Trends in wild adult steelhead (*Oncorhynchus mykiss*) abundance for snowmelt-driven watersheds of British Columbia in relation to freshwater discharge

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Abstract: Snowmelt-driven rivers of British Columbia support primarily summer-run steelhead (*Oncorhynchus mykiss*) that may spend up to 5 years as juveniles in freshwater. Time series analyses revealed significant negative correlations between an annual index of wild adult steelhead abundance (catch-per-angler-day, CpAD) for these rivers and summer freshwater discharge when these steelhead were juveniles. The strength of these relationships was related to latitude, with the more northerly rivers generating the strongest relationship between CpAD and freshwater discharge. Potential mechanisms by which interannual variation in freshwater discharge can modulate adult steelhead abundance include reduced juvenile mortality due to lower flow velocities during the warm summer months and to the creation of more juvenile habitat in low-velocity refuges. Alternatively, interannual variability in adult steelhead abundance is driven by variability in ocean climate of which freshwater discharge is an index. Interpretation of the data and analyses was encumbered in part by particular factors affecting CpAD as an index of abundance. However, the analyses support an interpretation that steelhead survival to adulthood might be influenced by freshwater conditions more so in northern snowmelt-driven rivers than in rainfall-driven rivers because steelhead from those rivers spend more years in freshwater as juveniles.

Résumé : Les cours d'eau de la Colombie-Britannique dont le régime hydraulique est déterminé par la fonte des neiges abritent surtout des truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) qui effectuent leur avalaison en été et qui peuvent demeurer jusqu'à 5 ans au stade juvénile en eau douce. Des analyses de séries temporelles de données ont montré l'existence de corrélations négatives significatives entre un indice annuel d'abondance des truites arc-en-ciel adultes (prises par pêcheur et par jour, PPJ) dans ces cours d'eau et le débit estival d'eau douce quand ces truites étaient juvéniles. La force de ces corrélations était reliée à la latitude, les rivières les plus septentrionales donnant les corrélations les plus fortes entre le PPJ et le débit d'eau douce. Au nombre des mécanismes possibles par lesquels la variation inter-annuelle du débit d'eau douce peut moduler l'abondance des truites arc-en-ciel adultes, on compte la réduction de la mortalité juvénile en été quand la vitesse du courant est basse et la création d'habitat favorable aux juvéniles dans les refuges à faible courant. Par ailleurs, la variabilité inter-annuelle de l'abondance des truites adultes est fonction de la variabilité du climat océanique, dont le débit d'eau douce est un indice. L'interprétation des données et les analyses ont été compliquées par certains facteurs particuliers affectant la validité du PPJ comme indice d'abondance. Cependant, nos analyses laissent penser que la survie des truites arc-en-ciel jusqu'à l'âge adulte serait davantage fonction des conditions existant en eau douce dans les rivières septentrionales à régime hydraulique déterminé par la fonte des neiges que dans les rivières à régime hydraulique déterminé par les pluies, parce que les truites des premières demeurent un plus grand nombre d'années en eau douce au stade juvénile.

[Traduit par la Rédaction]

Introduction

It has recently been argued that abundance patterns for salmon of rivers adjacent to the Northeast Pacific are caused mostly by changes in ocean survivorship (Mantua et al. 1997; Francis et al. 1998; Beamish et al. 1999; Hare et al. 1999). These researchers have identified correlations over time between indices of oceanic–atmospheric climate and salmon abundance as estimated by commercial catch and escapement. The link between ocean climate and salmon abundance has led to the judgement that variability in salmon abundance is caused primarily by changes in ocean survivorship. Intellectual support for this judgement comes from known links between ocean climate and the productivity of lower trophic levels (Roemmich and McGowan 1995; Brodeur et al. 1996; see Francis and Hare 1997). Further, increased survivorship of groundfish following the 1977 climate shift (Beamish and Bouillon 1993; Beamish et al. 1999) supports the argument that the critical ecosystem changes that improved survival after 1977 occurred primarily in the ocean because these species have no freshwater life history phase.

Partitioning the effects of survival in marine and freshwater habitats on the abundance of adult salmon returning to

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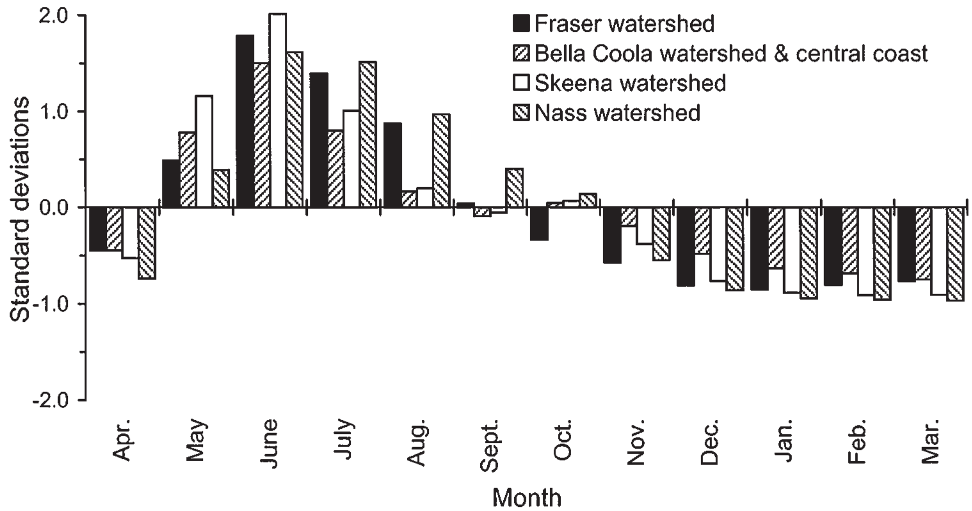
Fig. 1. Annual freshwater discharge profiles for four major snowmelt-driven regions expressed as deviations from their mean annual discharge for the years 1962 to 1994. No freshwater discharge monitoring stations qualified for the north coast rivers not within the Skeena and Nass watersheds.



their natal river is problematic, since mortality is integrated over both habitats (Bradford 1995). Further complicating this problem is the link between oceanic–atmospheric climate and the freshwater flow regimes of North American rivers. That is, interannual variability in freshwater discharge rates for rivers flowing into the North Pacific Ocean can be correlated with the prevailing oceanic–atmospheric climate (Mantua et al. 1997). Experimental separation of these effects has not been achieved for the five commercially fished salmon species (*Oncorhynchus* spp.), in part due to a lack of contrast in salmon abundance data among rivers experiencing different degrees of freshwater and oceanic influences on mortality.

Such contrast does exist for steelhead trout (*Oncorhynchus mykiss*) in British Columbia when angler success is used as an index of annual wild adult steelhead abundance for the fiscal (1 April to 31 March) years 1967–1968 to 1995–1996. Steelhead populations in British Columbia can be categorised as having natal rivers that tend to be either small and coastal with a rainfall-driven freshwater discharge (see fig. 1 in Smith and Ward 2000) or large and inland with a snowmelt-driven freshwater discharge (Fig. 1). Wild steelhead of coastal rainfall-driven regions are primarily the winter-run type (see table 1 in Smith et al. 2000) and have a 2- to 3-year freshwater residency (about one half of their life expectancy) before heading out to sea for the first time (Withler 1966; Ward 1996). On the other hand, wild steelhead of northern inland snowmelt-driven rivers tend to be the summer-run type (Slaney et al. 1996) and spend as long as 4–5 years in freshwater residency before smolting and emigrating to the ocean (Whately 1975). Anecdotally, Peven et al. (1994) aged two steelhead smolts of the inland Columbia River watershed at 6 and 7 years. Since steelhead from rainfall-driven and snowmelt-driven rivers appear to have the same oceanic distribution and generally spend 1–3 years at sea (Burgner et al. 1992), length of freshwater residency is a life history feature that discriminates steelhead of each river type.

