

Abstract.—To characterize the impact of spring floods on the survival of juvenile chinook salmon in the unstable, braided rivers on the east coast of New Zealand's South Island, I examined correlations between spring and summer flows in the mainstem of the Rakaia River and fry-to-adult survival for chinook salmon spawning in a headwater tributary. Flow parameters that were investigated included mean flow, maximum flow, and the ratio of mean to median flow (an index of flow variability), calculated during peak downriver migration of ocean-type juveniles (August to January). Survival was uncorrelated with mean or maximum flow but was positively correlated with the ratio of mean to median flow during spring (October and November). The correlation suggests that pulses of freshwater entering the ocean during floods may buffer the transition of fingerlings from fresh to saline waters and thus partly compensate for the lack of an estuary on the Rakaia River. A positive correlation between spring flow variability and the proportion of ocean-type chinook in relation to stream-type chinook is also consistent with this hypothesis. All correlations were relatively weak, reinforcing earlier results that production is primarily controlled by marine influences. These findings further demonstrate the considerable ability of chinook salmon to adapt to new habitats.

Survival of chinook salmon, *Oncorhynchus tshawytscha*, from a spawning tributary of the Rakaia River, New Zealand, in relation to spring and summer mainstem flows

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To understand the population dynamics of anadromous Pacific salmonids (*Oncorhynchus* spp.), it is important to isolate and characterize the influence of varying environmental factors on annual production. In the course of their life cycle salmon inhabit a succession of freshwater and marine environments, where prospects for survival depend on prevailing conditions. Spawning and incubation success may be adversely affected by substrate disturbance during floods; the suitability of riverine waters as habitat for rearing juveniles is dependent on both flow and temperature and may be reduced by flows that are too low or too high; and adult survival within the marine environment is at least partly determined by environmentally controlled factors such as oceanic water masses and the availability of suitable prey. Numerous studies have demonstrated significant correlations between environmental variables and indices of survival and growth, at scales ranging from local to global. Although correlation analysis in fisheries studies has been criticized for its potential for misuse and for a propensity to produce weak results of little practical value (Walters and Collie, 1988), other authors have noted that provided the method is used with discretion, biologically meaningful re-

sults can be derived (Kope and Botsford, 1990).

Despite the importance of in-stream habitats for rearing juvenile chinook salmon (*O. tshawytscha*), the relation between flow and brood year survival has received comparatively little attention. Interannual trends in the abundance of chinook salmon in the Fraser River, British Columbia, have been linked to flow variations in the mainstem (Beamish et al., 1994) and in the Nechako River tributary (Bradford, 1994). In the former study, annual production was inversely related to mean annual discharge, whereas in the latter study, juvenile survival in the upper Nechako appeared to decline as a result of flow diversion for hydroelectric generation, and the proportion of spawning fish using the upper river appeared to be negatively correlated with August flows. However, in the Nechako River study, as in some other studies linking downriver migration to river flows (e.g. Kjelson et al., 1982), low flows were often associated with increased water temperatures, making it difficult to differentiate between flow-related and temperature-related effects. Williams and Matthews (1995) found that survival of Snake River spring and summer chinook salmon juveniles was reduced during low flow conditions but concluded that these

losses were primarily due to problems with passage through hydroelectric dams rather than to low discharge per se. The effects of flow variability on survival have also received little attention. Increased downstream movement of newly emerged salmonid fry following sudden increases in discharge has been well documented (e.g. Irvine, 1986; Saltveit et al., 1995), but only rarely has flow variability been used as a predictor variable in population studies (Berggren and Filardo, 1993).

Whenever brood year survival is estimated from stock-recruitment or similar data, a search for correlations between river flow and survival will usually involve deriving a single flow index, such as the annual mean, for each cohort. Most such studies conducted to date have used flow averaged over periods from three months (Kope and Botsford, 1990) to one year (Beamish et al., 1994), but it is by no means obvious that these are the most informative or biologically meaningful parameters to use. A single catastrophic flood during the incubation period may cause large-scale destruction of redds and loss of alevins through bed scour (Montgomery et al., 1996) without having much effect on the mean annual flow. Prior to smolting, fry may be susceptible to short-term floods that carry them prematurely into seawater, when the same floods a few months later would have little impact. In addition, mean flow is not necessarily the most relevant statistic for characterizing flow regimes; it is possible that in the two examples given above, some other parameter (such as maximum flow or the coefficient of variation) might be more informative (e.g. Hvidsten and Hansen, 1988). For example, in New Zealand, where high flow variability is a defining characteristic of riverine ecosystems (Biggs, 1995), statistics such as the proportion of the time the flow exceeds three times the median (Clausen and Biggs, in press) and the ratio of mean flow to median flow (Jowett, 1990), have been successful in elucidating relations between flow regime and biological parameters. To explore fully the relation between flow and survival, therefore, it is necessary to consider not only the type of flow statistic that is likely to be of interest but also the duration and seasonal timing of the period over which the statistic is to be calculated.

Since the introduction of fall-run Sacramento River stock to New Zealand in the early 1900's (McDowall, 1994a; Quinn et al., 1996), chinook salmon have maintained self-sustaining populations in all major rivers on the east coast of the South Island (McDowall, 1990; Quinn and Unwin, 1993). Like most New Zealand rivers, these rivers (whose wide, braided shingle beds drain steeply mountainous catchments on the South Island main divide) are characterized by highly vari-

able flows (Jowett and Duncan, 1990), flooding quickly whenever snow and ice melt in the headwaters is augmented by heavy orographic rainfall. These floods occur at any time of year but are particularly common in spring. In rivers such as the Rakaia they cause massive bed movement (Ibbitt, 1979) and reduce the abundance and diversity of invertebrate fauna (Sagar, 1986) for up to one month afterwards. The impact of these events on seaward-migrating juvenile chinook has generated some debate. Several authors have remarked that survival of New Zealand chinook fry may be adversely affected during floods (McDowall, 1990; Flain¹). Other studies suggest that, although some fry may be lost during extreme floods, flow fluctuations in a more typical season do not have a serious negative impact on migration (Hopkins and Unwin, 1987).

Chinook salmon spawning populations in Glenariffe Stream, a headwater spawning tributary of the Rakaia River (Fig. 1), have been monitored since 1965 by means of an upstream counting fence (Quinn and Unwin, 1993). In this study I analyzed brood year survival, for chinook spawning in Glenariffe Stream, in relation to Rakaia mainstem discharge during spring and summer (August to January). My primary objectives were to examine various flow statistics as possible correlates with survival and to determine the sensitivity of any resulting correlations to changes in the interval used to calculate each statistic. A secondary objective was to examine evidence that spring floods were detrimental to brood year survival.

Chinook salmon in New Zealand

New Zealand chinook salmon are broadly similar to their Sacramento ancestors in terms of both their general life history (Unwin, 1986) and genetic make up (Quinn et al., 1996). Present day stocks comprise a mixture of ocean- and stream-type fish (Gilbert, 1913; Healey, 1983), corresponding to juveniles that spend 3–6 mo or 12–15 mo in fresh water before entering the ocean (Unwin and Lucas, 1993). In the Rakaia River, the most thoroughly studied of the major salmon producing rivers, ocean-type fish make up about two-thirds of the returning adults (Quinn and Unwin, 1993).

