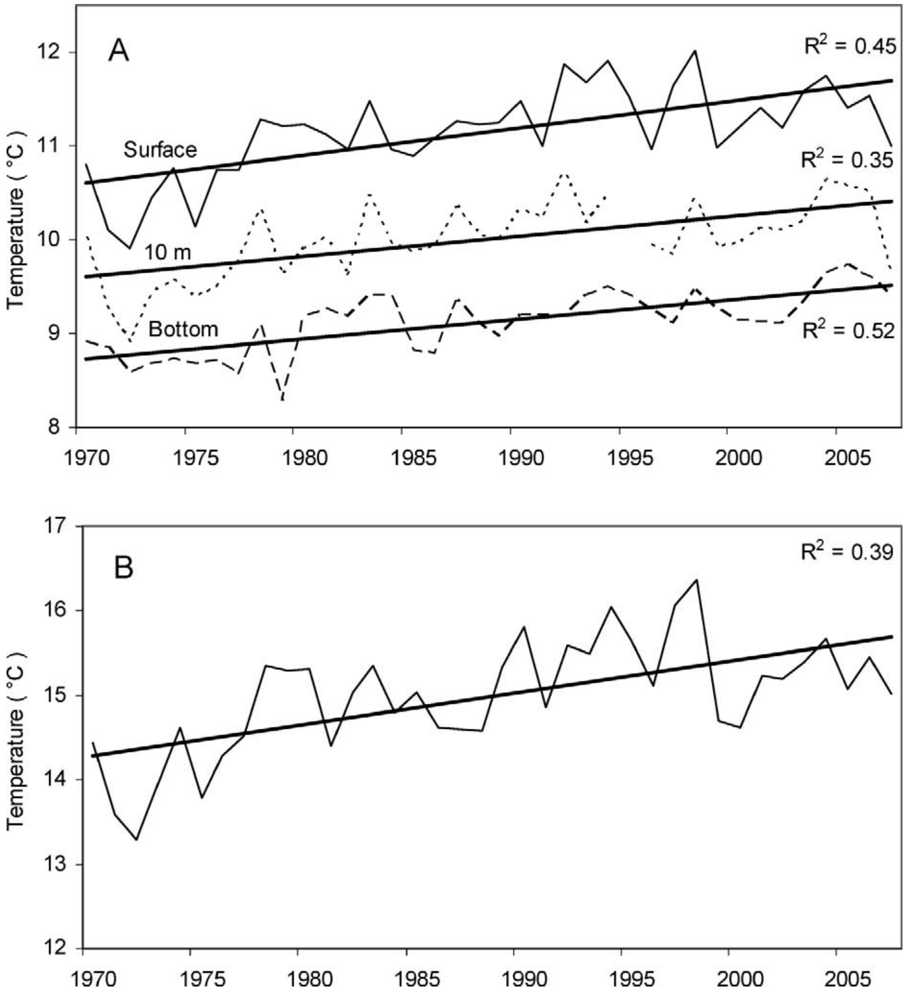

FIGURE 8.—Average temperatures in the Strait of Georgia at the Nanoose Bay site from 1970 to 2007: **(A)** average annual temperature at the surface, 10 m, and bottom and **(B)** average May–September sea surface temperature.

they indicate that our estimates of early marine mortality are most likely an indicator of the true early marine mortality given the consistency of the estimates from the two approaches.

Although other factors may contribute to the observed trends in marine survival, two significant factors were wind-driven mixing of surface waters in the Strait of Georgia and changes in sea surface temperature. There appeared to be a step change in the declining trend of early marine survival in 2002, and this change was coincidental with an increase in the number of days when the sustained wind speed exceeded 25 km/h. The negative relationship between strong winds during the early marine rearing period and early marine survival suggests that periods of relatively high wind speeds may inhibit the production or accessibility (or both) of the prey resources used by juvenile coho salmon. In spring and early summer, the freshwater plume from the Fraser River extends far out into the lower portion of the Strait of Georgia, covering as much as one-quarter to one-third of the entire strait. It is certainly plausible that increased mixing of the surface water at this time affects both salinity and zooplankton production, which in turn negatively affects marine survival. The timing of this change in early marine survival is similar to the shift in the Bering Sea ecosystem reported by Grebmeier et al. (2006). A recent study of trends in ecosystem indicators also identified a shift during 2001–2002 off the coast of Alaska (Litzow and Mueter 2009). Thus, the shift in early marine survival for coho salmon in 2002 may be part of a larger-scale impact of climate.