Motivated by this distinction, I present the results of time series analyses that relate trends in wild adult in-river steelhead abundance, as indexed by angler success, for the snowmelt-driven rivers of British Columbia to freshwater discharge during the years that these steelhead were juveniles in these rivers. The most northerly Taku and Stikine watersheds could not be considered in these analyses due to a lack of data. However, a convincing relationship was identified for north coast rivers, including those of the Skeena and Nass watersheds. The more southerly snowmelt-driven Bella Coola and Dean rivers revealed similar, but less convincing, relationships with freshwater discharge, but this lack of success is arguably attributable to less and uncertain information on steelhead abundance. No relationship between adult steelhead abundance and freshwater discharge was identified for the even more southerly snowmelt-driven Fraser watershed, perhaps in part due to steelhead of the predominant Thompson River smolting after only 2 years as juveniles, but my analyses were also encumbered by limited and uncertain data.

Very poor, and statistically insignificant, correlations were obtained between freshwater discharge and wild adult in-river steelhead abundance for four rainfall-driven regions of British Columbia ranging from the Queen Charlotte Islands south to the lower mainland of British Columbia near Vancouver. Based on these dichotomous results, I argue that steelhead survival to adulthood might be influenced by freshwater conditions more so in northern inland snowmelt-driven rivers than in coastal rainfall-driven rivers because steelhead from snowmelt-driven rivers spend more years in freshwater as juveniles.

Methods

Adult in-river wild steelhead abundance

Wild adult steelhead abundance for individual rivers of the Skeena, Fraser, Bella Coola, Nass, central coast, and north coast snowmelt-driven watersheds was indexed by using catch-per-angler-day (CpAD) as a measure of angler success (see figs. 5 and 6 in Smith et al. 2000). This index was calculated using catch and effort data collected by an angler questionnaire, the Steelhead Harvest Questionnaire (SHQ), managed by the British Columbia Ministry of Fisheries. To compare trends among series and execute time series analyses unencumbered by differences in absolute

Table 1. Indices of the reliability of the annual wild adult steelhead CpAD data used to investigate time series relationships between wild adult CpAD and freshwater discharge anomalies for the snowmelt-driven watersheds.

	Complete series[e]	Mean angler-days (river^{-1}·year^{-1})[f]	% of missing CpAD values[g]	Average deviation[h]	Variance ratio[i]	WSC[j]
Region or watershed						
Fraser watershed[a]	2	891	20	0.41	1.2	7
Bella Coola watershed[b]	0	750	0	0.38	2.7	4
Central coast[c]	0	271	30	—	—	4
North coast	2	2 225	1	0.33	2.6	0
Skeena watershed[d]	7	4 725	<1	0.16	4.8	9
Nass watershed	0	343	29	0.36	0.8	2
Individual rivers						
Thompson River	1	10 016	0	—	—	—
Bella Coola River	1	3 230	0	—	—	—
Dean River	1	4 008	0	—	—	—
Babine River	1	1 988	0	—	—	—

Note: The Skeena watershed stands out as having the most reliable data. It also has the largest number of freshwater discharge monitoring stations from which to calculate its freshwater discharge history. Note that four rivers provide suspicious data on trends in wild adult CpAD because (*i*) they are known to receive particularly high angling pressure (the Thompson River), (*ii*) they are designated as a classified waters because of desirable angling qualities (the Thompson, Dean, and Babine rivers), or (*iii*) they have a wild steelhead conservation problem (the Bella Coola River; Nelson et al. 1998).

[a]Excluding the Thompson River.
[b]Excluding the Bella Coola River.
[c]Excluding the Dean River.
[d]Excluding the Babine River.
[e]Number of rivers (including the "complement") without any missing river–year values for wild adult CpAD.
[f]Average number of angler-days (AD) used to calculate each river–year value for wild adult CpAD.
[g]Percentage of river–year values for wild adult CpAD missing because the number of angler-days for the calculation of CpAD was fewer than 100.
[h]Average deviation of any river–year value for standardised wild adult CpAD from the mean value for that year.
[i]Ratio of the among-years variance in standardised wild adult CpAD to the within-year variance in standardised wild adult CpAD.
[j]Number of Water Survey of Canada (WSC) monitoring stations with sufficient freshwater discharge data to qualify them for inclusion in this study.

CpAD among waterbodies of different sizes and productivities, CpAD was calculated and standardised to a zero mean and unit variance, as described in Smith et al. (2000).

Steelhead generally return to their natal rivers in what is known as either a winter run or a summer run. 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. Calculated values for CpAD are prone to certain biases; however, Smith et al. (2000) concluded that these biases generally do not interfere with interpretation of general trends over time in steelhead abundance when CpAD is calculated using data from several rivers and several years.

Freshwater discharge data

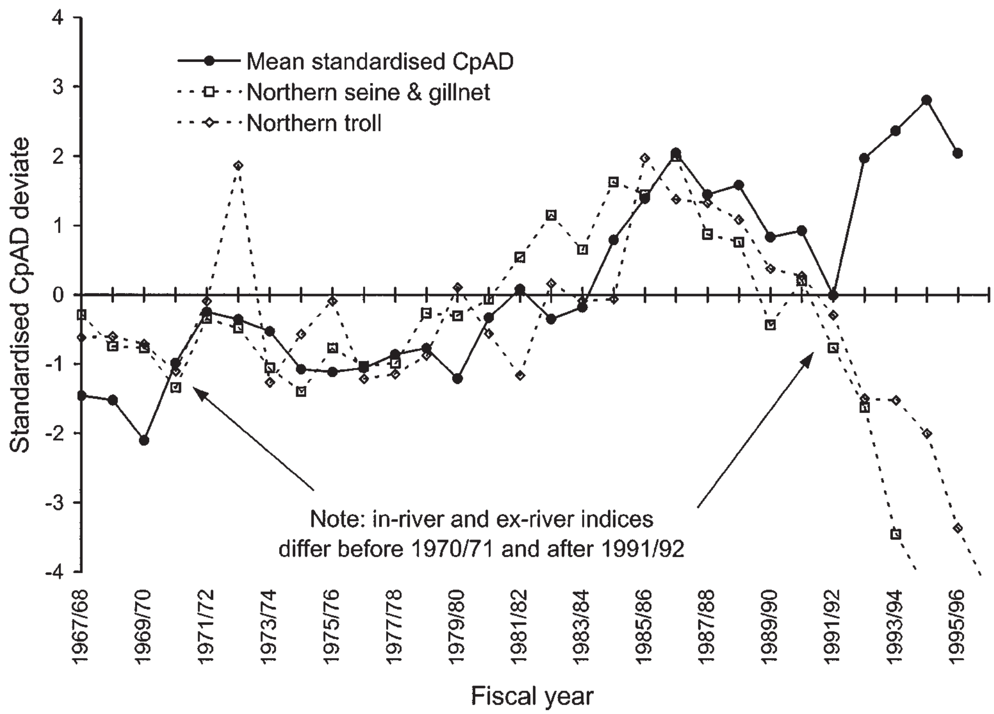
Water Survey of Canada freshwater discharge data were obtained from Environment Canada for all years available up until 1994 and for all regions of British Columbia. Monitoring stations for each region or watershed were then selected if (*i*) the data series began no later than 1962, (*ii*) the last year for which there are data is 1993 or 1994, (*iii*) there are no major gaps in the data series, (*iv*) there are no obvious discharge features related to water control, i.e., dams, and (*v*) the measure of discharge rate is cubic metres per second. These criteria resulted in the data for 65 monitoring stations representing the four rainfall-driven regions (the east and west coasts of Vancouver Island, the lower mainland of British Columbia near Vancouver, and the Queen Charlotte Islands) and five of the six snowmelt-driven watersheds (Fraser, Bella Coola, Skeena, Nass, central coast, and north coast) being accepted for analysis. Insufficient discharge data for north coast rivers meant that data for the Skeena watershed had to be used with those rivers.

