

The influence of phylogeny, size and behaviour on patterns of covariation in salmonid life histories

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We evaluated covariation in eight life history traits within the family Salmonidae. Principal components analysis defined a primary tactic ranking salmonids from large, early-maturing, semelparous individuals bearing few, large, rapidly developing eggs to the opposite suite of characters in small, iteroparous individuals. The analysis also defined a secondary cline from anadromous to freshwater forms, and a tertiary tactic describing variation in development. Clustering of species on the basis of life history traits reflected taxonomic affiliations. Life history traits appear to co-evolve and form successful life history strategies best suited to the biology and environment of a given taxon. Migratory behaviour and life histories are closely linked. The correspondence between behaviour and life histories may lead to unanticipated but nevertheless successful life history strategies.

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Мы оценивали ковариацию 8 параметров жизненных циклов в семействе *Salmonidae*. Анализ основных компонентов выявил первичное тактическое ранжирование лососевых от крупных, рано созревающих однократно нерестящихся особей, выметывающих немного крупных быстро развивающихся икринок до противоположного набора признаков у мелких многократно нерестящихся особей. Анализ выявил также вторичный клин от анадромных до пресноводных форм и тактику третьего порядка, описывающую различия в развитии. Группирование видов на основе особенностей жизненного цикла отражает таксономические связи. Отдельные особенности жизненного цикла по-видимому коэволюционируют и формируют стратегию жизненного цикла, наиболее подходящие для биологии и условий обитания данного таксона. Миграционное поведение и жизненные циклы тесно связаны. Соответствие между поведением и жизненным циклом может привести к формированию неожиданных, но тем не менее успешных стратегий жизненного цикла.

Introduction

Suites of life history traits should co-evolve to form adaptive tactics of reproduction and survival (Stearns 1976). Genetic, physiological, and developmental pathways constrain these tactics so that any given phylogenetic lineage has a limited number of reproductive and survival alternatives (Stearns 1980, 1983, Brown 1983). Similarly, allometric constraints with body size limit or preclude certain life history tactics within and between phylogenetic lines. This raises several interesting questions (Stearns 1980, 1983): To what degree does our perception of life history tactics depend upon phylogeny? How many of these perceived tactics are really allometric constraints of body size? What is the relationship between behaviours and life histories?

Mammalian life histories are related to body size (Millar 1977, 1981, Tuomi 1980, Eisenberg 1981) which accounts for most of the covariation among traits (Stearns 1983). Weight and phylogenetically-related covariation among mammalian life history traits define a primary tactic of r- to K-strategists and a secondary tactic of altricial to precocial forms (Stearns 1983).

Reptilian life history tactics are also constrained by body size but to a lesser degree than in the mammals (Stearns 1984). Again, the first classwide component describes a tactic ranking reptiles from r- to K-strategists. Life history tactics appear to be lineage dependent in reptiles and mammals (Stearns 1983, 1984). This general dependency of life histories on phylogeny suggests that microevolutionary trends in life histories are constrained within evolutionary lines.

But this gives little insight into how traits may have co-evolved in those ancient lineages. Did the common ancestors possess a wide or narrow array of life history traits? How many of the observed phylogenetic constraints have evolved through selective elimination of alternative tactics, as opposed to divergence of tactics along different phylogenetic lines?

We suggest that the answers to these questions can be found by careful examination of life history variation in closely related groups of organisms. We begin this analysis by looking at the Salmonidae, a well-studied fish family with complex life histories. We ask three explicit

questions related to covariation and evolution of salmonid life histories: 1) How do life history traits covary within the family Salmonidae? 2) Does size effect patterns of covariation in life history traits among salmonids? 3) What is the relation between life style (i.e. anadromy, freshwater residency) and life history?

The family Salmonidae contains three subfamilies, nine genera, and about 68 species (Behnke 1972). Five genera are recognized within the subfamily Salmoninae (salmons, trouts, chars): *Brachymystax*, *Hucho*, *Oncorhynchus*, *Salmo*, and *Salvelinus*. The subfamily Thymallinae (graylings) consists of a single genus, *Thymallus*, with four species. Three genera (*Coregonus*, *Prosopium*, and *Stenodus*) are recognized within the subfamily Coregoninae (whitefishes, ciscoes).

