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The paradox of ‘premature migration’ by adult anadromous salmonid fishes:
Patterns and hypotheses

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Abstract

In several groups of anadromous fishes but especially the salmonids, some populations migrate from the ocean to fresh water many months prior to spawning. This ‘premature migration’ reduces growth opportunities at sea, compels them to occupy much less productive freshwater habitats, and exposes them to extremes of flow and temperature, disease, and predation. We first review migration in salmonids, and find great variation in timing patterns among and within species, relative to the timing of reproduction. Premature migration is widely distributed among species but not in all populations, and we propose two hypotheses to explain it. First, the fish may be making ‘the best of a bad situation’ by entering early because access to suitable breeding sites is constrained seasonally by flow or temperature regimes, so they sacrifice growing opportunities at sea. Alternatively or additionally, some populations may be ‘balancing risks and benefits’ as they trade off the benefits of growth at sea against the risk of mortality there. In this model, the reduced risk of mortality at sea must be balanced against the risk of mortality in freshwater habitats from thermal stress, disease, and predators. Premature migration may be favored where temperatures and flows are moderate, or where lakes provide safety from predators and reduce energetic expenditure. Consistent with this hypothesis, early return is characteristic of larger, older salmonids (that would benefit less from additional time at sea to grow than would smaller fish). Finally, we consider the vulnerability of premature migrants to climate change and selective fisheries. Migration timing is an important part of the portfolio of phenotypic diversity that conveys resilience to species, population complexes, and the fisheries that depend on them. The premature migrants are often especially valued in fisheries and also often of particular conservation concern, and the phenomenon merits further research.

Introduction

The need to obtain energy for maintenance, growth, and reproduction drives a wide range of behavioral and ecological processes. Migratory animals take advantage of seasonally predictable patterns of resource availability in different habitats, either by foraging sequentially in a series of habitats, migrating between foraging and breeding areas, or combinations of patterns (Baker 1978). Many fishes migrate within marine or freshwater habitats but diadromous species migrate between marine and freshwater habitats. Diadromy is relatively unusual, displayed by < 1% of fish species, but is widely distributed among evolutionary lineages (McDowall 1988) and many of the species are important in traditional, commercial, and recreational fisheries. Diadromy is hypothesized to evolve when the costs (energetic demands of migration, stress from adaptation to different osmotic environments, exposure to predators, etc.) are exceeded by the benefits, which are generally seen as the growth opportunities in feeding grounds distant from the suitable breeding areas (Gross et al. 1988). The cline from a higher proportion of anadromous species (spawning in fresh water and growing primarily at sea) in high latitudes to predominately catadromous species (spawning at sea and growing primarily in freshwater) in low latitudes has been interpreted to reflect the typically superior growth opportunities in high latitude marine systems compared to freshwater habitats, and the reverse at low latitudes (Baker 1978; Northcote 1978; Gross et al. 1988).

If the ocean affords better growth opportunities for anadromous fishes, they should stay at sea as long as possible, and return to fresh water in time to migrate to their spawning sites and reproduce. However, 'premature migration' into fresh water longer in advance of reproduction than would be necessary to reach the spawning grounds upriver is known in all three major genera of salmonids (*Oncorhynchus* in the Pacific Ocean, *Salmo* in the Atlantic Ocean, and

Salvelinus in the Atlantic, Pacific, and Arctic oceans). Premature migration is also known in lamprey (Beamish 1980; Moser et al. 2015), and is a fundamental aspect of the biology of anadromous fishes (Berg 1959). Here we consider premature migration in salmonids but the concepts apply to other fishes as well. Premature migration in salmonids is distinct from return migration by individuals that will not breed in that year such as the so-called “half-pounders” in steelhead, *O. mykiss* (Kesner and Barnhart 1972; Savvaitova et al. 2005), immature Dolly Varden, *Salvelinus malma* (Armstrong 1974), or anadromous brown trout, *Salmo trutta* (Thomsen et al. 2007) colloquially known as “finnock” in Ireland and Scotland and “whitling” in much of England and Wales.

The present paper 1) defines the phenomenon of premature migration, 2) reviews the general patterns of migration and spawning timing in anadromous salmonids to determine whether there are distinct modes of migratory timing (i.e., premature migration and migration by fully mature fish) or a continuum, 3) documents co-variation between migration timing and the size, age, or sex of the migrants, 4) proposes hypotheses to explain the phenomenon based on the benefits and costs associated with early entry into freshwater and the costs of remaining at sea, and confronts them with the observed patterns. Finally, we consider the influences of climate change and fisheries on these migration patterns, and note the contributions of migration timing to the diversity and resilience of salmonid species and population complexes.

Defining Premature Migration

The term premature migration implies arrival in fresh water farther in advance of breeding than is necessary for the fish to migrate to the breeding grounds and complete reproduction, and the completion of sexual maturation in freshwater rather than at sea. Is there a

sharp distinction between populations with premature migrations and ones that migrate when fully mature? Such bimodality would allow unequivocal categorization of runs as premature or not, and that would facilitate some analyses. First, we need to consider how long it might take to migrate to the breeding grounds. Salmon are famous for their long migrations but most populations spawn in short, coastal rivers. Chinook salmon, *O. tshawytscha*, ascend up to 3000 km in the Yukon River system but a sample of 86 populations showed a mean of 396 km and a median of 135 km to the breeding grounds (Roni and Quinn 1995). Of 55 lakes supporting sockeye salmon, *O. nerka*, the maximum distances were 1064 km in the Fraser River system and 1444 km in the Snake River but the mean was 229 km and the median was 100 km (Bjornn et al. 1968; Burgner 1991). Of 132 rivers in eastern Canada supporting Atlantic salmon, *Salmo salar*, the maximum was 343 km, the mean was 45 km and the median was 32 km (Schaffer and Elson 1975). On the other hand, Atlantic salmon migrate 800 – 1000 km up the Loire-Allier River system (Baisez et al. 2011), restoration efforts are bringing anadromous brown trout and Atlantic salmon back to habitat formerly occupied some 1500 km up the Rhine River (Schreiber and Diefenbach 2005; Bölscher et al. 2013), and in the Pechora River system in Russia, Atlantic salmon ascend as much as 1800 km (Studenov et al. 2008). Even such distances, however, do not require long periods of time, as salmon can cover 30 - 50 km per day in free-flowing (Eiler et al. 2015) and impounded rivers (Quinn et al. 1997).

Is there a clear, bimodal distribution in arrival timing, relative to breeding timing? Many large rivers have multiple, genetically distinguishable breeding populations, each with its characteristic timing patterns, resulting in a continuum of migration and breeding timing in the complex as a whole. In some cases such as the Skeena River sockeye salmon (Beacham et al. 2014) and Klamath River Chinook salmon (Strange 2012) the runs grade into each other; some

are premature and some are not. The Skeena River's summer steelhead are an amalgamation of discrete populations, each with its own timing (Beacham et al. 2012), but all return so early (late July to late August) relative to spawning (mid-May to late June of the following year), that they are clearly premature migrants. Large rivers that support Atlantic salmon also have multiple, genetically distinguishable populations breeding in different parts of the system, such as the Varzuga River in Russia (Primmer et al. 2006), and the Moy (Dillane et al. 2008) and Foyle (Ensing et al. 2011) rivers in Ireland. Analysis of migration in such systems can be difficult because the timing of entry into fresh water is often only known for the river basin as a whole from fishery data or a downriver counting site, not for each breeding population.

