COMPARATIVE PHYLOGENETIC ANALYSIS OF THE EVOLUTION OF SEMELPARITY AND LIFE HISTORY IN SALMONID FISHES

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Abstract.—The selective pressures involved in the evolution of semelparity and its associated life-history traits are largely unknown. We used species-level analyses, independent contrasts, and reconstruction of ancestral states to study the evolution of body length, fecundity, egg weight, gonadosomatic index, and parity (semelparity vs. degree of iteroparity) in females of 12 species of salmonid fishes. According to both species-level analysis and independent contrasts analysis, body length was positively correlated with fecundity, egg weight, and gonadosomatic index, and semelparous species exhibited a significantly steeper slope for the regression of egg weight on body length than did iteroparous species. Percent repeat breeding (degree of iteroparity) was negatively correlated with gonadosomatic index using independent contrasts analysis. Semelparous species had significantly larger eggs by species-level analysis, and the egg weight contrast for the branch on which semelparity was inferred to have originated was significantly larger than the other egg weight contrasts, corresponding to a remarkable increase in egg weight. Reconstruction of ancestral states showed that egg weight and body length apparently increased with the origin of semelparity, but fecundity and gonadosomatic index remained more or less constant or decreased. Thus, the strong evolutionary linkages between body size, fecundity, and gonadosomatic index were broken during the transition from iteroparity to semelparity. These findings suggest that long-distance migrations, which increase adult mortality between breeding episodes, may have been necessary for the origin of semelparity in Pacific salmon, but that increased egg weight, leading to increased juvenile survivorship, was crucial in driving the transition. Our analyses support the life-history hypotheses that a lower degree of repeat breeding is linked to higher reproductive investment per breeding episode, and that semelparity evolves under a combination of relatively high juvenile survivorship and relatively low adult survivorship.

Key words.—Life history, phylogenetics, salmonids, semelparity.

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The semelparous state seems to be associated with reproductive recklessness on the part of the parent, and this strategy has probably evolved in association with adaptations that ensure a greater chance of survival of offspring. (Calow 1978)

Life-history theory seeks to explain the evolution of various traits that are often closely related to fitness, such as body size, age at first reproduction, number of breeding episodes, fecundity, and life span (Roff 1992; Stearns 1992). One of the most important developments in the genesis of this field was Cole's (1954) result that perennial reproduction was paradoxical, because ''for an annual species, the absolute gain in intrinsic population growth that can be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one more individual to the average litter size.'' Charnov and Schaffer (1973) resolved the apparent paradox by showing that optimal life history is a function of both fecundity and the relative survival rates of juveniles and adults. Thus, relatively low adult survival and high juvenile survival are expected to select for annual reproduction (or semelparity), and the reverse conditions should select for the perennial habit (or iteroparity; see also Stearns 1976; Bell 1980; Real and Ellner 1992; Bulmer 1994; Charlesworth 1994; Klinkhammer et al. 1997; Ranta et al. 2000a,b).

Empirical studies of semelparity and iteroparity have used comparisons between morphs or sexes within populations (Grosberg 1988; Oakwood et al. 2001), comparisons between populations within species (Leggett and Carscadden 1978; Sano and Morishima 1982; Lobon-Cervia et al. 1991), com-

parisons between related species (Calow and Woolhead 1977; Pitelka 1977; Calow 1978; Paine 1990; Young 1990; Miya and Nemoto 1991; Silverton 1996; Kaitala and Mappes 1997; Keeley and Bond 1999), and broad comparisons across taxa (Stearns 1976; Bell 1980; Dickhoff 1989; Young 1990; Roff 1992; Tallamy and Brown 1999). These studies have provided considerable support for the role of differences in mortality rates, especially adult mortality, in the evolution of reproductive effort and parity (see also Bertschy and Fox 1999). However, the evolution of parity mode and its associated life-history traits have yet to be analyzed in an explicitly phylogenetic context (as suggested by McPeek 1995; see also Harvey and Keymer 1991), so the selective pressures involved in the transitions between iteroparity and semelparity remain largely unknown.

Salmonid fishes (i.e., salmon, trout and char) are useful for analysis of the evolution of semelparity and iteroparity because: (1) they exhibit interspecific variation in parity, with semelparity in Pacific salmon but varying degrees of iteroparity in Atlantic salmon, trout, and char (Groot and Margolis 1991; Fleming 1998); (2) most species exhibit pronounced intraspecific variation in some phenotypic traits, such as migration distance, parity, and body size, that are related to life history (e.g., Rounesfell 1957, 1958; McDowall 1988; Elliott 1994); (3) their life cycles, behavior, and morphology have been generally well characterized (e.g., Groot and Margolis 1991; Fleming 1998); (4) reasonably robust phylogenies for salmonids have recently become available (Domanico and Phillips 1995; Domanico et al. 1997; Phillips and Oakley 1997; Oakley and Phillips 1999), allowing the analysis of life-history traits in their phylogenetic context; and (5) sal-

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monids are economically important and their life-history traits may be substantially impacted by ongoing human activities such as fishing and hatcheries (e.g., Ricker 1981; Fleming and Gross 1989, 1994).

In this study we present a comparative analysis of the evolution of life-history traits in salmonids, with emphasis on the selective pressures associated with the origin of semelparity. First, we use species-level analyses and independent contrasts analysis to test for evolutionary associations between body length, fecundity, egg weight, investment in gonad relative to soma, and parity (percent repeat breeding). Second, we reconstruct ancestral states for body length, fecundity, egg weight, and gonadosomatic index, to infer evolutionary trajectories in these traits. Finally, based on the results of these analyses, we propose a hypothesis for the transition from iteroparity to semelparity in salmonids, suggest ways that it can be tested further, and discuss the implications of our findings for life-history theory and salmonid management.

MATERIALS AND METHODS

Salmonid Fishes

Many salmonid species exhibit both anadromous and freshwater-resident forms, some species live only in fresh water (e.g., lake char and lenok), and in some species all females are anadromous but some males exhibit freshwater-resident forms (Dickhoff 1989; Groot and Margolis 1991). Anadromous and freshwater-resident forms may freely interbreed and produce fully viable progeny, and one individual may even exhibit both patterns within its lifetime (e.g., in brown trout; Elliott 1994). Such variation may be primarily facultative (Jonsson and Jonsson 1993; Fleming 1996; McDowall 1997; Thorpe 1998), sometimes with a strong component of latitudinal variation (e.g., Elliott 1994; McDowall 1997), or the two forms may exhibit genetic differences and considerable reproductive isolation (e.g., between sockeye and kokanee; Taylor et al. 1996). Anadromous species also display tremendous variation within and between species in the amount of time that they spend in fresh water and salt water, which is a function of such factors as latitude, water temperature, and growth rates (e.g., Healey 1986; Randall et al. 1987; Willson 1997).