Truly anadromous forms are found only in the salmonines. *Oncorhynchus* spp. (Pacific salmon) make extensive oceanic migrations and mature at sea, although freshwater forms of *O. masu*, *O. nerka*, and *O. tshawytscha* do exist. All individuals are semelparous. *Salvelinus* spp. exhibit the least degree of anadromy (e.g. *S. namaycush* has no anadromous form) and undergo restricted coastal and estuarine migrations. All members are iteroparous. *Salmo* spp. are intermediate between the other two genera in extent of oceanic migrations and degree of iteroparity.

Materials and methods

We selected only those species for which we could compile data on eight life history traits: hatching time of egg, egg size (diameter), number of eggs, age at maturity, length at maturity, maximum length, maximum age, and inter-brood interval. The references used to compile these data have been coded in Tab. 1 (cf. References). The final data set included 21 species, 29 forms (13 anadromous migrant, 16 freshwater resident), and seven genera representing all three subfamilies (Tab. 1). Values were recorded for females only. Maximum age was not used directly in the analyses because of increased error associated with the ageing of older individuals. Instead, maximum age and inter-brood interval were incorporated in an estimation of maximum broods per life where

$$\text{Maximum broods per life} = \frac{\text{Maximum age} - \text{minimum age at maturity}}{\text{inter-brood interval}}$$

We used a modification of Stearns' (1983, 1984) protocol for evaluating size constraints on life histories. First, we regressed each trait on maximum length. Next, we constructed principal components (PCI method; Anon. 1983) using all life history traits on all 29 forms. We repeated the principal components analysis (PCA) excluding maximum length. We repeated the PCA

again, after removal of body size effects by subtracting $b_i \times \text{maximum length}$ (b_i = slope of the regression of the i th trait on maximum length) from the i th trait on each form (Stearns 1984). We then used hierarchical clustering, based on Euclidean distances (Wishart 1978) of the component scores, to generate groups of fish with similar degrees of covariation in life histories.

Tab. 1. Mid-range values for each of seven traits in twenty-nine forms of the family Salmonidae.

Taxon	Hatching time (d)	Number of eggs	Egg size (mm)	Age at maturity (yr)	Length at maturity (cm)	Maximum broods/life	Maximum length (cm)	Reference code
<i>Coregonus artedii</i>	124.0	26374	1.95	4.0	31.8	12.0	57.2	A
<i>C. clupeaformis</i>	130.0	65272	2.50	6.5	42.5	21.5	64.0	B
<i>C. hoyi</i>	106.5	7851	2.00	2.5	25.0	9.0	31.5	C
<i>Prosopium cylindraceum</i>	140.0	10538	2.80	4.5	23.8	12.0	56.1	D
<i>P. williamsoni</i>	135.0	12785	2.80	3.0	38.5	16.0	57.2	E
<i>Stenodus leucichthys</i>	182.0	272500	2.50	10.5	60.5	4.7	150.0	F
<i>Thymallus arcticus</i>	15.5	9953	2.35	3.5	34.3	10.0	75.7	G
<i>Salmo clarki</i> (A)	45.5	2323	4.70	4.0	39.3	6.0	99.0	H1
<i>S. clarki</i> (F)	45.5	1255	4.70	3.5	20.0	7.0	99.1	H2
<i>S. gairdneri</i> (A)	47.5	4483	4.00	4.0	50.0	5.0	122.0	I1
<i>S. gairdneri</i> (F)	47.5	1500	4.00	4.0	42.0	5.0	91.5	I2
<i>S. salar</i> (A)	175.0	11196	6.00	5.0	67.0	11.0	140.0	J1
<i>S. salar</i> (F)	175.0	2384	5.25	5.0	21.5	10.0	99.0	J2
<i>S. trutta</i> (A)	89.5	1510	4.50	4.0	51.5	10.0	102.0	K1
<i>S. trutta</i> (F)	115.0	10588	4.25	3.5	29.0	11.0	82.6	K2
<i>Salvelinus alpinus</i> (A)	180.0	4582	4.35	7.0	63.0	18.0	96.0	L1
<i>S. alpinus</i> (F)	72.0	1576	4.30	8.0	27.7	12.0	55.0	L2
<i>S. fontinalis</i> (A)	125.0	2550	4.25	4.5	27.0	5.0	80.0	M1
<i>S. fontinalis</i> (F)	125.0	2550	3.85	2.5	20.0	8.0	86.0	M2
<i>S. malma</i> (A)	225.0	4250	4.50	8.0	37.5	11.0	127.0	N1
<i>S. malma</i> (F)	225.0	1412	3.55	5.5	15.1	12.0	75.0	N2
<i>S. namaycush</i>	117.5	10996	5.25	11.5	46.5	29.0	157.5	O
<i>Oncorhynchus gorbuscha</i>	94.0	1500	6.00	2.0	50.5	1.0	76.0	P
<i>O. keta</i>	120.0	3580	5.50	4.0	64.0	1.0	100.0	Q
<i>O. kisutch</i>	75.0	3570	5.25	4.0	53.0	1.0	96.0	R
<i>O. masu</i>	57.5	2286	7.00	3.5	55.0	1.0	74.3	S
<i>O. nerka</i> (A)	96.0	3643	5.95	4.5	60.0	1.0	84.0	T1
<i>O. nerka</i> (F)	140.0	1031	4.75	4.5	35.5	1.0	53.3	T2
<i>O. tshawytscha</i>	56.0	8931	6.50	5.0	77.5	1.0	149.0	U

