

SPECIAL SECTION

Strategies for Survival: Salmonids in Marginal Habitats¹

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Salmonid Flexibility: Responses to Environmental Extremes

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Abstract.—The responses of salmonid fishes to the problems posed by marginal habitats are genetic exercises in population insurance. The costs increase as the risks increase, but the risks are met by a wide repertoire of biological capacities. The most general proximate response to adversity is behavioral: ontogenetic niche shifts are an acknowledgment that a series of environments becomes marginal for all salmonids during development. Physiological tolerances and developmental flexibility govern the timing of these movements. Such shifts are the product of natural selection in relatively predictable environments, but less predictable or catastrophic events are accommodated at a different genetic level. Low spatial flexibility is counteracted by temporal insurance, and vice versa. Thus, high homing precision is coupled with complex multiple-age structures, and simple age structuring is coupled with relatively high spatial straying.

A symposium on salmonids in marginal habitats needs some description of marginality. By definition, marginal habitats imply conditions far removed from the preferendum of the species occupying them. Hence the fundamental scientific interest in species populations that live in marginal habitats lies in the mechanisms by which those species cope with adversity and in the differing life history strategies by which they solve the problem of reproduction there (Giesel 1976).

The range of habitats that a species occupies demonstrates its degree of morphological, physiological, behavioral, and ecological tolerance. That tolerance, while expressed at the individual level in these ways, is fundamentally a genotypic property, and so it is a genetic characteristic of the particular species as a whole. There is still much

discussion about the nature of variety in species like salmonids with geographically discontinuous populations, but evidence continues to accumulate for the adaptive nature of genetic differences between such discrete stock units (Taylor 1991).

Because the genotype is a blueprint for development, the characteristic tolerance of a species can be seen in the developmental flexibility of individuals. No animal normally occupies a totally constant environment, and the ways in which it copes with diel and seasonal change reflect its inherent (genetic) flexibility of response. When the scale of environmental changes exceeds the animal's capacity to respond in situ, the general biological response to adversity—migration—comes into play (Taylor and Taylor 1977). Within the fish's lifetime a sequence of different environments becomes marginal with respect to its current needs. When the animal's needs are being met, it stays where it is; when they are not, it moves until it finds appropriate conditions for its current demands. The migrations that characterize particular species are reflections of the major genetic boundaries defining those species within the limitations imposed by their environments.

Salmonids change habitat many times during development (Thorpe 1988), undergoing the so-called ontogenetic niche shifts. Each change in-

¹ This Special Section contains peer-reviewed papers from a symposium of the same title held during the American Fisheries Society's 121st annual meeting in San Antonio, Texas, September 9, 1991. Not all papers given at the symposium are represented here, but the first article, by J. E. Thorpe, summarizes the presentations. C. A. Dolloff and P. A. Flebbe, U.S. Forest Service, organized the program and coordinated papers for journal publication. Funding support for publication was provided by the U.S. Forest Service's Southeastern Forest Experiment Station.

volves a migration (Groot 1982). Hatching may be considered as the first of these migrations, prompted by the inadequacy of the restricted volume within the chorion for the completion of embryonic development. Then emergence from the gravel redd into open water—the second migration—represents an escape from the nutritional inadequacies of the gravel environment once the endogenous sources of nutrition have been depleted. Subsequent dispersal within the nursery environment of the stream represents movement away from the energetically unprofitable environment of densely aggregated sibling competitors. Later movement into pools at times of low water or drought represents escape from starvation, increased exposure to predation, and lethally high temperatures and low oxygen concentrations (Li et al. 1994; Nielsen et al. 1994, both this issue). Return to the gravel bed or to sheltered deep water in winter represents avoidance of freezing and conservation of energy resources (Metcalf and Thorpe 1992). Emigration from the stream into a lake, or to the sea, in spring represents abandonment of a trophically inadequate environment at a time of high food intake and also an inhospitable one at a time of reduced hyperosmotic regulatory ability (Primm et al. 1988). Finally, return to freshwater from the sea represents the abandonment of an environment that fails to provide for the specific needs of reproduction.

The organizers kindly invited me to review the papers given during a 1991 symposium on salmonids in marginal habitats. In the present paper I have referred to material offered for that symposium, some of which is published concurrently in this issue, and some not (denoted “unpublished” in the remaining text). I have considered the responses of the various salmonid species to marginality in terms of the predictability of changes in their environments, of the choices available to them developmentally, and of their behavioral ecology.

