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Reproductive guilds and the ultimate structure of fish taxocenes: amended contribution to the discussion presented at the mini-symposium*

Eugene K. Balon

Department of Zoology, College of Biological Science, University of Guelph, Guelph, Ontario N1G 2W1, Canada

The best strategy for a gambler may sometimes be a wait-and-hope strategy, rather than a bull-at-a-gate strategy.

Richard Dawkins (1976) in 'The Selfish Gene'

When Gene Helfman invited me to make a contribution during the final discussion in Ithaca I felt I had several serious points to make, but the unexpected provocation created no more than a whirlpool of thoughts. Consequently, the participants had to suffer through my struggle with the blackboard and endure a feeble attempt to make clear a concept most of them as yet knew nothing about. May I now address the same problem in a more relaxed way?

A recurring idea in different papers of these proceedings is that the ultimate densities of given species are dependent less on trophic webbs (see also Peters 1977) and competition (Keast, these proceedings) than on reproductive strategies. Even elsewhere it was suggested 'that populations may rather frequently be well below the equilibril sizes determined by resource supplies [and that] populations may be maintained at steady states below resource levels by consistent impact of predators (...) or by frequent and recurrent disturbances' (Wiens 1977). Reproductive strategies may play a major role in providing fish with the ability to fill available space or to maintain densities at equilibril sizes (whatever that means). In spite of this, the importance of reproductive strategies, though sometimes considered, has seldom been stressed. Since it is the theme developed in my papers on reproductive guilds (Balon 1975a,b), let me correct this omission. The whole concept of reproductive

guilds is new in North America, and it sometimes opposes and at other times supplements Root's (1967) trophic guilds. It is expanded and probably better explained in more recent papers (Chadwick 1976, Mahon & Balon 1977, Balon et al. 1977).

The reproductive guild theory is based on Kryzhanovsky's (1949) premise that 'adaptations of fishes for spawning and [early] development reflect not only the essential ecological factors of the embryonic period, but also the essential factors of all the other intervals of life. The adaptations mark the biology of adults, and define the type of migrations, invasion abilities and limits of distribution.' In other words, if we understand the principles of early ontogeny, we may understand the reasons behind life styles of adults. There is, however, neither a need nor would it be wise to treat fish in different intervals of ontogeny as separate taxa, as some have suggested. The various intervals of ontogeny of a given species should be treated as an inseparable continuum, but more accurate language (Balon 1975c), comprehensible to all (Jones 1972) should be employed.

The problem is which interval of ontogeny determines the structure of adult communities. I have been saying that embryonic and larval periods (if present, Balon 1977) are decisive intervals. Most authors still concentrate on adults.

Peter Sale's paper, for example, is replete with evidence in support of the reproductive guild theory. If the survival of a species and its ultimate density is dependent on a surplus of embryos and larvae, the species tends to develop pelagophilous adaptations which are energetically best suited for this purpose.

* This discussion forms part of the proceedings of a mini-symposium convened at Cornell University, Ithaca, N.Y., 18-19 May 1976, entitled 'Patterns of Community Structure in Fishes' (G. S. Helfman, ed.).

Members of the pelagophilous guild have eggs of the lowest density of all the guilds, containing 70–92% water and only 0.1–4.0% lipids. In view of the low energy content and small size⁺ of eggs a large quantity can be produced which then can be constantly available to fill the space freed at unpredictable intervals. Furthermore, the large quantity is necessary for dispersal into areas large enough, so that a few have a chance of survival. In spite of the tremendous mortality inherent in such an arrangement, the energy expenditure remains minimal. Possibly a lesser demand on buoyancy requirements in sea water may have favored the evolution of this strategy predominantly in oceanic environments and offers an alternate explanation to Helfman's (these proceedings). In addition to the production of low energy zygotes, adults expend little or no energy on parental care. The production of clutches numbering hundreds of thousands is commonplace.

In contrast, freshwater reefs of Lake Malawi are known to support a similar species diversity as coral reefs*, but the recruitment is guaranteed in a completely different strategy. Very few but very large, dense eggs are produced. For example, *Labeotropheus* spp. eggs contain 52% water and 45% lipids, and are deposited in lots of 20 to 50. Some cichlids in Lake Tanganyika (Brichard 1975) are known to produce and incubate two eggs per female only (D. J. Stewart, pers. comm.). Every single embryo is potentially earmarked as a replacement for an adult. Consequently, it is not only intensively guarded against predation, but mouthbrooded in isolation from the external environment. To eliminate exposure of the egg, using again the *Labeotropheus* example, every egg is released singly during rapid 'orgasmic loops', and immediately taken into the female's mouth; only there is it fertilized by the female consecutively sucking on the egg dummies on the anal fin of the male**. Furthermore, the large, dense yolk enables direct development of a fully formed juvenile, without the larval life interval, inside

⁺ See Russell (1976) except for parochial nomenclature.

* The apparent differences in fish diversity of coral reefs and tropical lakes (Emery, these proceedings) are due to an ecologically erroneous assumption which disregards comparisons per unit area. In some instances a comparison per hectare would reveal a reversed relationship (e.g. personal observations at Rincon de Guanabo, Cuba – Balon & Seneš 1967, and Lake Tanganyika – Bailey & Stewart 1977; see also Brothers' comment to Emery, these proceedings).

** Breeding without substrate contacts may be the explanation for the successful existence of some *Haplochromis* species in Lake Victoria (Greenwood 1974).

the female's buccal pouch, so that the released young is about 14% the size of its parent (Balon 1977).

The theory of reproductive guilds and its basic premise that predators and availability of oxygen play a leading role in the development of reproductive strategies (Balon 1975a: 823) is elegantly supported by Johannes (these proceedings) who explains the pelagophilous adaptations of coral reef fishes as a 'strategy of minimizing predation on young by exporting them offshore.' The whole reproductive strategy of pelagophils is aimed at maximizing this advantage of the marine environment. This is, however, not the only route that evolved to high diversity fish communities. We must be aware that an entirely opposite strategy exists in the Great Lakes of Africa, for example; some of the hazards of the pelagic phase are eliminated by adaptations enabling the entire ontogeny to occur entirely on one side of Smith's (these proceedings) 'filter screens'. Johannes' concept of quantity versus quality of offspring fits well within the reproductive guild theory (Fig. 1), the aim at quality being an energetically equal replacement for systems without a vast pelagial, and possibly, with oxygen limitations (Balon 1975a, 1977). To continue the Wall Street analogy of Sale (these proceedings) and Dale (these proceedings), the guild of bearing mouthbrooders with its heavy investment of energy into a single offspring is, consequently, not adapted to gamble in a lottery. All the investment went instead into real estate, considered by many the safest.

One is rather tempted to avoid the question of which strategy favors more speciation and less extinction. In my first definition of guilds I was convinced that their order, from pelagophils through guarders to livebearers, expresses a phylogenetic sequence from the more primitive to the better adapted for survival; from the energetically more wasteful to the less so. Although I am no longer convinced that it is so simple (Persov 1972), I am sure that adult trophic relationships are less important for the ultimate community structure than reproductive strategies.

Expanding this line of thought somewhat speculatively, one may distinguish sequences of maturation in any fish taxocene. Taxocenes with a high rate of colonization and extinction never attain high taxa diversity but consist of numerous reproductive guilds. In contrast, in highly diverse communities with low rates of colonization and extinction (in relative terms and evolutionary sense), reproduction and development fall mainly within the scope of a single guild, as for example the coral reef pelagophils and Malawian mouthbrooding cichlids. This can be related to greater

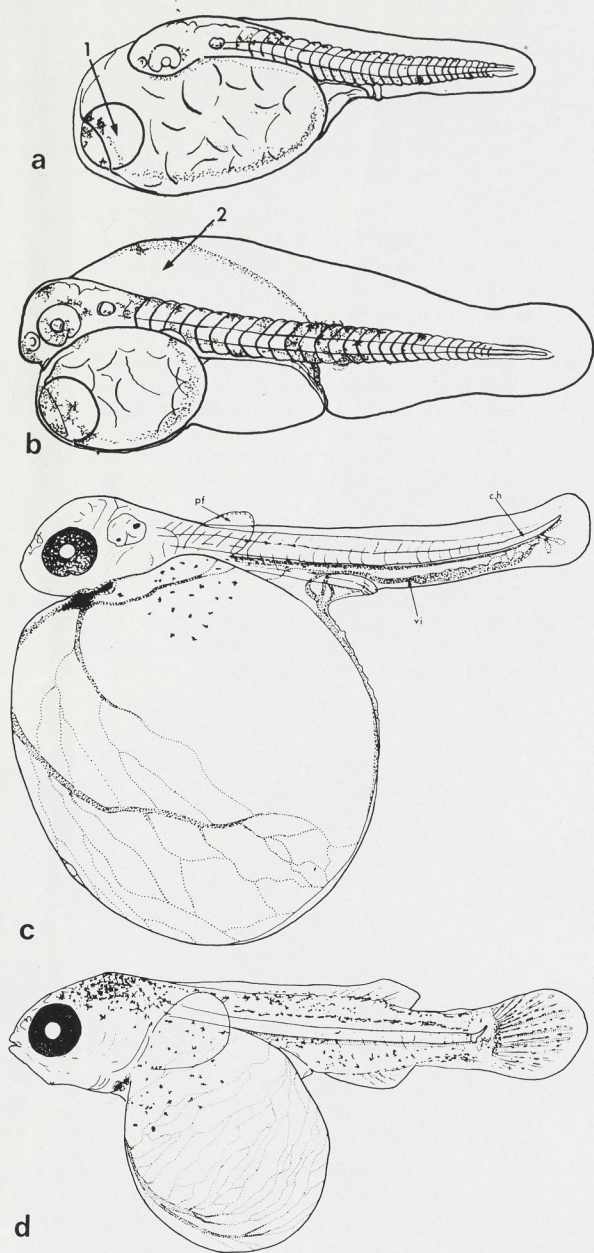


Fig. 1. The concept of quantity (pelagophilous guild) versus quality (guild of mouth brooders) illustrated on similar stages of ontogeny. Pelagic free embryos of *Caranx* (a,b) and in buccal pouch incubated free embryos of *Labeotropheus* (c,d): a,c, eleutheroembryos just after hatching (1 = oil globule, ch = chorda dorsalis, pf = pectoral fin, vi = vena caudalis inferior); b,d, eleutheroembryos at the beginning of rapid yolk absorption (2 = dorsal sinus).

environmental stability which allows and enhances speciation by positive feedbacks of nutrient recycling (Connell & Orias 1964). This in turn enables multiple reproductive strategies as compensators of environmental changes to relax. Consequently, the significance of reproductive strategies for the ultimate taxocene structures can be revealed: in mature (stable) systems, one strategy maintains the equilibrium, whereas in less mature (unstable) systems various strategies are on trial, a phenomenon involved also in the system (Armstrong & Gilpin 1977) of the 'r-K continuum' (MacArthur & Wilson 1967, Pianka 1970) or in 'b selection' and 'd selection', the latter replacing K-value for 'crowded populations which are regulated by resource limitations' (Hairston et al. 1970). Going even further, both pelagophilous and mouthbrooding strategies may be equal in energy cost and competitive pressures and may, therefore, be 'd-selected' (Grahame 1977), in contrast to the trial guilds which may be labelled as 'b-selected'. Pianka's (1972) theory of 'reproductive effort and expenditure per progeny against niche overlap' fits quite well in the hypothesis of trial guilds in unstable systems versus single guild of 'K-selected' nature in mature, stable systems. In my opinion this hypothesis forms a possible alternate or supplement to Helfman's (these proceedings) 'small target space'; only more evidence can resolve the apparent conflict.

