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X. THE MIGRATORY BEHAVIOUR OF JUVENILE ATLANTIC SALMON

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Abstract

Migration is a fundamental biological response to adversity. Salmon move progressively from one habitat to another as a habitat ceases to satisfy their changing needs. Hatching from the egg into the gravel redd, emerging from the redd onto the stream bed, moving away to establish a feeding territory, moving downstream to deeper water over winter, and finally emigrating from freshwater to sea - all these are abandonments of habitats once they can no longer satisfy the salmonsí needs. The downstream migration of smolting fish is interpreted chiefly as the eviction of an organism which is losing freshwater adaptation, involving physiological, behavioral and morphological components. Final passage through the estuary is complicated by rhythmical tidal current reversal and salinity increase, and temperature conditions modify the diel pattern of activity. Because the evolutionarily refined timing of arrival in the sea is critical for smolting salmon at any one river mouth, the construction of estuarine barrages poses serious problems for the maintenance of viable salmon populations in those rivers.

Introduction

Discussions about salmonid migration tend to focus on the ultimate regulators of the process, on the evolutionary advantages, and the mechanisms used by the animals in achieving migratory goals. But among the many definitions of migration the most useful is that of Taylor and Taylor (1977), that migration is a fundamental biological response to adversity. This turns the focus on to the proximate mechanisms. Put another way, this definition says that when an animalís needs are being met it stays where it is: when they are not, it moves until they are. So questions about the proximate causes of migration need to ask what was so wrong about the animalís current habitat that the animal was induced to leave it.

During ontogeny the needs of all animals change, and with those changes come niche shifts. It is the movements associated with these predictable patterns of change which characterise migrations, although the more dramatic long distance movements tend to dominate the discussions of salmonid migration. The sequence of Atlantic salmon migrations starts with hatching, followed by emergence from the gravel redd, movement away from the feeding areas, later movement to wintering areas, and then ultimately emigration from the freshwater nursery habitats to the pelagic adolescent growing habitat in the ocean.

1. The embryo stage

The embryo develops satisfactorily within the egg until the point where the protective advantage of the chorion is outweighed by its physical restriction for further growth. The hatching embryo trades this security for the relatively less restricted but potentially more dangerous environment of the gravel redd. The precise cues initiating this emigration from the egg are not entirely clear, but once the hatching gland is active the animal has some latitude in timing its emergence. Within the redd, embryonic growth can proceed protected from the majority of predators, and negative photoresponses ensure that any movements during early life take the animal deeper into the gravel. However, as the yolk becomes depleted to the point at which it is only just sufficient to maintain the formed embryonic tissue, survival is threatened and the alevin now trades the security of the redd for the opportunity to obtain external food. It emigrates into the surface gravel and eventually on to the open stream bed. Here, positive rheotaxis ensures that it takes up a position heading into the current on which are carried the drifting particles which will now constitute the majority of its diet. Further, positive thigmotaxis ensures that it remains in contact with the substratum, which serves to prevent downstream displacement, and keeps it close to shelter from potential predators.

2. The fry stage

Salmon redds may contain several thousand eggs, and so even if only 10% of the alevins survive to emerge as fry, this still implies densities of several hundred individuals in a few square meters of stream bed. Recent studies have shown that alevins may disperse within the gravel before emergence, such that fry may appear first above the gravel surface several meters away from the original redd. Within a single sibling group the individuals vary in their metabolic rate (Metcalfe *et al.*, 1995) and this is reflected in their social behavior (Metcalfe *et al.*, 1989). Individuals with high basal metabolic demands tend to be more aggressive, and to dominate those of lower metabolic rate. Social interactions lead to spacing of individuals on the stream bed, and gradually spatial territories are formed. This results in a mosaic pattern of occupancy of the stream bed, the territories consisting of a defended position on which the individual can sit and wait to obtain drift particles carried towards it on the current, and from which it has quick access to refuge from predators (Kalleberg, 1958). Recent work has shown that once these territories are established in the early summer, the population remains rather static, with little evidence of downstream movement until the autumn (Garcia de Leaniz, 1987). As individuals grow and their feeding demands increase, they tend to move up into the water column more frequently (Wankowski and Thorpe, 1979; Stradmeyer and Thorpe, 1987), from where their volume of search is greater.