Pacific salmonid runs tend to be categorized based on adult return timing. For example, 'summer steelhead' enter in summer and spawn the following spring, and 'winter steelhead' enter in winter and spawn that spring. These seasonal designations are imprecise because migration timing varies so much. Consequently, summer steelhead (or 'fall' in Alaska) are called 'stream-maturing' (Busby et al. 1996) because they enter in a relatively immature state and undergo final maturation in rivers; here we would call them premature. Winter steelhead (or 'spring' in Alaska) are 'ocean maturing' because most of the maturation process occurs in the ocean (Busby et al. 1996), and they are not premature. Chinook salmon are referred to as spring, summer, and fall, indicating when they enter freshwater. All spawn in the fall (Healey 1991) so the spring runs are premature whereas the fall runs are not. Some Chinook salmon migrate in the winter and spawn in late spring, an unusual pattern confined to the Sacramento River system, California (Healey 1991).

In many rivers, 'spring' Atlantic salmon enter in late winter or early spring and spawn the following fall or winter, and are certainly premature (Went 1964; Youngson 1994). However,

there can be a broad continuum of arrival timing (Shearer 1990), greatly complicating the distinction in some cases. Thus a cursory examination reveals no clear bimodality in timing of migration by salmonids, relative to spawning, that would support a simple distinction between populations with premature return timing and those entering at full maturity. For practical purposes, however, any delay exceeding three months in freshwater for populations other than those with exceptionally long migrations can be considered premature. What ecological processes drive this paradoxical behavior? To address this question, we take an inductive approach, examining first the patterns of migratory timing among and within salmonids, and then proposing two alternative ways of explaining that variation. The examples listed in the text are summarized in Table 1 but this should not be taken as an exhaustive or even fully representative list – only as examples of the diversity of migration timing within and among species.

Timing Patterns and Examples of Premature Migration

The genus *Salmo*: Atlantic salmon and brown trout

Both Atlantic salmon and brown trout (the anadromous form known as sea trout) spawn in the late fall but Atlantic salmon often spawn later and over a more protracted period than co-occurring brown trout (Jonsson and Jonsson 2011). The peak spawning date of salmon varies with latitude, from mid-October in the north (65 – 70° N) to mid-December farther south (Fleming 1996). Atlantic salmon are native to both sides of the ocean but there are more populations and wider range of patterns in Europe. In northern areas, return timing seems to be constrained by ice in the sea and the rivers, commencing soon after the ice leaves. For example, salmon migrated up the River Teno, in northern Scandinavia, primarily in June and July, when flows decreased and temperatures increased, and spawned in late September and early October

(Niemelä et al. 2000, 2006). Discrete breeding populations within this river system differ slightly in timing (Vähä et al. 2011) with no clear bimodality.

Atlantic salmon began to enter the River Tornionjoki, a Finnish tributary of the Baltic Sea, in late May or early June, when water temperatures in the lower part of the river were about 9 °C (Lilja and Romakkaniemi 2003). The migration peaked in mid-late June, about 7 weeks after the break-up of ice in the sea, as the river was warming. The authors concluded that, “The overall seasonal migration pattern is obviously an adaptation to the fairly regular, distinct climatic and hydrological changes found in the northern Baltic Sea. The break-up of an almost 1 m thick ice-cover in May and the subsequent annual peak flood restrict the start of the river entry, whilst the long in-river migration combined with a spawning season as early as September and October requires a relatively quick river ascent.” The river is about 500 km long but most spawning occurs about 100 – 300 km upriver from the mouth (Lilja and Romakkaniemi 2003), so it is not clear why the salmon require so much time to migrate this distance. In the Swedish tributary of the Baltic Sea, the Umeälven, the first salmon arrived in late June and early July, and the median was in late July and early August (McKinnell et al. 1994).

Salmon arrived somewhat later along the Atlantic coast of Norway than in the Baltic Sea, such as the River Vefsna, in northern Norway, where migration began in late June, peaked in July, and continued into early September (Jensen et al. 1986). The Imsa River salmon migration was later still, primarily in August through November (Jonsson et al. 1990). Spawning occurred primarily from about 10 November to 5 January (Bror Jonsson, pers. comm.), and the downstream migration of kelts was bimodal, in winter immediately after spawning, and in spring (Fig. 1, top). In an experiment, salmon representing eight Norwegian populations were reared in and released from the Imsa River (Jonsson et al. 2007). The four northern populations returned

earlier (median dates from 25 August to 13 September) than the salmon from the four southerly rivers, including the Imsa River (median dates from 3 October to 22 October), indicating a genetic basis for the timing of return.

In contrast to these Scandinavian populations of Atlantic salmon that return in the summer, with at most moderately premature migration, very protracted and premature migrations are common in Scotland and Ireland. Salmon were caught entering the Aberdeenshire Dee, Scotland throughout the February - August fishing season (Smith 1990), and similarly broad timing occurs in some Irish populations (Went 1964; Quinn et al. 2006). For example, electronic counts at a weir on the Blackwater River revealed upriver movement in all months of the year, with peaks in June and in October-November (Fig. 1, bottom). Doubtless, some of these fish entered the river earlier in the year, but commercial catches in the estuary occurred throughout the open season, from February through September, with the largest catches in June and July, and anglers took salmon in the lower reaches throughout the February - September season (Quinn et al. 2006). Similarly, "Fish entered the North Esk [Scotland] in every month in the year. Some fish entering in October of one year could not spawn until the following spawning season" (Shearer 1990). As with the salmon entering the Dee and the Irish rivers, the earliest returning fish tended to be older, 'multi-sea-winter' (MSW) fish, shifting to grilse (one sea-winter fish) later in the season; a pattern seen in the River Teno as well (Niemelä et al. 2006).

At the southern end of their European distribution, in northern Spain, the salmon migration was premature, as early as March (Valiente et al. 2011). At the southern part of the range in North America, remnant salmon populations in the Connecticut River system, USA peaked in late May to early June at the Farmington River, and in late June and early July upriver at the Holyoke Dam (Juanes et al. 2004). Thus they arrived prior to the annual maximum

temperatures ($>25^{\circ}\text{C}$ in July and August). In the Penobscot River, Maine the median was in late May and early June (Juanes et al. 2004). All of these would be considered premature migration, and the fish pass the warmest part of the year in the river prior to spawning. As with populations in Europe, the MSW salmon tended to arrive before the grilse but the separation was not nearly as great. The salmon migration in the Penobscot River was earlier than those in other rivers of Maine; data from nine rivers showed a continuum in timing rather than discrete early and late runs (Baum 1997). Farther north, in the Miramichi River, New Brunswick, the median entry was in September in the 1950s and 1960s, changing rather abruptly to July in the 1970s through 1990s (Juanes et al. 2004), and on the Torrent River, Newfoundland, the median was in late July to early August (Juanes et al. 2004).