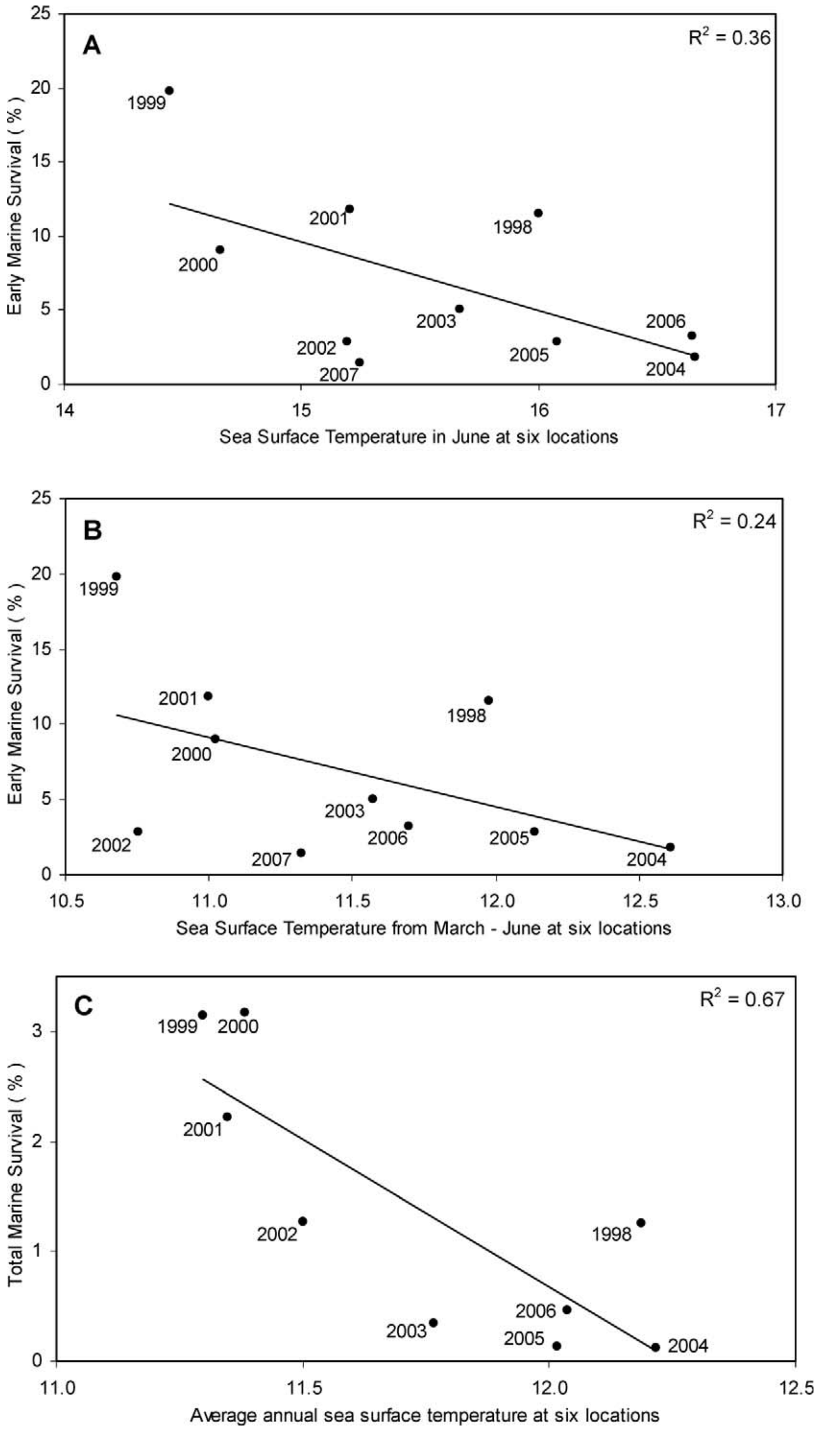

FIGURE 9.—Relationships between coho salmon survival and sea surface temperatures (SSTs) at six locations in the Strait of Georgia (listed in Table 1): **(A)** early marine survival versus June SST, **(B)** early marine survival versus average March–June SST, and **(C)** total marine survival versus average annual SST.

