

# Population stability in salmon species: effects of population size and female reproductive allocation

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## Summary

1. Population stability (i.e. level of temporal variation in population abundance) is linked commonly to levels of environmental disturbances. However, populations may also differ in their propensity to dampen or amplify the effects of exogenous forces. Here time-series of population estimates were used to test for such differences among 104 populations of six salmon species.

2. At the species level, Atlantic (*Salmo salar* L.), chinook (*Oncorhynchus tshawytscha* Walbaum) and coho salmon (*O. kisutch* W) were less variable than sockeye (*O. nerka* W) and pink salmon (*O. gorbuscha* W). Chum salmon (*O. keta* W) was more similar to sockeye and pink salmon. These differences may be related in part to differences in body size, and hence susceptibility to adverse environmental conditions, at the time when they migrate to the sea or lakes.

3. At the population level no effect of fecundity on variability was found, in contrast to findings for marine fishes, nor of egg size. Whereas substantial differences in the temporal stability of environmental factors among geographically close populations may override any effects of fecundity or egg size in fresh water, this is less likely in the marine environment where spatial autocorrelations of environmental variability are more pronounced.

4. Variation in population sizes was related positively to the duration of time-series when using standard deviations of ln-transformed population estimates, and also when using linearly detrended population variation, suggesting non-linear long-term abundance trends in salmon populations that extend beyond the 7-year period of the shortest time-series.

5. When controlling for differences among species, stability increased with increasing population size, and it is hypothesized that this is due to large populations having a more complex spatial and genetic structure than small populations due to wider spatial distribution. The effects of population size on stability, as well as differences in stability among species, suggest that population- and organism-specific characteristics may interact with exogenous forces to shape salmon population dynamics.

*Key-words:* density fluctuations, egg size, fecundity, phylogenetic comparisons, population dynamics.

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## Introduction

A major challenge for ecologists has been to understand the processes that shape variability in population abundances. In highly fecund species such as fishes,

much of the temporal variability in population abundance is believed to be determined during an early ‘critical period’ of the juvenile life, when high rates of mortality are commonly observed (Elliott 1989; Einum & Fleming 2000). Year-to-year variation in environmental conditions is believed to be one of the main forces behind fluctuations in fish populations. However, even in systems where exogenous forces appear to dominate (i.e. forces that affect population density but are not themselves affected by it, *sensu* Ellner & Turchin

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1995), there are reasons to believe that populations differ in their sensitivity to such forces.

One particular aspect of populations that may influence responses to exogenous forces is the pattern of resource allocation to offspring production, as influenced by trade-offs between egg size and number. If an organism is highly fecund, this should be reflected in high mortality from egg to adult (Koslow 1992). Thus, because of high mortality, a given level of environmental variation in mortality during juvenile stages may propagate into larger variation in adult abundance for highly fecund organisms. Conversely, populations that produce larger but fewer eggs may have more stable dynamics. Comparative data from moth populations appear to support this hypothesis (Spitzer, Rejmanek & Soldan 1984). It is also possible that egg size *per se* will affect population dynamics. Egg size may be important for offspring success during harsh environmental conditions, but not when environmental conditions are favourable (Einum & Fleming 1999). Thus, populations producing large eggs may have a higher persistence during years of unfavourable conditions (Pimm 1991).

In marine fish species, traditional interspecific comparisons have failed to provide evidence for a relationship between fecundity and population dynamics (Rothschild & DiNardo 1987; Mertz & Myers 1996). However, such cross-species analyses do not account for the evolutionary relatedness among populations or species, which may share life-history characteristics due to common ancestry (Harvey & Pagel 1991). They also tend not to control for other differences in life histories, ecology or behaviour among different taxonomic groups. To avoid such problems, Rickman *et al.* (2000) adopted a phylogenetic comparative approach and found that in comparisons of closely related taxa (e.g. stocks within species, and species within genera), high fecundity was matched by high recruitment variability in marine fishes. These results suggest that fecundity may be related to differences among fish populations in stability.

Population size may also influence stability. This may occur through demographic stochasticity in very small populations (less than about 100 individuals, Lande 1988), but one might hypothesize that similar relationships can be found even among larger populations. For example, within species, and particularly so for territorial organisms, larger populations tend to be distributed over larger spatial areas, consisting potentially of different subpopulations. Asynchronous local dynamics caused by asynchronous environmental stochasticity among these subpopulations, or by interactions between environmental stochasticity and local habitat quality, may then stabilize the overall dynamics (Kindvall 1996). This effect is analogous to that observed for metapopulations with asynchronous fluctuations in local populations, where these cancel each other out and the total population abundance is more stable (Ranius 2001). For small and less spatially structured

populations, environmental influences on the different individuals within the population may be correlated more strongly, causing larger fluctuations in total population abundance.