The migration patterns of age-0+ juvenile chinook salmon in the Rakaia River and a key spawning tributary, Glenariffe Stream (Fig. 1), have been studied in some detail, and are relatively well understood (Unwin, 1986; Hopkins and Unwin, 1987). From

¹ Flain, M. 1982. Quinnet salmon runs, 1965–1978, in the Glenariffe Stream, Rakaia River, New Zealand. Occasional Publ 28, N.Z. Ministry of Agriculture and Fisheries, Fisheries Research Div., 22 p. [Copy held at NIWA, Christchurch, New Zealand.]

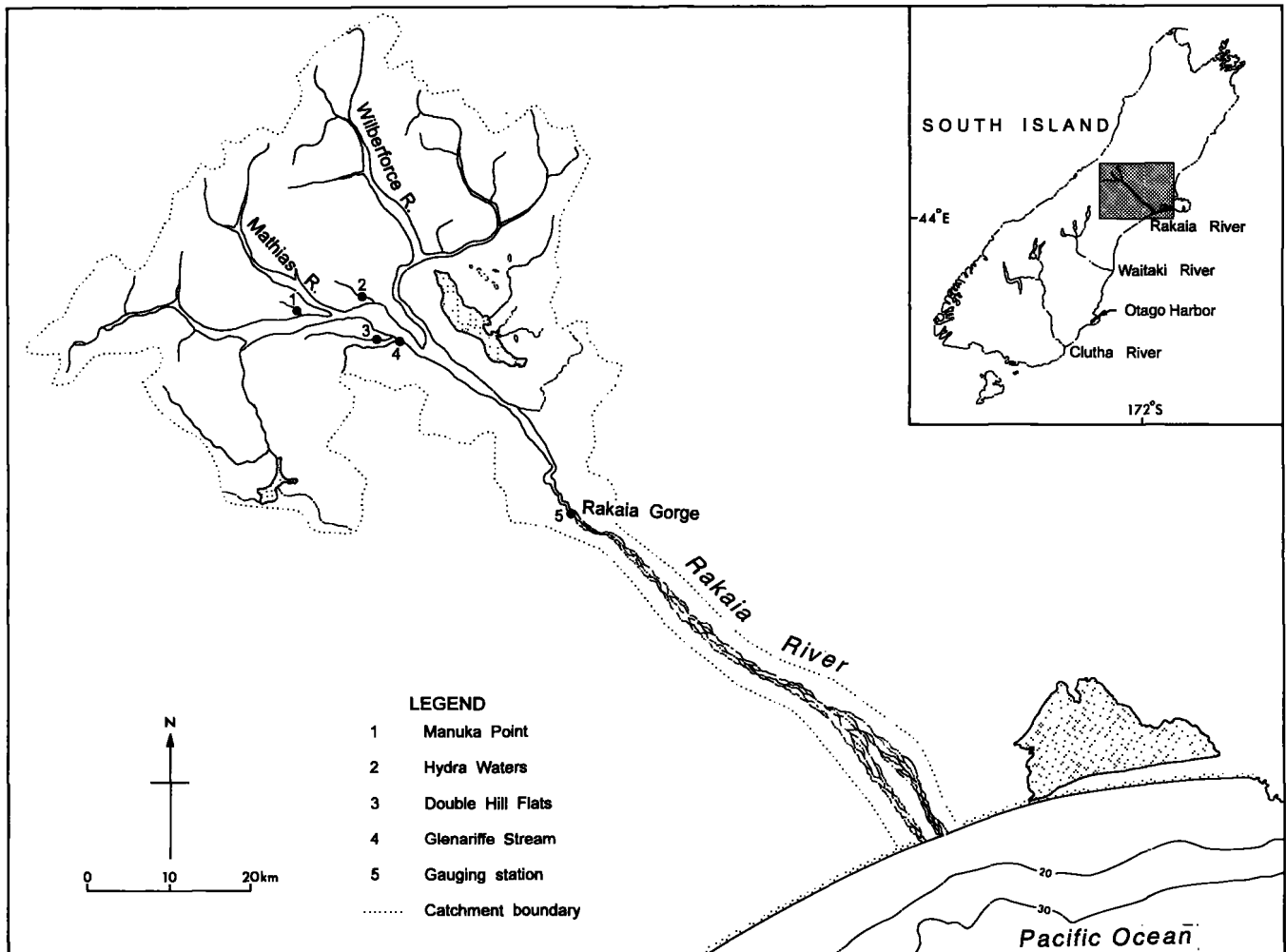


Figure 1

The South Island of New Zealand and the Rakaia River catchment, showing geographical features referred to in the text, the four main headwater tributaries used by spawning chinook salmon (1–4), and the 20-m and 30-m isobaths off the Rakaia mouth.

August to October (late winter to mid spring), large numbers of newly hatched fry emerge from the gravel in Glenariffe Stream and other spawning areas and begin to move downstream within 24 h of emergence. This migration appears to be driven by population pressure; the rearing capacity of Glenariffe Stream has been estimated at less than 100,000 fry, whereas annual fry production can exceed 3.7 million (Unwin, 1986). A second wave of larger fry, representing individuals remaining in their natal stream for up to 3 months, enters the upper river from November to January, but in Glenariffe Stream these fry represent less than 10% of the total production. This pattern appears to be typical for chinook populations within their native range (e.g. Lister and Walker, 1966; Reimers, 1973; Healey, 1991).

Within the upper reaches of the Rakaia River, fry quickly take up residence along the margins of the braided channels, where there is an abundance of

suitable rearing habitat (Glova and Duncan, 1985). Aquatic invertebrates, predominantly *Deleatidium* spp., are the primary prey in spring, but in summer the diet of fry is dominated by terrestrial species and chironomids (Sagar and Glova, 1987). From mid-August fingerlings gradually disperse downriver, growing steadily as the season progresses and reaching the lower river in mid-October at about 60–80 mm fork length (FL) (Hopkins and Unwin, 1987). Fingerlings remain abundant in the lower river until early February but show little tendency to increase in size; thus there appears to be a steady emigration of 90-day fingerlings into marine waters with continual replacement from upriver (Hopkins and Unwin, 1987). Similar patterns of movement have been observed in other New Zealand stocks (Davis and Unwin, 1989), in their ancestral Sacramento River (Kjelson et al., 1982), and elsewhere in North America (Healey, 1991). Mean FL at seawater entry

for these fingerlings is consistent with the back-calculated mean FL at seawater entry for ocean-type adults of Rakaia origin (Unwin and Lucas, 1993), confirming the importance of springtime mainstem rearing for ocean-type fry. Freshwater residence patterns of juvenile stream-type fish are less well understood, but there is some evidence that an initial period of tributary rearing lasting 3–6 mo is followed by mainstem rearing for the remainder of the first year (Unwin, 1986).

In the absence of a commercial marine fishery for salmon, very little is known about the marine phase of the salmon life cycle. Adult chinook are piscivorous and appear to feed opportunistically within the pelagic zone, although prey diversity is low and food availability is potentially limited by annual fluctuations in prey abundance (James and Unwin, 1996). Brood year survival rates for both naturally and hatchery-produced chinook of Rakaia origin vary by up to two orders of magnitude and appear to be predominantly related to marine influences (Unwin, in press). However, these results do not preclude the possibility that survival may also be partly influenced by conditions within the freshwater environment.

