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### 3. Spawning migrations

It is known from tagging studies that salmon in the open ocean that are becoming sexually mature swim toward their home rivers at the rate of 40-60 km/day (Ogura and Ishida, 1995). This is similar to the swimming speed which is energetically most efficient as estimated from laboratory experiments in swim tunnels (Brett, 1995; Webb, 1995). In order for salmon to achieve this migration speed, they must possess excellent orientation ability. Recently, tracking of individual sockeye, chum, pink and chinook salmon fitted with ultrasonic transmitters in the central Bering Sea confirmed that individual salmon swam in particular directions and speeds during day and night (Ogura and Ishida, 1995).

Interannual variation in the timing of spawning migration for several sockeye salmon stocks was shown to be correlated with sea surface temperature in the Gulf of Alaska (Blackbourn, 1987), where a simple temperature-displacement model was proposed to account for this relationship.

Average water temperature during egg incubation has an important influence on early development, and therefore, indirectly on timing of the spawning migration. Migration and spawning times are adjusted to ensure that fry emerge at the appropriate time (usually in spring). Sockeye salmon stocks returning to the Fraser River spawn over a period of five months, but each stock has its own specific migration and spawning time which has an annual variation of less than 10 days (Brannon, 1987). These stock-specific times are highly correlated with incubation temperatures; late spawning stocks return to streams that have higher incubation temperatures (Brannon, 1987).

The swimming speed of adult salmon migrating upstream is strongly influenced by temperature, with an optimum near 15°C (Brett, 1995). Recently, we captured migrating sockeye salmon in the Fraser River and subjected them to endurance tests in a swim tunnel at temperatures of 15, 17, 19 and 21°C; the distance traveled prior to exhaustion was greatest at 17°C but decreased sharply at 21°C (Clarke *et al.*, 1996).

## IV. PHYSIOLOGY OF MIGRATION IN SALMONIDS

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### Abstract

Most physiological studies of fish migration have focused on swimming and energetics; such studies on salmon migration have concentrated primarily on the adult spawning migration, and relatively less is known about juvenile migration. Data on growth and body

energy reserves of wild spring Chinook salmon (*Oncorhynchus tshawytscha*) parr and early migrating smolts indicate that energy is accumulated in advance to support migration and that stored protein may serve as an important energy source.

### **Introduction**

Salmonids use a variety of swimming modes; cruising, sprinting and accelerating (Webb, 1995). As true for most fish, salmonids use both white and red muscle types for propulsion. White muscle is the most massive and is used for burst swimming for prey capture, predator avoidance, and navigation in fast-flowing water. Red muscle is used for sustained swimming. White muscle is primarily anaerobic, using glycogen as fuel. Sustained swimming employs red muscle, which is aerobic and draws on lipid and protein for energy. In contrast to mammals, which depend on primarily on glycogen and lipids for muscular locomotion, fish rely on glycogen only for short bursts of locomotion. The salmonid diet is low in carbohydrates, in fact, salmonids are relatively intolerant to carbohydrates. Salmon do not show the ability to increase carbohydrate storage capacity as seen in mammals in response to physical training. Based on respiratory quotient measurements, Van den Thillart (1985) has shown that rainbow trout at rest may rely on 20% lipid and 80% protein oxidation, and in sustained swimming (80% of maximal sustained speed) they may use 10% lipid and 90% protein. These results indicate the importance of lipid and protein as energy stores to support sustained swimming of juvenile and adult migrations.

#### **1. Adult spawning migration**

During their final year before spawning, adult salmon grow and accumulate sufficient energy stores for migration to their natal stream. Once the adults enter fresh water, feeding opportunities are eliminated, so that all energy for swimming can come only from what has been stored. During migration adult salmon maintain glycogen stores, but their body lipids may become depleted. Additional energy is provided by protein breakdown, especially after lipid depletion (Idler and Clemmons, 1959; Mommsen et al., 1980; Brett, 1995).

