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ARTICLE

Anomalous Ocean Conditions May Explain the Recent Extreme Variability in Fraser River Sockeye Salmon Production

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Abstract

Record low returns of sockeye salmon *Oncorhynchus nerka* to the Fraser River in 2009 were followed by record high returns to the river in 2010, providing an unprecedented opportunity to examine links between oceanic factors and the survival of Pacific salmon stocks. The low returns in 2009 indicated poor early marine survival of juvenile sockeye salmon in 2007. The poor survival was likely due to low food levels arising from unfavorable wind and runoff conditions in the Strait of Georgia and the Queen Charlotte Sound–Hecate Strait region in the spring of 2007. Conversely, the high returns in 2010 were associated with a large smolt output from the Fraser River and good early marine survival in 2008. This enhanced survival was likely associated with adequate food levels arising from favorable oceanic conditions in the Strait of Georgia and the Queen Charlotte Sound–Hecate Strait region in the spring of 2008. We speculate that ocean factors during the subsequent marine years also affected brood year strength. Specifically, the back-to-back La Niña winters of 2007–2008 and 2008–2009 would have negatively influenced the survivability of the 2007 entry stocks, while the El Niño winter of 2009–2010 would have positively affected the survivability of the 2008 entry stocks. We conclude that poor early marine survival leads to low production. However, if large numbers of healthy fish survive the early marine entry, and if conditions during at least one of the two ocean winters in the Gulf of Alaska are favorable to stock survivability, then returns to the river can be high.

Sockeye salmon *Oncorhynchus nerka* originating from the Fraser River in British Columbia (Figure 1) support one of the most important fisheries on the Pacific coast of Canada. In addition to its economic and social importance, the fishery serves as an icon of environmental health and management (Ricker 1987; Beacham et al. 2004). Approximately 90 sockeye

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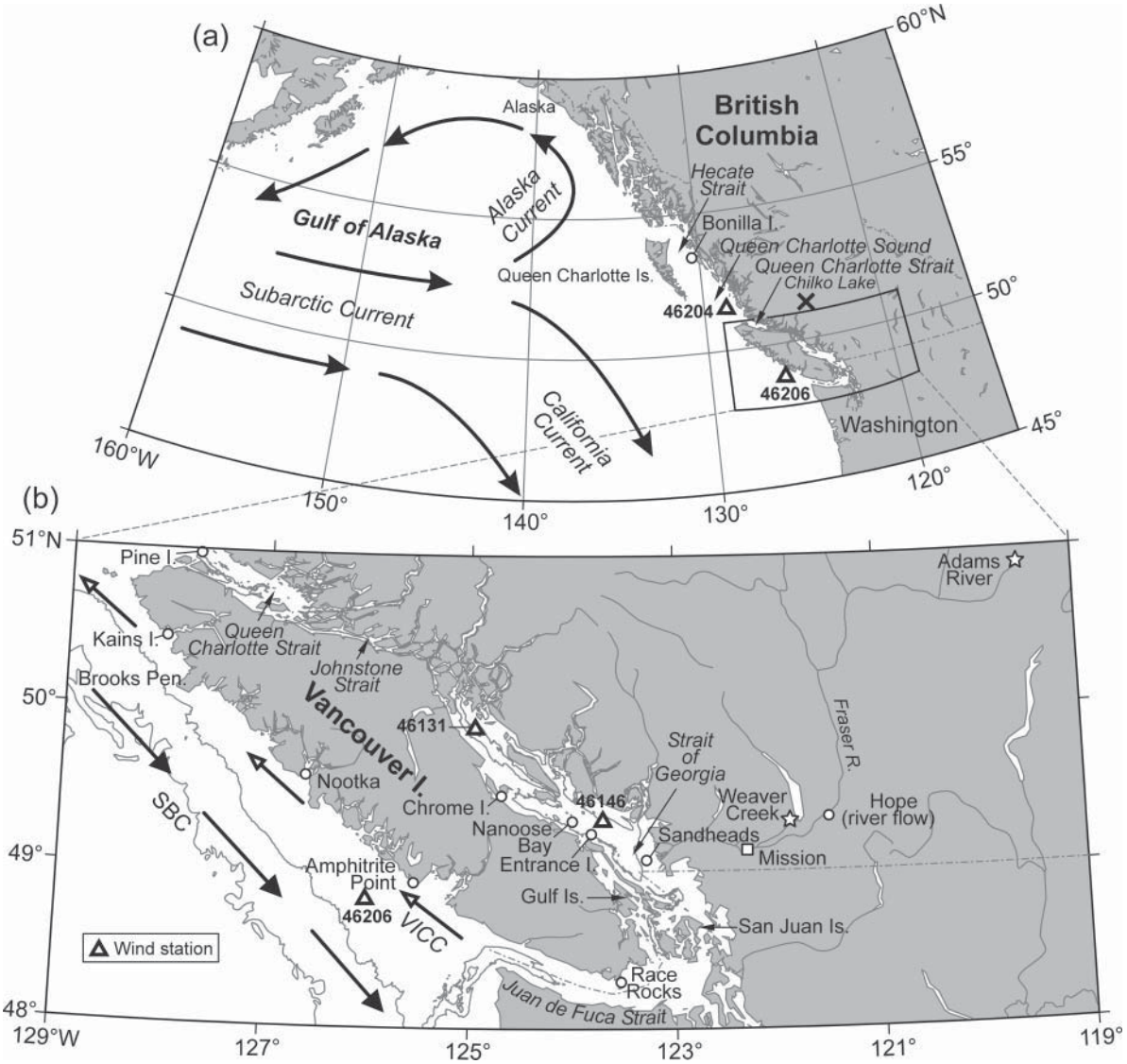


FIGURE 1. Maps of **(a)** the northeastern Pacific Ocean and **(b)** southern British Columbia showing the major ocean currents and sites at which the oceanic time series used in this study were recorded. Triangles denote wind stations (meteorological buoys 46131 [Sentry Shoal], 46146 [Halibut Bank], 46204 [Queen Charlotte Sound], and 46206 [La Perouse Bank]), and squares denote selected coastal lighthouse stations (Entrance, Chrome, Pine, and Bonilla islands). Nanoose Bay is on the central east coast of the Strait of Georgia. Currents are shown for summer only (SBC = Shelf-Break Current and VICC = Vancouver Island Coastal Current); current vector lengths are not scaled to speed. The small cross in panel (a) denotes the location of Chilko Lake.

salmon spawning populations have been identified in the Fraser River drainage system. Juveniles rear in about 24 nursery lakes, although most (about 90%) of the production is centered on fewer than 10 nursery lakes. Individual Fraser River sockeye salmon populations have characteristic timings when adults return to spawn and are broadly classified into four groups or "runs" for management purposes: early Stuart, early Summer, summer, and late (Gable and Cox-Rogers 1993).

Most juvenile sockeye salmon from the Fraser River leave their nursery lakes 1 year after they emerge from the gravel redd. They then enter the Strait of Georgia (Figure 1) over a 2-month period from late March until late May (Preikshot et al. 2012, this volume) and subsequently move northward through the Strait of Georgia over 5–6 weeks from roughly mid-May to mid-July (Beamish et al. 2012, this volume; Preikshot et al. 2012). Juveniles leave the Strait of Georgia to the north through the "Inside Passage" that takes them through Johnstone Strait, Queen Charlotte Strait, Queen Charlotte Sound, and Hecate Strait (Groot and Cooke 1987; Tucker et al. 2009; Welch et al. 2009, 2011). In the summer and fall, the juveniles move offshore and eventually into the Gulf of Alaska (Hartt and Dell 1986; Tucker et al. 2009), where they remain until they begin their return migration to the Fraser River in the spring and summer of their second year in the ocean. As a consequence of this life history, adult

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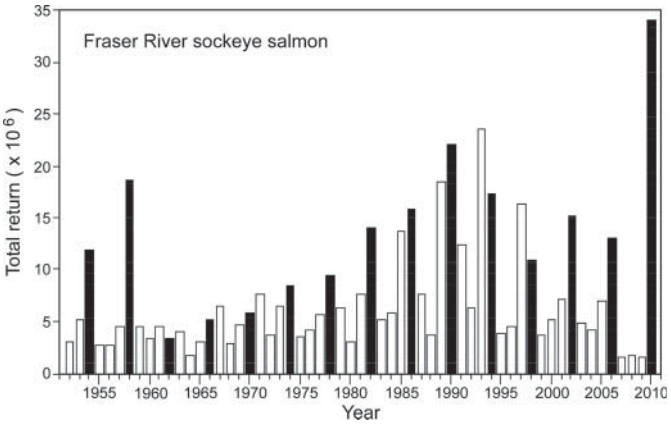


FIGURE 2. Total returns of sockeye salmon to the Fraser River. Dark bars indicate years when late-run Adams River stocks made a major contribution to the total salmon return. Return years 2007, 2008, and 2009 (brood years 2003, 2004, and 2005) were the lowest on record. The highest recorded return was in 2010.

sockeye salmon have a dominant age of four years and stocks undergo persistent cycles of abundance within this 4-year pattern (Figure 2). The present-day migration northward out of the Strait of Georgia may represent a change in direction from the westward migration through Juan de Fuca Strait postulated earlier by Healey (1980). This change would have occurred sometime in the late 1970s and could be related to the 1977 oceanic "regime shift" in the North Pacific (Preikshot et al. 2012).

As with other adult sockeye salmon, total returns of Fraser River stocks are highly variable throughout their distribution due, in part, to different production cycles and levels of marine survival. Ricker (1987) proposed that total "big year" returns in the early 1900s may have been around 100 million fish; other years presumably had substantially fewer returning fish. In the past 60 years, total annual returns have averaged approximately 7.8 million fish, with those in the big years (or dominant years, as they are now called) ranging from about 3.4 million to 22 million fish. This marked variability in adult returns is likely related to fishing and natural cycles (there is no consensus on the reasons for these cycles) and to the effects of climate. The most extreme variability in adult returns occurred between years 2009 and 2010, corresponding to the 2005 and 2006 brood years and the 2007 and 2008 ocean entry years, respectively. For 2009 and 2010, the expected returns were in the range of 10–11 million fish, whereas the actual returns were about 1.4 million and 29.6 million fish, respectively. The poor returns in the fall of 2009 led to a Canadian federal commission of inquiry (www.cohencommission.ca) while the good returns in the fall of 2010 (which included dominant-year late-run Adams River fish) established a record high for returning Fraser River stocks.

In this study, we show that the extreme, and unexpected, difference between the 2009 and 2010 sockeye salmon returns to the Fraser River was likely a consequence of several major factors, including environmental conditions in coastal British Columbia and the Gulf of Alaska, the freshwater production of smolts, and a life history strategy that requires that juveniles grow rapidly when they first enter the ocean. Our work extends the "critical size–critical period" hypothesis of Beamish and Mahnken (2001), which proposes that Pacific salmon brood year strength is determined in two stages during the first year in the ocean. According to this hypothesis, there is a large early-marine mortality that occurs shortly after juvenile salmon enter the ocean. This is followed by a physiologically based mortality during the first ocean winter that affects individuals that did not grow to a critical size and were unable to accumulate the necessary energy reserves during the previous summer and fall. The results presented here suggest that conditions in the second marine winter may also contribute to salmon survival in the Gulf of Alaska.

METHODS

Estimation of sockeye salmon smolts produced in the Fraser River drainage.—As noted in the introduction, ocean entry years 2007 and 2008—the years for which we wish to estimate the number of smolts produced in the Fraser River drainage system—correspond to spawning years 2005 and 2006 and to adult return years 2009 and 2010, respectively. The numbers of returning adults can be used to estimate the survival of the smolts to the adult stage.

Sockeye salmon smolts that enter the Strait of Georgia originate from a number of populations throughout the Fraser River drainage system. One of the major populations is from the Chilko Lake drainage (see Figure 1a for the location of the lake). Production from this system averaged 18.8% of the total returns to the Fraser River over the past 50 years (Grant et al. 2010). The number of sockeye salmon smolts leaving the drainage is estimated each year, and random samples are measured for length throughout the smolt migration out of the lake (Grant et al. 2010; T. Cone, Department of Fisheries and Oceans, personal communication). We used these estimates, and the relative proportion of the spawning population that produced the smolts to the total escapement in the Fraser River, to estimate the total number of sockeye smolts entering the Strait of Georgia from the Fraser River in 2007, 2008, and 2009. We acknowledge that determination of the number of smolts entering the strait is approximate and does not take into account freshwater mortality.

The estimated total marine survival for Chilko Lake smolts for return years 2009 and 2010 was 0.3% and 5.5%, respectively (Pacific Salmon Commission; http://www.psc.org). Assuming that these values were representative of all populations in the Fraser River drainage enables us to calculate the total sockeye salmon smolt production for the drainage region for the 2 years. A second method uses a proportional estimate of production. For example, if the sockeye salmon originating from Chilko Lake represent 10% of all adults returning to the Fraser River, then the number of smolts leaving the lake 2 years earlier would be 10% of all smolts produced. The method assumes that freshwater rearing conditions are similar

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for all populations and that marine survival is similar for all populations. Although there are obvious problems with both methods, they are intended only to provide an approximate estimate of the number of smolts that entered the ocean.

Trawl surveys for juvenile Fraser River sockeye salmon.—Trawl surveys were conducted in June and July 2007, 2008, and 2009 in the Strait of Georgia, Queen Charlotte Sound, and Hecate Strait. All surveys followed standard track lines, with net design and survey methodology reported in Beamish et al. (2000), Sweeting et al. (2003), and Tucker et al. (2009). The modified midwater trawl net had an approximate 30-m-wide, 15-m-deep opening and was fished for 30 min at an average speed of 2.6 m/s (5 knots) with headrope depths ranging from the surface to 30 m. Most sets were in the top 15 m of the water column. Catches for sets shorter than 30 min were standardized to a 30-min catch. Sets in the Strait of Georgia fished the top 30 m, whereas those in Queen Charlotte Sound, Queen Charlotte Strait, and Hecate Strait fished only the top 15 m. As a consequence, we compare catches for the surface 15 m only. For the 3 years being considered, the only survey in Queen Charlotte Strait was in 2009. The catches and the lengths of juvenile sockeye salmon for the Queen Charlotte Strait sample in 2009 were combined with those for Queen Charlotte Sound. Samples for DNA analysis are reported separately. Average catch is defined as the sum of the catch for each set divided by the number of sets. Fork lengths were measured from a subset of the catch. The stock composition of sockeye salmon in the trawl catches was determined with microsatellite DNA using the methods of Beacham et al. (2005).

