Trends in wild adult steelhead (*Oncorhynchus mykiss*) abundance for coastal regions of British Columbia support the variable marine survival hypothesis

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Abstract: Wild adult steelhead (*Oncorhynchus mykiss*) abundance for rivers in British Columbia was indexed using catch-per-angler-day (CpAD) calculated from data obtained using an angler questionnaire. Mean annual CpAD for primarily winter-run steelhead in rivers of four rainfall-driven coastal regions of British Columbia showed similar trends from the fiscal year 1967–1968 to 1989–1990. After 1989–1990 the trends diverged. The generally remote rivers of the west coast of Vancouver Island and the Queen Charlotte Islands maintained a steady or increasing trend in CpAD after 1989–1990. The long-term trend for these two regions correlated well with a joint index of winter and summer upwelling for the Coastal Upwelling Domain for the years that steelhead are at sea and is consistent with studies that relate marine survival of salmon to oceanic–atmospheric climate. In contrast with west coast Vancouver Island and the Queen Charlotte Islands, most rivers of the east coast of Vancouver Island and the lower mainland near Vancouver revealed declining trends since 1989–1990. Most of these rivers drain into the Strait of Georgia. Reasons for the discrepancy among regions after about 1990 are discussed. They include high angling pressure related to hatchery supplementation, differences in riverine and marine conditions, and smolt migration distance.

Résumé : Un indice de l'abondance des adultes de la truite arc-en-ciel anadrome (*Oncorhynchus mykiss*) sauvage dans les rivières de la Colombie-Britannique a été déterminé à l'aide des prises par pêcheur et par jour (PPJ) calculées à partir de données obtenues d'un questionnaire rempli par les pêcheurs à la ligne. Le PPJ moyen annuel pour des rivières comportant surtout des remontées d'hiver de truites arc-en-ciel de quatre zones côtières pluvieuses de la Colombie-Britannique présentait des allures semblables de l'exercice de 1967–1968 à celui de 1989–1990. Les allures ont ensuite divergé. L'allure obtenue pour les rivières généralement éloignées de la côte ouest de l'Île de Vancouver et des îles de la Reine-Charlotte indiquait un PPJ constant ou à la hausse après 1989–1990. L'allure à long terme de ces deux régions présentait une bonne corrélation avec un indice mixte des remontées d'eau d'hiver et d'été du domaine des remontées côtières pendant les années où les truites arc-en-ciel sont en mer et ce résultat est conforme à ceux d'études établissant une relation entre la survie en mer du saumon et les conditions océaniques et atmosphériques. Au contraire des rivières de la côte ouest de l'île de Vancouver et des îles de la Reine-Charlotte, la plupart des rivières de la côte est de l'île de Vancouver et du « lower mainland » à proximité de Vancouver présentent des allures à la baisse depuis 1989–1990. La plupart de ces rivières se jettent dans le détroit de Géorgie. Les raisons de ces écarts entre les régions notés vers 1990 font l'objet d'une discussion. Elles comprennent notamment une forte pression de la pêche à la ligne connexe à des apports d'origine piscicole, les écarts entre les conditions en rivière et en mer et la distance de migration des saumoneaux.

[Traduit par la Rédaction]

Introduction

Recent experimental work investigating ocean survival of steelhead (*Oncorhynchus mykiss*) has provided an opportunity to measure the influence of ocean survival on the abundance of wild adult steelhead that have returned to spawn in their natal river. A counting fence at the mouth of the rainfall-driven Keogh River of the northeast coast of Vancouver Island (Ward and Slaney 1988) has allowed an accurate census of the number of steelhead smolts entering the ocean and the number of adults subsequently returning to the river. Between 1977 and 1989, the smolt-to-adult survival of Keogh River steelhead averaged 15–16% but has declined to 3–4% in the most recent years (Ward 2000). This work on smolt-to-adult survival and evidence from a freshwater rearing study (Ward and Slaney 1993) provide the strongest evidence to date that ocean climate is a major determinant of the number of steelhead that return to the Keogh River to spawn and consequently also of the trend over time in adult steelhead abundance.

Several time series indices such as sea surface tempera-

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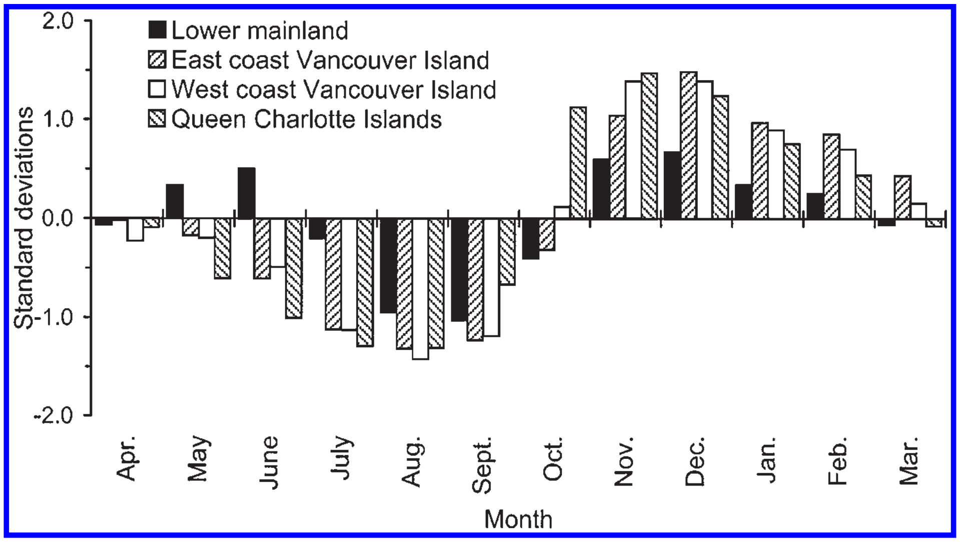
Fig. 1. Annual freshwater discharge profiles for the four major rainfall-driven regions. Profiles are expressed as deviations from the mean annual discharge for the years 1962 to 1994.



ture, salinity, sea level atmospheric pressure, and upwelling have been used as proxies for ocean climate (Mantua et al. 1997; Francis et al. 1998; Beamish et al. 1999*a*, 1999*b*). Among them, upwelling is a particularly compelling index of ocean climate (Bakun 1990), since its strength can be a critical factor affecting food chain connectivity and salmon survival perhaps as soon as they enter the ocean (Ware and Thompson 1991; Hsieh and Boer 1992; Roemmich and McGowan 1995; Brodeur et al. 1996; see Francis and Hare 1997). Upwelling is caused by offshore wind stress and results in cool, salty water being transported to the ocean surface. Upwelled water is generally rich in nutrients such as nitrates, phosphates, and silicates that are essential to biological production. In years of above (below) average summer upwelling, a positive (negative) anomaly of nutrient-rich water advects to the surface promoting higher (lower) than average rates of productivity of phytoplankton and zooplankton. Upwelling is a coastal phenomenon that occurs generally within 200 km of the Pacific coastline of North America from southern California to Alaska. However, not all regions of the coast experience the same degree of upwelling, and years of strong or weak upwelling do not coincide latitudinally (Ware and Thompson 1991). Likewise, not all sectors of the coast respond to upwelling with similar levels of productivity (Ware and McFarlane 1989).

In this paper, we investigate correlations between indices of summer and winter upwelling and the abundance of wild adult steelhead that have returned to their coastal rainfall-driven natal rivers. Unlike the commercially fished salmon species, whose adult abundance is estimated using commercial landing statistics and escapement counts, steelhead abundance is indexed by a measure of sport angler success. Here, we use catch-per-angler-day (CpAD) as an index of trends in wild adult steelhead abundance. Values of CpAD are calculated from angler catch and effort data collected by a mail-out questionnaire, the Steelhead Harvest Questionnaire (SHQ), managed by the British Columbia Ministry of Fisheries. This survey, which has been executed using essentially the same format since the fiscal (1 April to 31 March) year 1967–1968, facilitates the construction of trends in abundance for individual rivers, coastal regions, geographic regions, or watersheds (see figs. 5 and 6 in Smith et al. 2000). Analyses of these data indicated that trends in wild adult steelhead abundance yielded by this methodology were reliable, although individual values of CpAD could be biased by sampling uncertainty and dynamic factors such as a change in the level of angler effort over time (Smith 1999; Smith et al. 2000).