A semelparous life cycle is well documented for all females of coho, chinook, sockeye, pink, and chum, although freshwater resident males of coho, chinook, masu, and sockeye may sometimes breed more than once, at least under hatchery conditions (Dickhoff 1989; Unwin et al. 1999; Altukhov et al. 2000). Iteroparity is the norm in all other species (Stearley 1992; Willson 1997). The two main life cycles can be considered as discrete, because females of semelparous species exhibit genetically programmed, irreversible degeneration subsequent to breeding, whereas females of iteroparous species may breed more than once, even if most are unsuccessful in doing so (Rounesfell 1958; Weatherley and Gill 1995; Fleming 1998). However, iteroparity can also be considered as exhibiting continuous variation, because the degree of multiple breeding episodes varies between and within species (e.g., Fleming 1998).

Current variation within and among anadromous and fresh-

water forms apparently evolved after the latest round of glaciations for most extant populations (see Taylor et al. 1996; McCusker et al. 2000; Bernatchez 2001; Brunner et al. 2001; Taylor et al. 2001). By contrast, the divergences among *Salmo*, *Salvelinus*, and *Oncorhynchus* probably occurred on the order of 20 million years ago, and by 6 million years ago forms similar to extant sockeye, chum, and pink appear in the fossil record (Stearley 1992; McPhail 1997; Altukhov et al. 2000).

Phylogeny

Given our focus on the evolution of semelparity and associated life-history traits, we chose to include in our study five species of semelparous Pacific salmon (chinook, coho, sockeye, pink, and chum) and enough of their iteroparous relatives to achieve maximal statistical power while minimizing phylogenetic uncertainty. These related taxa included Pacific trout (rainbow and cutthroat), several char (lake, arctic, and Dolly Varden), and two species of *Salmo* (Atlantic salmon and brown trout). Masu salmon and brook char were excluded due to a relatively high degree of uncertainty about their phylogenetic positions. The phylogeny used here (Fig. 1) was derived from the analyses of the genes for growth hormone 1 and 2 Oakley and Phillips (1999), which exhibit very good bootstrap support for most nodes, and the analysis of ITS (Phillips and Oakley 1997) data for char (*Salvelinus*), which allows incorporation of Dolly Varden char as sister-taxon to arctic char (see also Brunner et al. 2001). Salmonid phylogeny has been a matter of considerable dispute for some time; nevertheless, this phylogeny represents a generally well-supported hypothesis of relationships, which is subject to revision as additional data become available.

By the phylogeny used here, we infer that semelparity evolved once, in the common ancestor of the five species of Pacific salmon (Fig. 1), and we assume that this single origin is the correct inference (see also Stearley 1992).

Datasets

The character data used here were taken almost exclusively from Hutchings and Morris (1985) for body length at maturity and fecundity and from Fleming (1998) for female percent repeat breeding, individual egg weight, and gonadosomatic index, which is measured as gonad weight relative to body weight (Roff 1992). Percent repeat breeding was arcsin transformed prior to all analyses. Egg weight rather than egg diameter was used because weight is a better indicator of egg size (Fleming and Ng 1987). Anadromous cutthroat trout gonadosomatic index, which was absent from Fleming's (1998) dataset, was estimated as 0.14 using data on egg weight, egg number, and body weight in Scott and Crossman (1973) and Fleming (1998). Because this estimate was approximate relative to all of the others in the dataset, we also conducted the analyses using values that ranged from 0.13 to 0.17 (a range of realistic possible values), and the main results were unchanged with regard to statistical significance. The value for fecundity of freshwater-resident *Salmo trutta* was corrected from 10,588 (a typographical error) to 1058 (J. A. Hutchings, pers. comm.). Our use of mean values from one or more studies (Fleming 1998) or species-typical values
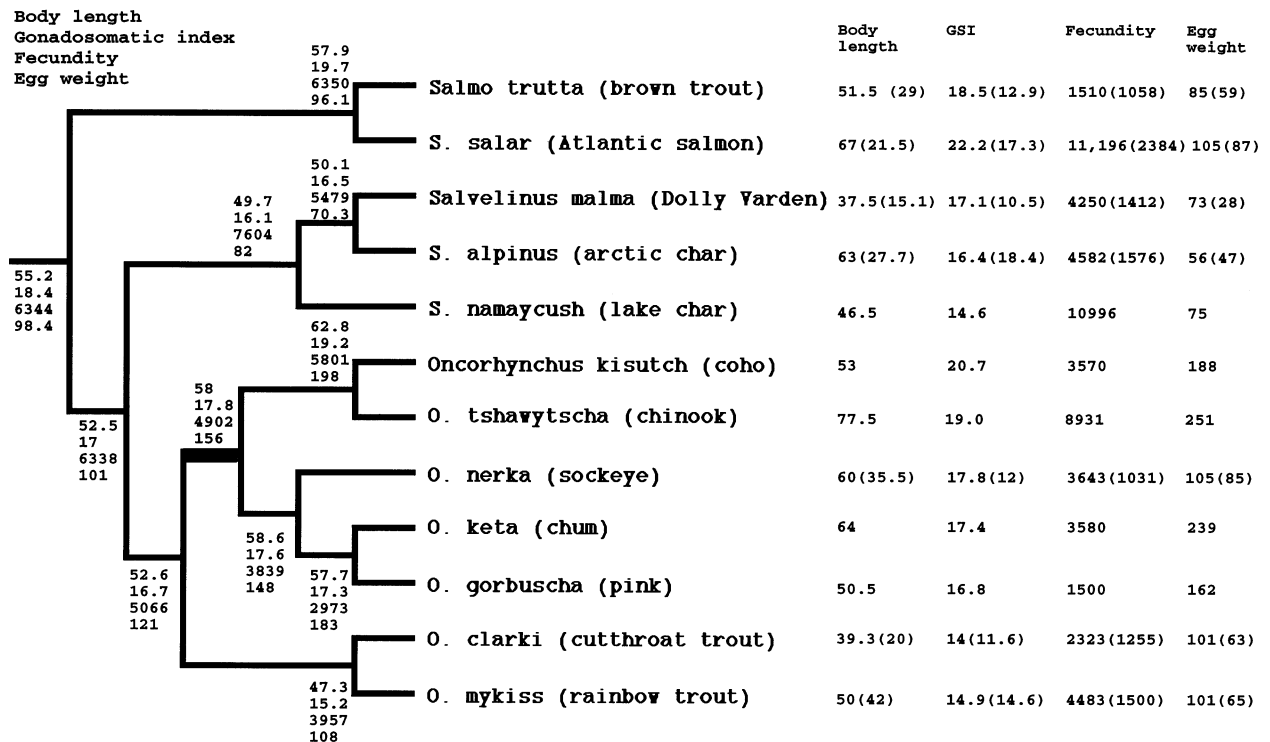
Body length
Gonadosomatic index
Fecundity
Egg weight