The marine migrations of sea trout are more complex than those of Atlantic salmon because both immature and mature fish return to freshwater. In addition, some sea trout spend a full year, including the winter, in marine waters but many only spend the summer, so the range of sizes and maturity states of returning fish can vary greatly. As with the southern populations of Atlantic salmon, the sea trout returning to northwest Spain migrated mostly from June through August (Fig. 2), and spawned from December through February (Caballero et al. 2006). Sea trout from Turkey fed in the Black Sea and migrated upstream as early as March, with a peak in May and June, and spawned in late October to late December (Okumus et al. 2006). Farther north, the migration tends to be in the fall, much closer to the timing of breeding. For example, sea trout ascended the River Imsa as early as April but the mode was in August to October (Jonsson and Jonsson 2002), and they spawned primarily in late October and early November (Bror Jonsson, pers. comm.). Even farther north, in the Vardnes River, the trout migrated in July to September

(Berg and Berg 1989a) and spawned in late September (Ole K. Berg, pers. comm., Fig. 3, top panel).

The sympatric sea trout and Atlantic salmon in County Mayo, in northwestern Ireland, illustrate the diversity of timing within a small geographical area. There are several rivers in close proximity to each other, including the Owenduff, and the Munhin, the outlet of Carrowmore Lake. Electronic resistivity counters detected passing fish, validated with images taken automatically as fish passed. Both rivers share the stable regimes of temperature and precipitation typical of this region. As an illustration, the Tarsaghaun, a major tributary of the Owenduff, had monthly mean temperatures ranging only from 6.3 °C (SD = 1.4) in January to 15.2 °C (SD = 1.2) in July, and stream height varied from a monthly mean low of 0.24 m (SD = 0.05) in June to 0.39 m (SD = 0.06) in December (Mary Dillane, Marine Institute, Newport, unpublished data). The fish could presumably easily enter in the fall, shortly before spawning but many do not, and the migrations are essentially year-round (Fig. 4).

The genus *Oncorhynchus*: Pacific salmon and trout

Among Pacific salmon, premature migration is best known in Chinook salmon; in some large systems such as the Sacramento River in California, adults returned in all months of the year (Healey 1991). These and other protracted runs such as the Klamath (Strange 2012), Columbia (Brannon et al. 2004; Keefer et al. 2004) and Fraser (Waples et al. 1990) rivers are amalgamations of separate populations, each with much narrower timing. All Chinook salmon spawn in the fall (with one exception, below), typically in August to November, but discrete populations spawn during much shorter periods within this range (Brannon et al. 2004). Fall Chinook salmon enter in the fall and spawn about a month or two later but many rivers,

especially in the central and southern end of the species' range, have premature migrants. Spring Chinook salmon enter early (e.g., April and May), migrate part way to their natal sites, seek cool refuges to minimize energy expenditures during the summer (Berman and Quinn 1991; Goniea et al. 2006), then complete their migration and spawn in fall. Some rivers also have what are termed summer runs. The cutoff between seasonal runs is sometimes arbitrary; some might be considered premature and some might not, depending on when they spawn, and how broadly the term is defined. Spring Chinook salmon generally migrate farther upriver to higher elevations than fall Chinook salmon, though there are exceptions. Spring Chinook salmon enter with more stored energy, an adaptation to sustain them during the migration and holding periods (Hearsey and Kinziger 2015). To add further complexity, winter Chinook salmon enter the Sacramento River in the late winter with a peak in March, and spawn in June in the upper reaches below Shasta Dam. Combined with what is termed a late fall run, the winter, spring and fall runs result in year-round entry of the species into the system (Fisher 1994).

Other than Chinook salmon, perhaps the Pacific salmon species with the widest range of migration timing is the sockeye salmon. Some populations that breed in the coastal region towards the southern end of the distribution, and also in the interior of the Columbia River system, show premature migration (Quinn and Adams 1996; Hodgson and Quinn 2002). For example, the Baker Lake population in northern Puget Sound, Washington enters primarily in July but does not spawn is not until October and November (Hodgson and Quinn 2002). They enter near the time of highest temperatures in the migratory corridor but this river stays quite cool (Fig. 5, top). The sockeye salmon migrating to Lake Ozette, along the coast of Washington, are even more extreme, entering in June and July (Fig. 5, bottom), even though they have a short, easy migration and do not spawn until late December (Hodgson and Quinn 2002). In this case,

273 however, the outlet of the lake is warmer, often exceeding 20 °C, and the early migration may
274 allow the fish to avoid high mid-summer temperatures. The populations with long delays in
275 freshwater tend to be in the southern end of the distribution, where warm temperatures in late
276 summer and early fall may select against entry a month or two prior to spawning. Rather, these
277 salmon enter early and often hold in lakes below the thermocline until fall, when they ascent
278 rivers to spawn (e.g., Newell and Quinn 2005).

279 Unlike Chinook and sockeye salmon, in which premature migration is common, the other
280 semelparous Pacific salmon species seldom show this pattern. The geographical distribution of
281 coho salmon, *O. kisutch*, overlaps broadly with Chinook salmon but where share the same
282 watersheds the Chinook salmon generally use the main river whereas coho salmon spawn
283 primarily in tributaries, or in small coastal streams (Sandercock 1991). In the early fall
284 (September and October) when many Chinook salmon spawn, these small streams often
285 experience very low flows until the fall and winter rains come. There is variation in arrival
286 timing, which Sandercock (1991) attributed to physical barriers to migration from flow
287 conditions. Access is even more difficult in small coastal California streams at the southern end
288 of the distribution of coho salmon because sandbars often completely block entry until heavy
289 rains open the mouths of the streams (Shapovalov and Taft 1954).

290 Most pink, *O. gorbuscha*, and chum salmon, *O. keta*, enter freshwater in an advanced
291 state of maturation and spawn only a short distance inland within a month of entry. Some pink
292 salmon travel over 100 km upriver (Heard 1991) but no populations seem to display premature
293 migration. The chum salmon that migrate over 1000 km up the Amur River and 2400 km up the
294 Yukon River enter in a much less advanced state of maturity than the coastal populations
295 because they have so far to travel (Brett 1995) but they would not qualify as premature. Some

areas also have what are known as ‘summer’ and ‘fall’ runs of chum salmon (Salo 1991). In Alaska, these groups tend to spawn in different areas and habitats; summer chum enter in June and July and spawn shortly thereafter in sites dominated by downwelling water, whereas fall chum enter later, in July and August, and spawn at sites where there is upwelling water, and so milder during the winter than the downwelling sites (Olsen et al. 2008). Three seasonal runs were described for rivers on Kamchatka but in each case spawning occurred within a few months of upriver migration (Kuzishchin et al. 2010), so these do not seem to be premature.

The distribution of masu salmon, *O. masou*, is limited to Asia but they are distributed over a range of latitudes, and anadromous populations vary in the timing of return and spawning (Kato 1991). In general they return in late spring or early summer, shortly after the snow melts, and spawn in early fall, and so are often premature but the extent of delay varies. Southern populations tend to enter earlier than northern population (April and May vs. June and July), and spawn later than northern ones (September and October vs August and September), so the southern populations spend more time in freshwater than the northern ones (Kato 1991).

All of the *Oncorhynchus* species described so far spawn in the fall, though that might be as early as July in the northern end of the range and as late as March in the south. However, the iteroparous Pacific trout species (steelhead, as anadromous rainbow trout are called, and coastal cutthroat trout, *O. clarkii clarkii*) characteristically spawn in the spring, when water temperatures are ascending rather than descending (Quinn 2005). Premature migration is characteristic of the many steelhead populations referred to as summer or river-maturing (Burgner et al. 1992; Busby et al. 1996). Stream-maturing steelhead tend to enter large rivers in the late summer and fall (Robards and Quinn 2002), migrate part way up, hold during the winter, and then ascend farther to spawn in spring. Ocean-maturing steelhead tend to enter coastal rivers, in a more advanced

state of maturity, in late winter and early spring, spawn, and then leave soon thereafter. Some rivers such as the Kalama River, a tributary of the Columbia River, have both seasonal runs of steelhead. The ocean-maturing steelhead entered from late fall to a peak in April, spawning in April (Leider et al. 1984), and the arrival of stream maturing steelhead peaked in July, continued into the winter, and most spawned in February (Fig. 6).

