Temporal and spatial responses of British Columbia steelhead (*Oncorhynchus mykiss*) populations to ocean climate shifts

D.W. WELCH,[1,]* B.R. WARD,[2]
B.D. SMITH,[3] AND J.P. EVESON[1]

[1]Ocean Sciences & Productivity Division, Pacific Biological Station, Department of Fisheries & Oceans, Nanaimo, BC, Canada V9R 5K6
[2]BC Ministry of Fisheries, Fisheries Research & Development Section, 2204 Main Mall, University of British Columbia, Vancouver, BC, Canada V6T 1Z4
[3]Environment Canada, Pacific Wildlife Research Centre, 5421 Robertson Road, Delta, BC, Canada V4K 3N2

ABSTRACT

The pattern of temporal change in recruitment of steelhead trout (*Oncorhynchus mykiss*) entering the ocean between 1963 and 1990 was geographically coherent in all regions of British Columbia. A major increase in recruitment was evident for smolts entering the ocean after 1977. Subsequently, an out-of-phase response occurred after 1990, indicating that the effect of a possible 1990 regime shift had both temporal and geographical structure. Steelhead entering northern regions had increasing recruitment, while steelhead entering southern BC coastal regions had sharply decreasing recruitment. The evidence clearly indicates that the overall recruitment response since 1977 was primarily shaped by changes in marine (not freshwater) survival. Similar sudden changes in adult recruitment also appear to be occurring for other species of Pacific salmon in BC and Oregon, such as coho (*O. kisutch*), which appear to occur suddenly and show considerable persistence. A possible explanation for the change is that ocean productivity declined in coastal regions of southern BC after 1990, reducing the marine growth of juvenile salmon. The Bakun upwelling index shows a pattern of geographical coherence along the west coast of North America that could in principle explain the observed pattern of changes in recruitment. However, no evidence for a temporal shift in this index occurring around 1977 and 1990 is apparent. The reason for the sudden and persistent decline in ocean survival is therefore uncertain.

Key words: Bakun index, coho, ocean climate, regime shift, salmon, steelhead, upwelling

INTRODUCTION

A shift in ocean climate occurred around 1977, which resulted in large-scale changes in biological productivity at several trophic levels in the Pacific Ocean (e.g. Hayward, 1997; McGowan *et al.*, 1998). Following 1977, both British Columbia (BC) and Alaskan salmon production increased sharply (Beamish and Bouillon, 1993; Francis and Hare, 1994; Hare and Francis, 1995; Magnuson *et al.*, 1996). Because the life history of salmon is divided into freshwater and ocean phases, it is generally difficult to discriminate the effects of freshwater from ocean survival changes on the recruitment to Pacific salmon. However, the concurrent increase in groundfish stocks (Beamish, 1993; Beamish and Bouillon, 1995) suggests that the critical changes affecting improved survival of salmon after 1977 occurred primarily in the ocean, because groundfish have no freshwater life history phase.

In addition to the relatively well-described temporal shift, there is also persuasive evidence that this shift in marine climate was not uniformly favourable, and that the climatic shift had significant geographical structure in addition to the temporal shift around 1977. Although zooplankton levels in the central Gulf of Alaska increased between the 1960s and the 1980s (Brodeur and Ware, 1992; Brodeur *et al.*, 1996), zooplankton abundances off California decreased to only 30% of their earlier levels (Roemmich and McGowan, 1995). Similar patterns of geographical change are evident for Pacific salmon populations, with stocks off Washington and Oregon decreasing at approximately the same time that more northerly populations began to increase (Pearcy, 1996; Mantua *et al.*, 1997; Hare *et al.*, 1999).

Some evidence for a shift in ocean climate occurring around 1989–90 has recently developed (Deser *et al.*, 1996; Trenberth and Hoar, 1996; Beamish *et al.*,

**Correspondence*. e-mail: welchd@pac.dfo-mpo.gc.ca
Revised version accepted 19 April 1999
Received 22 May 1998

1997a,b; Mantua *et al.*, 1997; Sugimoto and Tadokoro, 1997; Watanabe and Nitta, 1999). Watanabe and Nitta (1999) document perhaps the most extensive and persuasive evidence for abrupt changes in atmospheric circulation patterns throughout the Northern Hemisphere beginning around 1989. However, other atmospheric indices show more equivocal evidence for a persistent climatic shift. The Pacific Decadal Oscillation, a climatological index which has tracked past shifts in salmon production occurring in 1947 and 1977, reversed polarity in 1990, but subsequently weakened (Mantua *et al.*, 1997). The PDO index tracks an aspect of the geographical pattern of SST (sea surface temperature) anomalies in the North Pacific Ocean, and is also reflected in the pattern of central ocean SST anomalies. Deser *et al.* (1996) have also shown that these temperature anomalies propagate down from the surface through the thermocline to a depth of at least 400 m on a time scale of ≈1 year. The pattern of SST anomalies also shows evidence of having changed in 1990, indicating that the heat content of the upper ocean has also changed. Both chlorophyll and zooplankton levels also fell sharply in many areas of the Pacific Ocean and Bering Sea in the 1990s (Sugimoto and Tadokoro, 1997), at about the time when large-scale reductions in the exchange of water from the North Pacific into the Bering Sea were first observed (Stabeno and Reed, 1992).

More direct impacts on the physical structure of the ocean that should influence the food chain are also evident. Freeland *et al.* (1997) show that the thickness of the surface mixed layer at Ocean Station P has decreased over time, although the statistical fit of an abrupt step-like change in 1977 and a more gradual linear decrease over the entire time series is statistically indistinguishable (H. Freeland, *pers. comm.*). Sharp decreases in winter nitrate levels during the 1990s plus the thinning of the mixed layer have resulted in nitrate being completely depleted by midsummer for a broad region of the Gulf of Alaska west of the British Columbian shelf, reducing biological production at the base of the food chain by 40% (Whitney *et al.*, 1998).

There is also evidence for other recent and long-term changes in production for fish populations in the North Pacific Ocean that are clearly the result of climate changes rather than fishing (Kawasaki *et al.*, 1991; Kawasaki and Omori, 1995). For example, both Asian and Californian sardine populations increased rapidly following the climate shift of 1977, as did North American salmon populations (Klyashtorin and Sidorenkov, 1996; Klyashtorin and Smirnov, 1995). There are also very long-term (century-scale) changes in the productivity (or possibly shifts in the geographical distribution) of sardine populations off California that have occurred in the absence of any commercial fisheries (Baumgartner *et al.*, 1992). Similar sudden declines over the last five centuries in the abundance of some salmon populations in the northern North Pacific Ocean have also been found (Finney, 1998).

Despite many years of study, the relative effects of fishing and climate on determining the size of fish populations are still unclear. Recently, serious declines have occurred in the abundance of many of the salmon populations on which fisheries in south-central British Columbia are based. This paper presents evidence for a major climatological shift in the mean state of the ocean occurring around 1990, as indexed by the large changes in marine survival of steelhead trout (*Oncorhynchus mykiss*) populations that have occurred as a result. A unique aspect of this study is that we show that the 1990 climatological shift also had geographical structure – the population response of fish entering southern coastal waters had a very different pattern from that seen for fish entering northern BC coastal regions.

CONCURRENT CHANGES IN SALMON POPULATIONS

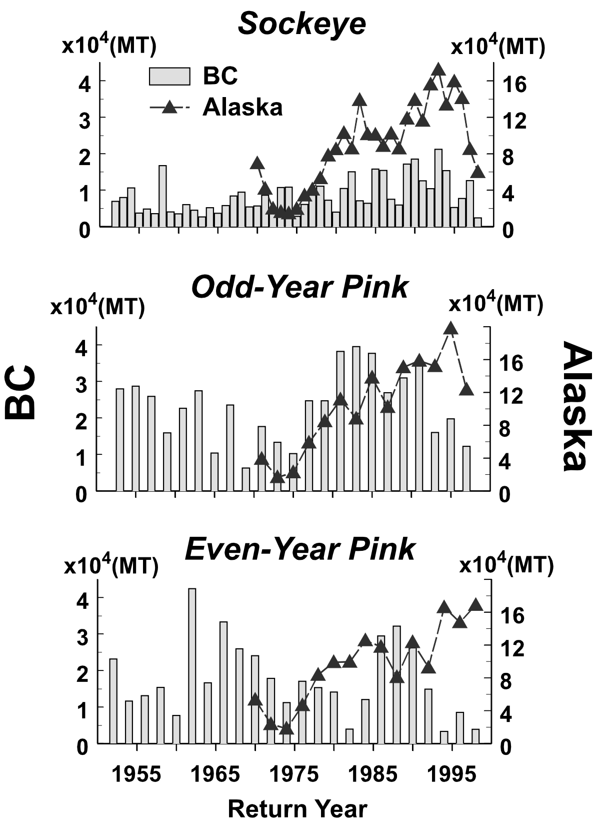
General patterns of the geographical response

Following the 1977 regime shift, both BC and Alaskan salmon production increased sharply (Beamish and Bouillon, 1993; Francis and Hare, 1994; Hare and Francis, 1995; Magnuson *et al.*, 1996). Alaskan sockeye (*O. nerka*) and pink salmon (*O. gorbuscha*) production increased greatly after 1976 (Fig. 1), and BC production also increased at more moderate levels. However, salmon production in Washington, Oregon and California showed the opposite response, beginning a downward slide which has resulted in the closure of most salmon fisheries. The dividing line between areas of improved salmon production post-1977 seems to have occurred at roughly the BC–Washington border. Although the specific reasons for the decline are still not understood, there is now a consensus that at least part of the cause was in the ocean, not freshwater (Emmett and Schiewe, 1997).