	Body length	GSI	Fecundity	Egg weight
Salmo trutta (brown trout)	51.5 (29)	18.5(12.9)	1510(1058)	85(59)
S. salar (Atlantic salmon)	67(21.5)	22.2(17.3)	11,196(2384)	105(87)
Salvelinus malma (Dolly Varden)	37.5(15.1)	17.1(10.5)	4250(1412)	73(28)
S. alpinus (arctic char)	63(27.7)	16.4(18.4)	4582(1576)	56(47)
S. namaycush (lake char)	46.5	14.6	10996	75
Oncorhynchus kisutch (coho)	53	20.7	3570	188
O. tshawytscha (chinook)	77.5	19.0	8931	251
O. nerka (sockeye)	60(35.5)	17.8(12)	3643(1031)	105(85)
O. keta (chum)	64	17.4	3580	239
O. gorbuscha (pink)	50.5	16.8	1500	162
O. clarki (cutthroat trout)	39.3(20)	14(11.6)	2323(1255)	101(63)
O. mykiss (rainbow trout)	50(42)	14.9(14.6)	4483(1500)	101(65)

Ancestral state values shown on the tree:

57.9 / 19.7 / 6350 / 96.1

50.1 / 16.5 / 5479 / 70.3

49.7 / 16.1 / 7604 / 82

55.2 / 18.4 / 6344 / 98.4

62.8 / 19.2 / 5801 / 198

58 / 17.8 / 4902 / 156

52.5 / 17 / 6338 / 101

58.6 / 17.6 / 3839 / 148

57.7 / 17.3 / 2973 / 183

52.6 / 16.7 / 5066 / 121

47.3 / 15.2 / 3957 / 108

FIG. 1. Phylogeny of salmonid fishes used here, with the origin of semelparity shown as a thick branch. Values for traits of anadromous forms are shown at the right (with values for freshwater-resident forms in parentheses), and inferred ancestral states are shown above and below the branches. Standard errors for ancestral states ranged from 11.5 to 18.1 (body length), 3.5 to 5.4 (gonadosomatic index), 1981 to 3123 (fecundity), and 26.8 to 42.3 (egg weight).

(Hutchings and Morris 1985) neglects the considerable intraspecific variation in these traits that is present within and among populations of most of the species included. The use of mean or typical values is not expected to bias the results of our analyses because levels of among-species variation in these traits are also substantial. The values used for each species and form in this study were not all collected from the same population, as ideally they would be; this heterogeneity will add noise to the results but likewise should not systematically bias the results. We encourage the future collection of sufficient life-history and intraspecific phylogeny data on salmonids to allow comparative tests that span the within- to between-species boundary (Garland et al. 1992), which would alleviate current data limitations and allow more robust partitioning of the causes of microevolutionary versus macroevolutionary changes in life-history traits.

Our full dataset included data from anadromous forms (12 species) and data from freshwater-resident forms for the seven of these 12 species that exhibit such forms (see Fleming 1998; Fig. 1). For the species-level analyses, all of these forms were included, for a total of 19 datapoints, which we refer to as the full dataset.

Analytic Methods

We used our character data and phylogeny to perform three main types of analyses: species-level associations, independent contrasts (Felsenstein 1985), and inference of ancestral states (Martins and Hansen 1997; Schluter et al. 1997; Garland et al. 1999; Garland and Ives 2000). The former two types of analysis primarily address the question of the extent to which pairs of characters are statistically associated with one another, in extant species only (species-level analysis) or throughout the history of the clade (independent contrasts).

Statistical validity of results from species-level and contrasts analyses requires that certain assumptions be met (Martins 2000). Species-level analyses, in which the values for extant taxa are treated as independent datapoints, can artificially inflate degrees of freedom because related species are statistically independent from one another only under two conditions: (1) a star phylogeny (with all lineages emanating simultaneously from a single point); or (2) a model whereby species do not undergo Brownian motion, but instead adaptively radiate via the filling of empty niches (Price 1997; Harvey and Rambaut 2000). Moreover, species-level analyses can also yield misleading results when unobserved, confounding third variables are hierarchically distributed on a phylogeny, such that associations between observed traits are mistakenly inferred (Ridley 1989). If these limitations do not obviate the results, species-level analyses can usefully depict current patterns of association between traits, whereas independent contrasts analyses yield insight into both historical patterns of diversification and associations among extant lineages (Ricklefs and Stark 1996).

For independent contrasts, the phylogeny and branch lengths (in units of expected character change) are assumed to be correct or subject to a small to moderate degree of error, and characters are assumed to evolve under (possibly correlated) Brownian motion (Felsenstein 1985; Martins 2000).

Independent contrasts are computed as branch-length standardized differences in trait values between pairs of sister-species (at the tips of the tree) or sister-lineages (for ancestral taxa). As such, they represent the evolved differences between pairs of lineages, which are statistically independent from one another under the Brownian model (Felsenstein 1985). Statistical significance of associations between traits (i.e., correlated evolutionary change) can be tested via regression of contrasts for one trait versus contrasts for another, with the regression forced through the origin (Garland et al. 1992). Adequate standardization of the contrasts (which is equivalent to equal weighting of the datapoints) is tested via regression of the absolute magnitude of the contrasts versus their standard deviations (branch lengths), with an absence of relationship indicating that adequate standardization is achieved. Inadequate standardization can be rectified via transformation of traits values, branch lengths, or both (Garland et al. 1992). Because our phylogeny was assembled using topologies inferred from two genes, we set all branch lengths equal to one. For our data, all contrasts were adequately standardized using the original branch lengths, except those for body length in the full dataset (the anadromous plus freshwater-resident dataset); these were adequately standardized by extending each terminal-tip branch to a length of five.

We used both independent contrasts and species-level analysis because the degree to which the assumptions of each are satisfied was difficult to ascertain and because any divergence in results between methods may indicate changes in the nature of selective pressures during diversification (Ricklefs and Stark 1996). We note, however, that results from species-level analyses are expected to be less conservative than results from independent contrasts.

Our independent contrasts analyses involved testing for evolutionary associations between pairs of traits, comparing sets of contrasts, conducting ANCOVAs to test for differences between semelparous and iteroparous forms, and using McPeek's (1995) single-branch isolation method to test for accelerated rates of change on the branch along which the origin of semelparity was inferred. For contrasts analyses, the data for anadromous and freshwater-resident forms were treated in three different ways.

First, we used the full dataset, with anadromous and freshwater-resident forms considered as sister-lineages in the phylogeny. This dataset allows analysis of the microevolutionary and ecophenotypic (intraspecific) changes between these pairs of forms, separately or in conjunction with the macroevolutionary (interspecific) changes at more-basal nodes, and it thus allows comparisons between macroevolutionary and microevolutionary patterns (Garland et al. 1992). One potential shortcoming of this full dataset is that the ancestors of species exhibiting both freshwater-resident and anadromous forms may have been similarly polymorphic in life history (McDowall 1988, 1997), and averaging across these two forms in the inference of ancestral node values may be unrealistic.