Salmonid fishes are ideal subjects for comparative studies of population dynamics for several reasons. First, although time-series of population sizes in most taxa are based almost invariably on a variety of estimates, such estimates for salmonid fishes are likely to be among the highest quality because adults can be counted as they ascend their natal river. Secondly, whereas defining a population may be problematic in many organisms due to the significant exchange of individuals among populations and the lack of structures delineating population boundaries, this is less of a problem for salmon, which return to their natal river with high fidelity (Stabell 1984). Finally, life-history characteristics of a great number of salmon populations are available, making studies of interrelationships between these characteristics and population dynamics feasible.

Despite the economic and conservation issues associated with fluctuations of salmon populations, little has been done to understand how characteristics of the populations themselves influence their dynamics. Here we compile time-series of adult counts, and match them with data on body size, egg size and fecundity from a total of 104 populations of six salmon species. These data are analysed using both traditional statistical analyses and phylogenetic comparative methods. Patterns of variation are examined at both species and population levels to test whether stability is species specific, whether stability depends on population size, and whether fecundity and/or egg size influence population stability.

## Materials and methods

We compiled data from the literature on time-series of population sizes (adult counts), body size and egg size (standardized to fresh egg weight following Fleming & Ng 1987) and/or fecundity (mean observed number of eggs per female). The species examined were Atlantic salmon (*Salmo salar* L.), chinook salmon (*Oncorhynchus tshawytscha* Walbaum), chum salmon (*O. keta* Walbaum), coho salmon (*O. kisutch* Walbaum), pink salmon (*O. gorbuscha* Walbaum) and sockeye salmon (*O. nerka* Walbaum) (Table 1). To normalize data, body size, egg size and fecundity were ln-transformed prior to analyses. Year-to-year variation in population size was calculated as standard deviations of ln-transformed population abundance estimates. This measure of variability is statistically independent of the mean value, but is less biased by long-tailed frequency distributions than coefficients of variation (McArdle, Gaston & Lawton 1990; Pimm 1991). It is influenced by long-term trends in population abundance, and hence can be regarded as a measure of long-term stability of populations. To control for long-term linear trends in abundance we detrended time-series by calculating residuals from

**Table 1.** Pairs of salmon populations and their mean fecundity (Fec), egg size (ES, mg) and body length (BL, mm). 'Pair Fec' indicates pairings of populations within species for fecundity analyses, and 'Pair ES' shows pairs of populations for egg size analyses. 'Var' denotes temporal variation calculated as the standard deviation of ln-transformed adult counts

Species	Pair Fec	Pair ES	Population	Fec	ES	BL	Population size <sup>a</sup>			Years	References <sup>b</sup>	
							Mean	Var	Time-series		Fec, BL and ES	
Atlantic	1	-	Gander R., Nfld	2 988	-	448	28 567	0.45	1980-97	1	2	
	1	-	Exploits R., Nfld	2 289	-	452	3 715	0.55	1980-97	3	4	
	2	-	Middle Brook, Nfld	3 107	-	442	1 064	0.43	1984-96	5	4	
	2	-	Terra Nova R., Nfld	2 839	-	441	1 636	0.38	1984-96	6	4	
	3	-	North-east R., Placentia	3 848	-	455	672	0.37	1986-95	7	4	
	3	-	Conne R., Nfld	3 090	-	434	3 463	0.55	1986-95	8	8	
	4	1	Restigouche R., NB	10 415	134	692	2 724	0.66	1971-81	6	9, 10	
	4	1	Miramichi, NB	5 665	108	552	1 826	0.50	1971-81	6	9, 10	
	5	-	St. John, Maritimes	4 244	-	530	10 405	0.45	1979-95	5	11	
	5	-	Liscomb, Nova Sc.	3 506	-	524	324	0.98	1979-95	12	12	
	Chinook	1	-	Sacramento R., CA	5 449	-	683	14 765	0.81	1967-94	13	14
1		-	Feather R., CA	5 423	-	-	36 680	0.46	1967-94	13	15	
2		-	Klamath R., CA	3 754	-	675	110	1.19	1984-94	13	14	
2		-	Trinity R., CA	3 498	-	633	8 866	0.98	1984-94	13	15	
3		1	Elk R., OR	4 920	283	733	2 080	0.32	1970-79	13	15	
3		1	Umpqua R., OR	3 826	240	671	6 438	0.24	1970-79	13	15	
-		2	Klrekitat R., OR	-	214	699	1 130	1.42	1967-80	13	15	
4		2	Clackamas R., WA	5 179	140	-	1 366/446	0.82/0.65	1976-87/1967-80	13	15	
4		-	Willamette R., OR	4 529	-	658	2 368	0.47	1976-87	13	15	
5		-	Yakima R., WA	5 245	-	654	1 755	0.45	1983-90	13	15	
5		3	Snake R., WA	3 923	227	639	21 163/17 677	0.53/0.67	1983-90/1977-91	13	15	
-		3	Methow R., WA	-	208	423	143	0.55	1977-91	13	15	
6		4	Samish R., WA	4 618	247	-	1 339	0.60	1974-82	13	15	
6		4	Skagit R., WA	4 483	296	741	7 259	0.29	1974-82	13	15	
-		5	Qualicum R., BC	-	309	756	1 097	0.70	1953-97	16	15	
7		5	Nanaimo R., BC	4 481	274	711	1 408	0.73	1953-97	16	17	
7		6	Cowichan R., BC	3 885	280	704	5 432/5653	0.57/0.57	1953-97/1953-94	16	17	
-		6	Nitinat R., BC	-	349	759	2 345	1.18	1953-94	16	17	
8	7	Quinsam R., BC	6 188	335	796	1 466	1.19	1978-97	16	17		
8	7	Puntledge R., BC	5 714	286	744	518	1.10	1978-97	16	17		
9	8	Clearwater R., BC	5 118	210	732	2122	0.63	1957-93	16	17		
9	8	Raft R., BC	4 728	204	691	273	0.73	1957-93	16	17		
10	9	Coldwater R., BC	3 715	132	587	395	0.82	1980-94	16	17		
10	9	Bonaparte R., BC	3 169	140	560	403	1.57	1980-94	16	17		
-	10	Upper Cariboo R., BC	-	172	706	1 054	0.63	1981-94	16	17		
11	10	Quessel R., BC	6 624	261	803	1 022/2101	0.72/1.39	1953-87/1981-94	16	17		
11	-	Cottonwood R., BC	5 487	-	680	206	0.97	1953-87	16	17		