After 1989–90, sharp reductions in total BC salmon production have occurred for all species. However, unlike the 1977 regime shift, the changes in BC salmon production observed in the 1990s are geographically disjunct.

Salmon returns to northern BC continued to increase, similar to the continuous increase seen since

Figure 1. Trends in BC (bars) and Alaska (line) catches of sockeye and pink salmon.



1977 in Alaska. For example, the 1996 catch of Skeena R. sockeye was the highest on record, and the 1996 Nass R. sockeye returns were also very high; both runs increased sharply in the 1990s (Wood *et al.*, 1997). However, salmon production in south and central coast regions of the province dropped sharply. Central coast sockeye stocks declined sharply after 1990, with marine survival of Rivers Inlet sockeye stocks near zero (McKinnell *et al.*, 1998).

Fine-scale evidence for a marine cause

Keogh River steelhead. The study of the population dynamics of Pacific salmon is complicated by the difficulty in partitioning the relative importance of freshwater and marine effects on survival. For almost all salmon populations in North America where both adult spawning numbers and subsequent recruitment can be estimated, it is not possible to separate these effects because the abundance of smolts as they enter the ocean is not measured. An exception to this problem is the Keogh River study (Ward and Slaney, 1988), where a counting fence positioned at the mouth of the river allows an accurate census of the number of steelhead smolts entering the ocean, and the number of adults that subsequently returned each year since 1977.

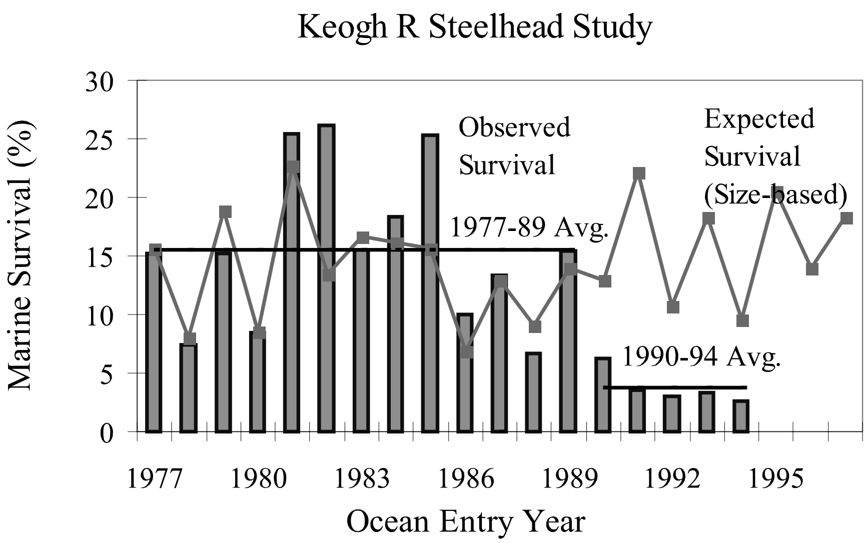
The Keogh River is at the north-eastern tip of Vancouver Island, in southern British Columbia. Between 1977 and 1989, the smolt-to-adult survival of Keogh R. steelhead averaged 15–16% (Ward, 1996) and deviations were strongly related to size at ocean entry (Fig. 2). Smolts entering the ocean at larger sizes subsequently experienced significantly higher survival (Ward *et al.*, 1989). However, smolt-to-adult (marine) survival dropped sharply beginning in 1990, to less than 4%, and size at ocean entry no longer provided a satisfactory prediction of subsequent survival. The years 1990 to 1994 have had the lowest ocean survivals on record. The resulting adult recruitment during the winters of 1996–1998 has been extremely low, leading to the emergency closure to fishing of most steelhead rivers along the east coast of Vancouver Island.

The Keogh study shows that a sharp change in marine survival occurred for Keogh smolts entering the ocean in 1990 and subsequent years. There are three important conclusions following from this result. (1) Marine survival of steelhead trout dropped in 1990, two years *before* mackerel (a predator on juvenile salmon) were observed on the west coast of British Columbia (Farrell, 1997), but at the time a number of climate indices were observed to change. (2) The change in survival affected relatively large fish. Keogh steelhead typically enter the ocean at 16–18 cm in length; thus the climatic change affected even relatively large fish, which were capable of foraging effectively. Match–mismatch and other theories associated with a critical period in the very early life history of fish are therefore not the explanation for the change in marine survival. (3) It is possible to distinguish between survival changes occurring in the ocean and freshwater, and to show that the changes in marine survival are an important component of the overall population response.

Geographical response of steelhead

Adult steelhead return with high fidelity to their natal stream (Burgner *et al.*, 1992). Change in adult recruitment levels to freshwater streams may therefore be associated with specific entry points for the smolts into the coastal ocean three years earlier (the approximate time from smolt entry until return as adults). A comparison of adult steelhead catch rates by anglers in individual BC streams permits a generalization of the recruitment response and an examination of how widespread the 1990 shift in marine survival was in British Columbia.

Figure 2. Changes in marine survival of Keogh River (northern Vancouver Island) steelhead trout relative to year of ocean entry. From 1977 to 1989, marine survival averaged 15.5% and deviations from this average were closely correlated with size of smolts at ocean entry; larger size at ocean entry resulted in higher subsequent survival. Marine survival in 1990 and later years dropped to only one-fourth of its former average and was no longer related to size at ocean entry. A broad-scale pattern of change in marine survival is also evident, with survival increasing to a maximum in the early 1980s and then declining; however, the sudden decline in 1990 is the dominant feature of the time series.



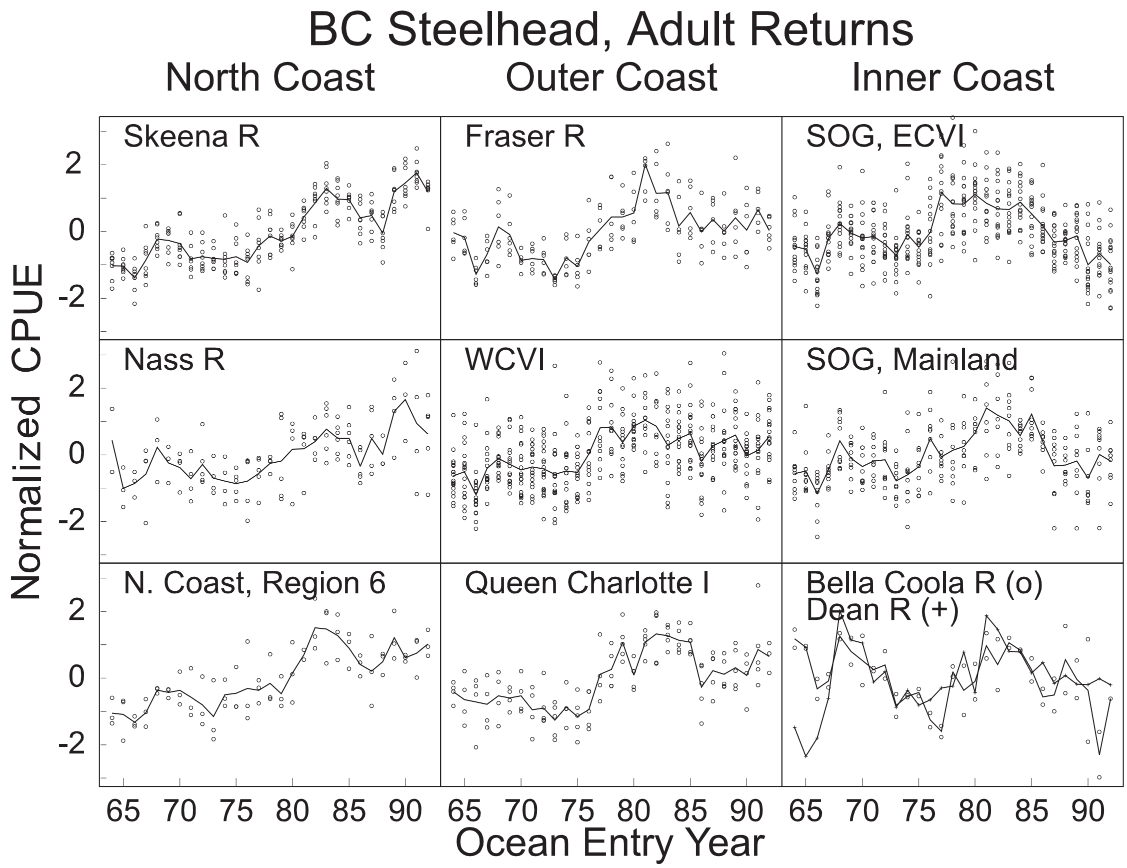
The Province of British Columbia has kept standardized records of steelhead angler success since 1966. The records permit a comparison of angler success as catch-per-angler-day (CPUE) for individual tributaries within all river watersheds in British Columbia. All time series were first square-root transformed to remove a dependence of the variance on the mean CPUE. We then calculated time series of standardized angler catch rates for individual tributaries within all watersheds by normalizing the resulting CPUE time series available from 1966 to 1996 for each individual tributary by subtracting the mean and dividing by the standard deviation (Fig. 3).