We focus here on trends in abundance observed for the coastal rainfall-driven rivers of British Columbia, specifically the east and west coasts of Vancouver Island, the lower mainland of British Columbia near Vancouver, and the Queen Charlotte Islands. Preliminary work indicated that these rivers share similar features of habitat and of steelhead population dynamics. All regions share a similar annual freshwater discharge pattern (Fig. 1), which contrasts them from the snowmelt-driven regions and watersheds, which have their own discharge pattern (see fig. 1 in Smith 2000). Rivers of the rainfall-driven regions generally flow directly into the ocean. They are characterised more by winter-run than by summer-run steelhead populations that smolt after an average juvenile freshwater residency of about 2–3 years (Withler 1966; Hooton et al. 1987).

For rivers of this set of four regions, we present results of time series analyses of the relationship between wild adult CpAD and upwelling anomalies for the Coastal Upwelling Domain off California, Oregon, and Washington and southern British Columbia (Ware and McFarlane 1989). We show that wild adult steelhead abundance and summer and winter upwelling anomalies relate in a manner consistent with current understanding of steelhead biology and ocean productivity processes for the two rainfall-driven regions least affected by anthropogenic influences (west coast Vancouver Island, the Queen Charlotte Islands). For the remaining two regions (east coast Vancouver Island, the lower mainland), steelhead populations have declined in numbers since about 1990 and in a manner inconsistent with predictions based on our proposed link between coastal upwelling and adult in-

Table 1. Number of rivers and the mean annual number of angler-days (AD) per river in the coastal rainfall-driven regions where wild steelhead have been caught.

	Count of rivers				
Region	Total	Complement	Complete series	Incomplete series	Mean AD (river^{-1}·year^{-1})
East coast Vancouver Island	56	41	12	4	2303
West coast Vancouver Island	89	69	7	14	912
Lower mainland	89	77	10	4	4514
Queen Charlotte Islands	24	20	3	2	727

Note: The "complement" refers to the number of rivers that contribute the last ≈10% of wild catch, when rivers are ranked in descending order of their contribution to wild catch from 1967–1968 to 1995–1996 (Smith et al. 2000). Complete series refer to rivers where CpAD is calculated for all 29 years from 1967–1968 to 1995–1996. Incomplete series are those missing a value for CpAD for at least one year due there being fewer than 100 angler-days of effort. The complement constitutes one of the complete series. The lower mainland includes 40 rainfall-driven Fraser River tributaries of which 37 form the complement. See Smith et al. (2000) for more details.

river wild steelhead abundance. We discuss this divergence in trends among these four regions with respect to high angling pressure related to hatchery supplementation of adult steelhead numbers, differences in riverine and marine conditions, and smolt migration distance.

Methods

Adult in-river wild steelhead abundance

Wild adult steelhead abundance for individual rivers of the four coastal rainfall-driven regions (Table 1) was indexed by using CpAD as a measure of angling success. We standardised CpAD to a zero mean and unit variance, as described in Smith et al. (2000), in order to compare CpAD trends among rivers and to execute time series analyses unencumbered by differences in absolute CpAD among rivers of different sizes and productivities. As will be introduced later, the period over which values for CpAD were standardised was chosen in accordance with the statistical hypothesis being tested.

Steelhead generally return to their natal river in either a winter run or a summer run (Withler 1966). The sport fishery for winter-run steelhead focuses on steelhead that return to freshwater generally between November and March, while summer-run steelhead tend to be angled during the fall of the year that they return. Thus, CpAD for a fiscal year is an index derived from data integrated over both run types where both occur in a river. The value of CpAD for any river and year is also affected by the survivorship of returning adults from cohorts with different residence times in freshwater and the ocean (Withler 1966; Burgner et al. 1992; Ward 1996). Wild steelhead of coastal, rainfall-driven regions are primarily winter-run type (see table 1 in Smith et al. 2000). Ageing, by scale analysis, of returning coastal steelhead found that most winter-run fish experienced 2 freshwater and 2 ocean years, while summer-run fish experienced 2 or 3 years in freshwater and 3 years at sea (Hooton et al. 1987). Unlike most other *Oncorhynchus* spp., steelhead are iteroparous, i.e., they can return to the ocean after spawning, although the percentage that survive to spawn a second time is low (Withler 1966; Hooton et al. 1987; Ward and Slaney 1988). Hatchery steelhead are abundant in certain rivers of east coast Vancouver Island, west coast Vancouver Island, and the lower mainland and are distinguished from wild steelhead by their lack of an adipose fin.

Bakun upwelling index

Bakun upwelling indices were obtained from the Pacific Fisheries Environmental Group of the United States National Oceanographic and Atmospheric Administration. The Bakun upwelling index is a measure of the rate of vertical movement of ocean water measured in cubic metres per second per 100 m of coastline. Monthly upwelling indices for the years 1946 to 1996 were obtained for seven locations along the west coast of North America identified by their latitude (N) and longitude (W) from 39°N, 125°W to 57°N, 137°W. Preparation of the monthly upwelling indices for statistical analyses used the following protocol. First, the summer and winter upwelling periods were identified from the seasonal upwelling pattern (Fig. 2*a*). Then, for each of the seven locations, average values of the upwelling index were calculated for the summer (April to September) and winter (October to March) time periods using the monthly data. Finally, for each latitude and time period, these averages were expressed as deviations from the average upwelling index for that latitude (Figs. 2*b* and 2*c*).

Time series analyses

Time series analyses (Hipel and McLeod 1994) were conducted as summarised in Smith et al. (2000). Briefly, these analyses included the use of transfer function-noise (TFN) and intervention models and were assisted by CuSum plots. In order to reduce the number of candidate time series models, the Bakun upwelling indices were first screened in exploratory correlation analyses with mean (over all series) standardised wild adult CpAD for the major regions and watersheds, including the snowmelt-driven regions. These exploratory analyses compared the time trends in mean standardised wild adult CpAD with summer and winter upwelling anomalies 0, 1, and 2 years prior to the year that the steelhead returned to their natal rivers to spawn. These lags correspond to the years that the steelhead are at sea following their entry into the ocean at about 2–3 years of age (Withler 1966; Ward 1996). Prior to these analyses, both the summer and winter upwelling anomalies were first scrutinised for serial autocorrelation. Both the winter and summer series at all latitudes were found to contain negligible serial autocorrelation and therefore were not subjected to prewhitening.

Until the fiscal year 1969–1970, the catch information from which the CpAD data were calculated was obtained only by polling steelhead anglers about the number of steelhead that they had caught and kept. Thus, a step intervention in 1970–1971 was included in all exploratory and final analyses to mark the beginning

Fig. 2. (*a*) Bakun upwelling indices expressed as monthly deviations from the annual means for the years 1946 to 1996. Note that deviations are above average for the so-called summer months (April to September) and below average for the so-called winter months (October to March). Bakun upwelling indices for 48°N, 125°W (*b*, *c*) are expressed as anomalies averaged over the fiscal (1 April to 31 March) years 1962–1963 to 1993–1994. Anomalies are presented for two organisations of the data, (*b*) summer and (*c*) winter, and are accompanied by the cumulative deviations (CuSums).