Review of the Symposium

Predictability

The examples of marginal habitats discussed in the symposium can be graded by relative predictability. When conditions are relatively predictable, even when predictably extreme, different successful strategies may evolve to allow species to exploit the limited possibilities open to them. Arctic salmonids solve their survival problems in a relatively highly predictable environment. J. B.

Reynolds (University of Alaska, unpublished) described two general ways in which salmonids overcame the severe limitations imposed by high-latitude climatic extremes: spawning in spring or early summer, which allows the progeny to accumulate their own energetic insurance against the physiological challenge of extreme cold in winter; or spawning in autumn, with the adults providing that energetic cushion for the fry in the form of yolk. Both tactics are compromises for the adults. In the first case, the adult misses the full advantage of the early increase of productivity in the spring, while it spawns, but then makes up for that loss by feeding heavily for the rest of the summer, and so should enter the winter with its stores well filled. In the second case, the adult feeds heavily from the beginning of the spring productivity boost, but loses some of its accumulated energy at spawning in autumn, before its own period of severe demand has begun. Reynolds also noted that this compromise in the partitioning of net energy gain results sometimes in failure to reproduce every year after maturity is reached.

The Mount St. Helens eruption, which strongly affected salmonid populations in that part of Washington State (P. A. Bisson et al., Weyerhaeuser Company, unpublished) epitomizes extreme unpredictability—a catastrophic event that may be statistically predictable, but only in time intervals much longer than the generation time of salmonids. However, even that level of predictability can be accommodated by the species in a genetic sense, and I will return to this below.

Episodic acidification is by definition unpredictable, but even when escape for the fishes is possible, marginality is not always solved successfully this way. C. J. Gagen et al. (Pennsylvania State University, unpublished) did record increased downstream movement of brook trout *Salvelinus fontinalis* in streams subject to acidic episodes, but they also noted up to 33% mortality in these streams. In comparable, but unaffected streams, there was no net movement of brook trout and no mortality during the study intervals. They also noted that the trout did not use the opportunities available to them of staying in point sources of more alkaline water.

Developmental Choice

Flexibility of maturation highlights another aspect of a fish's physiological repertoire. The normal developmental process involves a sequence of physiological choices—to maintain a particular course of development, or to change to another.

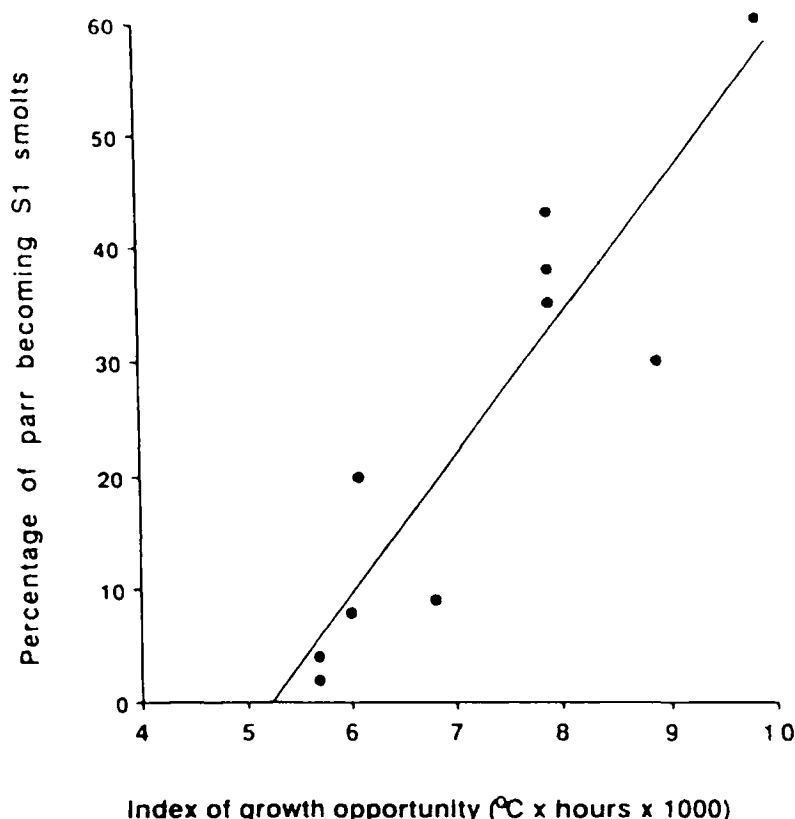


FIGURE 1.—The percentage of juvenile Atlantic salmon that became smolts at age 1 (S1) in relation to an index of growth opportunity (daylight hours multiplied by temperature) experienced by the fish in July. Data are for 10 subpopulations of the same family exposed to different conditions (after Thorpe et al. 1989).