Environmental data.—The physical environmental data examined in this study include daily mean wind velocity from meteorological buoys; daily salinity and sea surface temperature (SST) from British Columbia lighthouse stations; monthly mean discharge for the Fraser River and other rivers bordering the Strait of Georgia and southern Queen Charlotte Sound (Whitfield and Spence 2011); gridded (1.9° latitude × 1.9° longitude) monthly mean National Centers for Environmental Prediction and National Center for Atmospheric Research (NCEP/NCAR) Reanalysis-1 atmospheric sea level pressure and wind stress (Kistler et al. 2001); and gridded (1° latitude × 1° longitude) monthly mean Optimum Interpolation SST Version-2 data (Reynolds et al. 2002). We also examined monthly mean satellite-derived chlorophyll (ocean color) time series for British Columbia coastal waters derived from the Seaviewing Wide Field-of-View Sensor and Moderate Resolution Imaging Spectroradiometer (G. Borstad and L. Brown, ASL Environmental Sciences, Inc., 2011, personal communication). However, given the numerous gaps in the satellite data and the unknown relationship between surface chlorophyll concentration and depth-integrated production (total plankton biomass), we have left detailed investigation of these data to future study.

The meteorological time series serve as proxy variables for oceanic factors such as surface currents that could be affecting fish production (see Thomson and Hourston 2011). We use wind stress, $\tau = \rho_{air} C_D |U| U$, rather than wind velocity (U) to characterize the effects of surface currents because it is wind stress that appears as a driving force in the Navier-Stokes equations that govern physical oceanographic dynamics (here, ρ_{air} is the air density and C_D is the drag coefficient). Wind stress is available as part of the Reanalysis data; for meteorological buoys, we have estimated wind stress from wind velocities assuming neutral stability conditions (Smith 1988). We have also determined a pseudo–mixed layer depth derived from conductivity–temperature–depth (CTD) profiles collected by the Canadian Navy at Nanoose Bay in the west-central Strait of Georgia (http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/search-recherche/profiles-eng.asp). We use the prefix "pseudo" here because the minimum mixed layer depth we can derive from the CTD temperature, salinity, and density profiles is 2.5 m. This is the minimum depth that can be resolved by our mixing layer detection algorithm, which uses a split-and-merge curve fitting method to detect inflection points in water property profiles (Thomson and Fine 2003). Profiles which show no surface mixed layer were specified to have a mixed layer depth of 0 m. Close examination of the profile data for the strait shows that the absence of a surface mixed layer was typically due to a high surface density gradient, coinciding with a near-zero mixed layer depth. We note that each individual profile used in the derived monthly averages was carefully examined and any erroneous data (such as those with inverted surface density gradients) were rejected.

RESULTS

Fraser River Sockeye Salmon Smolts Entering the Strait of Georgia in 2007 and 2008

Smolts entering the Strait of Georgia in 2007 were produced from a total spawning escapement of 3,307,950 adult fish in 2005, of which Chilko Lake sockeye salmon accounted for 15.7%. In 2007, the estimated number of sockeye smolts leaving Chilko Lake was 77,128,000, about twice the previously recorded high for this lake. When we combine the 15.7% Chilko Lake fish for the total 2005 escapement return with the observed number of smolts leaving the lake in 2007 (and assume smolt-to-adult uniformity among stocks), we obtain an estimate of 491,563,000 sockeye salmon smolts produced in the entire watershed. Our second estimate of smolt production uses the estimation of 0.3% for the total marine survival of Chilko Lake smolts that went to sea in 2007. If we assume that this survival was representative of the survival of all sockeye salmon smolts and use the total observed return of 1,443,000 adult fish in 2009, we find that approximately 416,729,000 smolts entered the ocean in 2007. The average of the two estimates, roughly 454,146,000 smolts, represents the possible number of sockeye salmon smolts produced in the Fraser River drainage in 2007.

A total of 73,000,000 sockeye salmon smolts was counted leaving Chilko Lake in 2008. As with 2007, this was roughly twice the previously recorded high. The percentage of Chilko

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Lake sockeye salmon in the 2006 escapement was 15.2%. Using this percentage to determine the total smolt production, we calculate that 480,565,000 sockeye salmon smolts were produced in the Fraser River drainage in 2008. Our second estimate was obtained from an estimated marine survival of 5.4% for the Chilko Lake sockeye salmon smolts that went to sea in 2008. If we assume that this marine survival is representative of all stocks, approximately 556,944,000 smolts would have needed to enter the ocean in 2008 to produce the total observed return of 29,600,000 adults in 2010. The average of the two estimates yields roughly 518,754,000 sockeye salmon smolts produced in the Fraser River drainage in 2008, or 14.2% more smolts than in 2007.

In 2009, a total of 27,515,000 smolts was estimated leaving Chilko Lake. The adult return to Chilko Lake in 2007 was 28.9% of all returns to the Fraser River. Using these values, and applying the same methodology that we used for the 2007 and 2008 entry years, we estimated that 95,009,000 smolts were produced in the Fraser River drainage in 2009. This amounts to only 21% of the number of smolts produced in 2007. (The numbers of smolts produced in 2009 could not be estimated using the second method, as estimates of the marine survival for 2011 were not available at the time of this study.)

Lengths of Juvenile Sockeye Salmon Leaving Chilko Lake

In all 3 years, the samples measured for length were collected throughout the migration out of Chilko Lake, which started in late April in 2007 and 2008 and in early May in 2009, and ended in late May (Figure 3). The average length of 88.4 mm (SD = 6.6 mm) was largest in 2007. In 2008, the average length

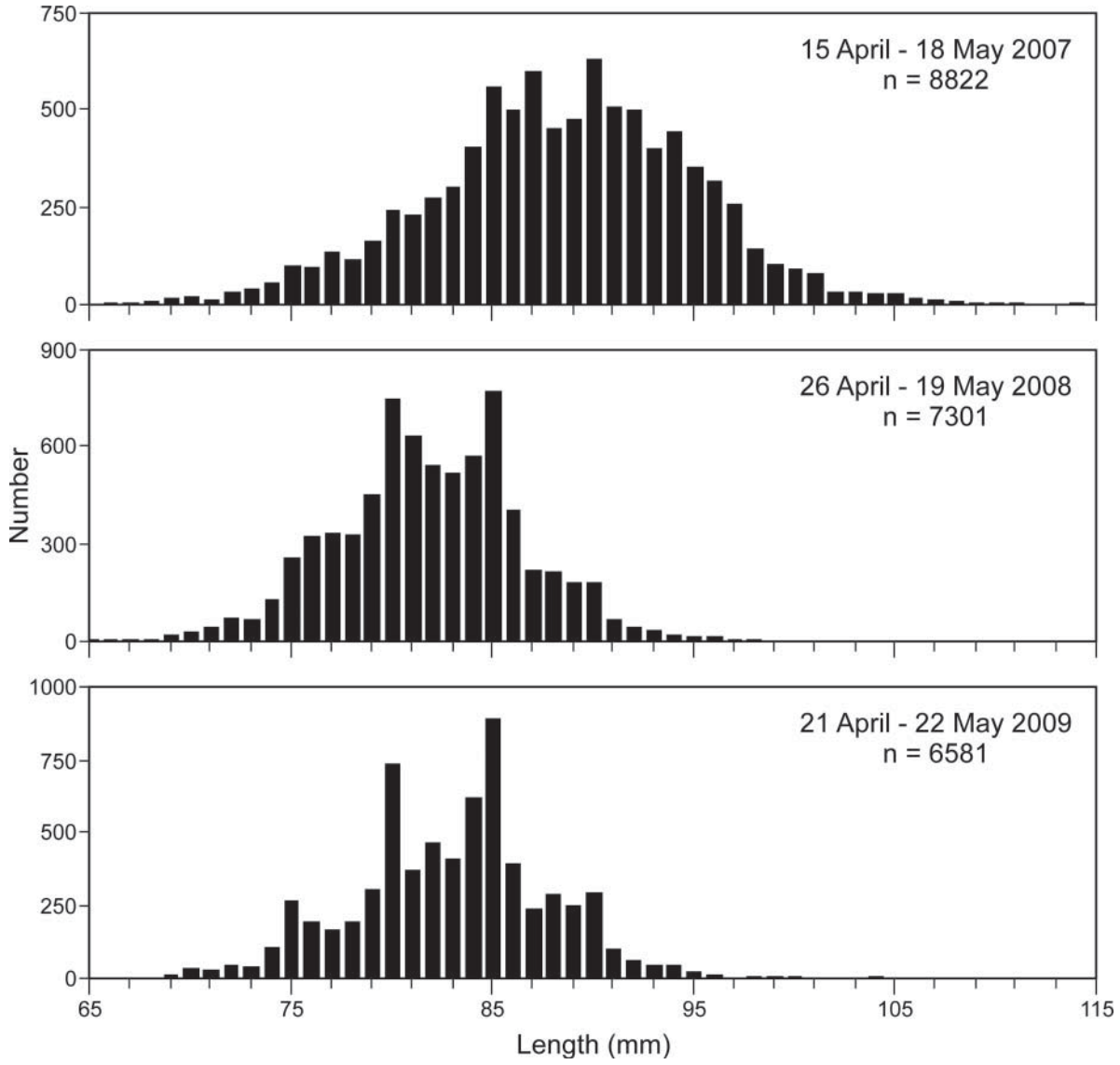


FIGURE 3. Length-frequency distributions of Fraser River sockeye salmon smolts leaving Chilko Lake; *n* denotes the total number of samples.

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was 81.9 mm (SD = 4.7 mm) and in 2009, 82.9 mm (SD = 4.8 mm).

Average Catches of Juveniles and Stock Composition in the Trawl Surveys (2007–2009)

In 2007, 74 trawl sets were conducted in the Strait of Georgia from July 8 to July 15. Twenty-one of these sets captured juvenile sockeye salmon and 53 had zero catch. All 65 fish were caught in the 0–15-m stratum. No individuals sampled were analyzed for stock composition. The average catch in the surface 15 m was 1.9 juvenile sockeye salmon per 30-min set (Figure 4a).

In 2008, 90 trawl sets were conducted in the Strait of Georgia from June 27 to July 6. Forty-four of these sets captured juvenile sockeye salmon and 46 sets had zero catch. A total of 1,597 sockeye salmon (96%) were captured in the 0–15-m depth range and 65 fish (4%) in the 15–30-m depth range. The average catch in the surface layer was 34.0 sockeye salmon per 30-min set (Figure 4a). A total of 167 fish was analyzed for stock composition, and all (100%) were from the Fraser River. The stock composition according to run timing was as follows: late, 73%; early summer, 20%; and summer, 7% (Figure 5a). Similar compositions were obtained for the Gulf Island region (Figure 5b). These percentages were generally similar to the expected stock percentages for the adult return for this brood year (Figure 5e); specifically, 82% late, 9% early summer, 8% summer, and 1% early Stuart.

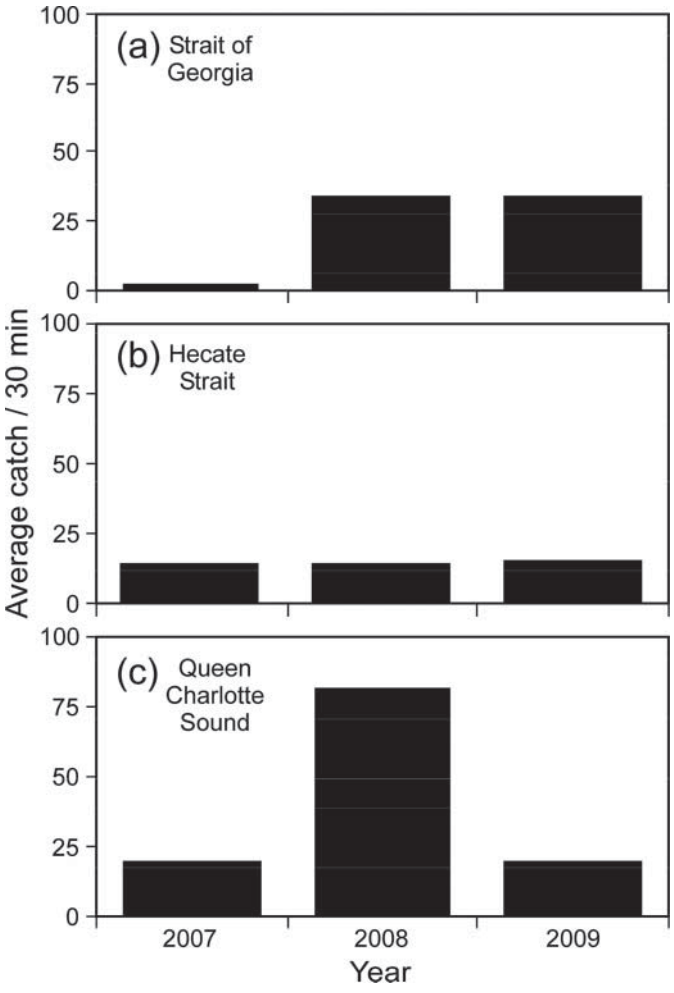


FIGURE 4. Average catch of juvenile sockeye salmon in July in standardized (30-min) sets for 2007, 2008, and 2009 for **(a)** the Strait of Georgia, **(b)** Hecate Strait, and **(c)** Queen Charlotte Sound.