Data sources and methods

The Rakaia River

The Rakaia River is a large, braided, glacier-fed river draining a 2,910 km² catchment that spans 70 km of the Southern Alps and rises to 2,800 m. Apart from a gentle 5-km gorge where the flow is briefly confined to a single channel, the river occupies an unstable, highly braided shingle bed up to 5 km wide (see Fig. 2 of Glova and Duncan, 1985). After collecting water from two major headwater tributaries (the Mathias and Wilberforce), the lower section (90 km) of the river flows directly into the Pacific Ocean with no significant tributary input. All major salmon spawning waters are located upstream of the Wilberforce confluence (Fig. 1). River gradient is virtually constant below this point, averaging 4.5 m/km, and the river discharges into the ocean via a small freshwater lagoon extending inland from the open sea for less than 100 m. The term "lagoon" is used in preference to "estuary" because there is no ebb and flow of the tide (although there is a tidal backup of fresh water) and because the area supports few, if any, predominantly estuarine life forms.² A detailed de-

scription of the river and its catchment is given by Bowden.³

Continuous flow data for the Rakaia River have been collected since 1959 by means of recorders at the downstream end of the gorge, 62 km above the mouth. For the purposes of this study, all flow statistics were calculated from the daily mean discharge (Q). Discharge (annual mean 200 m³/s) shows a moderately seasonal pattern, monthly means varying from 127 m³/s in July to 265 m³/s in November.³ The mean annual flood (the average of the annual maximum flow) is 1 448 m³/s, with a peak instantaneous discharge of 5,600 m³/s (estimated to have a return period of 60 yr) recorded in January 1994. The bank-full discharge (the instantaneous flow which results in complete inundation of the river bed as individual braids coalesce) ranges from 800 m³/s just below the gorge to about 2,500 m³/s in the lower river. Flood waters move rapidly downriver, typically reaching the mouth 8–12 h after passing through the gorge, although peak velocity increases with flood intensity, and travel times as short as 3.5 h over 40 km have been observed.^{4,5} Over the months relevant to this study, daily mean water temperatures in the lower river (23 km above the mouth) range from 6°C in August to 16°C in January (Unwin, 1986).

Glenariffe Stream spawning runs

Glenariffe Stream is a spring-fed tributary joining the Rakaia River 100 km above its mouth at an altitude of 430 m (Fig. 1). The flow regime is exceptionally stable, with a mean discharge of 3.4 m³/s and a maximum recorded discharge (over a seven-year period) of 16 m³/s. Chinook salmon spawning runs in Glenariffe Stream have been monitored annually by means of a counting fence installed in 1965 (Quinn and Unwin, 1993; Flain¹). The modal age-at-maturity is three years, with smaller numbers of 2-year and 4-year-olds and very few 5-year-old fish. The angler interception rate varies little between years, typically ranging from 30% to 40%.^{6,7} Since 1980,

² Eldon, G. A., and A. J. Greager. 1983. Fishes of the Rakaia Lagoon. Fisheries Environmental Report 30. N. Z. Ministry of Agriculture and Fisheries, Fisheries Res. Div., Christchurch, 65 p. [Copy held by NIWA, Christchurch, New Zealand.]

³ Bowden, M. J. 1983. The Rakaia River and catchment—a resource survey, vol. 2. North Canterbury Catchment Board and Regional Water Board, Christchurch, New Zealand, 101 p. [Copy held by NIWA, Christchurch, New Zealand.]

⁴ 1997. Unpubl. data, NIWA, Christchurch, New Zealand.

⁵ Horrel, G. 1997. Canterbury Regional Council, PO Box 345, Christchurch, New Zealand. Personal commun.

⁶ Unwin, M. J., and S. F. Davis. 1983. Recreational fisheries of the Rakaia River. Fisheries Environmental Report 30. New Zealand Ministry of Agriculture and Fisheries, Fisheries Research Division, Christchurch, New Zealand. [Copy held by NIWA, Christchurch, New Zealand.]

⁷ Millichamp, R. 1997. North Canterbury Fish and Game Council, 3 Horatio Street, Christchurch, New Zealand. Personal commun.

spawning stocks have been supplemented by hatchery releases, but scale-pattern analysis and coded-wire tag recoveries of spawning fish intercepted at the fence allow each run to be partitioned into hatchery-reared and naturally spawning components (Unwin and Glova, 1997). The stability of the flow regime ensures that pre-emergence mortality of ova and alevins is not flow-dependent and is reflected by the lack of interannual variation in egg to fry survival for naturally spawning fish (Unwin, 1986; Unwin, in press). Over five years (1973–76, and 1992) of record egg-to-fry survival ranged from 38 to 52% and averaged 48%. On this basis, annual production can be consistently expressed in terms of the number of fry leaving Glenariffe Stream (Unwin, 1997).

For this study, I used the data set in Table 1 of Unwin (1997), summarizing fry-to-adult survival (S) for the 26 years from 1965 to 1990, expressed as live adult spawners reaching Glenariffe Stream (summed over all year classes for each cohort) per 10,000 fry. These data are reproduced here as Table 1. Survival ranged from 1.3 (for the 1971 brood year) to 117 (for the 1973 brood year), with an annual mean of 8

spawners per 10,000 fry (0.079%). These data were log-normally distributed (Unwin, 1997); therefore I used log-transformed values for all calculations (see also Bradford, 1995).

Data analysis

For each year from 1965 to 1990, I calculated mean flows (\bar{Q}) for each calendar month, for the two three-month periods August–October (“spring”) and November–January (“summer”), and for the full six months. As indices of flow variability, I determined the maximum flow (\hat{Q}), and the ratio of the mean to the median flow (\bar{Q}/\tilde{Q}), for the same monthly, three-monthly and six-monthly intervals. Although other measures of flow variability are possible, such as skewness, coefficient of variation (CV), and baseflow index (which measures the ratio of the volume of base flow to the volume of total runoff), these all tend to be highly correlated and there is no one measure which represents the “best” index (Jowett and Duncan, 1990). I chose \bar{Q} because it is more robust (i.e. insensitive to extreme outliers) than statistics

Table 1

Spawning population size, fry production, adult returns, and fry-to-adult survival (adults per 10,000 fry, rounded to the nearest integer) for naturally spawning Glenariffe Stream chinook, 1965–90. Fry production for 1973–76 was estimated from trapping records; all other figures are based on a mean egg-to-fry survival of 48% (Unwin, 1997).

Brood year	Number of female spawners	Estimated fry production (thousands)	Number of returning adults	Adults per 10,000 fry
1965	1,278	2,988	4,676	16
1966	573	1,513	1,334	9
1967	746	1,760	505	3
1968	1,781	4,310	2,642	6
1969	1,286	3,249	2,760	8
1970	248	655	474	7
1971	1,084	2,573	330	1
1972	1,618	3,418	1,731	5
1973	160	275	3,207	117
1974	173	426	1,242	29
1975	799	1,834	2,045	11
1976	1,522	3,436	2,943	9
1977	778	1,614	1,341	8
1978	863	1,810	1,787	10
1979	1,413	2,138	546	3
1980	481	826	548	7
1981	856	1,978	1,097	6
1982	276	643	2,815	44
1983	326	784	1,766	23
1984	772	2,037	3,037	15
1985	1,800	4,722	950	2
1986	970	2,136	493	2
1987	669	1,400	1,151	8
1988	838	2,074	526	3
1989	391	767	615	8
1990	295	676	504	7

such as CV or skewness, which involve raising flows to the second and third power, respectively. I also calculated several indices related to the incidence of flood peaks, including the number of days when the daily mean discharge exceeded 500 m³/s, 1,000 m³/s, and 1,500 m³/s, and the mean of the ten highest flows over the six months from August to January. The complete set of flow parameters used is summarized in Table 2.