Preparation of monthly average flow rates for statistical analyses used the following protocol. First, for each month–year datum, flow rate was converted to ln[monthly flow rate] to standardise the variance in monthly flow rates among years. Second, for each monitoring station the average and SD of ln[monthly flow rate] over all years were calculated. Third, values for ln[monthly flow rate] were expressed as SDs from the average monthly flow rate over all years. Fourth, monitoring stations were amalgamated according to region or watershed and an average SD anomaly within a watershed was calculated. The freshwater discharge time series were found to be absent of identifiable serial autocorrelation and therefore were not prewhitened before being used in time series analyses.

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. Preliminary analyses explored for correlations between mean annual standardised CpAD and annual (fiscal) freshwater discharge anomalies for all 10 regions or watersheds. The freshwater discharge anomalies were challenged with explaining the trends in mean annual standardised CpAD by simultaneously analysing all rivers in each watershed. The exploratory analyses suggested that only the snowmelt-driven regions be the focus of formal analyses to identify relationships between trends in standardised CpAD and freshwater discharge. I then focused particularly on the Skeena watershed because both the CpAD time series and the freshwater discharge data seemed to be

Fig. 2. Comparison of two ex-river indices of wild adult steelhead abundance with in-river wild adult CpAD for the fiscal years 1967–1968 to 1995–1996. All three series are standardised over the comparable period 1970–1971 to 1991–1992. Mean standardised CpAD provides an index of abundance of wild steelhead that have entered the Skeena watershed. Standardised CpDF by the marine commercial seine, gillnet, and troll fisheries for salmon provides an index of steelhead abundance as they approach and enter the Skeena watershed. Note the discrepancy between CpAD and CpDF from 1967–1968 to 1969–1970, before the SHQ polled anglers on the number of steelhead that they caught and released in addition to those that they caught and kept. Note also that a sharp divergence between the in-river and ex-river indices begins in 1992–1993 coincident with the implementation of provincial regulations enforcing the release of steelhead caught in freshwater by sport anglers and federal mitigation to reduce the incidental interception of steelhead by the marine commercial salmon fisheries (Smith et al. 2000).



most reliable for that watershed, as judged by several measures of data quality (Table 1). Attempts to relate trends in standardised CpAD for each river of that watershed to freshwater discharge for each month of the year led to the identification of the summer months, particularly August, as the time of year when freshwater discharge best explained trends in CpAD. On the basis of that discovery, I then attempted to relate trends in CpAD for all snowmelt-driven watersheds to August freshwater discharge for those watersheds.

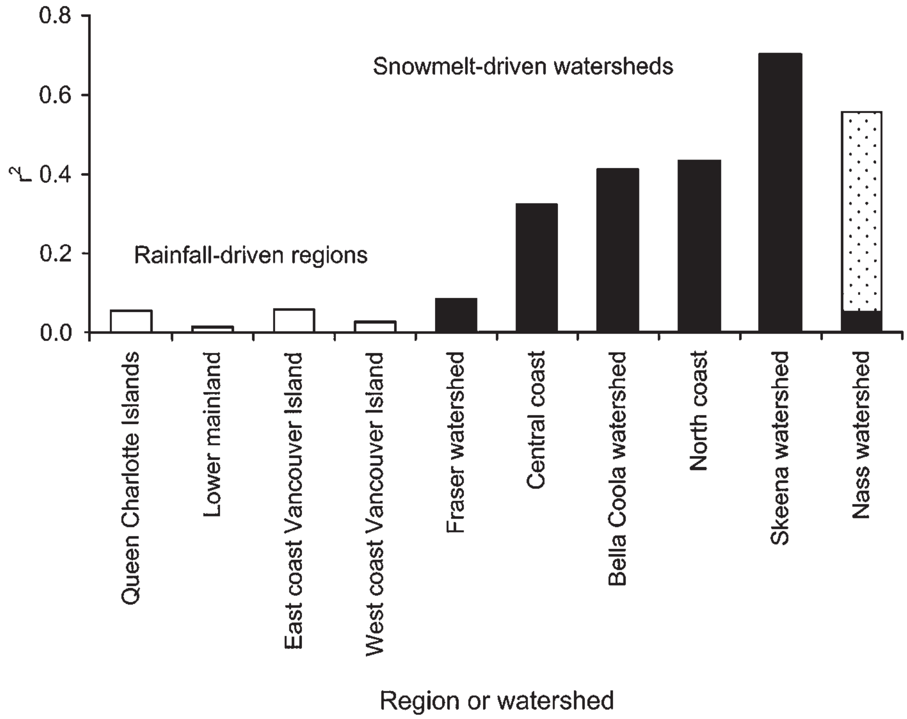
Both the exploratory and formal time series analyses were executed with consideration to suspected biases in CpAD introduced by changes in the SHQ methodology over time and in steelhead management practices (Smith et al. 2000). For example, from 1967–1968 to 1969–1970, CpAD was calculated using data only on steelhead caught and kept by anglers. Beginning in 1970–1971, anglers were also asked to provide information on steelhead that they caught and released (Smith et al. 2000). This abrupt upward shift in mean CpAD (apparent in Fig. 2 for rivers of the Skeena watershed) was accommodated in the exploratory and formal time series analyses for all 10 regions or watersheds by introducing a step intervention in 1970–1971, as described in Smith et al. (2000) and as applied in Smith and Ward (2000).

There is also good evidence that one particular management action is very likely to have affected standardised CpAD as an index of wild steelhead abundance for the Skeena and Nass watersheds. This action was mitigation to reduce the rate of steelhead interception by the commercial salmon fleet in marine waters approaching the mainstem Skeena and Nass rivers of their respective watersheds in 1992–1993. For the Skeena watershed, for which data are available, strong correlations were obtained for four independent indices of wild steelhead abundance standardised over the fiscal years 1970–1971 to 1991–1992 (Fig. 2). However, beginning in 1992–1993, the catch-per-day-fished (CpDF) of the commercial northern seine, gillnet, and troll fisheries began a sharp decline. At the same time, the number of adult returns indexed by both angler CpAD and the Tyee test fishery index increased sharply. The Tyee test fishery is a gillnet test fishery operated at Tyee near the mouth of the Skeena River to index steelhead abundance as they enter the Skeena River.

