

**Anomalous ocean conditions may explain the recent extreme variability  
in Fraser River sockeye salmon production**

by

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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 develop a conceptual model that links oceanic factors and the survival of Pacific salmon stocks. The low returns in 2009 indicated poor early marine survival of juvenile salmon in 2007. This poor early marine survival was likely due to low food levels arising from unfavourable wind and river discharge 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 due to adequate food levels arising from favourable wind and runoff conditions in the Strait of Georgia and Queen Charlotte Sound-Hecate Strait region in the spring of 2008. Ocean factors during the subsequent marine years may also have affected brood year strength. Specifically, we propose that the extreme La Niña winter of 2008-09 negatively influenced survivability of the 2007 and 2008 entry stocks while the extreme El Niño winter of 2009-10 positively affected 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 most one of the two ocean winters in the Gulf of Alaska are unfavourable to stock survivability, then returns to the Fraser River are likely to be high. These causal relationships between the physical environment and fish survivability make it possible to predict returns of Fraser River sockeye up to several years in advance.

## INTRODUCTION

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 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 one year after they emerge from the gravel redd. They then enter the Strait of Georgia (Figure 1) over a two-month period from late March until late May (Preikshot et al., 2011) and subsequently move northward through the Strait of Georgia over five to six weeks ranging from roughly mid-May to mid-July (Beamish et al., 2011; Preikshot et al., 2011). 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., 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 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). Based on Healey (1980), this change would have occurred sometime between the mid-1970s and early 1980s.

As with other adult sockeye salmon, total returns of Fraser River stocks are highly variable throughout their distribution region 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 the “big year” 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-induced freshwater and ocean variability. The most extreme variability in adult returns occurred between years 2009 and 2010, corresponding to the 2005 and 2006 brood years, and ocean entry years of 2007 and 2008, respectively. For 2009 and 2010, the expected returns were in the range of 10 to 11 million fish, whereas the actual returns were about 1.4 million and 29.6 million fish, respectively. The returns in the fall of 2010 (which include dominant-year Late-run Adams River fish) established a record high return of Fraser River stocks; the poor returns in 2009 led to a commission of inquiry ([www.cohencommission.ca](http://www.cohencommission.ca)).

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) that 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. Subsequent studies have shown that reduced early marine growth is associated with increased over-winter mortality for coho salmon (*O. kisutch*) and pink salmon (*O. gorbuscha*) (Beamish et al., 2004; Moss et al., 2005). A recent study (Farley et al., 2011) indicated that the first marine winter may be a critical period for juvenile sockeye salmon survival in the Bering Sea; years when the juvenile sockeye salmon had low energy density were years when the brood year also had low marine survival. 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 adult return years 2009 and 2010, respectively. The numbers of returning adults can be used to estimate the survival of the smolts through to the adult stage. Most mortality is thought to occur in marine waters, but some occurs during migration within the river system.

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. Production from this drainage system averaged 18.8% of the total returns to the Fraser River over the past 50 years. The number of sockeye salmon smolts leaving the drainage is estimated each year. 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 Fraser River drainage region enables us to calculate the total sockeye salmon smolt production for the drainage region for the two years. A second method uses a proportional estimate of production. For example, if sockeye salmon originating from

Chilko Lake represented 10% of all adults returning to the Fraser River, then the number of smolts leaving the lake two years earlier would be 10% of all smolts produced. The method assumes that freshwater rearing conditions are similar for all populations and that marine survival is similar for all populations. (The numbers of smolts produced in 2009 could only be estimated using the second method as estimates of marine survival will not be available until the fall of 2011.) 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 mid-water trawl net had an approximate 30 m-wide, 15 m-deep opening and was fished for 30 min at an average speed of  $2.6 \text{ ms}^{-1}$  (5 knots) with head rope 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. 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. Stock composition of sockeye salmon in the trawl catches was determined with microsatellite DNA (see 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 ( $1.9^\circ$  latitude  $\times 1.9^\circ$  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 ( $1^\circ$  latitude  $\times 1^\circ$  longitude) monthly mean Optimum Interpolation (OI) SST Version-2 data (Reynolds et al., 2002). We also examined monthly mean satellite-derived chlorophyll (ocean colour) time series for British Columbia coastal waters derived from the Seaviewing Wide Field-of-view Sensor (SeaWiFS) and Moderate Resolution Imaging Spectroradiometer (MODIS) (G. Borstad and L. Brown, pers. comm., 2011). 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 (cf. 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,  $\rho_{air}$  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, 2007). 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. To obtain a second estimate of smolt production, we note that the Chilko Lake smolts that went to sea in 2007 had an estimated total marine survival of 0.3%. 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.

In 2008, a total of 73,000,000 sockeye salmon smolts was counted leaving Chilko Lake. As with 2007, this was roughly twice the previously recorded high. The percentage of Chilko Lake sockeye salmon in the 2006 escapement was 15.2%. Using this percentage to determine the total smolt production, we estimate that 480,565,000 sockeye salmon smolts were produced in the Fraser River drainage in 2008. A second value is obtained from an estimate that the Chilko Lake sockeye salmon smolts that went to sea in 2008 had a marine survival of 5.4%. Assuming that this marine survival is representative of all stocks, we calculated that 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 were 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.

***Average catches of juveniles and stock composition in the trawl surveys (2007-2009)***

In 2007, seventy-four trawl sets were conducted in the Strait of Georgia from July 8 to 15. Twenty-one of these sets captured juvenile sockeye salmon and 53 had zero catch. All 65 fish were caught in the 0 to 15 m stratum. No individuals sampled were analyzed for stock composition. The average catch in the surface 15 m was 1.8 juvenile sockeye salmon per 30-min set (Figure 3a).

In 2008, ninety 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%) was captured in the 0 to 15 m depth range and 65 fish (4%) in the 15 to 30 m depth range. The average catch in the surface layer was 34.0 sockeye salmon per 30-min set (Figure 3a). A total of 179 fish was analyzed for stock composition and all (100%) were from the Fraser River. The stock composition according to run timing was: late 73%, early summer 20%, and summer 7% (Figure 4a). Similar compositions were obtained for the Gulf Island region (Figure 4b). These

percentages were generally similar to the expected run timing percentages for the adult return for this brood year (Figure 4e); specifically, late 82%, early summer 9%, summer 8%, and early Stuart 1%.

In 2009, a total of 83 trawls sets was 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 (86%) captured in the surface layer (0-15 m) and 218 (14%) in the 15 to 30 m depth range. The average catch in the surface layer was 33.9 fish per 30-min set (Figure 3a). A total of 141 fish was analyzed for stock composition for the Strait of Georgia and all were from the Fraser River. The stock composition according to run timing was summer 51%, late 30%, early summer 18%, and early Stuart 1% (Figure 5a). As with the stock composition for the Gulf Islands (Figure 5b), the expected percentages for adults from this brood year were summer run 47%, late run 37%, early summer run 15%, and early Stuart run 1% (Figure 5f).

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 Hecate Strait, which had relatively little variation in the average catch for the three years (Figure 3b), there was almost a four times increase in the average catch in Queen Charlotte Sound in 2008 compared to 2007 and 2009 (Table 1; Figure 3c), suggesting that more juvenile fish survived the travel from the Strait of Georgia. In 2009, the average catch in the Strait of Georgia was 58% larger than in Queen Charlotte Sound.

There were no samples collected for DNA analysis in the Strait of Georgia in 2007; however, in Queen Charlotte Sound, summer stocks represented about 2/3 of the sample with the remaining stocks about equally distributed among the early Stuart, early summer and late run stocks. The observed stock compositions in Queen Charlotte Sound and Hecate Strait in 2007 (Figure 6a,b) were almost identical, and these were generally similar to the expected stock composition (Figure 6c). In 2008, the stock composition in Queen Charlotte Sound (Figure 4c) was generally similar to the composition in the Strait of Georgia (Figure 4a). However, the stock composition of the sample in Hecate Strait (Figure 4d) 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 the Strait of Georgia and the Gulf Islands. In 2009, the stock composition in Queen Charlotte Strait and Hecate Strait (Figures 5c,e) was generally similar to the composition in the Strait of Georgia region (Figures 5a,b) whereas those in Queen Charlotte Sound (Figure 5d) were different from those in the Strait of Georgia.

#### *Size of juvenile sockeye salmon in the trawl catches*

Juvenile sockeye salmon in the trawl catches in the Strait of Georgia and Queen Charlotte Sound in 2007 were the smallest in the study years and were not significantly different between the two areas ( $t$  test,  $p \geq 0.05$ ; Table 2). Juvenile sockeye salmon were the smallest in each area in 2007 for all years studied (ANOVA,  $p \leq 0.05$ ). In all years, the juvenile sockeye salmon in the catches in Hecate Strait were significantly larger than in all other areas (ANOVA,  $p < 0.05$ ).

### *Timing of the Spring Transition*

Although details vary from region to region, meteorological time series for the west coast of British Columbia (Figure 7) 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 two years earlier (i.e., at the times of marine entry in years 2005, 2006 and 2007, respectively) (Figure 7). In each of these three years, the “Spring Transition” from predominantly northward directed (i.e., “southerly”) winds in winter to predominantly southward directed (i.e., “northerly”) winds in summer (cf. Strub et al., 1987; Thomson and Ware, 2005), was delayed by about one month relative to the twenty-year mean of mid-April. 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 7 that the reversal to northerly winds in 2008 occurred up to several months earlier than normal (Table 3). In 2008, the prevailing northerly wind that followed the transition was generally stronger than those for other years.

The Spring Transition is generally followed by a reduction in rainfall and cloud cover, and 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 (Figure 8) 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. 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 8a) becomes dominated by snowmelt-derived discharge from the Fraser River. Similar wind and runoff conditions apply to the Queen Charlotte Sound and Hecate Strait regions (Figure 8b). 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 away from the 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 between return years 2009 and 2010, we focused on oceanographic and metrological variables observed in the spring entry years of 2007 and 2008, respectively. Several major features emerge from the various environmental time series. 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 into the Strait from both the mainland and Vancouver Island side of the basin in the spring of 2007 but anomalously low runoff into the Strait from these regions in the spring of 2008 (Figures 8a,b); (2) prolonged southeasterly wind forcing in the Strait from during the spring of 2007 in contrast to moderate northwesterly wind forcing over the Strait during the spring of 2008 (Figure 9a); and (3) exceptionally low surface salinities throughout the Strait of Georgia from May through November 2007 compared to anomalously high surface salinities in the Strait from February through June 2008 (Figure 10a). Similar conditions were observed in Queen Charlotte Strait and in the Queen Charlotte Sound-Hecate Strait region (Figures 8c,d; 9b, and 10b). We note that persistent southeasterly winds also prevailed along the coast in the spring of the low production marine entry year 2005 (but not the low production year 2006); marine entry years 2009 and 2010 were marked by moderate northwesterly wind conditions similar to those in the high production entry year 2008 (Figure 9a). The winter and spring of 2007 were noteworthy for their anomalously high rainfall and relatively few hours of bright sunshine (A. McCarthy, Environment Canada, 2011, pers. comm.).

As noted previously, the persistent southeasterly winds and high runoff that prevailed over the Strait of Georgia and Queen Charlotte Sound-Hecate Strait region in early 2007 would have facilitated the northward transport and, in the case of the Strait of Georgia, the storage of silt-laden river runoff within the upper layer of the Strait. These accumulative effects, which generally began occurring before the time that juvenile Fraser River sockeye salmon were resident in the different regions, likely account for the



anomalously low surface salinities observed throughout much of the region that spring and summer (Figure 10). Freshwater retention in the Strait of Georgia also accounts for the magnitudes of the observed surface salinity anomalies (see Appendix A) 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 11). The shallow mixed layer was unprecedented in its timing and duration for the period 1980 to 2010 for which we have near continuous data. Moreover, satellite-derived chlorophyll data for the Strait of Georgia for the period 1997 to 2010 (Figure 12) reveal an early (February-March) bloom in the Strait in 2007, consistent with Collins et al. (2009) modeling results that link 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 12), the February-March bloom took place too soon to be utilized by zooplankton in the Strait 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. Chlorophyll levels in the Strait of Georgia in the spring of summer of 2005 were also anomalously low. 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 retention of brackish surface water presumably increased the surface stratification and reduced the downward light penetration into the euphotic layer of the

396 Strait of Georgia. Increased stratification also would have led to reduced vertical mixing  
397 and weaker entrainment of nutrient-rich water from the underlying marine layer, limiting  
398 the duration and vertical extent of upper layer primary productivity. These factors, in  
399 conjunction with reduced light penetration, may have confined plankton growth within a  
400 shallow (and therefore relatively low, depth-integrated biomass) surface layer around the  
401 time that the smolts were entering the strait. The cloudy and overcast “winter” skies that  
402 typically precede the Spring Transition also may have helped confine plankton  
403 productivity to a relatively shallow surface layer in the Strait. (We note that the same  
404 physical processes can lead to different responses for the central coast and west coast of  
405 Vancouver Island, as outlined in the Discussion.)

