HOMING IN PACIFIC SALMON: MECHANISMS AND ECOLOGICAL BASIS

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Summary

Pacific salmon (*Oncorhynchus* spp.) are famous for their homing migrations from oceanic feeding grounds to their natal river to spawn. During these migrations, salmon travel through diverse habitats (e.g. oceans, lakes, rivers), each offering distinct orientation clues and, perhaps, requiring distinct sensory capabilities for navigation. Despite these challenges, homing is generally precise and this philopatry has resulted in reproductively isolated spawning populations with specialized adaptations for their natal habitat. This paper reviews the mechanisms underlying all aspects of salmon homing but emphasizes the final, freshwater phase governed by olfactory recognition of homestream water. Prior to their seaward migration, juvenile salmon learn (imprint on) odors associated with their natal site and later, as adults, use these odor memories for homing. Our understanding of this imprinting process is derived primarily from studies using artificial odorants and hatchery-reared salmon. Recent findings suggest, however, that such studies may underestimate the complexity of the imprinting process in nature.

Key words: salmon, homing, olfactory imprinting, thyroid hormones, *Oncorhynchus* spp.

Introduction

The life history, ecology and evolution of salmonid fishes (salmon, trout and char) is dominated by their strong tendency to home to their natal site for reproduction. Homing characterizes the family but is best studied in the anadromous (i.e. 'sea run') forms. Typically, salmon spawn in streams or lakes and, after a variable period of freshwater residence (0–3 years, depending on the species and population), the offspring migrate to the ocean, presumably to take advantage of increased productivity and foraging opportunities (Gross *et al.* 1988) (e.g. Fig. 1A). Salmon remain in the ocean until they begin to mature and then return to their natal site to spawn (Fig. 1B,C). For many species and populations, these migrations pose extraordinary bioenergetic and navigational challenges. Homing migrations often begin thousands of kilometers from the mouth of the home river and, for some populations, in-river migrations back to their natal site may be as long as the ocean migration. These diverse marine and freshwater habitats provide distinct sets of orientation clues and pose distinct challenges for orientation. Despite these challenges, homing is generally precise, and fidelity to the natal site has resulted in reproductive isolation of spawning populations and specialized adaptations of these populations for their natal habitat.

In this paper, we briefly review the mechanisms underlying homing at all stages of the Pacific salmon (*Oncorhynchus* spp.) migration but emphasize the final, freshwater phase. Specifically, we examine the process by which juvenile salmon learn olfactory clues associated with their home stream and later use these retained odor memories to guide their return to the natal site as adults. The mechanism and timing of olfactory learning or 'imprinting' has been extensively studied (reviewed by Hasler and Scholz, 1983; Quinn and Dittman, 1992) but much of this work has involved olfactory learning by hatchery- or laboratory-reared fish using artificial odorants. In this review, we discuss olfactory imprinting and homing by wild salmon in the context of the complex freshwater habitats experienced by juvenile salmon and the fine scale of homing often demonstrated by adults.