I have long suspected that the general principles which guide the ultimate structure of fish taxocenes are similar for topographically comparable marine and freshwater habitats. Again, the case of the Lake Tanganyika sardines can serve as an example for a community structure similar to many marine pelagials in upwelling areas (Coulter 1970, Woodward 1974, Balon 1971, 1974). Furthermore, the increase in number of species and density after repeated rotenone samples at Nurse Cay, Bahamas (Smith 1973 and these proceedings) is very similar to the density and juvenile fish increase I obtained in a repeatedly rotenoned stream-cove of a tropical Zambezi reservoir (Balon 1974: 475). Given more data and also more communication between scientists active in marine and freshwater systems, I believe, most of the seemingly chaotic patterns will arrange themselves according to Mayr's (1976) idea that '... the solution of Darwin's paradox is that natural selection itself turns accident into design.'

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Department of Agriculture and Fisheries for Scotland
Freshwater Fisheries Laboratory
Faskally Pitlochry Perthshire PH16 5LB
Telephone STD 0796 2060

All communications to be addressed to The Officer in Charge

Dr R J Behnke
Department of Fisheries and Wildlife Biology
Colorado State University
FORT COLLINS
Colorado 80523, USA

Your reference

Our reference

JET

Date

8 July 1981

Dear Dr Behnke

I enclose a copy of the text of a paper which I presented at the Salmon and Trout Migratory Behaviour symposium, at the College of Fisheries, Seattle, in June this year. If you have time, I should be most grateful for your comments on the ideas embedded in it.

The paper was presented to provoke discussion, rather than to be assertive! It seems to me that the case for a marine or a freshwater origin of salmon and trout must remain an open one, but I find the argument in favour of a marine origin a useful working hypothesis in thinking about smoltification. It permits discussion of the behavioural, physiological and morphological changes associated with smolting in terms of proximate rather than ultimate factors, and avoids much of the teleology implicit in current views of the smolting process. What do you think?

I believe that you have recently completed a monograph on the American Salmoniformes: could you give me the complete reference to this, so that I can ensure our library obtains a copy rapidly? (If this is an official government sponsored publication, and you have spare copies, I should be most grateful for one myself, but I appreciate that you may not have these available for distribution.)

I look forward with interest to your comments.

Yours sincerely

JOHN THORPE

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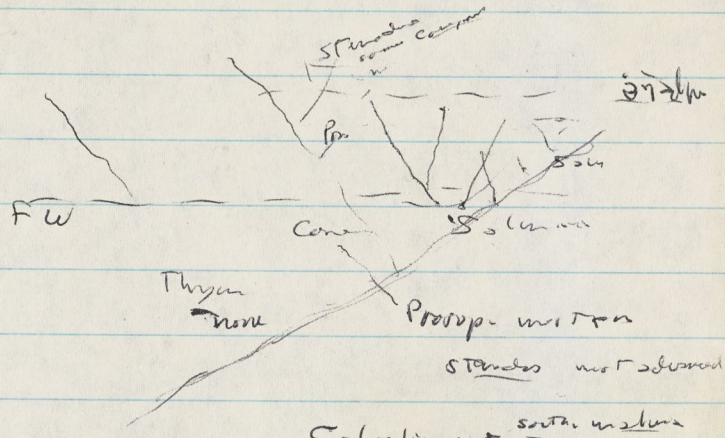
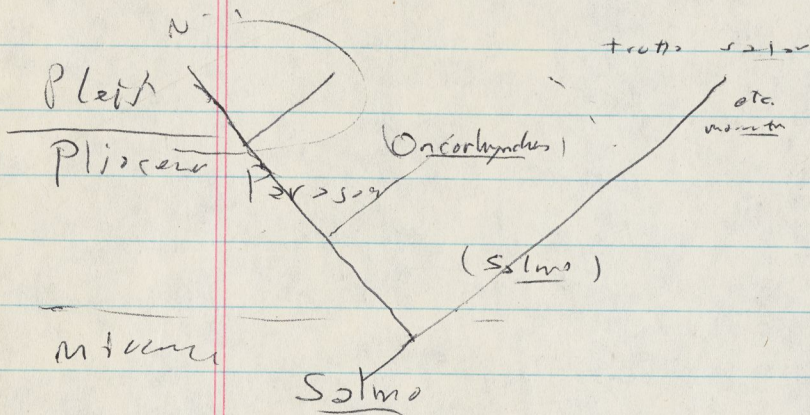
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- fossils

- O. not more prim. than Salmo

74 → 52 chrom & genome
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- Belen: Errors in chromosome pairs

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68 p. 1 - first submitted GC to Copps ^{revised to GC} rhodani Mason garbusha
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- Tms, p. 5 - Evol. trend in family appears to be toward total dependence on FW away from dependence on sea - ^{is} wrong.

- origin as marine pelagic fish - ^{Evolution from} 41,100 but ^{100,000} cretaceous

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MIGRATION IN SALMONIDS, WITH SPECIAL REFERENCE TO
JUVENILE MOVEMENTS IN FRESHWATER.

J. E. THORPE

FRESHWATER FISHERIES LABORATORY, PITLOCHRY. SCOTLAND.

MIGRATION IN SALMONIDS, WITH SPECIAL REFERENCE TO JUVENILE MOVEMENTS IN FRESHWATER.

J.E.Thorpe. Freshwater Fisheries Laboratory, Pitlochry. Scotland.

Abstract:

Balchen argued that migratory behaviour was a means of maximising comfort for the migrant. This paper considers life-history strategies of salmon, especially their migratory components within freshwater, from this point of view. Behavioural specialisations at successive growth stages represent compromises by the species, consequent on long-term genetic optimisation. Interpretations of the nature of these compromises depend on assumptions about the evolutionary history of salmonids. The historic arguments in favour of either a freshwater or a marine origin for the group are reviewed, and emphasis is given to Balon's interpretation of salmonids as neotenic marine fishes. The major implication of this argument is that specialisations during early life-history are adaptations of a marine animal to a freshwater habitat. Migrations during this period are interpreted as the consequences of a set of discomforts experienced by a marine animal, as each successive behavioural compromise is replaced by another.

Tinbergen (1963) pointed out that in order to understand behavior patterns it is necessary to study how the behavior adapts the organism to its environment, how the behavior evolved, how the behavior develops within the organisms own lifetime, and what mechanisms underlie that behavior. Crews (1960) has recently attempted such an integrated study of reproductive behavior in anoline lizards. The present short and selective review is an attempt to approach the subject of salmonid migrations at the juvenile freshwater stages from these four directions.

Migration: Balchen's hypothesis.

Balchen (1976) argued that fish migration was the outcome of "a simple-minded local process of maximising 'comfort'" for the migrant individual. By 'comfort' he implied some kind of nervous sensation which the fish acted to maximize or to minimize. Since the individual was simultaneously stimulated through a range of sensory modalities, its observed behavior might be interpreted as a compromise solution to a range of different types of 'comfort' problems. For example, Neill and Magnuson (1974) interpreted the behavior of yellow perch, Perca flavescens, which aggregated in water outside a thermal plume in Lake Monona, as behavioral thermoregulation which took precedence over the animals' feeding behavior which might otherwise have induced them to aggregate in an inshore area of more plentiful food organisms but a lethally high temperature. However, in experimental tanks, such fish would make forays from areas of preferred temperature to areas both above and below this temperature level to obtain food. In such a case the primary 'comfort' was optimal temperature, but 'discomfort' due to lack of food could ultimately compromise this, at least temporarily.

Balchen noted further that as hormonal activity changed seasonally, and as physiological tolerances changed with such activity and with stage of development, so the fish experienced changes in comfort which induced it to move and ultimately to settle in the situation of least discomfort. Such behavioral optimization he viewed as acting at 3 levels (Table 1), which he distinguished as momentary, dynamic, and genetic. His 3 levels lead to 3 levels of biological success: momentary optimization represents an instantaneously appropriate response to an external stimulus, resulting in survival of the individual. Such responses, repeated and refined over time define the dynamic level of optimization which results in the opportunity for the individual to grow and develop. The accumulation of a set of such dynamic optimizations defines the genetic level,

Behavioural Optimisation	Biological Success
Momentary Dynamic Genetic	Survival Growth Reproduction

since those individuals whose behaviour has been sufficiently close to optimal throughout development will succeed in reproducing, leading to the long-term fixation of evolutionarily proven successful behavioral strategies.

Salmonid life-history, strategy, and origins

Viewed from this stance, genetic optimization of behavior appears to have resulted in extensive migrations in the Salmonidae. But it is also clear that within the group as a whole the extent of these movements differs greatly between and within species. A range of complexity of life-history is found within each of the four main salmonine genera (Table 2), Oncorhynchus, Salmo, Salvelinus and Hucho. (cf. Rounsefell 1958, 1962) The simplest pattern in O.gorbuscha, the pink salmon, with almost total dependence on the marine environment, and a practically exact 2-year life-history; and perhaps the most complex in O.nerka, the sockeye salmon, with multiple year classes present simultaneously in freshwater and the sea, ability to mature before leaving freshwater, and ability to form wholly landlocked populations. This interspecific and intergeneric complexity of life-history strategy has led to discussion and argument about the evolutionary origins of the group. In considering the nature of migration in salmonids, and its motivation, it is appropriate to review these hypotheses briefly, as our concepts of the nature of these fishes assume one or other of the hypotheses implicitly.

The central question has been: did the salmonids originate in the sea, or in freshwater? Day (1887) and Regan (1911) considered that the family had a marine origin, probably derived from an ancestor similar to the modern wholly marine Argentina, and they argued that the present day distribution of salmonids could best be accounted for this way. They noted that no truly freshwater fishes (e.g. Cyprinidae) existed on oceanic islands, whereas salmonids did.

Genus	Anadromous only	Both	Non-anadromous only
Oncorhynchus	gorburcha	nerka	rhodurus (?)
Salmo	-	salar	aguabonita
Salvelinus	-	alpinus	namaycush
Hucho	-	perui	hucho

However, Tchernavin (1939) argued forcibly and authoritatively in favour of a freshwater origin for the group. He suggested that the simultaneous presence of freshwater resident and migratory forms within species indicated recent divergence, in which case the ancestral form should predominate. As there were no wholly marine forms among modern salmonids, then they could not have had a marine origin. This implied that Salmo, being least marine, was more primitive than Oncorhynchus. He explained the current distribution pattern of the family by analogy with that of many freshwater animals and other terrestrial organisms, proposing that distribution routes had been by freshwater, and that marine migration had only developed since the glacial period. Further, he argued that all Salmonidae breed in freshwater, require a current to ensure aeration of eggs in gravel redds, that their eggs are not fertilisable in seawater, and that homing to freshwater indicated the origin of the migratory habit. He speculated that the ancestral salmonids were small brightly coloured fish living in cool streams and lakes of the northern hemisphere, for whom habitat deterioration during glacial times forced emigration to sea, leading to size increase, and the development of smolt changes.

Neave (1958) assumed a freshwater origin for the genus Salmo, and argued that it had entered the Pacific coastal drainage by a freshwater route through North America. He considered that Oncorhynchus was derived from this invading Salmo, by isolation in an enclosed brackish sea in the Sea of Japan region during a lowering of sea level in the Pleistocene within the last million years. Subsequently the sea level rose, the newly evolved genus adapted to full seawater life, and invaded the rest of the North Pacific seaboard. In this argument he concurred with Tchernavin in the implication that Salmo was more primitive than Oncorhynchus, and that landlocked forms were relicts. Hoar (1958, 1976) accepted his argument, and on its basis concluded that those Oncorhynchus species which relied least on the freshwater environment, O.gorbuscha and O.keta, the pink and chum salmon, were the most specialised.