406  
407 In contrast to 2007, the more northwesterly winds and low runoff in the Strait of  
408 Georgia and Queen Charlotte Sound-Hecate Strait regions in the spring of 2008 (Figures  
409 8c,d, 9b) were conducive to the flushing of somewhat more saline, less stratified surface  
410 waters towards the open ocean. In the case of the Strait of Georgia, flushing of brackish  
411 surface waters seaward through passes between the Gulf and San Juan islands would have  
412 increased light levels in the surface of the Strait and allowed deeper wind mixing to more  
413 easily entrain nutrients into the upper layer of the basin, possibly leading to more  
414 vertically extensive and sustained plankton production in the spring and summer. We  
415 expect that food levels for the migrating juvenile sockeye salmon stocks would have been  
416 considerably higher than for the 2007 juveniles. The physical factors can account for the  
417 relatively high surface salinities observed throughout the strait in the early spring of 2008  
418 (Figure 10a), for the deep to average pseudo wind-mixed depths observed at Nanoose

Bay in the central Strait for that time period (Figure 11), and the delayed spring bloom in the Strait of Georgia that year (cf. Collins et al., 2009; Figure 12). 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 volume 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 NW British Columbia and SE 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 ( $\sim 100$  to 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 windstress associated with the cyclonic Aleutian Low and not the windstress directly which determines the degree of upwelling (Cummins and Lagerloef, 2002). In particular, the positive curl in the windstress associated with the Aleutian Low leads to divergence of the surface wind-driven Ekman layer and upwelling of the subsurface isopycnal surfaces; a negative curl in the windstress (such as that within the North Pacific High

pressure system in the subtropical Pacific) leads to convergence of the wind-generated surface Ekman layer and downward movement of isopycnal surfaces.

Based on the monthly mean property distributions presented in Figures 13 and 14, Fraser River sockeye salmon from the 2007 entry year would have been in the Gulf of Alaska during relatively low SSTs and moderately unfavourable upwelling wind conditions during the winter of 2007-08 (their first marine year). We assume these factors 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 2008-09, 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 14b). This would have led to greatly reduced upwelling and presumably confused circulation in the region, which we assume had a negative effect on Fraser River salmon stocks from both the 2007 and 2008 entry years.

The extreme La Niña winter of 2008-09 was followed by the strong El Niño winter of 2009-10, 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 13c), the anomalously intense Aleutian Low that accompanied the 2009-10 event (Figures 13c and 14c) would have supported intensified wind-driven upwelling in the Gulf of Alaska. This would have helped lift nutrients (and, possibly, overwintering plankton) higher in the water column so that they were more readily entrained in the

surface mixed layer. We assume that this led to great plankton productivity in the ensuing spring and had a positive effect on the survival of the 2008 and 2009 marine entry stocks.

## **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 Queen Charlotte Sound in 2008.

Trawl catches in all areas 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 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 residence time of juvenile sockeye salmon in the Strait of Georgia is not well

known. Preikshot et al. (2011) show that the average residence time is approximately 35 days. The average maximum number of smolts passing by Mission in the lower Fraser River, about 80 km from the Fraser River estuary, presently occurs on May 6. The average date at which 5% and 95% of the smolts pass Mission is approximately April 23 and May 28, respectively. Thus, it takes an average of 37 days for 90% of the sockeye salmon smolts to leave the Fraser River. The maximum number of juvenile sockeye salmon in the Strait of Georgia has been estimated to be June 12 while the average date when virtually all lake-type juveniles (about 98% of all life history types are lake type) leave the Strait of Georgia is July 12. Thus, on average, it takes about 32 days from the maximum smolt abundance in the strait until all juvenile sockeye salmon have died or left the Strait of Georgia. During this time juvenile sockeye salmon remain and grow in the Strait of Georgia (Preikshot et al. 2011.). Over an average residence time of about five weeks, juvenile sockeye salmon would be exposed to conditions within the Strait of Georgia that would affect their growth, condition, and survival.

***What was unusual about juvenile fish survival in the Strait of Georgia in 2007?***

The ocean entry years of 2007 and 2008 produced adult returns that were dramatically different despite the apparent similarity in total smolt production. The total return of 1,443,000 fish from the ocean entry year of 2007 (brood year of 2005 and return year of 2009) was the lowest in history while the total return of 29,600,000 fish from ocean entry year 2008 (brood year of 2006 and return year of 2010) was the highest in nearly 100 years. In Beamish et al. (2011), it is shown that all juvenile Pacific salmon that entered the Strait of Georgia in 2007 and survived through to the trawl survey in mid-

July showed signs of encountering a major shortage of prey. Coho and chinook salmon were the smallest in the eleven years of research surveys, resulting in the lowest condition since the trawl surveys started in 1998. These fish also had either the highest or second 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 was also the lowest in the odd-numbered survey years. (There are virtually no juvenile pink salmon in the Strait of Georgia in odd-numbered years). In 2008, when the adult coho salmon returned to the rivers flowing into the Strait of Georgia, the estimated marine survival was extremely poor and the lowest on record (Beamish et al., 2011). These observations provide convincing evidence that coho salmon entering the Strait of Georgia in 2007 had poor survival. Although survival information is not available for chinook salmon as they return as age-4 fish in 2010 and age-5 fish in 2011, we speculate that the marine survival of the chinook salmon will also be poor. Juvenile chum salmon catches in the trawl surveys in the Strait of Georgia were the smallest in the 11 years of surveys. The low number of returning adults to the Strait of Georgia in 2010 is consistent with very poor total survival (Beamish et al., 2011), supporting the notion that the small catches in 2007 resulted from poor early marine survival. Juvenile Pacific herring also survived very poorly in 2007 resulting in very poor recruitment to the commercial fishery in the Strait of Georgia in 2010 (Cleary et al., 2009; Beamish et al., 2011). In 2009, the percentage of the age-2+ recruiting year class (which hatched in 2007) was 66.6%. In 2010, this percentage decreased to 2%, which was the lowest on record, indicating a virtual failure of the 2007 year class.

Juvenile Pacific salmon and herring represent 98% of all fishes caught in the surface 30 m of the Strait of Georgia in the daytime trawls since 1998 (Beamish et al., 2011). Thus, the generally poor growth and poor survival of both of all juvenile Pacific salmon and herring is convincing evidence of a major change in the Strait of Georgia ecosystem in early 2007. 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. 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 fishes (Hjort, 1914; Houde, 1987; Pearcy, 1992; Beamish and Mahnken, 2001; Quinn et al., 2005).

The large numbers of smolts that were produced in fresh water in 2007 and 2008 would experience some mortality during their migration down the Fraser River, but there would still be hundreds of millions that enter the Strait of Georgia. It is to be expected that there will a large initial mortality in the Strait of Georgia even in years with exceptionally high adult returns, such as in the ocean entry year of 2008 (return year 2010). However, it is during the residence time in the Strait of Georgia of approximately 35 days that we propose that many of the sockeye salmon that went to sea in 2007 died or became increasingly susceptible to mortality because of their poor condition. Brood year strength can be determined early in the marine period according to the critical size and critical period hypothesis, 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 survived their residence period in the Strait of Georgia likely would



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, these fish would also experience poor feeding conditions in Queen Charlotte Sound, Hecate Strait, and in the Gulf of Alaska during their first and second winters thereby exacerbating the poor survival conditions experienced in the Strait of Georgia. Therefore, it was climate-scale ocean conditions that initiated the poor early marine survival of Fraser River sockeye salmon when they entered and dispersed through the Strait of Georgia in the spring of 2007. The coast-wide scale of these poor conditions would subsequently affect the fish that survived to leave the Strait of Georgia.

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, we contend that the high mortality was due mainly to a major failure of the production of prey that juvenile Pacific salmon require when they begin feeding early in the spring in the Strait of Georgia and that this production failure preceded any toxic algal blooms. Rensel et al. (2010) showed 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 would occur from about mid-May until early July when the Chilko Lake fish are in the Strait of Georgia.

As previously reported, the smolt production in 2008 was similar to 2007 and, for both years, twice the previously recorded maximum. However, the average catch estimates in late June 2008 in Queen Charlotte Sound and in the Strait of Georgia were substantially larger than in 2007, indicating that the early marine survival improved substantially. The juvenile sockeye salmon were larger than in 2007, but generally were small, which we suggest is a consequence of the increased density. The ocean entry year in 2008 was also a year when there were large numbers of juvenile pink salmon entering the Strait of Georgia. 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 was 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., 2011). Although the improved early marine survival of juvenile sockeye salmon would be the major contributor to the exceptional adult return in 2010, ocean conditions in the Gulf of Alaska after the juvenile sockeye salmon left the coastal areas could have had a positive secondary effect on the number of returns.

The almost constant average catch of juvenile Fraser River sockeye salmon in 2007, 2008 and 2009 in Hecate Strait (Figure 3b) is difficult to explain, considering the variation in average catches in the other areas. However, the average catch was small, relative to Queen Charlotte Sound, indicating that the fish that migrated into Hecate Strait

603 may not be a major percentage of the surviving population. The fish were also  
604 consistently larger than in Queen Charlotte Sound and the Strait of Georgia. The large  
605 size, as well as the stock composition of the fish in Hecate Strait, may be a consequence  
606 of faster growth or older ages. For example, approximately 5% of Chilko Lake sockeye  
607 salmon smolt at two years of age (Henderson and Cass 1991), which is higher than that  
608 typically displayed by other populations. Chilko Lake sockeye salmon were estimated to  
609 comprise 22% of Fraser River sockeye salmon caught in Hecate Strait in 2007, and 29%  
610 of Fraser River sockeye salmon caught in 2008, higher than the average 15-16% of Fraser  
611 River drainage escapement accounted for by the Chilko Lake population. Similarly, the  
612 Cultus Lake and Birkenhead River populations display higher proportions of two-year  
613 than typically observed in other populations. These two populations accounted for 11%  
614 and 4% of Fraser River sockeye salmon sampled in Hecate in 2007 and 2008,  
615 respectively, higher than would be expected based upon their relative contributions to  
616 drainage escapement. It thus seems likely that Fraser River sockeye salmon sampled in  
617 Hecate Strait in June were derived disproportionately from populations where individuals  
618 display older ages and larger sizes at smoltification. Unfortunately, as ages were not  
619 determined for any of the individuals sampled, it was not possible to confirm that  
620 individuals sampled in Hecate Strait in late June were typically older than those sampled  
621 in the Strait of Georgia in July. We suspect that the larger fish migrated faster out of the  
622 Strait of Georgia because of their size in fresh water, but this interpretation remains  
623 speculative until age composition of the fish in Hecate Strait is determined. It is relevant  
624 that, in 2007, the percentage of sockeye salmon from the Fraser River in Hecate Strait  
625 was the smallest in the three 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.

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 2009 displayed the largest body size of the three years in all areas. Unlike 2007 and 2008, average catches in the Strait of Georgia were larger than 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 was later than in 2008. These juveniles also encountered strong El Niño conditions during their first ocean winter in 2009-2010, which we consider was favourable for survival as evidenced by the large adult returns in 2010. The adult return in 2011 will confirm if the early marine survival and survival during the first ocean winter were exceptionally high in 2009.