Full details of the database and our assessment of the reliability of the data for tracking adult steelhead can be found in Smith *et al.* (2000). In general, the trends in adult steelhead recruitment indexed by these data show a good match with independent indices of steelhead abundance over time that can be generated from test fisheries operated at the mouths of rivers to estimate salmon abundance, and with snorkel surveys of in-river adult steelhead abundance conducted by provincial biologists. A calculation of the effect of implementing catch-and-release regulations in recent years suggests that although this might elevate CPUE values (because the same fish could be caught several times), it does not change the trend nor does it explain the difference in CPUE values between northern and southern BC described below.

A strongly coherent geographical pattern of returns of adult steelhead to British Columbia rivers is evident. Returns rose sharply for smolts entering the ocean in 1977 and later years in all regions of the province, consistent with the general response seen for other fish species (Fig. 4). Within a given region, the pattern of change in adult returns to nearby river systems is remarkably consistent, suggesting a common effect of the 1977 regime shift on different populations of British Columbia steelhead.

Comparison of the marine survival pattern for Keogh River steelhead with the adult returns shows that the province-wide increase in adult recruitment in the early 1980s was also evident in the pattern of change in marine survival for Keogh River steelhead (Fig. 4). For ocean entry years starting in the late 1980s a strongly disjunct response is evident (Fig. 5). Recruitment to northern BC rivers (Skeena, Nass and all other north coast rivers aggregated) increase in parallel. However, recruitment for south and central coast stocks declined continuously since the beginning of the 1990s, mirroring the marine survival pattern seen for the Keogh River study population, one of 26 rivers situated in the Strait of Georgia–Johnstone Strait region. Fraser River and outer coast stocks show an intermediate response. The Fraser River empties

Figure 3. Temporal changes in the relative returns of wild steelhead to individual tributaries within major watersheds or regions (circles). The average response for each region or river is also shown, applying equal weighting to the data for individual tributaries. (SOG, Strait of Georgia; ECVI, east coast Vancouver Island; WCVI, west coast Vancouver Island; see Fig. 6 for locations).



into the southern Strait of Georgia (Fig. 6). The coherence of adult steelhead recruitment with outer coast stocks suggests that steelhead smolts from Fraser River populations migrate out to the west coast of Vancouver Island through the Strait of Juan de Fuca and then north along the outer coast.

Comparative changes in ocean survival of coho. Steelhead and coho salmon share a number of common life history features, including an extended period of residence in rivers as juveniles followed by entry into the ocean at a rather large size relative to most other species of Pacific salmon. Pearcy (1996) discussed the pattern of changes in adult returns and ocean survival of Oregon coho up until the early 1990s and reviewed evidence for the effect of a number of marine factors on their survival. Beamish *et al*. (2000) show that more recent data indicate large-scale declines in the ocean survival of coho (*O. kisutch*) starting around 1990 for regions extending from Oregon north to southern British Columbia.

Although the exact times at which large-scale changes in marine survival occur are a matter of some debate, there have been significant changes in ocean survival of both species (Fig. 7). We calculated the average marine survival of Oregon (OPI) coho for the three regime periods of 1960–1977 (6.1%), 1978–1990 (3.3%) and 1991–1995 (0.5%). (We included survival for 1990 in the post-1977 period because the sudden drop in marine survival appeared to occur in 1991.) Marine survival in 1991 and later years declined to an average less than 1/5th the rate evident in the 1978–1990 period, and only 1/10th that holding prior to 1978. Although the time that the climatic shift had its impact on Oregon coho seems to be ≈1 year later than occurred for Keogh River steelhead, a sharp drop in ocean survival is evident for both regions in the 1990s that shows considerable persistence.

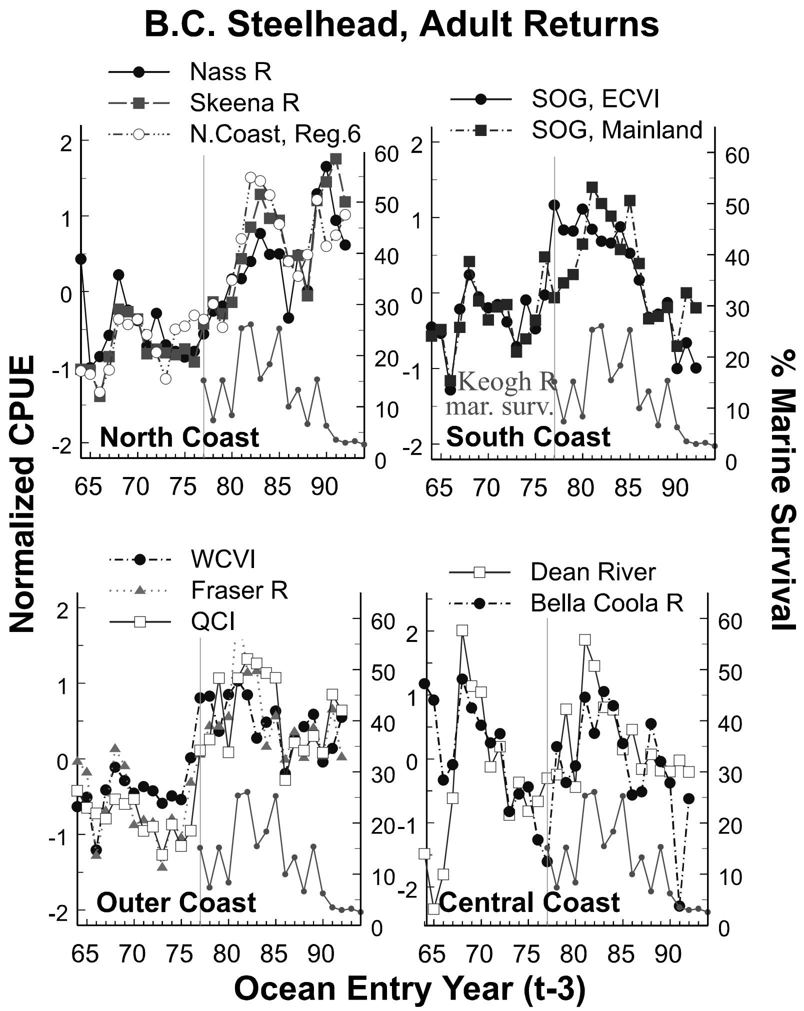


Figure 4. Changes in normalized angler catch rates for wild adult steelhead caught in British Columbia watersheds. Each time series was lagged back 3 years to the approximate year of ocean entry. Normalized abundance indices are grouped by geographical regions, with rivers with major steelhead populations shown separately, and rivers with minor populations aggregated. Following 1977 (vertical line), adult steelhead recruitment to all areas of the BC coast increased sharply. A period of high returns in the early 1980s is evident in all regions, as well as a smaller increase in the late 1960s. Steelhead abundance, based on CPUE, increased or stayed the same after 1990 for all rivers in northern BC, while south and central coast populations show sharp declines; outer coast stocks show an intermediate response. Marine survival for the Keogh R. population is superimposed on each graph.

A similar conclusion holds for a direct comparison of British Columbia steelhead and coho; the pattern of change in Keogh River wild steelhead survival from 1983 to 1993 was highly correlated with wild coho survival from British Columbia (data from Beamish *et al.*, 2000; $r^2 = 0.83$, $P < 0.05$).

Patterns of change in the Bakun wind index. The results in the previous sections indicate that large-scale coherent changes in survival of North American steelhead and coho occurred at the time of the 1977 climate shift. The response of steelhead and coho stocks indicates that a second climatic shift occurred around 1990, which resulted in decreased marine survival in coastal regions stretching from central British Columbia to as far south as Oregon, while survival in northern British Columbia and Alaska either increased or stayed the same. Thus the climatic shift did not include just a temporal change, but also a geographical change in the regions of good or poor marine survival. A candidate mechanism to explain this broad-scale pattern of changes in marine survival must therefore also show evidence for both a temporal change around 1990 and a simultaneous northward shift in the area of coherent effects from roughly the British Columbia–Washington border to central British Columbia waters.