Coastal cutthroat trout exhibit a range of migration patterns, including resident, adfluvial, and anadromous populations (Trotter 1989). In anadromous populations, the duration of marine residence and period in freshwater prior to spawning varies markedly. Populations in small streams along the coast of southeastern Alaska such as Eva Lake (Armstrong 1971) and Auke Creek (Fig. 7, top) migrate to sea in late spring, shortly after spawning, and return in late summer or early fall. This brief (e.g., May to September) period at sea leaves the fish in fresh water for about eight months prior to spawning. Interestingly, some of these small streams where cutthroat trout hold for long periods prior to spawning (Fig. 7, middle) have steelhead that enter just before spawning (Jones 1972, 1973; Fig. 7, bottom).

This protracted period in fresh water is not seen in all populations of coastal cutthroat trout. In Sand Creek, on the coast of Oregon, they left the sea in October-December, spawned in spring, and returned to sea in April-May (Sumner 1962). This pattern, with upriver migration in fall, and about a half-year in the river prior to spawning, was also reported for populations in Washington that used large rivers (Johnston 1982). However, populations migrate into small Puget Sound streams later (January-March), shortly before spawning, and leave primarily in April (Wenburg 1998). Small coastal streams in Oregon also enter just before spawning, in contrast to the more protracted patterns in some other rivers. In Deer and Flynn creeks, the modal upriver migration was in November through January and the downstream migration was

primarily in January and February (Lowry 1965). In these and similar systems, the early fish have spawned and returned to marine waters before the late fish have arrived.

The genus *Salvelinus*: The circumpolar char species

Anadromous species of the genus *Salvelinus* include brook trout, *S. fontinalis*, on the North American side of the Atlantic Ocean into Hudson Bay, white-spotted char, *S. leucomaenis* (Arai and Morita 2005), on the Asian side of the Pacific Ocean, bull trout, *S. confluentus*, on the North American side of the Pacific Ocean, Dolly Varden, *S. malma*, around the Pacific Rim and parts of the Arctic Ocean, and Arctic char, *S. alpinus*, in northern Atlantic, Pacific, and Arctic ocean drainages. All are fall-spawning, iteroparous, and facultatively anadromous, and display a range of migration patterns but generally do not show premature migration. The main reason for this seems to be that they typically migrate to sea in spring, spend only the summer there, and spawn in the fall so the scope for early migration is limited. For example, the anadromous brook trout from the Sainte-Marguerite River, Québec migrated downstream in May and maturing fish returned from August to October and spawned shortly thereafter (Lenormand et al. 2004). The upstream migration in the St-Jean River, Québec, was somewhat earlier (Castonguay et al. 1982), mostly in June through August, however.

Anadromous Dolly Varden enter marine waters over a range of latitudes, vary in the duration of marine residence and delay prior to spawning, and do not migrate very far inland (Bond and Quinn 2013). They generally spend only the summer at sea and spawn in the fall, so the period of holding in freshwater prior to spawning is brief but some populations enter earlier than needed to reach the spawning areas. For example, in Auke Creek, in southeastern Alaska, Dolly Varden migrate to marine waters in April and especially in May, and return from July

through October (Bond and Quinn 2013; Fig. 8). In the Buskin River, on Kodiak Island, Alaska, the upstream migration is primarily in July but fish return as early as May and as late as October. Dolly Varden often feed heavily on the eggs produced by sympatric Pacific salmon, and the return migration in many cases seems timed to take advantage of this rich food resource. Farther south, in Puget Sound, Washington, the anadromous char species is the bull trout, *S. confluentus*. They leave rivers in spring (primarily April and May) and by the end of June or July most have returned to freshwater (Hayes et al. 2011), though they do not spawn until October, so the migration is premature.

In the Vardnes River, northern Norway (69° 10' N), Arctic char migrated downstream primarily in May and June, returned primarily in July (Fig. 3, bottom), and spawned in October (Berg and Berg 1993). The Arctic char thus entered about a month earlier than sympatric sea trout (Fig. 3, top panel) described by Berg and Berg (1989b) and spawned a month later, so the short (only 1.2 km) migration would be considered premature for the char but not the sea trout. Arctic char in Svalbard, even farther north (79° 10' N), migrated downstream primarily in July and August and returned from mid-July to mid-September, for a marine residence of about 4 to 5 weeks (Gulseth and Nilssen 2000). Arctic char in the Fraser River of northern Labrador also migrated upstream in mid-July to late September and spawned in late October, and the larger fish returned earlier than the smaller ones (Dempson and Green 1985).

In the Canadian Arctic, many rivers have large runs of Arctic char, and the upstream migrations are typically very compressed. For example, runs in the Ekalluk, Jayco, Halovik and Laughlan rivers in the Cambridge Bay area were all between late August and early September (McGowan 1990). Similarly compressed runs, rising quickly to peaks in late August and largely finished by mid-September, were documented in the Meliadine River (McGowan 1992),

Freshwater Creek (McGowan and Low 1992) (Fig. 9, top), and the Koukdjuak River (Kristofferson et al. 1991). For example, in 1989 a very large and compressed run on the Ikaluit River (Read 2003) took place primarily in August, with 85% of the year's total of 282564 fish counted on eight consecutive days (Fig. 9, bottom). These migrations from the sea back to freshwater would not be considered premature because the Arctic char spawn in the fall.

An especially fascinating and complex migration pattern was documented for the Arctic char in the Nauyuk Lake system (Gyselman and Broughton 1991). Most char migrate downstream from Nauyuk Lake to marine waters, primarily in July, and return upriver in August (Fig. 10, top). However, this return migration is not for the purpose of spawning but to overwinter in the lake. Spawning in this system occurs in Willow Lake, upstream from Nauyuk Lake. The spawning migration is undertaken by a smaller fraction of the population that did not migrate to sea that year. They leave Nauyuk Lake and ascend Willow Creek in mid-June to mid-July (Fig. 10, bottom) because only then is there enough water to permit migration. The char remain in Willow Lake all summer, spawn in the lake in the fall, but cannot leave because the outlet is not passable that late in the season. They overwinter in Willow Lake and leave the following spring when the next cohort of spawning char is coming upstream.

In summary, this review of the timing patterns in anadromous salmonids revealed variation among species and locations, and what might be termed a species by location interaction. That is, some species (e.g., cutthroat trout) display premature migration whereas others (e.g., pink salmon) do not, but the cutthroat trout only display premature migration in certain locations. Moreover, in some of those locations sympatric steelhead trout do not display premature migration (Fig. 7), though they do elsewhere. Premature migration occurs in both semelparous and iteroparous species, and in both fall and spring spawning species. There are no

hard and fast rules but populations in the far north are less likely to display premature migration than ones farther south, as Youngson (1994) noted for Atlantic salmon. Some populations have very compressed migrations (typically in the far north, though in some southern populations as well), and others with year-round migration (typically in areas with moderate conditions). These diverse patterns of migration and spawning timing among species and populations have frustrated efforts to derive general explanations.

