BOOK REVIEWS

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EVOLUTION OF SALMON LIFE HISTORIES[1]

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Salmon, trouts, chars, and their relatives have been traditional sources of life-history observations, contributing to evolutionary theory since before Darwin. The writers and editors of the 13 chapters of *Evolution Illuminated* aim to inform evolutionists about hypotheses and tests in recent salmon research and also to bring modern evolutionary theory to the tool kit of salmon managers. These authors draw upon an extensive and sophisticated body of research. The book owes its existence to the evolutionary and economic importance of salmon as well as to the continuing loss of populations of Salmonidae through habitat destruction and commercial overexploitation.

Stephen Stearns and Andrew Hendry introduce readers to useful features of salmon diversity for research, such as high fecundity and variation in mortality rates, semelparity and iteroparity, sexual selection and alternative male strategies, postglacial recolonization from few to multiple habitats, philopatry versus dispersal, sympatric divergence and speciation, and hatchery facilities for studies of heritability, effects of selection, and plasticity. These features are exploited in subsequent chapters. The introduction also recognizes understudied opportunities for future research, including the roles of polyploidy, introgression, and metapopulation structure. I would also mention the opportunity to examine the striking morphological and life-history convergences implied by the (uncritical?) acceptance of some molecular phylogenies.

The most salient aspect of salmon life history is the tendency of five species of Pacific salmon to die after spawning (semelparity), unlike the iteroparity seen among other members of the family—Atlantic salmon, trouts, chars, huchen, taimen, *Brachymystax*, grayling, and whitefish. William Schaffer treats semelparity in the context of quantitative life-history theory. He finds support for the favored hypothesis that semelparity maximizes parental investment when start-up costs of reproduction are high. He includes tests of the roles of mating systems, age structure, and acquisition of traits that accelerate the dependence of effective fecundity on reproductive expenditure.

In chapter 2, A. P. Hendry, V. Castric, M. T. Kinnison, and T. P. Quinn examine six adaptive hypotheses to explain philopatry and four to explain variance in straying in return migration. Philopatry and dispersal are considered to be balanced alternatives. Some philopatry hypotheses are found unsupported (direct selection for access to suitable breeding sites) and several are found opaque to testing and are evaluated by rejection of the dispersal alternatives. Philopatry increases with conspecific precedence in a stream, and may improve access to parental resources through the transfer of resources between generations. Nutrients (from semelparous parental carcasses, benefiting grand-offspring) and relatively clean gravels (from long history of nest building) are explored with data, logic, and open minds, but will attract critical discussion. Evidence that dispersal (straying) evolves to buffer against temporal variation in habitat quality is ''equivocal but also wide-ranging and convincing.'' Cited studies provide evidence for and against hypotheses that dispersal is selected for by reducing competition among kin or decreasing inbreeding depression (inbreeding is rare in healthy, wild populations). These are evaluated comparatively and with discrimination, perhaps reflecting the multiple authorship—the chapter is a model for clearly laying out the hypotheses, predictions, and evidence in a formal, thorough manner.

Migration to the sea (which yields a growth advantage) is recognized as being ancestral in salmonids, but varying tradeoffs in cost and mortality have led to frequent changes in this behavior (summarized by A. P. Hendry, T. Bohlin, B. Jonsson, and O. K. Berg). Anadromy is positively correlated with the latitudinal gradient in differential productivity of marine and fresh waters. Observed variation in anadromy leads to consideration of the expectation that average fitness of nonanadromous individuals should decrease as they become more abundant but that reproductive success might be frequency dependent. Body size and condition are positively linked to anadromy. Different growth and size of males and females at maturity occur when their costs and benefits do not scale equally with change in growth rate. Migratory populations are shown to evolve traits and behaviors that decrease the proximate costs of migration.

The extensive literature on the relationship between egg number and egg size is comprehensively reviewed by S. Einum, M. T. Kinnison, and A. P. Hendry, with interesting observations: egg size is correlated with gravel size, but not because of the expected relationship to oxygen. Egg size is usually correlated with female body size, but when proportional increase in egg number exceeds the proportional increase in egg size, females with relatively greater investment increase egg number more than egg size. The ratio of egg number to egg size is shown to increase with migratory distance. Egg size decreases rapidly in a hatchery environment. This chapter (and others) might have benefited from more attention to the geology of salmon. Egg size is adapted to gravel size, as well as local nutrient availability, and determines hatching time. Gravel size is a function of responses of fluvial channels to sizes of fallen trees, in part, and erosion.

[1] *Evolution Illuminated: Salmon and Their Relatives.* A. P. Hendry and S. C. Stearns, Eds. 2004. Oxford Univ. Press, New York. x + 510 pp. HB $85.00, ISBN 01-951-4385-X.

Trees use the nutrients brought in by generations of semelparous salmon, so there are newly discovered ecological and historical relationships important to the evolution of life-history parameters (Montgomery 2003).

Life-history theory (reviewed by J. A. Hastings) predicts plasticity in organisms that encounter variable habitats, for example through widely dispersed offspring. Most salmonid examples of plasticity involve variations in growth and time of maturity. Slow-growing individuals optimize fitness by delay of maturity and large size; fast growth may increase fitness by permitting early maturity. These reactions are related to overwintering size and mortality. The tendency to be migratory responds to age of maturity among Atlantic salmon populations: old individuals are more likely to be anadromous, while younger-maturing populations are likely to be nonanadromous. The ability to produce different phenotypes across an environmental gradient is shown to have significant heritability in several examples.