As indicated by the above discussion, the effects of early marine survival on salmon rearing in the Strait of Georgia may differ among populations and individuals, and is likely dependent upon juvenile size at the time of smolting. Welch et al. (2011) estimated that, for 200 electronically-tagged sockeye salmon smolts migrating out of Cultus Lake in 2007, mortality in fresh water and the Strait of Georgia was 72% of smolts tagged. In their study, Welch et al. (2009) reported a mean fork length of 189 mm for the tagged smolts, and determined an average residence time in the Strait of Georgia of about 11 days according to travel times from the mouth of the Fraser River to a detection line in

the northern Strait of Georgia. Based on reported transit speeds, roughly two additional days were required for the fish to clear the Strait of Georgia. Thus, 72% fresh water and early marine mortality was observed for smolts of 189 mm fork length with a mean residence time in the Strait of 13 days. The mean fork length of the smolts examined by Welch et al. (2009) was considerably greater than the smolt fork length of  $107.9 \pm 16.7$  mm we observed in the Strait of Georgia in 2007, or the corresponding fork lengths of  $108.9 \pm 8.5$  and  $120.1 \pm 10.7$  mm observed in Queen Charlotte Sound and Hecate Strait, respectively (Table 2). As noted previously, the larger body size we observed in Hecate Strait in 2007 is consistent with faster northward migration rates of larger juveniles.

The residence time of 11 to 13 days for the Strait of Georgia reported by Welch et al. (2009) was considerably shorter than the average 35-day residence time estimated for juvenile Fraser River sockeye salmon by Preikshot et al. (2011). However, because the average size of juveniles we sampled in the Strait of Georgia in 2007 was considerably smaller than the size of juveniles tagged by Welch et al. (2009), it is highly probable that the smaller juveniles we observed reared for a longer period in the Strait of Georgia. If we assume that the smaller juveniles sampled in 2007 spent 22 to 24 days longer in the Strait of Georgia than the 11 to 13 days for the larger tagged juveniles used by Welch et al. (2009), then mortality rates for these fish were more likely in excess of 95% prior to exiting the strait. The strong correlation between Strait of Georgia herring survival (with herring juveniles residing in the strait for several months of initial rearing) and Chilko Lake sockeye salmon survival reported by Rensel et al. (2010) provides further corroboration of the importance of juvenile rearing in the Strait of Georgia subsequently

reflecting sockeye salmon brood year survival.

### *Effects of ocean conditions on salmon survival*

According to the above discussion, it was climate-scale ocean conditions that initiated the poor early marine survival of Fraser River sockeye salmon when they entered and dispersed through the Strait of Georgia in spring and summer of 2007. The coast-wide scale of these poor conditions would subsequently affect the fish that survived to leave the Strait of Georgia. The effects of these conditions are expected to differ among the different coastal and offshore regions.

### *Strait of Georgia*

Anomalously high runoff, combined with persistent southeasterly winds, in the spring of 2007 resulted in low surface salinities and a shallow surface mixed layer in the Strait of Georgia around the time of smolt entry. We assume that the winds were unable to break down the intensified surface stratification, resulting in shallowly confined plankton growth at the time the juveniles were entering the strait. 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 in 2009. In contrast, the low runoff and moderate northwest winds that prevailed in the strait in the spring of 2008 would have given rise to a relatively deep mixing layer and, presumably, relatively high food production in the late spring and summer of that year. 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 the disease would have further compromised the health of the out-migrating stocks. In contrast, the higher surface salinities encountered by smolts in the spring of 2008 may have been less stressful, minimizing possible autoimmune responses to diseases being carried by the fish.

Based on winds recorded at Halibut Bank in the central Strait of Georgia (Figure 6a), 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 stratification in the strait, may have been partially blocked by strong mixing in the passes (Griffin and LeBlond, 1990). In 2008, there were numerous northwesterly wind events so that the freshwater was flushed out on a more regular basis, diminishing the surface stratification and silt content, thereby allowing plankton growth over a greater depth range. Contrary to the 2007 entry year, the large numbers of 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

718 surviving fish that entered the central coastal waters. The persistent southeasterly winds  
719 that prevailed within southeastern Queen Charlotte Sound at that time (Figure 9b) would  
720 have driven the surface waters northward into Hecate Strait (Hannah et al., 1991),  
721 generating low salinities (Figure 10b) and presumably strongly stratified surface waters  
722 along the eastern boundary of the Sound. As a consequence, freshwater entering the  
723 sound from the Mainland rivers would not have contributed significantly to the salinity  
724 structure and establishment of an optimally deep mixed layer depth (cf., Gargett, 1997) in  
725 the central and seaward portions of the sound where the juvenile fish were migrating.  
726 Thus, in contrast to the Strait of Georgia, southerly winds over the central coast lead to  
727 weak vertical stratification and a less than optimally deep surface mixed layer in Queen  
728 Charlotte Sound. This argument is consistent with the low surface chlorophyll  
729 concentrations reported throughout southern Queen Charlotte Sound in April and May  
730 2007 (Borstad et al., 2011). The reverse conditions would have occurred during the  
731 northerly to light southerly winds and relatively low runoff (Figure 8c,d) that prevailed in  
732 the late spring of 2008. These winds would have made it easier for brackish surface water  
733 emanating from the mainland inlets to move seaward toward the entrance to Queen  
734 Charlotte Sound (Figure 1), leading to the vertical entrainment of nutrients and aiding in  
735 the establishment of a more optimally favourable mixed layer depth. Formation of a  
736 moderately deep surface mixed layer in Queen Charlotte Sound would be conducive to  
737 high plankton productivity. The seaward flushing of high chlorophyll concentration  
738 surface waters from the inlets is likely to have contributed to high productivity in the  
739 region (G. Borstad, 2011, pers. comm.).



*West Coast Vancouver Island and Pacific Northwest*

The response of salmon stocks from the Columbia River and Barkley Sound (west coast Vancouver Island) to the timing of the spring transition differs from that of the Fraser River stocks. Because the Spring Transition marks a shift from downwelling-favourable southerly winds to upwelling-favorable northerly winds along the outer coast, it also marks the time of enhanced nutrient and accelerated plankton growth in the upper layer of the ocean. On this basis, we would expect a late Spring Transition to have a negative effect on juvenile sockeye salmon survival. However, the coastal winds also affect the transport of brackish surface waters along the outer coast. During the months prior to the spring transition, the Columbia River plume is advected northward along the Washington coast (Hickey et al., 1998) and the buoyancy-driven Vancouver Island Coastal Current (VICC) reaches peak northward velocity of around  $0.5 \text{ ms}^{-1}$  along the west coast of the island. Both features extend about 25 km from the coast. In summer, following the transition, the Columbia plume is directed offshore or to the south but the VICC is weakened only slightly because of the compensating effect of increased Fraser River discharge during the spring freshet (Thomson et al., 1989; Thomson and Hourston, 2011). As a consequence, fish stocks migrating northward in these currents have a year-round energetic advantage that might offset any possible reduction in food sources caused by a delayed Spring Transition and associated upwelling. 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.

764 *Gulf of Alaska*

765         The juvenile Fraser River sockeye salmon that survived the 2007 marine entry  
766 period likely had low lipid reserves due to the adverse conditions they had encountered in  
767 British Columbia coastal waters. These fish would have been stressed even further as a  
768 result of the poor ocean conditions that prevailed in the Gulf of Alaska in the winters of  
769 2007-08 and 2008-09. Although adult fish from the 2008 entry year would also have  
770 been negatively impacted by the strong La Niña winter of 2008-09 in the Gulf, their  
771 healthier condition as juveniles and the favourable ocean conditions they subsequently  
772 encountered during the intense El Niño winter of 2009-10 would have contributed to their  
773 record returns in 2010. Based on this proposition, it is possible that returns in 2010  
774 would have been even higher had the winter of 2008-09 in the Gulf been less extreme.  
775 We further propose that relatively healthy fish from the 2009 entry year were positively  
776 affected by the intense El Niño event of 2009-10 (Figure 14c) but only marginally  
777 affected by the moderate La Niña event of 2010-11 (Figure 14d). If so, the returns of  
778 sockeye salmon to the Fraser River in 2011 are likely to be high.

779

780         As indicated by Figure 15, the atmospheric conditions in the Gulf of Alaska in the  
781 La Niña winter of 2008-09 (as well as the winters 2006-07 and 2007-08) coincided with a  
782 high positive North Pacific Index (NPI; Trenberth and Hurrell, 1994) whereas the El Niño  
783 winter of 2009-10 coincided with a high negative index. (A high NPI indicates higher  
784 than average sea-level pressure over the Gulf of Alaska and, in winter, a weaker than  
785 average Aleutian Low; and *vice versa*.) Thus, winter conditions in the Gulf of Alaska for  
786 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 winds during the winter preceding their return. The slightly positive index values recorded in the winter of 2010-11 (Figure 15) suggests a marginally positive open ocean effect on the returns of Fraser River sockeye salmon in the summer of 2011. Thus, we again predict relatively high returns based on the high numbers of healthy juveniles observed in coastal waters in the spring and summer of 2009.

## **SUMMARY AND CONCLUSIONS**

According to our findings, there is a strong link between Fraser River sockeye salmon production for extreme return years 2009 and 2010 and the occurrence, two years earlier, of highly anomalous environmental marine conditions in British Columbia coastal waters (brood year +2) and the Gulf of Alaska (brood year +3 and +4). 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 (Figure 16). 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 favourable 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 favourable coastal ocean conditions arising from relatively low freshwater runoff, an early Spring Transition (onset of northerly winds), and reduced surface stratification. In this case,

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. In particular, we speculate that the intense La Niña winter of 2008-09 had an added negative impact on the survival of the 2007 and 2008 marine entry stocks whereas the intense El Niño winter of 2009-10 had an added positive impact on the survival of the 2008 entry stocks. It is feasible that the 2010 returns might have been even more spectacular had the 2008 marine entry stocks encountered more favourable conditions in the Gulf of Alaska in the winter of 2008-09.

The highly anomalous (“negative”) ocean conditions that prevailed within the coastal waters of British Columbia in the spring of 2007 greatly reduced food availability and, consequently, 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 2007-08 and extreme La Niña of 2008-09 for the 2007 entry year) also would have contributed to the poor sockeye 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 (the region we consider to have the strongest impact on brood year strength), and fish-ocean interactions in the two subsequent years when the fish are in the Gulf of Alaska. Moreover, because winds and runoff associated with the Spring Transition along the west coast of North America have a 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 stocks and the Columbia River and Barkley Sound sockeye stocks. In particular, a delay in the Spring Transition along the outer coast is not necessarily problematic for the survival of west coast sockeye salmon stocks. Although 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 and a delayed 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). A delayed change in the prevailing currents over the shelf-slope region can be beneficial to the swimming energetics of sockeye salmon stocks from the Columbia River and Barkley Sound which migrate northward as juveniles along the outer coast of Vancouver Island.

This study generally supports the notion that ocean conditions from spring to early summer in the first marine year are critical to fish survival (cf., Beamish and Bouillion, 1993). Results further suggest that extreme winter conditions in the Gulf of

Alaska during the first and/or second marine winter can enhance (either negatively or positively) the survivability of the Fraser River stocks after they have migrated out of the coastal marine waters. These findings have led us to a testable hypothesis for sockeye production for the Fraser River stocks. Moreover, we can now combine environmental time series (coastal river discharge, winds, and vertical stratification) with marine entry 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 A**

In the spring and early summer of 2007, the monthly freshwater discharge anomalies for the Strait of Georgia ranged from roughly 500 to 3000 m<sup>3</sup>s<sup>-1</sup>. Using a conservative value of 1000 m<sup>3</sup>s<sup>-1</sup>, yields a seasonal (three month) discharge volume anomaly of 7.8 km<sup>3</sup>. This compares with a volume of 150 km<sup>3</sup> for the upper 30 m of the entire Strait (cf., Table 3 in Thomson and Foreman, 1998). Here, 30 m is a representative depth scale 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

879 freshwater is uniformly mixed over the 30 m, we obtain a volume ratio of 0.026.  
880 Multiplying this ratio by a mean salinity for the upper layer of the Strait of around 32 psu  
881 yields a basin-wide, seasonally integrated salinity anomaly of roughly -0.8 psu. This  
882 anomaly increases to -1.6 psu if we assume that the freshwater is mixed linearly (rather  
883 than uniformly) over the 30 depth range. These estimates are consistent with the -1 to -2  
884 psu anomalies in surface salinity observed at the coastal lightstations (Figure 10a).  
885

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## Figure Captions

Figure 1. Map of the northeast Pacific (a) and southern British Columbia (b) showing major ocean currents and sites recording oceanic time series records used in this study. Open triangles denote wind stations [meteorological buoys 46131 (Sentry Shoal), 46146 (Halibut Bank), 46204 (QCS), and 46206 (La Perouse Bank)] and open squares denote selected coastal lightstations (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 vectors lengths are not scaled to speed.

