

The evolutionary ecology of alternative migratory tactics in salmonid fishes

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ABSTRACT

Extensive individual variation in spatial behaviour is a common feature among species that exhibit migratory life cycles. Nowhere is this more evident than in salmonid fishes; individual fish may complete their entire life cycle in freshwater streams, others may migrate variable distances at sea and yet others limit their migrations to larger rivers or lakes before returning to freshwater streams to spawn. This review presents evidence that individual variation in migratory behaviour and physiology in salmonid fishes is controlled by developmental thresholds and that part of the variation in proximal traits activating the development of alternative migratory tactics is genetically based. We summarize evidence that alternative migratory tactics co-exist within populations and that all individuals may potentially adopt any of the alternative phenotypes. Even though intra-specific genetic divergence of migratory tactics is uncommon, it may occur if female competition for oviposition sites results in spawning segregation of alternative phenotypes. Because of their polygenic nature, alternative migratory tactics are considered as threshold traits. Threshold traits have two characteristics: an underlying 'liability' trait that varies in a continuous fashion, and a threshold value which is responsible for the discreteness observed in phenotypic distribution. We review evidence demonstrating that body size is an adequate proxy for the liability trait controlling the decision to migrate, but that the same phenotypic outcome (anadromy or residency) may be reached by different developmental pathways. The evidence suggesting a significant heritable component in the development of alternative migratory tactics is subsequently reviewed, leading us to conclude that alternative migratory tactics have considerable potential to respond to selection and evolve. We review what is known about the proximal physiological mechanisms mediating the translation of the continuous value of the liability trait into a discontinuous migratory tactic. We conclude by identifying several avenues for future research, including testing the frequency-dependent selection hypothesis, establishing the relative importance of adaptive phenotypic plasticity in explaining some geographic gradients in migratory behaviour and identifying the physiological and genetic basis of the switching mechanisms responsible for alternative migratory tactics.

Key words: anadromy, developmental thresholds, liability traits, heritability, selection, phenotypic plasticity, partial migration.

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I. INTRODUCTION

The repetitive, long-distance movements referred to as migration vary so much in pattern and scale among animals that it has proved difficult to reach generalizations about control mechanisms and their adaptive significance. The existence of considerable variation in the propensity to migrate and the pattern of migration seen within populations suggest that benefits do not accrue equally to all individuals. Individual variation in the expression of migratory behaviour thus becomes the focal point in understanding the evolution and persistence of migration. An increasing number of studies demonstrate that some individuals within populations migrate between habitats whereas others remain resident in a single habitat. Such observations are reported for a wide variety of taxa including insects, fish, birds and mammals (Chapman *et al.*, 2011). Our objective here is to understand the mechanisms generating variation in migratory behaviour using salmonid fishes of the subfamily Salmoninae (charr, trout and salmon) as a case study.

A diversity of migratory patterns co-exists within populations of most salmonid fishes. The phenomenon is commonly, and somewhat misleadingly, referred to as partial migration (Jonsson & Jonsson, 1993); part of a fish population may complete their entire life cycle in freshwater streams (residency) whereas another part may migrate to sea (anadromy) or to larger rivers or lakes before returning to freshwater streams to spawn. Here, 'partial' refers to the population and not the individual performance, the focus of the present discussion. Migration to sea encompasses a complex sequence of biochemical, behavioural and morphological changes which are collectively referred to as smolting (McCormick, 2009). In this process, the darkly pigmented, bottom-dwelling freshwater juvenile (generally known as parr) is transformed into the pelagic, silvery smolt adapted to living in a marine environment.

Major differences exist in the pattern and characteristics of the partial migration system among salmonid species and between sexes (Table 1). Intraspecific diversity in the timing and pattern of migratory movements and the proportional incidence of the different phenotypes among populations can vary enormously (Quinn, 2005; Jonsson & Jonsson, 2011). This diversity has been considered to co-evolve with other life-history traits to form adaptive strategies. Thus, aspects of their variation must be controlled by genetic variation (Hutchings & Morris, 1985; Jonsson & Jonsson, 1993; Hutchings & Myers, 1994; Hendry *et al.*, 2004).