For each parameter, I looked for evidence of a relation with the log-transformed Glenariffe Stream survival data by calculating the correlation coefficient for the paired data sets over the 26 years of record. I examined bivariate scatter plots and residual plots for any data sets showing a significant relation ($P < 0.05$). For these preliminary results I did not correct for the effect of multiple tests (i.e. the possibility of finding an artificially inflated correlation with one of the 32 flow parameters purely by chance); therefore P -values for each correlation overestimated their true significance (Walters and Collicie, 1988; Kope and Botsford, 1990). For these parameters, my next level of analysis was to recalculate the appropriate flow statistic for periods ranging in duration from one week to four months, dating from 1 June to 31 January (representing 805 periods in total), and to recalculate the correlation with the survival data for each choice of date and duration. I then constructed contour plots depicting variations in the correlation coefficient as a function of starting date and duration and examined these "surfaces of correlation" for the presence of local extrema. My motivation for this analysis was not to identify a single period that maximized the correlation, but rather to gauge the sensitivity of the correlation to small changes in interval, and hence to identify seasonal periods for which significant correlations between flow indices and survival persisted over biologically meaningful time scales.

All statistical calculations were performed with version 6.0 of SYSTAT software (Wilkinson, 1996). Contour and surface fits were accomplished with version 6 of SURFER for Windows' implementation of Kriging smoothing (Keckler, 1994) applied to a grid of correlation coefficients calculated at 5-day intervals on both the date and period axes.

Results

River flows

Over the period covered by this study (August 1965 to January 1991), monthly mean discharge ranged from 146 m³/s to 306 m³/s (Table 2). Individual

Table 2

Flow parameters used for correlation analysis, together with their mean and range over the period 1965 to 1990.

Parameter	Symbol	Mean	Range
Measures of flow volume (m³/s)			
Mean annual flow, Feb–Jan	\bar{Q}_{Annual}	209	156–277
Mean flow, Aug–Jan	$\bar{Q}_{\text{Spring/Summer}}$	237	157–329
Mean flow, Aug–Oct	\bar{Q}_{Spring}	190	86–348
Mean flow, Nov–Jan	\bar{Q}_{Summer}	283	186–456
Mean flow, Aug	\bar{Q}_{Aug}	146	80–293
Mean flow, Sep	\bar{Q}_{Sep}	181	71–570
Mean flow, Oct	\bar{Q}_{Oct}	243	106–493
Mean flow, Nov	\bar{Q}_{Nov}	282	131–457
Mean flow, Dec	\bar{Q}_{Dec}	306	160–589
Mean flow, Jan	\bar{Q}_{Jan}	262	148–416
Measures of flood peaks (flows in m³/s)			
Maximum flow, Aug–Jan	$\hat{Q}_{\text{Spring/Summer}}$	1,488	630–2,800
Maximum flow, Aug–Oct	\hat{Q}_{Spring}	975	167–2,470
Maximum flow, Nov–Jan	\hat{Q}_{Summer}	1,279	540–2,800
Maximum flow, Aug	\hat{Q}_{Aug}	385	86–2,470
Maximum flow, Sep	\hat{Q}_{Sep}	502	83–2,230
Maximum flow, Oct	\hat{Q}_{Oct}	755	133–2,030
Maximum flow, Nov	\hat{Q}_{Nov}	783	203–1,960
Maximum flow, Dec	\hat{Q}_{Dec}	1,006	282–2,800
Maximum flow, Jan	\hat{Q}_{Jan}	806	222–2,470
Mean of 10 highest flows, Aug–Jan	$\hat{Q}_{10\text{max}}$	854	443–1,410
Number of days $Q > 500$ m ³ /s, Aug–Jan	N_{500}	13	3–26
Number of days $Q > 1,000$ m ³ /s, Aug–Jan	$N_{1,000}$	2	0–8
Number of days $Q > 1,500$ m ³ /s, Aug–Jan	$N_{1,500}$	1	0–4
Measures of flow variability			
Mean/median, Aug–Jan	$\bar{Q}_{\text{Spring/Summer}}$	1.33	1.04–1.73
Mean/median, Aug–Oct	\bar{Q}_{Spring}	1.32	1.01–1.92
Mean/median, Nov–Jan	\bar{Q}_{Summer}	1.29	1.09–1.52
Mean/median, Aug	\bar{Q}_{Aug}	1.14	0.98–2.25
Mean/median, Sep	\bar{Q}_{Sep}	1.15	1.00–1.91
Mean/median, Oct	\bar{Q}_{Oct}	1.22	0.94–1.64
Mean/median, Nov	\bar{Q}_{Nov}	1.23	1.02–1.75
Mean/median, Dec	\bar{Q}_{Dec}	1.27	1.04–2.11
Mean/median, Jan	\bar{Q}_{Jan}	1.27	1.02–2.03

monthly means varied from 71 m³/s (September 1977) to 734 m³/s (December 1979). The mean maximum August to January flow (effectively the mean annual spring and summer flood) was 1,488 m³/s; values for individual seasons ranged from 630 m³/s in 1980 to 2,800 m³/s in 1979. Flow variability was lowest during August and September, although highly variable flows ($\bar{Q} > 1.6$) were recorded in all months.

Hydrographs for 1977 (a low-flow season) and 1984 (an above average season) illustrate the sharp peaks and rapid recession typical of Rakaia floods (Fig. 2). In the November 1984 event, discharge increased by a factor of 10 (from 172 m³/s to 1,710 m³/s) over 48 h and then fell from 1,960 m³/s to 455 m³/s over 72 h. Despite the contrast between the two seasons, both hydrographs also show a common period of low and relatively stable base flows in August and September, followed by more frequent floods as the season progresses.

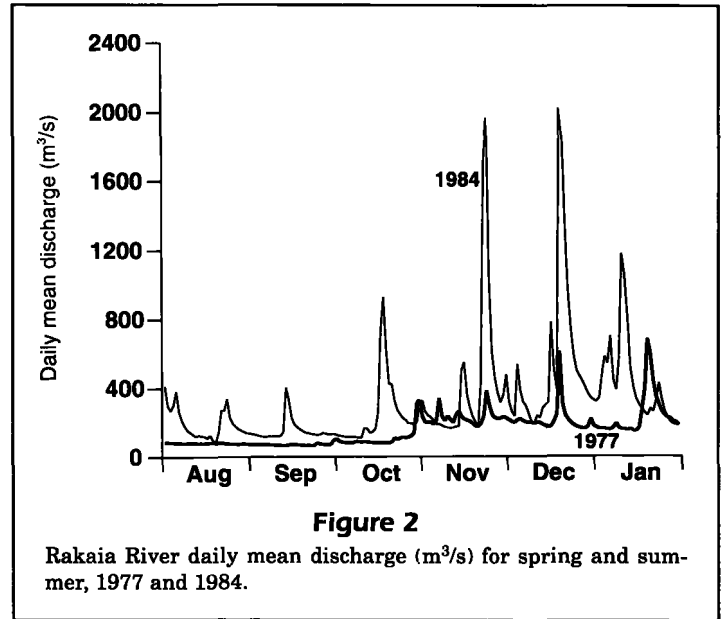


Figure 2

Rakaia River daily mean discharge (m³/s) for spring and summer, 1977 and 1984.