In 2009, 83 trawls sets were undertaken in the Strait of Georgia from June 26 to July 7. Of these, 53 sets captured juvenile sockeye salmon and 30 sets had zero catch. There were 1,354 fish (85%) captured in the surface layer (0–15 m), 218 (14%) in the 15–30-m depth range, and 16 fish (1%) in water deeper than 30 m. The average catch in the surface layer was 33.9 fish per 30-min set (Figure 4a). A total of 141 fish was analyzed for stock composition for the Strait of Georgia and all were from the Fraser River (Figure 6a). The stock composition according to run timing was as follows: summer, 51%; late, 30%; early summer, 18%; and early Stuart, 1% (Figure 6a). The stock composition for the Gulf Islands (Figure 6b) differed slightly from that for the Strait of Georgia. However, for both the open strait and the Gulf Islands, the stock composition was similar to the expected percentages for adults from this brood year, specifically, summer, 47%; late, 37%; early summer, 15%; and early Stuart, 1% (Figure 6f).

There were 56 trawl sets in Queen Charlotte Strait, Queen Charlotte Sound, and Hecate Strait from 2007 to 2009, and all sets were conducted at the end of June or early July (Table 1). Unlike in Hecate Strait, which had relatively little variation in the average catch for the 3 years (Figure 4b), there was an almost fourfold increase in the average catch in Queen Charlotte Sound in 2008 compared with 2007 and 2009 (Table 1; Figure 4c).

There were no samples collected for DNA analysis in the Strait of Georgia in 2007; however, in 2008 and 2009, all samples from the surveys were from the Fraser River. In Queen Charlotte Sound, summer stocks from the Fraser River represented about two-thirds of the sample, with the remaining Fraser River stocks being about equally distributed among the early Stuart, early summer, and late stocks. The observed Fraser River stock compositions in Queen Charlotte Sound and Hecate Strait in 2007 (Figure 7a, b) were almost identical, and these were generally similar to the expected stock composition (Figure 7c). In 2008, the stock composition in Queen Charlotte Sound (Figure 5c) was generally similar to the composition in the Strait of Georgia (Figure 5a). However, the stock composition of the Fraser River sockeye salmon sample in Hecate Strait (Figure 5d) had substantially larger numbers of summer stocks and substantially fewer late-run stocks than expected. The stock composition in Queen Charlotte Strait was also generally similar to that in the Strait of Georgia and the Gulf Islands. In 2009, the stock composition in Queen Charlotte Strait and Hecate Strait (Figures 6c, e) was generally similar to the composition in the Strait of Georgia region (Figures 6a, b), whereas those in Queen Charlotte Sound (Figure 6d) were different from those in the Strait of Georgia.

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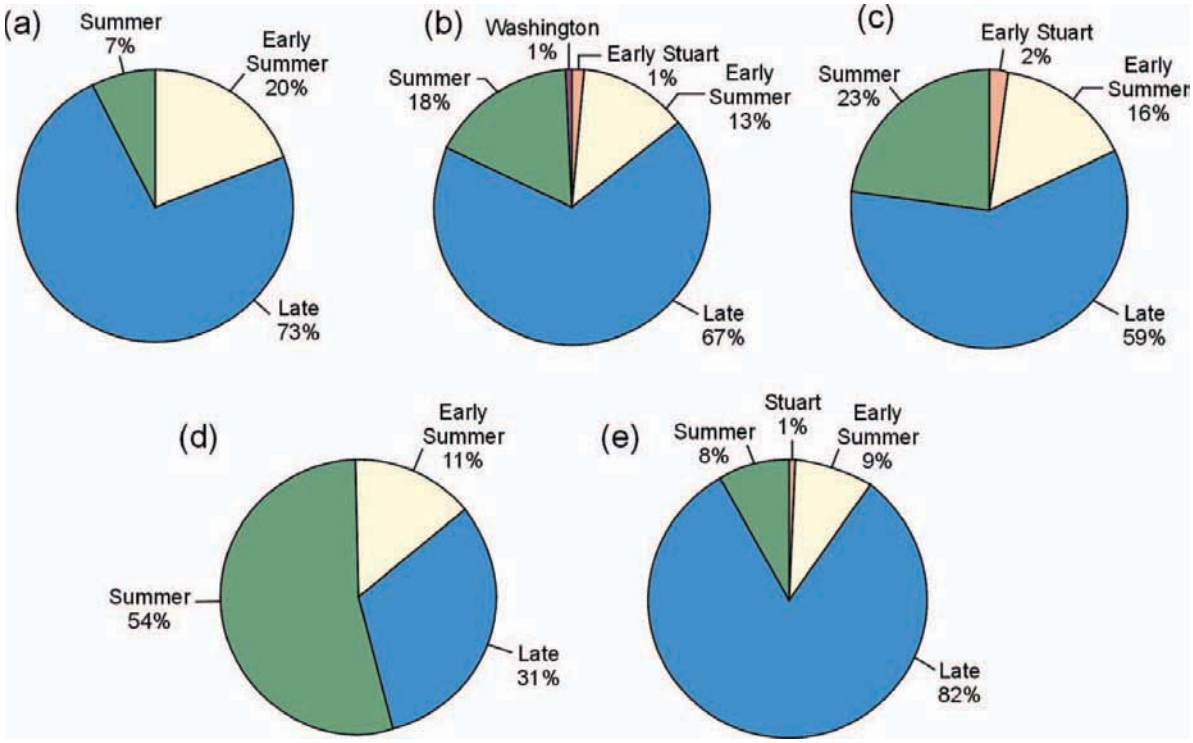


FIGURE 5. Stock structure as identified from DNA analysis of Fraser River sockeye salmon collected in 2008 for **(a)** the Strait of Georgia (June 27–July 16; $N = 179$), **(b)** the Gulf Islands (June 20–27; $N = 153$), **(c)** Queen Charlotte Sound (June 25; $N = 87$), and **(d)** Hecate Strait (June 26–27; $N = 103$), along with **(e)** the stock composition expected for returning fish in 2010.

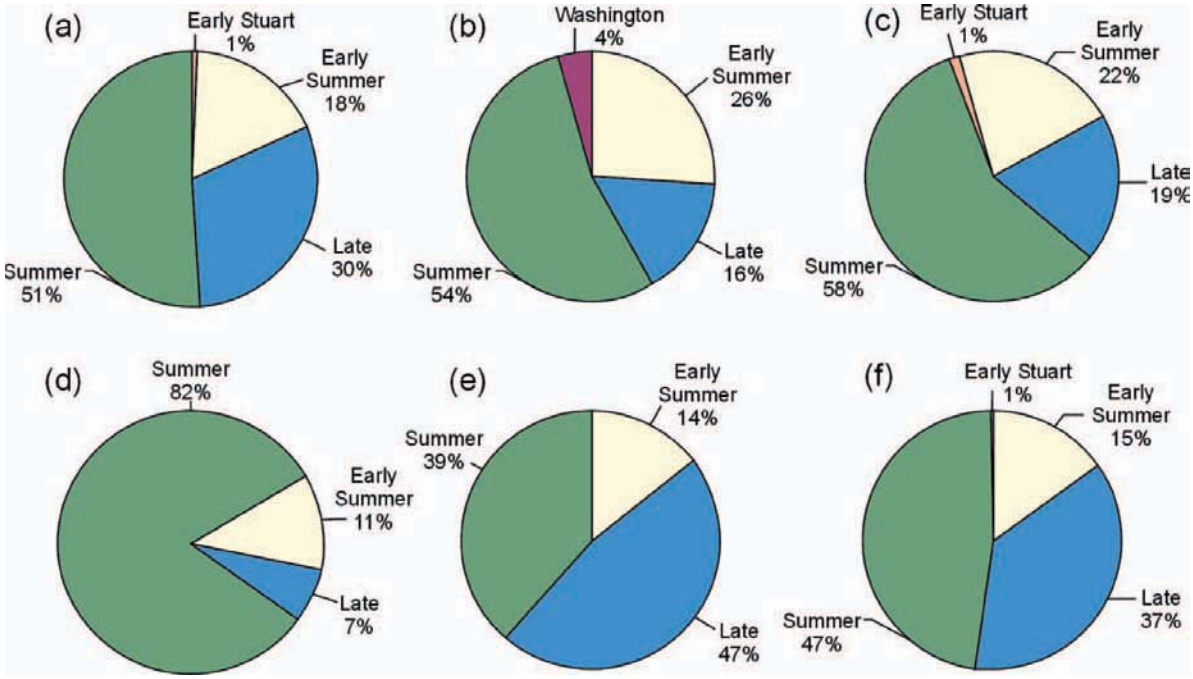


FIGURE 6. Stock structure as identified from DNA analysis of sockeye salmon collected in 2009 for **(a)** the Strait of Georgia (June 26–July 7; $N = 141$), **(b)** the Gulf Islands (June 1–5; $N = 146$), **(c)** Queen Charlotte Strait (June 24; $N = 79$), **(d)** Queen Charlotte Sound (June 23; $N = 61$), and **(e)** Hecate Strait (June 24–25; $N = 83$), along with **(f)** the stock composition expected for returning fish in 2011.

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TABLE 1. Results from analysis of trawl fishing sets in the Strait of Georgia, Queen Charlotte Strait, Hecate Strait, and Queen Charlotte Sound for sockeye salmon smolt marine entry years 2007 to 2009; NA = not available, NR = not relevant.

Year	Date	Location	Number of sets in top 15 m	Total sockeye salmon catches in top 15 m	Percentage of sockeye from the Fraser River (number analyzed for DNA from all depths)	Estimated catch of Fraser River sockeye	Average catch of Fraser River sockeye salmon/set in top 15 m	Percentage of sockeye salmon from populations on the West Coast of Vancouver Island
2007	Jul 8–15	Strait of Georgia	36	65	NA	65	1.9	NR
	Jun 28	Queen Charlotte Sound	5	103	98.4 (62)	101	20.2	0%
	Jun 29–30	Hecate Strait	13	400	45.4 (238)	182	14.0	47.1%
2008	June 27–July 6	Strait of Georgia	47	1,597	100 (167)	1,597	34.0	NR
	Jun 25–Jul 3	Queen Charlotte Sound	5	486	100 (88)	486	97.2	0%
	Jun 26–27, Jul 3	Hecate Strait	13	278	63 (165)	175	13.5	30.3%
2009	Jun 26–Jul 7	Strait of Georgia	40	1,354	100 (140)	1,354	33.9	NR
	Jun 24, Jul 2–3	Queen Charlotte Sound	5	118	93.8 (138)	111	22.1	0%
	Jun 25–26	Hecate Strait	8	188	56.8 (146)	107	13.4	15.8%
	Jun 24	Queen Charlotte Strait	7	96	90.8 (96)	87	13.7	0%

Size of Juvenile Sockeye Salmon Entering the Strait of Georgia and in the Trawl Catches

In all years, the juvenile sockeye salmon in Hecate Strait were significantly larger than those in all other areas (Table 2; analysis of variance [ANOVA], $P < 0.01$). Juveniles were the smallest in Hecate Strait in 2007 (Table 2; $P < 0.01$) and in Queen Charlotte Sound in 2007 (Table 2; $P < 0.05$). The average size of juvenile sockeye salmon in Queen Charlotte Sound was larger than that in the Strait of Georgia in all years, but only significantly larger in 2008 and 2009 (Table 2; $P < 0.05$). The average length of juvenile sockeye salmon in the Strait of Georgia was the smallest in 2008, but not significantly smaller (Table 2; $P > 0.05$).

Timing of the Spring Transition

Although details vary from region to region, meteorological time series for the West Coast of British Columbia (Figure 8) revealed that return years 2007, 2008, and 2009 were associated with anomalously late reversals in the alongshore winds over southern coastal British Columbia in spring 2 years earlier, i.e., at the times of marine entry in years 2005, 2006, and 2007, respectively. (The mean ± SE for the wind reversals for this region is April 16 ± 5 d for the period for which there are meteorological buoy observations [1980 to 2011]. There is no detectable long-term trend.) In each of these 3 years, the "spring transition" from predominantly northward directed (i.e., "southerly") winds in winter to predominantly southward directed (i.e., "northerly") winds in summer (see Strub et al. 1987; Thomson and Ware 1996) was delayed by about 1 month relative to the mid-April long-term mean. Moreover, the prevailing northerly winds that followed the transition in 2007 were generally weaker than those of other years. Conversely, the high returns in 2010 were associated with an anomalously early spring transition during the 2008 marine entry year. The transition occurred over several weeks beginning around mid-January and was characterized by anomalously weak southerly winds punctuated by periods of moderately strong northerly winds. Although this variability makes it difficult to pinpoint the exact time of the 2008 spring transition, it is clear from Figure 8 that the reversal to northerly winds in 2008 occurred up to several months earlier than normal (Table 3). The prevailing northerly wind that followed the

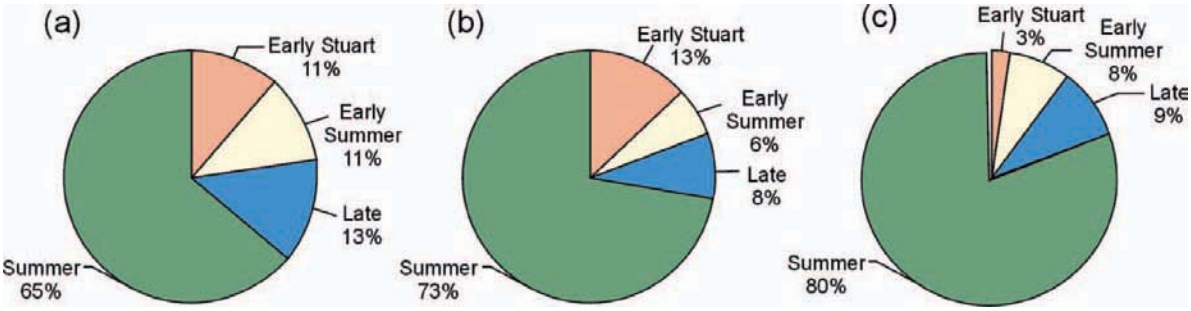


FIGURE 7. Stock structure as identified from DNA analysis of sockeye salmon collected in 2007 from **(a)** Queen Charlotte Sound (June 28; $N = 61$), and **(b)** Hecate Strait (June 29–30; $N = 108$), along with **(c)** the stock composition expected for returning fish in 2009.