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

Figure 3. Average catch of juvenile sockeye salmon in July in standardized (30-min sets) for years 2007, 2008, and 2009 for: (a) Strait of Georgia; (b) Hecate Strait; and (c) Queen Charlotte Sound.

Figure 4. Stock structure as identified from DNA analysis of sockeye salmon collected in 2008: (a) the Strait of Georgia June 27-July 16, 2008, sample size  $N = 179$ ; (b) the Gulf Islands June 20-27, 2008,  $N = 153$ ; (c) Queen Charlotte Sound June 25, 2008,  $N = 87$ ; (d) Hecate Strait June 26-27, 2008,  $N = 103$ ; (e) The stock composition expected to return in



2010.

Figure 5. Stock structure as identified from DNA analysis of sockeye salmon collected in 2009: (a) the Strait of Georgia June 26-July 7, 2009, sample size  $N = 141$ ; (b) the Gulf Islands June 1-5, 2009,  $N = 146$ ; (c) Queen Charlotte Strait June 24, 2009,  $N = 79$ ; (d) Queen Charlotte Sound June 23, 2009,  $N = 61$ ; and (e) Hecate Strait June 24-25, 2009,  $N = 83$ ; and (f) The stock composition expected to return in 2011.

Figure 6. Stock structure as identified from DNA analysis of sockeye salmon collected in 2007 from (a) Queen Charlotte Sound June 28, 2007,  $N = 61$ ; (b) Hecate Strait June 29-30, 2007,  $N = 108$ ; and (c) The stock composition expected to return in 2009.

Figure 7. The alongshore component of daily mean wind stress ( $\tau_y$ , positive toward  $300^\circ$  True) at (a) Meteorological Buoy C46206 and (b) NCEP Reanalysis site  $49^\circ 12'N$   $126^\circ 34'W$  ( $48^\circ 34'N$ ;  $125^\circ 38'W$ ) off southwest Vancouver Island for years 2005 through 2010 (see Figure 1). Inverted triangles show the approximate time of the “Spring Transition” when the prevailing winds switched from southeasterly (to the northwest) to northwesterly (to the southeast). Similar wind timing conditions occurred within the Strait of Georgia and central coastal regions of Hecate Strait and Queen Charlotte Sound.

Figure 8. Monthly time series of total river discharge for (a) the Strait of Georgia (SoG) and (b) the Queen Charlotte Sound/Strait region of British Columbia (BC) for the period from 1 January 2000 to 1 January 2010. Right-hand 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 SoG (a) consists of the sum of the Fraser River discharge recorded at the eastern end of the Fraser River valley at Hope, from the central and lower portions of the river downstream of Hope and its tributaries, and from freshwater inputs from Central Vancouver Island (C VI) and the BC mainland. The total discharge into the Queen Charlotte Sound/Strait region (c) is comprised of freshwater inputs from the Wannock River (Mainland BC) 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 recorded anomalously high runoff in mid- winter, 2007 was the only year to record anomalously high runoff throughout the entire year for both the Strait of Georgia and central coast waters.

Figure 9. 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 1 January 2000 to 1 January 2010. (a) Strait of Georgia: Meteorological buoy sites MB46131 on Sentry Shoal (northern Strait) and MB46146 on Halibut Bank (central Strait), and Sandheads Lightstation off the Fraser River Delta; and (b) Queen Charlotte Sound: Meteorological buoy MB46204 on West Sea Otter Bank ( $51^{\circ}22.1'N$ ,  $128^{\circ}45.0'W$ ), Reanalysis grid point  $52.0^{\circ}N$ ,  $129.1^{\circ}W$ , and North American Regional Reanalysis (NARR) site at  $51.5^{\circ}N$ ,  $129.1^{\circ}W$  (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.

Figure 10. 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.

Figure 11. Monthly anomaly of “pseudo” mixed layer depth for the period 2000 to 2010 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). (a) Mean anomaly; and (b) standard deviation. Anomalies were obtained by subtracting the mean monthly values for the full observation period 1969 to 2009 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 winds too weak for a true mixed layer to form (see text for further explanation). Similar mixed layer depth values are obtained using temperature and salinity profile data separately.

Figure 12. Monthly mean surface chlorophyll-a anomalies for the entire Strait of Georgia region. Gaps in the original 8-day series have been interpolated using linear regression and a least squares annual cycle (obtained from the monthly data for the record 1997 to 2010) subtracted from the interpolated time series. (Courtesy G.A. Borstad and L. Brown,

ASL Environmental Sciences, Inc.)

Figure 13. Monthly mean sea level pressure (mb), sea surface temperature, SST ( $^{\circ}\text{C}$ , in color) and windstress vectors for the winter periods November through April that stocks were in the Gulf of Alaska. (a) 2007-08; (b) 2008-09; (c) 2009-10; and (d) 2010-11.

Figure 14. As for Figure 13 but for anomalies in which the seasonal cycle (mean monthly values) have been subtracted from the distributions to produce monthly anomalies.

Figure 15. Time series of the North Pacific Index (NPI) anomaly for the past 10 years. The index is the area-weighted sea level pressure over the region  $30^{\circ}\text{N}$ - $65^{\circ}\text{N}$ ,  $160^{\circ}\text{E}$ - $140^{\circ}\text{W}$ . [The NP Index Data was provided by the Climate Analysis Section, NCAR, Boulder, USA; Trenberth and Hurrell (1994); Climate Dynamics 9:303-319. Data can be obtained from: <http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html>

Figure 16. Schematic relating the affect of ocean conditions along the coast and in the Gulf of Alaska (GoA) on the net production of Fraser River sockeye salmon. Darker shading denotes the time that the stocks were within coastal waters; lighter shading corresponds to time the fish were in the Gulf of Alaska. Brood years are also presented.

1172 Table 1. Results from analysis of trawl fishing sets in Strait of Georgia, Queen Charlotte Strait, Hecate Strait, and Queen Charlotte  
 1173 Sound for 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	Percentage of sockeye from the Fraser River (number analyzed for DNA)	Catch of Fraser River sockeye	Average catch of Fraser River sockeye salmon/set	Percentage of sockeye salmon from populations on the west coast of Vancouver Island
2007	July 8-15	Strait of Georgia	36	65	NA	65	1.9	NR
2007	June 28	Queen Charlotte Sound	5	103	98.4% (62)	101	20.2	0%
2007	June 29,30	Hecate Strait	13	400	45.4% (238)	182	14.0	47.1%
2008	June 27 – July 6	Strait of Georgia	90	1,662	100% (179)	1,662	34.0	NR
2008	June 25- July 3	Queen Charlotte Sound	5	486	100% (88)	486	97.2	0%
2008	June 26,27, July 3	Hecate Strait	13	278	63% (165)	175	13.5	30.3%
2009	June 26 – July 7	Strait of Georgia	83	1,572	100% (141)	1,572	33.9	NR
2009	June 24, July 2,3	Queen Charlotte Sound	5	118	93.8% (138)	111	22.1	0%
2009	June 25,26	Hecate Strait	8	188	56.8% (146)	107	13.4	15.8%
2009	June 24	Queen Charlotte Strait	7	96	90.8%	87	13.7	0%

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 deviation (SD), and number of fish (*N*) used for each estimate. Lengths for fish caught in the Strait of Georgia, Queen Charlotte Sound, and Hecate Strait in 2007 were significantly smaller than those caught in 2008 and 2009 (ANOVA,  $p \leq 0.05$ ).

Year		Strait of Georgia (1)	Queen Charlotte Strait (2)	Queen Charlotte Sound (3)	Hecate Strait (4)
2007	Length	107.9		108.9	120.1
	±SD ( <i>N</i> )	±16.7 (65)		±8.5 (61)	±10.7 (108)
	Weight	12.7		11.3	16.7
	±SD ( <i>N</i> )	±5.3 (51)		±11.3 (61)	±5.1 (108)
2008	Length	110.9		112.8	133.9
	±SD ( <i>N</i> )	±11.0 (388)		±7.2 (87)	±13.5 (103)
	Weight	11.9		11.8	22.8
	±SD ( <i>N</i> )	±5.2 (361)		±2.7 (87)	±8.2 (103)
2009	Length	116.4	121.2	114.2	159.4
	±SD ( <i>N</i> )	±10.3 (1163)	±8.4 (79)	±6.9 (61)	±14.8 (83)
	Weight	16.6	16.7	14.9	44.2
	±SD ( <i>N</i> )	±5.1 (310)	±3.5 (79)	±2.9 (61)	±13.9 (83)

1181 Table 3: Timing of the spring transition based on the daily alongshore component of wind  
 1182 stress from Meteorological Buoy MB4206 and NCEP/NCAR Reanalysis site  
 1183 49°N126°W. The mean transition date is around April 15.

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Year	MB46206	Re-analysis	Comment
2005	26 May	25 May	late
2006	22 April	20 April	normal
2007	7 May	7 May	late
2008	14 March	28 March	early
2009	4 March	26 March	early
2010	12 April	9 April	normal

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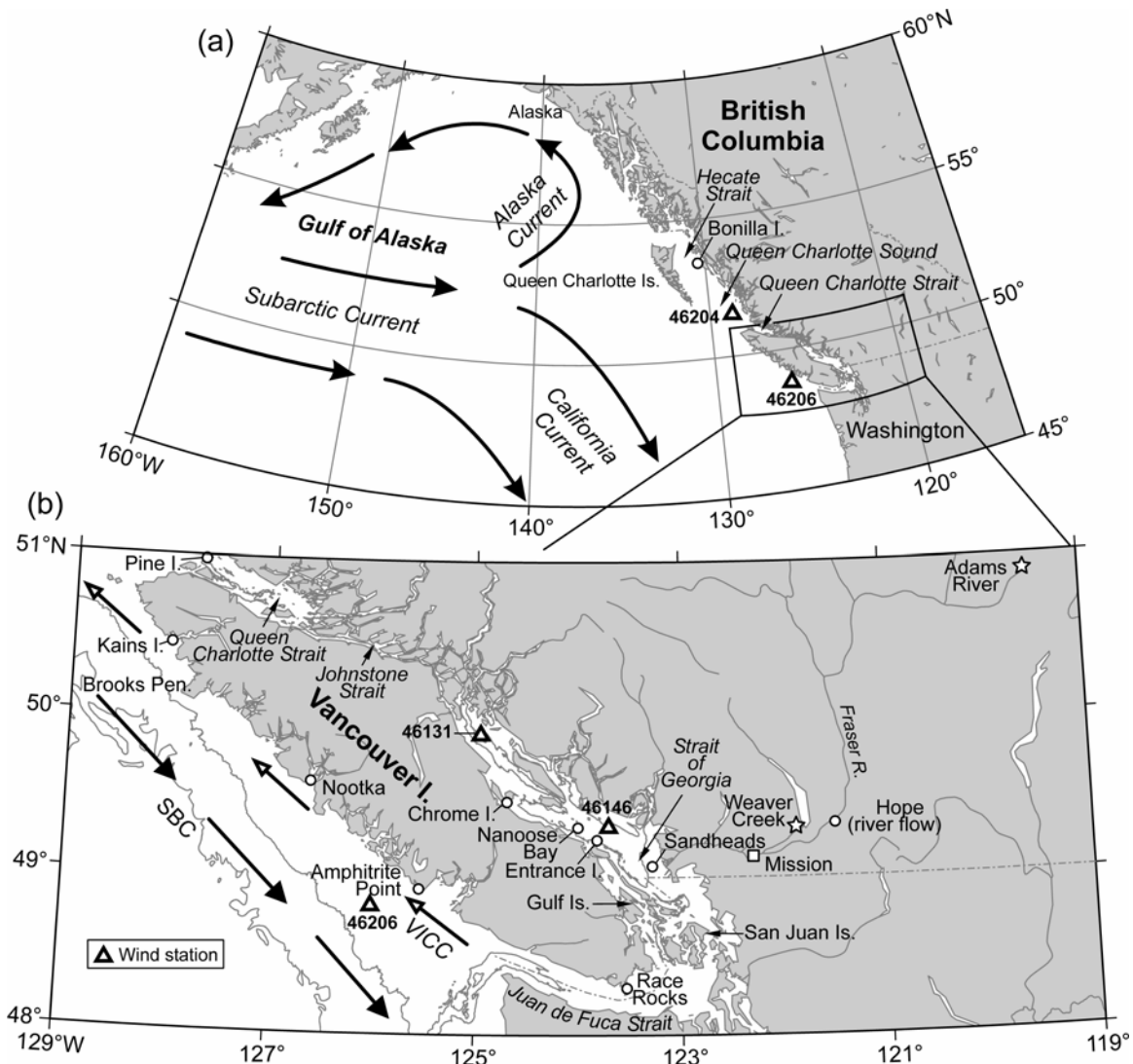