This divergence among indices in 1992–1993 coincides with the Canadian Department of Fisheries and Oceans promoting new conservation practices to reduce the mortality of steelhead incidentally caught in commercial marine salmon fisheries (Mr. S. Cox-Rogers, Department of Fisheries and Oceans, North Coast Division, Prince Rupert, B.C., personal communication; Mr. B. Hooton, British Columbia Ministry of Fisheries, Smithers, B.C., personal communication). These mitigation actions included setting a target of a 50% reduction in the rate of steelhead interception by the marine commercial salmon fleets as they approach the Skeena and Nass watersheds (Department of Fisheries and Oceans statistical areas 3X, 3Z, and 4). The fiscal year 1992–1993 also saw the introduction of strict rules enforcing the release of wild steelhead caught by sport anglers (see table 2 in Smith et al. 2000). Alternatively, Welch et al. (2000) argued that the abrupt increase in steelhead abundance in the Skeena and Nass watersheds beginning in 1992–1993 is due to an ocean climate regime shift that occurred about 1990 and resulted in increased survival of returning adult salmon a few years later.

This abrupt shift in mean CpAD between 1991–1992 and 1992–1993 was accommodated in both exploratory and formal time series analyses for the Skeena and Nass watersheds by introducing a step intervention in 1992–1993, as described in Smith et al. (2000). This 1992–1993 intervention was not applied to the remaining north coast rivers of coastal Region 6 (see fig. 1 in Smith et al.

Fig. 3. Exploratory squared correlations (r^2) between annual mean (over all series) standardised wild adult steelhead CpAD and the CuSums of historical mean annual freshwater discharge for the four rainfall-driven regions (open bars) and six snowmelt-driven watersheds (solid bars). Note that freshwater discharge data for the Skeena watershed were used for the north coast rivers. The stippled bar illustrates the result obtained for the Nass watershed using the more reliable freshwater discharge data for the adjacent Skeena watershed. 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. These values for r^2 were calculated assuming that the step interventions in 1970–1971 and 1992–1993 apply to the appropriate regions or watersheds, i.e., the parameters associated with those interventions were free to be estimated. Likewise, the r^2 values for east coast Vancouver Island and the lower mainland also include linear trend interventions beginning in 1990–1991 to account for observed downward trends in CpAD for these two rainfall-driven regions that were not observed for west coast Vancouver Island and the Queen Charlotte Islands (Smith and Ward 2000).



2000), since there is no argument to include it and the values for CpAD do not suggest an abrupt increase in steelhead abundance in those rivers at that time (see Fig. 7). Finally, to be consistent with Smith and Ward (2000), linear trend interventions beginning in 1990–1991 were included for east coast Vancouver Island and the lower mainland near Vancouver to account for an observed downward trend in CpAD for these two rainfall-driven regions that was not observed for west coast Vancouver Island and the Queen Charlotte Islands. The inclusion of an intervention in any analysis means that the step or slope parameter associated with that intervention was free to be estimated.

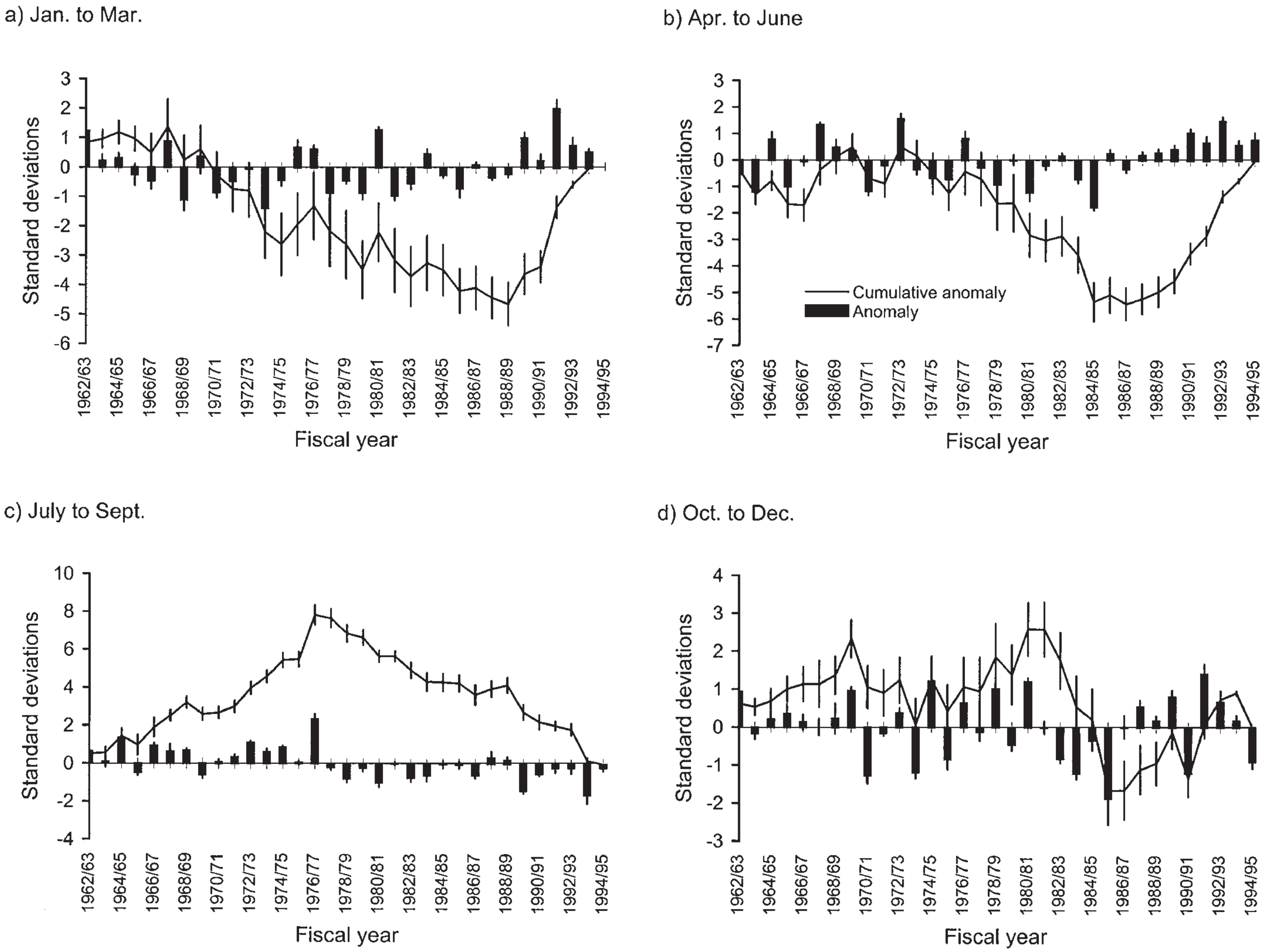
Results

Exploratory analyses of mean annual standardised CpAD versus freshwater discharge (Fig. 3) clearly distinguished the rainfall-driven regions from the snowmelt-driven watersheds. For all four rainfall-driven regions the correlation between annual anomalies of freshwater discharge and CpAD was close to zero. In contrast, correlations for the snowmelt-driven watersheds were much higher and as high as 0.70 for the Skeena watershed. The tendency is for the degree of correlation to increase toward the north, an obvious exception being the Nass watershed when using freshwater discharge data for that watershed. A much better correlation was obtained using the more reliable freshwater discharge data for the adjacent Skeena watershed. This qualitative result that discriminates between coastal rainfall-driven regions and inland snowmelt-driven watersheds is opposite to that obtained using coastal upwelling as the covariate series (Smith and Ward 2000).