#### **2. Energy accumulation of wild spring chinook salmon juveniles**

Since laboratory- and hatchery-reared fish fed commercial diets do not experience the normal extremes of seasonal change in temperature and nutrition, we began a study of wild spring chinook salmon in the Yakima River Basin, which is a tributary of the Columbia River and is located in central Washington State. The wild salmon fry emerge from the gravel in the spring and spend one year in fresh water before migrating to the ocean as yearlings. We collected fry and parr throughout the year by electroshocking streams near the spawning ground, which is located approximately 700 km from the ocean at an elevation of 800 m. During the spring, we collected outmigrating smolts at an irrigation diversion

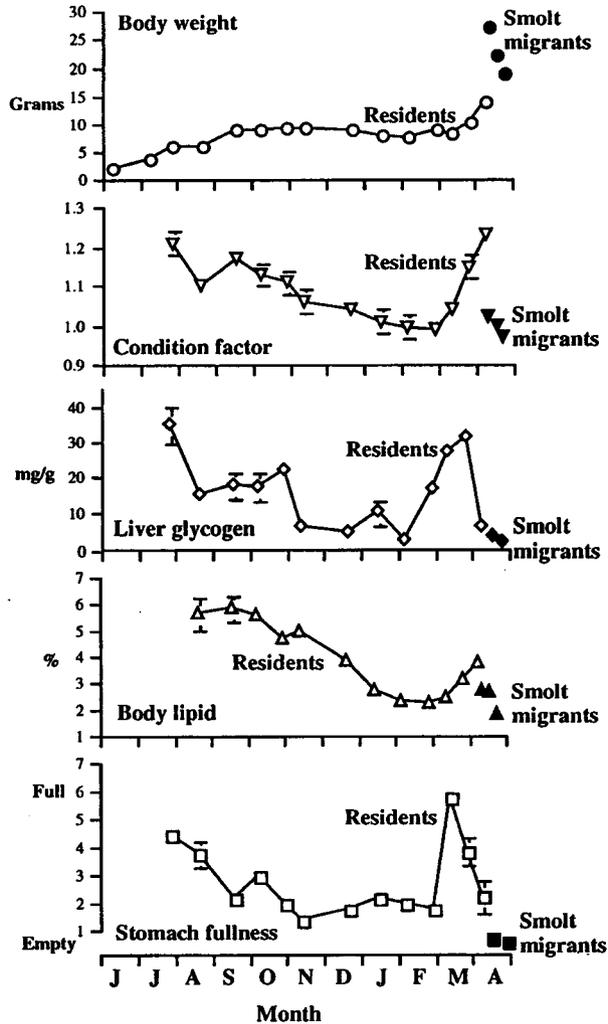


Fig. 5. Body weight, condition factor, liver glycogen, body lipid and stomach fullness for wild spring chinook salmon during their first year in fresh water. Data on resident fry and parr (open symbols) were obtained from fish sampled by electroshocking. Data on migrant smolts (closed symbols) were obtained from fish caught in a trap 250 km downstream from the electroshocking site.

dam located 250 km downstream from the site where we collected resident fish. The smolt collection site is about one-third of the distance that the fish must travel. Fish samples were analyzed for length, weight, condition factor, liver glycogen, body lipid, and stomach fullness. The results are summarized in Figure 5. Fish grew primarily in the first summer

and fall. Little growth was observed during the winter, probably because of low water temperature (1-3°C). Growth resumed in the late winter and spring coincident with the parr-to-smolt transformation. Migrating smolts were larger than the resident parr and transitional fish. Condition factor was high in the summer, declined during winter, and then increased sharply in the spring. Smolt migrants had reduced condition factor as is characteristic of smolts. Liver glycogen declined during the winter and then increased markedly in the spring in resident fish. Liver glycogen was depleted in smolt migrants. Body lipid levels were highest in the summer, declined in the winter, and then became elevated again in the spring in resident fish. Body lipid levels of migrant smolts were low (1-3%), among the lowest that we have seen in salmonids. Stomach fullness was correlated with growth and energy storage; it was high in the summer, low in the winter, and then increased sharply in the spring.

The pattern of change in body weight, stomach fullness, and body energy storage of resident fish is dynamic during the year. The high anabolic state in the summer contrasts with the low levels of energy in the winter. In the late winter and spring parr begin feeding and resume growth, coincident with body lipid and liver glycogen stores becoming replenished. Both live glycogen and body lipid are depleted in the smolt migrants, which were captured after only one-third of the seaward migration had been completed. This suggests that additional energy to support migration must come from food captured during migration or from stored protein. We speculate that large body size and growth during the parr-smolt transformation are important in building up stored energy as protein to be used to support smolt migration.

## V. EVOLUTION OF LIFE HISTORY AND MIGRATION IN FISH

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### Abstract

This paper reviews my hypothesis for the evolution of diadromous migration in fish (Gross, 1987; Gross *et al.*, 1988), and suggests additional hypotheses for amphidromy and intraspecific variation in migration.

### Introduction

Movement from one location to another is common in fish. A different location may have fewer costs, such as less predation, competition or disease. Or it may provide higher