Table 1. Continued

Species	Pair		Population	Fec	ES	BL	Population size <sup>a</sup>			Var	Years	References <sup>b</sup>	
	Fec	ES					Mean	BL	ES			Time-series	Fec, BL and ES
Chum	12	11	Cheakamus R., BC	6 242	223	742	626	1.13	1953-93	16	17		
	12	11	Ashlu Cr., BC	6 098	214	753	250	0.86	1953-93	16	17		
	-	12	Bowron R., BC	-	246	736	1 845	1.01	1961-94	16	17		
	-	12	Torpy R., BC	-	152	-	742	0.83	1961-94	16	15		
	-	13	N. Thompson R., BC	-	233	746	1 620	0.44	1964-90	16	17		
	-	13	Finn Cr., BC	-	209	708	665	0.52	1964-90	16	17		
	-	14	Bella Coola R., BC	-	325	-	21 807	0.29	1986-97	16	18		
	-	14	Atmarko Ch., BC	-	308	738	119	1.80	1986-97	16	17		
	-	15	Babine L., BC	-	312	-	1 326	0.88	1953-94	16	19		
	-	15	Kitimat R., BC	-	292	821	5 597	0.82	1953-94	16	18		
	-	-	Cowichan R., BC	2 555	-	588	64 216	0.62	1953-97	16	20		
	-	1	Chemainus R., BC	2 856	224	571	11 731/12 088	0.87/0.90	1953-97/1953-89	16	20, 21		
	2	1	Nitinat R., BC	2 448	242	546	29 437	1.25	1953-89	16	20, 22		
	2	-	Tlupana R., BC	2 688	-	570	1 408	1.54	1953-89	16	20		
	3	2	Mathers Cr., BC	2 711	271	557	3 229	1.20	1950-97	16	17, 20		
3	2	Pallant Cr., BC	2 567	218	542	12 088	1.39	1950-97	16	20, 21			
4	-	Bella Coola R., BC	3 475	-	608	40 946	0.79	1950-97	16	17			
4	3	Necleetsconay R., BC	2 463	231	575	2 231	1.11	1950-97	16	17			
-	3	Thorsen Cr., BC	-	232	620	428	1.16	1950-97	16	17			
-	4	Chehalis R., BC	-	244	581	26 903	0.80	1953-86	16	23			
-	4	Weaver Cr., BC	-	214	554	5 064	1.85	1953-86	16	19			
-	5	Stagoo Cr., BC	-	276	-	4 770	1.09	1968-90	16	21			
-	5	Kshwan R., BC	-	269	-	6 063	1.06	1968-90	16	21			
Coho	-	1	Nanaimo R., BC	-	190	503	1 826	0.26	1983-91	16	17		
	1	1	Millstone R., BC	2 653	181	546	47/72	1.36/1.08	1983-93/1983-91	16	17		
	1	-	Cowichan R., BC	2 329	-	520	12 965	0.68	1983-93	16	14, 24		
	2	-	Oyster R., BC	2 638	-	508	3 715	1.03	1953-97	16	25		
	-	2	Black Cr., BC	-	201	493	781	1.04	1985-96	6	25		
	2	2	Puntledge R., BC	2 310	232	518	3 641/2724	1.00/1.19	1953-97/1985-96	16	17		
	3	3	Siddle Cr., BC	2 916	171	484	351	1.14	1957-93	16	25		
	3	3	Pye Cr., BC	2 665	207	518	81	0.92	1957-93	16	25		
	-	4	Mamquam R., BC	-	167	533	351	0.28	1980-86	16	25		
	4	4	Tenderfoot Cr., BC	3 032	158	497	1 119	1.03	1980-86	16	17		
	4	-	Ashlu Cr., BC	2 878	-	509	171	0.67	1980-86	16	17		
	5	-	Mathers Cr., BC	3 255	-	557	2 143	0.85	1975-97	16	17		
	5	5	Pallant Cr., BC	2 790	253	542	2 724/2752	0.52/0.46	1975-97/1972-91	16	17		
	-	5	Kitimat R., BC	-	173	572	9 897	0.79	1972-91	16	17		
	-	6	Chehalis R., BC	-	240	563	498	0.78	1984-91	13	19, 24		