Second, to address these potential drawbacks, we also analyzed a dataset that included only the anadromous forms plus lake char (which only inhabits fresh water). This dataset represents only macroevolutionary processes.

Third, we analyzed a dataset that included these macro-

evolutionary contrasts plus the seven contrasts from the comparisons of anadromous and freshwater-resident pairs of forms, with these two sets of contrasts computed separately and combined for the analyses of evolutionary associations between pairs of traits. This third dataset avoids some of the potential difficulties of the first dataset, but it uses the species values of seven of the anadromous forms (the ones with freshwater-resident counterparts) in the computation of two sets of contrasts, which could also affect the outcomes.

The results from independent-contrasts analyses were qualitatively similar for almost all of the analyses using these three different datasets, with the main quantitative differences coming from reduced statistical power in the purely macroevolutionary and purely microevolutionary datasets. Thus, for independent contrasts, we focus mainly on the full dataset, and present results from analyses of the other two datasets where useful and appropriate.

For the inference of ancestral states, we present results only from the macroevolutionary data set (comprising the 12 anadromous forms and the one obligately freshwater species), but the results from analyses using the full dataset were very similar.

We conducted independent contrasts using McPeek's program, CONTRAST (provided by the author), and ancestral states were reconstructed in the software COMPARE (Martins 2001) using the method of Martins and Hansen (1997), which provides standard errors for estimated values at the nodes.

<center>RESULTS</center>

<center>*Species-Level Analyses*</center>

Correlations between traits

Body length, fecundity, egg weight, and gonadosomatic index were all positively correlated with one another, significantly so for all pairwise correlations except fecundity with egg weight (Fig. 2A). By contrast, percent repeat breeding was negatively correlated with length and egg weight, but uncorrelated with the other variables. The substantial positive correlations between length, fecundity, egg weight, and gonadosomatic index suggested that each of these variables reflects variation in general size, so principal components (PCs) analysis was conducted on the correlation matrix of these four traits to reduce their dimensionality and evaluate the biological significance of the components. PC1 exhibited consistent, positive loadings on all four traits and accounted for a large proportion of the variance; as such, it reflects a general size factor (Table 1). PC2, which is expected to be largely independent of the effects of general size, apparently reflects an interspecific trade-off between fecundity and egg weight; it shows strong but oppositely signed loadings for egg weight and fecundity. Finally, PC3 loads primarily on gonadosomatic index, and as such it appears to reflect variation in this trait that is independent of PC1 and PC2.

Differences between semelparous and iteroparous forms

Semelparous forms were longer, had heavier eggs, and showed higher values for PC1 score (larger general size) and
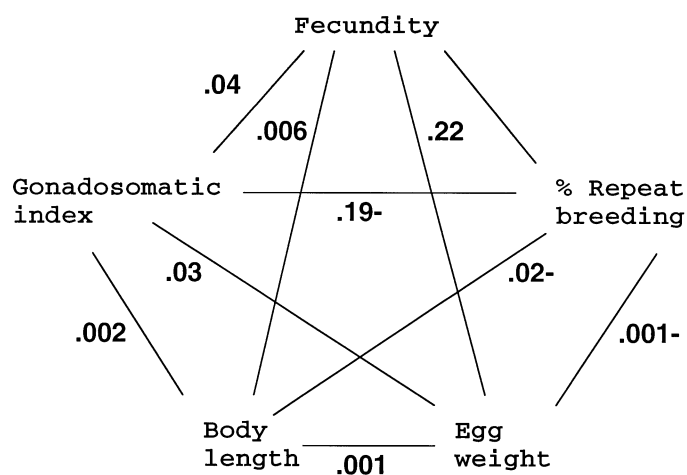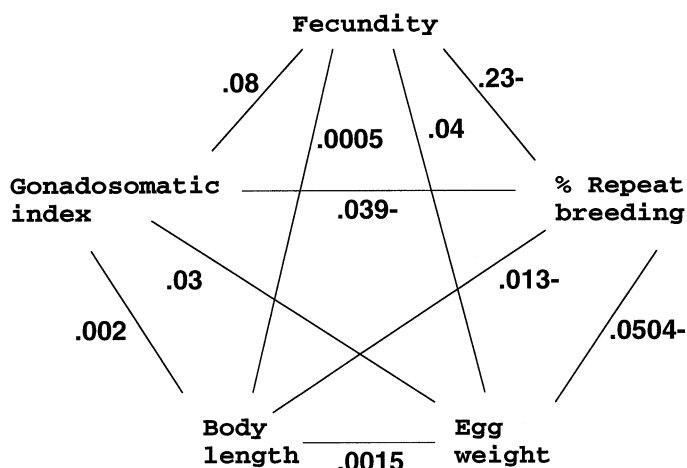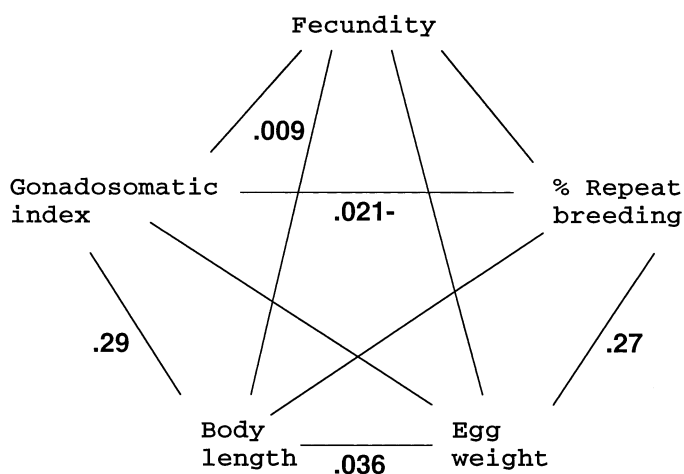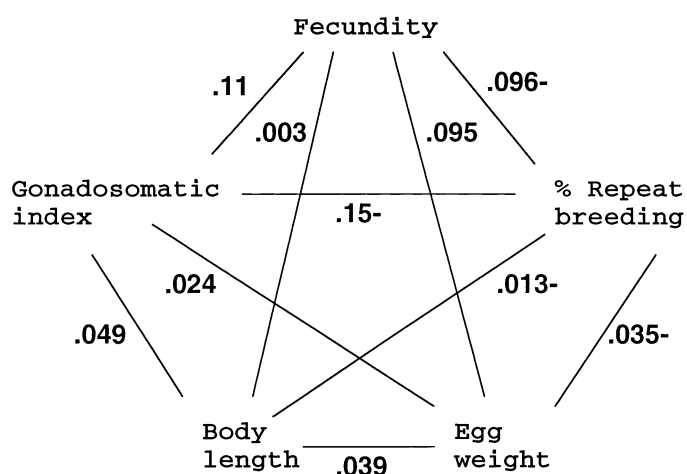
FIG. 2. Results from analyses of correlations between traits. *P*-values (below 0.30) are shown, and a hyphen after the value designates a negative correlation. (A) species values (raw data), full dataset; (B) independent contrasts (full dataset); (C) independent contrasts (anadromous-forms dataset); (D) independent contrasts (microevolutionary/ecophenotypic dataset, using only tips with anadromous-freshwater resident pairs).

lower values for PC2 score (higher egg weight relative to fecundity) than iteroparous forms. However, the two parity forms did not differ in gonadosomatic index, fecundity, or PC3 score (Table 2).