The two most striking choices that face anadromous salmonids are, in time sequence, smolting and sexual maturation. It has been shown that these choices are taken in response to specific seasonal signals (Scott and Sumpter 1983; Villarreal 1983; Thorpe 1986; Villarreal et al. 1988), but that the direction of choice depends on some internal process of assessment of performance at that time, performance that is almost certainly associated with energy status (Thorpe 1986; Rowe et al. 1991).

Experimentally, Thorpe et al. (1989) showed that the probability that a parr of Atlantic salmon *Salmo salar* would smolt in a given year depended on its growth opportunity (that is, on how marginal its environment was) during the previous July (Figure 1). This opportunity (or degree of marginality) was expressed as an index incorporating mean temperature and number of daylight hours—because the salmon feeds when it can see and is more active when it is warm. Applying this

argument to the species as a whole, Metcalfe and Thorpe (1990) showed that the average age at smolting in 182 Atlantic salmon rivers over a 40° latitudinal range was predictable on a similar basis (Figure 2). P. A. Ryan and T. R. Marshall (Ontario Ministry of Natural Resources, unpublished) used another index of marginality—physicochemical quality—to predict the suitability of various lakes for the production of lake trout *Salvelinus namaycush*.

As regards the maturation choice, Rowe et al. (1991) showed that those male Atlantic salmon parr that matured in the autumn were the ones that had started to replenish their mesenteric lipid store the previous April. If the parr had delayed this replenishment until May, they failed to mature that year. The authors emphasized that the physiological decision to commit resources to maturation occurred well before spawning, and gonad growth in Atlantic salmon has recently been found to increase sharply in the previous Novem-

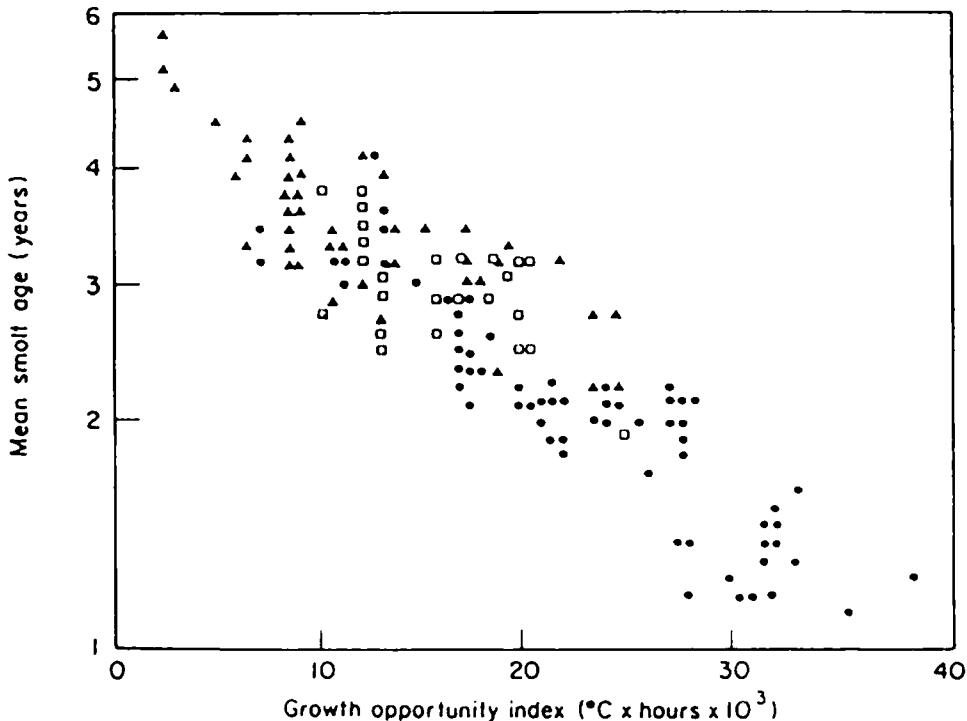


FIGURE 2.—The mean age of Atlantic salmon smolts in different rivers in relation to an index of growth opportunity similar to that of Figure 1. Data are from 182 rivers in Canada (triangles), east Europe (squares), and west Europe (circles) (after Metcalfe and Thorpe 1990).

ber, 12 months before spawning (Thorpe 1994). However, Rowe and Thorpe (1990b) suggested that maturation could be suppressed later if feeding and fat deposition were inadequate in the spring. Future opportunities for accumulating energy would depend on the length and warmth of the growing season. A cold spring would reduce these opportunities, whereas an early warm spring would not limit them to the same degree, and would not compromise reproductive success. So internal assessment of a set point related to fat status in spring could be a mechanism on which selection could act, adjusting a physiological switch to suppress further maturation if that set point has not been exceeded.