Correlation analysis

Of the 32 flow parameters listed in Table 2, 29 showed no correlation with survival rates for Glenariffe Stream chinook (Table 3). Correlation coefficients for these indices ranged from -0.223 to 0.283, none of which differed significantly from zero ($P > 0.16$ in all cases). The three exceptions were the mean flow \bar{Q} , the maximum flow \hat{Q} , and the ratio of the mean to median flow \check{Q} , for the month of November. All three measures were positively correlated with survival ($\bar{Q}_{NOV}, P = 0.045$; $\hat{Q}_{NOV}, P = 0.003$; $\check{Q}_{NOV}, P = 0.006$). By contrast, there was no correlation between sur-

vival and the same set of flow variables for the adjacent months of October and December.

The strongest and most consistent set of correlations involved the ratio of mean to median flow, calculated over periods of 30 to 90 d duration centered on or about November 1 (Fig. 3A). Over much of this range the correlation between \check{Q} and log S exceeded 0.5, with a maximum value of 0.667 for \check{Q} calculated over the 40-day period from 9 October to 17 November. More generally, survival tended to be high for broods corresponding to years when flow variability during October, November, and early December was high. For periods centered on the four weeks between

Table 3

Correlations between log-transformed brood year survival rates for Glenariffe Stream chinook and 32 indices of Rakaia mainstem flows, 1965-90. See Table 2 for definitions of symbols. Asterisks denote correlations significant at the 95% level (*) and 99% level (**).

Period	Flow parameter						
	\bar{Q}	\hat{Q}	\check{Q}	N_{500}	$N_{1,000}$	$N_{1,500}$	\hat{Q}_{10max}
February-January (year)	-0.091						
August-January (spring and summer)	-0.105	0.109	0.182	-0.062	0.261	0.165	0.164
August-October (spring)	-0.195	-0.140	-0.218				
November-January (summer)	0.046	0.205	0.269				
August	-0.068	-0.054	-0.066				
September	-0.082	-0.191	-0.159				
October	-0.223	-0.053	0.283				
November	0.397*	0.558**	0.520**				
December	-0.214	-0.112	-0.088				
January	-0.070	0.053	0.141				

18 October and 15 November, of five to nine weeks duration, the correlation between \bar{Q} and $\log S$ averaged 0.493. Taken as an isolated result, this correlation corresponds to an average significance level of $P < 0.01$ and an average coefficient of determination (r^2) of 0.243. There was some evidence of a weaker and more transient period of negative correlation between \bar{Q} and $\log S$ earlier in the season. For \bar{Q} calculated over periods of seven to nine weeks duration and centered on the fortnight from 6–19 September, the correlation with $\log S$ averaged -0.404 , corresponding to an r^2 of 0.16. The symmetric upright “V” shape apparent in the contours of Fig. 3A, centered on the beginning of November, is an artifact caused by the tendency for data sets representing \bar{Q} over periods of similar duration centered on the same date to be highly correlated.

Maximum flow (\hat{Q}) and mean flow (\bar{Q}) were generally only weakly correlated with survival, and the few periods during which correlations stronger than ± 0.4 were recorded showed little tendency to persist over temporal scales of more than a few days (Fig. 3, B and C). In addition, these correlations tended to become stronger at shorter time scales, suggesting that for \bar{Q} , and possibly for \hat{Q} , the correlations apparent in Table 3 were a transient effect of a fortuitous sequence of flood events. By contrast, the persistence of a positive correlation between \bar{Q} and $\log S$ for flows averaged over periods of up to 90 days suggests that the relation is much more robust and hence likely to be of biological significance. The correlations between \bar{Q} , \hat{Q} , and \bar{Q} are also consistent with this interpretation. Whereas \bar{Q}_{NOV} and \hat{Q}_{NOV} were highly correlated ($r=0.84$), \bar{Q}_{NOV} was only moderately correlated with both parameters ($r=0.61$ in both cases), confirming that \bar{Q} captured information on flow variation not measured by either \bar{Q} or \hat{Q} .

The relation between \bar{Q} and $\log S$ was moderately influenced by the 1973 brood (for which the survival rate was unusually high) but was not dependent on it. The 1965, 1974, 1982, and 1983 broods (for which survival was also relatively high) and the 1985, 1986, and 1988