Ocean migrations

The processes underlying open-ocean migrations by salmon have been debated for years but little experimental evidence exists regarding the sensory mechanisms and clues used in these migrations. The dearth of experimental evidence is largely due to the expense and difficulty of working with salmon in the open ocean. In lieu of direct experimentation with homing adults, much of our understanding of salmon homing in the open ocean has been inferred from their distribution patterns at sea, tag–recapture studies, simulation models of adult behavior and experiments on the orientation capabilities of juveniles. Although some models have simulated homing from the open ocean with little orientation (e.g. Saila and Shappy, 1963; Jamon, 1990), the assumptions and outputs of these models are contradicted by the wealth of information on the movements of salmon from the open ocean to the mouth of their natal river (Royce *et al.* 1968; Quinn and Groot, 1984; Hiramatsu and Ishida, 1989; Quinn, 1991). Data from commercial and research fisheries and from salmon
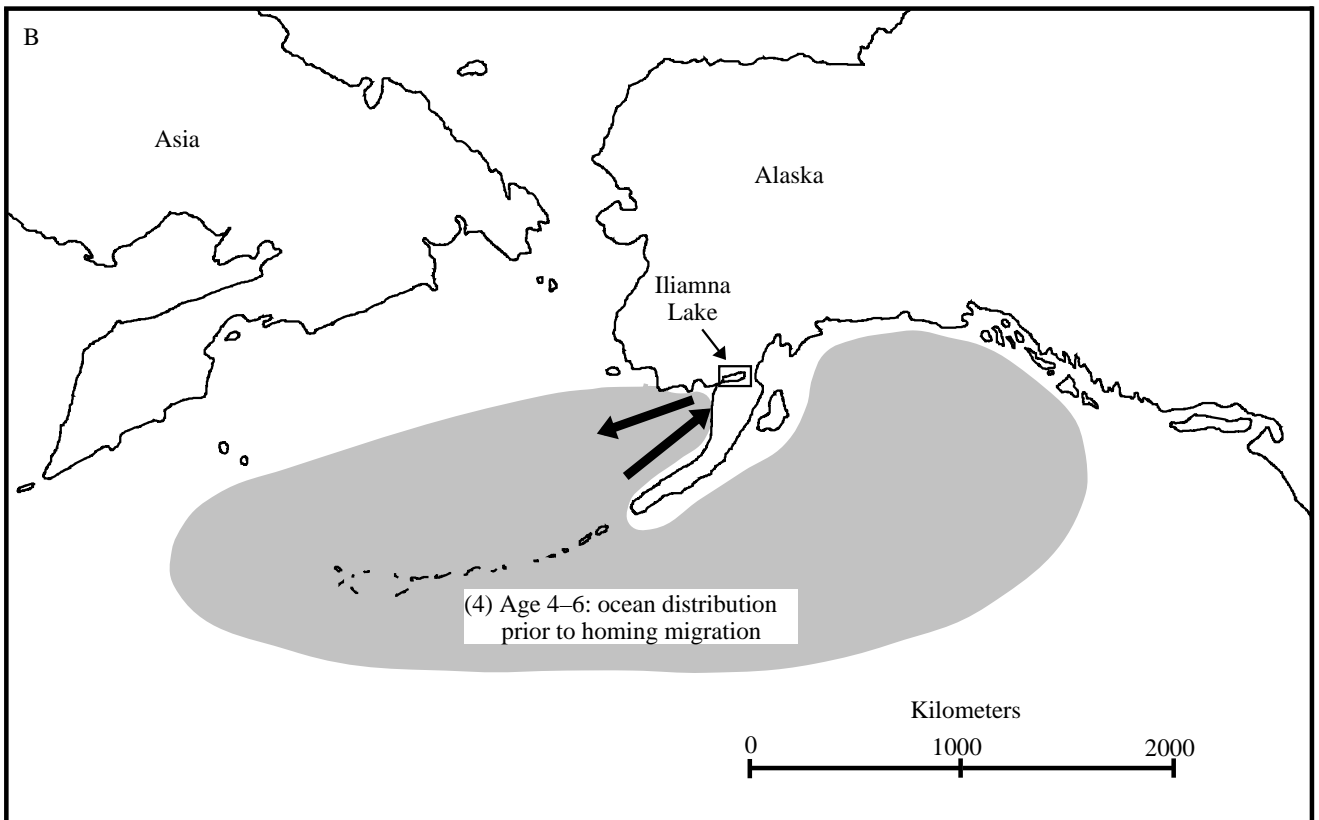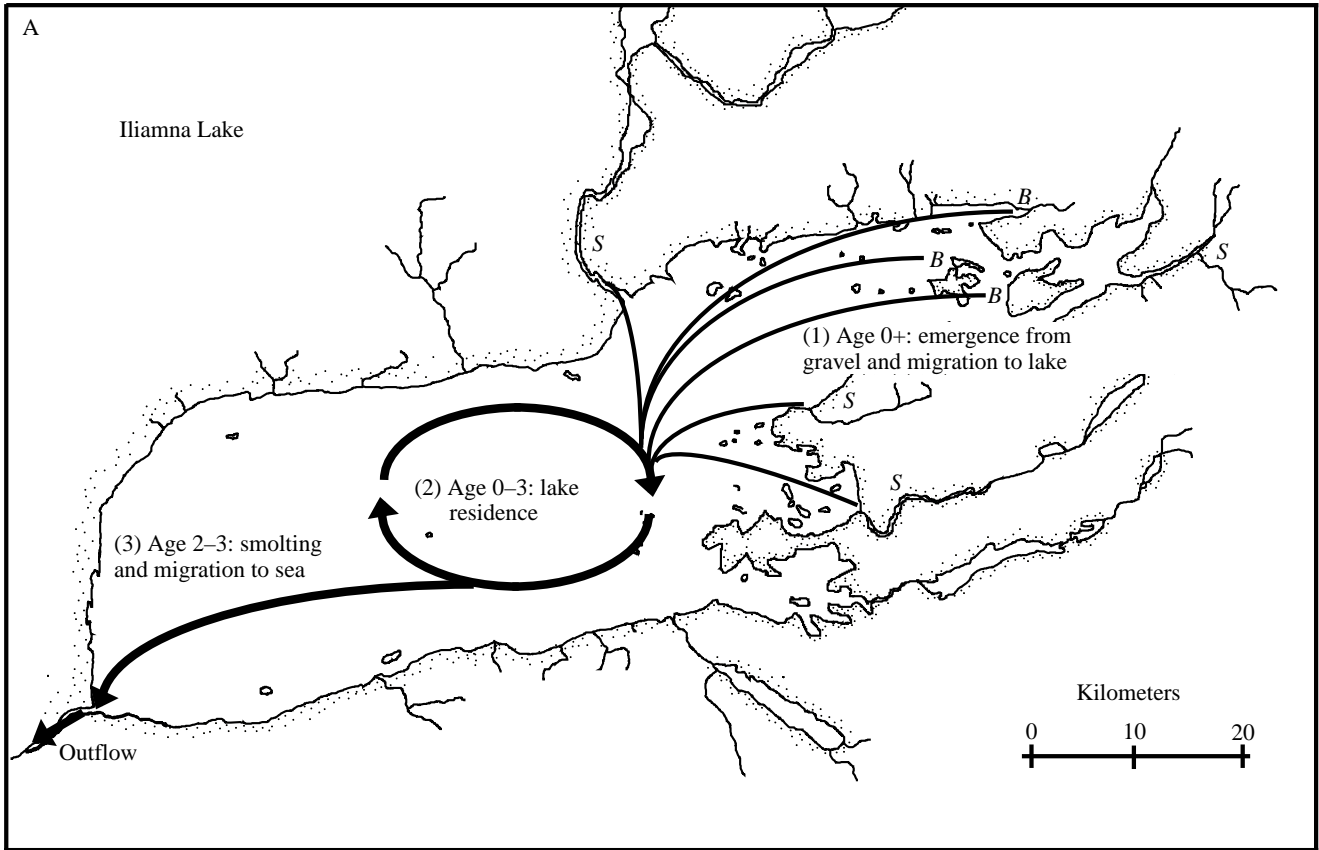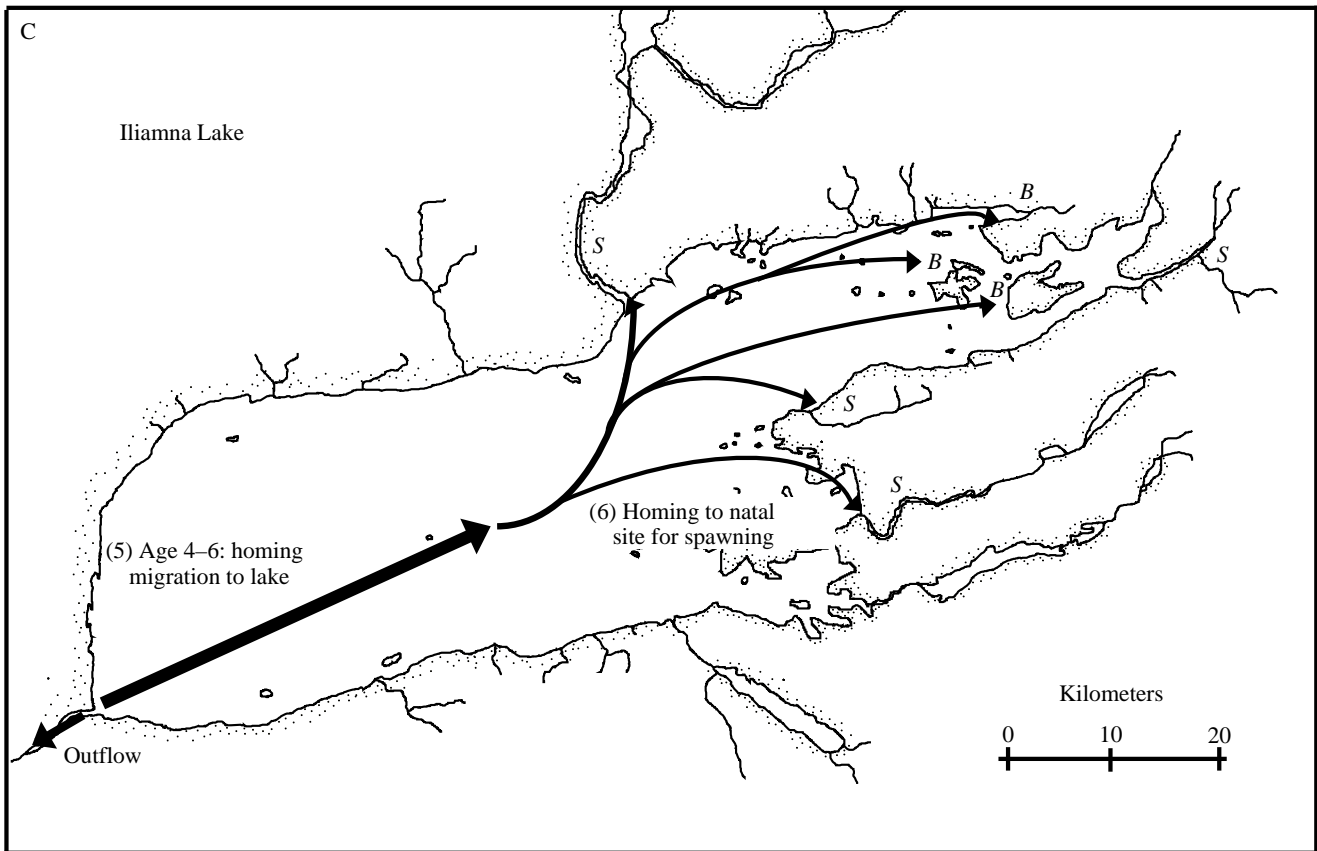
Fig. 1A,B