3. Parr movements

At the end of summer there is evidence of downstream displacement of a proportion of the population in many streams (Buck and Hay, 1984; Rimmer *et al.*, 1984). The migrants continue to feed and grow during the winter, while those that remain behave like hibernators (Huntingford *et al.*, 1992). Evidently it is difficult to maintain a sufficient food intake on the shallower riffle territories during winter than it is in the deeper water downstream. The autumn movement ceases in November, but movement downstream begins again in mid-winter, and this occurs among the same group of fish that were moving down in the autumn (Youngson *et al.*, 1983). It is likely that in large river systems, such movements allow growth in more capacious and perhaps more productive habitats of those individuals with higher metabolic demands.

4. Smolt migration: the psssive model

Among those moving in the streams in mid-winter are some individuals whose needs are more than trophic ones. Primmett *et al.*(1988) showed that as the season progressed from February to May, smolting Atlantic salmon became progressively less able to maintain their plasma sodium balance (Fig. 14). In parallel with this they began to produce greater quantities of urine (Eddy and Talbot, 1985), showing that they were becoming more permeable to water, and had to pump more out. This progressive reduction in the efficiency of hydromineral balance was accompanied by an increase in gill Na+/K+ATPase, and in plasma cortisol levels (Thorpe *et al.*, 1987). The increased plasma cortisol in turn increased succinic dehydrogenase activity (Langdon *et al.* 1984), which indicated increased ion transport by the chloride cells (Chernitsky, 1980). It was also paralleled by a reduction in the plasma levels of prolactin, allowing efficient regulation in freshwater (Prunet and Boeuf, 1989). Traditionally, these changes have been interpreted as indicators that the fish were "preparing for seawater", but it is clear that the changes were occurring long before they would be needed for seawater adaptation. It seems more probable that the increased gill enzyme activity and corticosteroid levels occurred in response to failing efficiency of freshwater adaptation, and reflected attempts to compensate by increasing the inward pumping of sodium from the surrounding water (Thorpe, 1982; Langdon and Thorpe, 1985; Simpson, 1985; Primmett *et al.*, 1988). These conditions characterise the smolting juvenile. Such gradually increasing maladaptation encourages downstream displacement, as the fish becomes more lethargic, and less willing to work to hold station against a current (Thorpe and Morgan, 1978; Thorpe *et al.*, 1988). At this time the fish becomes more buoyant (Saunders, 1965), and tends to rise in the water column, which further enhances downstream displacement. The flanks of the fish become silvery, adopting a camouflage appropriate to the more open upper water habitat and they lose the cryptic coloration which had protective value near the stream bed.