Hypotheses to Explain Premature Migration, and Weaknesses Therein

Genetic and Environmental Influences on Migration

The first step towards explaining premature migration is to consider whether the patterns reflect phenotypic plasticity, genetic adaptations, or non-adaptive variation. Inter-annual variation in migration timing is often correlated with environmental conditions in marine and freshwater environments (e.g., Hodgson et al. 2006; Anderson and Beer 2009), sometimes strongly (Mundy and Evenson 2011) but often not (Smith 1990; Lilja and Romakkaniemi 2003). Davidson et al. (1943) compared pink salmon migration up two streams, and noted that in both streams the salmon arrived in the near-shore area at about the same time every year. In the stream with stable, lake-fed flows, the salmon ascended at the same time, regardless of flow or temperatures changes, and held in the stream for final maturation. Flow in the other stream, without a lake, increased rapidly with precipitation, and the salmon entered only when they were fully mature, as soon as rain caused the stream to rise. So, the timing of migration from the sea was very regular in both populations but in one stream the final ascent was affected by local conditions (see also California coastal coho salmon: Shapovalov and Taft 1954). In general, the arrival timing of salmon in the vicinity of streams prior to upriver ascent varies by days or at

most a few weeks from year to year, and so the magnitude of variation between seasonal runs (often many months) cannot be ascribed to phenotypic plasticity.

Several lines of evidence indicate that migration and breeding timing are heritable. First, the median heritability of 0.51 for phenological traits was much higher than for any other category of traits in salmonids (Carlson and Seamons 2008). The genetic control of timing has been revealed in several salmonid species, often as part of selective breeding programs (Siitonen and Gall 1989; Sato et al. 2000; Neira et al. 2006; Abadía-Cardoso et al. 2013). Second, migration timing evolves in contemporary time-frames, as indicated by the differences among populations arising from common ancestors transplanted to a new environment (Quinn et al. 2000, 2011), in rivers experiencing climate change (Quinn and Adams 1996; Crozier et al. 2011), and in hatcheries preferentially spawning early-arriving fish (Quinn et al. 2002, Tipping and Busack 2004). Third, fish from different populations released experimentally from a common facility showed their ancestral return timing patterns (Ricker 1972; Hansen and Jonsson 1991; Stewart et al. 2002; Jonsson et al. 2007). Fourth, in iteroparous species such as steelhead, individuals that return early on their first migration tend to return early on subsequent migrations (Leider 1985; Abadía-Cardoso et al. 2013). Fifth, studies revealed an association between the circadian clock gene *Ots-Clock1b* and return timing in two different salmonid genera: Chinook salmon (O'Malley et al. 2013) and Atlantic salmon (O'Malley et al. 2014).

Migration timing has been studied for many decades but often the goal has been to explain how temperature and discharge affect migration on daily or other short time periods that might constitute phenotypic plasticity (Jensen et al. 1986; Smith 1990; Trépanier et al. 1996; Erkinaro et al. 1999) rather than explain the broader timing patterns. However, there have been efforts to explain premature migration patterns. Hawkins (1989) suggested that the early entry by

457 Atlantic salmon in some rivers was related to the long upriver migration, whereas in western
458 Scotland, late migration might be the only option because the small rivers lack suitable holding
459 habitat. Hawkins (1989) further hypothesized that some rivers are too warm in the lower reaches
460 and estuaries for fall ascent, and so the salmon enter early and hold prior to making the final
461 ascent to spawning grounds much later in the year. Can such a hypothesis be generalized to the
462 myriad patterns seen in salmonids?

463 Given the variation in environmental conditions in freshwater and marine habitats around
464 the rims of the Atlantic, Pacific and Arctic oceans occupied by salmonids (e.g., from Spain to
465 Svalbard, the Connecticut River to the Canadian Arctic, Korea to Kamchatka, and California to
466 the Bering Sea), no single factor explains all the patterns of timing and separation between
467 upriver migration and breeding. Consequently, we seek a framework for examining the
468 conditions in each location and species, even though the specific factors controlling timing may
469 vary. The primary selective factors operating on anadromy are the relative growth opportunities
470 and the risks of mortality in the marine and freshwater habitats.

471 High latitudes typically provide poorer growing conditions for fishes in freshwater
472 compared to marine habitats, and the prevalence of anadromy among diadromous fishes in these
473 regions likely reflects this difference (Baker 1978; Northcote 1978; Gross et al. 1988). So, fish
474 should stay at sea as long as possible, to maximize growth that can be translated into
475 reproductive success through increased egg number and egg size, and increased competitive
476 ability of larger fish. Indeed, Youngson (1994, p. 12) wrote “No entirely convincing explanation
477 has been proposed for why springers [early-returning Atlantic salmon] choose to exercise their
478 unusual style of life. By migrating to the oceans, all salmon increase their growth rate and their
479 size at sexual maturity. It might be wondered why if springers take steps to go to the ocean

feeding grounds to grow large, they cut short this phase of their lives by leaving the ocean at what appears to be an unnecessarily early stage.”

Hypotheses to Explain Premature Migration

We propose two different but not mutually exclusive perspectives on the phenomenon of premature migration (Appendix Figure 1). First, early migration may be a matter of making the ‘best of a bad situation.’ If headwater streams are highly suitable for breeding and juvenile rearing but access is limited by some physical factor such as temperature or flow, such that adults could not ascend shortly before spawning, they may enter early, and pay an energetic cost in terms of egg size to account for the metabolic demand from a summer of fasting (Healey 2001). In addition to the energetic cost of fasting, the fish also lost foraging opportunities at sea, and thus are smaller than they would be, had they spent the extra months at sea and returned later. Finally, freshwater environments are not without risk. A number of diseases can cause mortality during upriver migration, and are often exacerbated by high temperatures (St-Hillaire et al. 2002; Kocan et al. 2004). Ulcerative dermal necrosis afflicts early-returning Atlantic salmon, and episodic outbreaks coinciding with high density can be devastating, though they last only a few years (Roberts 1993). There is also risk from predators such as bears (Quinn et al. 2001) or otters (Carss et al. 1990) unless the fish have safe holding areas.

This ‘best of a bad situation’ hypothesis seems to explain why timing patterns often vary systematically within large river systems. For example, spring Chinook salmon and summer (stream-maturing) steelhead typically predominate in the upper reaches and tributaries of rivers like the Columbia and Fraser, whereas fall Chinook and ocean-maturing steelhead predominate in the lower parts of the system. This would seem to argue that features of the migratory corridor

and spawning sites rather than aspects of ocean conditions (which would presumably apply to all populations in the system) drive selection on timing. Likewise, similar timing patterns are seen among populations in different river systems that share similar physical conditions such as the sockeye salmon towards the southern end of their distribution that enter early, hold in lakes all summer, and spawn in fall (Hodgson and Quinn 2002).

However, in some cases the physical factors are not challenging enough to support the hypothesis that premature migration has evolved to avoid them. Some areas of Scotland and Ireland have very moderate flow and temperature regimes, and the late spawning of Atlantic salmon and short rivers would seem to allow adults to enter when the water was cool, and easily reach the spawning grounds yet they enter very early. Thus while temperature and flow regimes may in some cases result in the evolution of premature migration, they are sufficient in all cases. Very protracted runs (other than amalgamations of multiple populations) may reflect complex and disruptive selection on timing, as was documented by DNA parentage analysis of 19 consecutive brood years of steelhead (Seamons et al. 2007). Thus the extended runs in Ireland and Scotland may reflect different selective agents, which do not operate in all years.