However, Mottley (1934) examined the interrelationships of rainbow trout populations (Salmo gairdneri) in western North America, and concluded that the species was differentiating into distinct forms as a result of physical isolation. It was implicit in his argument that the anadromous steelhead was the type form, and the various landlocked rainbow populations were derived from it. Similarly, the migratory coastal cutthroat trout populations (S. clarki) were the type form from which their landlocked populations of the interior had been derived.

The paucity of the fossil record has permitted the persistence of these speculative and inconclusive arguments. Teleosts are believed to have evolved in the sea (Darlington 1957). Recently Cavender (1970) concluded that the Salmonidae were relatively primitive, by comparing them morphologically with the earliest known teleost family, the Jurassic Leptolepidae. The salmonines departed slightly from the leptolepid pattern in the neurocranium, jaws, and jaw suspension, suggesting specialisations among salmonines to feeding predaceously. These earliest teleosts were probably highly successful exploiters of the pelagic habitat. Cavender and Miller (1972) then described a giant salmonid, Smilodonichthys rastrusus from Pliocene deposits in California and Oregon, which was evidently a pelagic planktivore. This 190 cm long fish possessed more than 100 long toothless rakers on each gill arch, toothless maxillae, and the fossils had a pair of huge premaxillary breeding teeth. The form of the premaxilla, breeding teeth, and dermal bone structure suggested closest similarities to Oncorhynchus among modern salmonid genera. Furthermore, alongside some of the fossil material were further fossils almost identical with present day O. kisutch, the coho salmon. This find, being about 5 million years old, calls in question Neave's whole argument about the relatively recent origin of Oncorhynchus, and the similarities between this genus and the extinct pelagic

Smilodonichthys suggest that it rather than Salmo may be the more primitive.

An argument from a quite different direction lends support to this. Balon (1968) reviewed the literature on the interrelationships between the different forms of Salmo trutta, the sea, brown and lake trout of Eurasia, and concluded that the landlocked forms had arisen by neoteny from the type-form, the sea trout. These forms reproduced at a generally smaller size than the anadromous form, but more importantly retained many juvenile characteristics when mature. (Exactly the same observation was made for rainbow trout by Mottley (1934), although he did not suggest neotenic development.) Recently Balon (1980) extended his argument to the salmonine fishes as a whole, and using the Russian system of classification of developmental intervals (Kryzhanovskii, 1949; Balon 1975) he pointed out that metamorphic changes at the adult stage were evident in Oncorhynchus in exaggerated form (dorsal humps, enlarged skulls and premaxillae), while only evident in reduced form in other salmonines (e.g. kype in large Salma salar, thickened skin in S. trutta). In these other genera reproduction occurring before such metamorphosis, without irreversible changes in form and function, allowed multiple spawning (Table 3). Such telescoping of developmental intervals, and the development of iteroparity, point to the advanced rather than primitive evolutionary status of Salmo as compared to Oncorhynchus.

Since it is the landlocked populations which show evidence of evolutionary advance through juvenilization, the evolutionary trend in the family appears to be toward total dependence on freshwater, and away from dependence on the sea. It is then appropriate to view the Salmonidae as relatively primitive teleosts, of probable marine pelagic origin, whose specialisations are associated with reproduction and early development in freshwater. A major implication of this assumption is that the freshwater phases of the life-history of salmonids are enabled by specific

Developmental periods	Oncorhynchus	Salmo
Embryonic	√	√
Larval	X	X
Juvenile	√	√ ISp
Adult	√ Sp	√ ISp ISp
Senescent	√	(√)

adaptations, which are superimposed on a basically marine organism. If that organism is to return to its ancestral environment (i.e. downstream migration to sea) and survive there, it must abandon such adaptations progressively.

What then are these adaptations, in what way do they change during freshwater residence of juvenile salmonids, what may motivate such changes, and what are the consequences in terms of migration?

Adaptations to freshwater life.

Embryonic period

At hatching the alevins are buried in gravel. It has been shown experimentally (Mason 1976; Dill 1977; Godin 1980a, b; Carey and Noakes 1981) (Woodhead 1951; Roth and Geiger 1963; Bams 1969; Dill 1969; Brannon 1972) that they are negatively photokinetic at this time, positively rheotactic, and also positively geotactic. All these features ensure that they remain protected in the stream or lake bed until shortly before their yolk supply is used up, when, if they are to maintain formed tissue and grow they must switch to an external source of food. At this time the sign of geotaxis is reversed, photonegativity becomes less intense, and rheotaxis varies between and within species. As a consequence they emerge from the gravel bed and enter an environment subject to high ranges of light intensity and water velocity. Positive thigmotaxis ensures contact with the substrate and aided by positive rheotaxis enables them to avoid immediate displacement downstream on the current.

Juvenile period

Thigmotaxis gives way to orientation with respect to conspecifics at different rates in different species. Hoar (1956) observed with pink salmon

fry that stream-bed oriented shelter responses were replaced by schooling responses within a day or two of emergence. Such behavior maintained the fish in mid-water, and although they were extremely active and positively rheotactic by day, their downstream migration at night would be aided by loss of visual orientation and passive displacement. Other authors (MacKinnon and Brett 1955; Neave 1955) recorded active downstream migration and vigorous swimming by pink fry. Emigration of this species and of chum (Hoar 1958) appeared to be achieved by both active and passive processes. In sockeye Brannon (1972) determined that the fry aggregated in shallow water either upstream or downstream of their emergence point according to the relative intensity of their rheotactic behavior and the velocity of the water, and that schooling behavior was evident almost immediately upon arrival in a lotic environment. Positive rheotaxis was maintained, so that these schools were not displaced downstream out of a lake, as Hartman et al. (1962) had also found. Among coho salmon Hoar (1958) noted habituation to environmental stimuli, such that an initial positive rheotaxis became station-holding rather than an attempt to swim into a current, and the fish did not respond greatly to changes in current velocity at that station. In Atlantic salmon, thigmotactic behavior persists for months or years after emergence. Positive rheotaxis ensures position holding in the stream, and this is reinforced by territorial behavior, implying attachment of an individual to a specific site, and defence of this site against conspecifics through elaborate agonistic behavior (Kalleberg 1958; Keenleyside 1962; Keenleyside and Yamamoto 1962). Similar social behavior has been reported in other salmonids with an extended juvenile period of residence in streams (Hoar 1951; Stringer and Hoar 1955; Lindroth 1956; Newman 1956; Kalleberg 1958; Chapman 1962; Hartman 1963, 1965; Jenkins 1969; Everest and Chapman 1972; Stanley and Northcote 1974; Chiszar et al. 1975; ^{Dill 1977; Cole and Noakes 1980).} Territoriality is associated primarily with occupation of a suitable station from which food can be acquired (Symons 1968, 1971; Wankowski and Thorpe 1979a). As optimal food particle size for growth increases

as fish sizes increases, the nature of territory must change to permit an adequate observation range over which the fish can intercept progressively scarcer particles of appropriate size (Wankowski and Thorpe 1979a, b). In Atlantic salmon such changes may lead to an alteration of social structure away from individual territoriality towards a hierarchial grouping and alteration of habitat into deeper or more open water (cf. MacCrimmon 1954; Saunders and Gee 1964). This is the first sign of a reduction in thigmotaxis and increased orientation towards conspecifics in young Atlantic salmon, but positive rheotaxis ensures that position is maintained usually close to the maximum locally available current velocity. Similar movement into areas of faster water velocity and open substrate occurs in coho and chinook salmon (*O. tshawytscha*) (Lister and Genoe 1970), and brook trout (*Salvelinus fontinalis*) (Saunders and Smith 1955) with growth.

Ontogenetic changes in adaptations, and migration.

Fry stage

It is clear that the juvenile salmonid is preoccupied with current velocity. Adaptations to contend with this dominating environmental feature may be modified seasonally - for example, at low winter temperatures stream-dwelling species are inactive, and hiding behavior in the gravel bed or deep pools ensures that the fish are not carried out of the system.

In sockeye Brannon (1972) showed that the threshold velocity at which a particular population of fry would hold station, or would actively swim upstream was genetically determined, and from his examples and descriptions it is likely that selection for high thresholds had occurred only where spawning took place downstream of nursery lakes suitable for the growth of fry. In other situations there would be little biological sense in wholesale upstream migration of fry,

since by implication this would be towards a less productive and less spacious environment, and any genetic tendency towards high levels of rheotaxis and high velocity thresholds would be selected against. Northcote (1969) reviewed work on the upstream and downstream lakeward movements of trout (rainbow, cut-throat and brown), and noted that the young of a Salmo species "may demonstrate almost as much variability in migratory behavior as is found among young of the whole Oncorhynchus complex". He found evidence of changes in direction of net movement of rainbow trout fry in the Lardeau River as temperatures rose from $<14^{\circ}$ to $>15^{\circ}\text{C}$, such that fry then moved 200 m upstream into Trout Lake instead of 56 km downstream into Kootenay Lake as the bulk of the population had done earlier. He verified experimentally that warmer water enhanced the likelihood of upstream migration of these fry. Whether the direction or the intensity of the fishes response is modified is not clear from Northcote's paper, but Keenleyside and Hoar (1954) showed that a sharp rise of $4 - 5^{\circ}\text{C}$ would induce a switch from positive (holding) to negative rheotaxis in chum and coho fry. The pronounced genetic control of response to current velocity that Brannon demonstrated for sockeye fry was not shown in the trout studies reviewed by Northcote. However he did suggest it in comparing the current responses of rainbows from above and below falls on Kokanee Creek. Among fry above the falls no downstream movement was recorded over a 15-month period: downstream movement was found from the fry below the falls during the summer and autumn. Without a high response threshold to current the population could not have been maintained above the falls. Brannon showed further that upstream migration at current velocities below the threshold level was modified olfactorily: sockeye fry would swim upstream only into a current originating from a lake. Responses to light also differed between populations of sockeye. Byrne (1971) recorded that fry were night-active at emergence from the gravel, but became day-active about 10 days later. However Brannon found that among those populations that migrated upstream from the redds to lakes, that migration took place "during or very close to daylight". He suggested that "fry need visual orientation to

complement a positive rheotaxis in sustaining upstream movement". Upstream migration of rainbow trout was also characteristically by day (Northcote 1969), and downstream movement by night. It would seem that there were adaptations reducing the likelihood of loss of position through passive downstream dispersal in mid water at night when visual orientation was lost. Such a mechanism of downstream migration was postulated by Hoar (1954), but Brannon did not accept this. He noted that downstream migrant sockeye observed by Hartman et al. (1962) at Brooks Lake, Alaska had shown negative rheotaxis, and swimming movements. The authors stated that these fish were "usually swimming faster than the current flowed", but gave no data on swimming speeds or the intervals over which the fish were active (cf. MacKinnon and Brett 1955; Neave 1955).