These encouraging exploratory correlations between CpAD and annual freshwater discharge for the snowmelt-driven watersheds prompted me to further investigate this relationship for each month of the year. I began by analysing the CpAD time series for the Skeena watershed because both the CpAD time series and the freshwater discharge data were most reliable for that watershed (Table 1). I excluded the Babine River from these analyses because it does not present a pattern of CpAD consistent with that of the other rivers of the Skeena watershed (see Fig. 7; see fig. 6 in Smith et al. 2000). It is among a few rivers in the province with very high values for CpAD. These values are possibly biased by an annual fishing-down of the steelhead population in that river (Smith et al. 2000) in the years when percent catch and release was low.

For each month of the year, I specifically tested the hypothesis that freshwater discharge anomalies (Fig. 4) 2–5 years prior to the year that steelhead return to their natal river to spawn (i.e., while they were juveniles in freshwater) could explain trends in standardised CpAD for each river of the Skeena watershed. I also included the possibility that freshwater discharge during the year that steelhead return to

Fig. 4. Annual and cumulative annual anomalies (CuSums) of freshwater discharge for the Skeena watershed according to season. An abrupt change in the slope of a CuSum plot indicates a change in the mean level of a time series. Error bars represent 1 SE.

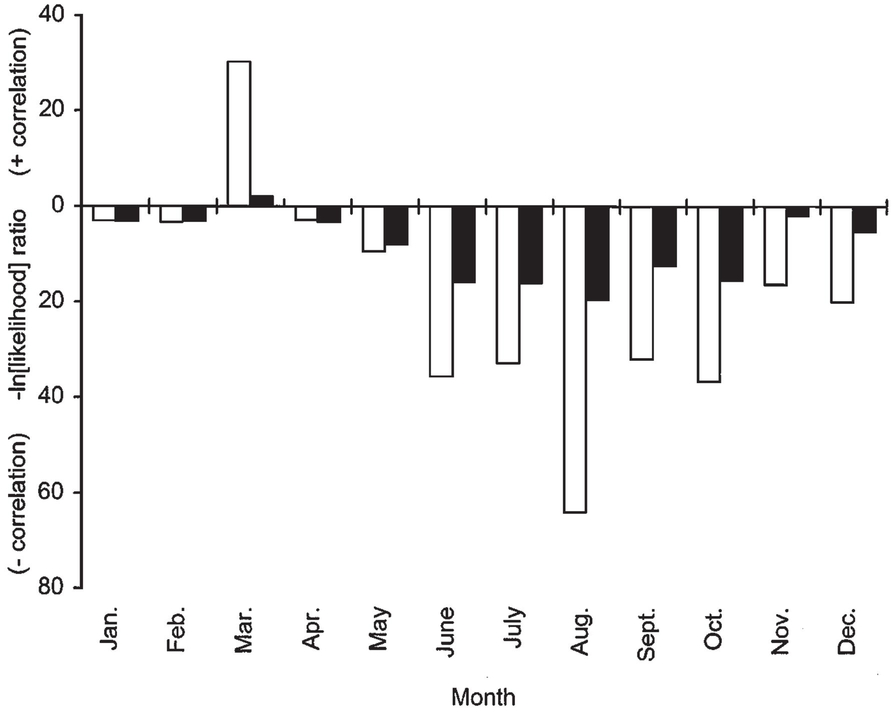


spawn could influence CpAD as an index of wild adult steelhead abundance. This latter correlation could be caused by high-flow conditions negatively affecting steelhead catchability by sport anglers. I identified almost exclusively negative correlations between monthly freshwater discharge anomalies 0 and 3–5 years prior to the year that steelhead return to spawn in their natal river of the Skeena watershed and standardised annual CpAD. Likelihood ratio comparisons identified August as the month having the closest correlation between CpAD and current and historical freshwater discharge, followed by the months that shoulder August (Fig. 5).

Results of the above analyses prompted me to perform four more analyses, one each for the Fraser watershed, the Bella Coola watershed, coastal Region 5 (the Dean River), and the north coast rivers (including the rivers of the Skeena and Nass watersheds), using freshwater discharge data for the month of August (Fig. 6). For this latter analysis, I used the freshwater discharge data for the Skeena watershed as the candidate covariate series, since the freshwater discharge data for the Nass watershed were of poor quality. I also limited the analysis of CpAD for the Nass watershed to the three rivers missing fewer than five years of values for CpAD.

I report the three formal time series analysis results for August (Tables 2–4; Fig. 7). No significant relationship between CpAD and freshwater discharge could be identified for the Fraser watershed using the $\alpha = 0.05$ rejection standard. The Bonferroni correction for $\alpha = 0.05$ for 12 monthly trials is 0.0043, but this is an overly conservative rejection standard for these analyses because flow rates for adjacent months are closely correlated and the risk of rejection of a real correlation is sharply increased. The three models reported accounted for 62, 58, and 40% of all variation in CpAD for the north coast, Dean River, and Bella Coola watersheds, respectively. Within this, 28, 14, and 29% of total variance can be attributed to annual variability in August freshwater discharge 3–5 years prior to the years that steelhead return to their natal river to spawn. The analyses for the Dean River and the Bella Coola watershed each required a linear trend intervention to account for a decline in CpAD of 0.11 and 0.05 SD, respectively, that could not be explained by the general trend over time in freshwater discharge for those two watersheds. There are few rivers in those watersheds, casting

Fig. 5. Comparison of differences in likelihood ratio support for time series TFN models of monthly flow rate deviations fit to standardised annual steelhead CpAD. The monthly models were fit to standardised annual CpAD for wild adult steelhead returning to seven rivers of the Skeena watershed (excluding the Babine River). The correlations between flow rate deviations and CpAD were predominately negative, the month of March being an exception. Results are presented for models that both include and exclude the autoregressive term AR(1), since autoregressive parameters tend to weaken support for candidate TFN relationships. Open bars, without autoregressive AR(1) term; solid bars, with autoregressive AR(1) term.



some doubt on the reliability of the trends in CpAD for those rivers (Smith et al. 2000).

The weak, negative relationship of CpAD to freshwater discharge during the year that steelhead return to their natal rivers to spawn accounted for only about 1–2% of total variance. Such a negative relationship would be expected if higher flow rates tend to reduce steelhead catchability by sport anglers. One effect of reduced catchability would be a tendency for CpAD to overestimate steelhead abundance in years of lower than average flow rates and vice versa. Summer and annual flow rates have been generally lower than average since about 1980 (Fig. 4), but the statistical evidence is weak that reduced catchability in the summer of years with higher than average flows is an important factor affecting CpAD as an index of adult steelhead abundance. However, the effect of high flow rates might be much more important in other seasons.