Fig. 1. Life cycle and migratory patterns of sockeye salmon populations in Iliamna Lake, Alaska. (A) Freshwater residence period encompassing emergence from natal gravel on beaches (*B*) or streams (*S*) to seaward migration as smolts. (B) Ocean distribution of maturing Iliamna Lake salmon prior to homing migration (French *et al.* 1976). (C) Homing migration to Iliamna Lake and natal site for spawning.

tagged in the ocean and recaptured at or near their home stream indicate that salmon converge on their river of origin with remarkable spatial and temporal precision despite initiating homeward migration from widely distributed feeding areas (Royce *et al.* 1968; Burgner, 1980). These observations are consistent with the hypothesis that homing salmon are guided by a map and compass system on the open ocean (Quinn, 1982), though some evidence indicates that only compass orientation need be invoked (Blackbourn, 1987). Experiments with Atlantic salmon (*Salmo salar*) indicated that the general orientation towards the coast did not require experience gained on the outward journey but that more precise homing did depend on such experience (Hansen *et al.* 1993).

The mechanism(s) underlying orientation by homing salmon at sea are not known, but experiments with juvenile sockeye salmon (*O. nerka*) migrating in large lakes have revealed sensory systems and orientation clues that could be involved in open ocean migrations. Juvenile salmon are able to orient to the sun's position, to polarized light patterns and to the earth's magnetic field (Groot, 1965; Quinn, 1980; Quinn and Brannon, 1982; Hawryshyn *et al.* 1990). Biogenic magnetite crystals, which may be used for magnetoreception, have been isolated from the head or lateral line of several salmon species (Walker *et al.* 1988; Moore *et al.* 1990; Ogura *et al.* 1992). It remains

to be demonstrated whether these sensory mechanisms are involved in ocean migrations and how they are integrated with other orientation systems.

River migrations

Although little experimental evidence exists regarding orientation mechanisms in the ocean, the final freshwater phase of the homing migration has been extensively studied. It is generally believed that as salmon enter their natal river there is a transition from oceanic orientation mechanisms to mechanisms more appropriate for riverine migration (Hasler, 1971). The interface between open ocean and up-river migration is the complex of coastal and estuarine waters. These waters pose special challenges, and salmon may use elements of many orientation systems there (Quinn *et al.* 1989; Pascual and Quinn, 1991; Olson and Quinn, 1993). Experimental evidence indicates that the freshwater homing migrations of salmon are governed primarily by olfactory discrimination of homestream water (Hasler and Scholz, 1983). It is unclear to what extent genetic factors (McIsaac and Quinn, 1988) and other sensory systems may also play some role in freshwater orientation (e.g. compass mechanisms in large lakes), but olfaction is essential for successful completion of the homing

migration (Wisby and Hasler, 1954; Dittman *et al.* 1995). The olfactory imprinting hypothesis for salmon homing was first proposed by Hasler and Wisby (1951) based on behavioral experiments demonstrating that fish can discriminate between the waters of different streams on the basis of odors. This hypothesis has several components: (1) streams differ in chemical characteristics that are stable over time; (2) salmon can distinguish these differences; and (3) salmon learn the chemical characteristics of their natal stream prior to or during their seaward migration, remember them without reinforcement during ocean residence, and respond to them as adults. To test this hypothesis, Hasler and his colleagues exposed juvenile coho salmon (*O. kisutch*) to one of two synthetic chemicals, morpholine or β-phenylethyl alcohol (PEA), and were able to attract the salmon into unfamiliar streams scented with one of these chemicals during their spawning migration 1.5 years later (Cooper *et al.* 1976; Scholz *et al.* 1976).