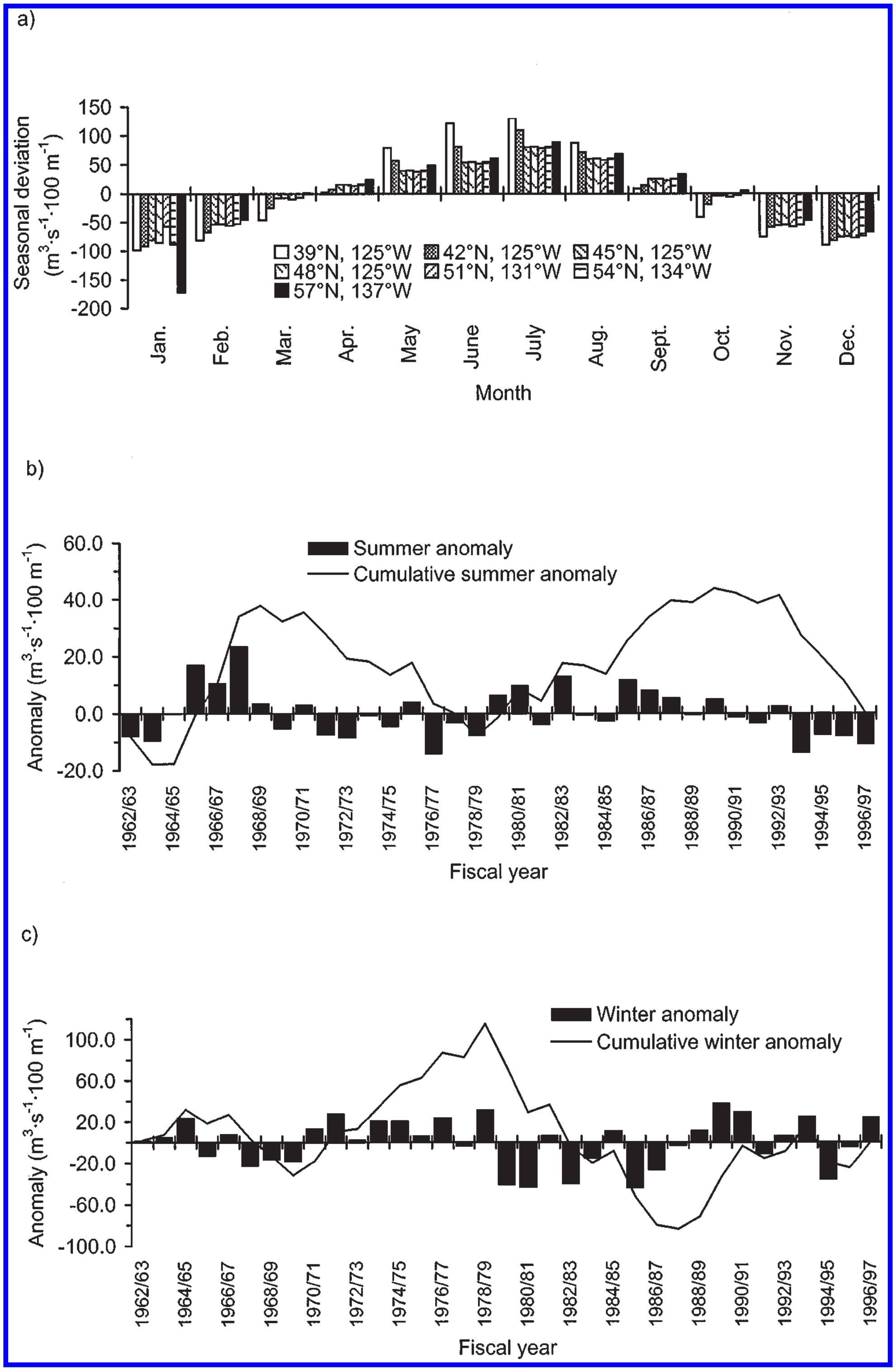
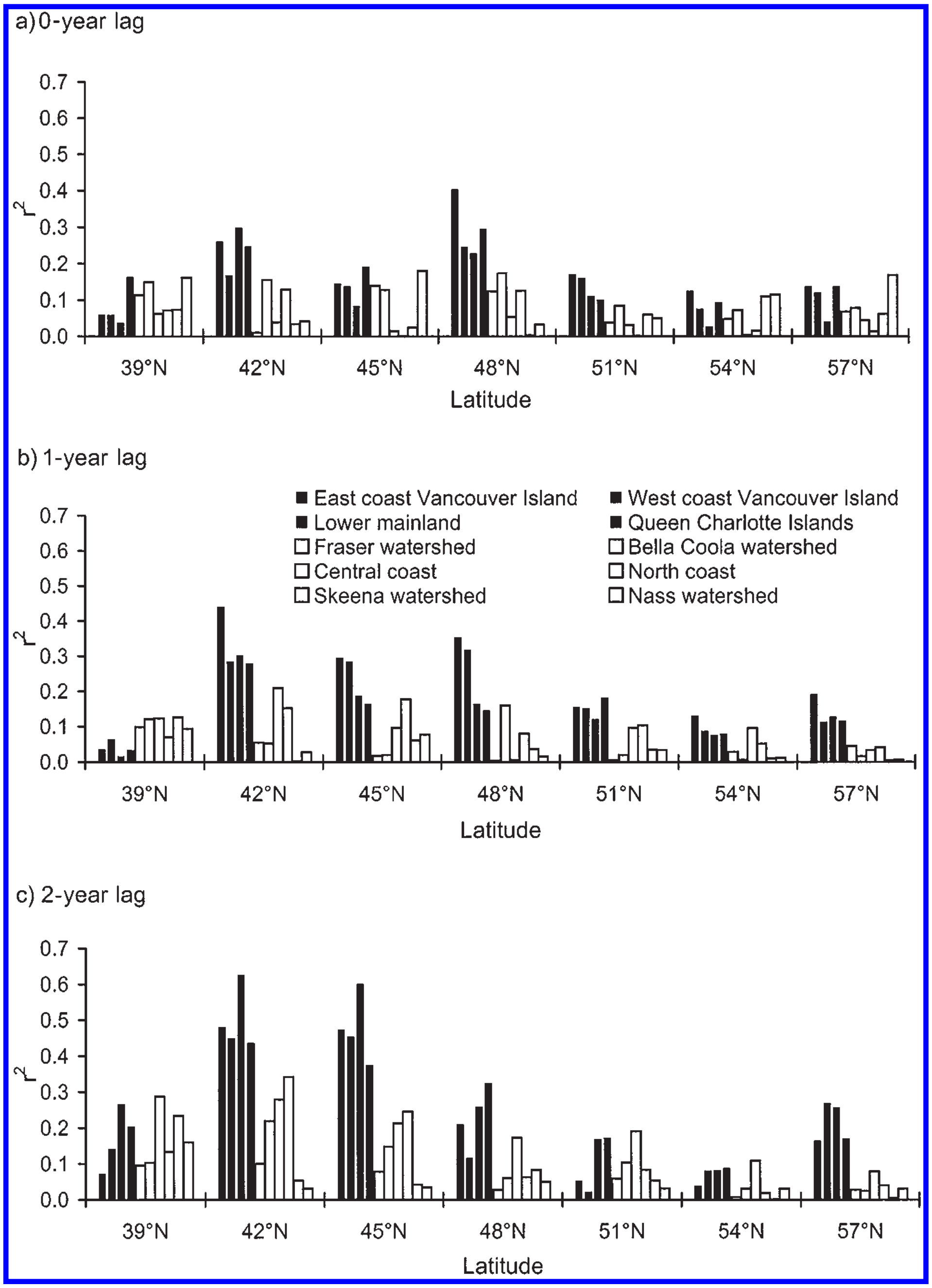


Fig. 3. Exploratory squared correlations (r^2) between mean standardised wild adult steelhead CpAD and jointly the summer and winter upwelling index anomalies for the specified latitudes at (*a*) 0, (*b*) 1, and (*c*) 2 years prior to the year that the steelhead return to spawn in their natal rivers. Correlations are portrayed according to whether the regions or watersheds are rainfall driven (solid bars) or snowmelt driven (open bars).



of the use of steelhead caught and released in addition to those caught and kept to calculate CpAD (see fig. 3 in Smith et al. 2000). During the exploratory time series analyses, wild adult CpAD was standardised over the entire period for which data were available, i.e., the fiscal years 1967–1968 to 1995–1996.