Atmospheric winds show large-scale patterns of geographical and temporal coherence, as well as a sudden change in the winter of 1989, that make them a good candidate for forcing changes in the ocean (Watanabe and Nitta, 1999). We examined the patterns of coherence in the upwelling-favourable winds along the west coast of North America at 15 standard locations (Fig. 8) calculated by the NOAA Pacific Fisheries Environmental Group (http://www.pfeg.noaa.gov/products/upwell.html). The Bakun upwelling indices are based on estimates of offshore Ekman transport driven by geostrophic wind stress, and averaged to monthly values. They are expressed in

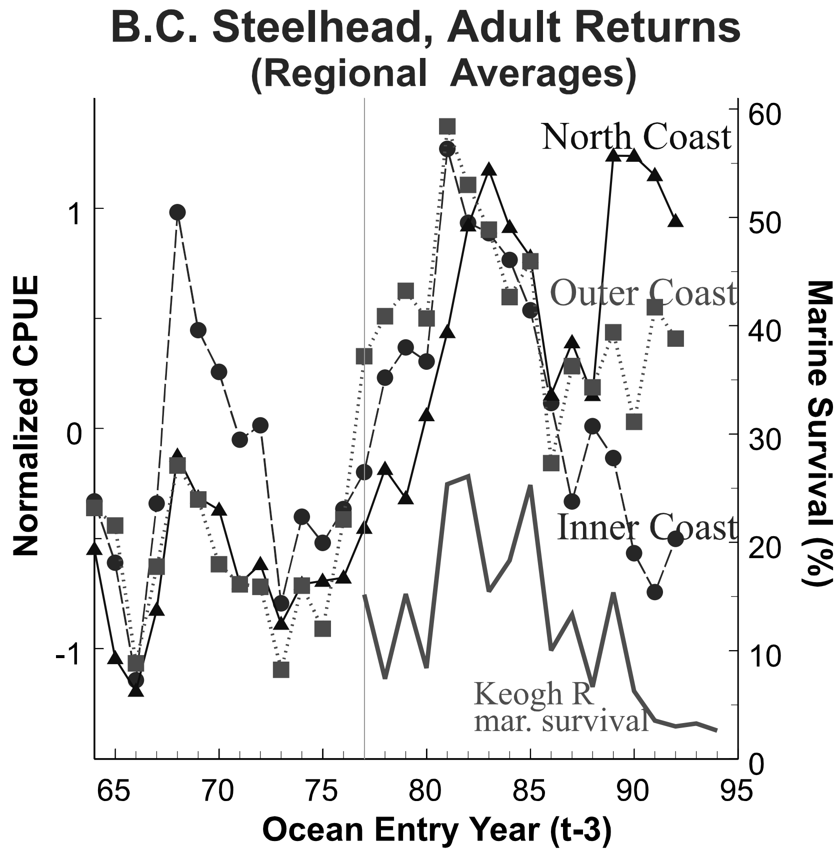


Figure 5. Aggregated steelhead recruitment patterns for three regions of the BC coast. Adult returns to north coast rivers increased sharply for smolts entering the ocean in 1989 or later years, and dropped for south and central coast regions. Outer coast stocks show an intermediate response. 'Inner Coast' is the response averaged over all south and central coast rivers.

units of cubic metres of upwelling per second per 100 metres of coastline. Monthly values of the Bakun winds were analysed for the period January 1946 to March 1997. We first conducted a hierarchical cluster analysis on the correlation matrix of upwelling indices to examine the groups into which the months or regions clustered, so as to reduce the dimensionality of the data set.

To do so we averaged over all 15 regions, to obtain a single set of 12 monthly values for the upwelling indices in the years 1946–1997, and then performed a cluster analysis on the monthly time series to identify seasons of similarly varying winds for the whole coast (Fig. 9). We then aggregated the monthly indices indicated by these clusters into three seasonal indices: winter (Oct.–Feb.), spring (March–June), and summer (July–Sept.). For each of these three seasons we then compared the pattern of geographical clusters to identify regions of geographical coherence in the pattern of upwelling-favourable winds.

The clearest spatial clusterings are for summer (Fig. 10), the period of strongest upwelling, and the season following the April–May entry of juvenile salmon into the ocean. The results from the cluster analysis indicate that the summer winds fall into a series of internally coherent geographical regions. Stations in the northern Gulf of Alaska (A–E) positively covary, and clearly cluster separately from Stations F–O lying to the south.

Stations E and F are near the northern and southern ends of Vancouver Island, respectively, close to the coastal region showing sudden changes in ocean survival relative to areas to the north after 1990. The two stations fit into different clusters, indicating that the patterns of coherence in the Bakun winds are different between regions E and F. Curiously, there is some indication for an intensification in upwelling-favourable summer winds for station F after 1977, but not for the regions to the north where most of the improvement in salmon survival actually occurred (Fig. 11). Following 1990 there is a weakening of the Bakun index for Station F and a somewhat reduced pattern of coherence in the pattern of change in the winds between Station F to the south and Stations A–E to the north.

The sudden change in the geographical pattern of survivals in southern British Columbia and Oregon could be explained if the pattern of regional coherence

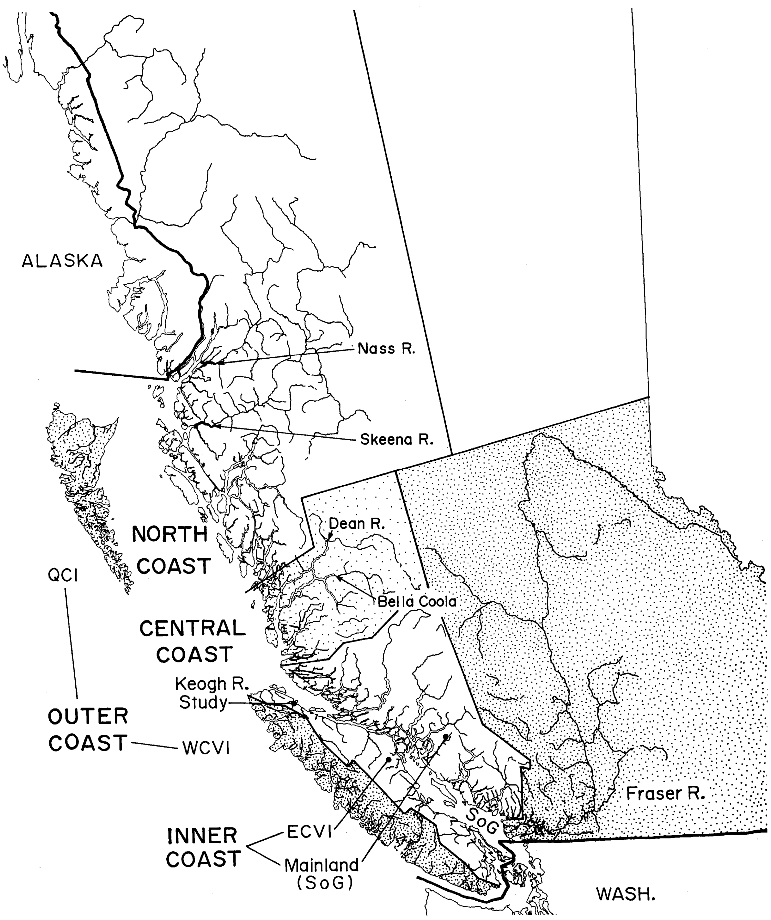


Figure 6. Location of the tributaries contributing data on angler CPUE, with major rivers indicated. Areas with similar patterns of coherent steelhead abundance responses are shown by shading. North Coast region includes rivers north of the Dean R. and south of Alaska. The Central and South Coast region includes stocks that must enter either the Strait of Georgia (SoG) or the area just to the north; the Keogh R. is indicated. The outer coast region (stippled) includes west coast Vancouver Island and Queen Charlotte Island (QCI) stocks plus the Fraser River watershed.

in upwelling-favourable wind flows changed after 1990. However, to be consistent with the change in observed survivals for steelhead and coho, a change in upwelling-favourable winds should occur about 1990, and the coastal region indexed by Station E (near the Keogh River) should also follow the wind pattern for regions to the south.

However, there is little convincing evidence for either change in the winds. Thus, although there was a marked intensification of the Aleutian Low following 1977, the Bakun index shows little evidence of a change in the degree of coastal upwelling. Analysis of the changes in sea surface temperature (SST) occurring in the 5-year periods before and after 1990 showed that a slight warming of about 0.5°C was evident around Vancouver Island, but again provided little convincing evidence for major oceanographic change.

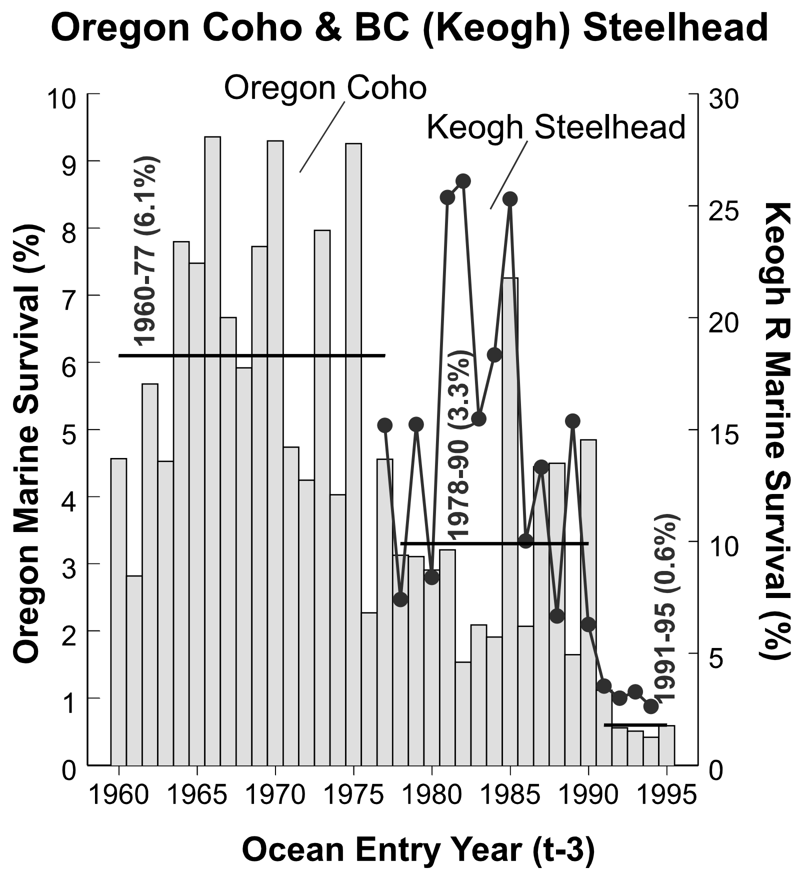
Changes in size at return. An analysis of the evidence for a decline in ocean productivity based on the size of returning sockeye shows that the late 1980s again seems to be a pivotal period. We calculated the average length of female sockeye measured on the eight major spawning grounds in the Fraser River, and then divided the annual mean lengths by the stock average. We then cubed the index to provide a rough measure of the change in weight that occurred. Sharp declines in adult size are evident for most stocks of Fraser sockeye beginning around 1989 (Fig. 12).