Parr and smolt stages

As downstream migration at the fry or any subsequent stage could be accomplished by passive displacement there seems little biological advantage in the migrant expending scarce energy resources in actively swimming. However Neave (1955) suggested that such behavior reduced the length of exposure to predators en route. The pattern seems to be associated with the schooling group - pink, chum and sockeye, and less evident, if present at all, in the territory holders - coho, chinook and Atlantic salmon. Tytler et al. (1978) tracked Atlantic salmon smolts through the lower reaches of two Scottish rivers, using ultrasonic tags. They proposed that emigration of this species was characterized by loss of affinity for a preferred site, resulting in downstream displacement in water velocities greater than 2 body lengths per sec ($b.l.s^{-1}$) between dusk and dawn in spring, with probable additional daytime displacement in summer. The data of Fried et al (1978), LaBar et al (1979) and McCleave et al (1978) for movement of smolts through the Penobscot estuary, Maine, were consistent with this model. They noted passive drift of smolts in surface flows in the estuary, and that here flow became the

the dominant factor controlling movement. Solomon (1978) concluded that because the smolts in a chalk stream were not migrating continually throughout 24 h, and that because they showed high activity levels, then migration must be active and not passive. But high activity also occurs in non-migratory fry at this time, and is independent of displacement: response to water velocity appears to be the critical feature (see below). However, a wholly passive emigration process might not account for movement through lakes. Thorpe et al. (1981) recorded the rate of passage of tagged smolts through Loch Tummel, Scotland, over two years. Hydrographic drogues set at 1 m depth travelled through the loch 3.7 times as fast as the smolts. If the fish had been displaced passively, they would have had to have been exposed to surface currents for only 6.5 h in any 24 h period: from data presented in Thorpe and Morgan (1978) the weighted mean diel period of activity of Loch Tummel smolts during March - May was 7.9 h, occurring at night. Movement of sonically tagged fish in Loch Voil confirmed that their movement occurred at night, was randomly oriented, and net displacement during their active period was equivalent to that of a drogue drifting at 1 metre depth. In these two lakes smolt migration could be accounted for by passive displacement, and no directional navigation needed to be postulated.

In this regard Atlantic salmon differ from the schooling sockeye smolts where Groot (1965) showed a well-directed active migration towards the lake outlet, at speeds of 2.3 - 3.9 b.l.s.⁻¹, equivalent to the fishes maximum sustained speed. Thorpe and Morgan (1978) found that Atlantic salmon smolts were unwilling to swim at more than 2 b.l.s.⁻¹, whereas as parr Wankowski and Thorpe (1979a) had recorded them holding position at up to 8.3 b.l.s.⁻¹ in the wild. Similar reduced swimming performance has been recorded in coho salmon smolts (Glova and McInerney, 1977; Flagg and Smith 1979). In Atlantic salmon, the authors interpreted this behavior as reduction in intensity of rheotaxis,

which resulted in passive downstream displacement at flows above 2 b.l.s^{-1} .

it would appear that the same mechanism may occur in coho, and enable a similar passive displacement response in this territorial riverine oncorhynchid.

It was noted above that progressive habitat change occurred in several stream-dwelling salmonids as they grew. These changes, being in the direction of faster flows and more spacious environments, lead down rather than upstream. Consequently at the final abandonment of freshwater at the smolt emigration a proportion of the downstream journey has already been traversed whereas for lacustrine species, after the initial movement from redd to lake such stepwise emigration may not occur. This difference could account for retention of an active directed emigration of sockeye, compared to its reduction or loss in the more advanced territorial riverine species.

Among several populations of Atlantic salmon downstream movements of juveniles have been noted in autumn (e.g. Calderwood 1906; Meister 1962; Mills 1964; Riddell and Leggett 1981; Youngson and Buck, in press). These movements may be associated with habitat deterioration during winter, and become fixed genetic traits (Riddell and Leggett 1931), but a recent study (Youngson and Buck, in press) has revealed a different element. The Girnock Burn is a small headwater stream in Aberdeenshire, Scotland. Migrants in this system have been censused at a trap close to its discharge into the River Dee, since 1967: the autumn emigration of juveniles has occurred over the period of upstream spawning movement of adults. The authors recorded a significant inverse relationship between the proportions of mature male parr among downstream migrants and the numbers of adult spawners ascending through the trap. In 197 no adults were permitted to pass upstream: in that year, mature parr made up over 50% of the downstream run of juvenile fish. King *et al.* (1939) recorded upstream migrations of mature Atlantic salmon parr at spawning.

These observations suggest an increased intensity of rheotaxis at spawning among mature juveniles, at a time of reduced rheotactic behavior among immature fish. Further, they suggest that the increase is transitory and that if spawning is not released, rheotactic intensity declines and the fish are displaced downstream. This would indicate the involvement of the pituitary-gonadal axis influencing behavioral response to water velocity, and a probable competitive relationship between maturation and downstream emigration. Thorpe and Morgan (1980) postulated such interference between smolting and maturation in this species from the consistent observation that fish which matured as parr one year and emigrated as smolts 6 months later, then returned as mature fish not 6 but 18 months after that (fig.4). Likewise, the faster-growing siblings in their hatchery populations smolted before reaching a size at which they would mature, but did not return to freshwater 6 months later when the slower growing siblings in these populations became ripe. Such a conflict of behavior could form a basis on which segregation into resident (residual) and migrant morphae occurs in sockeye (cf. fig.5, based on Ricker's (1938) study of the sockeye of Cultus Lake), masu (Oncorhynchus masou), and many Salmo and Salvelinus species. From such physiological competition it is easy to visualize the evolution of wholly landlocked forms, independent of physical barriers to downstream passage, and from these, through subsequent isolation, to new species.

Motivation for movement.

The behavioral changes discussed in the previous sections imply complex patterns of physiological change about which little is known for salmonids for the greater part of their freshwater juvenile period. Most physiological studies have concentrated on the parr-smolt transformation. These have been reviewed several times recently (Bern 1978; Wedemeyer et al. 1980; Folmar and Dickhoff 1981), and so will not be repeated here. The common implicit assumption of these studies

Spawning season	Age (yr)	Growth type	
		Fast	Slow
√	0	smolt	mature ♂ parr smolt
	0.5		
√	1	(a few mature)	mature ♂ parr smolt
	1.5		
√	2	mature	mature
	2.5		
√	3		
√	3.5		

Sibling: Salmo salar

Growth rate	Life - history type	
	Residual	Migrant
Very fast	✓	
Fast		✓
Average		✓
Slow	✓	

Oncorhynchus nerka :-
Sockeye salmon

has been that salmonids are freshwater fish, and the processes of smoltification are prospective adaptations, preparing the animal for life at sea. The teleological aspects of this argument do not arise if the alternative assumption is made, that salmonids are marine fish. Then the processes of change at smolting would be seen as reversions to basic patterns of control and regulation which have been suppressed during earlier developmental stages, as part of the complex of adaptations to freshwater life. This is the physiological equivalent of the model which envisages behavioral change by progressive abandonment of freshwater adaptations. Since physiologists generally have not adopted this assumption of the marine nature of salmon the model has not been tested, but some recent evidence exists in support of it.

Much physiological research on juvenile salmonids has been concerned with salinity relationships and hydromineral balance. In the sea salmonids must continually excrete sodium to maintain ionic balance. Prolactin has been shown to have osmoregulatory function, serving to reduce sodium efflux (Bentley 1971; Ng et al., 1980), necessary for ionic balance in freshwater. The activity of the prolactin producing mammotropes of the coho pituitary shows a progressive decrease from the freshwater parr stage to the smolt arriving in the sea (Bern 1978). These cells are rapidly reactivated if such smolts are transferred back into freshwater (Nagahama et al. 1977). Zambrano et al. (1972) noted a change in neurosecretory innervation of the prolactin secreting cells of masu salmon at smolting, and suggested that this was correlated with inhibition of prolactin secretion. Kubo (1955) and Folmar and Dickhoff (1981) showed that blood electrolyte levels were lowered in masu/at smolt migration. Thus prolactin is a prime candidate as an inhibitor of a marine regulatory process, which permits the salmon to live in freshwater, and when its activity is reduced progressively the fish leaves freshwater. This causal relationship has yet to be shown, but the removal of such an inhibitor would provide internal motivation for movement of the fish.

Weber and Smith (1980) have suggested a means by which this prolactin inhibition system is itself controlled. Melatonin increases plasma prolactin in rats, and removal of the pineal gland from goldfish Carassius auratus dampens the prolactin diurnal rhythm. Thus the pineal may regulate prolactin secretion through melatonin production. Their experiments on steelhead trout suggested that, as in rats, melatonin was synthesised in the dark, and that therefore increasing photo period in the spring would reduce melatonin production, thereby also reducing prolactin secretion. The importance of this light-pineal-pituitary axis for migration was emphasised, in that in mammals melatonin inhibits thyroid activity also, and pinealectomy of goldfish has suggested the same effect in fish (Fenwick 1970). Numerous authors have pointed to a role for thyroid hormones in salmonid migration (see Hoar 1976), through their effects on central nervous function, increasing responsiveness to external stimulation and their locomotor activity. The spring reduction of melatonin production would then release inhibition of thyroid hormone production, and the permissive role of these hormones would promote appetitive behavior exposing the fish to greater probability of displacement. Hoar and Bell (1950) noted that chum fry in freshwater were "under metabolic stress" which might increase activity. Baggerman (1963) showed that thyroid activity and salinity preference were positively correlated in juvenile Pacific salmon. Thus the removal of melatonin inhibition adds another inducement to the fish to move. Baggerman (1960) observed that sockeye fry tested in shallow tanks, preferred high salinities (‰) throughout the year in freshwater. But most sockeye fry stay in freshwater during that time, preferring a deepwater habitat in lakes by day, from very soon after emergence from the gravel (Brett 1971). Does the reduced light intensity at depth sustain melatonin production and thus inhibition of high thyroid activity and of seawater preference? In those populations of sockeye and of rainbow trout that moved upstream to lakes it was observed that they did so by day, whilst the downstream migrating stocks moved by night. Does light facilitate this movement,

by depressing the melatonin inhibition of thyroxine production thus maintaining a high level of response to water flow and high activity, until such time as deep lake water is encountered?

The brown trout of Loch Leven, Scotland, emigrate downstream from nursery areas into the loch during their first and second years, and at least the latter group have acquired the streamlined silver appearance of smolts at this time. On entry to the loch they are found on the shallow littoral for a short time, and then move to an offshore benthic habitat (Thorpe 1974; Arawomo 1977). Does this adoption of a low-light habitat reinstate the melatonin inhibition system?

Periodicity of movement in Atlantic salmon smolts was reviewed by Thorpe and Morgan (1973). Whereas downstream movement occurred in the spring during the expected nocturnal activity period, such movements were augmented by daytime activity in early summer. Furthermore, on entry to saline estuarial waters sonic tagged smolts were found to be displaced throughout 24 h periods in both a small Scottish estuary (Tytler et al 1978), and a large American one (La Bar et al. 1979). Such movement patterns may represent the waning effects of melatonin regulation as the photoperiod lengthens, and finally as the preferred ancestral saline environment is reached.

Another inhibition system may act through the gonads. It was noted above that mature Atlantic salmon parr are inhibited from autumn downstream migration. Peter (1978) recorded increased prolactin secretion influenced by oestradiol in Gillichthys mirabilis. This suggests that the influence of gonadal steroids on the osmoregulatory system would repay study in salmonids also.

Conclusions

The speculations of this paper are deliberate, to provoke reconsideration of the nature, motivation and control of the movements observed among juvenile salmonids in freshwater. Balon's hypothesis of the evolution of salmonid life-history strategies through penetration of freshwater by a pelagic marine fish, and progressive restriction of life-history to the freshwater habitat demands the acquisition of adaptations permitting survival, growth, and reproduction there. The salmonine genera show several ranges of evolutionary progression in this direction, with generally greater flexibility among Salmo and Salvelinus than among Oncorhynchus species. Behaviorally, the dominating physical feature of the freshwater environment with which the evolving fish had to contend was water velocity, and the common solution has been the evolution away from a schooling habit to individualistic, territorial, positively rheotactic stream-bed related behavior, ensuring retention in the system. The least advanced species in this respect, pink salmon, schools almost immediately on emerging from the gravel, and abandons freshwater promptly. The intermediate species show progressive delay before orientation to conspecific overrides orientation towards the river bed. Finally, the most advanced species are those which complete their life-cycle without leaving freshwater at all - Oncorhynchus rhodurus, and the "landlocked" morphae of O.masou, O.nerka, most Salmo and Salvelinus species. O.nerka shows an alternative solution to the problem, through adoption of lacustrine pelagic life, achieved without territorial development at the stream stage.