Results

A distinctive outcome of the exploratory analyses of the relationship between mean standardised CpAD and upwelling was the emergence of a dichotomy between two groups of regions or watersheds. The rainfall-driven regions (Fig. 3) showed particularly promising correlations with coastal upwelling. In contrast, the snowmelt-driven watersheds were generally more weakly correlated with coastal upwelling. Our interpretation of this result is that interannual variability in marine survival is more evident in the CpAD trend for steelhead originating in rivers of coastal rainfall-driven regions than it is for steelhead of inland snowmelt-driven regions. We expect that steelhead of rainfall-driven

Fig. 4. Exploratory squared correlations (r^2) between mean standardised wild adult steelhead CpAD for the four rainfall-driven regions and jointly the CuSums of summer and winter upwelling index anomalies for the three latitudes (42, 45, and 48°N) within the northern part of the Coastal Upwelling Domain (Ware and McFarlane 1989). The CuSum values were calculated starting at a lag of 0 years, i.e., the year that steelhead return to their natal river to spawn.

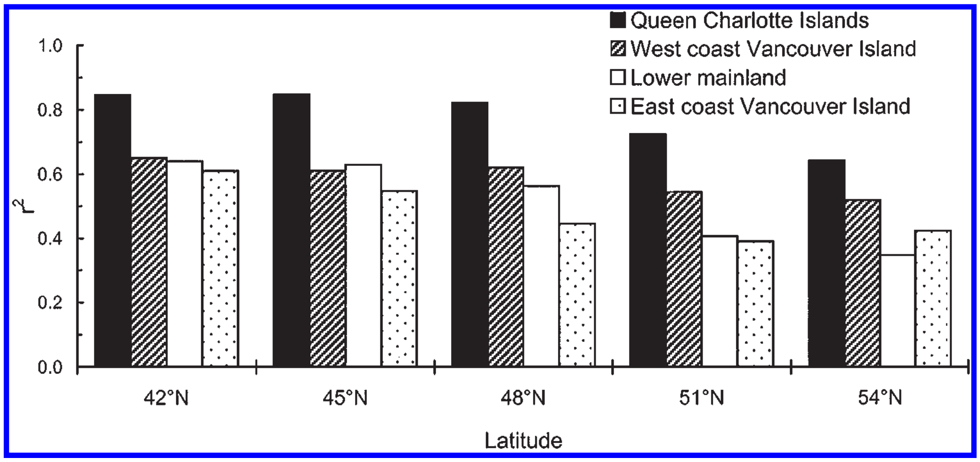


Table 2. Four covariate series associated with the four interventions reported in Table 3.

	Intervention series applies to:			
Fiscal year	(1) all rivers	(2) all rivers	(3) east coast Vancouver Island rivers	(4) lower mainland rivers
1967–1968	0	0	0	0
1968–1969	0	1	0	0
1969–1970	0	2	0	0
1970–1971	1	3	0	0
—	—	—	—	—
1989–1990	1	22	0	0
1990–1991	1	23	1	1
1991–1992	1	24	2	2
—	—	—	—	—
1995–1996	1	28	6	6

Note: Intervention series: (1) step intervention in 1970–1971 when the SHQ first started recording steelhead caught and released in addition to those caught and kept, (2) linear trend intervention beginning in 1968–1969 to account for a trend over time in CpAD unexplainable by the summer and winter upwelling anomalies, and linear trend interventions in CpAD after 1989–1990 for (3) east coast Vancouver Island and (4) the lower mainland.

regions and snowmelt-driven regions experience similar marine survival rates. However, the longer freshwater residence time of juvenile steelhead in the larger northern snowmelt-driven regions probably results in interannual variability in marine survival being more difficult to detect in those regions (Smith 2000).

Among the rainfall-driven regions the most promising relationships between standardised CpAD and upwelling occurred at latitudes 42, 45, and 48°N. These latitudes happen to correspond to an important upwelling region off California, Oregon, Washington, and southern British Columbia known for high marine productivity (Ware and McFarlane 1989). The similarity in strength of the relationships between steelhead CpAD and the summer and winter upwelling indices for these three latitudes led to the decision to further explore them using CuSum series (see Figs. 2*b* and 2*c*). These analyses identified the Queen Charlotte Islands as the region bearing the most promise for finding a statistical relationship between CpAD and the upwelling indices at these three latitudes, followed by west coast Vancouver Island, the lower mainland, and east coast Vancouver Island (Fig. 4).

The exploratory analyses led to three formal time series analyses challenging the ability of the summer and winter upwelling covariate series to explain wild adult steelhead CpAD for all four rainfall-driven regions. These analyses were also influenced by the consideration that the Queen Charlotte Islands and west coast Vancouver Island provided the best preliminary correlations with upwelling anomalies among all the rainfall-driven regions. Further study of the trends for all four rainfall-driven regions led to the recognition that all four regions displayed quite similar trends over the fiscal years 1967–1968 to about 1989–1990. After that date the CpAD trends for both the Queen Charlotte Islands and west coast Vancouver Island tended to remain stable or increase, while those for east coast Vancouver Island and the lower mainland declined. Consequently, our formal time series model included two linear trend intervention covariate series to measure this departure after 1989–1990 (Table 2). We determined that a linear trend intervention was also required to account for a general tendency for CpAD to increase over time at a rate that could not be explained by the summer and winter upwelling anomalies. The previously justified step intervention in 1970–1971 was also included in the analyses. To be consistent with our hypothesis that all four regions varied similarly only from 1967–1968 to 1989–1990, wild adult CpAD was standardised to a zero mean and unit variance only over that period.

The winter and summer upwelling anomalies and the four intervention series were formally challenged with explaining wild adult CpAD simultaneously for all 56 rivers of the rainfall-driven regions. Acceptable models, i.e., those providing satisfactory diagnostics for model fit (see Smith et al. 2000), were obtained for summer and winter upwelling data for all three latitudes of the northern part of the Coastal Upwelling Domain (Ware and McFarlane 1989). The model fits yielded r^2 values of 33, 34, and 34% for latitudes 42, 45, and 48ºN,

Table 3. Analysis of variance for a simultaneous time series analysis of standardised wild steelhead CpAD for 56 rivers of four coastal rainfall-driven regions of British Columbia.

Summary					
Observations	1433				
r^2	0.34				
SE	0.82				
Analysis of variance	**SS**	**df**	**Mean SS**	**F**	**p**
Regression	495.06	10	49.51	73.29	<0.0001
Residual	960.60	1422	0.68		
Total	1455.66	1432			
Parameter	**Description**	**Value**	**SE**	**p**	**Cumulative r^2**
μ	Intercept (series mean in 1967–1968)	–1.21	0.099	<0.0001	0.00
$\omega_{0,1}$	Step intervention in 1970–1971 (all four regions)	0.92	0.126	<0.0001	0.06
$\omega_{0,2}$	Linear trend intervention after 1967–1968 (all four regions)	0.033	0.0046	<0.0001	0.08
$\omega_{0,3}$	Linear trend intervention after 1989–1990 (ECVI only)	–0.29	0.032	<0.0001	↓
$\omega_{0,4}$	Linear trend intervention after 1989–1990 (LM only)	–0.13	0.035	0.0002	0.21
$\omega_{0,5}$	Winter upwelling: 0-year lag	–0.0055	0.0011	<0.0001	↓
$\omega_{1,5}$	Winter upwelling: 1-year lag	–0.0029	0.0011	0.0090	↓
$\omega_{2,5}$	Winter upwelling: 2-year lag	–0.0035	0.0009	0.0004	↓
$\omega_{1,6}$	Summer upwelling: 1-year lag	0.010	0.0034	0.0027	↓
$\omega_{2,6}$	Summer upwelling: 2-year lag	0.010	0.0038	0.0103	0.30
θ_1	AR(1)	0.25	0.027	<0.0001	0.34

Note: Significant TFN relationships were identified with both winter and summer upwelling anomalies at 48°N (see Fig. 5). Four other intervention series were also indicated. A linear trend intervention beginning in 1967–1968 identifies a tendency for CpAD in all regions to increase at a rate faster than that of the upwelling indices, while a step intervention in 1970–1971 accounts for the commencement of the recording of steelhead caught and released by the SHQ. Two linear trend intervention series indicate the downward departure of trends in CpAD for east coast Vancouver Island (ECVI) and the lower mainland (LM) after 1989–1990 from the trend indicated by the upwelling anomalies for west coast Vancouver Island and the Queen Charlotte Islands.