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TABLE 2. Length (mm) and weight (g) of samples of juvenile sockeye salmon from the 2007, 2008, and 2009 trawl surveys for the different coastal regions. Values include the mean, standard error of the mean (SE = SD/$\sqrt{N}$ for sample standard deviation SD), and number of fish (N) used for each estimate. For 2009, the Queen Charlotte Strait data are combined with Queen Charlotte Sound data.

Year	Variable	Strait of Georgia	Queen Charlotte Sound	Hecate Strait
2007	Length ± SE (N)	107.9 ± 2.1 (65)	108.9 ± 1.1 (61)	120.1 ± 1.0 (108)
	Weight ± SE (N)	12.7 ± 1.8 (54)	11.3 ± 1.5 (61)	16.7 ± 0.5 (108)
2008	Length ± SE (N)	106.0 ± 0.3 (1,168)	112.8 ± 0.8 (87)	133.9 ± 1.3 (103)
	Weight ± SE (N)	12.1 ± 0.3 (299)	11.8 ± 0.3 (87)	22.8 ± 0.8 (103)
2009	Length ± SE (N)	116.5 ± 0.3 (1,024)	118.1 ± 0.7 (140)	159.4 ± 1.6 (83)
	Weight ± SE (N)	16.9 ± 0.3 (276)	15.9 ± 0.3 (140)	44.2 ± 1.5 (83)

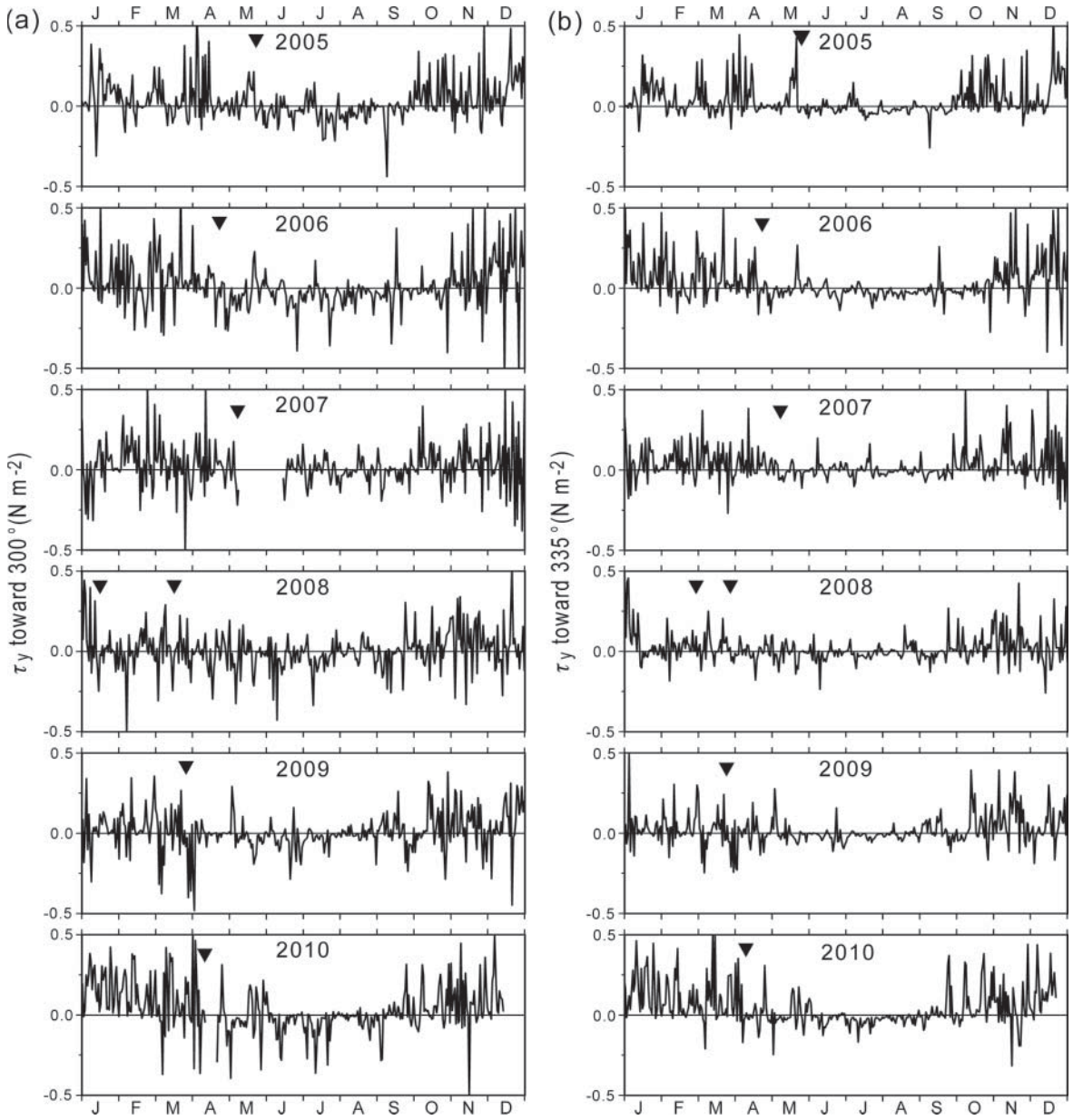


FIGURE 8. Alongshore component of daily mean wind stress (τ_y) at **(a)** Meteorological Buoy C46206 (48°50.1′N, 125°59.9′W, τ_y positive toward 300° true) and **(b)** NCEP reanalysis site 49N, 126W (48°34′N, 125°38′W, τ_y positive toward 335° true) off southwestern Vancouver Island for years 2005 through 2010 (see Figure 1). Inverted triangles mark the approximate times of the "spring transition," when the prevailing winds switch from southeasterly (to the northwest) to northwesterly (to the southeast). The mean date is April 16 ± 5 d (see text). Similar wind timing conditions occurred within the Strait of Georgia and central coastal regions of Hecate Strait and Queen Charlotte Sound.

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TABLE 3. Timing of the spring transition based on the daily alongshore component of wind stress from Meteorological Buoy MB4206 and NCEP/NCAR reanalysis site 49°N, 126°W. The mean transition date is around April 16.

Year	MB46206	Reanalysis	Comment
2005	26 May	25 May	Late
2006	22 Apr	20 Apr	Normal
2007	7 May	7 May	Late
2008	14 Mar	28 Mar	Early
2009	4 Mar	26 Mar	Early
2010	12 Apr	9 Apr	Normal
2011	2 Apr	1 Apr	Normal

transition in 2008 was generally stronger than those for other years.

The spring transition is generally followed by a reduction in rainfall and cloud cover as well as accelerated snowmelt. Prior to the transition, the prevailing southeasterly winds in the Strait of Georgia are conducive to the northwestward transport (and hence retention) of freshwater runoff entering the strait from the Fraser River and from the numerous smaller rivers located along the East Coast of Vancouver Island and the mainland side of the basin (Figure 9). In winter, the volume of freshwater entering the Strait of Georgia from pluvial-fed rivers can be equivalent to that entering the strait from higher elevations in the Fraser River drainage system. In the spring and summer months following the spring transition, the total discharge into the strait (Figure 9a) becomes dominated by snowmelt-derived discharge from the Fraser River. Similar wind and runoff conditions apply to Queen Charlotte Sound and Hecate Strait (Figure 9b). A principal difference with the Strait of Georgia is that most of the discharge on the central British Columbia coast originates from the mainland side. As a consequence, the southerly winds that prevail prior to the transition will tend to drive the brackish surface waters entering from the mainland inlets northward in Queen Charlotte Sound (Hannah et al. 1991). Conversely, the northerly winds that follow the transition will help drive the outflow from the coastal inlets into the sound (Borstad et al. 2011).

Effect of the Spring Transition Timing on Juvenile Salmon Survival

To determine the possible contribution of early marine conditions to the extreme difference in fish production observed

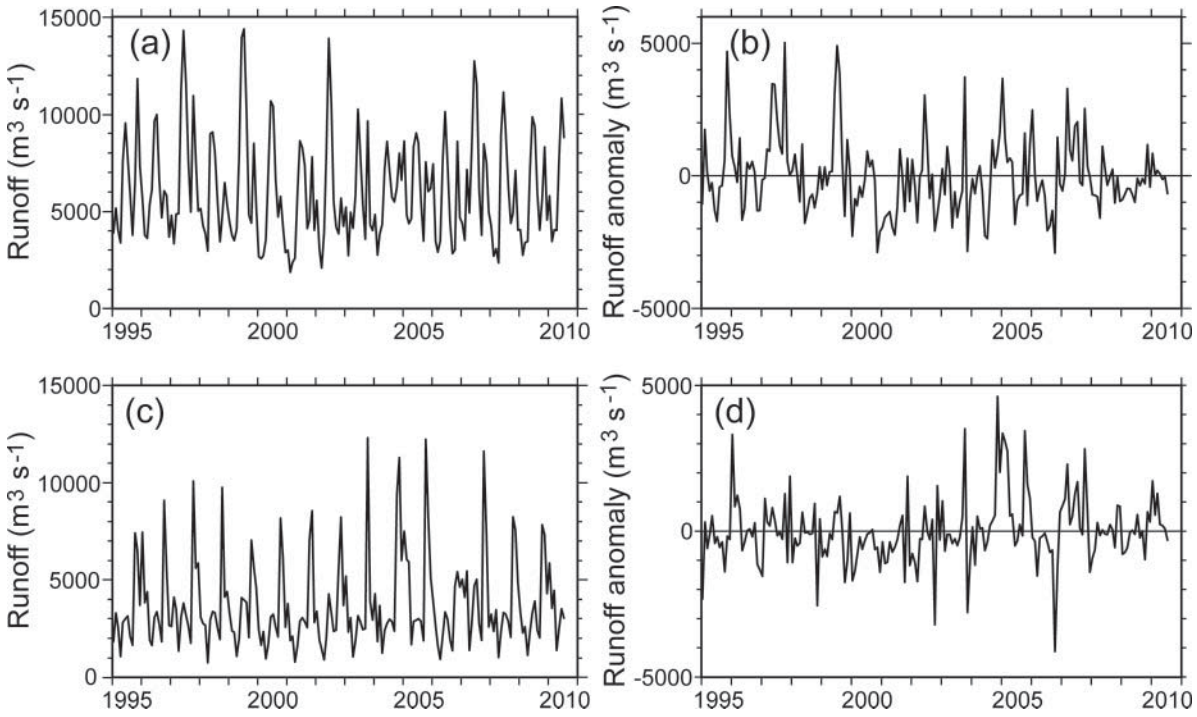


FIGURE 9. Monthly time series of total river discharge for **(a)** the Strait of Georgia and **(c)** the Queen Charlotte Sound–Strait region of British Columbia for the period from 1 January 2000 to 1 January 2010; panels **(b)** and **(d)** show the corresponding monthly mean anomalies. Anomalies were obtained by subtracting the seasonal cycle (mean monthly values) from each data series. The total discharge into the Strait of Georgia consists of the Fraser River discharge recorded at the eastern end of the Fraser River valley at Hope, that from the central and lower portions of the river downstream of Hope and its tributaries, and that from freshwater inputs from Central Vancouver Island and the British Columbia mainland. The total discharge into the Queen Charlotte Sound–Strait region is comprised of freshwater inputs from the Wannock River (mainland British Columbia) to the east of buoy 46204 in Figure 1a, from small rivers on the coast of northern Vancouver Island (not shown separately), and from rivers on the mainland coasts of Queen Charlotte Sound and Queen Charlotte Strait. Although several years experienced anomalously high runoff in midwinter, 2007 was the only year in which anomalously high runoff was recorded throughout the year for both the Strait of Georgia and central coastal waters.

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between return years 2009 and 2010, we focused on oceanographic and meteorological variables for the spring entry years of 2007 and 2008, respectively. Of particular significance are the marked differences in monthly mean river runoff, time-integrated (seasonal) winds, and monthly mean surface salinity observed from early to late spring in 2007 and 2008 in the coastal regions. In the case of the Strait of Georgia, we find (1) anomalously high runoff from both the mainland and Vancouver Island sides of the strait in the spring of 2007 but anomalously low runoff from these regions in the spring of 2008 (Figures 9a, b); (2) prolonged southeasterly wind forcing in the strait during the spring of 2007, in contrast to moderate northwesterly wind forcing over the strait during the spring of 2008 (Figure 10a); and (3) exceptionally low surface salinities throughout the region from May through November 2007 compared with the anomalously high surface salinities in the region from February through June 2008 (Figure 11a). Similar conditions were observed in Queen Charlotte Strait and in the Queen Charlotte Sound–Hecate Strait region (Figures 9c, 9d, 10b, and 11b). The winter and spring of 2007 were also noteworthy for their anomalously high rainfall and relatively few hours of bright sunshine (A. McCarthy, Environment Canada, personal communication).

The anomalous wind and runoff conditions that prevailed along the British Columbia coast in early 2007 (prior to the time that juvenile Fraser River sockeye salmon were resident in the different regions) likely account for the low surface salinities observed throughout much of the region that spring and summer (Figure 11). Freshwater retention in the Strait of Georgia also accounts for the magnitudes of the observed surface salinity anomalies (see appendix) and for the anomalously shallow pseudo–mixed layer observed at Nanoose Bay in the central sector of the strait throughout the spring and summer of 2007 (Figure 12). The shallow mixed layer was unprecedented in its timing and duration for the period 1980 to 2010, for which we have nearly continuous data. Moreover, satellite-derived chlorophyll data for the Strait of Georgia for the period 1997 to 2010 (Figure 13) reveal an early (February–March) bloom in the strait in 2007, which is consistent with Collins et al.'s (2009) modeling results linking the timing of plankton blooms to the depth of the wind mixed layer in the strait. Specifically, the much earlier than normal, short-lived bloom in 2007 supports our contention of an anomalously shallow mixed layer depth within the strait in early spring. Unlike the plankton bloom that occurred in the strait from May through August 2007 (Figure 13), the February–March bloom took place too soon to be utilized by zooplankton and therefore was not indicative of high spring productivity. (The only other year in the data series with an especially early spring bloom was 2005, another marine entry year that led to poor adult returns.) In contrast, marine entry year 2008 had relatively high surface chlorophyll levels from May through August, consistent with relatively high plankton productivity and deep mixed layer depths.