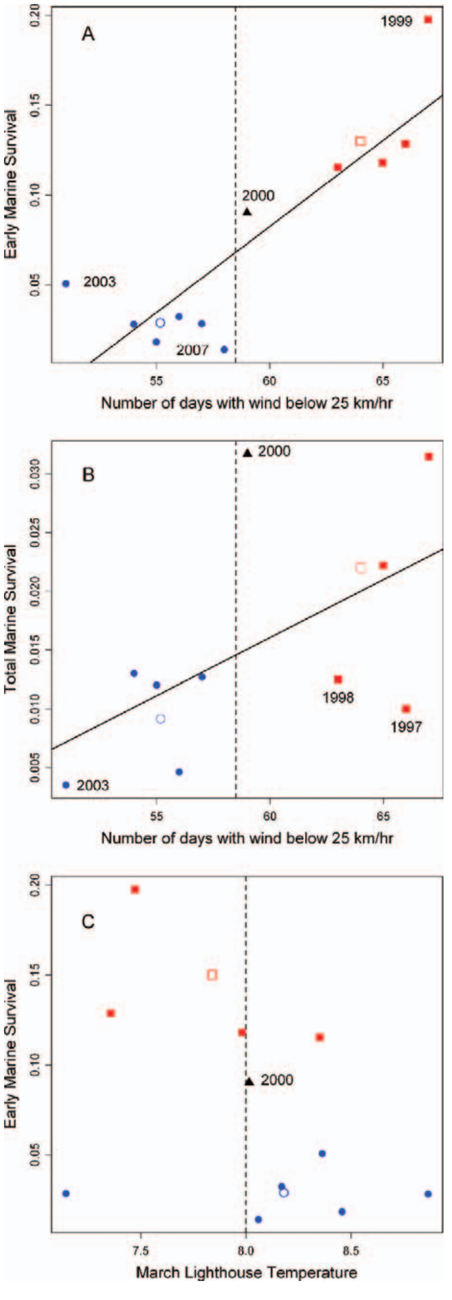

FIGURE 10.—Relationships between coho salmon survival and Strait of Georgia environmental factors: **(A)** early marine survival versus the number of May–July days with wind speeds below 25 km/h, **(B)** total marine survival versus number of May–July days with wind speeds below 25 km/h, and **(C)** early marine survival versus March lighthouse temperatures. Solid squares and solid triangles represent data from 1998 to 2001 (open square = centroid for these data); solid circles represent data from 2002 to 2007 (open circle = centroid). The vertical dashed line at 58.5 d represents the break point between the two regimes.

Increasing average annual sea surface temperatures were negatively related to total marine survival, whereas June sea surface temperatures were negatively associated with declines in early marine survival. The similarity between increasing temperature and winds and decreasing marine survival may indicate that a suite of factors is affecting coho salmon survival. Quinn et al. (2005) found that sea surface temperature was a good index of marine survival, but food availability conditions that smolts experience when they first enter the ocean may also be important. Most juvenile pink salmon and chum salmon enter the Strait of Georgia before coho salmon (Groot and Margolis 1991). Currently, these species are very abundant relative to coho salmon (Beamish et al. 2008), and we have evidence that they are growing to larger average sizes now than in the 1970s (King and Beamish 2000). The coho salmon diet overlaps with the diets consumed by pink salmon and chum salmon (King and Beamish 2000; Sweeting et al. 2004; Sweeting and Beamish 2009), indicating that juvenile pink salmon and chum salmon may affect the ability of juvenile coho salmon to find prey. A combination of increased temperatures and decreased prey may restrict the ability of coho salmon to acquire the additional food needed to compensate for the increased metabolic costs in the warmer surface waters. The changing environment of the Strait of Georgia may also result in early prey production that matches less closely with the ocean entry times of coho salmon than with the ocean entry times of their competitors, such as pink salmon and chum salmon.