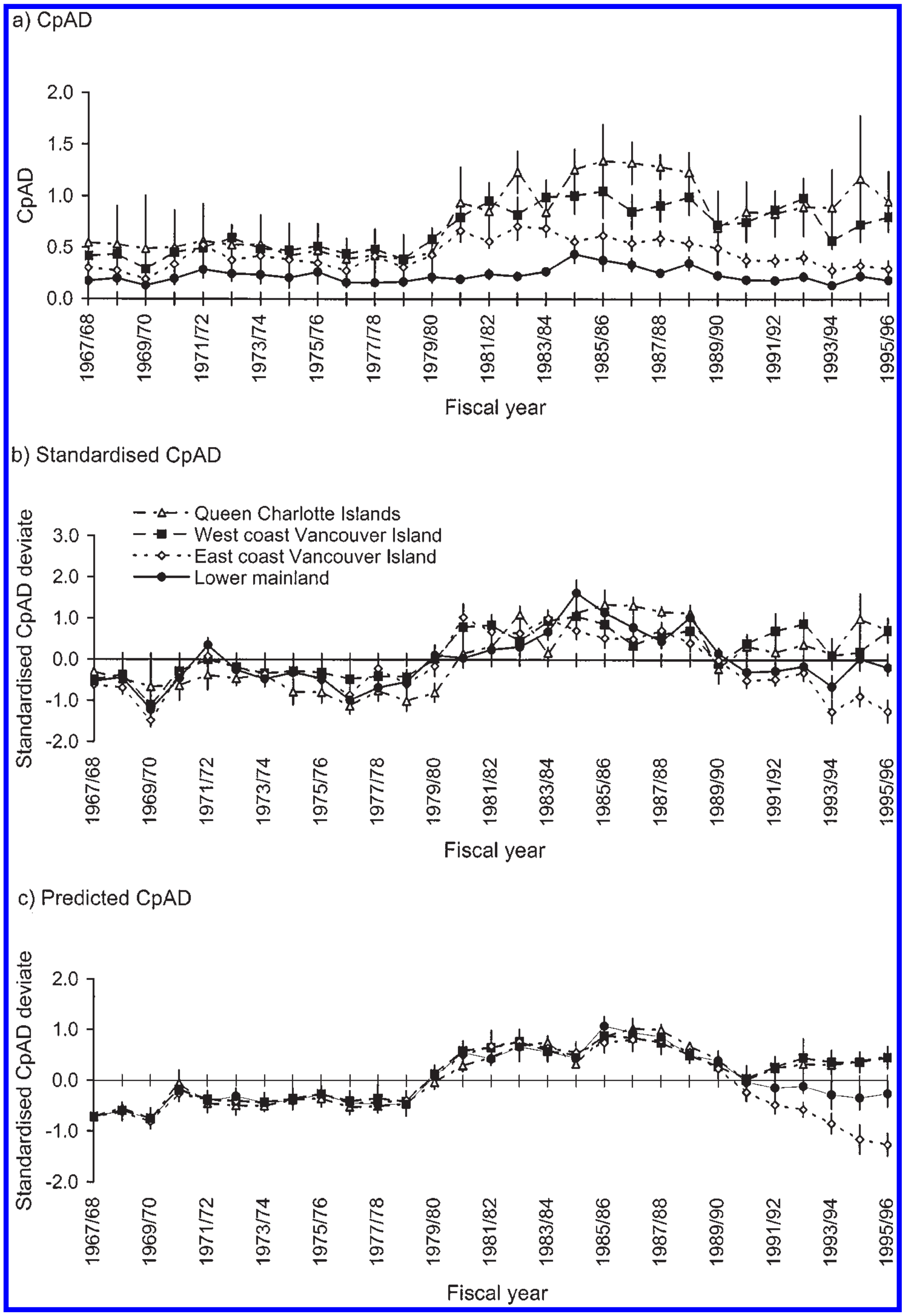
respectively. Given the similarity and consistency of the model fits, we report here only the results for 48ºN, since this is the latitude closest to the steelhead natal rivers in British Columbia (Table 3). A posteriori likelihood ratio tests supported our decision to simultaneously analyse all 56 time series as opposed to analysing the CpAD time series for each region separately (Akaike information criterion support is 14.5 for 48ºN). That is, our proposed single model that includes upwelling as a covariate, and the four intervention series, satisfactorily explains all 56 time series of CpAD.

The result for 48ºN (Table 3; Figs. 5 and 6) presents a parsimonious relationship between CpAD trends and upwelling anomalies, once the other identified shocks to the series are filtered by the chosen intervention series. One of these shocks is the step intervention in 1970–1971 ($\omega_{0,1}$). This shock captures a jump of 0.92 SD (from –1.21 to –0.30 SD) in the level of the CpAD series due to the inclusion of steelhead caught and released in the calculation of CpAD. A steadily increasing trend of 0.033 SD annually ($\omega_{0,2}$) accounts for an unexplained difference in trends over time between standardised CpAD and the upwelling indices. Most dramatically, after 1989–1990, standardised CpAD for east coast Vancouver Island and the lower mainland drops at a rate of 0.29 and 0.13 SD, respectively, relative to the Queen Charlotte Islands and west coast Vancouver Island. Overall, the nonrandom shocks to CpAD filtered by the four intervention series account for about 21% of the total variance in CpAD among years and rivers.

The TFN relationships identified significant correlations between standardised CpAD and winter upwelling at lags of 0–2 years ($\omega_{0,5}$, $\omega_{1,5}$, $\omega_{2,5}$) and summer upwelling at lags of 1 and 2 years ($\omega_{1,6}$, $\omega_{2,6}$) prior to the year that steelhead return to their natal river to spawn. When the upwelling series are considered as a suite, this relationship accounts for about 9% of total variance in standardised CpAD, or about 11% of the variance remaining after that filtered by the four intervention series. An autoregressive (AR) term (θ_1) accounts for 4% of total variance. Note that this nonzero value for θ_1 (Table 3) accounts for all of the within-year variability in predicted CpAD (Fig. 5*c*). Although 11% seems an unimpressive component of total variance, the summer and winter upwelling covariate series satisfactorily explain the observed variability in CpAD occurring at frequencies that Francis and Hare (1994), Mantua et al. (1997), and others refer to as decadal scale.

The entire model accounts for only 34% of the total variance in standardised CpAD because of the high degree of unexplainable intraannual variability among rivers. We have not formally investigated if this variability is related to sam-

Fig. 5. Mean (*a*) observed and (*b*) standardised wild adult steelhead CpAD for the four rainfall-driven regions from 1967–1968 to 1995–1996 and (*c*) mean predicted standardised CpAD according to the time series model of Table 3. Error bars indicate the SE of the predicted mean CpAD for each region. The SEs in Fig. 5*c* are due to the autoregressive (AR) term θ_1 (Table 3). Wild CpAD was standardised to a zero mean and unit variance over the years 1967–1968 to 1989–1990.