J. Nielsen's suggestion (U.S. Forest Service, unpublished) that coho salmon *Oncorhynchus kisutch* mature faster in marginal habitats is in direct contradiction to this interpretation, and therefore deserves particular mention. Although mammals and plants respond to adverse conditions by cutting their losses and reproducing, fishes generally respond to such conditions by postponing maturation (Stearns and Crandall 1984). The apparent

anomaly of lower growth rates of juvenile coho salmon yet higher development rates (earlier maturity?) may be explained on two possible grounds. Growth rates are characteristically assessed over periods of a year, or at least over whole growing seasons. But as already noted, the physiological decisions concerning maturation are taken early in the year over a matter of a few weeks, and they relate to the performance characteristics at that time. Juvenile coho salmon are small at this time, and over such a short interval the fishes' needs may be fully met and their growth rapid, even in habitats classified as marginal when considered over the whole period of occupancy by the fish. Rapid growth for only a few weeks during this critical time may permit considerable gonad development (Adams and Thorpe 1989), even if it is arrested when growth becomes restricted later in the summer. Growth rate assessed over the whole season would appear slow, obscuring the fact that it was fast over the critical interval that influenced maturation. This is the common fallacy that leads to the description of mature Atlantic salmon parr as dwarfs. Such individuals ac-

usually show inherently high growth rates, but because they grow over a shorter interval than their immature siblings, the latter eventually overtake them in size (Murphy 1980; Rowe and Thorpe 1990a).

Alternatively, the particular coho salmon population studied by Nielsen could have been selected for a very low set point for the physiological decision to mature. Controlled rearing experiments in comparison with other coho salmon stocks from supposedly optimal environments would be required to evaluate and distinguish between these possibilities.

Behavioral Ecology

The long-distance migrations between wintering and feeding grounds and between feeding and spawning areas that characterize Reynolds' Arctic salmonid populations (unpublished) are extreme instances of movements from inadequate to more adequate habitats, and they illustrate many times over the fundamental importance of mobility. The selection of thermal refugia by steelhead anadromous rainbow trout *Oncorhynchus mykiss* in Californian rivers in summer (Nielsen et al. 1994), by the same species in streams in arid areas from which the shelter of riparian vegetation has been removed (T. N. Pearsons et al., Oregon State University, unpublished), by the various southwestern trout species in equally arid areas (J. N. Rinne, Arizona State University, unpublished), and by the drought-affected trout in the Great Smoky Mountains (S. E. Moore, Great Smokey Mountains National Park, unpublished) represent similar proximate responses but on a much smaller geographic scale. In all these cases the final choice of habitat was a compromise; none of the environments was ideal, but each chosen habitat represented the least adverse solution available. This was illustrated nicely by Li et al. (1994), whose rainbow trout in high-altitude desert streams occupied habitats of relatively low productivity and food availability, avoiding those where the temperatures were approaching the upper lethal limit for the fish.

However, in the study of Pearsons et al. (unpublished), physiological restriction of trout to the lower-temperature stream sections resulted in increased vulnerability to predation, especially among smaller fishes. In this environment the summer flow had ceased, the stream had become a series of disconnected pools, and escape was very limited. For very many individuals this meant death. It is likely that the survivors were those

that were genetically more perceptive and whose avoidance reactions were more acute. M. E. McDonald et al. (University of Minnesota, unpublished) found that predator avoidance would confine young-of-the-year lake trout to the shallow littoral zone of an Arctic lake, and they showed experimentally that this would have kept the fish in an area that was trophically inadequate. Hence, to grow, habitat choice had to be a compromise between gaining adequate food and risking predation. It seems likely that the lake trout would have foraged intermittently in the trophically profitable but risky areas, but have spent most time in the safer but trophically poor littoral. Neill and Magnuson (1974) recorded an analogous stragem of balancing advantages. In Lake Monona, Wisconsin, the heated effluent from a power station harbored a density of zooplankton much higher than in the cooler lake water. At over 29°C, the water was above the incipient lethal temperature level for several lake fishes, which consequently did not live in the thermal effluent. In laboratory experiments, however, the authors showed that yellow perch *Perca flavescens* would make brief incursions into such inhospitable temperatures to feed.