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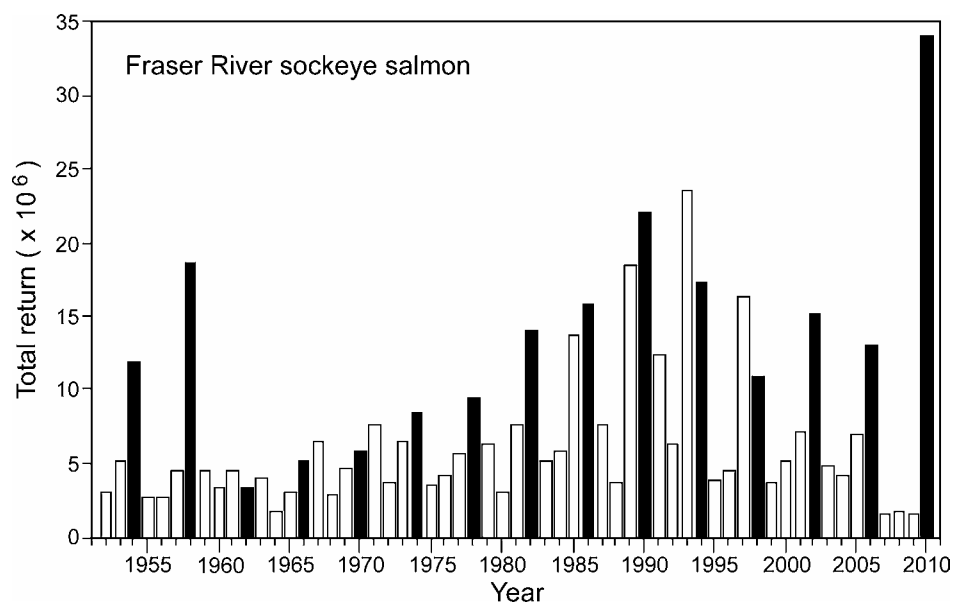


Figure 2. Total returns of sockeye salmon to the Fraser River. Dark bars indicate those years when Late-run Adams River stocks make a major contribution to the total salmon return. Return years 2007, 2008, and 2009 (brood years 2003, 2004, and 2005) were the lowest in the record. The highest recorded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

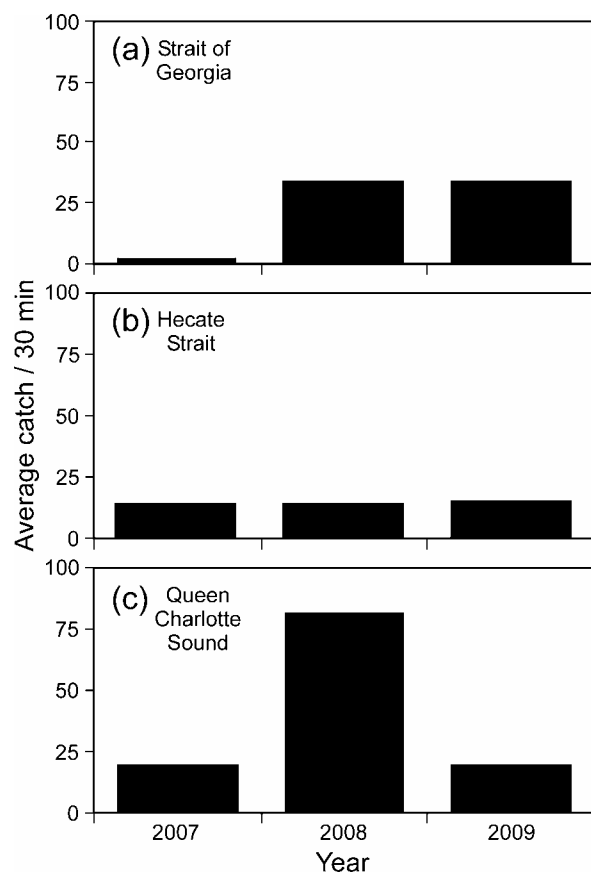


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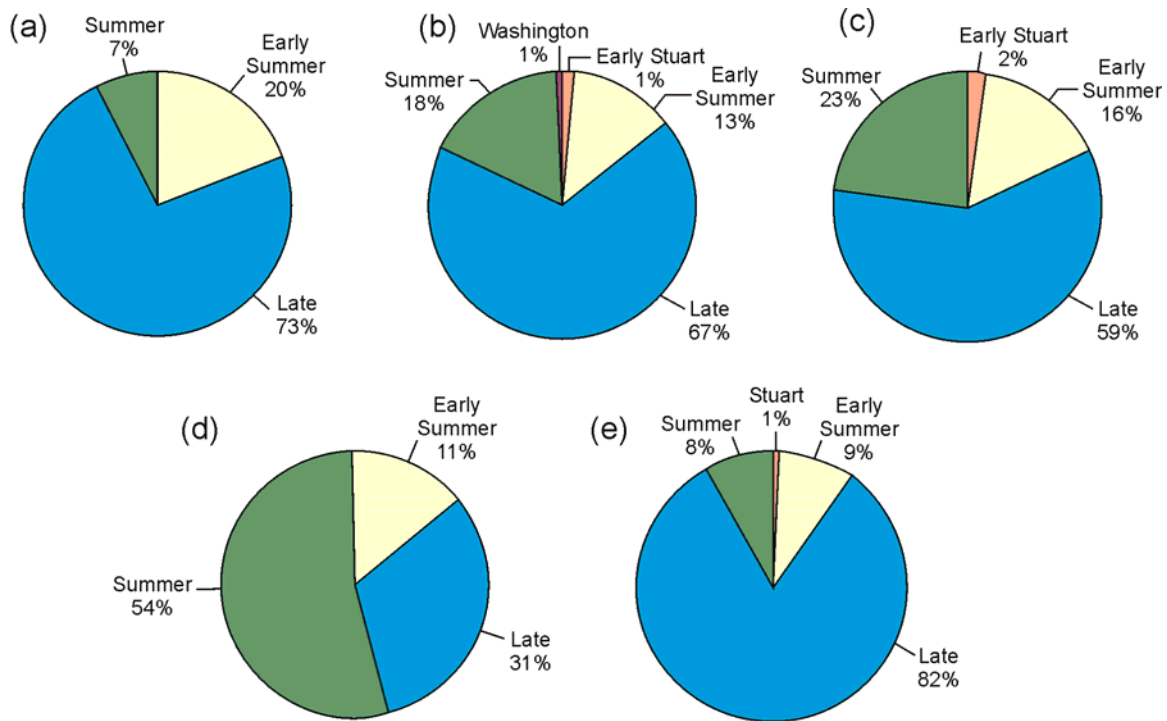


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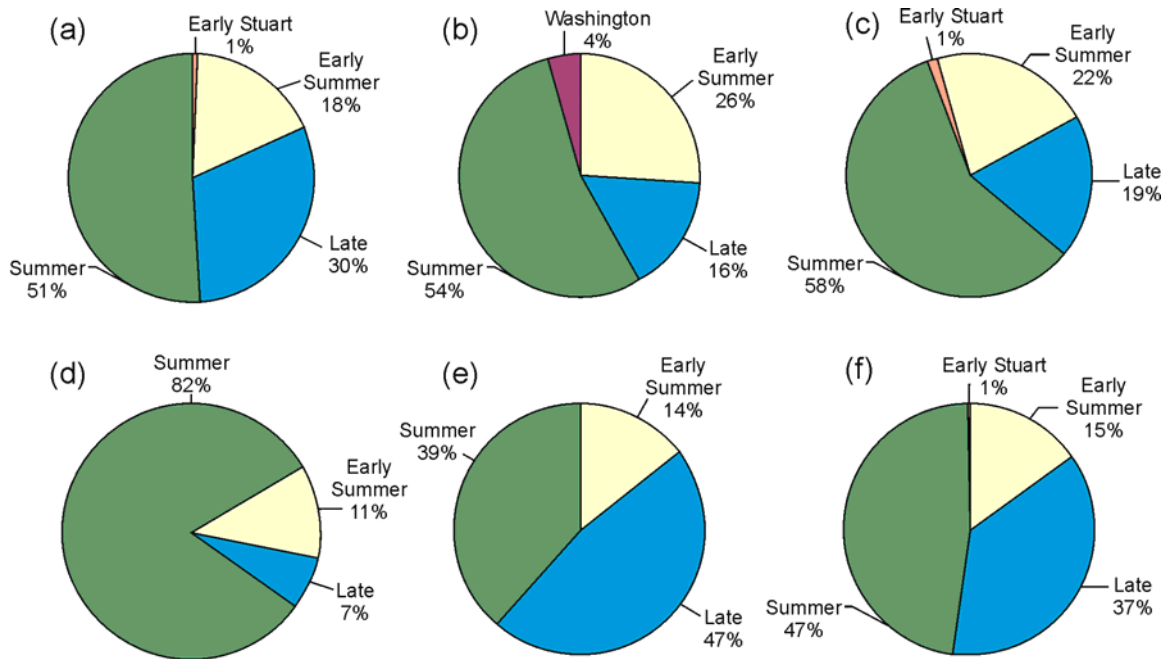


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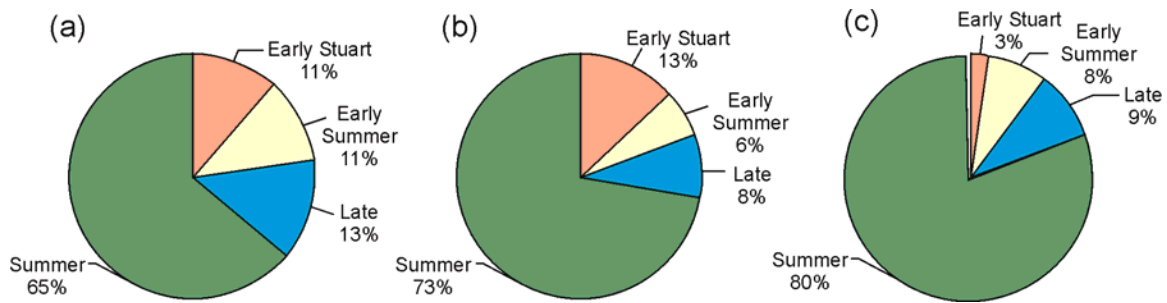