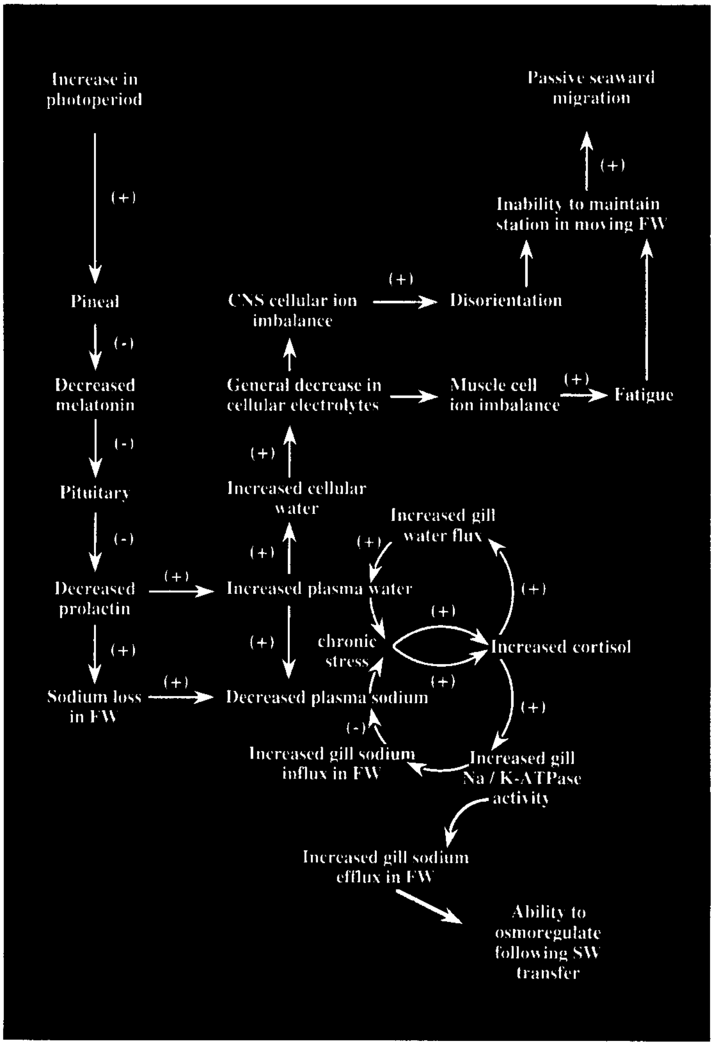

Fig. 14. Conceptual model of the changes in juvenile Atlantic salmon in the winter and spring, which result in its passive movement seaward (see text for details).

In addition to these seasonal physiological changes, another behavioral characteristic of salmon also promotes this downstream movement. At summer temperatures salmon are active throughout the day and night, but it has been shown recently (Fraser *et al.*, 1993) that as the temperature drops below about 10 ∞C they become less and less active by day, so that at temperatures characteristic of most of their geographic range they are nocturnal during the winter. This response, driven by temperature and not by light, has been interpreted as a predator avoidance mechanism, since, as the water cools, the speed of the fish's neuromuscular responses declines, and it is less efficient at avoiding endothermal predators such as goosanders (*Mergus merganser*), cormorants (*Phalacrocorax carbo*) and herons (*Ardea cinerea*) which feed on smolts by day (Kennedy and Greer, 1988). Even though the salmon are inefficient feeders at night, the advantage of feeding by day at cold temperatures is outweighed by the risk of being eaten. Becoming active by night, and moving up into the water column, they are likely to lose station through poor position-holding by sight, even though at such low temperatures their scotopic vision is relatively improved by increased proportions of porphyropsin in the retina (Allen *et al.*, 1982; Fraser *et al.*, 1993). As the season progresses, and the temperature increases, the salmon become gradually more active by day. By the end of May and early June the days have lengthened, the nights are short, and the smolting salmon are moving at all hours. Comparison of the proportion of smolting salmon caught in traps by day or by night over much of the geographic range of the species, shows that this temperature-regulated diel activity behavior is a general characteristic of the species (Thorpe et al., 1994) (Fig. 15).

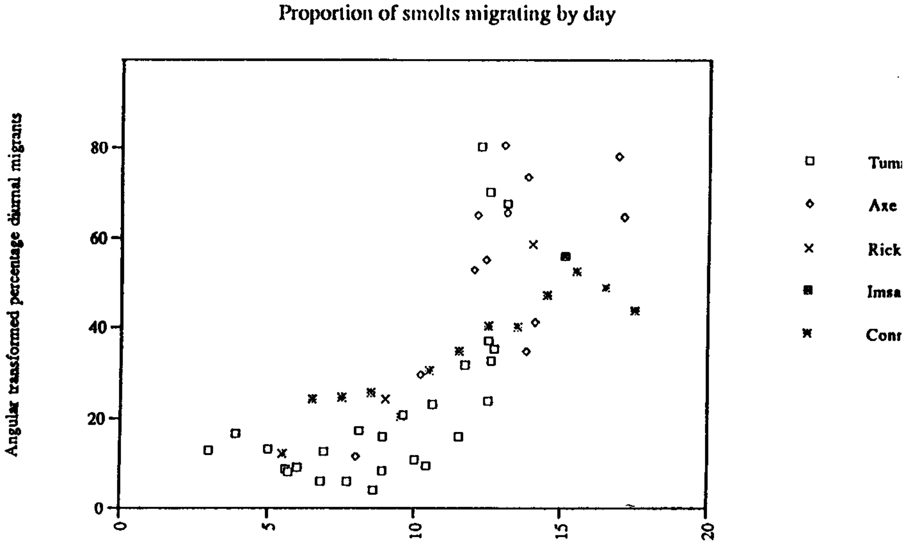
Proportion of smolts migrating by day

Fig. 15. The proportion of smolting Atlantic salmon captured during daylight hours, at different temperature, on five different river systems in Europe and North America.