Covariance analyses

The slope of the regression of egg weight on length was steeper for the semelparous forms than for the iteroparous forms ($F = 10.1$; df = 1,15; $P = 0.014$ for the interaction term; Fig. 3A). By contrast, there was no difference in slope ($F = 0.21$; df = 1,15; $P = 0.65$) or intercept ($F = 0.92$; df = 1,15; $P = 0.35$) between semelparous and iteroparous forms for the regressions of fecundity on length (Fig. 3B), or for the regressions of gonadosomatic index on length (slope $F = 0.05$; df = 1, 15; $P = 0.83$; intercept $F = 0.18$; df = 1,15; $P = 0.67$).

Independent Contrasts Analyses

Evolutionary correlations between traits

Across all forms and species, changes in gonadosomatic index were negatively correlated with changes in percent repeat breeding; changes in body length were positively cor-

TABLE 1. Results of principal components analysis on the correlation matrix of four morphological traits, using the full dataset ($N = 19$). Eigenvectors and loadings were very similar for the dataset that included only anadromous forms ($N = 12$).

Character	PC1 (65.7%)	PC2 (17.7%)	PC3 (11.4%)
Body length	0.569	−0.048	0.161
Egg weight	0.474	−0.653	0.384
Fecundity	0.444	0.756	0.342
Gonadosomatic index	0.505	0.001	−0.843

TABLE 2. Comparisons between semelparous and iteroparous salmonids, using species values as datapoints (mean, SE). Table 1 shows principal component (PC) eigenvectors and loadings. All results were qualitatively the same with regard to significance values for the dataset that included only anadromous forms ($N = 7$ interoparous and $N = 5$ semelparous), except that the body length difference was nonsignificant ($t = 1.6$, df = 10, $P = 0.14$) as was the PC1 difference ($t = 1.94$, df = 10, $P = 0.081$).

Character	Iteroparous $N = 13$		Semelparous $N = 6$		t (df = 17)
Body length	39.24	(4.34)	56.75	(6.39)	2.3*
Egg weight	72.70	(11.5)	171.70	(17.0)	4.8***
Fecundity	3732.00	(918)	3709.00	(1352)	0.0
Gonadosomatic index	15.62	(0.86)	17.28	(1.26)	1.1
PC1	−0.504	(0.41)	1.09	(0.60)	2.2*
PC2	0.34	(0.19)	0.75	(0.28)	3.3**
PC3	−0.10	(0.19)	0.22	(0.28)	0.96

related with changes in egg weight, fecundity, and gonadosomatic index and negatively correlated with changes in percent repeat breeding (Fig. 2B). In the purely macroevolutionary (anadromous) dataset, changes in gonadosomatic index remained negatively correlated with changes in percent repeat breeding, and changes in body length were positively correlated with changes in egg weight and fecundity (Fig. 2C). In this analysis, changes in body length were not significantly correlated with changes in gonadosomatic index or percent repeat breeding.

The contrasts that represented the differences between the seven anadromous and freshwater-resident pairs of forms (i.e., the six microevolutionary and ecophenotypic contrasts) showed similar patterns of associations between traits to those in the full dataset and the macroevolutionary dataset, albeit with reduced statistical power (Fig. 2D).

Covariance analyses

As in the species-level analyses, the slope of the regression of egg weight contrasts on body length contrasts was steeper for the semelparous forms than for the iteroparous forms (F = 5.8; df = 1,18; $P = 0.029$ for the interaction term, full dataset). By contrast, there was no difference in slope ($F = 0.9$; df = 1,15; $P = 0.36$) or intercept ($F = 0.49$; df = 1,15; $P = 0.49$) between semelparous and iteroparous forms for the regressions of fecundity contrasts on length contrasts. Similarly, gonadosomatic index did not exhibit a slope difference ($F = 0.13$; df = 1,15; $P = 0.91$) or an intercept difference ($F = 0.58$; df = 1,15; $P = 0.46$) between forms.

McPeek's test

The magnitude of the egg weight contrast along the single branch on which semelparity was inferred to have originated was significantly greater (65.3) than the set of all other contrasts (mean = 22.3, SD = 18.4, $t = 2.27$, df = 16, $P = 0.037$, full dataset), which indicates a strikingly large increase in egg weight along this branch. This difference in contrasts was comparable in magnitude for the purely macroevolutionary dataset (56.1 vs. 25.7), but did not reach statistical significance ($t = 1.3$, df = 9, $P = 0.23$).

One notable result from these analyses was that the contrasts corresponding to changes in egg weight within semelparous lineages appeared to be substantially greater than those within iteroparous lineages. Indeed, mean contrast magnitude within semelparous lineages (mean = 42.8, SD = 18, $N = 5$) was over twice as great as contrast magnitude within iteroparous lineages (mean = 16.2, SD = 11.8, $t = 3.64$, df = 15, $P = 0.0024$, contrast at origin of semelparity excluded, full dataset). The difference in contrasts was even more pronounced using the purely macroevolutionary dataset (semelparous contrasts: mean = 50.7, SD = 8.2, $N = 4$; iteroparous contrasts: mean = 12.2, SD = 13.0, $N = 6$; $t = 5.2$, df = 8, $P = 0.0008$; contrast at origin of semelparity excluded).