Physiologically the dominating problem was probably maintenance of hydro-mineral balance. Few experimental data are available to examine the evolutionary solutions to this problem, but inhibition of sodium loss was probably achieved chiefly through prolactin control, a mechanism probably regulated through a light-pineal-pituitary axis. The least advanced species show least evidence of

suppression of seawater preference, and early emigration from freshwater occurs. How the shallow water riverine species maintain inhibition of sodium efflux during long photoperiods remains to be shown, but a clue may exist in the apparent competitive relationship between smolt emigration and sexual maturation, suggesting an involvement of sex steroids in the maintenance of prolactin activity.

Salmonid migration viewed this way consists of progressive abandonment of specialised behavior and physiological mechanisms, differing in degree between species according to their level of development of such specialisations. It leaves a wealth of questions unanswered, but the present review is offered as an alternative framework within which to consider the nature of those migrations and their motivation.

Tables:

1. Balchen's levels of behavioral optimisation, and their corresponding results in terms of biological success.
2. Complexity of life-history strategy within Salmonid genera.
3. Developmental periods (*sensu* Balon 1975) in Oncorhynchus and Salmo, and spawning periods (Sp).
4. Age at smolting and at maturation in sibling populations of Atlantic salmon reared through the freshwater stage at the Almondbank smolt rearing station, Scotland.
5. Production of residual and migrant morphae among Cultus Lake sockeye salmon (after Ricker, 1938).

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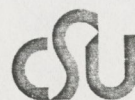
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Department of Fishery and Wildlife Biology

AIR MAIL



Colorado State University
Fort Collins, Colorado
80523

23 July 1981

Dr. John Thorpe
Freshwater Fisheries Laboratory
Faskally Pitlochry Perthshire
Scotland PH16 5LB

Dear Dr. Thorpe:

I enjoyed reading your speculations on the origins of salmonid migratory behavior. You wrote that your paper is intended to provoke discussion. This being the case, I will print out what I consider to be some serious logical flaws in the arguments you use to support your point of view.

I find two major problems: The first is that support for your contentions is based at phylogenetic levels--family, genus and species--and the second problem, which relates to the first, concerns making phylogenetic interpretations based on a character (anadromy) that must be considered as a plesiomorphous (a shared primitive state) character that also exhibits considerable convergence. That is, if I apply your ideas on anadromy to attempt to construct a phylogeny of salmonidae and compare it with a phylogeny based on other taxonomic evidence of primitive and derived character states some obvious nonconcordance results.

For contemplation on matters of the origin of Salmonidae--marine or freshwater--some thought must be given to defining Salmonidae and the original separation of the progenitor of the family from the other, most closely related, families in the order Salmoniformes--Osmeridae, Plecoglossidae, Salangidae (Northern Hemisphere) and Galaxiidae, Aplochitontidae, Retro pinnidae (Southern Hemisphere). The bulk of species in all of these family is anadromous. Thus, it appears that a common Mesozoic ancestor to all of them was anadromous. The anadromous ancestor to all of these families must have been derived, in turn, from a marine salmoniform that adapted to an anadromous way of life. The strictly marine ancestry in the phylogeny leading to Salmonidae must be very ancient; at a point prior to the separation of families of salmonoid fishes.

Polyploidy evidently played a role in the origin of Salmonidae. The subfamilies Thymallinae, Coreogoninae, and Salmoninae, all have about twice the DNA content in comparison to other salmoniform families. This polyploid progenitor of Salmonidae almost certainly spawned in freshwater, but was probably anadromous or estuarine, with the ability to osmoregulate in the ocean.

The origin of Salmonidae is probably very ancient. Fossils are known only since the Eocene but I suspect the origin is perhaps in the Cretaceous. Unless the fossil record becomes much better known and can contribute to our knowledge on the life history types of ancient ancestors, it is fallacious to argue for marine or freshwater origin of the family based on the degree of anadromy of living species. This is because, as can be observed among species of a genus, and even within a single species,

anadromy is highly variable and subject to convergent evolution--subject to change in evolutionary periods measured in thousands of years. To attempt to extrapolate these data from living species to monophyletic interpretations spanning perhaps 100,000,000 years since the origin of the family, is simply erroneous.

Your main contention is that a high degree of anadromy (more time spent in the sea) is primitive and a lesser degree of anadromy or a completely freshwater life history is the derived or advanced condition. The actual evidence is overwhelmingly against such a contention if the phylogeny based on the best available data is examined at the subfamily, genus, and species level.

The graylings are strictly freshwater. The most primitive genus of whitefishes, Prosopium, is strictly freshwater, while a few of the more advanced species of Coregonus are estuarine or semimigratory. Stenodus leucichthys, the sheefish, is anadromous (some populations) but is derived from a Coregonus-like ancestor. Thus, in the earliest branching of Salmonidae, a definite indication of a more completely freshwater life cycle is evident in two of the subfamilies. In Salmoninae, a strictly freshwater species, Salmothymus ohridanus, retains the most primitive osteological characters. Brachymystax is entirely freshwater. In Salvelinus, the evidence is variable but the most advanced forms (arctic charr, northern Dolly Varden), based on chromosome numbers and meristic characters (low numbers generally primitive, high numbers generally advanced), exhibit the highest degree of anadromy. In Salmo, the evidence is also variable but in the subgenus Parasalmo, the cutthroat trout species retains the more primitive structural features in comparison to the rainbow trout and is also much less anadromous than the rainbow trout. The Pacific Salmon (Oncorhynchus) is the most highly anadromous salmonid genus, but Oncorhynchus is not primitive. The evidence (skeletal features, lack of basibranchial dentition, high meristic counts, chromosomes) indicates a common origin for Oncorhynchus and Parasalmo after a separation from the subgenus Salmo (brown trout, Atlantic salmon). In Oncorhynchus, the most marine species, O. gorbuscha, is also the most advanced. Its chromosome number (52) is the lowest in the family and follows a regular trend of Robertsonian fusion within the genus from 74 to 52.

Salmo is certainly ancestral to Oncorhynchus, but as the fossil record now indicates and as can be observed from karyotypes, Oncorhynchus was not derived from a rainbow trout ancestor in the Pleistocene as proposed by Neave. In any event, your statement on page 5 that the evolutionary trend in Salmonidae appears to be towards a total dependence on freshwater is simply not supported and, in fact, contradicted by the taxonomic evidence correlating phylogeny with anadromy. At the subfamily, generic, and species level (comparing pairs of closely related species or subspecies within a species), the evidence is not completely uniform but there are certainly clear-cut trends that freshwater life cycles are primitive and anadromous life cycles are the derived condition.

Evidently you were influenced by Balon's publications. Balon originally submitted his 1968 paper to an American journal and I reviewed it. I found it full of wild, unsubstantiated speculation and with some outright errors. Balon is a charming gentleman but has the propensity to take bits and pieces

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of information and contort them to fit a preconceived idea. I saw Balon at a meeting in Canada in May and commented on his latest ideas concerning the correlation of salmonid phylogeny with his notions on embryology. He'll probably publish the work anyway and mislead others.

I wrote a "Monograph of the native trouts of the genus Salmo of western North America" for the U.S. Fish and Wildlife Service in 1979. This work was not published but some xerox copies were produced for distribution. You can write to Mr. Lee Mills, U.S. Fish and Wildlife Service, P.O. Box 25486, Denver Federal Center, Denver, CO 80225, and request a copy. I am now reorganizing and rewriting the original work. Hopefully it will be published this time before funds expire.

Sincerely,

Robert J. Behnke

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Ecology of Freshwater Fish

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Movement of brook trout (*Salvelinus fontinalis*) in four small subalpine streams in northern Colorado

Riley SC, Fausch KD, Gowan C. Movement of brook trout (*Salvelinus fontinalis*) in four small subalpine streams in northern Colorado. Ecology of Freshwater Fish 1992; 1: 112–122. © 1992 Munksgaard

Abstract – We studied the movement of brook trout (*Salvelinus fontinalis*) in four small streams in northern Colorado using mark-recapture methods and weirs. The recapture rates of marked adult trout were low for all streams, and large numbers of unmarked adult trout, apparently immigrants, were found each year. Significantly more trout immigrated into sections that were experimentally modified by installing low log dams, which increased depth, pool volume and the amount of overhead cover. The number of immigrant and resident trout was significantly related to the amount of cover in the sections. Resident trout were larger than immigrants in all streams in the last year of sampling. Most mobile brook trout moved upstream during summer on the two streams where weirs were operated, and upstream migrants were significantly larger than downstream migrants on both streams. We suggest that a high degree of movement may be an adaptive response by brook trout to the heterogeneous nature of small mountain streams.

S. C. Riley*, K. D. Fausch, C. Gowan

Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, USA

*Present address: Ocean Sciences Centre, Memorial University of Newfoundland, 4 Clark Place, St. John's, Newfoundland, Canada A1C 5S7

Key words: movement; dispersal; *Salvelinus fontinalis*; habitat; stream

S. C. Riley, Ocean Sciences Centre, Memorial University of Newfoundland, 4 Clark Place, St. John's, Newfoundland, Canada A1C 5S7

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Despite the existence of several classic papers on the subject (Skellam 1951; Howard 1960), the role of dispersal in the ecology of animal populations has not been firmly established. Dispersal behavior is heritable in a wide variety of taxa (Hilborn 1975; Rasmuson, Rasmuson & Nygren 1977; Ritte & Lavie 1977; Greenwood, Harvey & Perrins 1979; Berthold & Querner 1981), and several recent studies (Gill 1978; den Boer 1981) have elegantly demonstrated its importance to metapopulation dynamics. Although several models have been developed in an attempt to understand the adaptive significance of dispersal in heterogeneous environments (Gadgil 1971; Hamilton & May 1977; Comins, Hamilton & May 1980; Hastings 1983), our understanding is hampered by a lack of empirical studies.

Although the ecological and adaptive significance of anadromous salmonid migrations have attracted much attention (Leggett 1977; Quinn & Dittman 1990), the role of dispersal in the ecology of stream-resident salmonids is relatively poorly studied. In an influential paper, Gerking (1959) surveyed a number of studies on movement and

homing, and concluded that restricted movement of individuals was characteristic of many stream fish populations. Many studies on stream-resident salmonid populations (Miller 1957; Shetter 1968; Leclerc & Power 1980; Bachman 1984; Harcup, Williams & Ellis 1984; Nakano, Kachi & Nagoshi 1990; Heggenes, Northcote & Peter 1991) have also reported limited movement, and the general consensus among researchers is that the majority of adult stream-resident salmonids in a given population move very little.

Since stream-dwelling salmonids may often compete for space in streams (Chapman 1966), the nature of the available habitats may play an important role in determining movements (Northcote 1992). In this study, we attempted to determine the effects of an experimental habitat manipulation on the movement of adult (age 2 and older) brook trout in four small streams.