Table 1. Continued

Species	Pair Fec	Pair ES	Population	Fec	ES	BL	Population size <sup>a</sup>		Var	Years	References <sup>b</sup>	
							Mean	BL			Time-series	Fec, BL and ES
Pink	-	6	Hicks Cr., BC	-	147	475	464	0.87	1984-91	16	25	
	1	-	Seton R., BC	1 690	-	425	179 872	1.13	1953-91	16	17	
	1	-	Thompson R., BC	1 570	-	422	187 213	1.51	1953-91	16	17	
	2	1	Quinsam R., BC, odd years	1 719	140	463	2 322	1.21	1957-75	16	17, 26	
	2	1	Quinsam R., BC, even years	1 191	154	387	2 592	1.13	1958-76	16	17, 26	
	-	2	Keogh R., BC, even years	-	170	379	62 944	0.50	1954-80	16	26	
	-	2	Keogh R., BC, odd years	-	140	396	5 324	1.35	1953-79	16	26	
	-	3	Yakoon R., BC	-	189	398	240 386	1.14	1950-96	16	26	
	-	3	Deena Cr., BC	-	181	402	48 533	1.09	1950-96	16	26	
	-	4	Kitwanga R., BC, even years	-	184	392	80 017	1.06	1950-96	16	26	
Sockeye	-	4	Kitwanga R., BC, odd years	-	175	418	128 027	0.76	1951-97	16	26	
	-	5	Kitumkalum R., BC	-	166	415	45 707	1.93	1977-93	16	26	
	-	5	Khutzeymateen R., BC	-	134	399	24 588	1.19	1977-93	16	26	
	1	-	Cedar R., WA	3 627	-	437	198 789	0.54	1977-91	13	27	
	1	-	Okanogan R., WA	2 595	-	368	2 143	0.68	1977-91	13	27	
	2	-	Birkenhead R., BC	4 645	-	-	28 854	0.83	1948-92	6	27	
	2	1	Weaver Cr., BC	4 333	118	476	13 095/19 791	1.02/1.01	1948-92/1953-92	6	18, 27	
	-	1	Harrison R., BC	-	96	435	7 406	1.11	1953-92	16	28	
	3	-	Henderson L., BC	4 364	-	-	15 522	0.85	1953-82	16	29	
	3	-	Hobitton L., BC	2 757	-	-	4 675	0.74	1953-82	16	29	
4	2	Horsefly R., BC	3 504	66	469	2 465	3.32	1948-93	6	27, 28		
4	2	Chilko R., BC	2 872	85	450	108 012	1.03	1948-93	6	27, 28		
5	-	Awun R., BC	3 262	-	-	3 715	0.84	1978-88	16	29		
5	-	Mercer Cr., BC	2 825	-	-	2 276	0.53	1978-88	16	29		
6	-	Curtis Cr., BC	3 956	-	-	2 276	1.11	1978-93	16	29		
6	-	Devon L., BC	3 386	-	-	1 737	1.28	1978-93	16	29		
7	-	Early Stuart R., BC	4 343	-	467	23 156	1.48	1948-94	6	27		
7	3	Stellako R., BC	3 669	69	468	37 533/37 049	0.70/0.70	1948-94/1953-92	6	27, 28		
-	3	Nadina R., BC	-	76	443	6 568	1.35	1953-92	16	28		

<sup>a</sup>Separate values for mean population size and variation are given for those populations where different lengths of time-series were used in fecundity and egg size contrasts. The first mean size, variation and time-series given refers to fecundity contrasts, and the second to egg size contrasts. <sup>b</sup>1. Dempson *et al.* (1998a). 2. O'Connell, Ash & Walsh (1998). 3. Burgeois, Murray & Mercer (1998). 4. O'Connell, Dempson & Reddin (1997). 5. Chaput & Prevost (1999). 6. Ransom Myers' stock recruitment database (fish.dal.ca/~myers/data.html). R.A. Myers, Department Biol., Dalhousie University, Halifax, Nova Scotia. 7. O'Connell, Reddin & Mullins (1996). 8. Dempson, Furey & Bloom (1998b). 9. Randall (1989). 10. J.A. Hutchings, Department Biol., Dalhousie University, Halifax, Nova Scotia, unpublished data. 11. Marshall, Harvie & Jones (1998). 12. O'Neil, Harvie & Longard (1997). 13. StreamNet database (www.streamnet.org). M. Banach, Pacific States Marine Fisheries Commission, Gladstone, Oregon. 14. Rounsfell (1957). 15. Myers *et al.* (1998a). 16. Salmon Escapement Database, E. Grundmann, Canadian Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C. 17. Beacham & Murray (1993). 18. Beacham & Murray (1989). 19. Murray (1980). 20. Beacham (1982). 21. Beacham & Murray (1987). 22. Beacham & Murray (1985). 23. Beacham & Murray (1986). 24. Weitkamp *et al.* (1995). 25. Fleming & Gross (1990). 26. Beacham & Murray (1988). 27. Gustafson *et al.* (1997). 28. Groot & Margolis (1991). 29. Manzer & Miki (1986).