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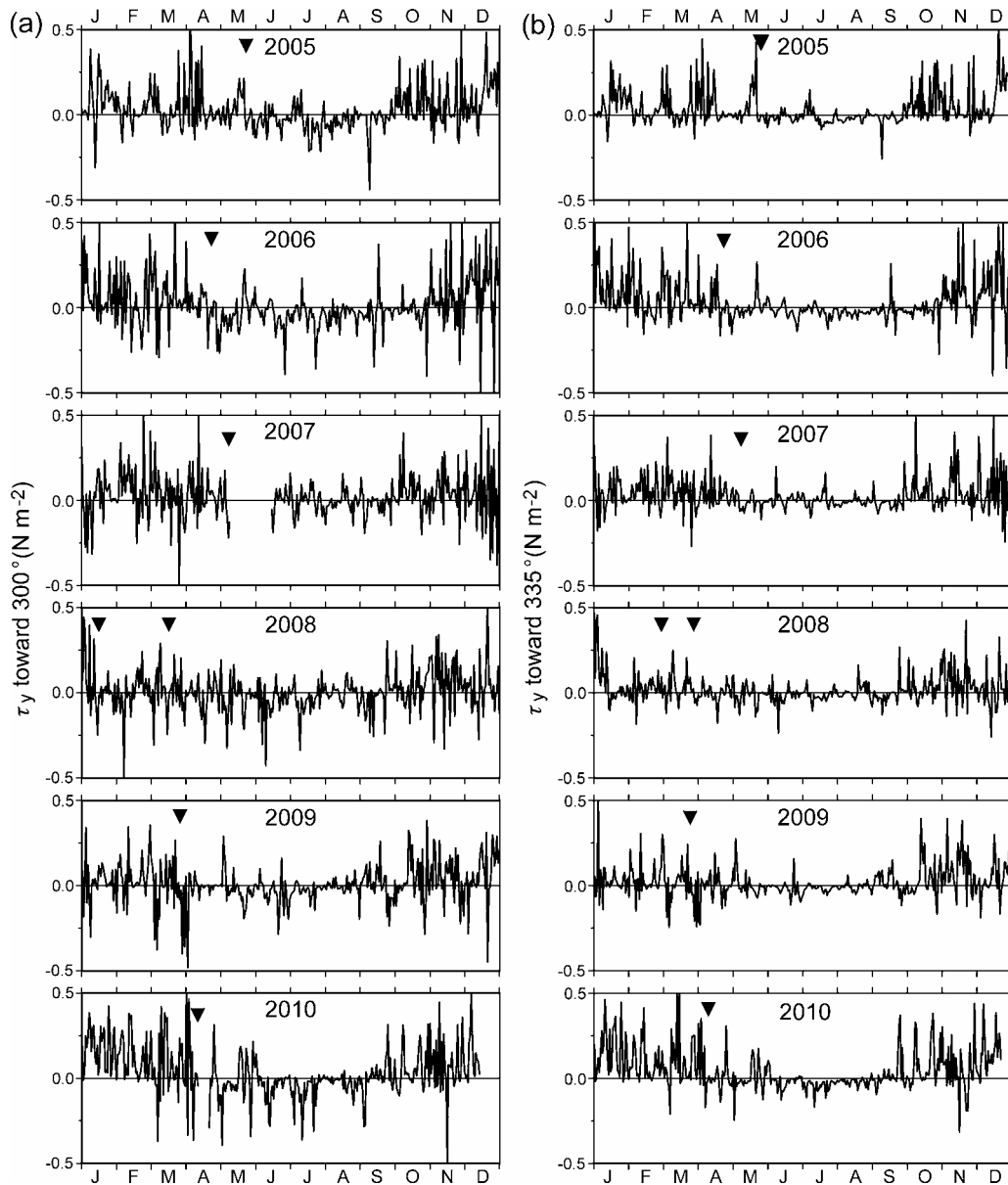


Figure 7. The alongshore component of daily mean wind stress ( $\tau_y$ , positive toward  $300^\circ$ True) at (a) Meteorological Buoy C46206 and (b) NCEP Reanalysis site  $49^\circ N 126^\circ W$  ( $48^\circ 34' N$ ;  $125^\circ 38' W$ ) off southwest Vancouver Island for years 2005 through 2010 (see Figure 1). Inverted triangles show the approximate time of the “Spring Transition” when the prevailing winds switched from southeasterly (to the northwest) to northwesterly (to the southeast). Similar wind timing conditions occurred within the Strait of Georgia and central coastal regions of Hecate Strait and Queen Charlotte Sound.

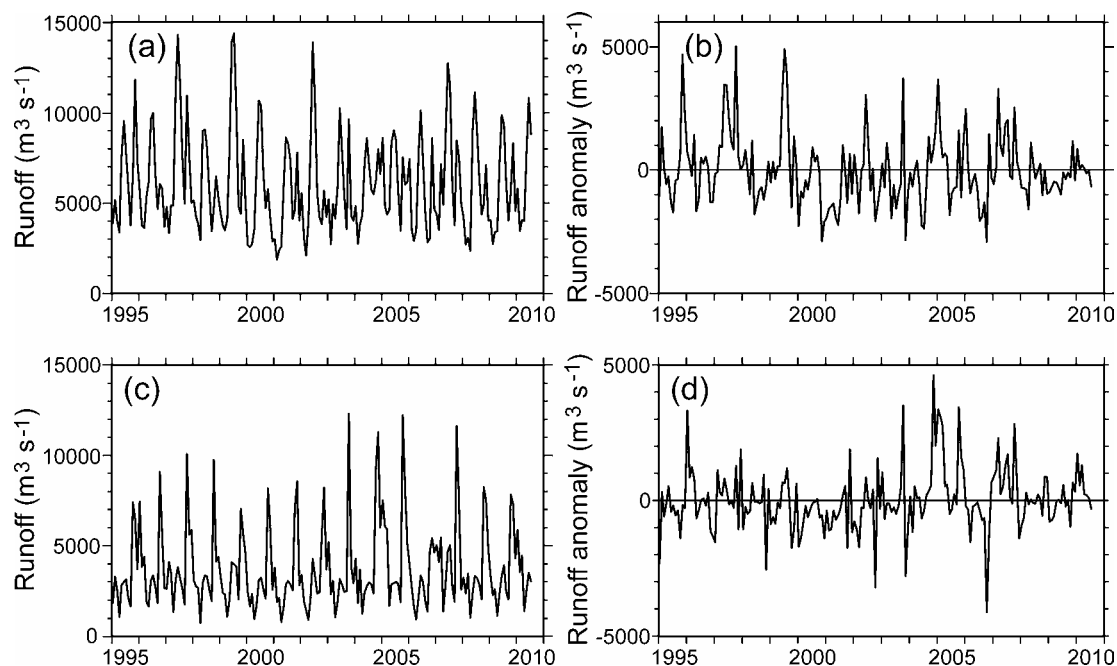


Figure 8. River discharge for selected catchment basins of southern British Columbia (BC) for the period from 1 January 2000 to 1 January 2010. Left-hand panels (a) and (c) show monthly mean discharge rates into the Strait of Georgia (SoG) and Queen Charlotte Sound/Strait regions, respectively; right-hand 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 SoG (a) consists of the sum of the Fraser River discharge recorded at the eastern end of the Fraser River valley at Hope plus the discharge from the central and lower portions of the river downstream of Hope and its tributaries, and from freshwater inputs from Central Vancouver Island (C VI) and the BC mainland. The total discharge into the Queen Charlotte Sound/Strait region (c) is comprised of freshwater inputs from the Wannock River (Mainland BC) to the east of buoy 46204 in Figure 1a, from small rivers on the coast of Northern Vancouver Island, and from rivers on the mainland coasts of Queen Charlotte Sound and Queen Charlotte Strait. Although several years recorded anomalously high runoff in mid- winter, 2007 was the only year to record anomalously high runoff throughout the entire year for both the Strait of Georgia and central coast waters.

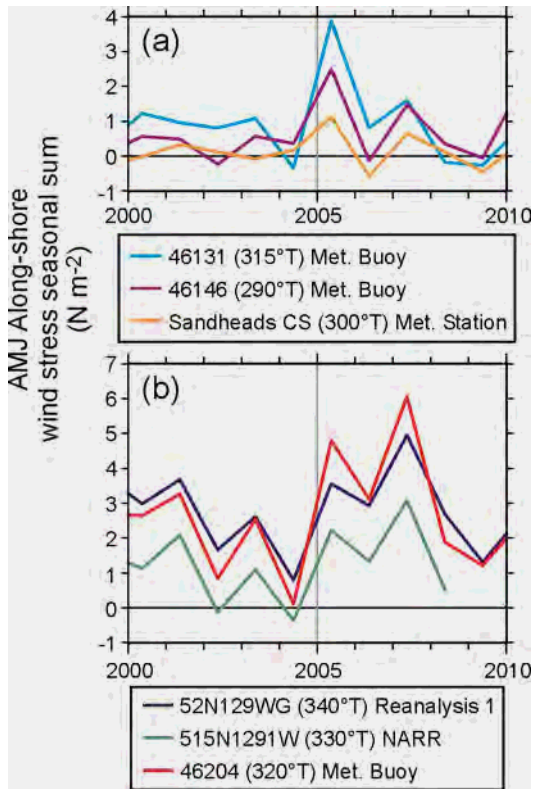


Figure 9. Time-integrated, along-channel component of the wind stress for the months of March, April, and May for Meteorological stations and Reanalysis sites in the study region for the period 1 January 2000 to 1 January 2010. (a) Strait of Georgia: Meteorological buoy sites MB46131 on Sentry Shoal (northern Strait) and MB46146 on Halibut Bank (central Strait), and Sandheads Lightstation off the Fraser River Delta; and (b) Queen Charlotte Sound: Meteorological buoy MB46204 on West Sea Otter Bank (51° 22.1'N, 128°45.0'W) and Reanalysis grid point 52.0°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.



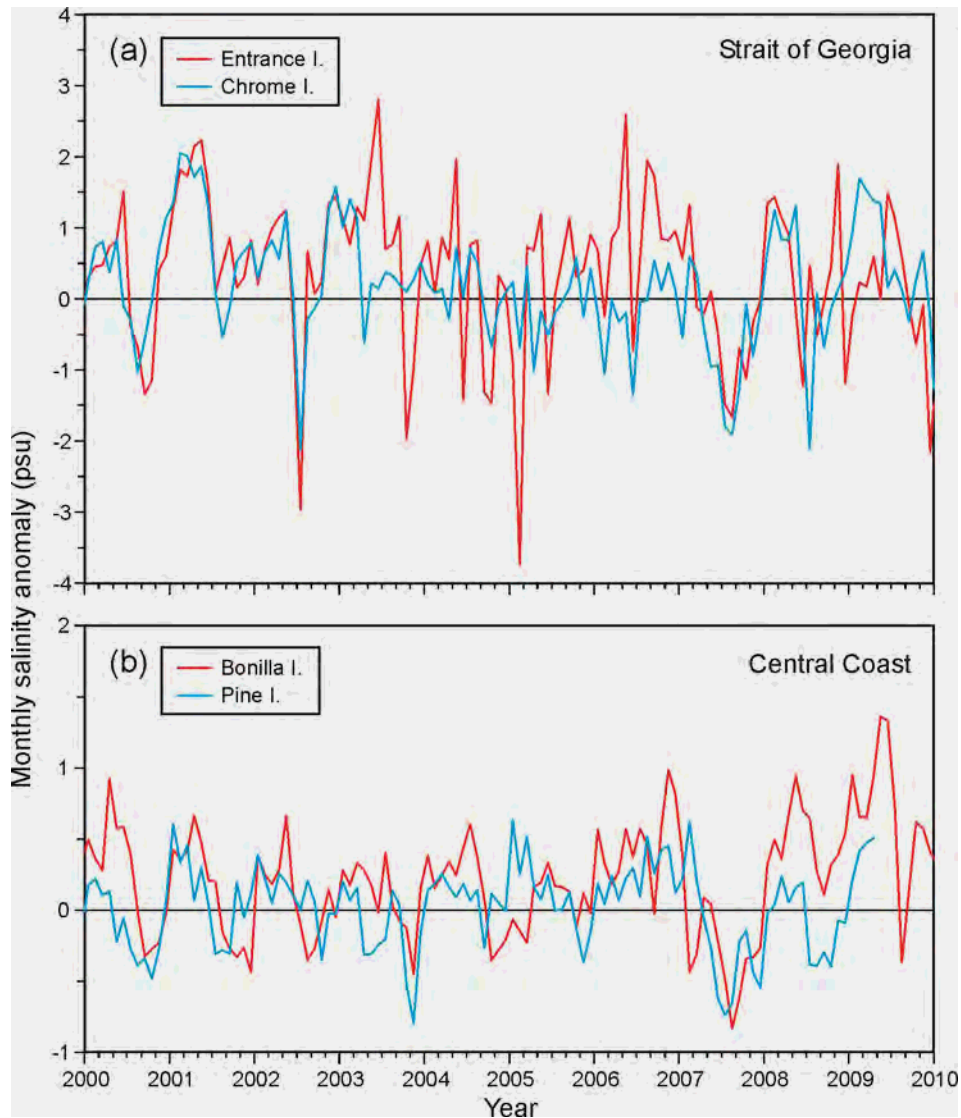


Figure 10. Monthly mean surface salinity anomalies for lightstations on the coast of British Columbia for the period 2000 to 2010. (a) Entrance Island (Strait of Georgia); (b) Chrome Island (Strait of Georgia); (c) Pine Island (Queen Charlotte Strait); and (d) Bonilla Island (Hecate Strait) (see Figure 1 for locations). Monthly anomalies were obtained by subtracting the seasonal cycle (mean monthly values) from each data series.