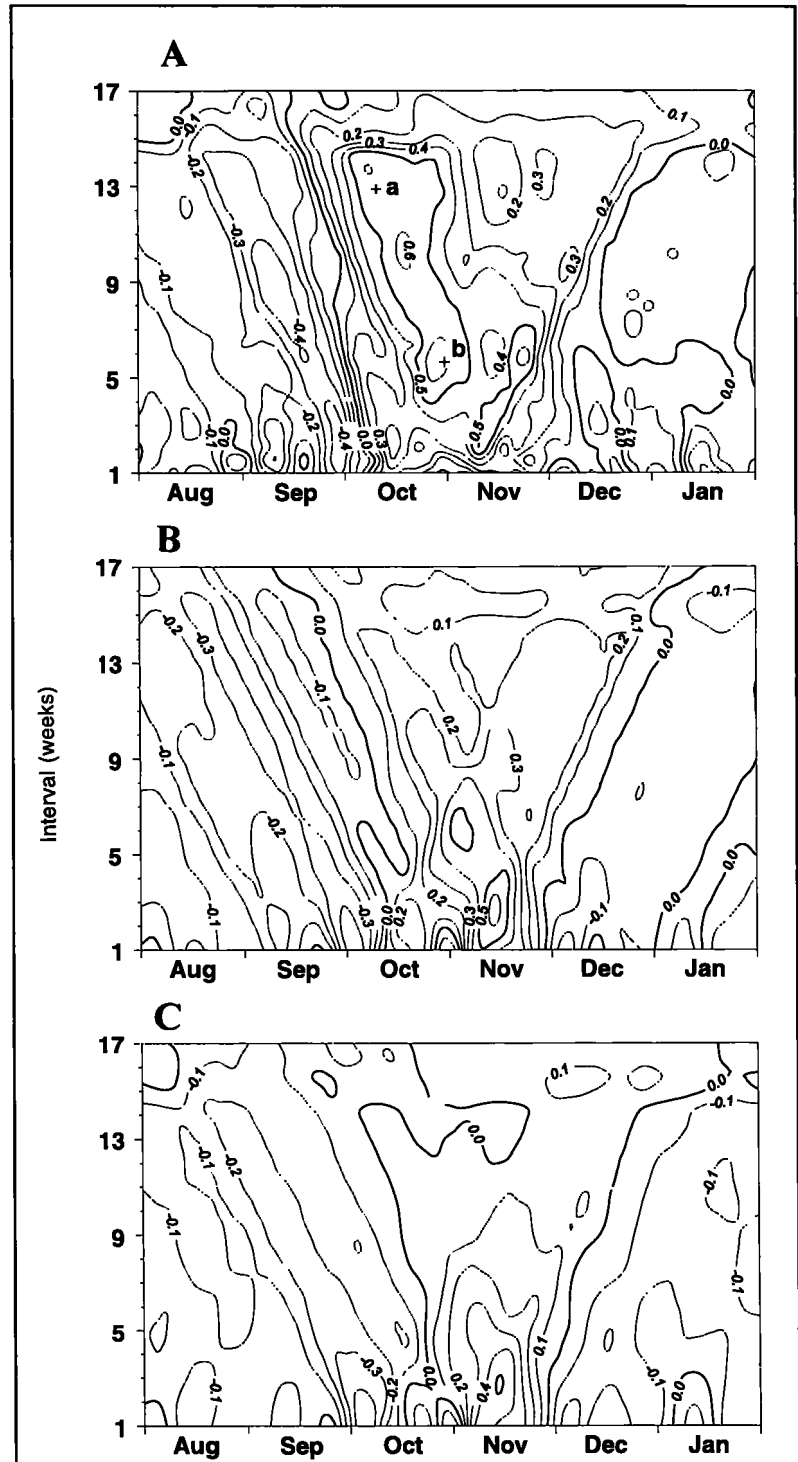


Figure 3

Correlations between log-transformed survival data for Glenariffe Stream chinook salmon and Rakaia River mainstem discharge expressed as the ratio of mean to median discharge (A), maximum discharge (B), and mean discharge (C), as a function of the period used to calculate each flow statistic. For each point, the locations on the x- and y-axes represent the mid-point of the period, and the duration, respectively. The points “a” and “b” correspond to the two intervals represented in Figure 4.

broods (for which survival was low) conform to the general trend irrespective of the duration of the period used to calculate \bar{Q} (Fig. 4). With the exception of the 1969 brood, the value of \bar{Q} during October and November was not highly sensitive to the choice of interval.

Discussion

Correlations and flow parameters

This study shows that, although fry-to-adult survival of Glenariffe Stream chinook salmon is correlated with the occurrence of springtime flood events in the Rakaia River, both the magnitude and the direction of the observed correlation depend strongly on the flow parameter used and the period over which this parameter is calculated. Survival was most strongly correlated with flow variability (as measured by the ratio of mean to median flow), the correlation being moderately negative for flows averaged over the period from mid-August to mid-October, and rather more strongly positive from mid-October to November. Similar but weaker correlations were apparent between survival and maximum flow, but mean flow was a poor predictor of survival irrespective of the time interval used.

The correlations reported here have two key features. First, although quite strong in a biological context, they are nevertheless relatively weak, accounting for at most 25–30% of the observed variation in

log survival. Even if the maximum positive correlation ($r=0.667$) is taken at face value, its predictive power allows years to be categorized only as “above average” or “below average,” at best (Prairie, 1996). This result is consistent with an earlier finding that annual survival rates for New Zealand chinook are primarily determined by marine rather than fresh-water influences (Unwin, 1997; see also Bradford, 1995). Second, the tendency for survival to be positively correlated with flow variation but uncorrelated with mean flow suggests that increased flow variability (in the sense illustrated in Fig. 5) at the appropriate time of year is beneficial to survival. This is in sharp contrast to the generally held view that spring floods have a detrimental impact on chinook fry in the Rakaia and other New Zealand rivers (Waugh, 1980; McDowall, 1990; Flain¹).

The three key flow parameters used in this study—mean flow, maximum flow, and ratio of mean flow to median flow—are by no means the only ones possible and can only capture some of the information contained in the hydrograph for a given time period. Mean flow essentially measures the total volume of water passing through the river over the interval in question, without conveying any information about the magnitude or distribution of floods. For example, a 90-day mean of 200 m³/s could arise from 90 consecutive days at exactly 200 m³/s each, or from 89 days at 180 m³/s and one day at 1,980 m³/s. Maximum flow characterizes peak flood intensity, but not flow variability, so that a flow period with one 2,000 m³/s flood will outrank another period with ten 1,900 m³/s floods.

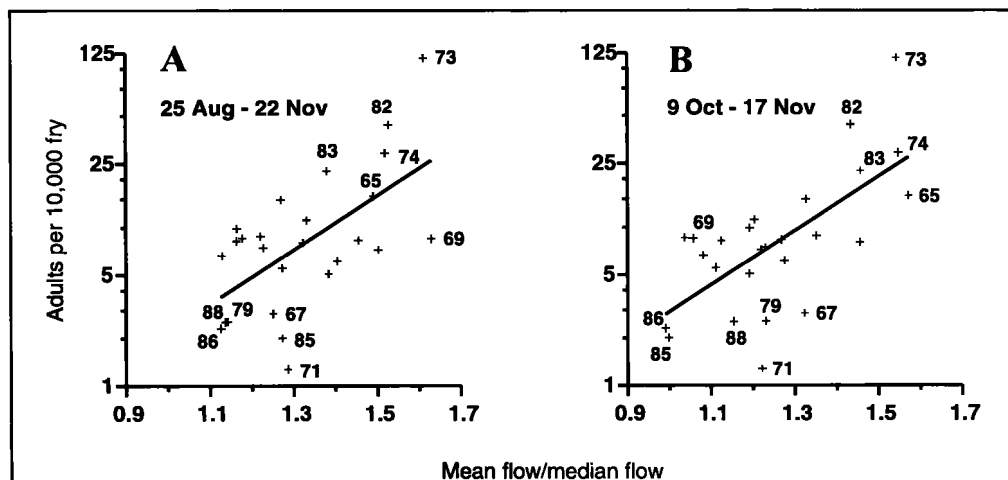
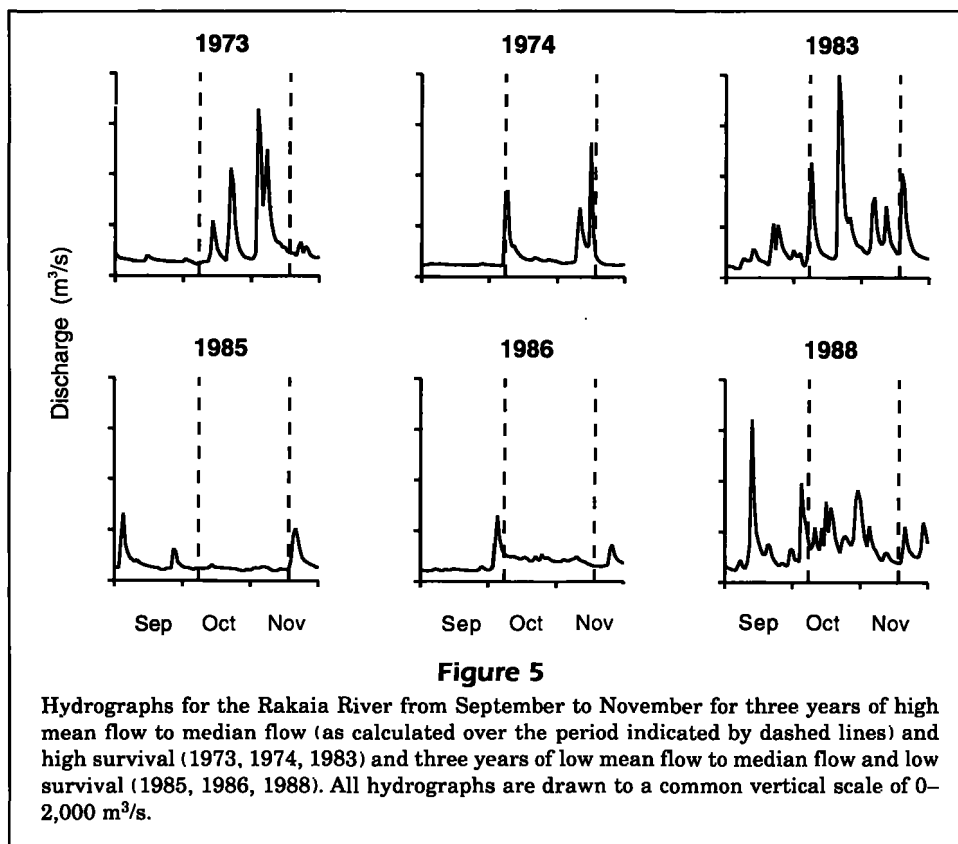