(A) = anadromous.
(F) = freshwater resident.

Tab. 2. Correlation and regression of each trait on maximum length.

Trait ^a	Mean ^b	r	p	Slope	Intercept
Hatching time	113.2	0.00	0.491	0.007	1.979
Egg size	4.32	0.45	0.007	3.928	-3.283
Number of eggs	16989.6	0.17	0.188	0.591	2.555
Age at maturity	4.90	0.48	0.004	0.533	-3.796
Length at maturity	41.69	0.49	0.004	0.572	0.478
Maximum broods/life	8.70	-0.01	0.470	-0.111	2.917

a. Hatching time, egg number, age at maturity, and length at maturity were log-transformed. A square-root transformation was performed on maximum broods/life. Egg size was not transformed.

b. Untransformed means.

Results

All traits showed considerable variation among salmonid forms and, in general, there appeared to be more variation among taxa than within (Tab. 1). Maximum length accounted for significant variation in only three traits (egg size [$r = 0.45$], age at maturity [$r = 0.48$], and length at maturity [$r = 0.49$]), all of which were positively correlated with body size (Tab. 2).

Loadings on all three principal components remained essentially unchanged whether maximum length was in-

cluded or not (Tab. 3). In both cases, the first component described an axis at one end of which were small, late-maturing fish bearing many, small, slowly developing eggs in many broods per lifetime, and at the other end of which were large, early-maturing fish with few, large, rapidly developing eggs in a few broods per lifetime. The second component distinguished large, late-maturing forms with many, large eggs from small, early-maturing forms having few, small eggs. The third component described a cline from small fish bearing few, large, slowly developing eggs to large fish having many, small, rapidly developing eggs.

Tab. 3. Unrotated component loadings for principal components 1, 2, and 3 before and after removal of length effects.

Trait	PC1	PC2	PC3
A. Length effects not removed, maximum length included			
Hatching time	.466	.233	.603
Egg size	-.796	.374	.381
Number of eggs	.606	.442	-.554
Age at maturity	.438	.725	.234
Length at maturity	-.405	.705	-.388
Maximum broods/life	.821	.067	.136
Maximum length	-.197	.838	.068
% variance explained	32.7	30.3	14.9
B. Length effects not removed, maximum length excluded			
Hatching time	.499	.210	.651
Egg size	-.714	.468	.415
Number of eggs	.675	.399	-.515
Age at maturity	.563	.589	.268
Length at maturity	-.273	.861	-.309
Maximum broods/life	.822	-.166	.102
% variance explained	38.0	25.6	17.3
C. Length effects removed			
Hatching time	.476	-.095	-.739
Egg size	-.796	.058	.505
Number of eggs	.682	.617	-.191
Age at maturity	.684	.086	.440
Length at maturity	-.306	.886	.179
Maximum broods/life	.813	-.257	-.082
% variance explained	42.5	20.9	17.8