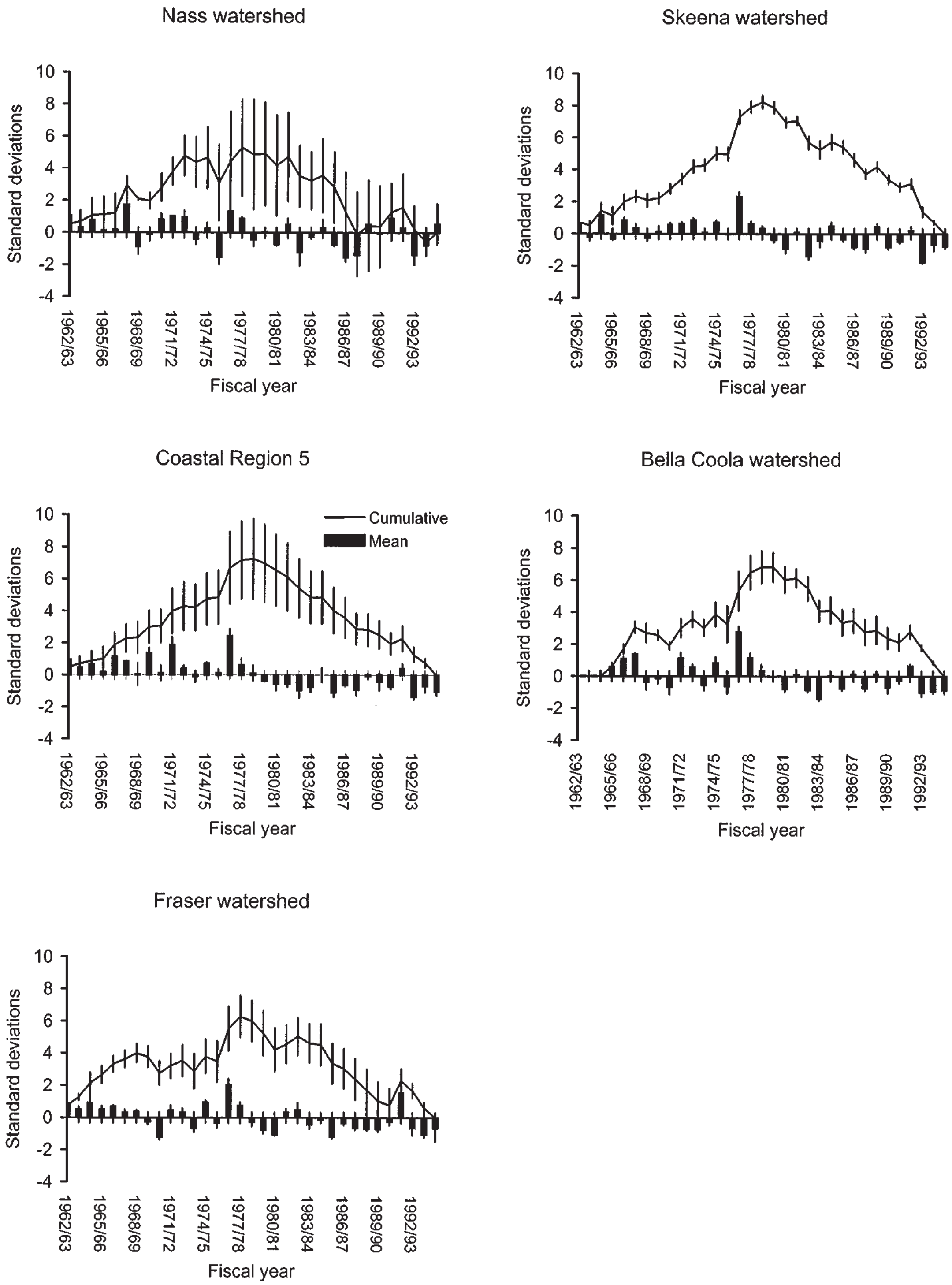
The autoregressive (AR) (θ_1) and (or) moving average (MA) (ϕ_1) terms account for the final few percentages of total variance. The nonzero values for these terms account for the within-year variability in predicted standardised CpAD represented by the error bars in Fig. 7. Note also that the step interventions in 1970–1971 and 1992–1993 account for factors that would otherwise cause CpAD to overestimate the increasing trend in steelhead abundance evident for the north coast rivers. Thus, steelhead abundance in the north coast watersheds has apparently not increased in abundance as dramatically as indicated by the observed values for CpAD (Fig. 7; see fig. 6 in Smith et al. 2000).

Discussion

Time series analysis detected a statistically significant relationship between standardised CpAD for wild adult steelhead and August freshwater discharge anomalies for the most northerly of the snowmelt-driven watersheds in British Columbia subjected to analysis. These analyses allow the interpretation that summer flow conditions 3–5 years prior to the year that adult steelhead return to their natal river to spawn (Fig. 6) might be an important determinant of adult steelhead abundance (Fig. 7; Tables 2–4). Once having accounted for variation in standardised CpAD arising from the step interventions in 1970–1971 and 1992–1993, no explanation other than the history of August freshwater discharge is required to explain about 36% of interannual variability in standardised wild adult CpAD in snowmelt-driven north coast rivers over the past two to three decades.

I found the strongest support for the proposition that freshwater discharge rates affect future adult steelhead abundance for the more northerly rivers. The CpAD and freshwater discharge data for the Dean River and rivers of the Bella Coola watershed ranked lower in reliability than the data for the more northerly rivers by several measures of quality (Table 1), thereby weakening the power of my analyses to detect relationships between CpAD and freshwater discharge. No relationships could be identified for the Fraser watershed, but I note that the Thompson River of the Fraser watershed receives very high angling pressure (Table 1) and is unique in that Thompson River steelhead smolt after 2 years

Fig. 6. Annual and cumulative annual anomalies (CuSums) of freshwater discharge for five snowmelt-driven watersheds for the month of August. An abrupt change in the slope of a CuSum plot indicates a change in the mean level of a time series. Error bars represent 1 SE.



(Mr. B. Ward, British Columbia Ministry of Fisheries, Vancouver, B.C., personal communication). The Thompson River, along with the Dean River of the central coast and the Babine River of the Skeena watershed, are designated as classified waters because of their desirable angling qualities. The Dean and Babine rivers have high and variable values for CpAD when compared with other rivers in their watershed (see fig. 6 in Smith et al. 2000) and may be seriously biased by an annual fishing-down of the steelhead population in those rivers, especially in the years prior to catch and release being a common practice (Smith et al. 2000). The CpAD trend for the Bella Coola watershed is suspect because the Bella Coola River is known to have a wild steelhead conservation problem related to overfishing (Nelson et al. 1998).

I caution readers not to take the quantitative results of

Table 2. Analysis of variance for a time series analysis of standardised wild adult steelhead CpAD for two rivers, plus the complement of 28 rivers, for the north coast (coastal Region 6, CR6); six rivers, plus the complement of 30 rivers, for the Skeena watershed; and two rivers, plus the complement of 12 rivers, for the Nass watershed.