DISCUSSION

Most ocean fisheries for salmon exploit a mixture of populations, complicating the reconstruction of trends for individual populations. In addition, because Pacific salmon spend the first phase of their life history in freshwater and the second phase in the ocean, it is frequently difficult to establish whether declines in productivity are due to marine or freshwater effects.

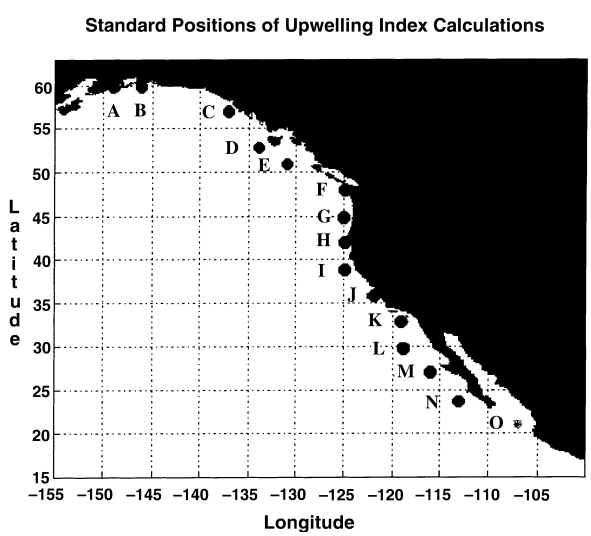
Winter-run steelhead trout (*O. mykiss*) return to their natal streams much later than other species of salmon, eliminating confounding effects on recruitment from commercial fishery interceptions. Escapement to freshwater therefore indexes the changes in total recruitment over time. Because the relative

Figure 7. Comparison of the changes in marine survival of Oregon coho (bars) and Keogh R. steelhead (line). A large drop in ocean survival occurred in both regions during the 1990s. Horizontal lines indicate average marine survival for Oregon coho during three potential regime periods.



recruitment of adult steelhead to individual freshwater streams can be indexed by changes in angler success over time in British Columbia (Smith *et al.*, 2000), and steelhead return to their natal streams with high fidelity (Burgner *et al.*, 1992), changes in adult recruitment can be related to very specific geographical entry points for the juveniles along the coast of British Columbia about three years earlier.

Figure 8. Station locations used in the upwelling analysis (data provided by NOAA Pacific Fisheries Environmental Group, Monterey, California).



The pattern of adult recruitment in British Columbia steelhead trout indicates that these changes in productivity are the result of sudden declines in ocean survival occurring in south-central regions of the province. Furthermore, these changes in survival appear to have sharply defined geographical as well as temporal features. This general finding is not affected by whether the rivers for which only winter-run stocks of steelhead are selected for examination, which are not subject to commercial fishery interceptions, or the broader base of rivers which includes both winter- and summer-run populations. The data therefore suggest that both the geographical and temporal boundaries defining the time periods and geographical regions of climatic 'regimes' can shift suddenly in the oceans.

The geographical clustering and strong temporal coherence of adult returns indicates that recruitment of British Columbia steelhead improved in all regions of the province after the 1977 climate shift. In the

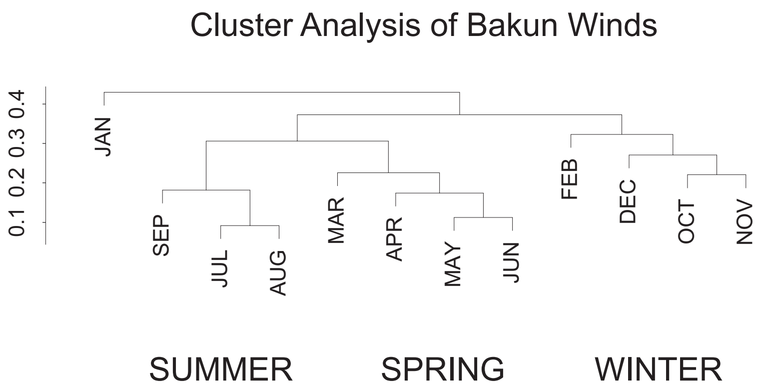


Figure 9. Seasonal clustering of the Bakun wind index. Data for all stations were averaged to form a single monthly value for the 1946–1997 time series.

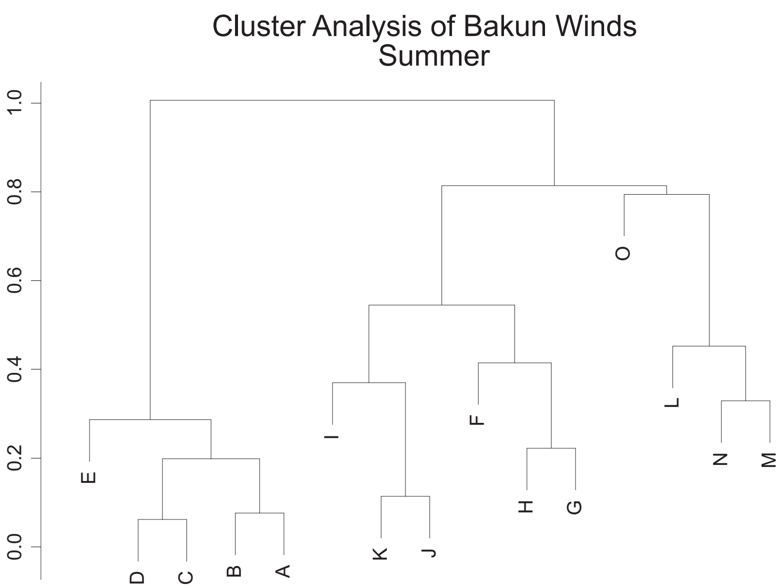


Figure 10. Cluster analysis of the summer winds. The data for July–September were averaged to form a summer time series for each station. The largest differences are between Stations A–E to the north and all areas to the south. Stations E and F are located near the northern and southern ends of Vancouver Island, at roughly the locations separating poor and good ocean salmon survival after 1990 and 1977, respectively. The two stations lie in different clusters.

years following 1977 (when data for Keogh River steelhead are available), the pattern of increase then decline in marine survival during the 1980s and its consistency with adult recruitment suggests that the major factor influencing the overall recruitment pattern was change in ocean rather than freshwater survival.

There is clear evidence for a second climatic shift affecting steelhead around 1990. However, unlike the 1977 shift, which affected all areas of the province similarly, the 1990 shift had a different effect depending upon the region of the coastal ocean the juvenile steelhead entered. Ocean survival of steelhead entering coastal waters from rivers in the southern region of BC decreased, causing large-scale declines in steelhead populations after 1990. Steelhead entering the coastal zone from rivers in northern BC or outer coastal regions in southern BC experienced stable or improved recruitment at this time. It is of note here that Fraser River steelhead, which first must enter the Strait of Georgia, show the same pattern of change as west coast of Vancouver Island and Queen Charlotte Island stocks, suggesting that the migration paths of these fish follow those of the outer coast stocks, and that they likely spend little time in the Strait of Georgia or its northern extension, Johnstone Strait.