Figure 4

The relation between log-transformed survival data for Glenariffe Stream chinook salmon and the ratio of mean to median discharge in the Rakaia River mainstem for two periods near local maxima in Figure 3A. Twelve points corresponding to broods with extreme survival or flow indices for at least one of the two periods shown are identified by year.



The ratio of mean to median flow is a direct measure of flow variability, but it does not necessarily follow that low values of \bar{Q} correspond to low and stable flows. Flow regimes where \bar{Q} is close to one (i.e. mean flow differs little from the median) can arise in two different ways, only one of which corresponds to an extended period of low flows (Fig. 5). The other possibility is a period of highly variable flows superimposed on a high base flow, so that even though flows vary greatly from day to day, the flow distribution is only moderately skewed. By contrast, high values of \bar{Q} are more consistently associated with highly variable flows, tending to correspond to intervals when a lengthy period of low, stable base flows is punctuated by a relatively small number of short and sharp flood events. Both the 1973 and 1974 seasons ($\bar{Q}_{9 \text{ Oct} - 17 \text{ Nov}} = 1.54$ and 1.55 , respectively) were characterized by low and stable base flows during September, followed by two or three relatively short-lived flood events during October and November. The 1985 and 1986 seasons ($\bar{Q}_{9 \text{ Oct} - 17 \text{ Nov}} = 1.00$ in both cases) were characterized by uniformly low and stable flows, with no floods over the six weeks from 1 October. The effect of high base flows on flow variability is illustrated by comparing the 1983 and 1988 seasons ($\bar{Q}_{9 \text{ Oct} - 17 \text{ Nov}} = 1.46$ and 1.15 , respectively). Whereas base flows were low throughout 1983, so

that a 2,000 m³/s event in late October generated a high figure for \bar{Q} , the absence of a major flood during October and November 1988 produced a lower figure for \bar{Q} despite high and rapidly fluctuating base flows over most of the period shown.

The other flow parameters examined during the initial phase of this study, such as the number of days from August to January when flows exceeded a certain level, showed no correlation with survival. Although in principle it would have been possible to subject these parameters to the same level of analysis used for \bar{Q} , \hat{Q} , and \tilde{Q} , this analysis becomes progressively less meaningful at shorter time scales. For example, given that $N_{1,000}$ ranged from 0 to 8 over a six month period (Table 2), the same statistic calculated over monthly intervals would typically take on only a few discrete integer values and would be inappropriate for correlation analysis.

Mechanisms

The topography of the correlations between \bar{Q} and survival, as illustrated by the qualitative features of Fig. 3A, coincides to a striking degree with several key events in the migration patterns of juvenile ocean-type fry in the Rakaia River. The period of highest positive correlation between flow variability

and survival, mid-October to November, coincides with the period when fingerlings first become abundant in the lower river and begin their transition to oceanic waters. The period centered on mid-September, when there is some evidence of a negative correlation between flow variability and survival, corresponds to the earlier time when fry are still migrating downriver and have yet to grow to the point where they are able to withstand the transition to salt water. Survival is not correlated, either positively or negatively, with flow variability at the beginning of the season (August, when most fry have yet to hatch) or at the end of the season (January, by which time most fingerlings have left the river). The correlation also tends to disappear when flow variability is averaged over more than about 100 days, a period that is consistent with the 90-day freshwater residence period of Rakaia fingerlings.

The tendency for survival to be positively correlated with flow variability rather than flow volume (as measured by \bar{Q}), and the short duration of each individual flood peak, suggest that these flood pulses must be an integral part of any plausible linking mechanism. Maximum survival appears to result when stable flows prior to mid-October are followed by a few (perhaps two or three) large floods over the next four to six weeks. By contrast, seasons when there are no major floods during October and November seem to result in poor survival irrespective of flows earlier in the season. Although any discussion based solely on the present results is speculative, I suggest that sudden increases in Rakaia discharge coinciding with peak emigration of fingerlings from the river mouth may increase survival by buffering the transition from fresh to saline waters in the vicinity of the offshore plume. If so, these pulses may help to compensate for the lack of an estuary at the Rakaia mouth and the low importance of the lagoon as a salmon rearing habitat,² one of the key features distinguishing the Rakaia (and other New Zealand salmon-producing rivers) from the extensive tidal basins below the Sacramento River mouth (Kjelson et al., 1982). The effect may be compounded by the well-documented tendency for downstream migration rates to increase with flow, both in New Zealand (Irvine, 1986) and North American populations (e.g. Kjelson et al., 1982; Berggren and Filardo, 1993), so that each flood pulse increases both the number of fingerlings leaving the river and their prospects for successful acclimation to salt water. Outflow of turbid flood waters may also increase survival by reducing visibility, and hence decreasing losses to inshore marine predators such as kahawai (*Arripis trutta*), although reduction in visibility is likely to be no more than a secondary effect (cf. St.

John et al., 1992). A positive correlation between survival of hatchery-reared Atlantic salmon (*Salmo salar*) and maximum river discharge during the first seven days after release has been attributed to reduced predation at higher flows (Hvidsten and Hansen, 1988).

A distinguishing feature of chinook salmon compared with other species of *Oncorhynchus* is their gradual acquisition of seawater tolerance while still in fresh water, without the sudden transition associated with smoltification in species such as coho (*O. kisutch*) or steelhead (*O. mykiss*) (Hoar, 1976). By early November, Rakaia fingerlings are of an age and size close to the generally accepted minima for successful transfer to seawater (Clarke and Shelbourn, 1985; Franklin et al., 1992), and water temperatures in the Rakaia River (12–15°C; Unwin, 1986) and at sea (12–14°C)⁸ appear to be within the optimal range for juvenile chinook salmon reported by these studies. However, acclimation to seawater also depends on the rate of transition. A gradual transfer to saline waters allows even very young fish to acclimatize successfully (Hoar, 1976), as evidenced by the abundance of chinook fry in low salinity estuarine waters in North America (Reimers, 1973; Healey, 1980; Levy and Northcote, 1981), including the lower Sacramento River (Kjelson et al., 1982). Changes in estuarine ecology during low-flow seasons in the Snake-Columbia River system have been suggested as a factor contributing to reduced survival of Snake River chinook (Williams and Matthews, 1995). In the Strait of Georgia, where the Fraser River plume forms a well-developed halocline at a depth of 5–10 m, juvenile salmonids showed a preference for surface waters of low salinity (10–15 ppt) in the plume, compared with the more saline waters (25–30 ppt) in other regions of the Strait (St. John et al., 1992). The Georgia Strait study also reported a tendency for plankton and larval fish to align with the plume boundary, providing enhanced feeding opportunities.