Following removal of length effects, the total explained variance increased marginally from 77.9% to 81.2%. The first component remained relatively unchanged, whereas the second described a gradient from large fish having many eggs to small fish having few eggs. The interpretation of the third principal component differed substantially after length effects were removed, with a gradation from late-maturing fish bear-

Tab. 4. Arithmetic means of seven life history traits in anadromous and freshwater forms of *Salmo clarki*, *S. gairdneri*, *S. salar*, *S. trutta*, *Salvelinus alpinus*, *S. fontinalis*, and *S. malma* (calculated from mid-range values recorded in Tab. 1).

Trait	Anadromous migrant	Freshwater resident
Hatching time (d)	126.8	115.0
Egg size (mm)	4.61	4.27
Number of eggs	4413	3038
Age at maturity (yr)	4.7	4.6
*Length at maturity (yr)	47.9	25.0
Maximum broods/life	9.0	9.3
*Maximum length (cm)	109.3	84.0

*Trait values are significantly ($p < 0.05$) different between the two forms.

ing large, slowly developing eggs to early-maturing fish bearing small, rapidly developing eggs. Many of these relations with size may be a reflection of differences in anadromy within species. Anadromous forms were significantly larger than their freshwater counterparts (Tab. 4).

Differences in the second and third principal components before and after removal of length effects were caused by changes in the dependence structure among traits following removal of length effects. Removing the correlations with maximum length reduced the correlations of egg size and age at maturity with length at maturity, the trait with the highest loading on PC2 (Tab. 5). This explains why loadings on egg size and age at maturity were reduced on PC2 following the removal of length effects. Correlations of all traits with hatching time, the most important trait on the third principal component, remained unchanged, whether the correlation with length was included or not. With length effects removed, the correlation of egg size with age at maturity increased whereas that with length at maturity decreased. This accounted for the inclusion of age at maturity and exclusion of length at maturity on PC3.

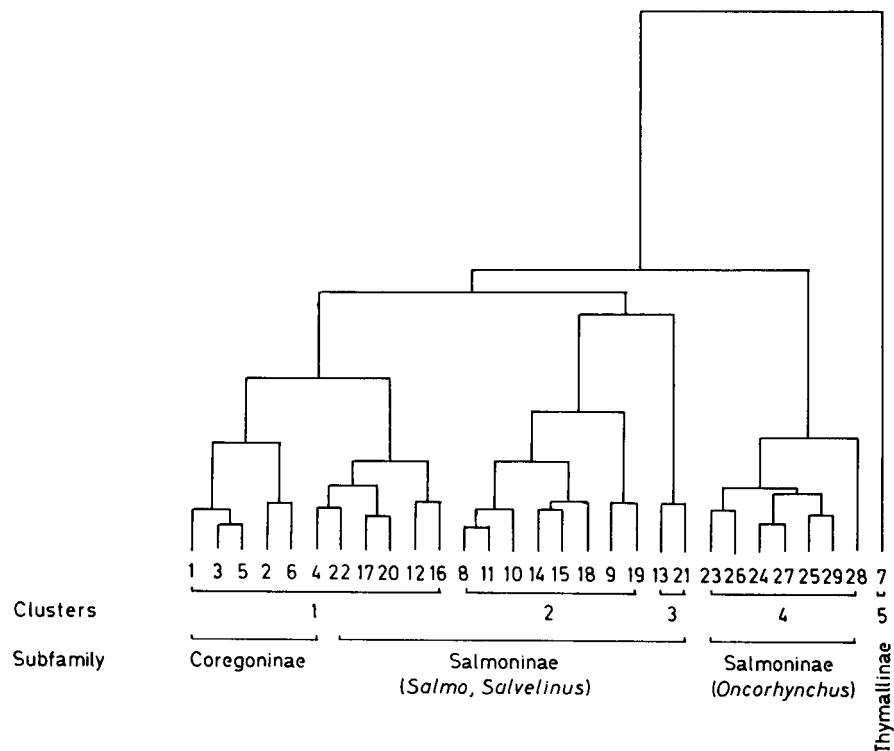
The cluster analysis revealed an interesting convergence of life histories among five groups of salmonids

Tab. 5. Correlation among salmonid life history traits with lengths effects included (below diagonal) and with length effects removed (above diagonal).