linear regressions between year and ln-transformed population estimates.

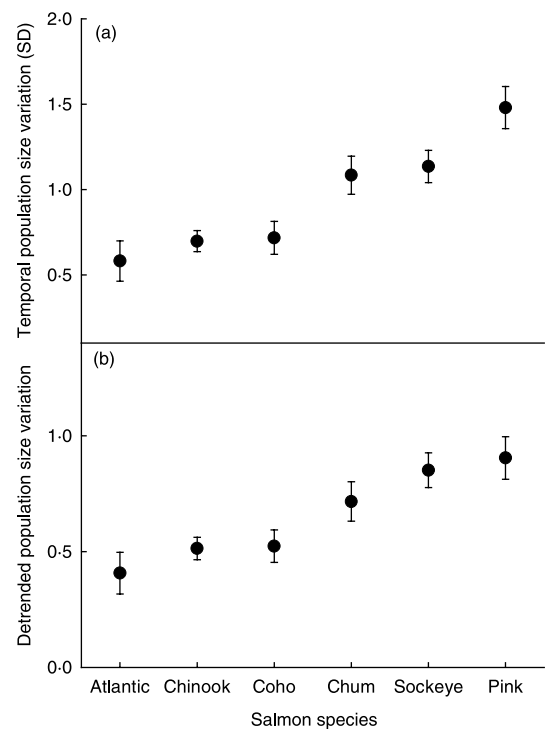
Two sets of analyses are reported. First, data were analysed without incorporating relatedness among populations and species. In these analyses, effects of species, duration of time-series (i.e. number of years), mean population size, fecundity and egg size on population stability were tested. For pink salmon, which have a fixed 2-year life cycle, even- and odd-year populations were considered separate populations. Secondly, paired independent contrasts were used (Harvey & Pagel 1991). In these contrasts, differences in population variability, fecundity and egg size were calculated between pairs of conspecific populations which were located closer to each other geographically than to any other populations of the same species in the sample. In addition, for pink salmon, even- and odd-year populations within the same river were compared. For all species, time-series of adult counts were selected such that data for populations within pairs were from identical time periods, giving a total of 35 pairs for each test (Table 1). In selecting our pairs, we assumed that geographical distance among populations reflects degree of genetic relatedness (Olsen *et al.* 1998; Nielsen, Hansen & Loeschcke 1999). To verify that these contrasts yielded data that are phylogenetically independent, mean values of fecundity and egg size were calculated for each pair, and tests of correlations between these and absolute differences in these traits within pairs were performed (Freckleton 2000). The statistics from the paired independent contrasts are reported for regressions forced through the origin (Harvey & Pagel 1991) and also as binomial tests. For those populations where body lengths were available, a second set of paired contrasts that controlled for differences in body length among populations were obtained by calculating residuals of fecundity or egg size from an ANCOVA with body length (postorbital hypural) as a covariate and species as a factor.

**Results**

Using the data from all populations, we initially examined differences in annual population variation among species, with mean population size and number of years sampled as covariates. This analysis included the longest time-series of population sizes available for each population (Table 1). There were significant differences

among species, and annual population variation decreased with mean population size for both standard deviations and detrended variation (Table 2). In addition, both measures of variation increased with increasing number of years sampled. Comparisons of marginal means of standard deviations for the different species (i.e. means adjusted for the covariates [number of years and mean population size]) showed that Atlantic, chinook and coho salmon were less variable than sockeye and pink salmon, and with chum being more similar to sockeye and pink (Fig. 1, Table 3). For detrended variation a similar pattern emerged (Fig. 1, Table 3).

There were no significant correlations between mean egg size or mean fecundity and contrasts in these traits for population pairs (egg size:  $n = 35, r_s = -0.17, P = 0.342$ ; fecundity:  $n = 35, r_s = 0.06, P = 0.713$ ), suggesting that the pairwise approach was successful in



**Fig. 1.** Comparison of (a) mean ( $\pm 1$  SE) temporal population size variation (standard deviation of ln-transformed data) and (b) detrended population size variation among salmon species after adjustment for variation in mean population sizes and numbers of years sampled.