Increasing temperatures and associated changes that reduce aerobic scope and decrease food availability when increased food is required may be a stressor for juvenile coho salmon that reduces fitness and makes an individual more susceptible to predation or disease as has been reported for Chinook salmon in Lake Michigan (Stewart and Ibarra 1991; Rand and Stewart 1998). Fry (1947) developed the concept of "scope for activity," which identified the basic amount of energy needed by a species to survive up to the maximum sustainable energy that may be metabolized. Species differ in their scope for activity but can be characterized by their aerobic scope, which is the difference between basal (or standard) and maximum metabolic rates (Fry 1971). There is a loss of aerobic scope at temperatures higher than an optimum, termed the upper pejus temperatures (pejus means "turning worse"; Pörtner 2002; Pörtner and Knust 2007; Pörtner and Farrell 2008). Critical temperatures that can be lethal to fish have much broader upper and lower ranges than upper and lower pejus temperatures. An example of an impact at the population level was shown by Pörtner and Knust (2007), who linked a long-term increase in summer temperatures with a long-term decline in the abundance of an indicator species of bottom fish.

Food supply and food quality affect growth, and optimal temperatures for growth decline as the daily ration declines, exacerbating the effect of a warmer habitat (Beauchamp 2009). Thus, the warming of the Strait of Georgia over the past decades—particularly the warming of surface waters in the early marine period—would be expected to increase the energy needed for basal metabolism (Brett 1970, 1971; Neill and Bryan 1991). Increased metabolic costs reduce the aerobic scope (Farrell et al. 2008), which can reduce marine survival of juvenile Pacific salmon (Ryding and Skalski 1999; Cole 2000; Koslow et al. 2002). A reduction in prey supply due to either competition or changes in nekton composition would further stress an individual fish or reduce fitness. Predation is always an important source of mortality, but now disease could also be an important source of mortality. It is known that increased temperature and reduced prey can increase the susceptibility of juvenile Pacific salmon to common diseases (Richter and Kolmes 2005). It is also known that hatchery fish can lose natural resistance to common diseases (Hemmingsen et al. 1986; Bakke 1997), making them more susceptible to disease than wild coho salmon.

Disease in hatchery fish is not uncommon, and a large percentage (~64%) of the 654 reported cases investigated in British Columbia between 1975 and 1997 involved coho salmon (Noakes et al. 2000). The number of cases involving coho salmon is disproportionately high considering that hatchery coho salmon represented only 6% of the total production (excluding sockeye salmon from spawning channels and other enhancement facilities) during the same period. We also suspect that a great many cases of disease are not reported or investigated because the hatchery fish do not exhibit clinical signs of disease (or hatchery staff may not recognize the clinical signs of disease) despite one or more disease pathogens being present. The lethal and nonlethal consequences of these disease issues have not been evaluated—partly because the data are not generally available or because there has simply been no analysis or evaluation conducted. Since disease is almost always identified as a possible factor related to a decline in returns, it would make sense to collect and report disease information whenever possible. This is difficult to do for wild coho salmon, but it would be beneficial if hatcheries were required to screen a random sample of fish before they are released; document any disease or fish health concerns, including the presence of specific disease pathogens; and ensure that these data are publicly available.

The declining total marine survival in relation to climate-related changes in a marine ecosystem is consistent with the findings of a number of other Pacific salmon studies in general and coho salmon studies in particular (Nickelson 1986; Fisher and Pearcy 1988; Holtby et al. 1990; Pearcy 1992; Friedland et al. 2000; Beamish and Mahnken 2001; Beamish et al. 2004). If temperature and climate are indices of processes that are associated with the reduction in marine survival for coho salmon in the Strait of Georgia and if these changes to the ecosystem continue as many scientists suggest (IPCC 2007), it seems probable that the average early marine survival will remain low. This is a serious issue for management agencies as wild populations of coho salmon could diminish in numbers and some populations could be lost. As populations of wild coho salmon are lost or diminished, the wild salmon policy (DFO 2005b) and the Species at Risk Act (Government of Canada 2003) could be used to attempt to rebuild the populations that are declining. However, it is possible that the declines cannot be stopped and that some populations cannot be rebuilt. Dr. Bill Ricker advised that he had learned to expect the unexpected when studying Pacific salmon. One way to minimize future surprises is through continued research and monitoring to determine whether the low early marine survival reported in this study will continue. Research is also needed to determine whether wild coho salmon are better adapted to the changing conditions in the early marine period. We suggest that the results of this study indicate that strategies need to be developed quickly to manage hatchery and wild coho salmon in the changing environment in the Strait of Georgia.

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