5. Tests of the passive model of smolt migration

Such evidence would suggest that smolt migration within freshwater was probably largely passive displacement. To test this hypothesis, wild fish were tagged in the late winter, and their progress downstream was followed by recapture at traps downstream of the tagging site. It was found that inanimate objects (hydrographic drogues) travelled downstream through a 25-km river and loch section at about 4 times the speed of a migrating smolt (Thorpe *et al.*, 1981). This suggested that the fish were displaced at about the speed of the water, but only during their period of nocturnal activity. This was tested more carefully by tracking fish and drogues acoustically simultaneously through a loch. This showed that the fishes moved at night, in relatively short steps, in no consistent direction, but during their period of activity were displaced along the axis of the loch in the direction of the wind-driven surface water (Thorpe *et al.*, 1981).

6. Smolt emigration through estuaries

Similar trials have been made releasing acoustically tagged fish just upstream of the tidal influence in estuaries. Early trials (Fried *et al.*, 1978; McCleave, 1978; Tytler *et al.*, 1978) found that the fish held station until the currents exceeded 2 body lengths per second and were then displaced downstream. In the Eden estuary (Scotland), where the freshwater flow reverses briefly at high tide, the fish were carried back upstream. However, since net water movement was out to sea, the fish were eventually transported through the estuary.

More recently, detailed studies on wild Atlantic salmon smolts have been carried out in the Avon (England), Conwy and Tawe (Wales) estuaries (Moore *et al.*, 1990a,1992, 1995; Moore and Potter, 1994). Smolts were tagged in fresh water using miniature 300-kHz acoustic transmitters. The transmitters were surgically implanted into the peritoneal cavity of the smolts (Moore *et al.*, 1990b), and after full recovery the fish were released to continue their downstream migration. This technique of transmitter attachment has been shown to have negligible physiological and behavioral effects on salmon smolts (Moore *et al.*, 1990b). The movements of the smolts within the freshwater and estuarine environments were monitored using an array of 300 kHz acoustic sonar buoys (Moore *et al.*, 1992, 1995; Moore and Potter, 1994).

In all three river systems, the migration of smolts in freshwater was predominantly nocturnal, supporting the observations from previous studies (Thorpe and Morgan, 1978; Thorpe *et al*,. 1981; Lundqvist and Eriksson, 1985; Hansen and Jonsson, 1985; Greenstreet, 1992a). However, in the River Conwy the smolt run became less strictly nocturnal as the season progressed and the temperature rose, consistent with prediction (Thorpe *et al.*, 1994). During the latter part of the season, a significant proportion of the smolts switched to movement during both day and night. This change in the smolt migratory pattern of behaviour was reflected in a significant seasonal change in the residency time of the smolts, with fish tagged later in the season spending less time in freshwater before migrating into coastal waters. As a result of this seasonal shift in behavior, a significant proportion of the smolts migrated out of the estuary over a brief five-day period (Moore *et al.*, 1995). This period may represent the optimal time or window of opportunity for smolts to migrate from freshwater into the marine environment. This supports the observation that the timing of the migration of Atlantic salmon smolts from fresh to saltwater is critical to their subsequent survival and successful return as adults (Hansen and Jonsson 1989). However, it is still not understood what environmental mechanisms are operating during this initial marine phase, that make this timing so crucial.

It has been argued that salmon smolt migration in estuaries is either passive (Huntsman, 1962; Tytler *et al.*, 1978; Thorpe *et al.*, 1981; Greenstreet, 1992b), partly active (Thorpe and Morgan, 1978; McCleave, 1978; Solomon, 1978; Kennedy *et al.*, 1984) or active (Hansen and Jonsson, 1985). In the River Conwy estuary there was evidence that the migratory behavior differed both temporally and spatially, and it was not possible to ascribe a single method of migration to the smolts.