The geographically disjunct response suggests that whatever change occurred in the ocean that reduced salmon survival in Washington and Oregon waters moved quickly northward following 1989/90, so that salmon entering south-central BC coastal waters experienced the same poor conditions for survival first experienced by Washington and Oregon salmon after 1977. In southern British Columbia waters, ocean survival decreased to less than one-quarter of its previous value beginning in the summer of 1990. Because the ocean changes following 1990 also decreased coho survival in Oregon rather than improving them, the

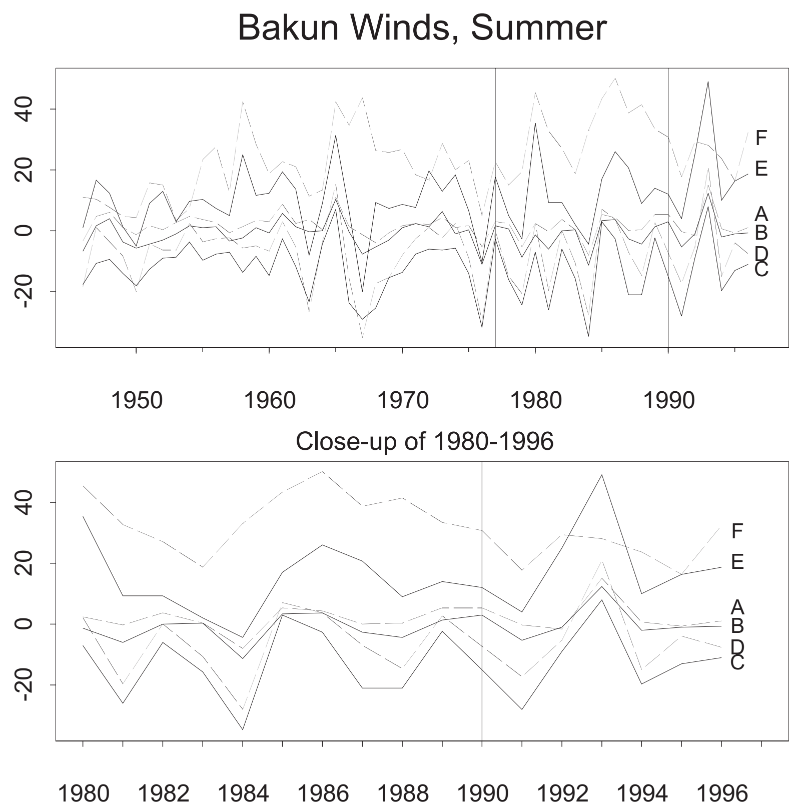


Figure 11. Changes in the Bakun upwelling index for Stations A–F (summer average). No marked changes are evident at the time of either the 1977 or the 1990 climate shift.

1990 event is best described as a geographical extension (and possible intensification) of those conditions occurring after the 1977 climate shift, rather than a reversion to previous conditions.

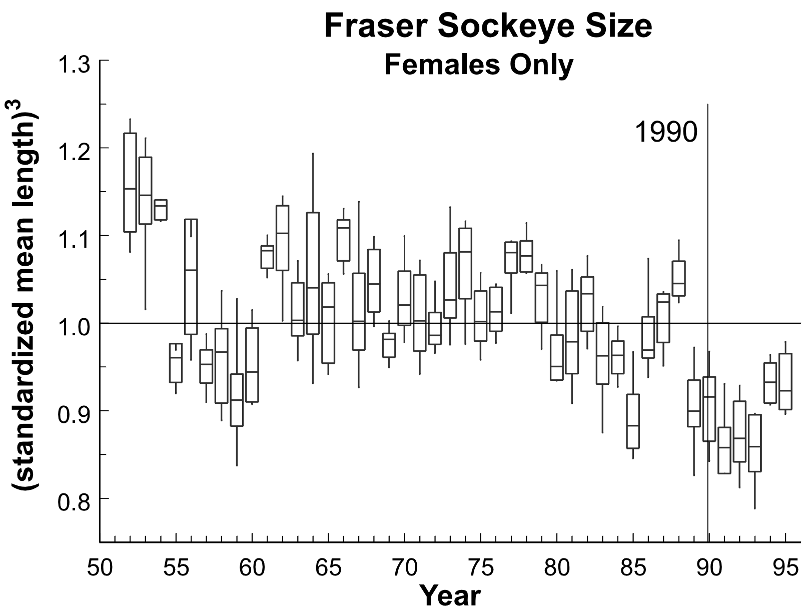
The rapidity of the decline in survival is particularly remarkable because juvenile steelhead and coho enter the ocean at large size (16–18 cm and 9–11 cm, respectively), and are capable predators in their own right. It is thus very unlikely that the cause of the decline in survival can be due to a match/mismatch mechanism where larval fish fail to encounter a patch of sufficiently dense plankton.

Juvenile salmon migrate northwards along the continental shelf of the Americas in the summer (Hartt and Dell, 1986). By the late autumn and early winter, most appear to have moved at least as far as the Aleutians while remaining strictly on the continental shelf (Welch *et al.*, 1997a, 1997b, 1998). As a result, juveniles entering southern coastal regions of the ocean must eventually migrate north through regions where marine survival for those stocks to the north had improved. Thus the factors contributing to poor survival in the 1990s probably occurred in the coastal regions defined by the river mouths of those stocks with poor survival. A second possibility is that changes in offshore pelagic regions of the ocean might also have resulted in reduced survival, but this seems less likely because the juvenile migration paths of most salmon species confines them to the continental shelf.

There is some evidence that juvenile steelhead have a different pattern of ocean migration, and move directly offshore rather than north along the shelf (Hartt and Dell, 1986; Burgner *et al.*, 1992), and that individuals from the same population may school together while offshore (McKinnell *et al.*, 1997). This would imply a potentially greater role for offshore processes in determining survival. However, most juvenile steelhead that have been tagged were tagged along the continental shelf around Kodiak Island, and the single return for a Washington–Oregon steelhead tagged as a juvenile at sea was for an Oregon fish tagged on or near the shelf off Kodiak Island, Alaska (Hartt and Dell, 1986). Therefore, although some proportion of the juvenile steelhead may move directly offshore, there is also direct evidence that at least some of the juveniles move northwards along the continental shelf, and thus reach the coastal regions favourable to marine survival in northern British Columbia.

The sharp changes in ocean survival taking place in the 1990s are coincident with the shallowing of the mixed layer in this region (Freeland *et al.*, 1997) and

Figure 12. Changes in mean size of female sockeye salmon carcasses measured on eight major spawning grounds within the Fraser River. Annual mean lengths for each stock were standardized by dividing by the long-term mean to correct for differences in size between stocks, and then the resulting value cubed to give an approximate estimate of the change in weight over time. Results are expressed as a box-and-whisker plot of the stock-specific annual means; the horizontal line shows the median size and the whiskers show the range. A sharp drop in mean adult weight is evident beginning around 1989, the time when significant changes in atmospheric circulation were first noted (Watanabe and Nitta, 1999).



the summertime depletion of nitrate in offshore waters of the Gulf of Alaska in the 1990s in a region some 400–600 km wide (Whitney *et al.*, 1998). Both observations suggest that a fundamental change in the ecosystem dynamics of the NE Pacific from an iron-limited to nitrate-limited ecosystem for at least part of the year might be occurring. During the winters of 1994–95, widespread mortality of pelagic seabirds (especially northern fulmars, *Fulmarus glacialis*) owing to starvation was observed from Vancouver Island south to the coast of Oregon. Post-mortem examination of these birds revealed no food in their guts, and no residual stores of body fat, and the conclusion was that the birds died from emaciation and stress-responses associated with starvation (CCWHC, 1996). The size of adult sockeye returning to all major spawning grounds in the Fraser River also dropped by 15% in 1989, suggesting reduced feeding success during their return migration through offshore and/or coastal waters. Both changes suggest either that the productivity of coastal regions was affected directly by the climatic shift or that the export of productivity from offshore pelagic regions to the shelf was reduced.

Two lines of evidence point to a reduction in net biological productivity. First, prior to the drop in the mean size of sockeye salmon in the 1990s, average size had remained stable since the 1960s. The decline in length is equivalent to about a 15% decline in weight; if the growth reduction is assumed to be confined to the last marine year, this would require a 30% drop in marine growth rates because sockeye approximately double their weight each year of life in the ocean (Ricker, 1962, 1976). Sample sizes for Keogh R. steelhead are much smaller, but these data also indicate that marine growth of steelhead may have dropped after 1990.

Prior to 1990, size at ocean entry was a good predictor of mean survival rates for Keogh R. steelhead (Ward and Slaney, 1988), with marine survival increasing from 5% at an initial smolt size at ocean entry of 16 cm to 35% for smolts entering at 22 cm; for each 1 cm increase in ocean entry between 16 and 20 cm, survival to recruitment increased by 5%. To put this increase in perspective, each 1 cm increase in initial size *doubled* survival over that obtained at 16 cm, and therefore doubled steelhead recruitment. Similar size-related mortality relationships have also been reported for other species such as coho (Holtby *et al.*, 1990) and chum salmon (Healey, 1982).

In 1990 and later years, the positive relationship between size at ocean entry and subsequent survival failed for Keogh steelhead (Fig. 2). A possible explanation for the sudden decline in steelhead survival after 1990 and the change in growth of adult sockeye in 1989 is that reduced ocean productivity led to reduced growth rates for maturing sockeye during their migration from offshore feeding grounds in the central and western Gulf of Alaska, and reduced growth rates for juvenile steelhead entering southern and central coastal areas. Slower juvenile growth would result in steelhead remaining in smaller size groups with consequently higher mortality rates for longer periods of time; predator populations would not necessarily have to change to cause the observed change in salmon survival. However, the growth of juvenile steelhead and other salmon stocks in northern areas of the province and in SE Alaska must have remained as high as (or higher than) in the 1980s for this mechanism to be a consistent explanation for the differences in marine survival between these areas.

Increases in the intensity of upwelling off Oregon were positively related to Oregon coho survival before 1977, but appeared to have only a statistically negligible (and negative) relationship afterwards (Pearcy, 1996). Holtby *et al.* (1990) also reported a possible influence of upwelling-favourable winds on coho survival off the west coast of Vancouver Island, again with a possible change in the pattern of the relationship around 1977.