Alternatively, the fish may be striking an optimal balance between the costs of early departure from the ocean (lost feeding opportunity, energetic demands of fasting for a protracted period in freshwater, and mortality risk in freshwater) against the costs of remaining at sea. Research on mortality at sea has tended to emphasize the period immediately after ocean entry (e.g., Halfyard et al. 2013; Moore et al. 2015). However, the life history of salmon implies that the ocean is risky; they stay at sea only as long as necessary to reap the reproductive benefits of larger size. The largest individuals of each cohort leave the ocean and return to spawn, and the smaller ones of the cohort stay at sea to repeat the process (remain or return) the next year

(Parker and Larkin 1959; LaLanne 1971). Thus maturation is sensitive to the costs and benefits of returning or delaying for another year, and this tradeoff is size-selective. It is very difficult to estimate the mortality risk per unit time when salmon are at sea. Models assume that larger fish are safer than smaller ones (Ricker 1976; Furnell and Brett 1986) but estimated annual mortality rates are about 20-40% in the last year at sea for Pacific salmon (Fredin 1965, Mathews 1968, Mathews and Buckley 1976). Marine mammals (Ford and Ellis 2006) and sharks (Nagasawa 1998; Hulbert et al. 2005) are large enough to eat sub-adult and adult salmon, and killer whales, *Orcinus orca*, selectively feed on larger, older Chinook salmon rather than smaller ones (Ford and Ellis 2006).

The risk of mortality at sea presents a viable alternative to physical constraints in freshwater as an explanation for the premature entry of some populations. If the mortality risk associated with additional time at sea is greater than the potential growth-related benefits for reproduction and the energetic and mortality costs of in-river holding, then premature migration may be advantageous. One implication of the marine predation risk hypothesis is that the cost-benefit balance may depend on the size of the fish.

It is well-known that the early returning Atlantic salmon are typically large, multi-sea winter fish, whereas the grilse enter the same river several months later (Shearer 1990). The variation in size and age with respect to timing is much less dramatic in Pacific salmon but in a number of species older fish arrive before younger ones within unimodal runs (Quinn 2005; Anderson and Beer 2009; Abadía-Cardoso et al. 2013). The earlier arrival of larger and older fish might be explained by at least three processes, which are not mutually exclusive. First, if all salmon were feeding in the same area and commenced homeward migration at the same date, the larger fish would swim faster and arrive earlier. This might be termed the ‘swimming

performance hypothesis.’ Second, smaller fish might benefit from a longer period of feeding at sea, as they would grow more in proportion to their size than larger fish, and so the optimal date to commence migration depends on size. This ‘optimal departure date hypothesis’ is consistent with the report that in years when Atlantic salmon grilse were in poor condition (i.e., lower weight for a given length) they returned later in the season than in years when they were in better condition (Todd et al. 2012). Further evidence that migration timing can reflect energetic tradeoffs was presented by Halttunen et al. (2013). The downstream migration of Atlantic salmon kelts depended on body condition; “...individuals with low energy reserves migrated early to the risky but productive marine habitat, whereas individuals with greater energy reserves stayed in the safe but less productive river habitat until staying became energetically more costly than migrating (p. 1063).” Finally, there may be processes on the spawning grounds that select against early arriving females. The ability of females to dig deep nests depends on body size (Quinn 2005, Steen and Quinn 1999), so if small females spawned early they might have their nests disturbed by larger females spawning later in the season. The lower probability of nest disturbance late in the season allows smaller females to be successful. This might be termed the ‘size-dependent optimal breeding date hypothesis.’ Late breeding females tend to be smaller than those breeding earlier but size did not explain much of the variation in breeding date in sockeye salmon, for example (Hendry et al. 1999; Doctor and Quinn 2009).

One complication for hypotheses regarding the earlier arrival of larger salmon is that this is not always the case, at least in Pacific salmon. In Waddell Creek, California coho salmon jacks (males that spent only the summer at sea) returned earlier than the older (1 sea-winter) males (Shapovalov and Taft 1954). Similarly, jack Chinook salmon ascended the Babine River, B.C. earlier than to older males but the timing of sockeye salmon in the same river did not differ with

age (Jordan 1967). Undoubtedly, a complete review would reveal cases of earlier arrival of larger or older fish, other cases where smaller or younger fish arrive first, and still others where there is no pattern at all. Perhaps there would be a “weight of evidence” in support of the hypothesis of earlier migration by larger fish but there might be enough exceptions to question its generality.

In addition to age, arrival often varies between males and females. As early as 1937, Pritchard wrote (p. 408) “It is commonly stated that during the spawning runs of anadromous fishes the males arrive first” and his data on pink salmon showed this pattern (Pritchard 1937). Similarly, data on coho salmon (Shapovalov and Taft 1954) and kokanee (Lorz and Northcote 1965) also showed that males arrived prior to females on average. This seems to be a general pattern (Morbey 2000, Quinn et al. 2009), likely evolved to maximize the reproductive success of males. This is paradoxical because the females select, prepare, and guard the nest site so it might seem that males should arrive after females. However, the females spawn soon after arriving, and so males would lose less in breeding opportunities by being a bit early (i.e., prior to the arrival of females) than late (i.e., after most females have bred). In this ‘conservative bet-hedging’, given the uncertainty in arrival timing of females, males tend to arrive early. However, the earlier migration of males in coastal waters and earlier arrival on spawning grounds is usually a matter of days to weeks rather than weeks to months, as can be the case with age-classes, so different processes are probably operating.

Climate change, fishing, and the phenology of salmon migrations

For at least the past two decades it has been recognized that salmon survival and productivity are affected by broad-scale climate processes in the Pacific (Beamish and Bouillon 1993, Mantua et al. 1997) and Atlantic oceans (Friedland et al. 2003, Friedland et al. 2014).

Climate also affects migration through a mix of proximate environmental stimuli at sea and in rivers, and through natural selection from such factors as temperature and flow regimes in rivers, and the opportunities for growth and the risk of mortality at sea. Models and empirical trends generally indicate milder winters, leading to smaller snowpack and earlier spring runoff in rivers of western North America in the future (Stewart et al. 2005; Hamlet and Lettenmaier 2007; Arismendi et al. 2013). These physical changes might alter the flow or temperature cues stimulating upriver migration, and they would also change the regimes of selection. Changes in ocean temperature might also alter timing cues, selection regimes, and growth, and the ratio of grilse to MSW Atlantic salmon was affected by climate (Scarnecchia et al. 1991; Gudjonsson et al. 1995; Summers 1995).

If salmon migrate into freshwater early to avoid lethal or stressful summer temperatures (Hodgson and Quinn 2002), climate changes have great conservation consequences. Either phenotypic plasticity or selection may drive fish to arrive even earlier in future generations, and spawn later in the fall, widening the duration of holding as the summers get warmer or drier over the years. Such a trend towards earlier arrival was noted in Columbia River sockeye salmon and hypothesized to result from selection (Quinn and Adams 1996). Subsequent analyses indicated that selection against fish arriving too late, experiencing warm conditions, and dying *en route* was a plausible explanation, though phenotypic plasticity seemed to explain some of the shift in timing (Crozier et al. 2011). Similarly, Reed et al. (2011) predicted that 21st century climate change will lead to the evolution of earlier migration by Fraser River sockeye salmon that arrive before summer temperatures peak. Salmon use cool refuges during the summer (Berman and Quinn 1991; Baigun et al. 2000) but increased mean air temperature would increase groundwater temperatures (Meisner et al. 1988), so the refuges might also get warmer, stressing the fish.