This review presents evidence that variation in migratory behaviour and physiology in salmonid fishes is controlled by developmental thresholds and that part of the variation in proximal traits activating the development of alternative migratory tactics (AMTs) is genetically based. The general term 'alternative tactic', or its synonym 'alternative phenotype', refers to the discontinuous patterns of variation expressed at the same life stage within populations that are the result of divergent developmental programs. Such discontinuity, also referred to as polyphenism, may pertain to all levels of phenotypic organization (behaviour, physiology, morphology or life history) and in salmonids is often conspicuous in body size frequency distributions (Jonsson & Jonsson, 1993).

Contrary to the observed genetic polymorphisms associated with some alternative phenotypes in other taxa (e.g. the marine isopod *Paracerceis sculpta*: Shuster & Wade, 1991), alternative migratory tactics in salmonids share features with a special class of polygenic traits, called 'threshold traits' (Hutchings & Myers, 1994; Roff, 1996; West-Eberhard, 2003; Emlen, 2008). Threshold traits have two characteristics: an underlying 'liability' trait that varies in a continuous fashion, and a threshold value which is responsible for the discreteness observed in the phenotypic distribution at a given point in time (e.g. freshwater residency *versus* smolting and emigration) (Falconer & Mackay, 1996).

Table 1. Synopsis of the principal alternative migratory phenotypes occurring sympatrically in salmonine species.

Species	Range	Parity	Alternative migratory phenotype	Description	Sex ratio	References
Atlantic salmon <i>Salmo salar</i>	North Atlantic Ocean	I	Anadromous ^a grilse	Return to FW to spawn after 1 year at sea	Male biased	Power (1981) and Bacon <i>et al.</i> (2009)
			Anadromous multi sea winter	Return to FW after 2 or more years at sea	Female biased	Power (1981) and Bacon <i>et al.</i> (2009)
			FW resident parr (precocious parr)	Sexually mature FW parr (age at maturity may overlap with that of large anadromous males)	Uniquely male	Hutchings & Jones (1998)
			Ouananiche ^b	FW residents	Equal sex ratio	Adams (2007)
Brown trout <i>S. trutta</i>	Europe and western Asia	I	Anadromous (whiting, finnock)	Return to FW after six months in coastal areas	Male biased	Elliott (1994) and Cucherousset <i>et al.</i> (2005)
			Anadromous sea trout	Return to FW after at least 18 months in coastal waters	Equal sex ratio	Titus & Mosegaard (1992)
			FW resident parr (precocious parr)	Sexually mature FW parr	Male biased	Dellefors & Faremo (1988)
			Resident trout	Trout that remain in natal streams to complete their life cycle	Equal sex ratio	Elliott (1994) and Cucherousset <i>et al.</i> (2005)
			FW migrants	Migration to lakes or rivers before returning to natal streams	Both sexes	Elliott (1994) and Cucherousset <i>et al.</i> (2005)
Brook charr <i>Salvelinus fontinalis</i>	Eastern North America	I	Anadromous sea trout	Return to FW after 1 or more years in coastal waters	Sex ratio varies with age at migration (overall sex ratio equal)	Power (1980) and Lenormand, Dodson & Ménard (2004)
			FW resident (speckled trout)	Trout that remain in FW (including lakes, rivers and streams) to complete their life cycle	Equal sex ratio	Power (1980)
Bull trout <i>S. confluentus</i>	Western North America	I	Anadromous	Poorly documented	Both sexes	Brenkman & Corbett (2005)
			Fluvial FW migrant	Migrates to rivers prior to returning to natal streams	Both sexes	McPhail & Baxter (1996) and Mogen & Kaeding (2005)
			Adfluvial FW migrant	Migrates to lakes prior to returning to natal streams	Both sexes	McPhail & Baxter (1996) and Mogen & Kaeding (2005)
Arctic charr <i>S. alpinus</i>	Holarctic	I	Anadromous ^c	Return to natal lakes after 1 or more years at sea or in coastal waters	Female-biased or equal sex ratio	Nordeng (1983) and Gulseth & Nilssen (2001)
			Large FW resident	Trophic polyphenism	Male-biased or equal sex ratio	Nordeng (1983) and Klemetsen <i>et al.</i> (2003)
			Small FW resident	Trophic polyphenism	Male-biased or equal sex ratio	Nordeng (1983) and Klemetsen <i>et al.</i> (2003)
White-spotted charr <i>S. leucomaenis</i>	Far east of Asia	I	Anadromous	Northerly populations only; multiple migrations between the sea and fresh water prior to spawning	Female biased	Arai & Morita (2005)
			FW resident	Fluvial or lacustrine residents	Uniquely male in the north of range, equal sex ratio in the south of range	Yamamoto <i>et al.</i> (1999)