For none of the other variables did the difference in contrast magnitudes between the branch at the origin of semelparity and the other branches approach statistical significance, nor were there any significant or near-significant difference in contrast magnitudes for these variables between semelparous and iteroparous lineages.
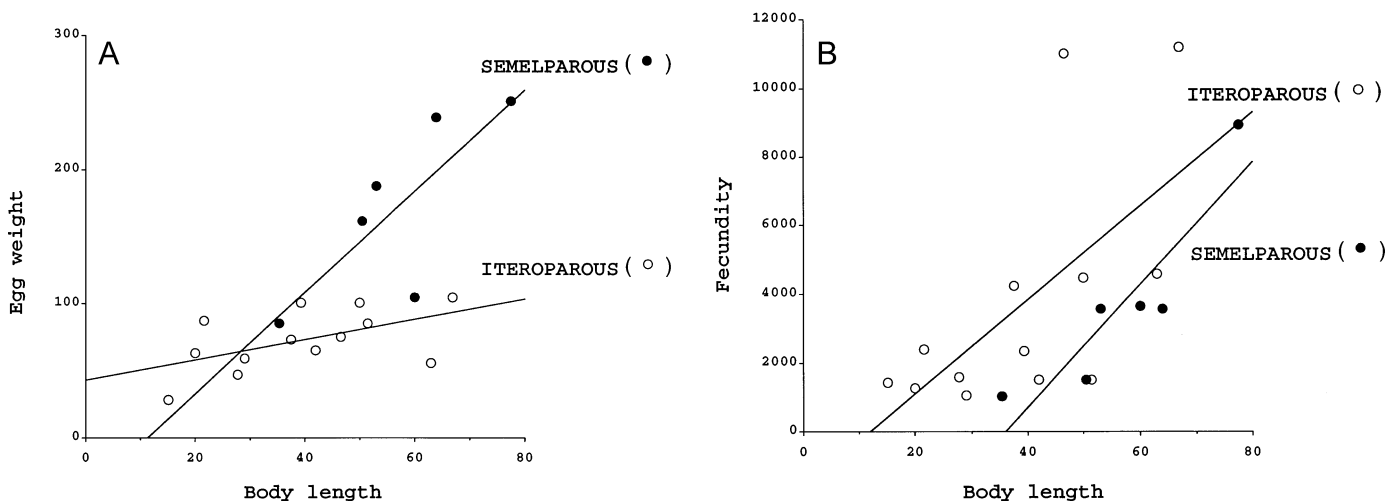

FIG. 3. Regressions of (A) egg weight and (B) fecundity on body length, for semelparous and iteroparous forms.

Inference of Ancestral States

Using the method of Martins and Hansen (1997), there were substantial increases in both body length and egg weight at the origin of semelparity (Fig. 1), but fecundity decreased somewhat and gonadosomatic index increased only a small amount along this branch. However, as for virtually all other studies that have derived standard error estimates for inferred ancestral states of continuous traits, the standard errors are sufficiently large that none of the inferred changes can be ascribed statistical significance. As such, these inferred values should be taken as suggestive and ancillary with respect to the other analyses described above.

DISCUSSION

The most important novel finding of our study is that the origin of semelparity in salmonids was associated with a substantial increase in egg weight. This finding is supported by the mean difference in egg weight between semelparous and iteroparous forms (see also Hutchings and Morris 1985; Fleming 1998), McPeek's tests of evolutionary rates, and the reconstruction of ancestral states. Moreover, the evolutionary significance of egg weight for the evolution of parity mode is also highlighted by the steeper slopes of the regressions of egg weight on length in semelparous forms and the accelerated evolutionary rates of egg weight change within semelparous lineages.

Understanding these results, with regard to the selective pressures involved in the transition from iteroparity to semelparity, requires putting the evolution of salmonid egg weight and associated traits into their life-historical context.

Egg Size and Semelparity

Substantial effects of the female on egg size are three-fold. First, as found here and in many other studies, larger female salmonids tend to produce larger eggs, within and between populations and among species (Beacham and Murray 1985; Healey 1986; Quinn et al. l995; Fleming 1996; Heath and Blouw 1998; Hendry et al. 2001). Because egg weight is a property of offspring determined by mothers, this correlation apparently represents a maternal effect (Heath and Blouw 1998; Einum and Fleming 2000a,b), which in this case appears to have strong macroevolutionary life-historical effects. Second, egg weight and egg number trade off with one another, within females and among and within populations, especially after adjusting for body size (Fleming and Gross 1990; Quinn et al. 1995; Fleming 1996; Jonsson and Jonsson 1999; Einum and Fleming 2000b; Kinnison et al. 2001). Thus, selection on egg number may cause correlated changes in egg size or vice versa (e.g., Fleming and Gross 1990; Hendry et al. 2001). This trade-off is also supported at the interspecific level by the bipolar loadings of PC2 for egg weight and fecundity in our species-level analysis. Third, increased maternal care is predicted to favor the evolution of larger eggs because care reduces mortality during this stage (Sargent et al. 1987; Clutton-Brock 1991).

Notable effects of prehatching environment on egg size in salmonids include gravel size and temperature. Thus, larger gravel size tends to select for larger eggs, since eggs are better oxygenated under these conditions; by contrast, smaller eggs, which have a smaller surface area to volume ratio for gas exchange, tend to have higher survival than larger eggs in smaller gravels (Beacham and Murray 1985; Fleming and Gross 1989, 1990; Quinn et al. 1995; Hendry et al. 2001). Because larger females within Pacific salmon species are generally able to secure better nests with larger gravel (Healey 1986; Hendry et al. 2001), this effect can reinforce or favor a positive association between female size and egg size (Quinn et al. 1995). The other main prehatching effect on egg size is temperature: among populations, higher temperature tend to select for larger eggs, due to lower conversion efficiency of yolk to tissue in warmer weather (Beacham and Murray 1985; Fleming and Gross 1990; Jonsson and Jonsson 1999).

Post-hatching environment selects on egg size mainly via the close relationship between egg size and the size of individuals at later stages. In virtually all species of salmonids examined, larger eggs tend to yield larger fry and juveniles, which exhibit higher growth and survivorship due to mitigated effects of competition, predation, or both (Fowler 1972; Hutchings 1991; Elliott 1994; Heath and Blouw 1998; Einum and Fleming 1999, 2000a; Hendry et al. 2001). This relationship may be especially important because, on average, the juveniles of semelparous salmonids migrate to sea considerably earlier in life than do the juveniles of iteroparous forms (i.e., a substantial proportion go to sea at age 0 or 1; Randall et al. 1987; Pearcy 1992), and juvenile mortality tends to be especially high during the transition from fresh water to the sea (Peterman 1987; Pearcy 1992; Hansen and Quinn 1998). However, despite clear advantages to juveniles of larger eggs, females are under selection to maximize their fitness under the size-number trade-off. In many iteroparous salmonids, breeding females have been shown to produce relatively more, smaller eggs under relatively good juvenile-feeding conditions, whereas production of fewer, larger eggs is favored under worse juvenile-feeding conditions (Thorpe et al. 1984; Hutchings 1991, 1997; Jonsson et al. 1996; Einum and Fleming 1999; Einum et al. 2002).

What are the implications of these selective pressures for the origin of semelparity in Pacific salmon? First, as noted by Bell (1980) the association of larger eggs with higher juvenile survivorship is consistent with predictions from theory that semelparity can be favored by an increase in juvenile survivorship (Charnov and Schaffer 1973; Stearns 1976; see also Miller and Brannon 1981; Dodson 1997). This is an interesting result, but as described below, its importance can only be assessed in the context of other selective pressures involved in the origin of semelparity.

Second, only in the semelparous Pacific salmon has female nest-guarding been documented (van den Berghe and Gross 1986; Groot and Margolis 1991). As noted above, such guarding should favor increased egg size as it does in other fishes (Sargent et al. 1987). Thus, the origin of semelparity was also apparently associated in time with the evolution of increased maternal care, although the sequence of these two events is difficult to ascertain (Tallamy and Brown 1999).