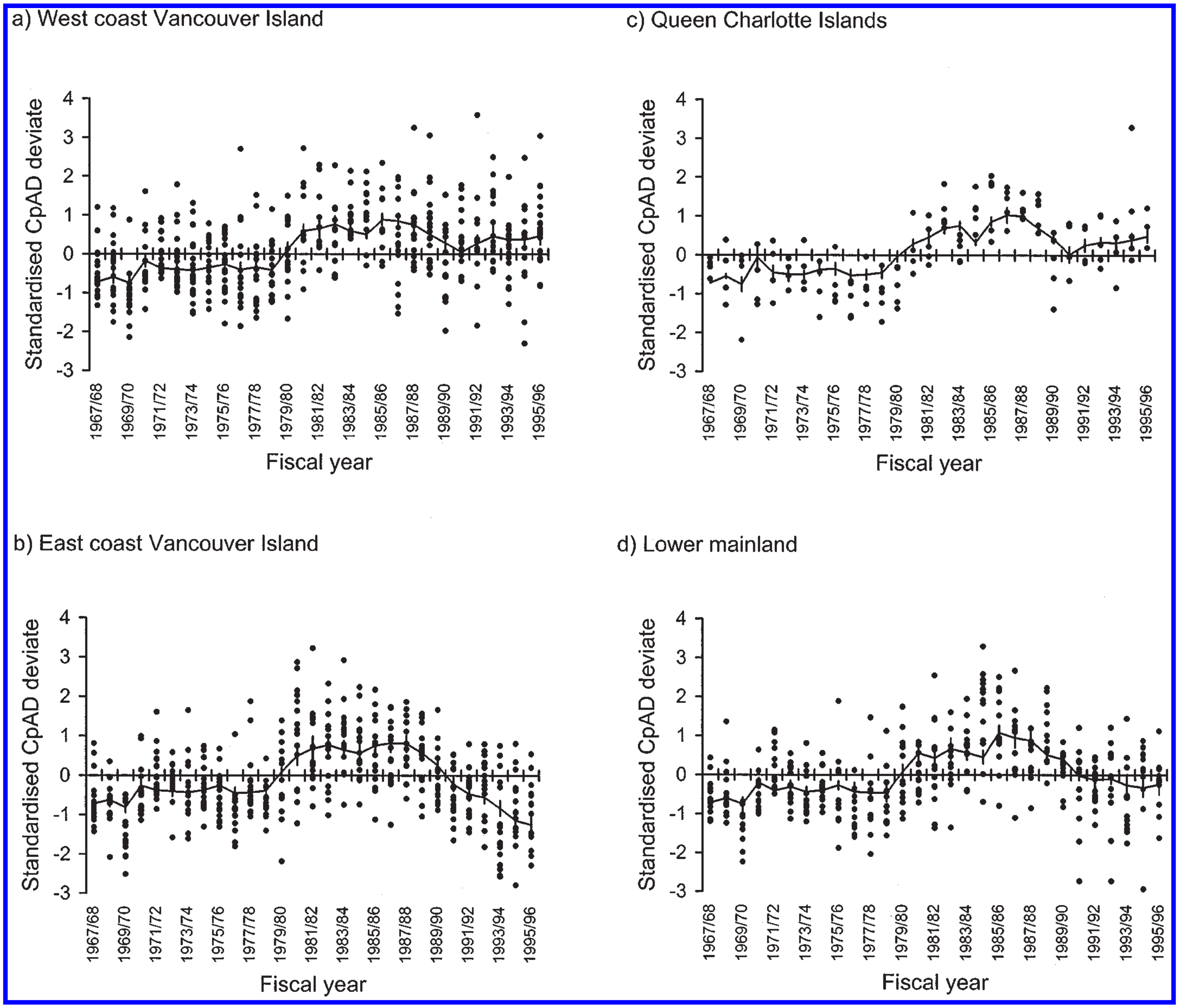


pling or real differences among rivers. We made an effort to reduce sampling variability by restricting the calculation of CpAD to those river–year entities having had at least 100 angler-days of effort (see Smith et al. 2000), so this prompts us to suggest that there are important real differences among rivers. When we performed an analysis equivalent to the one reported in Table 3 on only those four standardised CpAD series representing the mean CpAD for all rivers in each region (i.e., to remove intraannual variability among rivers; analysis not reported), the full model accounted for 74% of the total variance, with the suite of upwelling terms accounting for 23% of total variance, or a more impressive 44% of the remaining variance remaining after that filtered by the four intervention series.

Discussion

Recent work has shown that the return rate of adult salmonids to their natal rivers can be influenced in an important way by their survival rate during their marine life (Hare

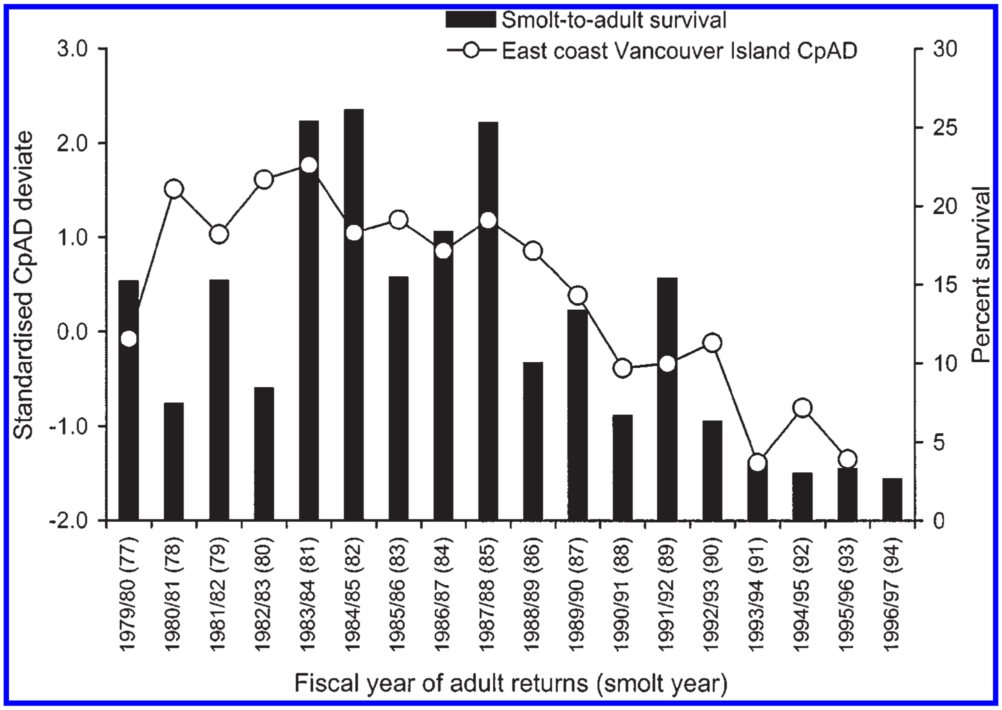
Fig. 6. Values observed for individual rivers and mean predicted standardised wild adult steelhead CpAD for the four rainfall-driven regions from 1967–1968 to 1995–1996 using the model of Table 3 but with parameters values optimised for each region. Error bars indicate the SD of the predicted values of CpAD for each river in the region. These SDs are due to the nonzero values for the autoregressive (AR) term θ_1. Wild CpAD was standardised to a zero mean and unit variance over the years 1967–1968 to 1989–1990.



and Frances 1995; Mantua et al. 1997; Ward 2000). The importance of coastal upwelling in this regard has been considered as an index of both general ocean climate and coastal marine productivity (Ware and Thompson 1991; Hsieh and Boer 1992). Our results are in concert with those of previous studies in that we report satisfying correlations between an index of returning wild adult steelhead abundance (CpAD) and coastal upwelling within the northern part of the Coastal Upwelling Domain (Ware and McFarlane 1989), a coastal area off western North America known for high marine productivity. We found steelhead abundance to be positively related to summer upwelling anomalies and negatively related to winter upwelling anomalies during the years that steelhead are at sea. We also found a generally increasing trend in CpAD of about 0.033 SD·year^{-1} ($\omega_{0,2}$, Table 3) that is unexplained by the summer and winter upwelling anomalies but that is possibly related to ocean climate having been generally favourable for salmon production in northern waters during the last two decades (Francis and Hare 1994; Hare and Frances 1995; Mantua et al. 1997).