Summary							
Observations		343					
r^2		0.62					
SE		0.58					
Analysis of variance		SS	df	Mean SS	F	p	
Regression		183.2	11	16.65	50.09	<0.0001	
Residual		110.0	331	0.33			
Total		293.2	342				
Parameter	Description			Value	SE	p	Cumulative r^2
μ_{CR6}	CR6 intercept (series mean) in 1967–1968			–0.70	0.24	0.003	↓
μ_{Skeena}	Skeena intercept (series mean) in 1967–1968			–0.66	0.16	<0.001	↓
μ_{Nass}	Nass intercept (series mean) in 1967–1968			–0.52	0.28	0.066	0.00
$\omega_{0,1}$	CR6 step intervention in 1970–1971			0.88	0.25	<0.001	↓
$\omega_{0,2}$	Skeena step intervention in 1970–1971			0.71	0.17	<0.001	↓
$\omega_{0,3}$	Skeena step intervention in 1992–1993			0.78	0.20	<0.001	↓
$\omega_{0,4}$	Nass step intervention in 1970–1971			0.46	0.30	0.119	↓
$\omega_{0,5}$	Nass step intervention in 1992–1993			0.82	0.29	0.006	0.25
$\omega_{3.6}$	August discharge: 3-year lag			–0.18	0.05	<0.001	↓
$\omega_{4,6}$	August discharge: 4-year lag			–0.16	0.05	<0.001	↓
$\omega_{5,6}$	August discharge: 5-year lag			–0.12	0.05	0.002	0.53
$\omega_{0,6}$	August discharge: 0-year lag			–0.14	0.04	0.014	0.54
θ_1	AR(1)			0.54	0.06	<0.001	↓
ϕ_1	MA(1)			0.28	0.09	0.001	0.62

Note: The Babine River of the Skeena watershed is excluded for reasons explained in the text, as are three rivers of the Nass watershed because they are missing values for wild CpAD for five or more years. The model identifies a significant (α = 0.05) relationship between CpAD and August freshwater discharge 0 and 3–5 years prior to the year that wild adult steelhead return to their natal river to spawn. The model includes two step interventions each for the Skeena and Nass watersheds: one in 1970–1971, the first year that the SHQ polled anglers on the number of steelhead that they caught and released as well as on those caught and kept, and another in 1992–1993 associated with the implementation of measures to mitigate steelhead mortality caused by commercial fishers and sport anglers. Only the 1970–1971 intervention applies to the north coast rivers.

Table 3. Analysis of variance for a time series analyses of standardised wild adult steelhead CpAD for the Dean River of coastal Region 5.

Summary							
Observations		27					
r^2		0.58					
SE		0.78					
Analysis of variance		SS	df	Mean SS	F	p	
Regression		16.26	7	2.32	3.77	0.0099	
Residual		11.70	19	0.62			
Total		27.96	26				
Parameter	Description			Value	SE	p	Cumulative r^2
μ	Intercept (series mean) in 1967–1968			–1.04	0.12	<0.001	0.00
$\omega_{0,1}$	Step intervention in 1970–1971			3.06	0.15	<0.001	↓
$\omega_{0,2}$	Linear trend intervention in 1967–1968			–0.11	0.01	<0.001	0.43
$\omega_{3,3}$	August discharge: 3-year lag			–0.47	0.06	<0.001	↓
$\omega_{4,3}$	August discharge: 4-year lag			–0.047	0.06	<0.001	↓
$\omega_{5,3}$	August discharge: 5-year lag			–0.18	0.05	0.002	0.57
$\omega_{0,3}$	August discharge: 0-year lag			–0.22	0.08	0.009	0.58
ϕ_1	MA(1)			0.16	0.08	0.051	0.58

Note: The model identifies a significant (α = 0.05) relationship between CpAD and August freshwater discharge 0 and 3–5 years prior to the year that wild adult steelhead return to the Dean River to spawn. The model includes a step intervention in 1970–1971, the first year that the SHQ polled anglers on the number of steelhead that they caught and released as well as on those caught and kept, and a linear trend beginning in 1968 to account for a general decline over time in CpAD that occurs at a rate (0.11 SD·year^{-1}) greater than can be explained by the time series of freshwater discharge.

Table 4. Analysis of variance for a time series analysis of standardised wild adult CpAD for the Bella Coola River, plus the complement of three rivers, for the Bella Coola watershed.

Summary							
Observations		54					
r^2		0.40					
SE		0.73					
Analysis of variance		SS	df	Mean SS	F	p	
Regression		17.06	5	3.41	6.40	0.0001	
Residual		25.59	48	0.53			
Total		42.65	53				
Parameter	Description			Value	SE	p	Cumulative r^2
μ	Intercept (series mean) in 1967–1968			0.88	0.37	0.024	0.00
$\omega_{0.1}$	Step intervention in 1970–1971			–0.08	0.46	0.870	↓
$\omega_{0.2}$	Linear trend intervention in 1967–1968			–0.05	0.02	0.038	0.04
$\omega_{3.3}$	August discharge: 3-year lag			–0.36	0.13	0.007	↓
$\omega_{4.3}$	August discharge: 4-year lag			–0.38	0.12	0.003	0.33
ϕ_1	MA(1)			–0.42	0.16	0.014	0.40

Note: The model identifies a significant (α = 0.05) relationship between CpAD and August freshwater discharge 3 and 4 years prior to the year that wild adult steelhead return to their natal rivers to spawn. The model includes a step intervention in 1970–1971, the first year that the SHQ polled anglers on the number of steelhead that they caught and released as well as on those caught and kept, and a linear trend beginning in 1968 to account for a general decline over time in CpAD that occurs at a rate (0.05 SD·year^{-1}) greater than can be explained by the time series of freshwater discharge.

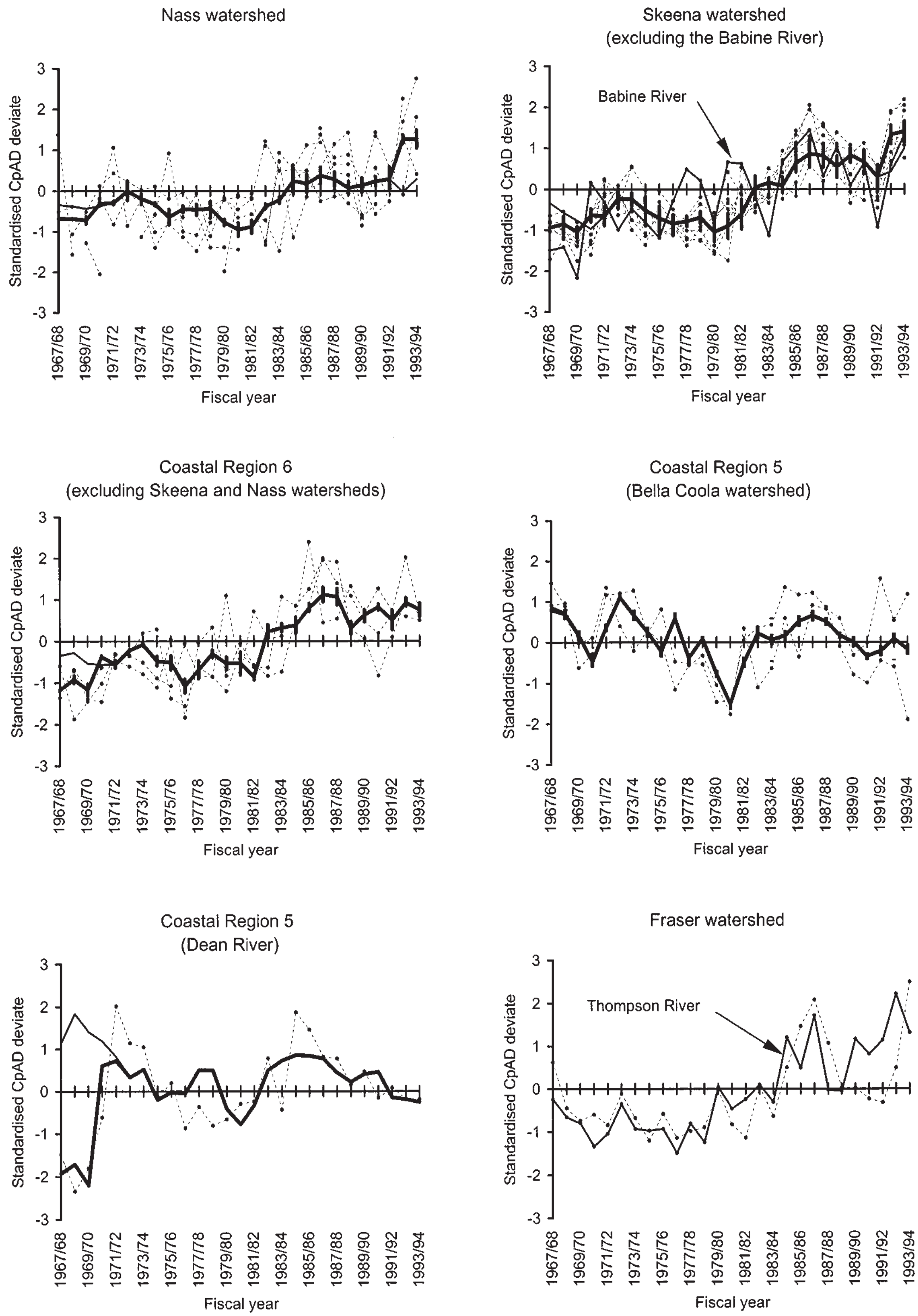
these analyses too literally, since there are several important constraints to their interpretation. There is undoubtedly some influence of variability in ocean climate on the abundance of adult steelhead returning to spawn in their natal rivers. Also, CpAD is an index calculated for an entire fiscal year (Smith et al. 2000). Therefore, for some rivers, CpAD indexes the abundance of both summer-run and winter-run steelhead returning at different times of the year, with each run possibly comprising several cohorts. Nevertheless, the quantitative results allow the qualitative interpretation that the abundance of wild adult steelhead returning to rivers of the more northerly snowmelt-driven watersheds might be determined more by the summer and autumn flow conditions that these steelhead experienced as juveniles in freshwater than is the case for steelhead of rainfall-driven regions. Steelhead of snowmelt-driven watersheds are known to spend up to 5 years as juveniles (Whately 1975) in these cold, unproductive waters compared with an average about 2–3 years for juveniles of the warmer and more productive rainfall-driven regions (Hooton et al. 1987; Ward 1996).