Trait	Trait					
	Hatch	Eggsize	Eggs	Agemat	Lengmat	Maxbrood
Hatch						
Eggsize	-0.06					
Eggs	0.20	-0.49				
Agemat	0.35	-0.01	0.37			
Lengmat	-0.11	0.45	0.27	0.20		
Maxbrood	0.28	-0.51	0.34	0.41	-0.33	
Maxlength	0.00	0.45	0.17	0.48	0.49	-0.01

Abbreviations: Hatch = hatching time; Eggsize = size of egg; Eggs = number of eggs; Agemat = age at maturity; Lengmat = length at maturity; Maxbrood = maximum broods/life; Maxlength = maximum length.

Fig. 1. Life history clusters of salmonids. The numbers correspond to species as follows (A = anadromous migrant, F = freshwater resident): 1. *Coregonus artedii*. 2. *C. clupeaformis*. 3. *C. hoyi*. 4. *Prosopium cylindraceum*. 5. *P. williamsoni*. 6. *Stenodus leucichthys*. 7. *Thymallus arcticus*. 8. *Salmo clarki* (A). 9. *S. clarki* (F). 10. *S. gairdneri* (A). 11. *S. gairdneri* (F). 12. *S. salar* (A). 13. *S. salar* (F). 14. *S. trutta* (A). 15. *S. trutta* (F). 16. *Salvelinus alpinus* (A). 17. *S. alpinus* (F). 18. *S. fontinalis* (A). 19. *S. fontinalis* (F). 20. *S. malma* (A). 21. *S. malma* (F). 22. *S. namaycush*. 23. *Oncorhynchus gorbuscha*. 24. *O. keta*. 25. *O. kisutch*. 26. *O. masu*. 27. *O. nerka* (A). 28. *O. nerka* (F). 29. *O. tshawytscha*.



(Fig. 1). The largest group (11 members) was comprised of the coregonines, *S. namaycush*, both forms of *S. alpinus*, and the anadromous forms of *S. malma* and *S. salar*. Both forms of *S. clarki*, *S. gairdneri*, *S. trutta* and *S. fontinalis* clustered in a second group. All Pacific salmon clustered together. The final two clusters consisted of the freshwater forms of *S. salar* and *S. malma* in one and *T. arcticus* in the other.

Oncorhynchus spp. are primarily anadromous fish that return from the ocean to spawn in fresh water. All individuals are semelparous. Eggs are large (6.8 mm), few in number (3900), and hatch over a short period of time (81 d) (Tab. 6). Maturity is achieved at a young age (3.8 yr) and large size (60 cm). In contrast, the coregonines (whitefishes, ciscoes) which reside in freshwater are iteroparous. Eggs are small (2.2 mm), numerous (47000) and require 136 d for hatching to occur. Rela-

tive to Pacific salmon, maturity is delayed (5.4 yr) and is attained at a small size (31 cm). Life history traits of the salmonines *Salmo* spp. and *Salvelinus* spp. are intermediate to those of Pacific salmon and coregonines. With the exception of *S. namaycush*, the species of both genera have anadromous and freshwater forms. For species with both anadromous and freshwater forms, egg size of the anadromous form was always equal to or greater than their freshwater counterparts (Tab. 1). Life history data on the freshwater *T. arcticus* are singularly distinct among salmonids, an appropriate reflection of its separate taxonomic designation.

Discussion

Previous studies on other vertebrates identified a primary reproductive tactic along an *r* – *K* continuum

Tab. 6. Arithmetic means of six life history traits in the family Salmonidae (calculated from mid-range values recorded in Tab. 1).