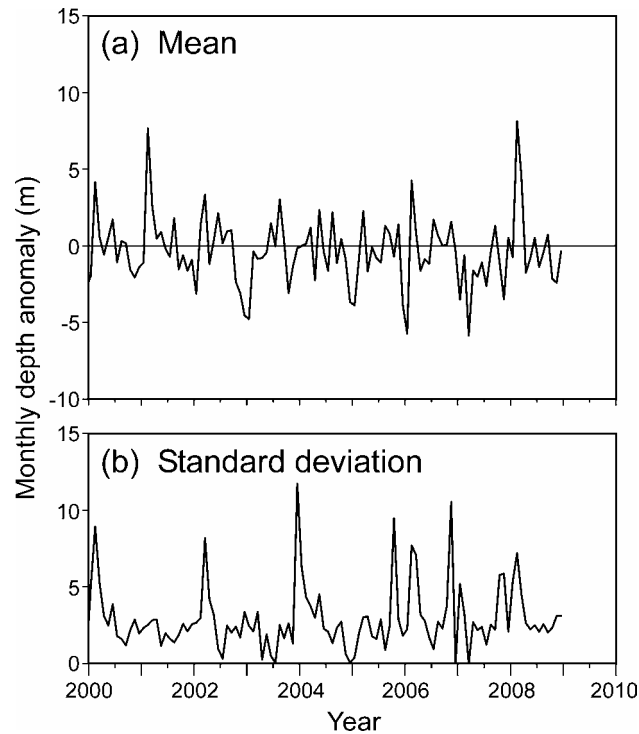


Figure 11. Monthly anomaly of “pseudo” mixed layer depth for the period 2000 to 2010 based on density profile data collected by the Canadian Navy at the Nanoose Bay Test Range centered near 49.19°N,124.00°W in the central Strait of Georgia (see Figure 1). (a) Mean anomaly; and (b) standard deviation. Anomalies were obtained by subtracting the mean monthly values for the full observation period 1969 to 2009 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 winds too weak for a true mixed layer to form (see text for further explanation). Similar mixed layer depth values are obtained using temperature and salinity profile data separately.

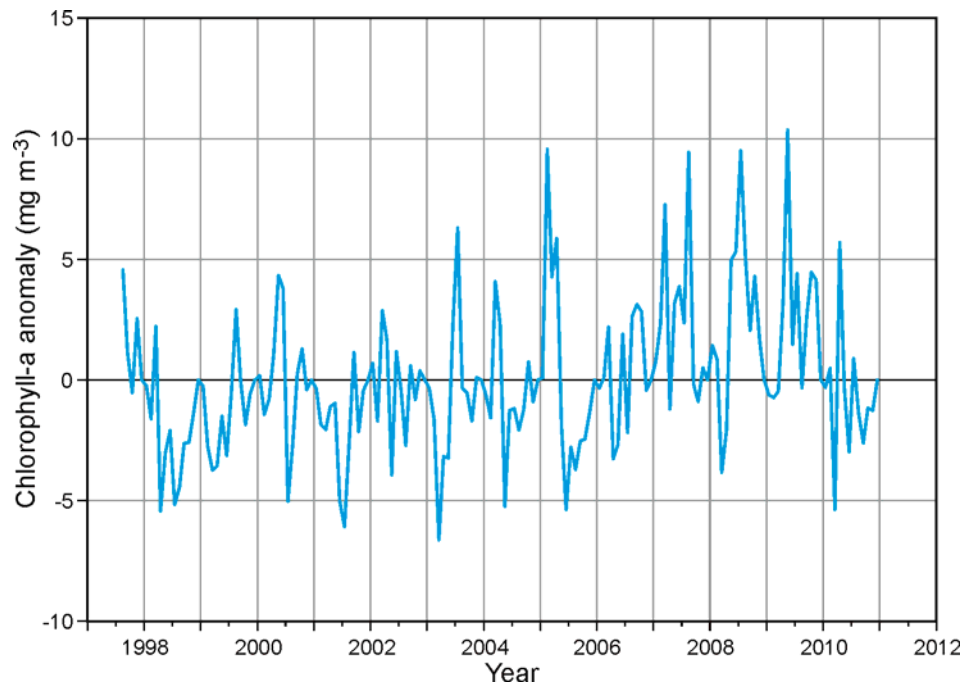


Figure 12. Monthly mean surface chlorophyll-a anomalies for the entire Strait of Georgia region. Gaps in the original 8-day series have been interpolated using linear regression and a least squares annual cycle (obtained from the monthly data for the record 1997 to 2010) subtracted from the interpolated time series. (Courtesy G.A. Borstad and L. Brown, ASL Environmental Sciences, Inc.)

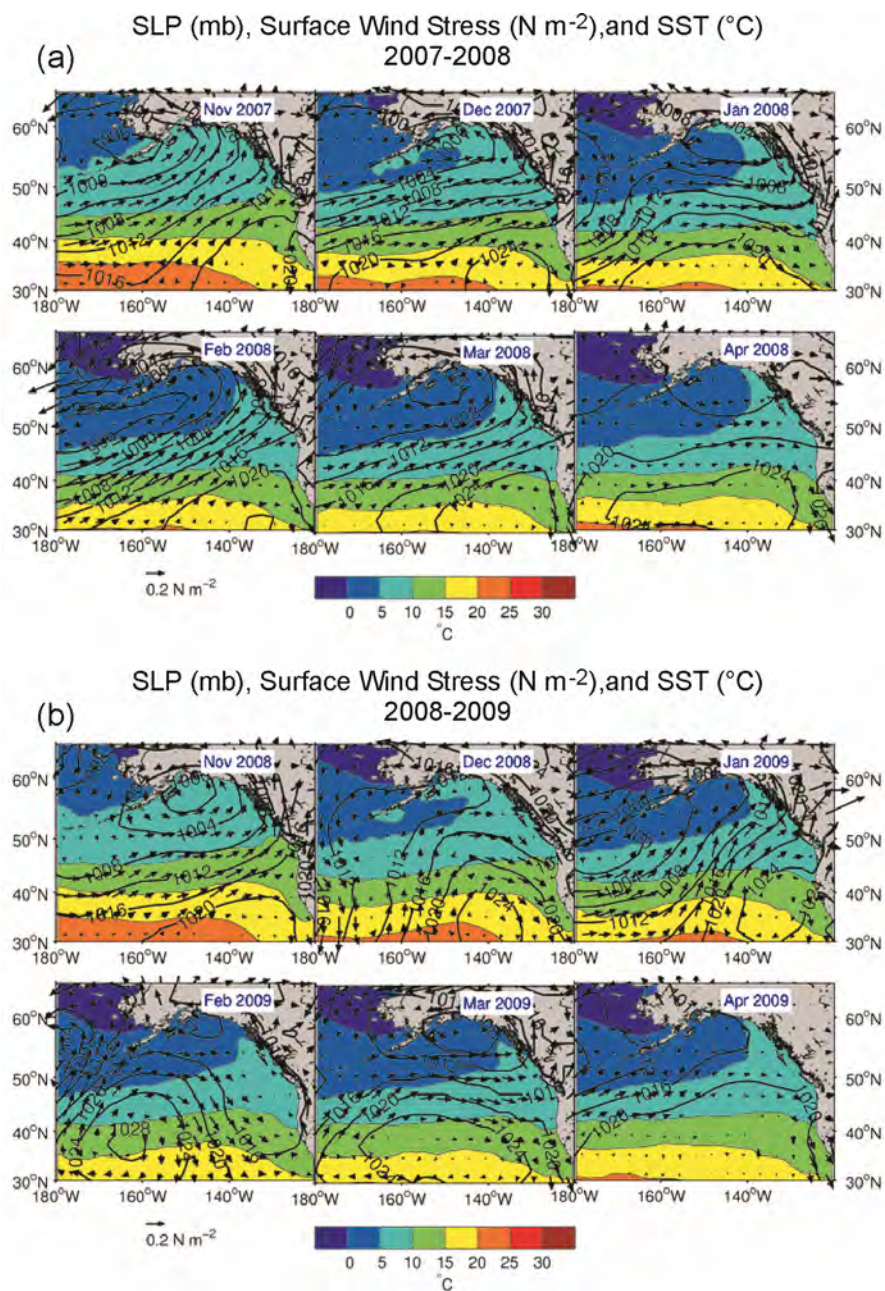


Figure 13. Monthly mean sea level pressure (mb), sea surface temperature, SST ( $^{\circ}\text{C}$ , in color) and windstress vectors for the winter periods November through April that stocks were in the Gulf of Alaska. (a) 2007-08; (b) 2008-09.



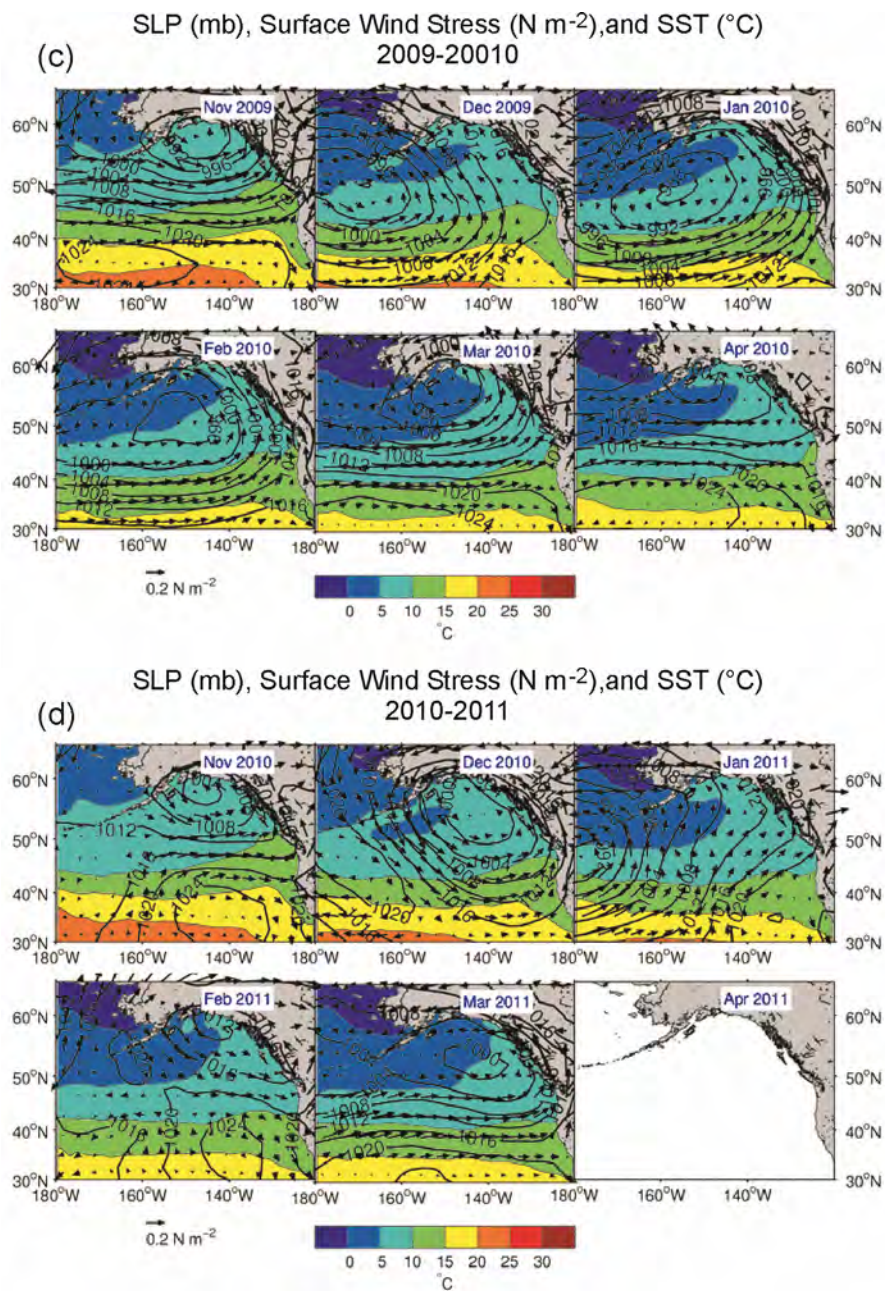


Figure 13 continued. (c) 2009-10; and (d) 2010-11.