Third, semelparous salmonids apparently breed under generally higher densities than those of iteroparous salmonids (Stearley 1992; Fleming 1996, 1998), which could select for

increased competition for food between juveniles and thus for larger eggs (Einum and Fleming 1999). Larger juvenile and egg size could also be favored in species with territorial juveniles (Hoar 1976; Pearcy 1992), and in populations and species with seaward migrations relatively early in juvenile life (Rounesfell 1958; Randall et al. 1987), in part because smolting success increases with size (e.g., Hoar 1976; Randall et al. 1987).

Finally, our data showing that semelparous salmonids are larger than iteroparous ones by species-level comparisons and the reconstruction of ancestral states showing a substantial inferred mean length increase suggest that body size also increased at the origin of semelparity. Because our results show that body size and egg size tend to be positively correlated among species and forms, larger body size itself may engender larger eggs via a positive genetic correlation or a stronger maternal effect (Heath and Blouw 1998).

Further evaluation of these hypotheses relating egg size to semelparity requires: (1) comparative estimates of juvenile and adult survivorship rates in Pacific salmon (Bradford 1995) versus anadromous rainbow and cutthroat trout; (2) analysis of the degree of density dependence in survivorship to adulthood (e.g., Peterman 1980, 1987), because density dependence can reduce the effects of juvenile survivorship variation on the evolution of parity (Bulmer 1994; Charlesworth 1994); (3) measurement of selection on egg size and number (e.g., Einum and Fleming 2000a,b); and (4) studies of juvenile survivorship in other fish taxa, such as eels, lamprey, and some gobies (Bell 1980; Dickhoff 1989), showing transitions between parity modes.

Body Size, Egg Size, and Parity

Our analyses suggest that body size increased, perhaps substantially, with the origin of semelparity. In salmonid fishes, larger size is associated with anadromy and feeding in the nutrient-rich temperate seas (Northcote 1978; Gross 1987; Gross et al. 1988; McDowall 1988; Jonsson and Jonsson 1993), and, for anadromous salmonids, larger fish tend to breed in larger rivers (Schaffer and Elson 1975; Thorpe and Mitchell 1981; Bernatchez and Dodson 1987; Beacham et al. 1988; Fleming and Gross 1989; Johnsson et al. 1991; L'Abee-Lund 1991; Taylor 1991; Stearley 1992; Blair et al. 1993; Roni and Quinn 1995; Fleming 1996).

One of the main effects of large size is that, all else being equal, larger fish swim more efficiently and faster in current (Brett and Glass 1973); the mass-specific energy costs of swimming decrease with body size, such that the trade-off between investment in gonads and migration distance decreases as body size increases (Schaffer and Elson 1975; Thorpe and Mitchell 1981; Roff 1988, 1991; L'Abee-Lund 1991; Weatherley and Gill 1995; Hogasen 1998). Despite this reduction in trade-off, larger Atlantic salmon, brown trout, and arctic char are more likely to breed only once than smaller ones (Dutil 1986; Jonsson et al. 1991, 1997; Jonsson and L'Abee-Lund 1993; Fleming 1998; see also Iguchi 1996), apparently in part because the energy loss of spawning is more difficult for larger fish to restore (Ware 1978; Dutil 1986). Taken together, these patterns provide strong links among large size, anadromy, and breeding once, and they are

consistent with the idea that the origin of semelparity in salmonids involved an increase in body size.

An important question is why semelparous species exhibit a steeper slope than iteroparous species for the regression of egg weight on body length (see also Heath and Blouw 1998), although slopes do not differ significantly for fecundity on body length (but see Rounesfell [1958, fig. 6], who did find a shallower slope in semelparous species for fecundity on weight, using a smaller dataset). The main differences in energy allocation trade-offs between semelparous and iteroparous forms are that semelparous forms apparently invest relatively more in secondary sexual characteristics (Fleming and Gross 1989, 1994; Fleming 1998), and iteroparous forms retain energy to facilitate postspawning survival (Dodson 1997). Larger fish species may have relatively more post-migration energy to allocate to reproduction (semelparous forms) or reproduction and survival (iteroparous forms); this is consistent with the positive correlations that we found between body length and gonadosomatic index. In larger semelparous forms, this increased energy may be differentially allocated to egg weight rather than egg number (as well as to sexual competition), for reasons discussed above. By contrast, larger iteroparous forms may differentially invest in fecundity and postspawning survival. These hypotheses can best be analyzed via further comparative and intraspecific (among-population) studies of iteroparous and semelparous fishes that relate variation in body size to variation in gonadosomatic index, egg weight, fecundity, migration distance, and parity.

Gonadosomatic Index and Parity

The negative correlations found here between percent repeat breeding and gonadosomatic index are consistent with predictions from life-history theory that lower survivorship is associated with higher reproductive effort (Reznick 1985; Roff 1992; Reznick et al. 2000; see also Hutchings 1993). This relationship has been found for various other fishes (e.g., Leggett and Carscadden 1978; Lambert and Dodson 1990; Reznick et al. 1990; Fox and Keast 1991; Hutchings 1993; Bertschy and Fox 1999); for salmonids, Fleming (1998) noted that anadromous forms have lower percent repeat breeding and higher gonadosomatic indices than their conspecific freshwater-resident forms.

Despite the association between gonadosomatic index and repeat breeding, semelparous salmonids do not have higher gonadosomatic indices than iteroparous ones, nor is there a notable increase in gonadosomatic index inferred for the origin of semelparity. Probably the best hypothesis offered to explain these findings is that Pacific salmon females tend to invest relatively more energy in competition for nest sites (Fleming and Gross 1989, 1994; van den Berghe and Gross 1989) and in defense of eggs than do related salmonids, and these activities come with a cost to investment in gonads (Healey and Heard 1984; Fleming and Gross 1989). In addition, the energetic costs of migration appear relatively high for semelparous species; indeed, some Pacific salmon engage in much longer migrations overall than do other salmonids (Rounesfell 1958), and in some Pacific salmon populations, well over 50% of body energy is spent in migrating to the

spawning grounds (Hendry and Berg 1999). Given the costs involved in sexual selection, parental care, and migration, gonadosomatic index is expected to underestimate reproductive effort more in Pacific salmon than in other salmonids (see also Vøllestad and L'Abee-Lund 1994).