Ware and McFarlane (1989) included the region from northern Vancouver Island south through Washington and Oregon as part of the Coastal Upwelling Domain, and regions to the north of the Queen Charlotte Islands as part of the Coastal Downwelling Domain (the intervening region was defined as a transitional zone). The coastal regions we identified in the 1990s as having improved or reduced marine survival roughly fit these geographical classifications, but we have been unsuccessful in identifying a change in a physical factor that can account for the changes that we see.

Our results for steelhead suggest that the geographical separation of good and poor survival regions shifted north to central British Columbia waters around 1990. Unfortunately, although this provides a possible basis to explain why steelhead populations in southern BC now experience different ocean survival conditions than do northern BC populations, patterns of geographical coherence in regions of upwelling-favourable winds show little evidence for the northward movement of the dividing line between the regions of coherent winds in 1990 to include the region up to northern Vancouver Island (nor little evidence of a change in 1977, the time of the first climatic shift). Thus, although the large-scale pattern of geographical coherence in the wind fields off the west coast of North America provides a promising mechanism to explain coherent patterns of change in ocean survival, the Bakun wind indices show little evidence of this change. The Bakun index is only a proxy for the effect of winds on the oceans. However, we have also examined regionally corrected wind fields for the west coast of Canada that include corrections for topographic steering and other factors on the strength and direction of the local winds (Faucher *et al.*, 1999), but again find no evidence for a consistent geographical or temporal change.

Direct measurements of the vertical rates of upwelling off Vancouver Island have shown poor correlation with estimates of upwelling derived from the Bakun index (Thompson and Ware, 1996), so caution is needed in making the conclusion that changes in the strength of upwelling have not driven the changes in survival. Nevertheless, the pattern of correlation in the regions of coherent upwelling-favourable wind patterns shows little evidence for the geographical shift northward around 1990 needed to explain the sudden decline in ocean survival of British Columbia steelhead in the 1990s.

Gargett (1997) has proposed that the out-of-phase shifts between salmon stocks in northern and southern regions of the eastern North Pacific are the result of changes in relative water column stability, changing the balance between relative light and nutrient levels affecting phytoplankton. We have not yet examined this hypothesis, but the evidence for a sharp change in ocean survival for stocks off southern and northern British Columbia in the 1990s makes this an attractive candidate for a field study.

The declines in marine survival we have found are so large that even the complete cessation of all fishing on southern stocks of British Columbia steelhead following 1990 would not compensate for the increased ocean mortality that has occurred. As a result, these populations will decline quite substantially even in the absence of fisheries. To put the rapidity and depth of the decline in perspective, consider the fate of a population experiencing suddenly decreased ocean survival conditions which then continues for three generations, as has occurred (Ward, 2000). For southern British Columbia steelhead, marine survival has dropped to one-fourth of its value in the 1980s. At the end of three generations of reduced survival the population will only be $(\frac{1}{4})^3 = {}^1/_{64}$th, or 1.6%, of its previous level. For Oregon coho, where marine survival is now only one-fifth its level in the 1980s, the population decline would be to 0.8%. These declines in ocean survival might be partially buffered by density-dependent increases in freshwater survival in some populations, but are still extremely serious. The Keogh River steelhead population, for example, has dropped from a spawning population of 3000–4000 wild adults in the late 1980s to fewer than 100 individuals in the spring of 1998.

No matter how accurately calculated, the productivity of fish populations measured by traditional stock assessments must necessarily be based largely on data collected prior to the time of sudden changes in ocean climate. Assessments are therefore based on statistical analysis of *past* levels of productivity. One implicit statistical assumption of most stock assessments is that sudden changes in mean levels do not occur, so that the gradual accumulation of new data can be weighted equally with older data. (In fact, for multi-age-class marine populations such as groundfish, more recent data are given *less* weight because they are considered less reliable.) Such analyses cannot easily incorporate the potential for sudden changes in mean state, because they attempt to measure average productivity and implicitly assume that runs of higher or lower productivity do not occur. As the simple calculations above show, it is critical that potential changes in productivity be identified and factored into management decisions as quickly as possible, so as not to overfish stocks during periods of low productivity.

Unless corrected for current oceanographic conditions, stock assessments will give misleading conclusions because the blending of data before and after a climate shift will mean that the assessment advice will largely be based on conditions applicable before the change. Making this correction will be extremely difficult because the underlying links between oceanographic change and biological effects on salmon populations are not yet clear. It is clear, however, that without this understanding, traditional assessments will probably always be too slow to react to sudden changes in the ocean environment of the form we have reported here.

CONCLUSIONS

The population dynamics of steelhead appear to be strongly associated with large-scale climatic changes that have major effects around the eastern rim of the North Pacific. Beamish *et al.* (2000) show that parallel changes in coho marine survival also occurred in 1990. Following the development of anomalous atmospheric circulation patterns in 1989 (Watanabe and Nitta, 1999), a sharp change in the mean state of the Pacific Ocean appears to have occurred. This climate shift, which resulted in warming of the central North Pacific following the cooling event of 1977, was accompanied by anomalous ocean conditions throughout much of the NE Pacific after 1990.

An important distinction needs to be made between the biological response of steelhead and coho populations to this change, and the atmospheric and oceanographic changes driving them. Some of the latter indices (such as the warming of the central Pacific or the changes in sea level pressure) indicate that a relaxation of ocean and atmospheric conditions back to the pre-1977 state appeared to occur. However, the response of coho and steelhead indicates that a progressive intensification of the conditions causing poor survival resulted after 1990, with the populations not showing a return to the higher marine survival conditions characteristic of the period prior to 1977 (e.g. Fig. 7).

The response of British Columbia fish populations to this regime shift also appears to depend strongly on the coastal region young fish enter. Based on the parallel between steelhead abundance and marine survival in Keogh River, the marine survival of steelhead dropped sharply in south-central regions of BC while either increasing or remaining stable in northern BC and Alaskan waters. Patterns of decline in angler success for steelhead by river system demonstrate that the decline in survival occurred for steelhead entering the ocean as smolts in 1990 and subsequent years, and extended from southern BC to an area just south of the Skeena River (northern BC). Steelhead returns to the Skeena and Nass Rivers, based on CPUE trends, continued to increase after 1990.

Although the precise cause of the change is unclear, it may be mediated by changes in ocean productivity that reduce the growth rates of both young and old fish. The result for young fish is that they remain small for longer periods of time, and therefore experience higher cumulative mortality. The changes in British Columbia after 1990 are clearly different from the normal critical period concept used in recruitment studies, with salmon entering the ocean at up to 18 cm length experiencing sharp increases in mortality. Although changes in abundance of predators such as mackerel also occurred in 1992–93, and have previously been implicated in declines in salmon populations, the mackerel invasion in BC occurred two years *after* the sudden decline in salmon survival (Farrell, 1997). As a result, the impact of mackerel on fisheries was of importance to some stocks, but is unlikely to have determined the overall dynamics of the recruitment fluctuations following either the 1977 or the 1990 climate shifts.

It is unclear at present how consistently the pattern of geographical and temporal change in steelhead, which we have shown, also occurs for the other species of Pacific salmon except for coho, partly because of the mixed-stock nature of ocean fisheries for these species. However, a rather clear case can be made for sudden and large changes in ocean conditions directly affecting steelhead and coho stocks throughout much of their range on the west coast of North America.

ACKNOWLEDGEMENTS

We thank Steven Hare for an especially useful review, and for introducing us to the paper by Watanabe and Nitta. This work forms part of the Canadian GLOBEC initiative.

REFERENCES

Baumgartner, T.R., Soutar, A. and Ferreira-Bartrina, V. (1992) Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. *CalCOFI Rep.* **33:**24–40.

Beamish, R.J. (1993) Climate and exceptional fish production off the west coast of North America. *Can. J. Fish. Aquat. Sci.* **50:**2270–2291.

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

Beamish, R.J. and Bouillon, D.R. (1995) Marine fish production trends off the Pacific coast of Canada and the United States. In: *Climate Change and Northern Fish Populations.* R.J. Beamish (ed.). *Can. Spec. Publ. Fish. Aquat. Sci.* **121:**585–591.

Beamish, R.J., Mahnken, C. and Neville, C.M. (1997a) Hatchery and wild production of Pacific salmon in relation to large-scale, natural shifts in the productivity of the marine environment. *ICES J. Mar. Sci.* **54:**1200–1215.

Beamish, R.J., Neville, C.E. and Cass, A.J. (1997b) Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. *Can. J. Fish. Aquat. Sci.* **54:**543–554.

Beamish, R.J., Noakes, D., McFarlane, G., Pinnix, W., Sweeting, R. and King, J. (2000) Trends in coho marine survival in relation to the regime concept. *Fish. Oceanogr.* **9:**115–120.

Brodeur, R.D. and Ware, D.M. (1992) Interannual and interdecadal changes in zooplankton biomass in the subarctic Pacific Ocean. *Fish. Oceanogr.* **1:**32–38.

Brodeur, R.D., Frost, B.W., Hare, S.R., Francis, R.C. and Ingraham, W.J. (1996) Interannual variations in zooplankton biomass in the Gulf of Alaska and covariation with California Current zooplankton. *CalCOFI Rep.* **37:**80–99.

Burgner, R.L., Light, J.T., Margolis, L., Okazaki, T., Tautz, A. and Ito, S. (1992) Distribution and Origins of Steelhead Trout (*Oncorhynchus mykiss*) in Offshore Waters of the North Pacific Ocean. *Int. N. Pac. Fish. Comm. Bull.* 51.