Hasler and Scholz (1983) further proposed that the process of olfactory learning and homing is intimately linked to hormone levels at different life stages. Their studies with artificial odorants suggested that juvenile coho salmon learn the odors of their home stream during a sensitive period termed the parr–smolt transformation (PST), a developmental process characterized by physiological and behavioral changes which prepare freshwater residents (parr) for life at sea. This type of unconditioned, irreversible learning during a sensitive period of development is reminiscent of filial imprinting, whereby young birds form an attachment to their mother; hence, the term imprinting has been applied to olfactory learning by salmon. The importance of the PST as a sensitive period for olfactory imprinting by coho salmon was recently confirmed using hatchery-reared coho salmon exposed to the odorant PEA as embryos, parr or smolts (Dittman *et al.* 1995). Only salmon exposed to PEA as smolts were attracted as adults to water scented with PEA. These results are consistent with the general finding that salmon reared at one site but released from a second site prior to, or during, PST return as adults to the release site, not the rearing site (Donaldson and Allen, 1957; Jensen and Duncan, 1971). However, recent studies by Tilson *et al.* (1994, 1995) indicated that kokanee (the non-anadromous form of sockeye salmon), which normally migrate from their natal site soon after emergence from the gravel, are able to imprint on artificial odorants as alevins and emergent fry as well as at the smolt stage.

Olfactory imprinting and thyroxine levels

Many of the changes that occur during the parr–smolt transformation are associated with surges in the plasma levels of the hormone thyroxine (Dickhoff *et al.* 1978; Dickhoff and Sullivan, 1987), and these elevated thyroxine levels may be involved in olfactory learning (Hasler and Scholz, 1983). Scholz (1980) demonstrated that presmolt coho salmon with artificially elevated thyroxine levels exposed to an odor were able to retain long-term memories of that odor whereas untreated control fish were not. Consistent with this hypothesis, Morin *et al.* (1989*a,b*, 1994; Morin and Doving, 1992) found a period of enhanced olfactory sensitivity during the PST which coincided with increased thyroid activity and imprinting ability in Atlantic salmon (*Salmo salar*). A correlation between transient increases in thyroxine levels and the ability to imprint on artificial odors at various developmental stages has also been observed for kokanee salmon (Tilson *et al.* 1994, 1995). Olfactory imprinting can occur in the absence of a distinct plasma thyroxine surge (Dittman *et al.* 1994), but this observation may reflect differences between thyroid hormone concentrations in tissue (at the site of action) and plasma levels of thyroxine (Specker *et al.* 1992). We recently demonstrated that the peripheral olfactory system of coho salmon is sensitized to a specific odorant after exposure to that odorant during the PST (Nevitt *et al.* 1994; Dittman, 1994). Thyroid hormones have been implicated as regulators of neurogenesis and maintenance in the peripheral olfactory system in other vertebrates (e.g. Burd, 1991; Paternostro and Meisami, 1989, 1991), and Kudo *et al.* (1994) recently demonstrated that the olfactory epithelium of smolting masu salmon (*O. masou*) is enriched in thyroid hormone receptors compared with that of parr. Therefore, thyroid hormone surges may influence neural development in the salmon olfactory system and facilitate olfactory imprinting (Nevitt *et al.* 1994).

Olfactory imprinting by wild salmon

The study of olfactory imprinting by salmon has focused on a few species and has mainly involved two general strategies: (1) experimental manipulation of artificial odorants using laboratory- or hatchery-reared fish and (2) transportation of hatchery fish from a rearing site to a remote release site and monitoring adult return patterns. While these approaches have yielded great insights into the mechanisms involved in imprinting and homing, they may present an unrealistically simplified picture of the processes of olfactory imprinting by wild salmon. Wild salmon experience constantly changing environmental conditions and a variety of water sources prior to seaward migration. In most hatcheries, however, salmon are reared in a single water source and under stable conditions (e.g. little variation in temperature and water flow). Furthermore, the chemical signature of the different natural water sources may be extremely complex, varying not only in composition but also in the concentration of specific components. These odor signatures undoubtedly experience both short- and long-term changes in response to natural seasonal events and less predictable human activities. Thus, although artificial odorants have been a useful tool for studying imprinting, the mechanisms by which wild salmon learn and recognize complex mixtures and sequences of odorants may differ from imprinting on a single artificial odorant (Sandoval, 1980; Dodson and Bitterman, 1989).