Material and methods

Study sites

This research was conducted in 500-m study reaches of four small, moderate-gradient (range 1.0–2.4%) streams in northeastern Colorado (Table

1). Study reaches on all streams contained little wood debris and had few pools. Late-summer baseflow discharge was less than $0.1 \text{ m}^3 \cdot \text{s}^{-1}$. Water chemistry is typical of subalpine streams in the area, with low alkalinity (range: $<5\text{--}51 \text{ mg} \cdot \text{l}^{-1}$), low conductivity (range: $35\text{--}117 \text{ }\mu\text{S}$), and barely detectable levels of nitrate nitrogen (range: $<0.02\text{--}0.18 \text{ mg} \cdot \text{l}^{-1}$).

The 500-m stream reaches were divided in half, and one section was randomly designated as the treatment section. In this way, the downstream sections of the North Fork of the Cache la Poudre River (hereafter the North Fork) and Walton Creek and the upstream sections of Colorado and Jack creeks were designated as treatment sections. Ten log-drop structures were installed in these 250-m treatment sections during the summer of 1988 by U.S. Forest Service personnel using only hand tools.

All of the streams support naturally reproducing populations of brook trout (*Salvelinus fontinalis*). Other fish species are rare in all streams except Jack Creek, which also supports a small (12–28% of fish caught) population of Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*). All streams were posted with signs declaring catch-and-release, fly-and-lure-only regulations within the research sections. These streams are remote, however, and creel survey data and time-lapse photography indicate that anglers visit them very rarely or not at all (Riley 1992).

Habitat

We used a transect method to describe the physical habitat of each study section. Permanent transects were established perpendicular to the stream flow at 5-m intervals. Depth, mean water velocity (measured at 0.6 total depth) and substrate (modified Wentworth classification; Orth 1983) were measured at 7 equidistant points on each transect at late summer baseflow in 1988, 1989 and 1990.

The pool volume of each section was estimated by measuring depths at 1-m intervals along transects established within areas identified as pools. Transects were spaced 1 to 5 m apart, depending on pool length. The volume of cells defined around each depth measurement was calculated, and summed to estimate total volume. Pool volumes were measured at baseflow, usually the same day as transect data were collected.

We carefully measured the lengths of 5 types of cover (undercut bank, log, overhanging vegetation, wetted brush and rock) in each section on the same day that pool volumes were estimated. To qualify as cover, objects were required to be at least 15 cm wide (except undercut bank, for which 10 cm was considered adequate), have at least 15 cm of water beneath them, and be no more than 15 cm above the water surface. Overhanging vegetation and brush were included as cover only if they concealed at least 50% of the area beneath from overhead view.

Electrofishing

We sampled each section during late summer baseflow at least once each year in 1987 through 1990. Jack and Walton Creeks were not sampled in 1987. We electrofished in an upstream direction using battery-powered electrofishing units operating at 250–400 volts direct current. The ends of each section were blocked with 5-mm-mesh seines before sampling to ensure population closure. In most cases, 3 electrofishing passes were made, although 4-pass estimates were conducted in Jack Creek (downstream section), Walton Creek (upstream section) and the North Fork (downstream section) in 1989. Care was taken to ensure that all habitat was electrofished and that effort remained constant on each pass (see Riley & Fausch in press for details). Both sections of each stream were usually sampled on consecutive days in any given year, and both were sampled within one week in all cases.

Table 1. Physical characteristics of study streams in northern Colorado. Trt=treatment, Ctl=control. Figures for pool volume and cover are means of all post-treatment estimates (1988–1990), while mean widths are expressed as the ranges for these years.

Stream	Longitude and latitude	Elevation (m)	Mean width (m)		Pool volume (m^3)		Cover (m)	
			Trt	Ctl	Trt	Ctl	Trt	Ctl
North Fork of the Cache la Poudre River	40°49' N 105°42' W	2730	4.0–4.5	2.9–3.8	132	19	89	57
Colorado Creek	40°28' N 106°37' W	2775	3.4–4.3	3.1–3.2	188	28	125	49
Walton Creek	40°23' N 106°42' W	2775	3.8	3.5–3.6	136	13	101	37
Jack Creek	40°25' N 105°59' W	2925	3.9–4.6	3.3–4.8	100	19	55	26

All fish captured during electrofishing were anesthetized (MS-222), measured (total length [TL] to the nearest mm), weighed (nearest g until fall 1988, nearest 0.01 g thereafter), fin-clipped (fish >69 mm only), retained in live baskets in the stream and released near their point of capture after processing. The left pelvic fin was excised on trout >69 mm captured in the downstream section of each stream on each sampling occasion, while the adipose fin was removed from those captured in upstream sections. Any previously excised fins that were beginning to regenerate were trimmed. In 1991, all brook trout >120 mm TL were marked with individually numbered Floy Fine Fabric anchor tags on Jack Creek and the North Fork.

In all streams, age-1+ trout were easily separated from older fish by examining length-frequency histograms. We calculated maximum likelihood removal estimates of trout population size for trout greater than 1 year old in each section using the generalized removal estimator of Otis et al. (1978) as computed by the computer program CAPTURE (White et al. 1982). We do not report the population estimates in this article, but we use the estimated capture probabilities to assess how well we sampled the sections.

On 10 occasions during 1988–1991, trout were held overnight in baskets to assess mortality associated with electrofishing and handling. Barrier nets were usually left in place to minimize the possibility of other trout immigrating during this period. Trout were released from the baskets the next day (14–18 h later) and mortality was recorded.

In August 1991, we electrofished the study sections on Jack Creek and the North Fork to look for fish tagged in the weirs (see below). On Jack Creek, we also electrofished 100 m upstream and 250 m downstream of the section enclosed by the weirs.

Weirs

In 1991, we constructed two-way weirs on Jack Creek and the North Fork. Three weirs were constructed on each stream (downstream end, between treatment and control, and upstream end) which allowed the capture of all fish moving into, out of, and between the study sections. Weirs were installed in reaches having mean column water velocities less than about $60 \text{ cm} \cdot \text{s}^{-1}$ and depths less than about 70 cm. It was not always possible to construct weirs at section boundaries because of unsuitable depths and velocities. On both streams, weirs were located within 50 m of the section boundaries, except the downstream weir on Jack Creek, which was located about 100 m below the downstream end of the control section.

Weirs consisted of upstream (i.e., opening facing downstream) and downstream traps separated by a series of panels oriented diagonal to the flow such that fish were directed to the appropriate trap. The weir design was similar to that described by Hall (1972). After installation, traps were checked via snorkeling and all gaps were repaired. Based on the mesh size and observations made while snorkeling, the weirs were effective at trapping fish >65 mm TL. Large cobbles and small boulders were placed in the traps to provide refuges for fish, and traps were covered to prevent predation.

The weirs were operated from July 15–August 18 and September 3–15 on Jack Creek and from July 13–August 15 and September 5–15 on the North Fork. Traps were checked daily when possible; checks were not made on a total of 10 days on Jack Creek and 8 days on the North Fork. Fish removed from traps were measured (TL, mm) and inspected for old fin-clips. For all fish <120 mm, a portion of a fin was excised which was unique to each weir: fish that passed the downstream, middle, and upstream weirs had portions of the right pelvic, right pectoral and anal fin excised, respectively. Fish >120 mm were tagged with uniquely numbered Floy Fine Fabric anchor tags except during July 19–29, when fins were excised as for smaller fish because of a shortage of tags.

Study sections were divided into subsections approximately 50 m long or shorter. The mid-point of each subsection was used to estimate the distances travelled by individual trout. For example, a fish marked at the downstream weir (0 m) and recaptured in the 50-m subsection immediately above it would be estimated to have moved a distance of 25 m. Thus, travel distances could be estimated to within approximately 50 m.

Results

Habitat

We present only a brief summary of the changes in habitat that resulted after log drop structures were installed (see Riley 1992). Log drop structures caused significant increases in pool volume and cover in treatment sections ($P < 0.05$ for both, by two-way analysis of variance (ANOVA)). Mean pool volume in treatment sections was 15.8 m^3 (SD = 15.9) before treatment and 128 m^3 (SD = 9.8) in 1990, while in control sections the means were 19.5 m^3 (SD = 9.2) before treatment and 17.8 m^3 (SD = 4.8) in 1990. The mean total cover in treatment sections increased from 41.6 m (SD = 32.6) before treatment to 76.2 m (SD = 11.2) in 1990, and total cover in control sections remained similar (35.6 m [SD = 14.8] before treatment, 28.6 m [SD = 16.0] in 1990). The mean depth was significantly

greater and the mean velocity significantly lower in treatment than in control sections after the installation of structures ($P < 0.01$ for both, by ANOVA).

Brook trout populations

Electrofishing. Estimated capture probabilities indicate that we captured at least 95% of the fish in each section on all but 6 of 30 sampling occasions, and at least 86% on 5 of these 6. The lowest percentage captured (76%) was in the North Fork in July 1988, which was most likely due to relatively high flows. In only 4 of 15 cases (North Fork July 1988, 1989, 1990; Jack Creek 1989) did the percentages estimated to have been captured in the two sections of one stream in a given year differ by more than 4%.

Of 2122 brook trout that were held overnight in baskets after electrofishing and handling, only 11 (0.5%) died. Eight of these fish were age 1+, and 3 were age 2+ or older. These results suggest that electrofishing mortality was very low on these 4 streams, especially for age-2 and older fish.

A large proportion (17.5–84.3%, median 52.0%, Table 2) of the age-2 and older brook trout sampled each year in all streams bore no fin clip that would

indicate that they had been captured previously. In 77% of the cases, fewer than 50% of the trout that we captured bore marks indicating that they were present in the section in question the year before. The possibility that fin regeneration may have rendered our marks unrecognizable is discounted because we have not observed this phenomenon on two similar nearby streams where trout > 125 mm were marked by both tagging and fin removal (S. C. Riley & K. D. Fausch, unpublished data). Moreover, recent data suggest that regeneration of the pelvic and adipose fins of age-0+ brown trout is not common (Johnsen & Ugedal 1988). Because very few age-1+ trout are too small to be marked, and our estimates of capture probabilities for this age class indicate that we generally capture > 85%, recruitment of a substantial number of unmarked yearlings from within the sections is also unlikely.

Table 2. Percentage of age-2+ and older brook trout sampled that bore finclips from previous sampling in 4 streams in northeastern Colorado. Stream codes: NFP=North Fork, CC=Colorado Creek, WAL=Walton Creek, JAC=Jack Creek. Treatment section is downstream in the North Fork and Jack Creek, upstream in Colorado and Walton Creeks.