Long-Term Solutions

There are circumstances in which the problem of marginality cannot be solved by escape. In their lake trout study, Ryan and Marshall (unpublished) described a real extreme. If the outlet to a lake becomes blocked, lake trout can only survive there if the temperature and oxygen conditions remain within quite restricted limits. If the lake becomes so enriched that oxygen concentrations decline further in summer, the fish have nowhere else to go. Comparable extremes are created by pollution, sometimes dramatically, as in the 25 rivers of southern Norway where Atlantic salmon are now virtually extinct, a decline attributed to the inability of the freshwater juveniles to tolerate the extreme levels of acidification reached there over the past 100 years (Hesthagen and Hansen 1991).

If the problem cannot be sidestepped, it has to be faced. There may not be any viable solutions, as perhaps in the case of the lake trout and the salmon of southern Norway. But in others there are. A catastrophic disaster like the eruption of Mount St. Helens (Bisson et al., unpublished) was lethal for almost all the individual fish in the rivers in its immediate vicinity. However, it was evidently not lethal for the total populations of those

fish, because they are still there, and have reached new high levels of production in the decade since the eruption. This is a form of genetic insurance against environmental instability.

The presumed advantages of high homing accuracy of adult salmonids to their natal streams—the maintenance of co-adapted gene complexes of proven value in stocks specific to particular river systems—carries with it a penalty. If that river is “destroyed,” as was Toutle Creek by Mount St. Helens in 1980, then its associated specific stocks are threatened too. However, most salmonid species, other than pink salmon *Oncorhynchus gorbuscha*, have insured against that risk through multiple-age structures. Hence, only a part of each species’ stock was present in the rivers at the time of the Mount St. Helens disaster, and the rest were at sea. Therefore, there was a reserve of genetic material of those stocks still available for reestablishment after the natural restoration of the river had begun. That this is a very successful stratagem was made clear by Bisson et al. (unpublished), who found that the populations were able to capitalize on the temporarily increased food availability following the various disasters. However, Bakshinsky (1980) pointed out that although species with multiple age-groups possess an insurance in time, their high homing precision reduces their insurance in space. By contrast, species such as pink salmon, which show almost no life history flexibility, have little insurance in time, but, straying more readily, possess more insurance in space. (However, evidence of relatively rapid colonization of recently deglaciated streams in Alaska by several other *Oncorhynchus* species suggests that they possess considerable insurance in space also [Milner and Bailey 1989; Thorpe, in press]).

Flebbe (1994, this issue) surveyed the distributional patterns of brook trout, rainbow trout, and brown trout *Salmo trutta* at the southern end of their geographic range in the Appalachians, and identified other ecophysiological limiting factors. When these become altitudinal and restrict fish to waters above a certain elevation, then escape from other vicissitudes is a limited solution to marginality. However, unavoidable adverse conditions may select for extreme genetic characteristics in a population, and such may be expected at the physiological extremes of the species ranges.

Recolonization, albeit artificial, has shown other aspects of marginality. N. H. Ringler et al. (State University of New York, unpublished), in reviewing a century of fish introductions into the Lake

Ontario drainage basin, showed that competition with 30 or more native species restricted the possibilities for the invaders. In upstream regions most suitable for juvenile salmonids, these authors found the predictable relationships between productivity, stream order, and morphometry—namely, that food availability and predation pressure both declined in an upstream direction—as described by Zalewski and Naiman (1985).

Finally, it is reassuring for a fish biologist to know that some events that may be perceived as disasters by humans are not received quite that way by the fish. Hurricane Hugo was none too gentle with the terrestrial environment, but apparently its effects on the world of the stream fish were minimal (Dolloff et al. 1994, this issue). No information was given on the downstream effect of the accumulation of woody debris flushed out of these streams, so it is not known if the impact was greater in the mainstream rivers than in the upper tributaries. It is also reassuring to a general conservationist that, because beaver dams result in increased stream temperatures, the beaver was exonerated from causing the decline of brook trout in Wisconsin (McRae and Edwards 1994, this issue).

Overall, the papers convey an impression of salmonid fishes as remarkably versatile organisms, behaviorally and physiologically, with a sufficiently wide genetic repertoire within species to enable them to adapt to a dramatic range of physical circumstances.

Acknowledgments

I thank Larry Nielsen and the organizers of this symposium for inviting me to present a summary paper, and for their kind hospitality at San Antonio throughout the Annual Meeting of the Society. The figures were reproduced by permission of Academic Press Ltd.

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