Migration through the upper and middle sections of the Conwy estuary was passive during the hours of darkness, but with some degree of orientation that maintained the smolts in the upper water column and within the main current (Moore *et al.*, 1995). This passive orientation was discontinued through the lower estuary and migration here was indicative of active, directed swimming. The speed of movement of smolts was in excess of the water current (Moore *et al.*,1995). Active tracking indicated that fish were moving in the upper water column and close to the maximum current speeds. LaBar *et al.*, (1978) also reported smolts swimming actively against the current in the lower sections of the Penobscot River estuary. A similar pattern of swimming behavior was demonstrated by smolts in a laboratory study when they transferred to seawater (Moore *et al.* 1995). It is possible that during the transition from freshwater to saltwater there is significant change in the smolts'behavior and they switch from moving passively with the current and actively swim seawards. It is not understood what causes this shift in swimming behavior, but it may be stimulated by the smolts migrating into water exceeding a particular salinity threshold.

In the River Conwy, there was evidence of a nocturnal selective ebb tide transport component to the smolt migration, similar to mechanisms demonstrated in other species (Harden Jones *et al.*, 1979). Although McCleave (1978) was unable to demonstrate a similar selective tidal transport component of the smolt migration in the Penobscot River estuary, he hypothesised that this particular orientation mechanism would need to exist to allow the movement of fish out of the estuary. In the Conwy estuary, smolts migrated close to the surface and were oriented to remain within the main flow of the channel (Moore *et al.*, 1995). Previous studies have also suggested that salmon smolts initiate their seaward movement through an estuary on an ebbing tide (Calderwood, 1908; White and Huntsman, 1938). Smolts migrating on an ebbing tide, close to the surface and within the main channel of the estuary, are within the section of the water column with the highest current velocities. Energetically this is the most advantageous strategy for migration through the estuary and would result in the rapid movement of smolts out into coastal waters (Fried *et al.*, 1978).

Movement through the estuary and into coastal waters appears to be unaffected by changes in water quality. Increasing salinity does not appear to act as a barrier to seaward migration of the smolts (Greenstreet, 1992b; Moore *et al.* 1992,1995), and there is no apparent period of saltwater acclimation required, as appears the case for some ocean type salmonids like sockeye *Oncorhynchus nerka* (Heifetz *et al.*, 1989) and chinook *O. tschawytsha* (Thorpe, 1994). Active tracking of salmon smolts in the River Tawe estuary indicated that the fish moved rapidly from freshwater and out into the open sea. A physiological requirement to leave the freshwater environment may be an important cue in initiating Atlantic salmon smolt migration in freshwater (Primett *et al.* 1988).

7. The effects of estuarine barrages

An understanding of smolt migration through estuaries has been important in evaluating the potential impact of estuarine constructions such as barrages on the behavior and survival of migratory salmonids. One major concern relates to the potential changes in the flow regimes above a barrage and the effects on smolt migration. Tidal currents within an estuary are important cues for moving smolts into coastal waters rapidly under the cover of darkness (Tytler *et al.*, 1978; McCleave, 1978; Thorpe *et al.*, 1981; Greenstreet, 1992b; Moore *et al.*, 1992; Moore *et al.*, 1995). The removal of a significant tidal cycle in the impoundment of a barrage results in a reduction of ebb-tide cues that would otherwise carry the fish seaward. The consequences of such an event have been demonstrated in the estuary of the River Tawe, South Wales where, in 1992, a barrage was constructed across the lower estuary. Here the smolts reside for longer periods within the impounded river above the barrage and are potentially more vulnerable to predation. The timing of the movement of the smolts into coastal waters is also delayed, and the fish may not migrate into the marine environment during the optimum period. As previously noted, the timing of smolt movement into coastal waters may be crucial to survival and return as adult fish (Hansen and Jonsson, 1989).

There is also concern about the potential impact of changes in water quality within impounded estuaries on the survival of salmonid smolts. The modified tidal cycle and retention of river water upstream of a barrage may concentrate contaminants and reduce water quality. The delay to smolt migration caused by the barrage will also increase the exposure time of fish to any adverse conditions. The exposure of smolts for extended periods to sublethal levels of contaminants and low oxygen levels may have significant effects on the subsequent survival of smolts in the marine environment.