The increased surface stratification in the Strait of Georgia in early 2007 would have led to reduced vertical mixing and weaker entrainment of nutrient-rich water from the underlying marine layer, limiting the duration and vertical extent of upper layer primary productivity. These factors, in conjunction with possibly reduced light penetration due to higher fluvial-derived particle concentrations, may have confined plankton growth to a shallow (and therefore relatively low, depth-integrated biomass) surface layer around the time that the smolts were entering the strait. The cloudy and overcast "winter" skies that typically precede the spring transition also may have helped confine plankton productivity to a relatively shallow surface layer in the strait.

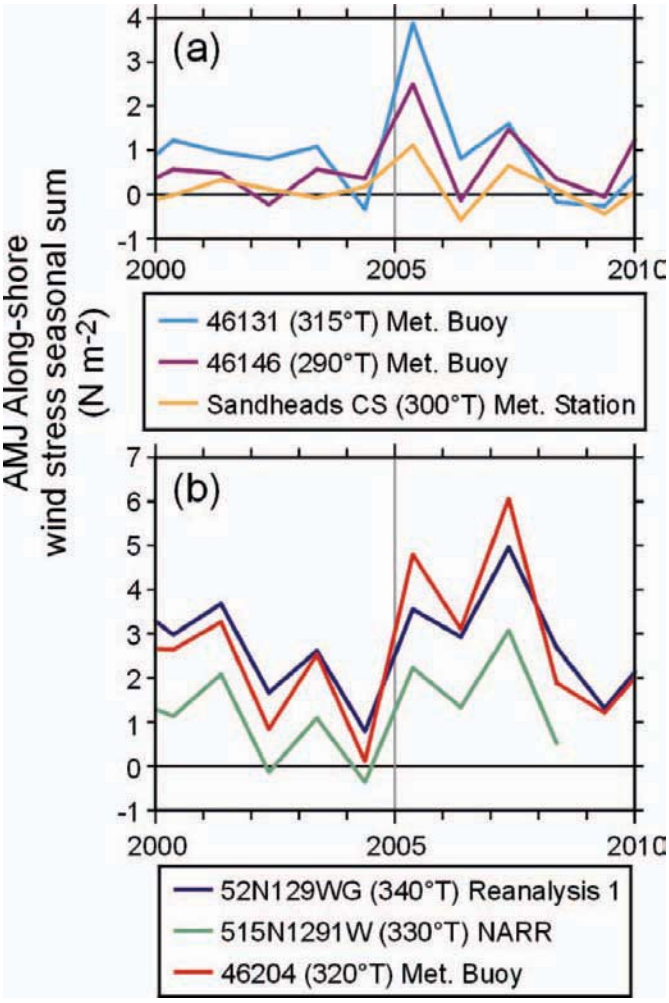


FIGURE 10. Time-integrated, along-channel component of the wind stress for the months of March, April, and May for meteorological stations and reanalysis sites in the study region for the period from 1 January 2000 to 1 January 2010. Panel **(a)** is for the Strait of Georgia (meteorological buoy sites MB46131 on Sentry Shoal [49°54.4′N, 124°59.1′W] and MB46146 on Halibut Bank [49°20.4′N, 123°43.6′W] and Sandheads Lightstation off the Fraser River Delta [49°6.6′N, 123°18.0′W]); panel **(b)** is for Queen Charlotte Sound (meteorological buoy MB46204 on West Sea Otter Bank [51°22.1′N, 128°45.0′W], reanalysis grid point 52.0°N, 129.1°W, and the North American Regional Reanalysis (NARR) site at 51.5°N, 129.1°W (see Figure 1). Positive alongshore directions are shown in brackets in degrees true compass bearing. The cross-shore components of the wind stress are much weaker and therefore not presented.

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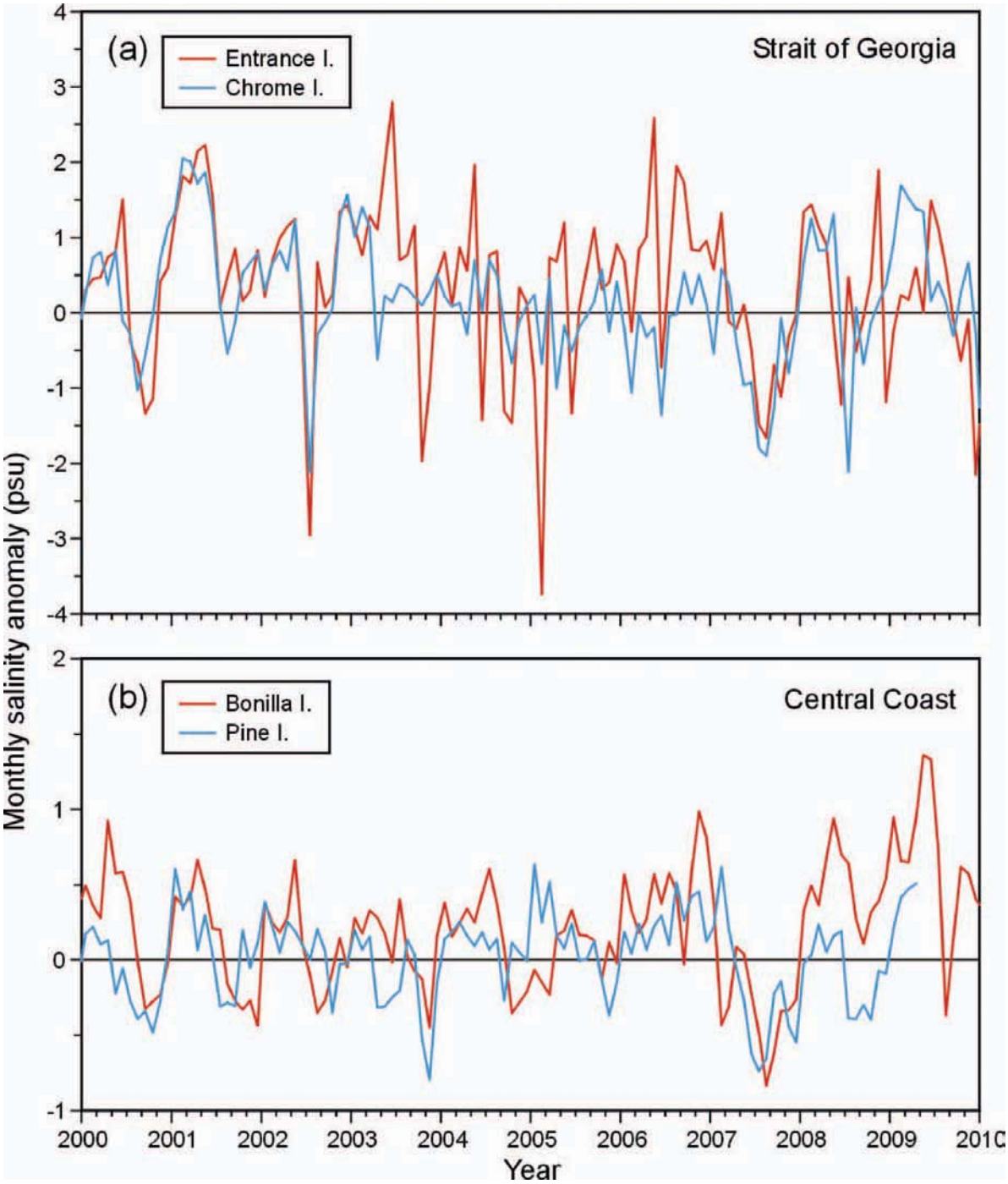


FIGURE 11. Monthly mean surface salinity anomalies for lightstations on the coast of British Columbia for the period 2000 to 2010: **(a)** Entrance Island (Strait of Georgia), **(b)** Chrome Island (Strait of Georgia), **(c)** Pine Island (Queen Charlotte Strait), and **(d)** Bonilla Island (Hecate Strait) (see Figure 1 for locations). Monthly anomalies were obtained by subtracting the seasonal cycle (mean monthly values) from each data series.

In contrast to 2007, in the spring of 2008 the marine conditions in the Strait of Georgia and Queen Charlotte Sound–Hecate Strait regions (Figures 9c, 9d, 10b) were conducive to the flushing of somewhat more saline, less stratified surface waters towards the open ocean. In the case of the Strait of Georgia, the flushing of brackish surface waters seaward through passes between the Gulf and San Juan islands would have increased light levels in the surface of the strait and allowed deeper wind mixing to more easily entrain nutrients into the upper layer of the basin, possibly leading to more vertically extensive and

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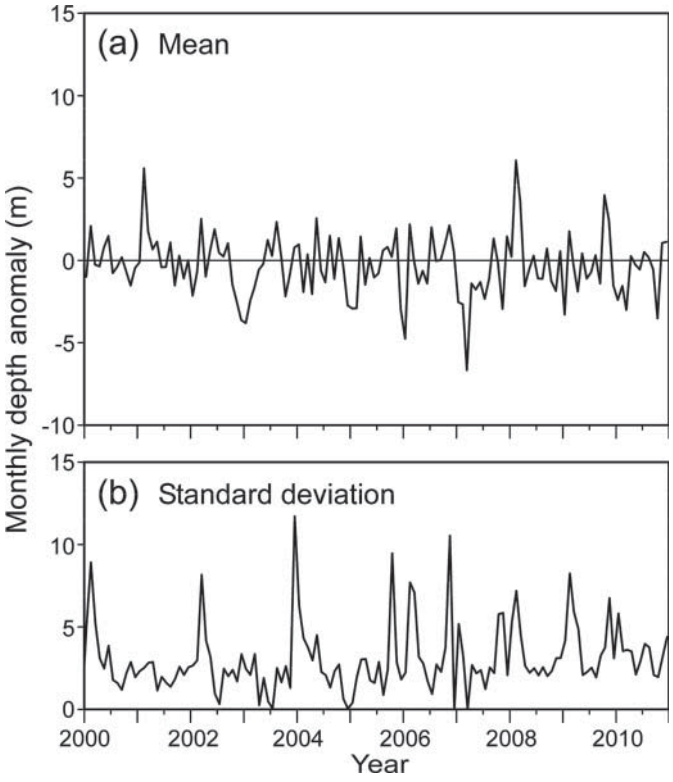


FIGURE 12. Monthly anomalies of pseudo–mixed layer depth for the period 2000 to 2011 based on density profile data collected by the Canadian Navy at the Nanoose Bay Test Range centered near 49.19°N, 124.00°W in the central Strait of Georgia (see Figure 1). Panel **(a)** shows the mean anomalies, panel **(b)** the corresponding standard deviations. The anomalies were obtained by subtracting the mean monthly values for the full observation period (1969–2010) from the monthly mean values. The term "pseudo" is used to describe the mixed layer depth because estimates may include the use of CTD observations which show no indication of a true mixed layer near the surface, either because the water is too stratified or the winds too weak for a true mixed layer to form (see text for further explanation). Similar mixed layer depth values were obtained using temperature and salinity profile data separately.

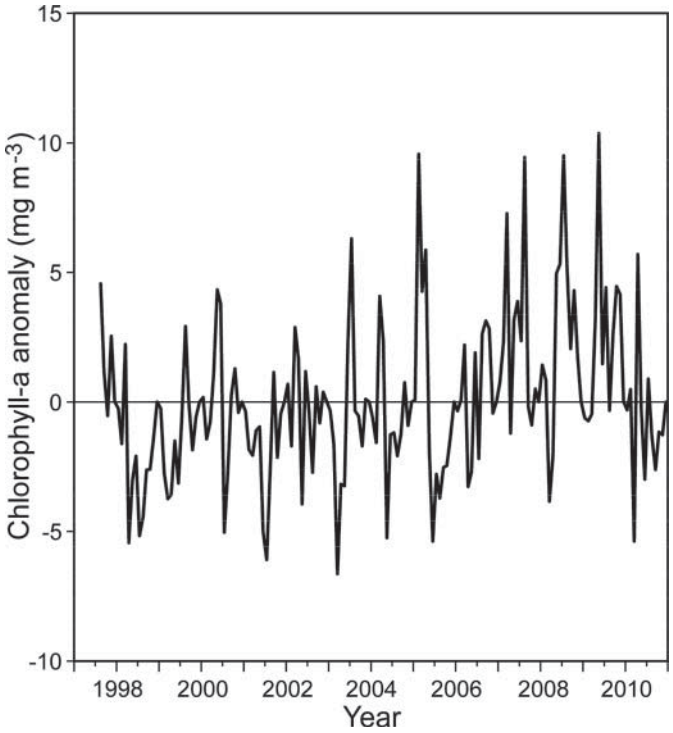


FIGURE 13. Monthly mean surface chlorophyll-*a* anomalies for the entire Strait of Georgia region. Gaps in the original 8-d series were interpolated using linear regression and a least-squares annual cycle obtained from the monthly data from 1997 to 2010 subtracted from the interpolated time series (G. A. Borstad and L. Brown, ASL Environmental Sciences)

sustained plankton production in the spring and summer. We expect that food levels for the migrating juvenile sockeye salmon stocks would have been considerably higher than those for the 2007 juveniles. The physical factors can account for the relatively high surface salinities observed throughout the strait in the early spring of 2008 (Figure 11a), for the deep to average pseudo–wind-induced mixed layer depths observed at Nanoose Bay in the central strait for that time period (Figure 12), and the delayed spring bloom in the Strait of Georgia that year (see Collins et al. 2009; Figure 13). The flushing mechanism would have been most effective during neap tides when turbulent tidal mixing within passages through the Gulf and San Juan islands exerts minimal "hydraulic control" on water exchange between the Strait of Georgia and Juan de Fuca Strait (Griffin and LeBlond, 1990; Masson and Cummins 2000; Thomson et al. 2007).