Table 1. Continued

Species	Range	Parity	Alternative migratory phenotype	Description	Sex ratio	References
Dolly Varden, <i>S. malma</i> ^a	North Pacific Ocean	I	Anadromous	Mature and overwintering immature fish return to FW after one summer in coastal waters	Female biased	Armstrong & Morrow (1980) and Maekawa & Nakano (2002)
Rainbow trout/steelhead <i>Oncorhynchus mykiss</i>	North Pacific Ocean	I	FW resident parr (residual parr)	Sexually mature FW parr	Uniquely male	Armstrong & Morrow (1980)
			FW resident	Lacustrine, spring or stream residents	Equal sex ratio	Armstrong & Morrow (1980)
		I	Anadromous (steelhead)	Return to natal streams after 1 or more years at sea or in coastal waters	Female biased	Busby <i>et al.</i> (1996)
			Fluvial and adfluvial FW migrants (rainbow trout)	Variable migration patterns within FW before returning to natal streams for spawning	Both sexes	Busby <i>et al.</i> (1996)
Masu salmon, or cherry salmon ^c <i>O. masou</i>	Far east of Asia		FW resident (rainbow trout)	Trout that remain in natal streams to complete their life cycle	Both sexes	Busby <i>et al.</i> (1996)
		I	Anadromous (sakuramasu)	Return to natal streams after at least 1 year in coastal waters	All females in the south, sex ratio equal at northern end of range	Kato (1991) and Tsiger <i>et al.</i> (1994)
			Jacks (anadromous)	Spend one summer in coastal waters before returning to natal streams	Uniquely male	Kato (1991) and Tsiger <i>et al.</i> (1994)
Coastal cutthroat trout <i>O. clarki clarki</i>	Pacific coast of North America		FW parr (precocious parr)	Sexually mature FW parr	Uniquely male	Kato (1991) and Tsiger <i>et al.</i> (1994)
			FW migrants (yamame)	Non-anadromous salmon; variable migration patterns between lakes and streams	Male biased	Kato (1991) and Tsiger <i>et al.</i> (1994)
		I	Anadromous	Mature and overwintering immature fish return to FW after one summer in coastal waters	Both sexes	Trotter (1989) and Orlay <i>et al.</i> (1999)
			Fluvial and adfluvial FW migrants	Variable migration patterns before returning to natal streams for spawning	Both sexes	Trotter (1989) and Orlay <i>et al.</i> (1999)
			Non-migratory FW residents	Remain in small headwater streams	Both sexes	Trotter (1989) and Orlay <i>et al.</i> (1999)
Sockeye salmon <i>O. nerka</i>	North Pacific Ocean	S	Anadromous	Mature fish return to natal streams after 1–4 years at sea	Sex ratio varies with age at migration	Burgner (1991) and Kaeriyama & Ueda (1998)
			Jacks and jills (anadromous)	Spend one summer at sea before returning to natal streams	Predominantly male, females (jills) rare	Burgner (1991) and Kaeriyama & Ueda (1998)
			Freshwater residual	Mature after 1 or 2 years in lakes, principally in more southerly populations.	Predominantly male	Burgner (1991) and Kaeriyama & Ueda (1998)

Table 1. Continued

Species	Range	Parity	Alternative migratory phenotype	Description	Sex ratio	References
Coho salmon <i>O. kisutch</i>	North Pacific Ocean	S	Anadromous	Mature fish return to natal streams after at least 18 months at sea	Sex ratio varies with age of migration	Sandercock (1991)
			Jacks (anadromous)	Spend one summer at sea before returning to natal streams	Uniquely male	Sandercock (1991)
Chinook salmon <i>O. tshawytscha</i> ^f	North Pacific Ocean	S	Freshwater residual	Mature after one or 2 years in lakes	Equal sex ratio	Foerster & Ricker (1953)
			Anadromous (stream-type)	Mature fish return to natal streams after 1 or 2 years at sea.	Sex ratio varies with age of migration	Healey (1991)
			Jacks (anadromous: stream-type)	Spend one summer at sea before returning to natal streams	Uniquely male	Healey (1991)
			FW resident parr (stream-type)	Mature after one or two summers in headwater tributaries	Male biased	Pearsons <i>et al.</i> (2009)

This synopsis ignores finer scale phenotypic variation in migratory pattern and life history within and among populations. FW, fresh water. Sex ratio, 'both sexes' indicates that sex-ratio estimates are either highly variable or not reported, but that both sexes are reported to express the designated phenotype. Parity: I, iteroparity- multiple reproductive events during life; S, semelparity- single reproductive event before death.