Stream	Section	Date	Number captured	Percentage bearing clips from			
				Section where marked	Other section	Both sections	None
NFP	Control	07/88	44	52.3	0.0	0.0	47.7
NFP	Treatment	07/88	47	42.6	4.2	0.0	53.2
NFP	Control	08/88	58	50.0	8.6	1.7	39.7
NFP	Treatment	08/88	107	25.2	2.8	0.0	72.0
NFP	Control	08/89	93	31.2	16.1	1.1	51.6
NFP	Treatment	08/89	175	32.0	3.4	0.0	64.6
NFP	Control	07/90	102	33.3	10.8	3.9	52.0
NFP	Treatment	07/90	174	37.9	8.0	2.9	51.1
CC	Control	07/88	158	39.2	4.4	0.7	55.7
CC	Treatment	07/88	147	44.2	6.8	0.7	48.3
CC	Control	08/89	196	37.2	1.5	0.0	61.3
CC	Treatment	08/89	365	31.2	12.9	2.2	53.7
CC	Control	08/90	286	31.8	4.9	5.2	58.1
CC	Treatment	08/90	352	44.6	9.4	4.5	41.5
WAL	Control	08/89	177	78.5	4.0	0.0	17.5
WAL	Treatment	08/89	117	53.0	8.5	0.0	38.5
WAL	Control	08/90	173	64.7	6.4	3.5	25.4
WAL	Treatment	08/90	194	39.7	1.5	4.1	54.7
JAC	Control	08/89	69	18.8	0.0	0.0	81.2
JAC	Treatment	08/89	89	10.1	4.5	1.1	84.3
JAC	Control	08/90	87	43.7	4.6	0.0	51.7
JAC	Treatment	08/90	115	33.9	17.4	0.9	47.8

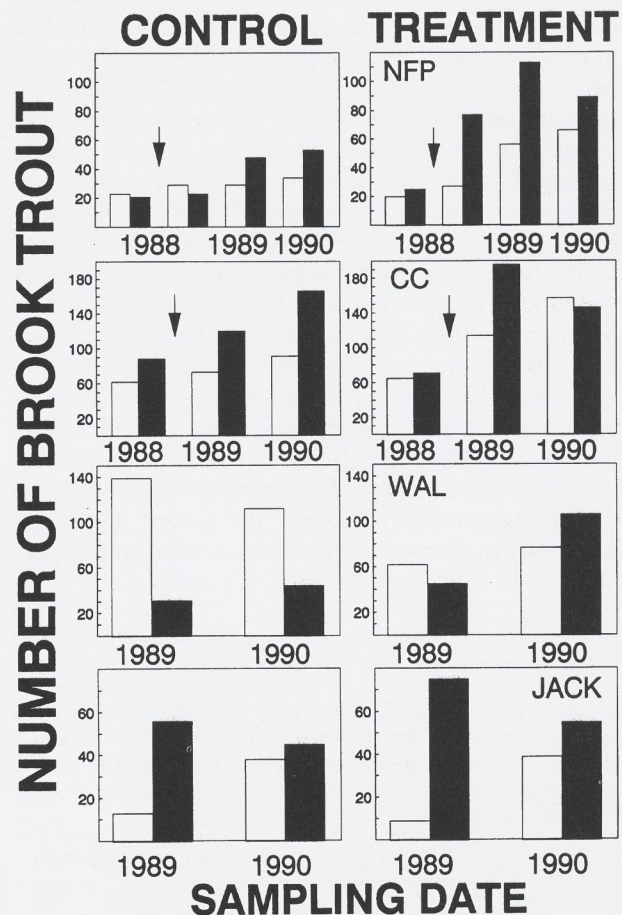


Fig. 1. The number of immigrant (solid bars) and resident (open bars) brook trout in treatment and control sections of four streams in northern Colorado. Stream codes are as in Table 2 and appear in the right panel. Arrows indicate the date when log-drop structures were installed; structures were installed the year before the first samples shown for Walton and Jack creeks. Immigrant trout were those with no finclip, while residents were those which bore only a finclip indicating prior residence in the section (see text).

Because we captured most of the population when we electrofished, most unmarked brook trout must have been immigrants to our sections. We did not consider as immigrants any trout that originated in the adjacent section in order to avoid any bias that might be due to fish displaced by our sampling, so our estimates of the number of immigrant trout are conservative.

There were more immigrant brook trout in treatment sections than in control sections in all post-treatment samples, except the 1990 sample from Colorado Creek (Fig. 1). The two pre-treatment samples (Colorado Creek 1988, North Fork July 1988), however, suggest that the numbers of immigrants in the treatment and control sections were similar before treatment. The number of immigrant brook trout in post-treatment samples was significantly greater in treatment than control sections ($P=0.03$ by paired t -test).

We estimated the number and percentage of trout that remained in the study sections between annual sampling occasions by comparing the number captured that bore the appropriate finclip with the number of marked trout known to have been present on the previous sampling occasion, including age-1+ fish (Table 3). We used only trout with the correct section finclip for this analysis, because trout with both finclips might have immigrated from the other section between samples. The number of appropriately marked brook trout that were captured in their section of origin (resident trout) was consistently less than 50% (22.1–41.6, median 30.2%) of the number of known to have been present on the previous sampling date. Overall, there was no significant difference between treatment and control sections with respect to the proportion of resident trout ($P=0.89$ by paired t -test on arcsine-transformed proportions). The mean per-

centage of fish that remained in the study sections was almost identical for treatment (31.9%) and control (31.5%) sections.

Although the percentage captured remained similar, the number of resident trout increased in the treatment sections of Colorado Creek and the North Fork after log drop structures were installed, while remaining similar in control sections (Table 3, Fig. 1). The number of residents also increased in the treatment section of Walton Creek in post-treatment samples, while declining in the control section, although initially there were more than twice as many residents in the control than the treatment. There appears to be no difference between the sections on Jack Creek.

We related the number of resident and immigrant trout in the sections to 3 habitat features that changed as a result of our treatment (pool volume, total length of cover, and the percentage of transect depths greater than 30 cm for both the year in question and the preceding year) using linear regression on post-treatment samples (1989 and 1990, $n=14$). All pairs of independent variables were significantly correlated both within and among years ($P<0.05$ in all cases), so multiple regression was deemed inappropriate. The number of immigrants was positively related to cover in the year of sampling ($r^2=0.34$, $P=0.03$), and the number of resident trout was positively related to the cover estimates for the preceding year ($r^2=0.33$, $P=0.03$).

The mean lengths of immigrant brook trout were not significantly different from residents on the first recapture occasion (1988 in Colorado Creek and the North Fork, 1989 in Walton and Jack creeks) in all sections except the upstream (treatment) section of Jack Creek, where residents were significantly larger (Table 4). Resident trout were significantly larger in both sections of Colorado Creek in 1989 and in both sections of all streams in 1990.

Weirs. A total of 322 brook trout were captured during the 49 days that the traps operated on Jack Creek. Trap mortality was 2.3% for fish captured in downstream traps (i.e. those with openings facing upstream) and 0.3% for upstream traps. Trap mortality was higher in the North Fork; 22 of 267 trout captured were found dead (8.2%), all in the downstream traps. It is unlikely that this was caused by the traps themselves, because the traps were of identical construction in both streams and were deployed in reaches with similar habitat characteristics. Fish found dead or dying in the North Fork traps were diseased, and many appeared to have died before reaching the traps. The

Table 3. Number of marked brook trout that remained between annual samples in treatment and control sections of four experimental streams in northeastern Colorado. Stream codes are as in Table 2. Trout that remained were those with only the correct section clip. Those with both finclips were not considered because they could have immigrated from the other section between sampling occasions. Numbers are also expressed as percentages of the number of trout with the correct finclips (including age-1+) known to have been present on the previous sampling date.

Stream	Section	1987–1988		1988–1989		1989–1990	
		<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
NFP	Control	36	36.4	29	31.2	34	26.0
NFP	Treatment	34	42.5	56	40.6	66	24.0
CC	Control	62	28.8	73	30.2	91	31.8
CC	Treatment	65	24.2	114	36.2	157	30.5
WAL	Control			139	36.6	112	41.6
WAL	Treatment			62	22.1	77	35.0
JAC	Control			13	23.2	38	30.2
JAC	Treatment			9	29.0	39	30.2

Brook trout movement

Table 4. Mean lengths of resident and immigrant brook trout in 4 streams in northeastern Colorado. Stream codes as in Table 2. Significance of differences in mean length between residents and immigrants by *t*-test is indicated in the far right column: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS=not significantly different.

Stream	Date	Section	Residents			Immigrants			
			Mean length (mm)	Standard deviation	<i>n</i>	Mean length (mm)	Standard deviation	<i>n</i>	
NFP	07/88	Control	150.9	26.5	23	153.9	30.1	21	NS
NFP	07/88	Treatment	154.1	24.1	20	147.2	28.7	25	NS
NFP	08/88	Control	157.7	26.6	29	163.3	30.7	23	NS
NFP	08/88	Treatment	163.5	25.9	27	162.5	24.6	77	NS
NFP	08/89	Control	148.0	29.6	29	142.7	23.2	48	NS
NFP	08/89	Treatment	156.4	30.8	56	148.1	26.6	109	NS
NFP	07/90	Control	158.5	36.0	34	130.3	26.2	53	***
NFP	07/90	Treatment	157.6	33.3	66	132.0	28.0	89	***
CC	07/88	Control	138.9	23.7	62	136.0	22.8	88	NS
CC	07/88	Treatment	134.8	26.0	65	138.0	28.7	71	NS
CC	08/89	Control	156.1	26.1	72	130.3	22.6	120	***
CC	08/89	Treatment	137.0	27.2	114	129.0	19.4	196	**
CC	08/90	Control	147.6	25.2	91	129.4	20.3	166	***
CC	08/90	Treatment	131.5	21.7	157	124.9	20.2	146	**
WAL	08/89	Control	157.9	18.1	139	157.0	15.5	31	NS
WAL	08/89	Treatment	164.5	16.7	62	161.6	17.1	45	NS
WAL	08/90	Control	164.5	20.1	112	145.1	15.1	44	***
WAL	08/90	Treatment	163.4	22.1	77	150.9	16.8	106	***
JAC	08/89	Control	165.2	25.8	13	152.6	26.4	56	NS
JAC	08/89	Treatment	183.0	24.4	9	155.1	26.6	75	**
JAC	08/90	Control	152.0	23.7	38	137.0	20.2	45	**
JAC	08/90	Treatment	152.6	26.8	39	138.1	24.2	55	**

reason for the high incidence of disease is unknown.

Brook trout movement in both streams was predominantly upstream; 79 and 71% of all trout captured were in upstream traps on Jack Creek and the North Fork, respectively. Upstream captures were significantly greater than downstream captures on both streams ($P < 0.0005$ by chi-square), as was a tendency for more total captures at downstream weirs ($P < 0.01$ for Jack Creek, $P < 0.05$ for the North Fork, by chi-square).

In Jack Creek, the number of brook trout captured decreased steadily from approximately 10 fish per day during the first three weeks to fewer than 2 fish per day by mid-September. Linear regression of trout captured per day by sampling date revealed that this trend was significant for fish moving both upstream ($r = 0.37$, $P < 0.01$) and downstream ($r = 0.46$, $P < 0.01$). By contrast, the total number of trout captured per day in the North Fork remained relatively constant at approximately 5 fish per day. This constant rate of capture represents a balance between an apparent, but not significant, increase in upstream captures and a significant decrease ($r = 0.31$, $P < 0.05$, by linear regression) in downstream captures over the sampling period.

Brook trout captured in downstream traps in Jack Creek were smaller (mean TL [SE] = 123.5 mm [3.8]) than those captured in upstream traps

(135.6 mm [2.0], $P < 0.05$ by *t*-test). The same was true in the North Fork, where upstream migrants averaged 164.2 mm TL (SE = 2.4) and those moving downstream averaged 139.5 mm (SE = 5.0, $P < 0.05$).

We conducted 3 electrofishing passes in the treatment and control sections of Jack Creek while the weirs were in place, allowing us to evaluate the effects of our sampling on trout movement. Movement rates in the 7-day periods before and after electrofishing in the control section (July 31, 1991) were not significantly different. Movement rates were also not different before versus after sampling the treatment section on August 14, except for a reduction to 2.5 trout per day on the day after sampling. This was likely caused by barrier nets above and below the section, which were left in overnight while fish were retained in live baskets to assess mortality. The movement rate increased to approximately 5 fish on the second day after electrofishing and remained there. These results lead us to conclude that our electrofishing had little effect on trout movement (cf. Moore, Larson & Ridley 1985) and certainly did not cause emigration.

There was no significant difference in the number of brook trout that emigrated from the treatment (98) and control (108) sections of Jack Creek during the trapping period. On the North Fork, however, significantly fewer fish emigrated from

the control section (58) than from the treatment (91) ($P < 0.01$). There were no significant differences between the number of trout immigrating into treatment and control sections on either stream.