The main inference of this result is that higher than average summer and autumn flows 3–5 years prior to the year that steelhead return to spawn in their natal rivers in the more northerly snowmelt-driven watersheds negatively affect adult steelhead abundance (Table 2; Fig. 7). Summer is the season of peak discharge in snowmelt-driven regions (Fig. 1). Years of lower than average summer freshwater discharge (Fig. 6), especially since the early 1980s, coincide with higher than average values for wild CpAD (Fig. 7). Consequently, a period of lower than average flow rates in the 1980s and early 1990s appears to have been favourable to steelhead abundance. Given that wild steelhead return to the Skeena watershed at 6–7 years of age (Mr. R. Ptolemy, British Columbia Ministry of Fisheries, Victoria, B.C., personal communication), this suggests that the mean age of greatest vulnerability is about 2–3 years, when most steelhead are probably parr (Hooton et al. 1987; Peven et al. 1994; Busby et al. 1996). Two mechanisms capable of increasing juvenile mortality are a direct loss of low-velocity habitat required as refuges for parr (Fausch 1993) during years of high flows and water levels and the premature flushing of juveniles out of suitable habitat or the river by high flows (Shirvell 1990; Nehring and Anderson 1993; Latterell et al. 1998). High flows could be particularly detrimental during the summer when the physiological stress imposed by high water temperatures, low dissolved oxygen concentrations, and silt load would be greatest (Northcote 1992).

No relationship could be identified between historical freshwater flow and adult steelhead abundance for the rainfall-driven regions (Fig. 3). Rainfall-driven regions are characterised by rivers with generally steeper slopes and higher energy gradients than snowmelt-driven rivers. Not detecting a relationship might seem surprising, given that coefficients of annual variance in July to October discharge rates for the rainfall-driven regions (65%) tend to be considerably higher than those for the snowmelt-driven regions (35%). One explanation is that the direct runoff characteristic of rainfall-driven regions results in short-duration extreme flow events not being captured in the average monthly flow rate data. Much of the precipitation on snowmelt-driven watersheds is stored as ice and snow. It tends to melt slowly, thus reducing the frequency, magnitude, and consequences of extreme flow events but prolonging the periods of above- or below-average flows.

The freshwater flow regime is intimately connected to ocean climate through rainfall (Mantua et al. 1997), and it is conceivable that the relationships that I identified between adult steelhead abundance and freshwater discharge reflect the influence of interannual variability in oceanic–atmospheric climate on both adult steelhead abundance and freshwater discharge rates. The trends in adult steelhead abundance for both the rainfall-driven regions and the snowmelt-driven watersheds show an increase in the late 1970s and early 1980s near the time of the first documented climate shift in 1977 (Beamish et al. 1999). Recent studies have also interpreted

Fig. 7. Mean time series predictions (thick solid lines) of standardised wild steelhead CpAD for north coast rivers (coastal Region 6) and the Skeena and Nass watersheds (Table 2, but with parameter values optimised for each watershed), the Dean River (Table 3), and the Bella Coola watershed (Table 4). No predictions are reported for the Fraser watershed, since no significant relationship between CpAD and freshwater discharge was identified. Error bars indicate the SDs of the predicted CpADs for each river in the watershed. These SDs are due to the nonzero values for the autoregressive (θ_1) and (or) moving average (ϕ_1) terms. Predictions that transcend the step interventions in 1970–1971 and 1992–1993 are represented by thin solid lines that merge with the thick solid lines at those years. Thin solid lines also identify the Thompson and Babine rivers. Thin broken lines with points represent standardised CpAD for individual rivers. The original, unstandardised time series of CpAD can be viewed in fig. 6 in Smith et al. (2000).



that a favourable ocean climate has been responsible for the generally increasing abundance of adult salmon in more northerly waters over the past few decades, while abundance in more southerly waters has declined (Hare et al. 1999; Welch et al. 2000). Freshwater discharge in British Columbia shows a similar decadal-scale pattern. For example, the start of the spring freshet in south and central British Columbia has advanced about 1 day·year^{-1} over the last two to three decades (Leith and Whitfield 1998). This advance has been accompanied by a lower flow rate in the late-summer and autumn seasons.

Welch et al. (2000) argued that this dichotomy in salmon productivity between north and south, which occurs at about 52°N latitude, appears in trends in wild adult steelhead CpAD after 1990 and is evidence of a possible regime shift in ocean climate about that time. I propose that this dichotomy might be due in part to a differential effect of freshwater influences on adult steelhead abundance in rainfall-driven versus the generally more northerly snowmelt-driven regions or watersheds. Given the confounding of atmospheric influences on both the oceanic and freshwater environments of salmonids of the Northeast Pacific Ocean (Mantua et al. 1997), the freshwater environment might be a more important determinant of decadal-scale variability in adult salmonid abundance than has been discovered to date. The tendency for salmon productivity in the Northeast Pacific Ocean over the past two to three decades to increase in the north and decrease in the south (see Hare et al. 1999) perhaps should also be considered in the context of decadal changes in freshwater flow regimes. However, juvenile steelhead have a considerably longer freshwater residency than do most salmonids (Groot and Margolis 1991) and are a more likely candidate for detecting an influence of the freshwater environment on adult abundance.

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