^aAnadromy is migration between freshwater for reproduction and early rearing and the sea for growth and maturation.

^bNon-anadromous Atlantic salmon that occur sympatrically with anadromous salmon in Newfoundland waters. Ouananiche occur allopatrically elsewhere in north-east North America. Native non-anadromous Atlantic salmon also occur in the River Namsen, Norway (Vuorinen & Berg, 1989), but are not called Ouananiche.

^cPrior to reproduction, northerly anadromous populations of Arctic charr, as well as other charr species, migrate annually from the sea to fresh water in the autumn to seek winter temperature refuges.

^dTwo forms, a northern and southern, are recognized in North America and Siberia. Both forms exhibit alternative migratory phenotypes. The southern form tends to overwinter in lakes and large rivers.

^eThe allopatric, largely FW, cherry salmon known as amago is considered a sub-species rather than a distinct species (*O. rhodurus*) (Gwo *et al.*, 2008).

^fTwo ecological forms of Chinook salmon exist; the stream-type perform extensive ocean migrations and are typical of Asian populations, northern-latitude populations and headwater tributary populations in temperate North America; the ocean-type spend most of their ocean life in coastal waters and are typical of populations on the North American west coast south of 56°N.

The liability may be thought of as a compound trait, such as social status, whose expression is the result of multiple interacting factors (Roff, 1996). Often, this liability trait is expressed in terms of a morphological trait, such as body size. If the liability takes values that surpass the threshold value at a sensitive time point during ontogeny, it causes the development of one particular tactic; however, if the liability takes values that lie below the threshold, then development of the alternative tactic occurs (Roff, 1996). Both the liability and the threshold value are proposed to be conditional on the environment encountered by individuals during development but also to be influenced by individual genotypes (West-Eberhard, 2003; Brockman & Taborsky, 2008). (See Appendix 1 for clarification of the terminological issues surrounding the use of the word ‘threshold’).

Our first objective is to consider the evidence that AMTs co-exist within populations and that all individuals may potentially adopt any of the alternative phenotypes. Treating AMTs as occurring within populations of interbreeding individuals then allows us to evaluate the evidence that these tactics are mediated by individual sensitivity to threshold values along a liability trait.

Our second objective is to describe how body size and other correlated measures of somatic condition influence the expression of migratory behaviour and determine whether these measures are useful proxies for the liability. We review the evidence for thresholds for AMTs in salmonids and explore whether multiple thresholds may control the development of alternative phenotypes.

Our third objective is to consider the evidence that genetic variation influences the traits involved in the development of alternative migratory tactics, as this is a necessary requirement for a response to natural selection. We then consider how gene–environment interactions acting on threshold traits may result in the local adaptation of AMTs. We illustrate this possibility by describing some dominant biogeographical patterns in the expression of salmonid AMTs.

We conclude by identifying the major shortcomings concerning our knowledge of AMTs, offer some suggestions for future research and look beyond salmonids to apply these principles to other taxa. Our intention is not to review the voluminous literature on alternative migratory behaviour in its entirety, but to analyse the phenomenon within the theoretical context of threshold traits and their genetic basis.

II. MIGRATORY TACTICS AS ALTERNATIVE PHENOTYPES WITHIN GENETIC POPULATIONS

Here we consider the evidence that AMTs co-exist within populations and that all individuals may potentially adopt any of the alternative phenotypes. Migratory phenotypes that are genetically distinct would preclude a role for alternative developmental pathways. In salmonids, AMTs are often associated with alternative reproductive phenotypes during spawning activity (Taborsky, 2008). Such alternative

reproductive tactics (ARTs) are generally represented by bourgeois males (the anadromous, migratory phenotype) that monopolize mates using their large body size and secondary sexual characteristics, and small sneaker males (which are either completely resident or undertake a brief marine migration) that exploit bourgeois males by sneaking fertilizations (Hutchings & Myers, 1994; Taborsky, 2008). In cases where residency is restricted to males, as in predominantly anadromous populations of Atlantic salmon *Salmo salar*, segregation into genetic populations cannot occur as sneaker males must necessarily spawn with anadromous females. In some species, resident females may be present but so rare (e.g. only 3.7% of resident brown trout, *Salmo trutta*, in small Norwegian streams; Jonsson *et al.*, 2001b) that most resident male parr must nevertheless spawn with anadromous females.