Populations entering after temperatures peak might evolve along with a warming climate, migrating and breeding later in the fall. Such long-term shifts in migration timing have been observed with increased temperatures (Robards and Quinn 2002; Goniea et al. 2006), though interpretation of the trends is complicated by changes in the relative abundance of component populations, and by artificial propagation. Some populations are more tolerant of high temperatures and perform better under difficult conditions than others within the same river system (Eliason et al. 2011), and populations differ in migration strategies to deal with thermal conditions (Strange 2012), so the responses will be complex. Changes in ocean productivity affecting growth and survival could also tip the balance for or against premature migration, shift the optimal month, or alter the extent to which the benefits differ by fish size and age. However, the extent to which fish life history and phenology track climate-driven ecological changes in marine and freshwater systems will depend and the relative roles of genetic adaptation and phenotypic plasticity.

There are also paradoxical changes in phenology that reveal how little we understand the links between climate and timing. Three Pacific salmon species (sockeye, pink and coho) were monitored for four decades in Auke Creek, in southeastern Alaska (Kovach et al. 2013). During this period the mean summer water temperatures increased markedly but of the three species (all migrating at or after the temperatures peaked), only sockeye salmon showed the predicted pattern of migrating later over time to avoid the warm water. The other two species migrated earlier, even though it meant that they experienced much warmer temperatures. In another perplexing case, late runs of sockeye salmon have been entering the Fraser River, British Columbia earlier in the year since 1995, experiencing high mortality rates along the migratory route and on the spawning grounds before reproducing (Hinch et al. 2012).

In addition to these climate-driven changes in timing cues and selection regimes, salmon also experience selection on timing from fisheries and other human activities. The present distribution of Chinook salmon in the Columbia River, with a small spring run and a dominant fall run, may not reflect the original pattern. The native runs were apparently dominated by later spring and summer fish, migrating upriver in June and July (Chapman 1986), currently a period of lower abundance than the spring and fall runs. Craig and Hacker (1940) concluded (p. 196) “In the very early days of the industry [1860s to 1880s] the fishing was largely confined to the spring and early summer, when fish of the best quality were present in the river. The result was that these races of the chinook salmon soon began to show the result of the heavy fishing imposed upon them and to show signs of depletion, which were commented upon as early as the late [eighteen] seventies... The period from 1890 to 1910 was one in which ... the less desirable races of chinooks entering the river during August and September were fished with increasing intensity and fishing gear and methods were being improved and made more efficient.”

The preference for early-migrating fish (when humans may have been hungry), especially if the fish were high in fat content, was shown by Native Americans as well (Swezey and Heizer 1977), so the spring runs may have been more heavily fished than later ones prior to industrial-scale fishing. In Europe, needless to say, humans have exploited salmon for millennia, and the current timing patterns may reflect some history of selection. Indeed, given this history, it is remarkable that the early runs persist at all, as they are highly sought in recreational (Consuegra et al. 2005) and commercial fisheries, and are more susceptible to angling than later arriving fish (Quinn et al. 2006). In contemporary periods, commercial fishing can also be selective on timing, and shifts in run timing were noted in Bristol Bay sockeye salmon (Quinn et al. 2007).

Finally, the past decade has seen an increasing appreciation of the role of population and life history diversity in the productivity of salmon populations. These ‘biocomplexity’ (Hilborn et al. 2003) and ‘portfolio effect’ (Schindler et al. 2010; Moore et al. 2014) concepts provide clear motivation to maintain population diversity through its association with stable, resilient runs. Conversely, reduced diversity characterizes declining population complexes (Carlson and Satterthwaite 2011). As this review has shown, the timing of migration and duration of holding prior to spawning are fundamental aspects of salmonid evolutionary ecology. These migration patterns reflect the diversity and complexity of selection regimes; the benefits that salmon convey to their ecosystems and to humans depend on maintaining the full spectrum of variation in populations.

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Figure captions

Figure 1. The timing of upstream (black bars), spawning, and downstream migration (cross-hatched bars) by Atlantic salmon in: top panel: the River Imsa, Norway (Jonsson et al. 1990), and bottom panel: the Blackwater River in Munster, Ireland (from Quinn et al. 2006).

Figure 2. Upstream migration by Iberian sea trout from 1995 to 2003, expressed as the mean monthly percent of the annual total (Caballero et al. 2006).

Figure 3. Upstream (black bars) and downstream migration (cross-hatched bars) of Vardnes River sea trout (top panel, from Berg and Berg 1989) and Arctic char (bottom panel, from Berg and Berg 1993).

Figure 4. Upstream (black bars) and downstream migration (cross-hatched bars) by Atlantic salmon and sea trout in two rivers in Ireland, expressed as monthly percentages of the annual total counts at electronic fences, provided by Richard Hewat, Alnabrocky House (Munhin data, 2006 – 2011), and Leo Layden, Lagduff Lodge (Owenduff data, 2008 – 2012).

Figure 5. Upriver migration by sockeye salmon to Baker Lake (top panel) and Lake Ozette, Washington, averaged over multiple years (from Hodgson and Quinn 2002, updated with additional unpublished data). Mean daily water temperature data from the Skagit River at Mt. Vernon for the Baker Lake and the Ozette River for Lake Ozette (note different Y-axis scales).

Figure 6. Upstream migration by adult winter (open bars) and summer steelhead (stippled bars) in the Kalama River, Washington (Washington Department of Fish and Wildlife data, modified from Quinn and Myers 2004). Peak spawning timing of each group from Leider et al. (1984).

Figure 7. Upstream (black bars) and downstream migration (cross-hatched bars) of cutthroat trout in Auke Creek, Alaska (top panel), expressed as monthly percent of the annual total (Alaska Department of Fish and Game annual reports). Middle panel: Petersburg Creek cutthroat trout, and bottom panel, Petersburg Creek steelhead (Jones 1972, 1973). In all cases the fish spawn in spring.

Figure 8. Upstream (black bars) and downstream migrations (cross-hatched bars) of Dolly Varden in Auke Creek, Alaska (data from Alaska Department of Fish and Game, Bond and Quinn 2013).

Figure 9. Top panel: upriver migrations by anadromous Arctic char in the Meliadine River (McGowan 1990) and Freshwater Creek, Canada (McGowan and Low 1992). Bottom panel: upstream migration timing of Arctic char in the Ikaluit River, Canada (Read 2003).

Figure 10. Migrations of adult Arctic char in the Nauyuk Lake system in Canada. Top panel: black line shows the upstream (but not spawning) migration from the sea and the dashed line shows the downstream migration to marine waters. Bottom panel: black line shows the spawning migration up Willow Creek to Willow Lake, and the dashed line shows the downstream migration of post-spawning fish back to Nauyuk Lake (Gyselman and Broughton 1991).

