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Australian continent had moved north after its separation from Antarctica, and was populated by the lineage of *A.reinhardti* from nearby Indonesia. Eels that inhabit the Australian continent thus now consist of two groups that may have arrived there by way of different routes at different times (Fig. 4).

The Japanese eel, *A.japonica*, is apparently not closely related to the Atlantic eels, as has previously been supposed, even though recent findings have shown them to have similar migratory and recruitment strategies (Tsukamoto, 1992). Instead, the Japanese eel is only distantly related to the North Atlantic eels, together with all eels which appear to have diverged from a common Indonesian ancestor. Keys to this scenario are the availability of the Tethys corridor and larval dispersal westwards and southwards on the paleo-circumglobal current. Our findings provide a new basis for further evaluation of the evolutionary implications of the remarkable life history strategy of freshwater eels of the genus, *Anguilla*.

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III. PHYSIOLOGICAL ECOLOGY OF PACIFIC SALMON MIGRATION

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Abstract

Anadromous Pacific salmon (genus *Oncorhynchus*) undergo a series of habitat shifts during their elaborate life cycle, characterized by various migrations, most notably between ocean feeding areas and freshwater spawning sites. The physiological preparation for and conduct of these migrations are adapted to annual cycles of temperature and photoperiod.

Introduction

The dramatic and accurate homing migration of adult salmon from the open ocean back to their natal streams has inspired observers for centuries. The complex life cycle of anadromous Pacific salmon involves a series of habitat changes, including outmigration of juveniles from rivers to the sea, a feeding migration in the North Pacific Ocean, and finally a purposeful migration of adults back to their native rivers, lakes and streams to reproduce and

die. Within this general pattern, there is considerable variation, not only among species but also among stocks with regard to the distance traveled and the seasonal timing of the migrations. This variation results from different patterns of residence in freshwater, estuarine and marine habitats (Groot and Margolis, 1991). One benefit of migrations is to enable salmon to increase feeding opportunities so as to augment size and fecundity. Another benefit is that migrations allow salmon to avoid unfavorable conditions in seasonally varying environments. Individual stocks of salmon conduct their migrations at precise times in order to arrive at the most favorable time for feeding or spawning in their particular habitats.

The aim of this paper is to give an overview of Pacific salmon migration in relation to temperature and photoperiod that are the major environmental cues synchronizing salmon growth and development. Research is continuing to unravel more details of these important physiological mechanisms which enable Pacific salmon to adapt to the diverse environments in which they live. One important practical application of such knowledge is to know the permissible range of environmental conditions in order that salmon habitat can be protected or rehabilitated in order to sustain individual populations. Another application is for the propagation of juvenile salmon in hatcheries and releasing them in support of fisheries. This latter aim has prompted intensive study of the early development of salmon (Bern and Nishioka, 1993; Clarke and Hirano, 1995).

1. Migration of fry and smolt

The successful completion of migrations of fry and smolts have a very important influence on the size of a stock because abundance, growth rate and mortality are highest at this phase of the life cycle (Godin, 1981). The early development of juvenile salmon involves a number of behavioral, morphological and physiological changes that prepare juvenile salmon for their feeding migration to the sea. This development therefore represents one of the most important adaptations in the salmon life cycle.

There is a strong seasonal rhythm to migration of salmon in response to selection pressures imposed by seasonally fluctuating environmental conditions. Hoar (1965) postulated that the physiology of ionic regulation in salmonids changes seasonally under the influence of an endogenous cycle that is synchronized by photoperiod. It has been shown that the annual cycle of photoperiod synchronizes the physiological development to the smolt stage in a number of species. Nevertheless, there is as yet no formal experimental proof that the seasonal smolting cycle in Pacific salmon involves an endogenous circannual rhythm (Clarke and Hirano, 1995).

Anadromous Pacific salmon in fresh water can be classified broadly into two categories: those that enter the sea as underyearlings and those that are yearling or older migrants. On the one hand, in pink salmon (*O. gorbuscha*), the preparatory phase for downstream migration to the sea is compressed into a short interval; by the time that the

yolk is absorbed, downstream fry migrants are able to hypoosmoregulate in sea water (Varnavsky *et al.*, 1993). This development is not characterized by obvious changes in morphology or coloration. On the other hand, salmon which develop for a year in fresh water undergo an obvious transformation from the parr stage to the smolt stage which migrates to the sea. The masu salmon (*O. masou*) is characteristic of this group in which the transformation from the cryptically colored stream-dwelling parr to the silvery smolt is controlled by growth opportunity; not all members of the population become smolts during the same year (Kubo, 1974).