When males and females exhibit both resident and anadromous phenotypes, such behaviour generally persists as true AMTs within common gene pools because of gene flow between the alternative phenotypes (Table 2). In the case of Atlantic salmon on the island of Newfoundland, anadromous and non-anadromous (ouananiche) phenotypes co-exist in a large number of watersheds where no barrier to migration exists (Hutchings, 1986). Although evidence of reproductive isolation in historically allopatric groups of anadromous and non-anadromous salmon exists (e.g. Vuorinen & Berg, 1989), truly sympatric anadromous and non-anadromous Atlantic salmon are not genetically differentiated (Adams, 2007). No genetic differentiation was observed between migratory and resident freshwater forms of bull charr (*Salvelinus confluentus*) in North-Eastern Oregon (Homel *et al.*, 2008), of coastal cutthroat trout (*Oncorhynchus clarki*) in the lower Columbia River (Johnson *et al.*, 2010) or between anadromous and freshwater brown trout in a river of western Norway (Hindar *et al.*, 1991). Similarly, extensive gene flow between anadromous and resident brown trout was observed in Normandy, France where the two phenotypes had access to the same spawning areas (Charles *et al.*, 2005, 2006). Thériault *et al.* (2007) demonstrated that gene flow occurred between the two life-history forms of brook charr, *Salvelinus fontinalis*, and was mediated by resident males mating with both freshwater resident and anadromous females. In this case, the sneaking reproductive behaviour by small males impedes any genetic segregation related to size-assortative mating.

In the case of resident rainbow trout and anadromous steelhead (*O. mykiss*), most evidence also indicates a lack of genetic differentiation between the two migratory phenotypes when in sympatry (Table 2). Nevertheless, two cases of apparent genetic divergence between the migratory phenotypes have been reported. However, one appears to be due to recent stocking with a genetically divergent steelhead stock (Narum *et al.*, 2004), whereas the second is due to the downstream movement of an artificially established population of rainbow trout that remains genetically isolated from the now sympatric steelhead component (Pearse *et al.*, 2009).

Table 2. Evidence for lack of genetic differentiation between sympatric alternative migratory tactics (AMTs) when both sexes exhibit the phenotypic dichotomy.

Species	Location	Comparison	Methodology	Differentiation	References
Atlantic salmon <i>Salmo salar</i>	Newfoundland	Morphological identification of sympatric anadromous salmon and ouananiche; four watersheds	Eight microsatellite loci	Diverse analyses, truly sympatric forms not differentiated	Adams (2007)
Brown trout <i>Salmo trutta</i>	Voss River, Norway	Scale characters to identify anadromous and resident types	Allozyme allelic frequencies	G_{st} between life-history types within sites; $P = ns$.	Hindar <i>et al.</i> (1991)
Brook charr <i>Salvelinus fontinalis</i>	Oir River, Normandy France	Stable isotope analysis of fry to classify progeny of resident or anadromous female trout	Six microsatellite loci	AMOVA between fry grouped by type and site or year; $P = ns$	Charles <i>et al.</i> (2005, 2006)
Brook charr <i>Salvelinus fontinalis</i>	Ste-Marguerite River, Québec	Parentage analysis of fry based on capture of upstream migrant and resident adults	Thirteen microsatellite loci	Multilocus θ_{st} between forms; $P = ns$	Thériault <i>et al.</i> (2007)
Rainbow trout/Steelhead <i>Oncorhynchus mykiss</i>	British Columbia	Morphological identification of mature rainbow trout and steelhead, five sites	Nuclear intron length variants + seven microsatellites + MHC polymorphisms	F_{st} values between the forms for all gene locus markers, $P = ns$; one significant F_{st} value based on microsatellite loci	Heath <i>et al.</i> (2008)
	Copper River, Alaska	Morphological identification of mature rainbow trout and steelhead	Thirteen microsatellite loci	G -tests and F_{st} estimates between forms; $P = ns$	Olsen <i>et al.</i> (2006)
	Kamchatka	Scale characters to identify anadromous and resident types	Ten microsatellite loci	Allele frequencies and multilocus genotypes between forms; $P = ns$	McPhee <i>et al.</i> (2007)
	Hood River, Oregon	Morphological identification of migrating steelhead and resident trout	Eight microsatellite loci	Grandparentage analysis reveals 20% of steelhead genes come from wild residents	Christie <i>et al.</i> (2011)
Arctic charr <i>Salvelinus alpinus</i>	Northern Norway	Morphological identification of mature anadromous and small and large resident phenotypes	Rearing and transplantation experiments	Young charr segregated into the three phenotypes irrespective of parental phenotype	Nordeng (1983)
Bull trout <i>Salvelinus confluentus</i>	North-East Oregon	PIT tag detections to define known migrants <i>versus</i> likely residents	Eight microsatellite loci	Pairwise F_{st} , $P = ns$	Homel <i>et al.</i> (2008)
Coastal cutthroat trout <i>O. clarki clarki</i>	Lower Columbia River	Sea-run and migratory/non-migratory freshwater types	Allozyme allelic frequencies	Single evolutionary lineage	Johnson <i>et al.</i> (2010)