On Jack Creek, most tagged brook trout tended to remain within 100 m of the location where they were originally marked (Fig. 2). Of the 91 recaptures by weirs and electrofishing, 41 (45%) were made within the same reach (approximately 50 m) as the initial capture. Most of these trout were captured passing upstream through a trap and then recaptured the next day passing downstream at the same weir. Of the fish that did move to other locations, 90% moved upstream. The mean distance moved by Jack Creek brook trout was 68.3 m upstream.

On the North Fork, unlike Jack Creek, most recaptured brook trout did not remain in the same reach, but moved upstream (Fig. 2). Of the 69 recaptures, 52 (75%) had moved upstream and only 11 (16%) remained in the same location. The mean distance moved by brook trout in the North Fork was 125.8 m upstream, almost twice the mean distance in Jack Creek.

Discussion

Dispersal is known to occur at several stages of the life history of stream-resident salmonids. Fry often disperse after emergence (Elliott 1966, 1987; Randall 1982; Moore & Scott 1988), and adults may move upstream to spawn (Schuck 1945; Solomon & Templeton 1976; Northcote 1978), although

the latter may not be necessary in streams where suitable spawning areas are ubiquitous (Needham & Cramer 1943; Miller 1957; Hesthagen 1988; Nakano et al. 1990). Considerably less is known about movement of stream salmonids between the end of the first year of life and maturity. An understanding of movement is essential if we are to effectively manage stream salmonid populations.

Several authors have postulated the existence of two components of stream fish populations: a large static and a small mobile component (Funk 1955; Gerking 1959; Flick & Webster 1975; Solomon & Templeton 1976; Harcup et al. 1984; Hesthagen 1988; Heggenes et al. 1991). Static trout establish territories or dominance hierarchies and remain within a restricted area, while mobile trout are presumably those that are unable to establish themselves.

Our results suggest that, among years, a large proportion of the brook trout in the four streams that we sampled are mobile (Tables 3, 4). Recapture rates of less than 50% have also been reported in other studies of trout and salmon (Shetter & Hazzard 1938; Logan 1963; Stefanich 1951; Holton 1953; Smith & Saunders 1958; Saunders & Smith 1962a, b; Hillman, Griffith & Platts 1987; Cunjak & Randall in press). It is important to note that low recapture rates alone do not necessarily indicate a high degree of movement, since mortality may be high. The fact that we observed large numbers of immigrant trout in our study sections, however, does indicate that many brook trout in these streams are mobile.

This suggests that movement of stream-dwelling trout may be common, yet the general consensus among salmonid ecologists is that resident trout undertake only limited movements (Miller 1957; Bachman 1984). This apparent contradiction may be because most studies focus on recaptured fish, and sampling rarely extends far enough to include long-range movements. What these data suggest is that movements of the static fraction of the population are limited.

The scale at which movements are studied varies widely, but the ability to detect and classify movements depends greatly upon the scale at which the research is conducted. For example, research conducted at smaller scales may be able to distinguish significant short-range movements, but gives no information about longer movements. Studies of salmonid movement are not at all standardized in this respect, and comparison of data is therefore difficult. It is doubtful that we will fully understand the significance of dispersal in salmonids until comparable experiments are conducted in a variety of streams in different biomes.

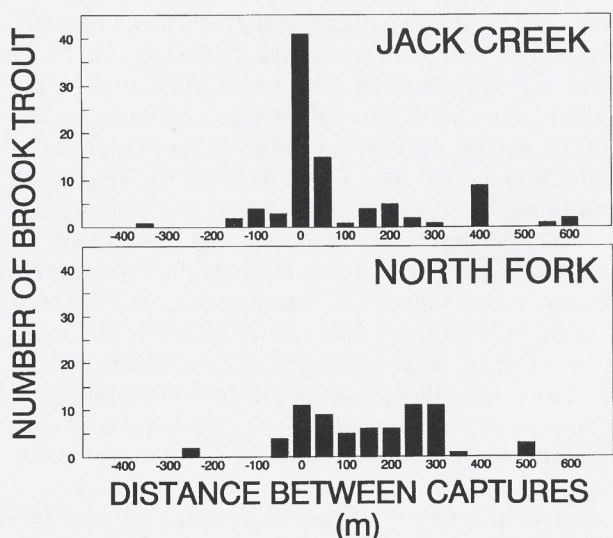


Fig. 2. Frequency distributions of the distance between captures of marked brook trout in Jack Creek and the North Fork of the Cache la Poudre River. Trout were captured in weirs and by electrofishing.

The results from our trapping and electrofishing indicate that brook trout in Jack Creek and the North Fork tended to move upstream during the summer. A tendency toward upstream movement by stream-resident brook trout has also been noted by Saunders & Smith (1962b) in New Brunswick and Flick & Webster (1975) in New York. Chisolm, Hubert & Wesche (1987), however, found that radio-tagged brook trout tended to move downstream during winter in Wyoming.

Most research dealing with the release of hatchery-reared salmonids has indicated a propensity for downstream movement (Cobb 1933; Hoover & Johnson 1937; Shetter & Hazzard 1940; Smith 1940; Trembley 1944; Cooper 1952; Cresswell 1981; Helfrich & Kendall 1982), but no such generalization is warranted for wild trout. Since hatchery trout may often be excluded from access to territories by residents (Bachman 1984), it is possible that subordinate trout may generally tend to move downstream. Our observation that brook trout moving downstream were smaller than upstream migrants supports this idea. Needham & Cramer (1943) also found that brown trout moving upstream in Convict Creek (California) were larger than downstream migrants, but the difference was not tested. Although our results suggest that downstream and upstream migrants are different, little can be inferred without further study.

Our results indicate that resident brook trout were larger than immigrants on all streams by 1990 (Table 4). A similar tendency for smaller salmonids to be more mobile has been noted in some studies (Miller 1957; Saunders & Smith 1962b; Nakano et al. 1990), but not in others (Harcup et al. 1984; Cunjak & Randall in press). Hesthagen (1988) found that mobile brown trout were larger in reaches with high population density. Heggenes et al. (1991) noted that larger cutthroat trout tended to move farther in a small British Columbia stream, although the relationship was weak.

A tendency for resident trout to be larger than immigrants would be expected if mobile trout were being excluded by larger, dominant individuals. This possibility is also supported by the observation that salmonid movement rates may be related to local population density (Jenkins 1969; Flick & Webster 1975; Harcup et al. 1984; Hesthagen 1988), although this has not always been observed (Bjornn 1971; Mense 1975; Heggenes 1988). Dominance and aggression among salmonids is thought to play a major role in controlling population density, and therefore emigration, in streams (Chapman 1962; Symons 1971; Grant & Kramer 1990). The fact that resident trout have not always been observed to be larger (such as the 1988 and 1989 results from this study), however, suggests

that other factors may be involved in initiating movements.

We observed significantly more immigrant trout in treatment sections than in control sections. In turn, the number of immigrant and resident trout was significantly related to the amount of cover, which along with pool volume and depth was significantly greater in treatment than control sections after logs were installed. Hunt (personal communication cited in Chapman & Bjornn 1969) found that habitat alterations which increased primarily cover, along with pool area and depth, resulted in a decreased rate of emigration from the treated section of a Wisconsin stream. The importance of cover in determining the distribution and dispersal of trout in streams has also been reported by other investigators (Chapman & Bjornn 1969; Hunt 1971; Devore & White 1978; Nielsen 1986; Cunjak & Power 1987; Mesick 1988). Our trapping data did not indicate that emigration was lower out of, or immigration greater into, treatment sections during summer, which suggests that habitat-related movements in these streams may be important during some other period. Several investigators have suggested that winter habitat plays an important role in salmonid movements (Bjornn 1971; Tschaplinski & Hartman 1983; Chisholm et al. 1987; Hillman et al. 1987; Cunjak & Randall in press); this possibility deserves further study.

Movement of stream salmonids may be affected by a number of factors, including water temperature (Chapman & Bjornn 1969; Bjornn 1971; Hillman et al.), flow regime (Manion 1977; Montgomery et al. 1983), fish size (Miller 1957; Solomon & Templeton 1976), local population density (Harcup et al. 1984; Hesthagen 1988), winter conditions (Cunjak & Randall in press), the presence of non-salmonids (Flick & Webster 1975), and habitat characteristics (Bjornn 1971; Hutchings 1986; Heggenes et al. 1991). The quality, quantity and location of habitats within a stream are likely to be among the more important factors controlling salmonid movements. Salmonids may change habitats between day and night (Edmundson, Everest & Chapman 1968; Bachman 1984), seasonally (Rimmer, Paim & Saunders 1984; Cunjak & Power 1986; Hillman et al. 1987; Baltz et al. 1991; Nickelson et al. 1992) and as they grow larger (Kalleberg 1958; Chapman & Bjornn 1969; Baltz & Moyle 1984), and all of these habitat shifts may require movement.

In general, one would expect dispersal to increase as habitats become patchier (Wiens 1976; Horn 1984). Because small mountain streams are patchy mosaics of shallow, relatively inhospitable riffles and deeper, quiet pools, salmonid movements within these streams may primarily be adap-

tive responses to shifting habitat availability and requirements. In this sense, habitat may be the ultimate factor controlling movements, and aggression by conspecifics simply a proximate stimulus (cf. Fretwell & Lucas 1970; Gadgil 1971; Lomnicki 1978). Movement may therefore largely be a function of population size and structure. For example, if recruitment is too great to be supported by the habitat, or if habitat quality is less than usual (such as in a year with low flow), one might expect a greater influence of territorial aggression on movement. This is supported by our observation that more brook trout moved, and moved farther, in the North Fork than in Jack Creek, since population density is greater in the North Fork (Riley 1992).

It is important that we develop a more complete understanding of the factors that affect movement in salmonid populations, because this will affect our ability to make inferences about other aspects of their biology. This is perhaps best illustrated by the example of correlative habitat models (for example, Binns & Eiserman 1979), which are becoming common management tools in the United States. If a substantial proportion of the individuals in a stream are transients, then abundance or biomass data collected for that population may not accurately reflect the quality of the habitat (cf. Van Horne 1983). Similarly, the degree of movement will affect the scale at which salmonid populations should be studied, since we observed that habitat manipulation affected immigration from outside the treated sections. Thus, a better understanding of dispersal in stream salmonid populations is necessary for good management.

Resumen

1. Hemos estudiado los movimientos de *Salvelinus fontinalis* en 4 ríos del norte de Colorado (USA), utilizando métodos de marcaje-recaptura y azudes.

2. En todos los ríos, la tasa de recaptura de adultos marcados fué baja y cada año se encontraron mayores números de truchas adultas no-marcadas, aparentemente inmigrantes.

3. Significativamente más truchas inmigraron dentro de aquellas localidades que fueron experimentalmente modificadas instalando pequeños azudes que resultaron en un incremento de la profundidad, el volumen y la cantidad de cubierta. El número de truchas inmigrantes y residentes está significativamente relacionada con la cantidad de cubierta en las localidades.

4. En todos los ríos, durante el último año de muestreo, las truchas residentes fueron mayores que las inmigrantes. Las más móviles, migraron aguas arriba durante el verano en los 2 ríos donde funcionaban los azudes. En ambos ríos, las migrantes río arriba fueron significativamente mayores que las migrantes río abajo.

5. Sugerimos que un alto grado de movimiento puede ser una respuesta adaptativa de las truchas a la naturaleza heterogénea de los pequeños ríos de montaña.

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