Evolution of Semelparity

The traditional explanation for the evolution of semelparity in Pacific salmon hinges on high costs of migration to the breeding grounds and concomitant low adult survival from one breeding episode to the next (Schaffer and Elson 1975; Dingle 1980; Roff 1992; Willson 1997; but see Schaffer 1979). Although costly migrations may be a necessary condition for the origin of semelparity (e.g., Bell 1980; Dickhoff 1989), two findings suggest that they are not sufficient for its origin or maintenance. First, many populations of anadromous steelhead and Atlantic salmon also undergo long, difficult migrations comparable to those of Pacific salmon, but they remain iteroparous (at least potentially) even though most individuals fail to repeat breed (Rounesfell 1958; Hoar 1976; Weatherley and Gill 1995; Fleming 1998). Second, migration costs are relatively low in pink, kokanee, most chum, some chinook (Rounesfell 1958), and many populations of the other Pacific salmon species, yet all of these remain semelparous. Thus, either the origin of semelparity represents an irreversible evolutionary transition (Bull and Charnov 1985) maintained by a lack of variation in female parity mode, or other demographic factors are involved in maintaining semelparity in these populations and species.

Based on the results of our analyses, we hypothesize that evolutionary increases in egg size (and probably also body size), coupled with costly migrations at least near the transition to semelparity, were sufficient for its origin. The ancestral Pacific salmon is surmised to have been most similar to extant coho, sockeye, or steelhead trout (Hoar 1958; Weatherley and Gill 1985; Healey 1986; but see also Miller and Brannon 1981), and these speculations are consistent with our ancestral state reconstructions (Fig. 1). Notably, these three species undergo longer freshwater migrations to breed, on average, compared to other Pacific salmon and trout (Rounesfell 1958; Hoar 1976; McDowall 1988), and in steelhead (as also in Atlantic salmon) longer freshwater migrations are known to engender lower adult survival to repeat breed (e.g., Meehan and Bjorn 1991; Stearley 1992; Willson 1997). We suggest that in such an ancestral form these long freshwater migrations selected for increased body size (Roff 1988, 1991), which may have made repeat breeding even less likely (Dutil 1986; Jonsson et al. 1991; Fleming 1998). Moreover, increased adult mortality may also have been caused by the more-extensive ocean foraging of Pacific salmon (Rounesfell 1958; Holtby and Healey 1990; Bradford 1995) if such foraging occurred in the iteroparous ancestor of this lineage, and an increase in the density of breeding adults, if it occurred in the ancestral Pacific salmon lineage, may also have selected for higher reproductive effort, via stronger competition for good breeding sites (Fleming and Gross 1989, 1994). Finally, for reasons still to be discerned, egg size underwent a spectacular increase, which presumably led to higher juvenile survivorship. The two demographic conditions selecting for semelparity—lower adult survival and higher juvenile survival—may thus have been jointly sufficient to drive the transition from one parity mode to the other (see also Miller and Brannon 1981; Stearley 1992; Dodson 1997).

A final process that may have notably affected the transition from iteroparity to semelparity is fertilization of streams by carcasses of spent adults, which has been shown to substantially enhance stream productivity and enrich rearing habitat for juveniles (Northcote 1967, 1978). As semelparity began to increase in frequency in the ancestral Pacific salmon, the decay of spawned-out adults would have increasingly provided locally concentrated nutrients to juveniles via stream enrichment, which would have been expected to increase offspring survivorship and production of juveniles. To the extent that juvenile density was correlated with adult density and that increased adult density was associated with increased intrasexual competition (e.g., Fleming and Gross 1994), consequent increased investment in each breeding episode and resultant stronger selection for semelparity may have produced a positive feedback loop that would have facilitated the transition from an iteroparous to a semelparous form. This process may have been especially important given the relatively unproductive freshwater environments of the regions currently inhabited by Pacific salmon (Northcote 1967).

Testing these hypotheses related to the origin of semelparity will be difficult because semelparous species have likely undergone numerous secondary adaptations related to parity, and the transition may have been irreversible. For salmonids, the best strategy may be to compare populations of steelhead that differ in adult and juvenile demographics, migration costs, breeding density, and perhaps egg size, especially because some steelhead exhibit a small and variable degree of somatic degeneration upon breeding (Robertson and Wexler 1959; Stearley 1992; for sex hormone changes see also McBride et al. 1986). More generally, tests of hypotheses for the iteroparity-semelparity transition will require phylogenetically based comparative analyses for other taxonomic groups.

Semelparity and the Adaptive Radiation of Salmonids

Major changes in life history, such as the origin of semelparity, may represent key innovations that can spur diversification (Givnish and Sytsma 1997). Among salmonids in general, the phylogenetic evidence suggests multiple evolutionary transitions from lineages that are highly plastic for phenotype and life history (e.g., brown trout, most char, and Pacific trout) to forms that are more specialized, such as obligately freshwater forms (e.g., lake char, lenok, kokanee) and more or less obligately anadromous species (coho, sockeye, chinook, chum, and pink salmon; Rounesfell 1958; Thorpe 1987; Taylor et al. 1996). The origin of semelparity may also have been fostered by high intraspecific plasticity in life history: coho, sockeye, and steelhead exhibit not only relatively long migrations but also relatively high amongpopulation variation in migration distance and freshwater and saltwater residence times (Withler 1966; Dingle 1980; Healey 1986, 1987; Randall et al. 1987). Such variability, coupled

with the highly developed riverine population subdivision of salmonids (Thorpe 1998) may have facilitated the evolutionary transition to semelparity in the ancestral Pacific salmon (see Ranta et al. 2000a). Thus, both for salmonids as a whole and for the iteroparity-to-semelparity transition, we suggest that facultative variation within species gave rise to fixed variation among species (Thorpe 1987; Jonsson and Johnsson 1993; see also West-Eberhard 1986). For salmonids, this hypothesis can be tested further via larger-scale phylogenies, between and within species, for the family as a whole.

Once semelparity originated, semelparous lineages apparently underwent an adaptive radiation with regard to egg size, showing greatly accelerated rates of change among lineages by our independent contrasts analysis. The selective basis for these rapid changes is unclear, but they are likely related to diversification in body size, migration pattern, spawning location, and gonadosomatic index (Stearley 1992; Willson 1997).

Overall, the semelparous life history appears to represent one end of a partially complete continuum: freshwater-resident salmonids have small bodies, small eggs, low gonadosomatic index, and high iteroparity; anadromous iteroparous forms have larger bodies (Gross 1987; Fleming 1998) and eggs, higher gonadosomatic index, and lower levels of iteroparity; and anadromous semelparous forms are generally larger still in body size and egg size, although without an increased gonadosomatic index. Such a continuum suggests that many of the selective pressures driving salmonid life-history variation are more or less consistent among forms and species (see also Rounesfell 1958; Hutchings and Morris 1985; Stearley 1992; Willson 1997; Fleming 1998).

Applied Implications

The main relevance of this study to salmonid conservation and management is that fisheries and habitat degradation have probably been increasing the adult mortality rates of many populations and species (e.g., Hansen and Quinn 1998; Thorpe 1998), and hatchery rearing may reduce juvenile mortality rates. Thus, human activities may be selecting strongly for semelparity in iteroparous species such as steelhead and Atlantic salmon; indeed, reductions in percent repeat breeding have been reported in some populations of Atlantic salmon (Altukhov et al. 2000, p. 45).

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