G_{st} , F_{st} and θ_{st} are different measures of genetic differentiation between populations. AMOVA: Analysis of Molecular Variance. $P = ns$: probability of differentiation not significant. MHC: major histocompatibility complex. PIT: passive integrated transponder.

(1) Female intrasexual competition and segregation of migratory phenotypes

In some cases, genetically segregated migratory phenotypes have been associated with the temporal or spatial segregation of spawning activities. Based on maternal origin, as determined from otolith microchemistry (and thus excluding male-mediated gene flow), all adult steelhead from an Oregon river were progeny of steelhead females and all resident rainbow trout were progeny of resident rainbow trout (Zimmerman & Reeves, 2002). The apparent differentiation of the two forms was associated with spatial and temporal segregation of spawning activities (but see Christie, Marine & Blouin, 2011). Similarly, the significant genetic differentiation of resident and anadromous individuals in a Quebec population of brook charr was related to the segregation of spawning sites (Boula *et al.*, 2002). What then could explain the segregation of spawning activities between different migratory phenotypes?

Such segregation may be related to competition among females. Generally, females compete for access to resources necessary for successful reproduction rather than for access to male gametes. Thus, the relative intensity of intrasexual competition in females may be strongly influenced by variation in resource distribution (Clutton-Brock, 2009). In salmonids, females generally compete with other females for quality oviposition sites; they excavate nests, spawn and then bury their eggs. In iteroparous species the nests are abandoned once buried, but in the semelparous Pacific salmonids, females guard the nests until death (Esteve, 2005). In non-guarding salmonids, loss of nests due to superimposition by later-spawning females can be very high, affecting between a third and one half of all nests (Essington, Sorensen & Paron, 1998). Among nest guards, female size is important in reducing egg loss because larger females dig deeper nests and are more successful in defending them from active take-over by other females (van den Berghe & Gross, 1989; Fleming & Gross, 1994).

There thus appears to be an opportunity for female salmonids to reduce intrasexual competition by selecting different oviposition sites based on their body size or adopting different reproductive phenologies to co-exist on the same spawning grounds (van den Berghe & Gross, 1989; Morbey & Ydenburg, 2003). An often-observed pattern within salmonid populations is that larger females tend to spawn in deeper and faster water than smaller females (reviewed in Morbey & Hendry, 2008). In general, salmonids can spawn in gravel beds with a median diameter approximately equal to 10% of their body length (Kondolf & Wolman, 1993). This suggests that smaller females can exploit smaller gravel sizes which are generally associated with habitats of slower water currents (Rice & Church, 1998). Smaller females may thus optimize reproductive success by selecting habitats with smaller substratum sizes (but poorer incubation environments) that are either inaccessible to or avoided by larger females. Under such a scenario, alternative female phenotypes (resident and migratory) in salmonids are unlikely to be under frequency-dependent selection as the mating success of one phenotype

will not affect the mating success of the alternative. Rather, female phenotype frequency will depend upon the relative abundance of the spawning habitats and on the strength of natural selection on fecundity.