The underyearling and yearling migrants differ with respect to their environmental requirements for development of the ability to enter seawater. The annual cycle of photoperiod is the main environmental cue that synchronizes the parr-smolt transformation in coho (*O. kisutch*) and masu salmon. In contrast, underyearling migrants are capable of entering seawater at a particular size and do not require a specific photoperiod cue.

The separation into underyearling and yearling migrants does not necessarily occur only among species. For example, chinook salmon (*O. tshawytscha*) are ecologically and geographically differentiated into two life-history types that differ in their migration from rivers into estuaries and the open ocean. "Ocean-type" chinook salmon migrate into estuaries as fry or fingerlings in the first year of life and grow there for up to six weeks

Table 1. Classification of freshwater life history patterns in Pacific salmon

SW migrant <1 year in fresh water	SW migrant >1 year in fresh water
Chum salmon	Stream-type chinook salmon
Pink salmon	Coho salmon
Ocean-type sockeye salmon	Masu salmon
Ocean-type chinook salmon	Lake-type sockeye salmon

before continuing their migration to the ocean. In contrast, "stream-type" chinook salmon spend one or more years in rivers before migrating to the sea as smolts; they are only transient residents in the outer portion of estuaries. The two life-history types have different responses to photoperiod (Clarke *et al.*, 1989). Hybridization experiments have shown that the photoperiod-independent smolting phenotype of ocean-type chinook is dominant and that the two phenotypes separate in the F2 progeny when the F1 hybrid is backcrossed to the stream-type parent (Clarke *et al.*, 1992, 1994). A similar example of intraspecific variation occurs in the sockeye salmon (*O. nerka*). Juvenile sockeye usually grow in lakes for at least one or two years before migrating seaward as smolts, although in some northern river

systems without lakes there are "ocean-type" stocks of sockeye salmon which enter the sea as underyearlings (Wood *et al.*, 1987). Because juvenile sockeye salmon are able to enter the sea at a small size, there is considerable potential for production of underyearling smolts for sea ranching (Clarke *et al.*, 1981; Kaeriyama, 1992). The two major patterns for Pacific salmon development are summarized in Table 1.

For species such as pink and chum salmon (*O. keta*) which may enter the sea soon after emergence, downstream migration to the sea is the only migration in fresh water. In comparison, sockeye salmon fry show a variety of migration patterns between the spawning beds and the nursery lake where they grow for a year or more until they develop into smolts (Groot, 1981). Fry which emerge in streams which discharge into the nursery lake migrate downstream with the current, typically after dusk. Sockeye fry emerging from spawning gravel in an outlet river below the nursery lake must first reach the shore where current velocities are low and then migrate upstream (Clarke and Smith, 1972). In contrast to the downstream migrants, the upstream migrants form large schools which swim along the shore in daylight hours and hold position during darkness (Godin, 1981). Sockeye fry migrating upstream use olfactory cues, including calcium ion to distinguish lake water from that of other tributary streams (Bodznick, 1978a,b).

2. Marine migrations

The duration and extent of adult feeding migrations vary considerably among species of Pacific salmon. Masu salmon spend one winter at sea and are caught mainly in the Sea of Japan and the Sea of Okhotsk; few of them are found in the offshore areas of the Pacific Ocean. Sockeye salmon, on the other hand, typically spend two years feeding in the open ocean and then start their homeward migration. They may be up to 4000 km offshore in the spring of their second year at sea (Groot and Quinn, 1987).

Several species are widely distributed in the North Pacific Ocean where most of their growth occurs. Despite a number of studies of the oceanographic factors associated with observed patterns of distribution, it is still not clear what limits the dispersal of Pacific salmon. A recent investigation by Welsh *et al.* (1995) found evidence for a sharply-defined southern boundary of the distribution of salmon in spring which was associated with a precise temperature for each species. They estimated the critical temperatures to be 10.4°C for pink and chum salmon, 9.4°C for coho salmon, and 8.9°C for sockeye salmon. A surprising aspect of these temperatures is that they are much lower than those associated with maximal swimming performance (Brett, 1995). The reason for these sharp boundaries to salmon migration are not known, although they might be an adaptation to maximize growth in relation to a limited food supply (Welch *et al.*, 1995). The strong temperature boundary in distribution suggests that changes in ocean temperatures could have strong effects on population levels of Pacific salmon (Hinch *et al.*, 1995; Welch *et al.*, 1995).

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