One explanation for our satisfactory result is that the productivity of lower trophic levels within the Coastal Upwelling Domain is an important factor directly affecting steelhead growth and survival soon after they enter the ocean. Although it has been argued that the strength of summer upwelling determines the level of coastal productivity (Ware and McFarlane 1989; Brodeur et al. 1996), winter upwelling is also an important covariate in our time series analysis of trends in wild adult steelhead CpAD. Winter upwelling tends to be at least as strong in magnitude as summer upwelling and is opposite in sign (Fig. 2*a*), suggesting that winter upwelling might be as persistent and reliable an

Fig. 7. Smolt-to-adult survival of wild winter-run steelhead of the Keogh River according to the year of adults returns. Smolt-to-adult survival is compared with the trend in standardised mean wild adult CpAD for east coast Vancouver Island.



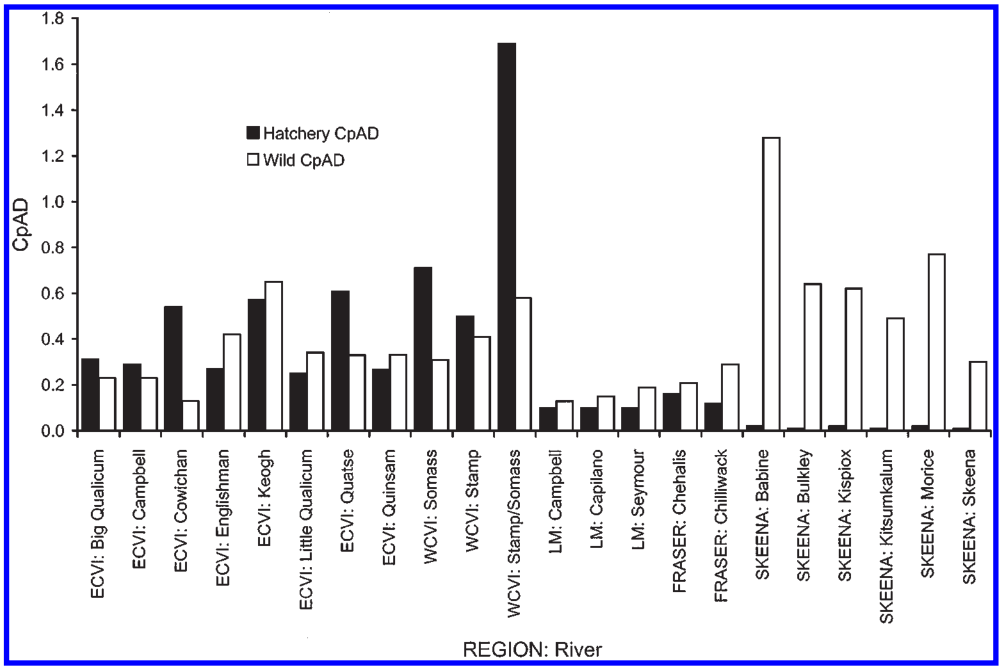
index of coastal productivity, with strong winter downwelling being associated with a future productivity benefit. Ware (1995) described how the summer marine climate off British Columbia, as measured by sea surface temperature, is decided largely by the previous winter's (December to May) weather. At that time of year the atmosphere is dominated by the Aleutian Low Pressure System (see Beamish et al. 1999*b*; Hare et al. 1999), which in turn would affect the rate of winter upwelling.

Alternatively, upwelling might just be one of the several known simple or composite indices of the general ocean climate, or productivity regime, during the years that steelhead are at sea (Mantua et al. 1997; Francis et al. 1998; Beamish et al. 1999*a*, 1999*b*). For example, other indices have been used to show that winter ocean climate appears to be an important factor affecting the recruitment success of certain groundfish species (Hollowed and Wooster 1992) and the migration pattern of Strait of Georgia coho salmon (*Oncorhynchus kisutch*) (Beamish et al. 1999*a*). Upwelling is almost certainly an imperfect index of ocean climate and trophic connectivity because the upwelling period might be short or weak, or upwelled water might be poor in nutrients if the thermocline is deep and nutrient-rich waters are not effectively transported to the ocean surface. We note also that Welch et al. (2000) found upwelling to be an uninformative index of the abrupt ocean regime shifts that occurred in 1977 and perhaps also in 1990 (Beamish et al. 1999*b*). Indeed, the argument that upwelling is just one of several indices of ocean climate is more consistent with current thinking in that since the late 1970s, the Central Arctic Domain of the Northeast Pacific shows a zooplankton production pattern inverse to that of the Coastal Upwelling Domain (Francis et al. 1998).

Our incomplete knowledge about the out-migration of steelhead smolts comes mainly from the Columbia River where Pearcy et al. (1990) reported that smolted steelhead tend to migrate offshore through the Coastal Upwelling Domain on their way to the subarctic waters of the North Pacific (Burgner et al. 1992). Based on recoveries at sea of tagged hatchery steelhead, McKinnell et al. (1997) suggested that hatchery steelhead from the Columbia River take a more direct route to the Aleutian region of the North Pacific Ocean than do hatchery steelhead of the Strait of Georgia. It is appropriate to ask if wild steelhead from coastal rainfall-driven regions of British Columbia take advantage of productivity in the Coastal Upwelling Domain before migrating to the Central Arctic Domain. Alternatively, is coastal productivity advected in a manner that benefits out-migrating steelhead?

The relationship that we propose between wild adult steelhead CpAD and ocean climate for rainfall-driven regions has support in experimental science. Ward and Slaney (1988, 1993), Ward et al. (1989), and Ward (1996, 2000) documented changes in smolt-to-adult survival rates for winter-run steelhead of the Keogh River near the northern tip of east coast Vancouver Island. Of particular note is that smolt-to-adult marine survival declined dramatically from the late 1980s and continued low during the 1990s (Fig. 7). Since winter-run Keogh steelhead are not vulnerable to interception in marine commercial salmon fisheries, the complication that this vulnerability would introduce to the interpretation of marine survival rates is eliminated. The work on the Keogh River provides compelling evidence that adult in-river wild steelhead abundance for rivers of rainfall-driven regions of British Columbia is influenced in an important way by marine survival. Cooper and Johnson (1992)

Fig. 8. Comparison of wild and hatchery adult steelhead CpAD according to river and region and averaged over the years 1981–1982 to 1995–1996. Only those regions and rivers where hatchery supplementation has occurred are portrayed. ECVI, east coast Vancouver Island; WCVI, west coast Vancouver Island; LM, the lower mainland near Vancouver.



also suspected a decrease in marine survival as the explanation for a low number of winter-run steelhead returning to coastal Washington in 1990–1991.