Figure 1

Figure 2

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Figure 10

Appendix Figure 1: Hypotheses to explain premature migration

Two non-mutually exclusive hypotheses to explain the phenomenon of premature migration, here operationally defined as return to freshwater more than three months in advance of spawning. Salmon may leave the ocean prematurely to avoid lethal or stressful temperatures in lower river reaches (Panel A, T_{max} = river temperature above which migration is restricted), or enter before low flows restrict access to spawning tributaries (Panel B, F_{min} = flow below which migration is restricted). In both cases, fish may be selected to migrate earlier than otherwise optimal (to the left of the vertical dotted lines, as indicated by the arrows). T_{max} and F_{min} will vary across species and populations. We refer to this as ‘making the best of a bad situation.’

Alternatively (or additionally), salmon may strike a balance between the costs of early ocean exit versus the costs of remaining at sea. Panel C describes a situation where cumulative mortality risk in saltwater (M_{SW}) increases the longer fish stay in the ocean, e.g. due to predation. Conversely, longer delay in freshwater prior to spawning increases the energetic

demands of fasting (plus some risk of predation and disease), so the cumulative mortality risk in freshwater (M_{FW}) is lower the shorter the freshwater holding period.

Finally, by leaving the ocean early, fish also forego growth opportunity and associated reproductive (R) benefits (Panel D). For females, R benefits of later ocean exit may be realized in terms of the total gonad mass (egg number $\times$ egg size, both positively related to body size). For males, R represents success in competition for access to mates, which is also positively related to body size and hence time of ocean exit relative to spawning. S represents cumulative survival probability, calculated as $(1-M_{SW})(1-M_{FW})$, and fitness is then calculated by multiplying R by S. In this toy example, the resulting fitness function peaks at -8, implying that the best time to leave the ocean is eight months prior to spawning, all else being equal. The scaling of the R and S functions is arbitrary and these functions should vary with the fish's sex, age or size, and the dynamics of reproductive success in the natal habitat. Optimal ocean exit times may thus be sex, age or size-specific, and population specific. For some populations or classes of individuals, the fitness function might be much flatter (i.e., weaker net selection on migration timing) and hence a range of ocean exit times may be viable within the same population. Similarly, inter-annual variation in oceanic or freshwater conditions could result in the optimum shifting across generations, and this fluctuating selection may then act to maintain genetic variation in migration timing within populations. In situations where reproductively isolated populations spawn in different parts of the same river system, sub-populations may experience different cumulative freshwater mortality risk (i.e. there is spatial variation in the M_{FW} function), or they may be subject to varying thermal or flow constraints on upriver migration at different times of year. This could produce adaptive divergence in ocean exit times among populations within the same river system that may experience similar mortality risks and growth opportunities at sea.

Table 1. Summary of salmonid migration timing examples in the text, listing the species, region, and whether the migration is premature or not. Populations are listed approximately north to south, with the exception of Arctic char whose distribution is circumpolar. This should not be taken as an exhaustive or representative list of the timing patterns of these species.

<u>Species</u>	<u>River and region</u>	<u>Return migration pattern</u>	<u>Reference</u>
Atlantic salmon	Teno, northern Scandinavia	June-July, premature	Niemelä et al. 2000, 2006
	Tornionjoki, Baltic Sea	June, premature	Lilja and Romakkaniemi 2003
	Umeälven, Baltic Sea	July-August, somewhat premature	McKinnell et al. 1994
	Vefsna, northern Norway	July-August, somewhat premature	Jensen et al. 1986
	Imsa, Norway	Sept.-October, not premature	Jonsson et al. 1990
	Dee and North Esk, Scotland	Very protracted, premature	Shearer 1990; Smith 1990
	Ireland	Very protracted, often premature	Went 1964; Quinn et al. 2006
	Northern Spain	As early as March, premature	Valiente et al. 2001
	Torrent, Newfoundland, Canada	July-August, premature	Juanes et al. 2004
	Miramichi, New Brunswick, Canada	July-Sept., somewhat premature	Juanes et al. 2004
	Maine, USA	Summer, some premature	Baum 1997
	Connecticut River, USA	May-June, premature	Juanes et al. 2004
Sea trout	Vardnes, Norway	July-September, not premature	Berg and Berg 1989a
	Imsa, Norway	August-October, not premature	Jonsson and Jonsson 2002
	Northern Spain	June-August, premature	Caballero et al. 2006
	Turkey	May-June, premature	Okumus et al. 2006
	Northwestern Ireland	Year-round, premature	Unpublished
Chinook salmon	Fraser River, Canada	Many populations, some premature	Waples et al. 1990
	Columbia River, USA	Many populations, some premature	Brannon et al. 2004
	Klamath River, USA	Many populations, some premature	Strange 2012
	Sacramento River, USA	Many populations, some premature	Healey 1991; Fisher 1994
Sockeye salmon	Skeena River, Canada	Many populations, some premature	Beacham et al. 2014
	Baker Lake, USA	July, premature	Hodgson and Quinn 2002
	Lake Ozette, USA	June-July, premature	Hodgson and Quinn 2002

	Columbia River, USA	Several populations, all premature	Hodgson and Quinn 2002
Coho salmon	Various	Late fall, seldom premature	Sandercock 1991
Pink salmon	Various	Late summer, seldom premature	Heard 1991
Chum salmon	North America	Fall, generally not premature	Salo 1991
	Kamchatka, Russia	Fall, not premature	Kuzishchin et al. 2010
Masu salmon	Japan and Russia	Late spring-early summer, premature	Kato 1991
Steelhead trout	Russia, USA and Canada	Many populations, many premature	Burgner et al. 1992; Busby et al. 1996
	Southeast Alaska	May, not premature	Jones 1972, 1973
	Skeena River, Canada	July and August, premature	Beacham et al. 2012
	Columbia River, USA	Many populations, many premature	Robards and Quinn 2002
	Kalama River, Washington	Two populations, one premature	Leider et al. 1984
Cutthroat trout	Southeast Alaska	Sept.-October, premature	Armstrong 1971
	Puget Sound, Washington	Fall or winter, premature or not	Johnston 1982; Wenburg 1998
	Sand Creek, Oregon	October-December, premature	Sumner 1962
	Deer and Flynn creeks, Oregon	November-January, premature	Lowry 1965
Brook trout	Sainte-Marguerite River, Québec	August-October, not premature	Lenormand et al. 2004
	St-Jean River, Québec	June-August, somewhat premature	Castonguay et al. 1982
Dolly Varden	Multiple populations, Alaska	Summer, mostly not premature	Bond and Quinn 2013
Bull trout	Puget Sound, Washington	June-July, premature	Hayes et al. 2011
Arctic char	Svalbard, Norway	July-September, not premature	Gulseth and Nilssen 2000
	Vardnes River, Norway	July, somewhat premature	Berg and Berg 1993
	Fraser River, Labrador, Canada	July-Sept., not premature	Dempson and Green 1985
	Cambridge Bay, Canadian Arctic	August-Sept., not premature	McGowan 1990
	Meliadine River, Canadian Arctic	August-Sept., not premature	McGowan 1992
	Freshwater Creek, Canadian Arctic	August-Sept., not premature	McGowan and Low 1992
	Koukdjuak River, Canadian Arctic	August-Sept., not premature	Kristofferson et al. 1991
	Ikaluit River, Canadian Arctic	August-Sept., not premature	Read 2003
	Nauyuk Lake, Canadian Arctic	August, premature	Gyselman and Broughton 1991