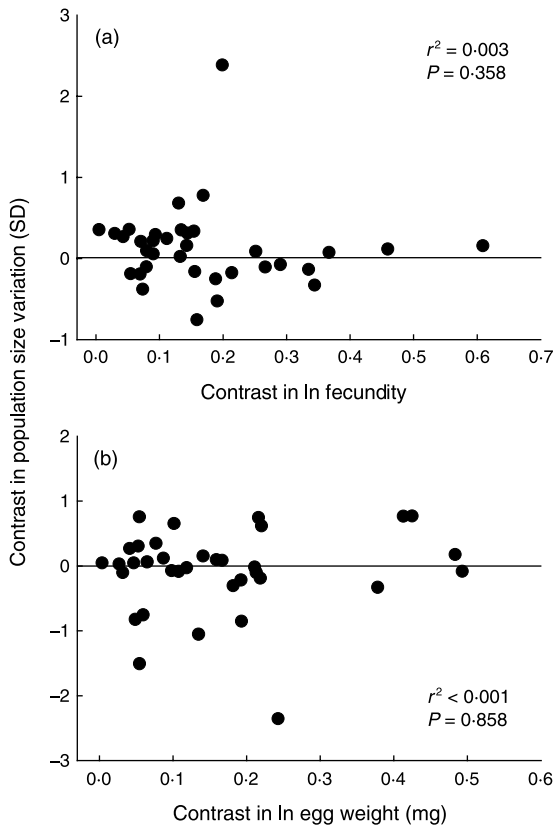
**Table 2.** ANCOVA of temporal population size variation (standard deviation and detrended variation) of six salmon species. Slopes of covariate regressions (b) are given to indicate direction of effect

	d.f.	Standard deviation			Detrended variation		
		b	F	P	b	F	P
Species	5, 96		8.26	< 0.001		5.30	< 0.001
Number of years	1, 96	0.01	7.56	0.007	0.01	6.18	0.015
Mean population size	1, 96	-0.10	17.69	< 0.001	-0.06	11.60	0.001

**Table 3.** *P*-values for pairwise *t*-test comparisons of temporal population size variation (standard deviation below diagonal, detrended variation above diagonal) among salmonid species after adjustment for variation in mean population size and numbers of years sampled

	Atlantic	Chinook	Coho	Chum	Sockeye	Pink
Atlantic	—	0.300	0.300	0.021	< 0.001*	0.001*
Chinook	0.381	—	0.903	0.043	< 0.001*	0.001*
Coho	0.361	0.857	—	0.098	0.003*	0.002*
Chum	0.004*	0.004*	0.020	—	0.207	0.146
Sockeye	0.001*	< 0.001*	0.004*	0.711	—	0.647
Pink	< 0.001*	< 0.001*	< 0.001*	0.020	0.023	—

\**P* < 0.05 after adjustment by sequential Bonferroni method.



**Fig. 2.** Relationship between phylogenetically independent contrasts in (a) fecundity and (b) egg size and temporal population size variation (standard deviation of ln-transformed data) of salmon fishes.  $r^2$ - and *P*-values for linear regressions forced through the origin are given.

controlling for phylogenetic correlations (Freckleton 2000). Pairwise contrasts in fecundity were not correlated with contrasts in temporal variation in population abundance measured either as standard deviations (Fig. 2a) or detrended variation ( $r^2 = 0.03$ ,  $P = 0.285$ ). The population with the highest fecundity had the highest variation in 22 of the 35 paired comparisons for standard deviations (Fig. 2a, binomial test:  $P = 0.176$ ), and in 14 of 35 paired populations for detrended variation ( $P = 0.310$ ). Fecundity was influenced significantly by body length and differed among species (ANCOVA: body length,  $F_{1,59} = 61.71$ ,  $P < 0.001$ ; species,  $F_{5,59} = 23.48$ ,  $P < 0.001$ ),

and using residuals from this analysis did not alter the findings significantly [the more fecund population was more variable in 14 of 27 paired comparisons when using standard deviation ( $P > 0.99$ ), and in 15 of 27 when using detrended variation ( $P = 0.700$ )].

To test for effects of fecundity on variability while controlling for population size, residuals from the analyses of covariance given in Table 2 were calculated, and these were compared in a pairwise fashion. The results were similar: the population with the highest fecundity had the highest population variation (controlled for population size) in 21 of the 35 paired comparisons when using both standard deviations and detrended variation ( $P = 0.310$ ). These results are therefore consistent with those obtained in traditional ANCOVA analysis, where phylogenetic relationships were ignored (Table 4).

There was no indication that egg size influenced population stability. There was no correlation between the extent of within-pair differences in egg size and the extent of population variation among pairs (Fig. 2b; detrended variation:  $r^2 < 0.01$ ,  $P = 0.838$ ). Moreover, the population with the largest eggs was least variable in 18 of the 35 paired comparisons when using standard deviations (Fig. 2b;  $P > 0.99$ ), and in 15 of the 35 comparisons when using detrended variation ( $P = 0.499$ ). Egg size was significantly influenced by body length and differed among species (ANCOVA: body length,  $F_{1,62} = 15.26$ ,  $P < 0.001$ ; species,  $F_{5,62} = 22.88$ ,  $P < 0.001$ ). Using residuals from this analysis we again found no effect, i.e. the population with larger eggs was less variable in 14 of 29 paired comparisons when using standard deviations ( $P > 0.99$ ), and in 15 of 29 when using detrended variation ( $P > 0.99$ ).