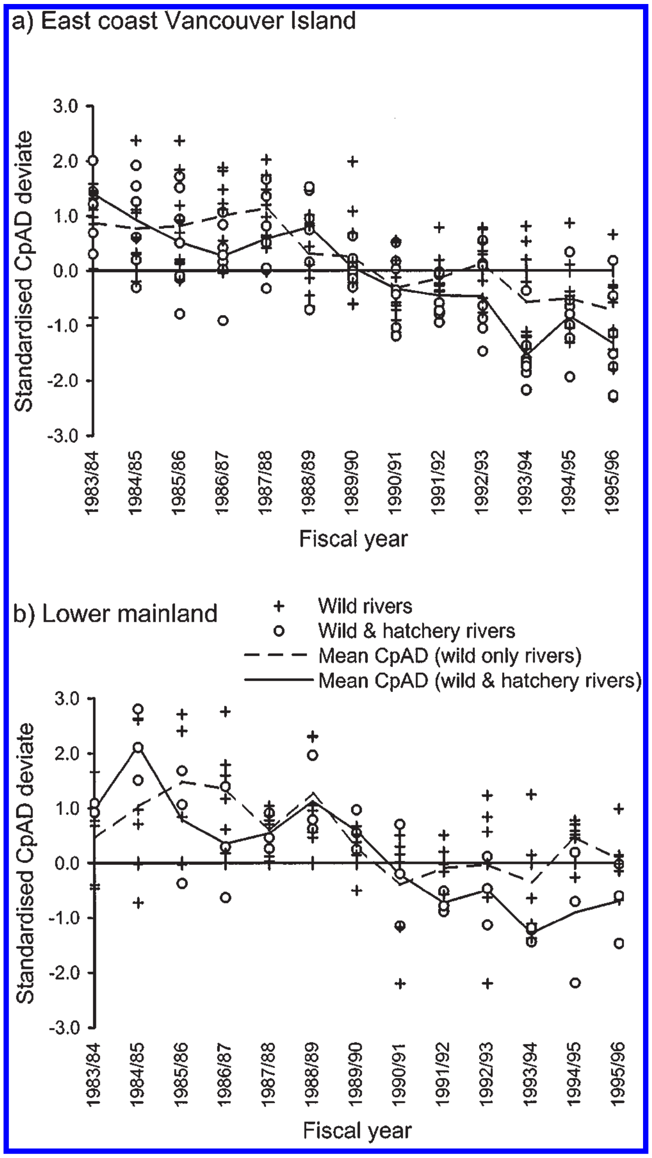
The pattern of smolt-to-adult survival for wild steelhead returning to the Keogh River bears a close resemblance to the CpAD trend for east coast Vancouver Island (Fig. 7). However, we are still suspicious that the decline in wild adult CpAD for east coast Vancouver Island and the lower mainland after about 1990 is greater than can be explained only by the prevailing rates of ocean survivorship measured for Keogh River steelhead. We note that desperately low numbers of winter-run wild steelhead were counted in 1996–1997 and 1997–1998 in certain rivers of east coast Vancouver Island selected for assessment. The returns of winter-run adult steelhead to some east coast Vancouver Island rivers have been so low that they probably received only a tenth of the number of steelhead needed to achieve desired escapement targets (Mr. J. Wightman, British Columbia Ministry of Fisheries, Nanaimo, B.C., personal communication). Arguably, the introduction of regulatory catch and release for wild fish in 1985–1986 and prohibitions to angling in 1997 have been crucial to the sustainability of these wild populations.

Several features distinguish much of east coast Vancouver Island and the lower mainland from west coast Vancouver Island and the Queen Charlotte Islands: smolt migration patterns, marine characteristics of the Strait of Georgia, regional weather patterns, river discharge patterns, a high degree of hatchery supplementation (Fig. 8), and urbanisation with an associated high number of anglers (Table 1). Thus, we pose that, notwithstanding these distinguishing features of east coast Vancouver Island and the lower mainland, all four rainfall-driven regions might have presented essentially the same pattern in wild CpAD over time. The two outer coastal regions (west coast Vancouver Island, the Queen Charlotte Islands) are relatively unperturbated by the anthropomorphic perturbations of hatchery supplementation and urbanisation; thus, our proposition is consistent with an interpretation of Busby et al. (1996) who concluded that the primarily winter-run steelhead populations of the remote outer northern coast of Washington State are not presently endangered. On the other hand, east coast Vancouver Island and the lower mainland would seem to be more vulnerable than west coast Vancouver Island and the Queen Charlotte Islands to anthropogenic threats. It is important to note that this distinction among regions is independent of any underlying explanatory model, such as coastal upwelling. It is the obviously disparate trends among regions after about 1990 that are at issue.

We did not formally examine or uncover riverine or marine factors capable of explaining the disparate trends in wild CpAD between the Strait of Georgia and the coastal Pacific after about 1990, as did Beamish et al. (1999*a*) for Strait of Georgia coho salmon life history as it relates to migration. These factors remain of interest, however, since it is conceivable that in the early 1990s, both freshwater and marine survival were lower in rivers south of the Keogh River, and particularly in the Strait of Georgia, than in the Keogh River. The more southerly rivers experienced summer drought conditions in the 1990s that may have increased the exposure of juveniles to excessive ultraviolet radiation (Walters and Ward 1998), and the smolts from those rivers had long migrations through atypically warm water.

At this time, we are also concerned that the decline in wild adult CpAD after about 1990 might be an indirect effect of hatchery supplementation. The presence of hatchery steelhead in a river attracts angling effort on both wild and hatchery steelhead (Smith 1999). This would cause unwel-

Fig. 9. Trends in standardised wild adult steelhead CpAD calculated from rivers with only wild steelhead and from rivers with both wild and hatchery steelhead for (*a*) east coast Vancouver Island and (*b*) the lower mainland. In the early years of hatchery supplementation, 1983–1984 to 1989–1990, no difference was detected for either region in mean standardised wild CpAD between rivers with and without hatchery supplementation (ANOVA, $p > 0.6$). From 1990–1991 to 1995–1996, rivers with hatchery supplementation had significantly lower values for mean standardised wild CpAD than rivers with only wild steelhead (east coast Vancouver Island: –0.47 SD, $p = 0.001$; the lower mainland: –0.95 SD, $p = 0.006$). Wild CpAD was standardised to a zero mean and unit variance over the years 1967–1968 to 1995–1996.



come incidental mortality of wild fish associated with multiple catches and releases. When catch and release of wild steelhead is mandatory, mortality results from hook injury or the stress of playing the fish or by an angler misidentifying a wild steelhead as a hatchery steelhead and not releasing it. Evidence that excessive mortality of wild steelhead might be a concern is our observation that mean wild CpAD is significantly lower from 1990–1991 to 1995–1996 in rivers of east coast Vancouver Island and the lower mainland that support both wild and hatchery steelhead than in rivers with only wild steelhead (Fig. 9). Given their proximity to a large urban population of anglers with easy access to these rivers, it seems that at least part of the explanation of the recent declines for east coast Vancouver Island and the lower mainland could be the marginal mortality inflicted by steelhead anglers on wild steelhead during a period of low marine survival.

Anthropogenic support of steelhead numbers by hatchery supplementation can also indirectly affect steelhead abundance in that hatchery steelhead might outcompete less abundant wild steelhead for habitat and resources when these are limiting. This competition can be exacerbated by the domestication of wild steelhead when wild and hatchery steelhead interbreed over successive generations (Waples 1991; Ryman and Laikre 1991), since hatchery-reared steelhead are seriously relaxed from natural selection (Reisenbichler and McIntyre 1977; Berejikian 1995; Mr. R. Reisenbichler, Northwest Biological Science Center, Seattle, Wash., personal communication). Thus the longer a population of steelhead is supported by hatchery supplementation, the greater the loss of fitness in wild fish and the greater the expectation that wild fish will decline in abundance. However, in British Columbia, hatcheries use only wild steelhead as brood stock and smolts are released into the lower reaches of watersheds. This practice appears to be effective in minimising negative interactions between wild and hatchery steelhead (Ward 2000).

To conclude, the arguments that we present are based on inference and follow from the identification of a statistical correlation between an index of wild adult in-river steelhead abundance (CpAD) and coastal upwelling for coastal rainfall-driven regions of British Columbia and obvious differences in trends inside and outside the Strait of Georgia since about 1990. We present no direct experimental evidence of the relationship between upwelling and CpAD; however, our arguments are consistent with trophic dynamics (Ware and Thompson 1991; Hsieh and Boer 1992; Roemmich and McGowan 1995; Brodeur et al. 1996) and recent theory that relates decadal-scale changes in the abundance of salmon in the Northeast Pacific to ocean climate (Francis and Hare 1994; Hare and Francis 1995; Mantua et al. 1997; Francis et al. 1998; Hare et al. 1999; Welch et al. 2000). That is, like other salmonids, British Columbia steelhead populations appear to have increased significantly after 1977 (Smith et al. 2000), the time of the first documented climatic shift (Beamish et al. 1999*b*). However, given the recent declines in the Strait of Georgia, there remains a need for further research to discriminate environmental and angling effects on these steelhead populations. In the meantime, we advocate a precautionary approach to steelhead management when wild abundance is low and yet hatchery returns are high.

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