There is also extraordinary diversity of freshwater habitats and migratory patterns within and among salmonid species.

For example, upon emergence from their natal gravel, juvenile salmon may migrate immediately to sea (e.g. chum, *O. keta*; pink, *O. gorbuscha*), remain in the stream (e.g. coho; chinook, *O. tshawytscha*) or migrate and rear in lakes (sockeye) (Groot and Margolis, 1991). Juveniles from different populations of chum salmon may emerge directly into estuarine water or may migrate thousands of kilometers to sea. In such cases, the seaward migration might require only one night or as much as 2 months. The generality of homing in salmonids in view of such variation in life histories and habitats suggests that the mechanisms involved in acquiring site-specific cues (i.e. imprinting) and subsequent use of these cues to guide the homing migration must be both spatially and temporally flexible.

In general, studies with hatchery fish (primarily coho and Atlantic salmon) have indicated that the sensitive period for olfactory imprinting is during the PST (Hasler and Scholz, 1983; Morin *et al.* 1989*a*,*b*; Dittman *et al.* 1995). However, Madison *et al.* (1973) suggested that the sensitive period for olfactory imprinting may differ between species or even between populations of salmon depending on their freshwater migratory patterns. Imprinting prior to the PST might be predicted in species such as sockeye salmon that migrate from their natal (i.e. incubation) site 1 or 2 years before the PST. Consistent with this prediction, hatchery-reared kokanee salmon imprint on artificial odorants at the end of embryonic development when they would typically emerge from their gravel nest and migrate to a lake (Tilson *et al.* 1994, 1995). The PST is the sensitive period for imprinting in hatchery-reared coho salmon. The migration patterns of *wild* salmon, however, suggest that they must imprint prior to the PST. Coho salmon often move downstream in the winter and subsequently experience PST (in spring) in the lower regions of rivers (Peterson, 1982), yet home as adults to their natal sites. Courtenay (1989) demonstrated that coho salmon formed long-term memories of odors they experienced shortly after or even before hatching, but these have not been experimentally linked to homing.

The natural migratory patterns of juvenile salmon in fresh water led Harden Jones (1968) and Brannon (1982) to propose that juvenile salmon learn a series of olfactory waypoints as they migrate through fresh water and later retrace this odor sequence as adults. This 'sequential imprinting' theory is consistent with the finding that juvenile salmon transported away from their rearing site tend to return as adults to their release site (e.g. Donaldson and Allen, 1957; Jensen and Duncan, 1971; Solazzi *et al.* 1991). However, the closer the release site is to the rearing site, the higher the percentage of fish that return to their rearing site as adults (Lister *et al.* 1981; Johnson *et al.* 1990). This correlation suggests that salmon may initially return to their site of release, but if they can detect the odors of their rearing site they will continue on to this site. If the sequential imprinting hypothesis is correct, salmon must have a flexible system for learning olfactory waypoints at appropriate times and places. However, many salmon populations do not migrate directly up-river to their spawning grounds, but rather enter fresh water long in advance of spawning, migrate part way, and then hold for many months in large rivers (e.g. Berman and Quinn, 1991) or lakes (e.g. sockeye salmon) before moving to the spawning grounds. Thus, the homing migration is not a simple response to stimuli; there are many complexities in the movements of juvenile and adult salmon that a complete hypothesis must explain.

Model for plasticity in olfactory imprinting

On the basis of previous findings that thyroid hormones are important for olfactory imprinting, the most obvious candidate for regulating the timing of olfactory imprinting is the thyroid system. The thyroid endocrine axis is a dynamic system under the control of endogenous developmental processes as well as external environmental cues. Although the major surge in plasma thyroxine levels occurs during the PST, more subtle peaks in thyroid hormone levels can occur earlier in development, particularly at hatching and at the time of emergence from the natal gravel (Dickhoff and Sullivan, 1987; Tilson *et al.* 1994, 1995). Such developmentally controlled peaks in thyroid activity may represent periods of sensitivity for imprinting at key landmarks during freshwater rearing (e.g. the natal site; site of initiating the seaward migration). Furthermore, the thyroid axis is sensitive to a number of environmental cues including exposure to novel water (Dickhoff *et al.* 1982; Hoffnagle and Fivizzani, 1990), lunar phase (Grau *et al.* 1981), temperature changes (Iwamoto, 1982; Lin *et al.* 1985), photoperiod (Hoar, 1976; Iwamoto, 1982) and water flow rates (Youngson and Simpson, 1984; Lin *et al.* 1985). All of these factors can apparently contribute to increases in thyroxine levels both independently and in conjunction with development-associated thyroxine surges. We have hypothesized (Dittman *et al.* 1994) that imprinting prior to the smolt stage is not observed in hatchery-reared coho salmon because the stable rearing conditions provide insufficient environmental stimuli for full thyroid function except during PST (Nishioka *et al.* 1985).