There have been no studies on salinity gradients off the Rakaia mouth, but nearshore salinity off Otago Harbour (on the east coast of the South Island 220 km south of the Rakaia) is inversely correlated with discharge from the Clutha River a further 100 km to the south (Jillett, 1969). The coastal shelf off the Rakaia River has a very gentle slope, with the 20-m isobath 5–10 km offshore (see Fig. 1). Consequently, peak Rakaia outflows should have a substantial impact on inshore salinity. For example, a daily mean discharge of 1 200 m³/s over 24 h (which is less than the mean annual spring flood) represents a total volume of fresh water of 0.1 km³, equivalent

⁸ 1997. NIWA, Christchurch, New Zealand. Unpubl. data.

to a 10 km² surface layer that is 10 m deep. Devolve- ment of the resulting halocline would presumably require considerable input of wave energy, and under calm conditions, a surface layer of low salinity water may persist for some days until dispersed to the north-east under the influence of the Southland current (Heath, 1972).

Implications

The analysis described in this study relates only to ocean-type fry. Because ocean-type fish make up approximately two thirds of the Rakaia adult population (Quinn and Unwin, 1993), fluctuations in their abundance would have a significant impact on brood year survival. However, one third of Rakaia adult chinook have a stream-type juvenile life history, and there is some evidence that the emergence of stream-type behavior in what was originally a fall-run stock represents an adaptive response to the lack of estuarine waters on New Zealand's salmon-producing rivers (Unwin and Glova, 1997). The freshwater habitat preferences and migration patterns of stream-type chinook in the Rakaia River are poorly understood, and their sensitivity to flow variations is unknown. However, the possibility that survival of ocean-type fry may increase in seasons of variable flow could provide a compensating selective force that would help to establish a balance between the incidence of the two phenotypes. If so, the ratio of ocean- to stream-type fry in any one annual cohort should also be positively correlated with the variability of spring flows into the Rakaia River during the first year of life.

To explore this hypothesis further, and hence to provide an independent test of the plausibility of the mechanisms outlined in the previous section, I examined archival material from NIWA's scale collections, aspects of which are summarized in Tables 2, 3, and 4 of Quinn and Unwin (1993). These records include scale samples from salmon taken in the Rakaia sports fishery for nine annual cohorts between 1965 and 1984. These scale samples permitted returning fish from each cohort to be classified according to juvenile life history. The incidence of ocean-type fish among 3-year-old adult chinook was positively correlated with mainstem flow variability over the period 9 October to 17 November ($r^2=0.54$, $P=0.025$; Fig. 6) during the year in which they emigrated as juveniles. Of particular interest is the high incidence of ocean-type fish in the 1973 and 1982 cohorts, which were also the broods for which survival was highest.

With regard to the New Zealand salmon fishery, which is managed purely for recreational anglers

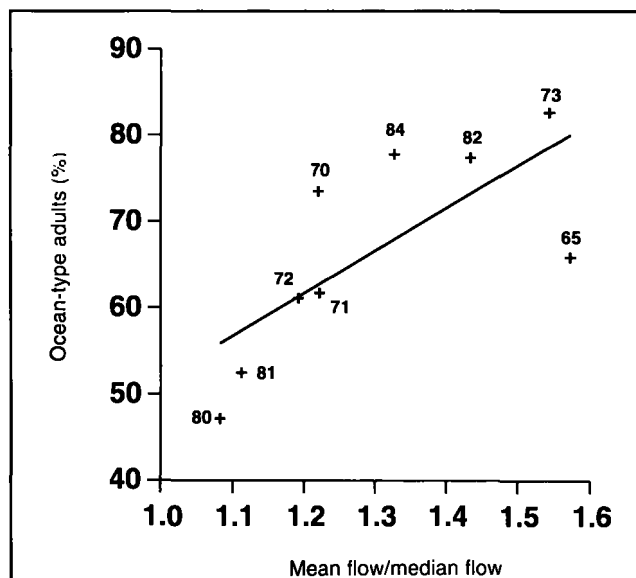


Figure 6

The relation between the incidence of ocean-type adults among 3-year-old chinook salmon caught by Rakaia River anglers over nine seasons from 1965 to 1984, and the ratio of mean to median discharge in the Rakaia mainstem for the corresponding juvenile cohort, for the same time interval (9 October to 17 November) as that represented in Figure 4B. Sample sizes averaged 127, and ranged from 36 to 373.

(McDowall, 1994b), the main conclusion to be drawn from this study is that despite the observed correlations between survival and flow variability, interannual variation in survival remains at best weakly predictable. However, spring flow variability is easy to analyze on a season by season basis, and the possibility of making at least a broad prediction identifying years of high or low survival up to two seasons in advance suggests the effort is worth making. The New Zealand Fish and Game Council (which is responsible for management of the sports fishery) have recently instituted annual monitoring programs for key spawning runs in all major salmon rivers,⁹ and these will eventually enable comparisons between survival and flows to be made for other major east coast catchments. My results also suggest that any reduction in flow variability resulting from development of storage impoundments for hydroelectric or irrigation purposes would have a significant negative impact on the fishery over and above any losses caused by barriers to upstream passage. The high bed load of major braided rivers such as the Rakaia makes them unattractive candidates for impoundment, but declines in salmon runs in two other riv-

⁹ Webb, M. 1997. Central South Island Fish and Game Council, PO Box 150, Temuka, New Zealand. Personal commun.

ers (the Clutha and Waitaki) following hydroelectric development (McDowall, 1990) may be partly linked to a reduction in the magnitude and frequency of spring floods. A positive association between salmon production and large offshore plumes is also consistent with the general distribution of salmon in east coast rivers (McDowall, 1990), with the largest populations confined to major rivers draining the main divide. Traditionally this distribution has been attributed to the presence of stable headwater spawning tributaries such as Glenariffe Stream, but this explanation is not fully convincing. Many minor east coast rivers support self-sustaining stocks of brown trout (Jowett, 1990; McDowall, 1990), and spawning requirements for chinook are not dissimilar.

From an evolutionary standpoint, the present results help to shed further light on the processes by which chinook salmon have been able to succeed in New Zealand waters. In addition to the emergence of stream-type fish as a significant component of modern New Zealand stocks, several other recent studies have noted differences between present-day New Zealand and Sacramento chinook at both phenotypic and genotypic levels (Quinn and Unwin, 1993; Quinn et al., 1996), suggesting that the process of adaptation may be ongoing. The somewhat unusual mechanisms which have apparently enabled New Zealand chinook salmon to establish the only self-perpetuating stocks outside their native range (Harache, 1992) underscore the great phenotypic plasticity of the species, and the value of the New Zealand populations as a laboratory for studying this plasticity.

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