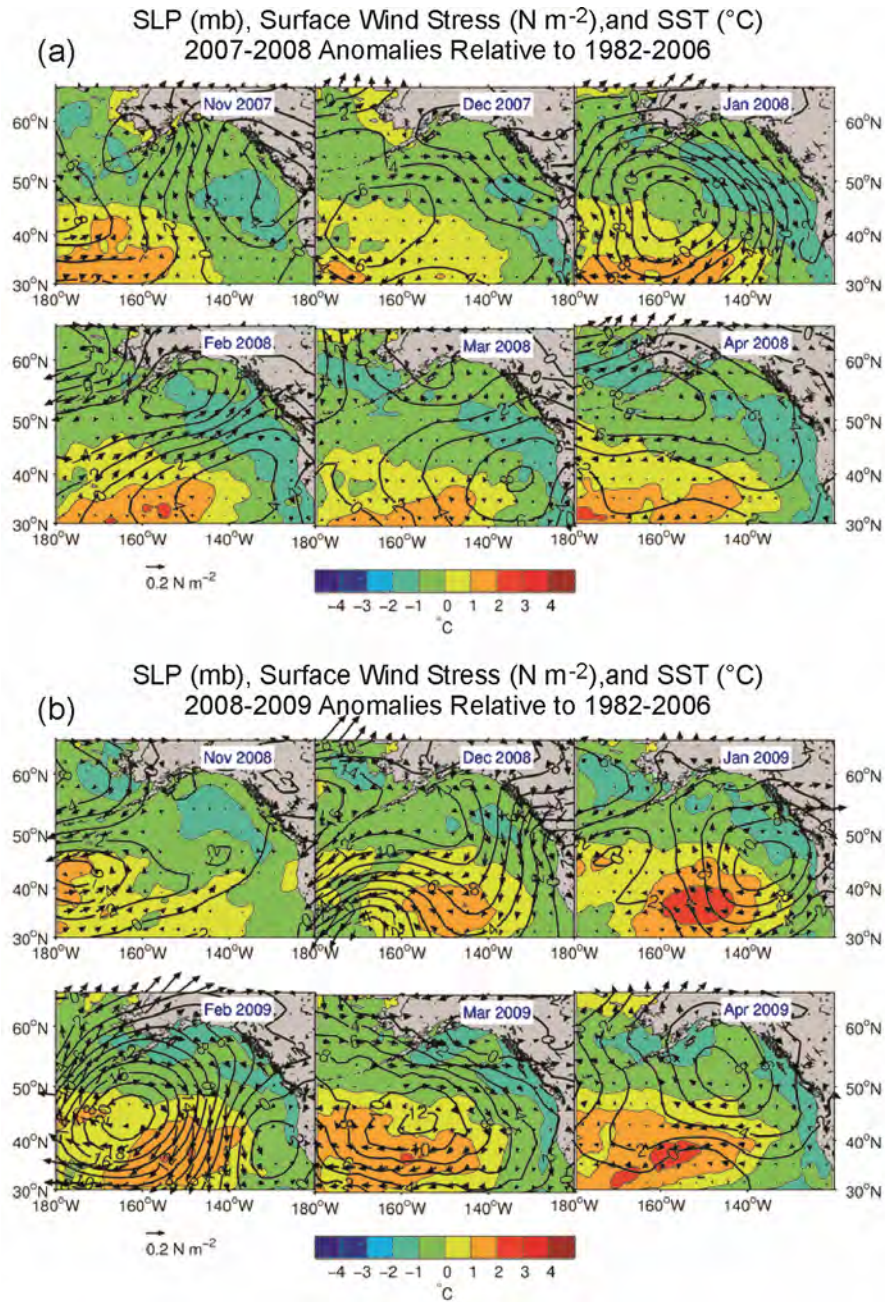
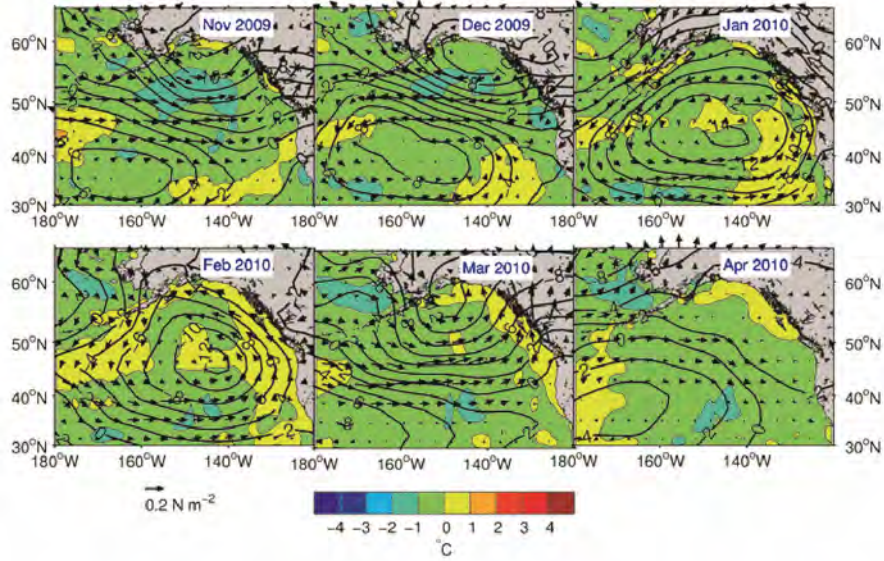


Figure 14. As for Figure 13 but for anomalies in which the seasonal cycle (mean monthly values) have been subtracted from the distributions to produce monthly anomalies. (a) 2007-08; and (b) 2008-2009.



(c) SLP (mb), Surface Wind Stress ( $\text{N m}^{-2}$ ), and SST ( $^{\circ}\text{C}$ )  
2009-2010 Anomalies Relative to 1982-2006



(d) SLP (mb), Surface Wind Stress ( $\text{N m}^{-2}$ ), and SST ( $^{\circ}\text{C}$ )  
2010-2011 Anomalies Relative to 1982-2006

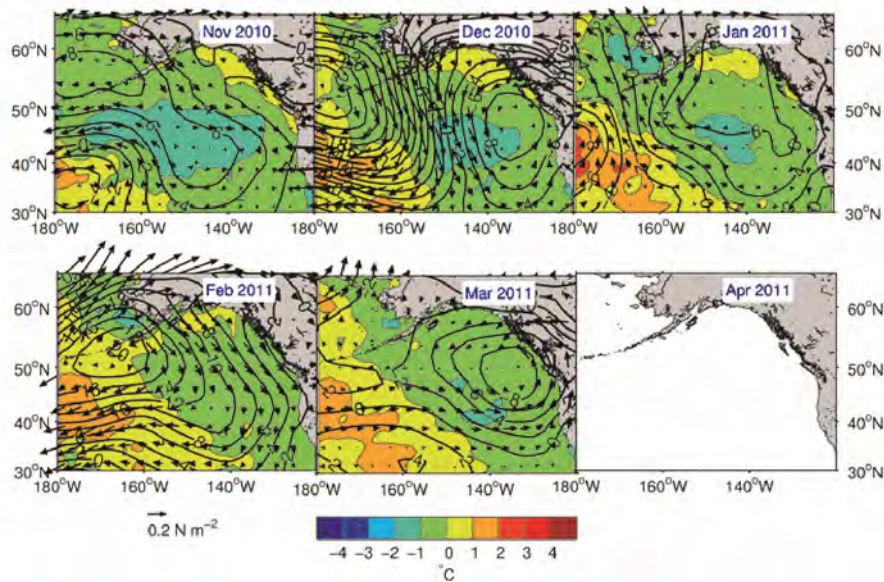


Figure 14 continued. (c) 2009-10; and (d) 2010-11.

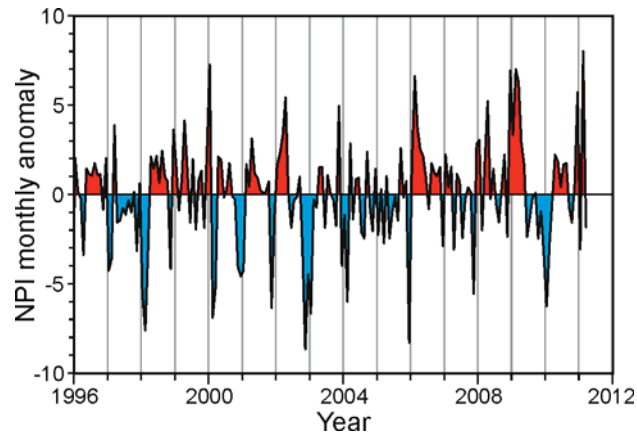


Figure 15. Time series of the North Pacific Index (NPI) anomaly for the past 10 years. The index is the area-weighted sea level pressure over the region 30°N-65°N, 160°E-140°W. [The NP Index Data was provided by the Climate Analysis Section, NCAR, Boulder, USA; Trenberth and Hurrell (1994); Climate Dynamics 9:303-319.] Data can be obtained from: <http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html>



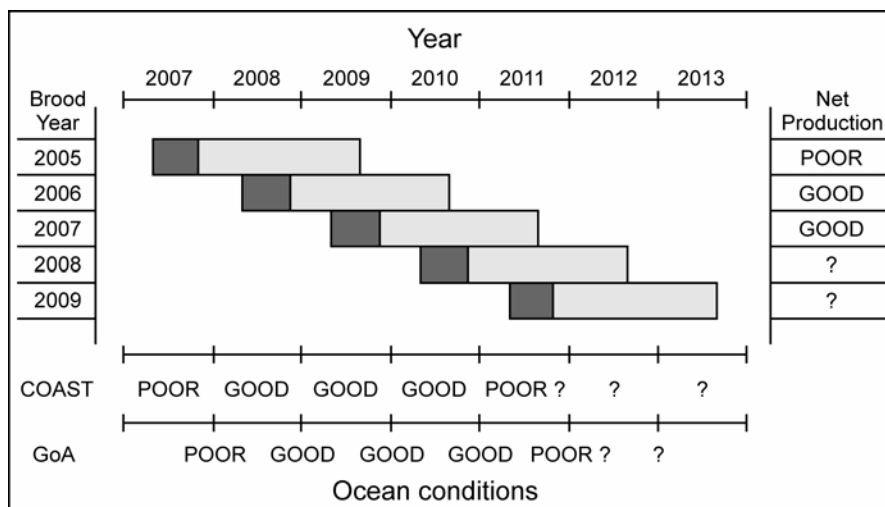


Figure 16. Schematic relating the affect of ocean conditions along the coast and in the Gulf of Alaska (GoA) on the net production of Fraser River sockeye salmon. Darker shading denotes the time that the stocks were within coastal waters; lighter shading corresponds to time the fish were in the Gulf of Alaska. Brood years are also presented.