Finally, tests for effects of egg size on variability while controlling for population size were performed by calculating residuals from the analyses of covariance given in Table 2, and then comparing these residuals in a pairwise fashion. No effect of egg size on variability was observed using this approach [the population with larger eggs was less variable in 18 of 35 paired comparisons when using standard deviations ( $P > 0.99$ ), and in 16 of 35 when using detrended variation ( $P = 0.735$ )]. Again, these results are consistent with those obtained when ignoring phylogenetic relationships (Table 5).

**Table 4.** ANCOVA of temporal population size variation (standard deviation and detrended variation) of six salmon species for which fecundity data were available. Slopes of covariate regressions (*b*) are given to indicate direction of effect

	d.f.	Standard deviation			Detrended variation		
		<i>b</i>	<i>F</i>	<i>P</i>	<i>b</i>	<i>F</i>	<i>P</i>
Species	5, 61		3.12	0.014		2.87	0.022
Number of years	1, 61	0.01	6.19	0.016	0.01	5.21	0.026
Mean population size	1, 61	-0.10	11.29	0.001	-0.07	10.17	0.002
Fecundity	1, 61	< -0.01	< 0.01	0.984	0.06	0.16	0.689

**Table 5.** ANCOVA of temporal population size variation (standard deviation and detrended variation) of six salmon species where egg size data were available. Slopes of covariate regression (*b*) are given to indicate direction of effect

	d.f.	Standard deviation			Detrended variation		
		<i>b</i>	<i>F</i>	<i>P</i>	<i>b</i>	<i>F</i>	<i>P</i>
Species	5, 61		3.73	0.005		4.06	0.003
Number of years	1, 61	< 0.01	0.23	0.634	< 0.01	2.44	0.124
Mean population size	1, 61	-0.12	9.10	0.004	-0.10	12.58	0.001
Egg size	1, 61	-0.03	0.01	0.909	-0.10	0.31	0.581

## Discussion

This study provides several insights into patterns of population fluctuations in salmon species. We found no effect of fecundity on annual variation in population sizes. Such an effect might have been expected based on findings in a recent study of marine fishes, where stocks with high fecundity have higher variation in recruitment than related stocks (Rickman *et al.* 2000). Unlike Rickman *et al.* (2000), we did not use recruitment estimates that controlled for spawning population size in our analyses (i.e. standard deviation of ln residuals from a Ricker spawner-recruitment function, cf. Rickman *et al.* 2000), because estimation of the spawner-recruitment functions requires accurate, population-specific information about age at maturation. The two estimates of variation, however, were closely correlated in salmon ( $n = 85$  populations,  $r = 0.80$ ,  $P < 0.001$ , data from Myers, Bridson & Barrowman 1995), and it is thus unlikely that the difference in approach causes our results to differ from those of Rickman *et al.* (2000). It is also unlikely that the contrasting results were due to differences in statistical power. While contrasts in fecundity (ratio of most to least fecund species/population within pairs) were, on average, larger in magnitude between marine fish species (*c.* 2; Fig. 2 in Rickman *et al.* 2000) than those between salmon populations (1.2), the results were consistent across the range of differences in fecundity within pairs for both studies, including regions of overlap. Furthermore, the sample size of paired contrasts for salmon populations was almost three times that for marine species. We also found no relationships between population variation and egg size. It is pos-

sible that differential exploitation on populations may have obscured relationships, for example, by affecting population characteristics such as variability in abundance. The exploitation of salmonid populations, however, occurs largely at regional scales and thus our pairwise analyses of geographically close populations during identical time periods minimize the potential influence of such effects.

One potential explanation for the lack of relationships between population variation and fecundity or egg size in salmon is that populations experiencing highly variable environments evolve to buffer the effects of such variation (e.g. Benton & Grant 1999). Alternatively, and perhaps more likely, temporal variation in exogenous forces is highly divergent even among streams that are geographically close. This hypothesis is supported by the lack of a correlation between population fluctuations among pairs of closely located populations ( $n = 62$ ,  $r = -0.07$ ,  $P = 0.611$ ). Thus, local environmental variation may be more important in determining relative levels of abundance fluctuations among populations reproducing in freshwater and using streams and estuaries as initial nursing habitat than in marine environments, where spatial autocorrelations of environmental variability are more pronounced (Myers, Mertz & Bridson 1997).

The duration of time-series was related positively to variation in population sizes when using standard deviations, and also when using detrended variation. Because the linear detrending did not remove the effect of time-series duration on variation, this suggests that there are long-term non-linear abundance trends in salmon populations that extend beyond the 7-year period of



the shortest time-series (i.e. long-term negative trends followed by long-term positive trends). Relationships between duration of time-series and variation have been reported previously in various taxa (Pimm & Redfearn 1988).