An outstanding review by I. A. Fleming and J. D. Reynolds links evolution of breeding systems to adult survival, influenced by ideas of George Williams and Stephen Stearns, and to game theory, to explain differences between males and females. Salmon are unusual among fishes in that females, not males, provide parental care. Female competition and mate-choice dynamics provide context to female parental investment, especially trade-offs between semelparity and iteroparity, and females' narrow temporal window of fertility and defense of nests until death. Males maximize the number of nests visited and exceed females in variability of reproductive success. Contrasts between alternative tactics are intricately related to reproductive timing and variation in success, related to evolution of body size and secondary sexual characters as honest signals. Our modern knowledge of these relationships owes much to the research of Hendry and his associates. This chapter also considers natural history, such as: Alaskan salmon body depth matches stream depth because of bear predation; landlocked sockeye salmon efficiently sequester rare carotenoids to manufacture breeding colors; some female salmon appear to use male colors and false orgasms to manipulate males' behavior; and early maturity of sneaker males is partially genetically determined, and at one-fifth or less the size of hooknose anadromous ''fighters,'' they are sometimes more successful at gaining fertilizations. The large literature on alternate male strategies in fishes is augmented by new data.

Life-history evolution is discussed as a conflict between historical contingency (vicariance and recolonization influenced by glaciation) versus determinism (natural selection and especially convergent or divergent evolution) in Chapter 7 by M. T. Kinnison and A. P. Hendry, subtitled ''Tempo and Mode in Salmonid Evolution.'' There is a discussion of theory and history, including a phylogeny with life-history information mapped upon it. Duplicate genes in tetraploids are discussed as possible factors in salmonid evolution. Introgression in chars is mentioned as confounding to reconstructing phylogenetic history, as are conflicts among molecular, biochemical, and life-history data. Anadromy is negatively correlated with iteroparity and also related to social and migratory behavior of juveniles, philopatry, strong mate choice, and strong secondary sexual characters. Discovery of a northern ''stream'' form and a southern ''ocean'' form of chinook salmon, with different behaviors and life histories, is important and bears on the question of whether adaptive divergence occurs before or after reproductive isolation. But there is no special reason for discussing it as a postglacial phenomenon (14,000 years), given fossil and phylogenetic evidence that the chinook lineage has probably been here for more than six million years. The authors close the chapter with a discussion of heritable and plastic responses to size-selective exploitation, which selects for decreased body size. Abundant examples of parallel and convergent responses in introduced populations support natural selection and provide estimates of rapid rates of evolution.

Later chapters are devoted to insights into effective population size (R. S. Waples), natural hybridization (E. B. Taylor), evolution under selective harvest (J. J. Hard), and preserving diversity (M. J. Ford). The most startling revelation in these chapters is that not only do hatchery practices select for nonadaptive characteristics, but the planting of hatchery-produced offspring back into their natural population *decreases* effective population size when it adds a narrowly restricted part of the overall gene pool (the Ryman-Laikre Effect, discussed by R. S. Waples).

L. Bernatchez applies a comparative genetic approach to the postglacial divergence of a host of whitefish species into empty niches left by retreat of the glaciers. Divergences result from competitive interactions and occupation of different adaptive zones. Reproductive isolation results from low fitness of intermediate phenotypes, but also as a byproduct of genetic change. Sympatric forms of whitefishes differ especially in the number and length of their gill rakers (food capture and sorting structures), shown to have high heritability. Common ancestry of clades is evaluated by molecular phylogenies based on DNA sequences, and a rate of 2% sequence divergence per million years is assumed, yielding a Pleistocene, even postglacial, divergence episode for most species. But the rate of 2% per million years may be two times too fast for salmonids, according to fossil calibrations (Smith et al. 2002). Bernatchez shows that high extinction rates are exceeded by high speciation rates in these fishes. Trait utility is demonstrated by transplant experiments and the role of selection in divergence is clearly demonstrated.

In the last chapter, K. A. Young appeals to evolutionary theory to change the past mismanagement of salmonid fishes, including such topics as: selection above the level of the individual, frequency- and density-dependent (soft) selection, and frequency/density-independent (hard) selection. Because these interact in important hierarchic ways in populations under exploitation, they should become part of ''contextual management,'' in which environmental and demographic manipulations are applied to affect persistence of stocks. Traditional management practices often select against whole populations; for example, exploitation of larger populations in mixed-stock fisheries frequently drives small populations toward extinction (the A. J. Nicholson effect). The reverse, benefit to nontarget populations, may result from selective exploitation. Ricker's demonstration of evolutionary changes in age and size of maturity caused by size-selective harvest (hard selection) in many stocks of Pacific salmon is tested against soft-selection hypotheses. The discussion extends to

examination of contextual management of alternative male strategies, bad hatchery practices, competition, and timing of spawning. Standard stock-recruitment and sustainable-yield models are shown to be unsustainable, in part because they are insensitive to exploitation effects on life-history evolution.

In summary, this is a most valuable and progressive look at salmon ecology, genetics, and evolution. The extensive tables of life-history data and 1300 references add to its value for teachers, researchers, managers, and conservationists. The critical tests of hypotheses for philopatry, semelparity, and dispersal, in particular, should broaden framing of future tests of life-history evolution in other organisms. The book advocates more sophisticated use of principles of effective population size and life-history evolution in salmonid management and should aid the scientific and political struggles to manage salmon sustainably.

Literature Cited

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