Effect of Gulf of Alaska Conditions on Salmon Survival

Plankton productivity in the Gulf of Alaska is maintained by the vertical flux of nutrients into the upper mixed layer in winter and early spring (Brodeur and Ware 1992; Ware and McFarlane, 1989; Thomson and Fine 2009). Westward propagating mesoscale eddies originating off northwestern British Columbia and southeastern Alaska (Tabata 1982; Thomson and Gower 1998) are also capable of delivering nutrients to the region (Ladd et al. 2009). Nutrient levels diminish through the summer and are renewed in winter through wind-driven upwelling of deep (>100-m), nutrient-rich waters below the permanent pycnocline (~100–200 m depth). Averaged over time and space, this upward winter flux of nutrients is dependent on the location and intensity of the Aleutian Low pressure system and the maximum depth of the surface mixed layer in late winter. Here, it is the curl of the wind stress associated with the cyclonic Aleutian Low and not the wind stress directly which determines the degree of upwelling (Cummins and Lagerloef 2002). In particular, the positive curl in the wind stress associated with the Aleutian Low leads to divergence of the surface wind-driven Ekman layer and an uplift of the subsurface isopycnal surfaces; a negative curl in the wind stress (such as that associated with the North Pacific High pressure system to the south) leads to convergence of the wind-generated surface Ekman layer and a depression of isopycnal surfaces.

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Based on the monthly mean property distributions presented in Figures 14 and 15, Fraser River sockeye salmon from the 2007 entry year would have spent their first marine winter in the Gulf of Alaska during a period of relatively low sea surface temperatures (SSTs) and moderately unfavorable winds associated with the 2007–2008 La Niña. These factors are assumed to have had a slightly negative effect on stock survival. While SST anomalies in the gulf were again negative in the second marine winter, wind conditions in the region were highly anomalous due to the extreme La Niña winter of 2008–2009, the second most intense La Niña recorded in the Pacific Ocean. The Aleutian Low shifted to the Bering Sea and anomalously weak cyclonic winds prevailed over the Gulf of Alaska from December 2008 through April 2009 (Figure 15b). This would have led to greatly

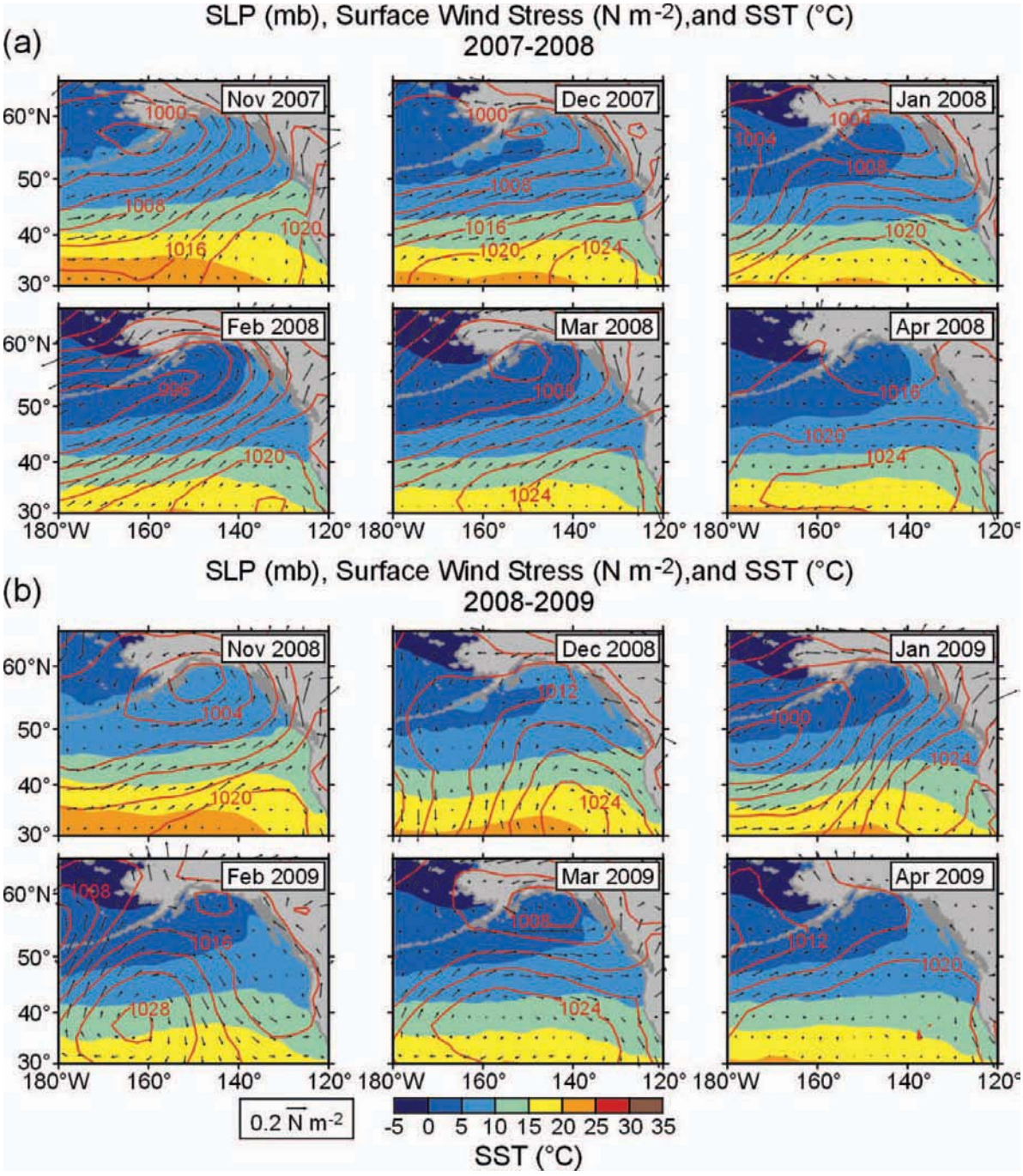


FIGURE 14. Monthly mean sea level pressure (SLP [mb]), sea surface temperature (SST [°C]; in color), and wind stress vectors for the winter periods November through April that stocks were in the Gulf of Alaska during **(a)** 2007–2008, **(b)** 2008–2009, **(c)** 2009–2010, and **(d)** 2010–2011.

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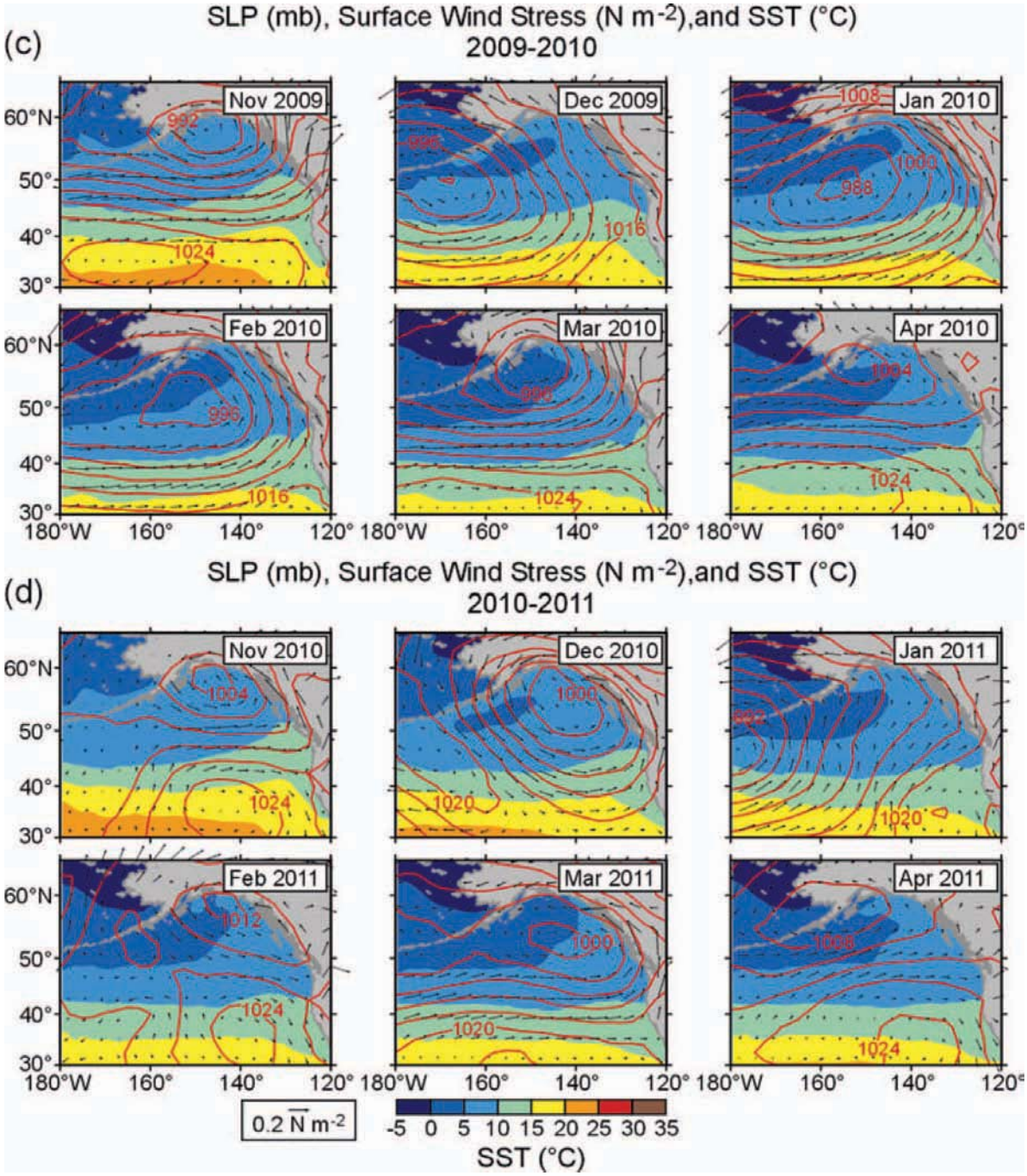


FIGURE 14. Continued.

reduced upwelling and possibly confused circulation in the region, both of which may have had a negative effect on Fraser River salmon stocks for both the 2007 and 2008 entry years.

The extreme La Niña winter of 2008–2009 was followed by the strong El Niño winter of 2009–2010, the most intense El Niño ever recorded for the central Equatorial Pacific. In addition to the higher than normal SST values along the coast of North America (Figure 14c), the anomalously intense Aleutian Low that accompanied the 2009–2010 event (Figures 14c, 15c) would have supported intensified wind-driven upwelling in the Gulf of Alaska. This would have helped lift nutrients (and, possibly, overwintering plankton) higher into the water column so that they were more readily entrained in the surface mixed layer. We assume that this enhanced plankton productivity in the ensuing spring and had a positive effect on the survival of the 2008 and 2009 marine entry stocks.

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DISCUSSION

We have estimated that about 14% more sockeye salmon smolts entered the Strait of Georgia from the Fraser River in 2008 than in 2007. However, trawl survey catches of juvenile sockeye salmon were approximately 400% larger in Queen Charlotte Sound and 1,800% larger in the Strait of Georgia in 2008 than in 2007. These comparisons between years and areas are problematic because of small sample sizes in Queen Charlotte Sound and sampling dates in the Strait of Georgia. Nonetheless, it does appear that the early marine survival in the Strait of Georgia was substantially greater in 2008 than in 2007, resulting in larger catches in the Strait of Georgia and in more fish surviving to travel into Queen Charlotte Sound in 2008.

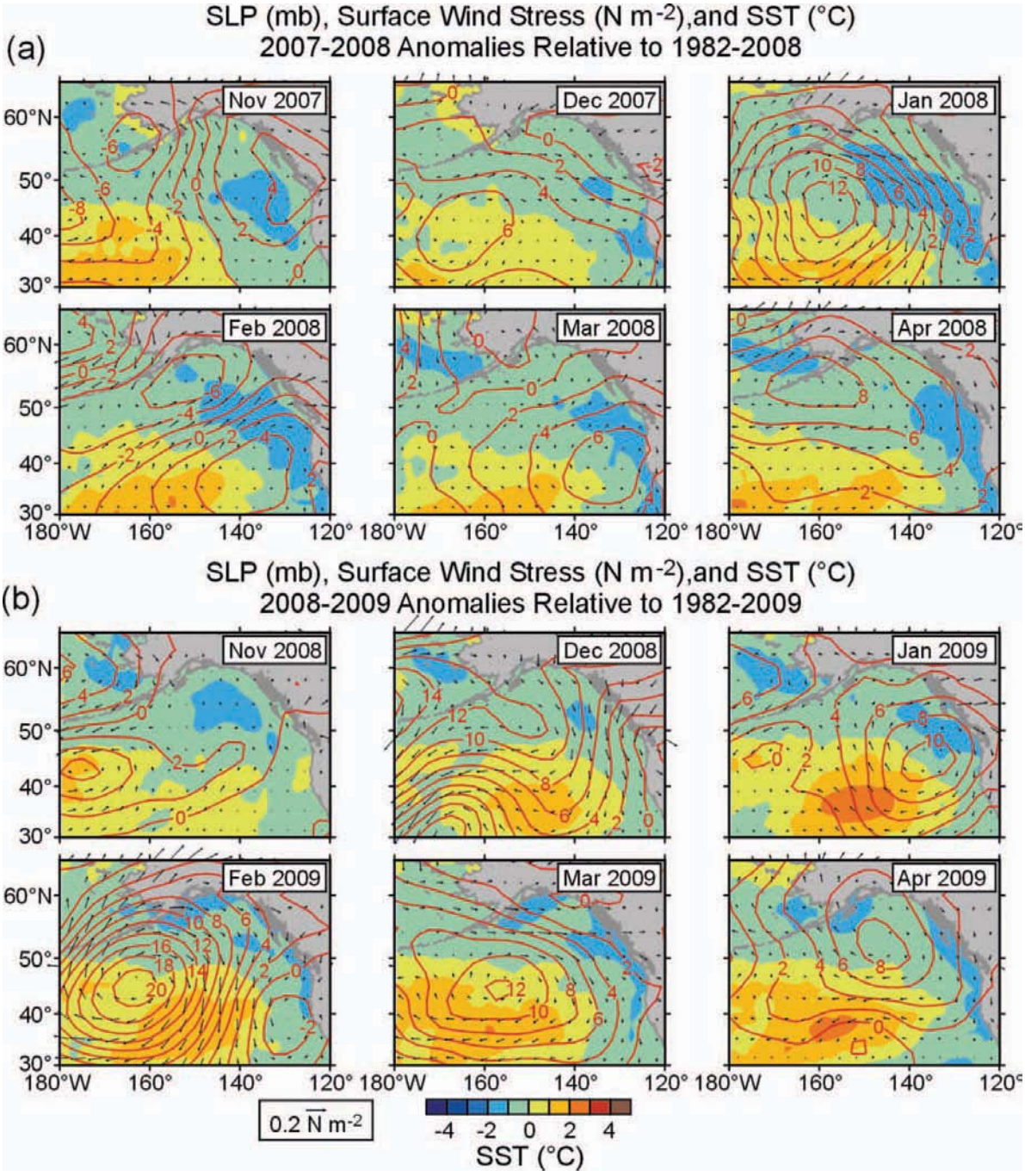


FIGURE 15. Anomalies in monthly mean sea level pressure (SLP [mb]), sea surface temperature (SST [°C]; in color), and wind stress vectors for the winter periods November through April that stocks were in the Gulf of Alaska during **(a)** 2007–2008, **(b)** 2008–2009, **(c)** 2009–2010, and **(d)** 2010–2011.