Thyroid hormones are also associated with migratory behavior (Hoar, 1976). In general, juvenile salmon migrating in fresh water have higher levels of plasma thyroxine than non-migrants (Youngson *et al.* 1989; Fujioka *et al.* 1990; McCormick and Bjoernsson, 1994). Iwata and Tagawa (1991) artificially elevated thyroxine levels in kokanee salmon and induced downstream migration. Conversely, migration may also influence thyroid activity. During migration, swimming rates often increase and salmon experience new environments with differing chemical compositions, temperatures and flow rates. These factors can stimulate thyroid hormone production (Dickhoff *et al.* 1982; Nishioka *et al.* 1985) and, hence, facilitate olfactory imprinting. Migrating salmon may therefore experience elevated thyroxine levels, providing a complex linkage between migration, thyroxine levels and imprinting. Consistent with this hypothesis, coho salmon held in captivity and not allowed to migrate during smolting exhibited impaired homing ability compared with fish released as smolts to migrate naturally (Dittman *et al.* 1995). A role of migration in

(A) Hatchery-reared salmon

Developmental and seasonal cues → Elevated thyroxine levels → Increased tendency to learn odors

Imprinting threshold

Thyroxine level

N D J F M A M J J A S O N D J F M A M J

Fertilization

Hatching

Emergence

Rapid growth

Parr–smolt transformation (hatchery release)

Seawater entry

(B) Wild salmon

Environmental stimuli (e.g. ↑ flow, novel water, temperature)

Developmental and seasonal cues → Elevated thyroxine levels → Increased tendency to learn odors