One of the most intriguing cases of genetic divergence between migratory lifestyles is observed in *Oncorhynchus nerka*. This species may exist as three ecotypes; anadromous sea/river sockeye salmon that spends its initial life stages in fresh water, anadromous lake sockeye which spends about half its life in nursery lakes before migrating seaward, and non-anadromous kokanee salmon that exist only in lakes (Wood *et al.*, 2008). Under suitable conditions, kokanee may occur sympatrically with lake-type sockeye. The potential for gene flow between the two morphs seems great as kokanee males sneak on spawning sockeye pairs (Foote & Larkin, 1988) and can fertilize up to 20% of a female sockeye's eggs (Foote, Brown & Wood, 1997). The progeny of sockeye and kokanee are fully viable and fertile when raised in a hatchery setting (Craig, Foote & Wood, 2005). Nevertheless, lake-type sockeye and kokanee ecotypes inhabiting the same nursery lake typically exist as reproductively isolated populations. Wood *et al.* (2008) found significant differentiation between the sympatric ecotypes in 7 out of 12 comparisons of lake-type sockeye and kokanee ecotypes. Pair-wise genetic distances between sympatric lake-type sockeye and kokanee were smaller than among populations of the same ecotype in different lakes, consistent with parallel evolution rather than a common origin of the kokanee ecotype.

What then accounts for the genetic divergence of alternative phenotypes in this species, when conditions should favour the maintenance of alternative reproductive and migratory tactics and impede genetic divergence? Food habitats of juvenile sockeye and kokanee are virtually identical and there is no evidence that trophic specialization could drive divergent selection (Wood, Foote & Rutherford, 1999). One possible explanation resides in the sexual preference of both sockeye and kokanee for the colour red during spawning (Foote, Brown & Hawryshyn, 2004). Kokanee, which inhabit carotenoid-poor lakes, are threefold more efficient at acquiring and storing such pigments from their diet than are sockeye, which inhabit the comparatively carotenoid-rich marine environment (Craig & Foote, 2001). The offspring of sockeye that remain in fresh water (residuals, Table 1) develop a far less attractive green colouration as do the non-anadromous progeny of crosses between sockeye and kokanee (Craig & Foote, 2001; Craig *et al.*, 2005). These authors argue that the unattractive colour of residuals and the non-anadromous progeny of crosses between sockeye and kokanee may promote sympatric differentiation of the two morphs (Craig & Foote, 2001). However, small green males may apparently adopt the sneaker behavioural tactic (and actually may profit from their cryptic colouration). The fate of anadromous progeny of crosses between sockeye and kokanee, which in principle should develop the red colouration in the carotenoid-rich marine environment, is unknown. One speculative explanation for the genetic divergence may involve negative

pleiotropy whereby kokanee's efficiency at acquiring and storing carotenoid pigments from their diet may somehow impair their ability to smolt. In such a situation, sockeye-kokanee hybrids would be at a disadvantage. Finally, female kokanee dig nests in areas of lower water velocity and finer gravel size than female sockeye (Wood & Foote, 1996), possibly contributing to isolation by female habitat selection. For the time being, the final answer to this question remains elusive.

Large anadromous males can displace or kill smaller males in a variety of salmonid species [e.g. coho salmon *O. kisutch* (Fleming & Gross, 1994), Atlantic salmon (Hutchings & Myers, 1987)]. In some cases, these large males apparently breed uniquely with anadromous females (brook charr: Thériault *et al.*, 2007). In other cases, anadromous males may fertilize the eggs of anadromous females first and then those of the resident females provided that they have access to them (e.g. lake Arctic charr *Salvelinus alpinus*: Jonsson & Hindar, 1982). If larger males and females are excluded from spatially constrained habitats (i.e. small tributary streams), small males may be restricted to breed with small females. In this case, both males and females could be released from frequency-dependent selection as the alternative, anadromous, tactic is not successful in such restricted habitat. This may lead to the establishment of isolated populations inhabiting small streams within the drainage basin and potentially to the evolution of the resident phenotype independently from the anadromous component, even when in sympatry (see Section IV.1). Such segregation would be further reinforced by the strong philopatry typical of salmonid fishes. However, we do not possess adequate data to test the hypothesis that disruptive selection for body size in females due to competition for oviposition sites may contribute to the genetic segregation of alternative migratory phenotypes.

The weight of evidence therefore suggests that genetic divergence of alternative migratory phenotypes generally does not occur and that AMTs in salmonids originate from common gene pools. We may then evaluate the evidence that these tactics are mediated by individual sensitivity to threshold values along a liability trait characterized by genetic variation. Genetic divergence between AMTs may sometimes occur if the different phenotypes segregate spawning activities. Female habitat choice may drive such segregation, but other proximal mechanisms potentially limiting gene flow between AMTs are unknown. Far more studies are required involving different species to identify the ecological conditions that may contribute to reduced gene flow between the alternative migratory phenotypes.