CCWHC (1996) A mortality event in Northern Fulmars in the Pacific Northwest. *Can. Coop. Wildlife Health Center Newsl.* **4:**8–9.

Deser, C., Alexander, M.A. and Timlin, M.S. (1996) Upper ocean thermal variations in the north Pacific during 1970–1991. *J. Climate* **9:**1840–1855.

Emmett, R.L. and Schiewe, M.H. (eds) (1997) *Estuarine and Ocean Survival of Northeastern Pacific Salmon: Proceedings of the Workshop.* U.S. Dep. Commerce, *NOAA* Tech. *Memo. NMFS–NWFSC* **29:**1–313.

Farrell, A.P. (1997) Effects of temperature on cardiovascular performance. In: *Global Warming: Implications for Freshwater and Marine Fish.* C.M. Wood and D.G. McDonald (eds). Cambridge, UK: Cambridge University Press, pp. 135–158.

Faucher, M., Burrows, W.R. and Pandolfo, L. (1999) Empirical–statistical reconstruction of surface marine winds along the western coast of Canada. *Clim. Res.* **11:**173–190.

Finney, B.P. (1998) Long-term variability in Alaskan sockeye salmon abundance determined by analysis of sediment cores. *N. Pac. Anadr. Fish Comm. Bull.* **1:**388–395.

Francis, R.C. and Hare, S.R. (1994) Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. *Fish. Oceanogr.* **3:**279–291.

Freeland, H., Denman, K., Wong, C.S., Whitney, F. and Jacques, R. (1997) Evidence of change in the winter mixed layer in the Northeast Pacific Ocean. *Deep Sea Res.* **44:**2117–2129.

Gargett, A.E. (1997) The optimal stability 'window': a mechanism underlying decadal fluctuations in North Pacific salmon stocks? *Fish. Oceanogr.* **6:**109–117.

Hare, S.R. and Francis, R.C. (1995) Climate change and salmon production in the northeast Pacific ocean. In: *Climate Change and Northern Fish Populations.* R.J. Beamish (ed.). *Can. Spec. Publ. Fish. Aquat. Sci.* **121:**357–372.

Hare, S.R., Mantua, N.J. and Francis, R.C. (1999) Inverse production regimes: Alaskan and West Coast Pacific salmon. *Fisheries* **21:**6–14.

Hartt, A.C. and Dell, M.B. (1986) Early Oceanic Migrations and Growth of Juvenile Pacific Salmon and Steelhead Trout. *Int. N. Pac. Fish. Comm. Bull.* **46:**1–105.

Hayward, T.L. (1997) Pacific Ocean climate change: atmospheric forcing, ocean circulation and ecosystem response. *Trends Ecol. Evol.* **12:**150–154.

Healey, M.C. (1982) Timing and relative intensity of size-selective mortality of juvenile chum salmon during early sea life. *Can. J. Fish. Aquat. Sci.* **39:**952–957.

Holtby, L.B., Andersen, B.C. and Kadowaki, R.K. (1990) Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **47:**2181–2194.

Kawasaki, T. and Omori, M. (1995) The impacts of climate change on Japanese fisheries. In: *Climate Change and Northern Fish Populations.* R.J. Beamish (ed.). *Can. Spec. Publ. Fish. Aquat. Sci.* **121:**523–528.

Kawasaki, T., Tanaka, S., Toba, Y. and Taniguchi, A. (eds) (1991) *Long-Term Variability Of Pelagic Fish Populations And Their Environment.* Oxford: Pergamon Press, 402 pp.

Klyashtorin, L.B. and Sidorenkov, N.S. (1996) The long-term climatic changes and pelagic fish stock fluctuations in the Pacific. *Izvestiya Pacific Res. Fish. Centre (TINRO)* **119:**33–54.

Klyashtorin, L. and Smirnov, B. (1995) Climate-dependent salmon and sardine stock fluctuations in the North Pacific. *Can. Spec. Publ. Fish. Aquat. Sci.* **121:**687–689.

McGowan, J.A., Cayan, D.R. and Dorman, L.M. (1998) Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* **281:**210–217.
McKinnell, S., Pella, J.J. and Dahlberg, M.L. (1997) Population-specific aggregations of steelhead trout, *Oncorhynchus mykiss*, in the North Pacific Ocean. *Can. J. Fish. Aquat. Sci.* **54:**2368–2376.
McKinnell, S.M., Wood, C.C., Rutherford, D.T., Hyatt, K.D. and Welch, D.W. (1998) The collapse of the Rivers Inlet sockeye fishery: the case against a freshwater cause. *N. Pac. Anadr. Fish. Comm. Tech. Rep.* (Unnumbered). 27–29.
Magnuson, J.J., *et al.* (14 authors) (eds) (1996) *Upstream: Salmon and Society in the Pacific Northwest*. Washington, DC: National Academy Press, 452 pp.
Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. and Francis, R.C. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteor. Soc.* **78:**1069–1079.
Pearcy, W.G. (1996) Salmon production in changing ocean domains. In: *Pacific Salmon and their Ecosystems: Status and Future Options*. D.J. Stouder, P.A. Bisson and R.J. Naiman (eds). Chapman & Hall, New York, NY, USA, pp. 331–352.
PFMC (Pacific Fishery Management Council) (1997) *Preseason Report 1. Stock Abundance Analysis for 1997: Ocean Salmon Fisheries*. February 1997. Appendices B-2 and B-3.
Roemmich, D. and McGowan, J. (1995) Climatic warming and the decline of zooplankton in the California Current. *Science* **267:**1324–1326.
Ricker, W.E. (1962) Comparison of ocean growth and mortality of sockeye salmon during their last two years. *J. Fish. Res. Bd. Canada* **19:**531–560.
Ricker, W.E. (1976) Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. *J. Fish. Res. Bd. Canada* **33:**1483–1524.
Smith, B.D., Ward, B.R. and Welch, D.W. (in press) Trends in wild adult steelhead (*Oncorhynchus mykiss*) abundance as indexed by angler success. *Can. J. Fish. Aquat. Sci.*
Stabeno, P.J. and Reed, R.K. (1992) A major circulation anomaly in the western Bering Sea. *Geophys. Res. Lett.* **19:**1671–1674.
Sugimoto, T. and Tadokoro, K. (1997) Interannual–decadal variations in zooplankton biomass, chlorophyll concentration and physical environment in the subarctic Pacific and Bering Sea. *Fish. Oceanogr.* **6:**74–93.
Thompson, R.E. and Ware, D.M. (1996) A current velocity index of ocean variability. *J. Geophys. Res.* **101:**14297–14310.
Trenberth, K.E. and Hoar, T.J. (1996) The 1990–1995 El Nino Southern Oscillation event: longest on record. *Geophys. Res. Lett.* **23:**57–60.
Ward, B.R. (1996) Population dynamics of steelhead in a coastal stream, the Keogh River, British Columbia. In: *Stock Assessment in Inland Fisheries*. I. Cowx (ed.). Oxford: Blackwell Scientific Publications, Fishing News Books, pp. 308–323.
Ward, B.R. and Slaney, P.A. (1988) Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. *Can. J. Fish. Aquat. Sci.* **45:**1110–1122.
Ward, B.R., Slaney, P.A., Facchin, A.R. and Land, R.W. (1989) Size-biased survival in steelhead trout: back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, B.C. *Can. J. Fish. Aquat. Sci.* **46:**1853–1858.
Ware, D.M. and McFarlane, G.A. (1989) Fisheries production domains in the northeast Pacific Ocean. *Can. Spec. Publ. Fish. Aquat. Sci.* **108:**359–379.
Watanabe, M. and Nitta, T. (1999) Decadal changes in the atmospheric circulation and associated surface climate variations in the Northern Hemisphere winter. *J. Climate* **12:**494–510.
Welch, D.W., Morris, J.F.T., Carlson, H.R., Farley, E.V., Van Hardenberg, B., Carmack, E.R. and Münchow, A. (1997a) Results from the CCGS W.E. Ricker Gulf of Alaska Salmon Survey, March 1997. *North Pacific Anadromous Fish Commission Doc.* **287**.
Welch, D.W., Morris, J.F.T., Eveson, J.P., Van Hardenberg, B., Carmack, E.R. and Münchow, A. (1997b) Results from the CCGS W.E. Ricker Gulf of Alaska Salmon Survey, October 1996. *North Pacific Anadromous Fish Commission Doc.* **288**.
Welch, D.W., Morris, J.F.T., Wittke, E. and Smorodin, V.I. (1998) CCGS W.E. Ricker Gulf of Alaska Salmon Survey, November–December, 1997. *North Pacific Anadromous Fish Commission Doc.* **308**.
Whitney, F., Wong, C.S. and Boyd, P.W. (1998) Interannual variability in nitrate supply to surface waters of the northeast Pacific Ocean. *Mar. Ecol. Prog. Ser.* **170:**15–23.
Wood, C.C., Rutherford, D.T., Peacock, D., Cox-Rogers, S. and Jantz, L. (1997) Assessment of recruitment forecasting methods for major sockeye and pink salmon stocks in northern British Columbia. *Can. Tech. Rep. Fish. Aquat. Sci.* **2187:**1–85.