Increased tendency to migrate

Imprinting threshold

Thyroxine level

N D J F M A M J J A S O N D J F M A M J

Fertilization

Hatching

Emergence

Rapid growth
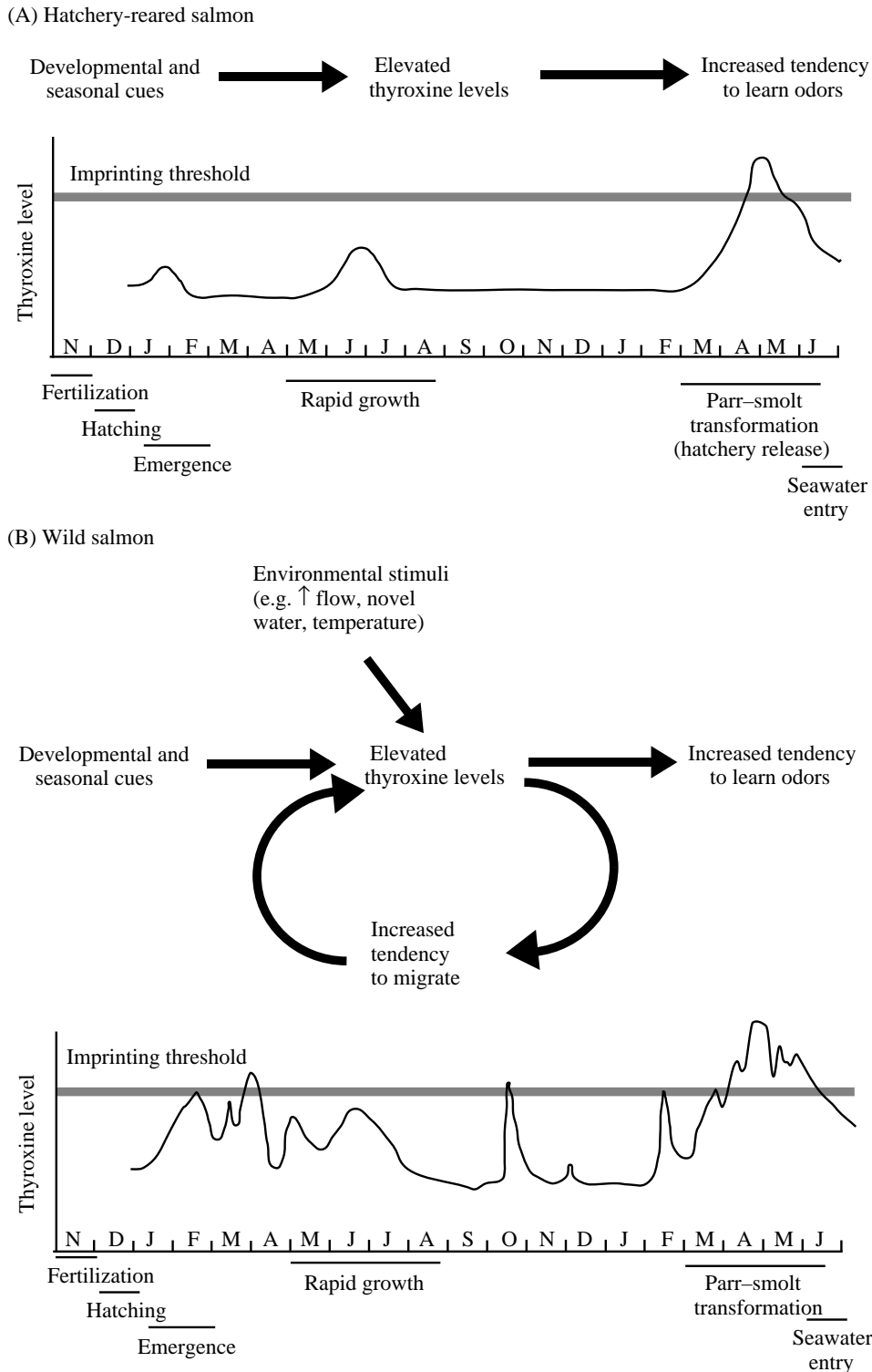
Parr–smolt transformation

Seawater entry

Fig. 2. Hypothetical relationship between thyroxine levels, olfactory imprinting and migration in (A) hatchery-reared and (B) wild coho salmon. Thyroxine data for hatchery fish from Dickhoff and Sullivan (1987). Thyroxine levels for wild salmon are purely hypothetical to illustrate the model.

controlling imprinting is appealing because during freshwater residence salmon would need to learn olfactory waypoints primarily during periods of movement.

We hypothesize that hatchery-reared salmon may experience sensitive periods for imprinting only during developmentally controlled thyroid hormone surges or after the radical environmental changes associated with release from the hatchery (Fig. 2A). In contrast, wild salmon may have several

periods of sensitivity for olfactory imprinting that are controlled by the thyroid endocrine axis (Fig. 2B). Thyroid activity changes during freshwater residence in response to changing developmental status and environmental conditions. Furthermore, thyroid activity both influences and is influenced by migratory status. Therefore, wild salmon have a flexible system of imprinting whereby they learn key freshwater landmarks at developmentally regulated periods, but they also learn opportunistically during migrations in response to novel environmental stimuli.

Ecological and evolutionary aspects of homing

Homing to natal sites has led salmon to evolve population-specific adaptations to the physical and biotic characteristics of these sites. Taylor (1991) has reviewed many of these 'local adaptations', but we will provide selected examples in sockeye salmon. These salmon home to the incubation site (not the site of smolt migration), as shown by genetic differentiation of populations within lake systems (Varnavskaya *et al.* 1994). The sockeye salmon populations within large lake systems in Bristol Bay, Alaska, consistently vary in life history traits related to specific features of their spawning and incubation habitats (Blair *et al.* 1993) (Fig. 1). Two notable traits that vary are egg size and male body size and shape. Populations spawning in areas with a fine substratum have smaller eggs than at nearby sites with a coarser substratum, even though all juveniles will rear in and leave as smolts from the same lake (Quinn *et al.* 1995). In addition, male reproductive success is associated with large size and especially with the development of an exaggerated dorsal hump (Quinn and Foote, 1994). However, males in shallow streams are small and shallow-bodied, apparently because the sexual selection for hump development and large size that is expressed in deep-water sites is opposed by natural selection, chiefly in the form of size-selective predation by brown bears (Hanson, 1992; T. R. Hamon, G. T. Ruggerone and T. P. Quinn, unpublished data).

These adaptations to the natal spawning and incubation sites depend on imprinting by juvenile salmon prior to, or at, emergence rather than at the smolt stage. However, returning adults must apply their olfactory memory to discriminate among increasingly similar water sources and, at some point, homing may give way to spawning site selection. For example, spawning takes place at specific sections of beaches on a series of islands bathed by wind-driven currents of lake water in the eastern end of Iliamna Lake, Alaska (Fig. 1). Do salmon home to the group of islands, to one particular island (their island of origin), to a specific beach on the island or to a particular section of the beach (Blair and Quinn, 1991; Hendry *et al.* 1995)? The distribution of spawning salmon observed from year to year must reflect a complex combination of homing and responses to habitat quality, intrasexual competition and availability of mates. These ecological factors culminate in the variation in reproductive success that is the evolutionary driving force behind homing in salmon.

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