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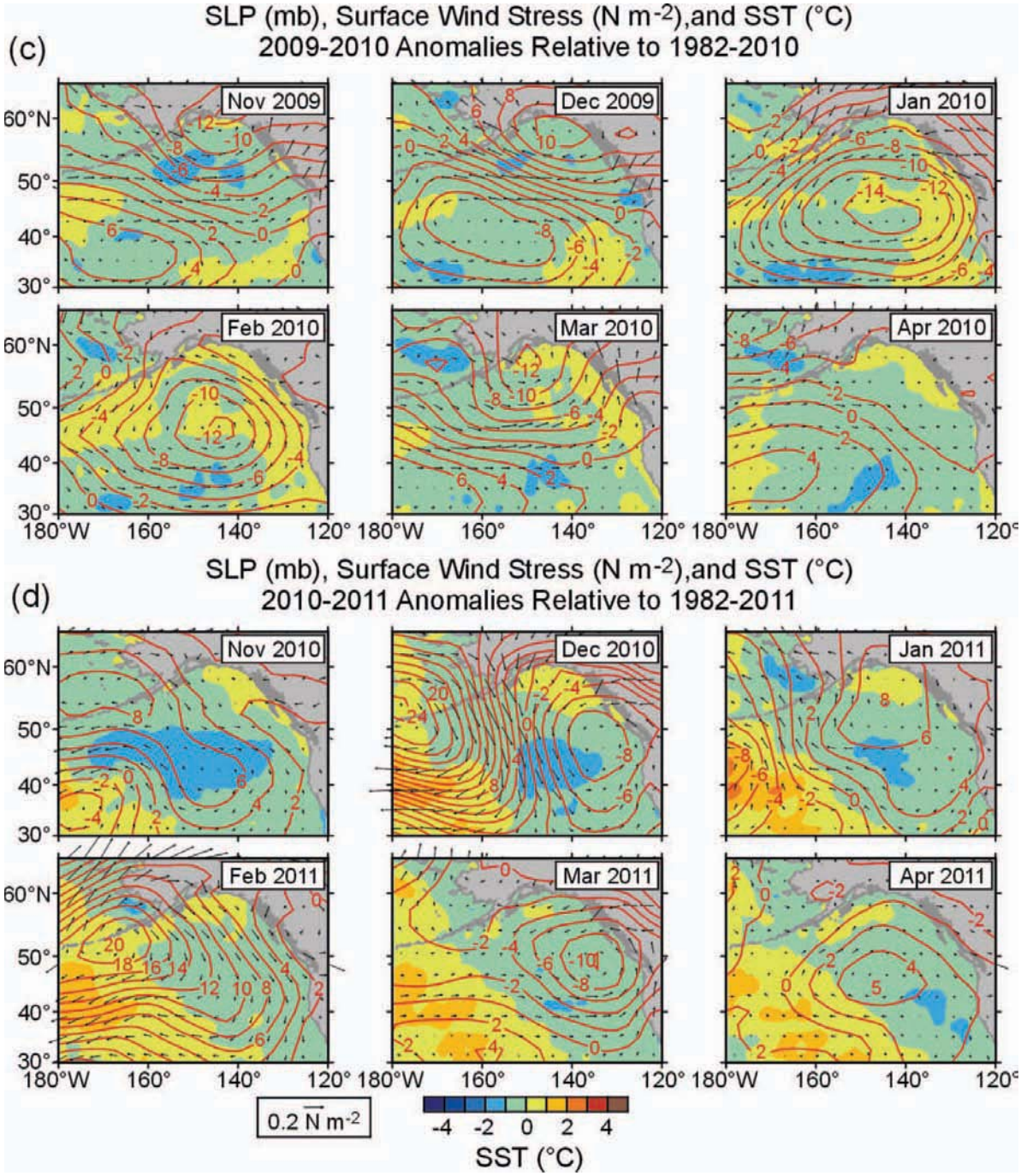


FIGURE 15. Continued.

The results of DNA analysis and the trawl catches in 2007, 2008, and 2009 show that juvenile sockeye salmon from the Fraser River are distributed from the Gulf Islands in the south to Hecate Strait in the north by late June and early July. This indicates that the migration out of the Strait of Georgia involves both dispersion throughout the Strait of Georgia and movement out of the strait. This pattern of migration also confirms that the patterns of juvenile sockeye salmon migration are complex and that all areas should be sampled repeatedly during the dispersal and migration phases. Until such studies are carried out, we are left to extrapolate from the existing data.

The catches of juvenile sockeye salmon in the trawls were much larger in 2008 than in 2007. Considering the relatively small (roughly 14%) difference in the smolts produced between the 2 years, we interpret the larger catches as representing much larger early marine survival. Moreover, ocean entry years 2007

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and 2008 produced adult returns that were dramatically different despite this apparent similarity in total smolt production. The total return of 1,443,000 adult fish from ocean entry year 2007 (return year 2009) was the lowest in history, while the total return of 29,600,000 adult fish from ocean entry year 2008 (return year 2010) was the highest in nearly 100 years. Beamish et al. (2012) find that all juvenile Pacific salmon *Oncorhynchus* spp. that entered the Strait of Georgia in 2007 and survived to the trawl survey in mid-July showed signs of encountering a major shortage of prey. Coho salmon *O. kisutch* and Chinook salmon *O. tshawytscha* were the smallest in the 11 years of research surveys, resulting in the lowest condition since the trawl surveys started in 1998. These fish also had the highest percentage of empty stomachs in the 11 survey years, indicating that they were probably having difficulty finding prey. The early marine survival for coho salmon from ocean entry until mid-September in 2007 was also very poor, which most likely explains the poor return of adults in 2008 (Beamish et al. 2012). Catches of juvenile chum salmon *O. keta* in the trawl surveys in the Strait of Georgia were the smallest in the 11 years of surveys. The low number of returning adult chum salmon to the Strait of Georgia in 2010 is consistent with very poor total survival, supporting the notion that the small catches in 2007 resulted from poor early marine survival. Perhaps the most convincing evidence of very poor conditions for juvenile fish survival in the surface 30 m of the Strait of Georgia in 2007 was the collapse of the 2007 year-class of Pacific herring *Clupea pallasii* (Beamish et al. 2012). Juvenile Pacific herring spawn in the spring, and juveniles remain throughout the Strait of Georgia for about 1 year. Routine surveys of juvenile Pacific herring in 2007 found very few young-of-the-year individuals. Samples of the stomach contents of juvenile Chinook and coho salmon in July 2007 had essentially no juvenile Pacific herring, indicating that most young-of-the-year herring had probably died before mid-July. Recruitment of the 2007 year-class of Pacific herring to the commercial fishery in 2010 was the lowest ever recorded, confirming that there was exceptionally poor survival of the young-of-the-year Pacific herring in the spring of 2007 (Cleary et al. 2009; Beamish et al. 2012).

Juvenile Pacific salmon and herring represent 98% of all the fish caught in the surface 30 m of the Strait of Georgia in the daytime trawls since 1998 (Beamish et al. 2012). Thus, the generally poor growth and/or poor survival of all juvenile Pacific salmon and herring in 2007 is convincing evidence of a major change in the Strait of Georgia ecosystem early that year. We propose that the ocean conditions described in this report resulted in a shift to exceptionally low production of the prey normally consumed by these fish during the critical early marine period for Pacific salmon. This is consistent with the generally accepted notion that it is during this early marine period that most of the marine mortality occurs for Pacific salmon and many other species of fish (Hjort 1914; Houde 1987; Pearcy 1992; Beamish and Mahnken 2001; Quinn et al. 2005; MacFarlane 2010), except that the conditions causing the mortalities in 2007 in the Strait of Georgia were extreme and possibly unique.

The juvenile sockeye salmon that were in the Strait of Georgia in late June and early July 2008 were smaller than those in 2007. The small size appears to be a consequence of the small ocean entry size compared with 2007. The small size of these fish could also result from an increased density of other competing species, as ocean entry year 2008 was also a year when there were large numbers of juvenile pink salmon *O. gorbuscha* entering the Strait of Georgia. If adjustments were made to standardize the lengths of trawl-caught fish with the ocean entry size of Chilko Lake smolts, the juvenile sockeye salmon in the Strait of Georgia in 2008 would be larger than the fish in 2007. We do not know whether using the lengths of Chilko Lake smolts in 2008 to standardize the average length of all smolts in the trawl catch would be representative of the population, but it is an indication that all juvenile sockeye salmon in 2008 grew more rapidly than the juveniles in 2007. If this standardization is representative of the population, then the juvenile Fraser River sockeye salmon that were distributed from the Strait of Georgia to Hecate Strait towards the end of June 2007 had the smallest size among the years 2007, 2008, and 2009. The exceptionally large adult return of pink salmon in 2009 of this brood year is evidence that conditions for marine survival for juvenile Pacific salmon were much improved in the spring of 2008. We note that the survival of juvenile Pacific herring was also much larger than in 2007 (Beamish et al. 2012).

The large numbers of smolts that were produced in freshwater in 2007 and 2008 would experience some mortality during their migration down the Fraser River, but there would still be hundreds of millions that entered the Strait of Georgia. It is to be expected that there will a large initial mortality in the Strait of Georgia. However, it is during the residence time in the Strait of Georgia of approximately 43–54 d (Preikshot et al. 2012) that we propose that many of the sockeye salmon that went to sea in 2007 died or became increasingly susceptible to sources of mortality because of their poor condition. Brood year strength is likely determined early in the marine period (Beamish and Mahnken 2001), even if the actual mortality occurs later, indicating that not all of the mortality would have to occur in the Strait of Georgia. Many of the juvenile sockeye salmon that survive their residence period in the Strait of Georgia presumably do not survive through the rest of the year and following winter because of their poor condition. It is not known how long the juvenile sockeye salmon are resident in Queen Charlotte Sound and Hecate Strait, but it is known that the juveniles migrate into the Gulf of Alaska, where they spend the first ocean winter. As indicated by our analyses, the 2007 entry year fish would also have experienced poor feeding conditions in Queen Charlotte Sound, Hecate Strait, and the Gulf of Alaska during their first and second winters, thereby exacerbating the poor survival conditions experienced in the Strait of Georgia. This interpretation is supported by studies showing that reduced early marine growth is also associated with increased overwinter mortality

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for coho salmon and pink salmon (Beamish et al. 2004; Moss et al. 2005). Farley et al. (2011) further show that the first marine winter also may be a critical period for juvenile sockeye salmon survival in the Bering Sea; years when the juveniles had low energy density were years when the brood year had low marine survival.

Rensel et al. (2010) suggest that mortalities of juvenile sockeye salmon in the Strait of Georgia in 2007 resulted from an accumulation of toxic algae. Toxic algae may have contributed to mortality in some areas of the Strait of Georgia; however, the nearly complete collapse of the 2007 Pacific herring year-class indicates that the cause of the generally poor survival of all juvenile fish in the surface 30 m must have been prevalent throughout the Strait of Georgia. Thus, the high mortality was probably due to a major failure of the production of prey required by juvenile Pacific salmon when they begin feeding in early spring in the Strait of Georgia. Rensel et al. (2010) show that from 1994 to 2007 there was a strong correlation between the total marine survival of Chilko Lake sockeye salmon and the early marine survival of age-0 Pacific herring in the Strait of Georgia. We suggest that this is additional evidence that conditions within the Strait of Georgia have a major influence on the brood year strength of Fraser River sockeye salmon. Furthermore, the relationship would indicate that the influence occurs from about mid-May until early July, when the Chilko Lake fish are in the Strait. It is likely during this time that most of the juvenile Pacific herring died.

The almost constant average catch of juvenile Fraser River sockeye salmon in 2007, 2008, and 2009 in Hecate Strait (Figure 4b) is difficult to explain, considering the variation in average catches in the other areas. On the other hand, the average catch was small relative to that in Queen Charlotte Sound, indicating that the fish that migrated into Hecate Strait were not a major percentage of the surviving population. The fish were also consistently larger than those in Queen Charlotte Sound and the Strait of Georgia. The large size, as well as the stock composition of the fish in Hecate Strait, may be a consequence of faster growth, older ages, or both. For example, approximately 5% of Chilko Lake sockeye salmon become smolts at 2 years of age and not at 1 year like most salmon (Henderson and Cass 1991). Chilko Lake sockeye salmon were estimated using DNA analysis to comprise 22% of the Fraser River sockeye salmon caught in Hecate Strait in 2007 and 29% of the Fraser River sockeye salmon caught in 2008, higher than the average 15–16% of Fraser River drainage escapement accounted for by the Chilko Lake population. Similarly, the Cultus Lake and Birkenhead River populations display higher proportions of 2-year-old fish than is typically observed in other populations. These two populations accounted for 11% and 4% of the Fraser River sockeye salmon sampled in Hecate Strait in 2007 and 2008, respectively, higher than would be expected based upon their relative contributions to drainage escapement. It thus seems likely that the Fraser River sockeye salmon sampled in Hecate Strait in June were derived disproportionately from populations where individuals display older ages and larger sizes at smoltification. Unfortunately, as ages were not determined for any of the individuals sampled, it was not possible to confirm that the individuals sampled in Hecate Strait in late June were typically older than those sampled in the Strait of Georgia in July. We suspect that the larger fish migrated out of the Strait of Georgia faster because of their size in freshwater, but this interpretation remains speculative until the age composition of the fish in Hecate Strait is determined. It is relevant that, in 2007, the percentage of sockeye salmon from the Fraser River in Hecate Strait was the smallest in the 3 years (Table 1), possibly indicating that there were fewer juveniles entering Hecate Strait from the Strait of Georgia in 2007 than in 2008 and 2009, which is consistent with the interpretation that there was a larger early marine mortality in the Strait of Georgia in 2007.