Our strongest finding was that increasing population sizes appear to lend stability to the dynamics. Variation in population size decreased with increasing population size, although the measures of variability used here have been suggested to be independent of population size in most species (McArdle *et al.* 1990; Pimm 1991). There are at least four biological processes that may cause negative correlations between variation and population size in salmonids. First, large populations may have a more complex spatial structure than small populations, consisting of subunits that do not fluctuate in perfect synchrony. Thus, such spatial structuring may be stabilizing if the relative success of different segments of a population vary from year to year, because the effect of exogenous forces on the total population is averaged out across years (Kindvall 1996; for a salmon model see Kocik & Ferreri 1998). It should be emphasized that the positive effects of population size on stability observed here represent among, rather than within population patterns. Unless a temporal decrease in population size is associated with loss of population subunits, variation in mean population size within populations should not be associated with stability.

A second hypothesis is that populations that are, on average, small are those populations that experience high environmental variance, and therefore also show high variability. For example, Benton, Lapsley & Beckerman (2002) found that increasing environmental variance increased population variance and decreased mean population size in experimental populations of soil mites (*Sancassania berlesei* Michael). This effect also skewed the distribution of population sizes negatively. Hence, if this is the explanation for the observed association between population size and stability in the present study, we would expect an association between population size and skewness. However, we found no effect of either species or mean population size on skewness (calculated following Sokal & Rohlf 2000: 111) among populations (ANCOVA: species  $F_{5,103} = 1.17$ ,  $P = 0.328$ ; mean population size  $F_{1,103} = 0.49$ ,  $P = 0.486$ ). Thus, factors other than environmental variability, such as the mean quality and amount of habitat are likely more important determinants of the broad patterns of spatial variation in population size.

Thirdly, if populations become sufficiently small, demographic stochasticity (caused by variation in contribution to the next generation among individuals for a given year) may influence relative levels of variation among populations of varying size. With the current data, however, this seems unlikely, because only two of the 104 population time-series examined had mean population sizes of less than 100 adult individuals.

Finally, if large populations have higher levels of density-dependent mortality than small populations,

and if this density-dependent mortality occurs later in life than most of the mortality due to external forces, then year-to-year fluctuations in external forces may have a smaller impact on adult population size in large than in small populations. Although this is possible, empirical data suggest that density-dependent mortality is strongest during the initial 'critical phase' of life (Elliott 1989) and the evidence for 'self-thinning' later in life is weak at best (Armstrong 1997).

At the species level, detrended population variation differed, with Atlantic, chinook and coho being less variable than sockeye and pink salmon, and with chum being more similar to sockeye and pink salmon. A similar pattern appeared when measuring variation as standard deviations. Although causal explanations for such differences among species are hard to test due to the pronounced differences in life histories and habitat use, we suggest that timing of migration to the marine environment may contribute to the observed patterns of dynamics. Whereas Atlantic, coho and components of chinook salmon populations typically spend substantial amounts of time (months to years) growing in freshwater rivers or estuaries prior to their migration to sea, pink and chum salmon migrate to sea shortly after they emerge from their gravel nests. Thus, due to their small size at migration, pink and chum salmon may be more susceptible to temporal variation in the marine environment of coastal areas (e.g. temperature, prey abundance, predation) than are the larger juveniles of Atlantic, coho or chinook salmon. Support for this hypothesis comes from release experiments of Atlantic salmon smolts (juvenile migratory stage), where annual variability in survival decreased with increasing smolt size (Salminen & Kuikka 1995).

At first glance, sockeye salmon do not appear to fit this pattern because they migrate to sea at a large size. However, shortly after emergence they do undertake a migration from their natal river to a freshwater lake, and may thus experience an associated temporal variability in survival, although somewhat diminished relative to that experienced by pink and chum salmon migrating to sea. Moreover, the mean variability in the sockeye salmon of this study is highly influenced by one extreme population (Horsefly River, BC, standard deviation = 3.32), and when removing this population from the analyses, mean variability decreases (adjusted mean SD = 1.00) to a point intermediate between that of coho and chum salmon and not significantly different from either ( $P > 0.05$ ). The Horsefly River population is one of the few sockeye populations that shows strong cyclic fluctuations, the reasons for which remain unclear (see Myers *et al.* 1998b).

Considering the distinct dynamics of the closely related species in this study, it may not be surprising that traditional cross-species comparative studies have failed to find a relationship between fecundity and recruitment variability in marine fishes (Rothschild & DiNardo 1987; Mertz & Myers 1996), whereas the single study that incorporated phylogenetic relationships did (Rickman

et al. 2000). At present, there is no evidence for similar effects of fecundity, or effects of egg size, on salmon dynamics. However, both the differences in variability among species and the relationship between population size and variability suggest that other organism-specific characteristics may be important in determining the extent to which populations dampen effects of exogenous forces.

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