Trait	Subfamily			Thymallinae
	Salmoninae <i>Oncorhynchus</i> *	Salmoninae <i>Salmo, Salvelinus</i>	Coregoninae	
Hatching time (d).....	81	121	136	16
Egg size (mm).....	6.8	4.5	2.2	2.4
Number of eggs.....	3900	4200	47000	10000
Age at maturity (yr).....	3.8	5.3	5.4	3.5
Length at maturity (yr).....	60	37	31	34
Maximum broods/life.....	1	11	11	10

*Excludes freshwater form of *O. nerka*.

(Stearns 1983, 1984). We did not find this to be the case in salmonids, thus substantiating Stearns' (1984) assertion that the strength of the pattern of r- and K-selection is dependent upon the taxonomic level examined. The first principal component ranked forms from large, early-maturing, semelparous fish bearing few, large, rapidly developing eggs to the opposite suite of characters in small, iteroparous fish. Small body size, early maturity and increased fecundity are expected to covary with one another (MacArthur and Wilson 1967, Pianka 1970, Stearns 1976, Horn 1978). Salmonids are more flexible in life history adaptations than the models used to predict patterns of covariation.

The second component (degree of anadromy) seems to be growth related. By adopting an anadromous life style, an individual increases its chances of attaining a large size, subsequently producing more eggs (Bagenal 1967). There were no significant differences in brood size between anadromous and freshwater forms. This may reflect the varying degrees of anadromy among *Salmo* spp. and *Salvelinus* spp.

The third component revealed yet another unique strategy (delayed reproduction with slowly developing eggs) which may be related to seasonality associated with the spawning and hatching of eggs. Time to hatching is negatively correlated with ambient water temperature (Scott and Crossman 1973, Johnson 1980). Many salmonids (e.g. *S. salar*, *S. fontinalis*) spawn during the autumn yet their eggs do not hatch until late in the following spring when conditions are favourable for growth and recruitment.

The life history clusters of salmonids are not dissimilar, at the generic level, to the phylogeny proposed for this family by contemporary systematists (Norden 1961, Behnke 1972, Scott and Crossman 1973, Nelson 1976). Wootton (1984) found similar clusters based on the reproductive traits of 162 Canadian freshwater fishes. The close association of salmonid life histories to within-family phylogeny is consistent with the contention that life histories themselves are adaptive and are molded by microevolutionary forces. The morphological similarity among salmonids suggests that body design is less likely to constrain life history evolution. Through evolutionary time, suites of co-adapted traits would diverge along different phylogenetic lines.

Size alone does not effect patterns of covariation in the life history traits of salmonids. This may reflect the relatively small size range within the family. Size probably constrains life history tactics in the class Osteichthyes where lengths at maturity may range from 18 mm in a goby (e.g. *Trimma taylori*) to 1630 mm in a sturgeon (e.g. *Acipenser transmontanus*) (Scott and Crossman 1973).

In contrast to the effects of body size, our analyses imply that life style (anadromy in this case) has great influence on covariation in life history traits. Anadromy may effect patterns of covariation in life histories or could itself have arisen as an adaptive strategy in re-

sponse to age-specific survival (Bell 1980). Some salmonid biologists have argued that anadromy was imposed upon primitive salmonid-like fish because of large-scale environmental disruptions which deteriorated freshwater fluvial habitats (Tchernavin 1939, Neave 1958, Hoar 1976). In this case, the traits one observes which are related to anadromy are probably caused by anadromy. But the anadromous life style is a mixed blessing. The benefits include an increased growth rate at sea relative to that in freshwater which results in a larger size at maturity (Northcote 1978). Among the costs is an exhausting migration up fast-flowing streams and rivers to suitable spawning sites. The degree of iteroparity in anadromous salmonids may be a compromise between these alternatives in terms of adult and juvenile survival (Schaffer and Elson 1975, Schaffer 1979). This view is bolstered by our and Bell's (1980) observation that egg size increases with the degree of anadromy. If juvenile survival depends upon egg size (Blaxter and Hempel 1963, Bagenal 1969), the selective advantage of anadromous forms would be enhanced. But setting anadromy and life histories as cause and effect alternatives may be misleading. Behaviour and life history traits should co-evolve to form optimal adaptive strategies which convey selective advantage in specific environmental contexts.

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