In 2009, the estimated production of sockeye smolts in the Fraser River drainage was about one-fifth that for 2007 and 2008. Juvenile sockeye salmon in the 2009 trawl survey displayed the largest body size of the 3 years in all areas. Unlike in 2007 and 2008, average catches in the Strait of Georgia were larger than those in Queen Charlotte Sound. Because of the limited number of sets in Queen Charlotte Sound, it is difficult to interpret the relatively large catch in the Strait of Georgia, other than to suggest that there had been a higher early marine survival or that the migration out of the Strait of Georgia in 2009 was later than in 2008. The average catch in the Strait of Georgia in 2009 was 58% larger than in Queen Charlotte Sound, perhaps indicating that the migration out of the strait was slower and that residence times vary.

Effects of Ocean Conditions on Salmon Survival

The effects of oceanic conditions on the survival of Fraser River sockeye salmon are expected to differ among the different coastal and offshore regions. These regions are examined in order of importance to marine survival.

Strait of Georgia.—Based on the winds recorded at Halibut Bank in the central Strait of Georgia (not shown but similar to the events shown in Figure 8 for the outer coast), winds capable of flushing brackish water from the Strait in the spring of 2007 occurred only during short-term events in late March and mid-May 2007 (data from mid-May to mid-June are missing). The first prolonged event did not occur until the first half of July, after most of the fish had left the strait. The wind events in the spring of 2007 occurred during periods of waning spring tides, so it is possible that the flushing events, which would help reduce surface stratification in the strait, were partially blocked by strong mixing in the passes (Griffin and LeBlond 1990). Thus, it appears that winds in early 2007 were unable to break down the intensified surface stratification, resulting in shallowly confined plankton growth at the time the juvenile sockeye salmon were entering the strait that year. The shallow mixing layer and thinly distributed plankton biomass in the spring of 2007 could have led to low sockeye prey concentrations during the 2007 entry year and ultimately contributed to the historically low returns

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in 2009. Although highly speculative, it is also feasible that the low surface salinity in 2007 served as a stressor that triggered an enhanced autoimmune response to possible diseases carried by the smolts as they migrated downstream from the spawning grounds to the marine environment (Miller et al. 2011). Response to disease would have further compromised the health of the out-migrating stocks. While disease may have been a contributor to the mortality of sockeye salmon in 2007, it is important to note that there were also exceptionally large mortalities of juvenile Pacific herring, which hatched throughout the Strait of Georgia that year.

In the spring of 2008 there were numerous northwesterly wind events, so that the freshwater was flushed out on a more regular basis, diminishing the surface stratification (and possibly the light-absorbing surface fluvial silt concentration), thereby enabling plankton growth over a greater depth range. The moderate northwest winds, combined with low runoff, would have given rise to a relatively deep mixing layer and, presumably, relatively high food production in the late spring and summer of 2008. Unlike in 2007, the smolts entering the strait in 2008 were less likely to have been compromised by a lack of prey prior to their northward migration through the strait.

Queen Charlotte Sound–Hecate Strait.—The ocean conditions that negatively impacted the juvenile Fraser River sockeye salmon within the Strait of Georgia in the spring of 2007 also negatively impacted the surviving fish that entered the central coastal waters. The persistent southeasterly winds that prevailed within southeastern Queen Charlotte Sound at that time (Figure 10b) would have driven the surface waters northward into Hecate Strait (Hannah et al. 1991), generating low salinities (Figure 11b) and presumably strongly stratified surface waters along the eastern boundary of the sound. As a consequence, freshwater entering the sound from the mainland rivers would not have contributed significantly to the salinity structure and establishment of an optimally deep mixed layer depth (see Gargett 1997) in the central and seaward portions of the sound where the juvenile fish were migrating. Thus, in contrast to the situation in the Strait of Georgia, southerly winds over the central coast led to weak vertical stratification and a less than optimally deep surface mixed layer in Queen Charlotte Sound. This argument is consistent with the low surface chlorophyll concentrations reported throughout southern Queen Charlotte Sound in April and May 2007 (Borstad et al. 2011). The reverse conditions would have occurred during the northerly to light southerly winds and relatively low runoff (Figure 9c, d) that prevailed in the late spring of 2008. These winds would have made it easier for brackish surface water emanating from the mainland inlets to move seaward toward the entrance to Queen Charlotte Sound (Figure 1), leading to the vertical entrainment of nutrients and aiding in the establishment of a more optimally favorable mixed layer depth. Formation of a moderately deep surface mixed layer in Queen Charlotte Sound would be conducive to high plankton productivity. The seaward flushing of high chlorophyll concentration surface waters from the inlets is likely to have contributed to high productivity in the region (G. Borstad, ASL Environmental Sciences, Inc., personal communication).

Gulf of Alaska.—The juvenile Fraser River sockeye salmon that survived the 2007 marine entry period likely had low lipid reserves due to the adverse conditions they had encountered in British Columbia coastal waters. These fish would have been stressed even further as a result of the poor ocean conditions that prevailed in the Gulf of Alaska in the winters of 2007–2008 (a moderate La Niña winter) and 2008–2009 (a strong La Niña winter). Although adult fish from the 2008 entry year would also have been negatively impacted by the strong La Niña winter of 2008–2009 in the gulf, their healthier condition as juveniles and the favorable ocean conditions they subsequently encountered during the intense El Niño winter of 2009–2010 would have contributed to their record returns in 2010. Based on this proposition, it is possible that returns in 2010 would have been even higher had the winter of 2008–2009 in the gulf been less extreme. We further propose that relatively healthy fish from the 2009 entry year were positively affected by the intense El Niño event of 2009–2010 (Figure 15c) but only marginally affected by the moderate La Niña event of 2010–2011 (Figure 15d). This may account for what preliminary results indicate is at least an average return of sockeye salmon to the Fraser River in 2011.

As indicated by Figure 16, the atmospheric conditions in the Gulf of Alaska in the La Niña winter of 2008–2009 (as well as the winters 2006–2007 and 2007–2008) coincided with a high positive North Pacific Index (NPI; Trenberth and Hurrell 1994), whereas the El Niño winter of 2009–2010 coincided with a high negative index. (A high NPI indicates higher than average sea-level pressure over the Gulf of Alaska and, in winter, a

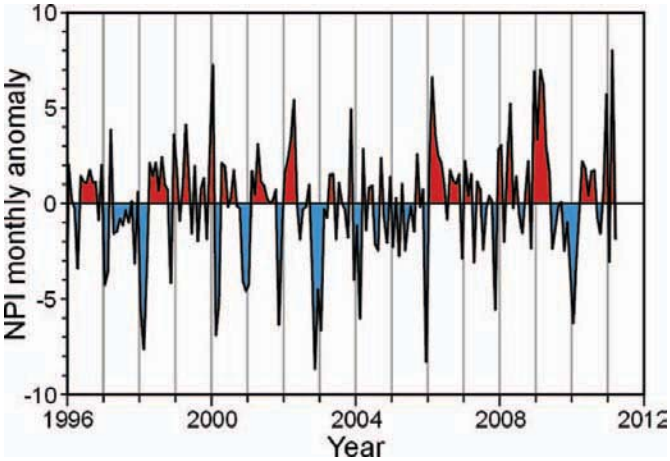


FIGURE 16. North Pacific Index (NPI) anomalies for the period 1996–early 2012. The index is the area-weighted sea level pressure over the region 30°N–65°N, 160°E–140°W. Data are from the Climate Analysis Section, National Center for Atmospheric Research, Boulder, Colorado, and Trenberth and Hurrell (1994); they can be obtained from: http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html.

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weaker than average Aleutian Low, and conversely for a low NPI). Thus, winter conditions in the Gulf of Alaska for the three lowest Fraser River sockeye salmon return years (ocean entry years 2005, 2006, and 2007) coincided with a positive NPI and major displacements of the Aleutian Low pressure system and associated winds during the winter preceding their return. The slightly positive index values recorded in the winter of 2010–2011 (Figure 16) suggest a marginally negative open ocean effect on the returns of Fraser River sockeye salmon in the summer of 2011.

Summary

According to our findings, there is a strong link between the extremes in Fraser River sockeye salmon production in 2009 and 2010 and the occurrence, 2 years earlier, of highly anomalous environmental marine conditions in British Columbia coastal waters. Wind forcing, river discharge, and surface stratification for the Strait of Georgia and Queen Charlotte Sound–Hecate Strait regions in spring appear to have been the most critical factors determining the health and survivability of the juveniles once they enter marine waters. Low production begins with the occurrence of high freshwater runoff, a delayed spring transition (continuation of persistent southerly winds), and pronounced surface stratification during the first few months that the fish enter the coastal ocean. Such adverse ocean conditions mean that even favorable ocean conditions in the Gulf of Alaska during the next two winters are unlikely to improve the brood year strength. Conversely, high production is possible provided the stocks initially encounter favorable coastal ocean conditions arising from relatively low freshwater runoff, an early spring transition (onset of northerly winds), and reduced surface stratification. In the latter case, the ocean conditions in the Gulf of Alaska during the first and/or second winter may have a secondary impact (positive or negative) on the overall brood year strength.

The highly anomalous ("negative") ocean conditions that prevailed within the coastal waters of British Columbia in the spring of 2007 probably greatly reduced food availability for, and consequently the survivability of, migrating Fraser River juvenile sockeye salmon for the 2007 marine entry year. Anomalously weak or reversed cyclonic winds in the Gulf of Alaska during the ensuing winters (as in the case of the weak-to-moderate La Niña of 2007–2008 and the extreme La Niña of 2008–2009 for the 2007 entry year) also would have contributed to the poor sockeye salmon return to the river in 2009. In contrast, the highly anomalous ("positive") ocean conditions that prevailed within the coastal waters in the spring of 2008 led to relatively high food levels and well-nourished and healthy juvenile salmon. The Fraser River sockeye salmon that entered the coastal marine waters in 2008 then encountered an intense Aleutian Low in the central Gulf of Alaska during the first ocean winter (the strong El Niño winter of 2009–2010), which likely contributed to the high returns to the Fraser River in 2010.

Our findings clearly distinguish between fish–ocean interaction in the first marine year (when the fish enter the estuarine environments of coastal British Columbia and Alaska) and fish–ocean interactions in the two subsequent years (when the fish are in the Gulf of Alaska). Moreover, because the winds and runoff associated with the spring transition along the West Coast of North America have large spatial and temporal footprints, and because outer coastal waters respond much differently to these physical factors than inner coastal waters, our findings are not inconsistent with the observed differences in adult returns between the Fraser River sockeye salmon stocks and the Columbia River and Barkley Sound stocks. Specifically, a delay in the spring transition along the outer coast is not necessarily problematic for the survival of West Coast sockeye salmon stocks. Although such a delay translates into a delay in coastal upwelling and a corresponding delay in spring plankton production, there is also a delay in the formation of the southward flowing shelf-break current, a delay in the reduction in the northwestward flow of the buoyancy-driven Vancouver Island Coastal Current along the inner shelf of Vancouver Island (Thomson et al. 1989; Hickey et al. 1991; Thomson and Hourston 2011), and a delay in the offshore or southward redirection of the poleward moving Columbia River plume off the coasts of Washington and Oregon (Hickey et al. 1998). As a consequence, fish stocks migrating northward in these flow regimes have an energetic advantage that might offset any possible reduction in food sources caused by a delay in the spring transition. Regardless of which mechanism dominates, the survival and returns of Columbia River and Barkley Sound stocks can be expected to differ from those of stocks originating from the Fraser River.

This study generally supports the "critical size–critical period" hypothesis of Beamish and Mahnken (2001) and leads to a testable hypothesis for sockeye salmon production for the Fraser River stocks. We propose that it should be possible to combine environmental time series (coastal river discharge, winds, and vertical stratification) and escapement numbers with early marine survival data for the Strait of Georgia and Queen Charlotte Sound–Hecate Strait region to forecast returns to the river up to a year in advance.

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APPENDIX

Surface Salinity Anomalies in the Strait of Georgia

In the spring and early summer of 2007, the monthly freshwater discharge anomalies for the Strait of Georgia ranged from roughly 500 to 3,000 m^3/s. Using a conservative value of 1,000 m^3/s yields a seasonal (3-month) discharge volume anomaly of 7.8 km^3. This compares with a volume of 150 km^3 for the upper 30 m of the entire strait (confer Table 3 in Thomson and Foreman 1998). Here, 30 m is a representative depth for the surface brackish layer within the strait (Thomson 1994). If we assume that 50% of this water is retained in the strait on a seasonal basis and that the freshwater is uniformly mixed over the 30 m, we obtain a volume ratio of 0.026. Multiplying this ratio by a mean salinity for the upper layer of the strait of around 32 practical salinity units (psu) yields a basinwide, seasonally integrated salinity anomaly of roughly –0.8 psu. This anomaly increases to –1.6 psu if we assume that the freshwater is mixed linearly (rather than uniformly) over the 30-m depth range. These estimates are consistent with the –1 to –2 psu anomalies in surface salinity observed at the coastal lighthouse stations (Figure 11a).

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