III. LIABILITY TRAITS, THRESHOLD VALUES AND THE EXPRESSION OF MIGRATORY BEHAVIOUR

Here we describe how body size and other traits correlated with somatic condition influence the expression of migratory behaviour and determine whether these traits are useful

proxies for the liability trait controlling the decision to migrate in salmonids. Characteristics such as the concentration of certain hormones, lipid storage or growth efficiency have been shown to affect the adoption of alternative phenotypes, and have been hypothesized as potential liability traits in a variety of invertebrate and vertebrate species (McCormick & Naiman, 1984; Hutchings & Myers, 1987; Rowe & Thorpe, 1990; Rowe, Thorpe & Shanks, 1991; Roff, 1997; Thorpe *et al.*, 1998; Forseth *et al.*, 1999; Emlen & Nijhout, 2000). Nevertheless, body size is the most commonly reported proxy of the liability trait in salmonids (e.g. Aubin-Horth & Dodson, 2004; Thériault *et al.*, 2007; Piché, Hutchings & Blanchard, 2008). Although part of this bias is due to the relative ease in measuring this trait (in mass or length), the evidence also suggests that body size adequately represents the liability trait. For example, through the study of genetic correlations, much of the genetic variance in body size is shared with the propensity to migrate in brook charr (Thériault *et al.*, 2007). Similarly, the timing of early sexual maturity in male Atlantic salmon, and hence the adoption of the resident tactic, is strongly genetically correlated with body size (Páez *et al.*, 2010). These strong correlations suggest that common genes affect both the incidence of AMTs and body size. More generally, this also suggests that such traits will change under selection either through a direct response (i.e. when selection acts directly on the trait) or through a correlated response (the trait changes in response to selection imposed on the correlated trait).

However, the role that body size and growth plays in the expression of AMTs is complex. One hypothesis states that faster growing individuals migrate to more productive feeding areas because they are energetically constrained in low-productivity habitats at a younger age and smaller size [brown trout (Forseth *et al.*, 1999), Arctic charr (Rikardsen & Elliott, 2000), brook charr (Morinville & Rasmussen, 2003), steelhead trout (Beakes *et al.*, 2010), chinook salmon *O. tshawytscha* (Beckman & Dickhoff, 1998)]. These studies led to the conclusion that fast growth results in migration to richer feeding grounds (Jonsson & Jonsson, 1993).

By contrast, other studies have shown that fast growth early in life is associated with freshwater residency and, in some cases, early sexual maturity. By reciprocally transplanting brown trout between two sections in a river, Olsson *et al.* (2006) demonstrated that migratory behaviour was characteristic in a river section with high brown trout densities and low specific growth rates, whereas non-migratory behaviour was more common in a section with low brown trout densities and high specific growth rates. In laboratory experiments, more brown trout became migrants when food levels were low than under high food levels (Olsson *et al.*, 2006; Wysujack *et al.*, 2009). Latitudinal variation in the growth and maturation of masu salmon *O. masu* also supports the hypothesis that freshwater residency is promoted by favourable growth conditions at southern latitudes (Morita & Nagasawa, 2009). In a study of several cohorts of a wild Atlantic salmon population, size was significantly greater for future mature parr than for immature males suggesting that

greater body size promotes residency and early maturity (Aubin-Horth & Dodson, 2004). What then is responsible for the apparently contradictory patterns in the expression of AMTs as a function of body size? An examination of threshold mechanisms responsible for migration to sea provides some insights.

(1) Critical threshold body length for migration

Elson (1957) first suggested that juvenile Atlantic salmon must attain, during autumn, a threshold body length of 10 cm to migrate the following spring. Several studies have subsequently supported the hypothesis of a critical threshold length for migration in salmonids (Kristinsson, Saunders & Wiggs, 1985; Skilbrei, 1991; Yamamoto & Nakano, 1996; Yamamoto & Morita, 2002; Thériault & Dodson, 2003), although growth rate may have a modifying effect on the specific threshold value (e.g. brown trout: Økland *et al.*, 1993). In some cases, the effect of a threshold size is evident as the length–frequency distribution of juveniles becomes bimodal some time before migration; fish in the upper modal group (i.e. the fast-growing individuals) migrate the following spring whereas those in the lower modal group remain as parr for an additional year (Thorpe, 1977; Kristinsson *et al.*, 1985; Hirata, Goto & Yamazaki, 1988; Yamamoto & Nakano, 1996; Utrilla & Lobon-Cervia, 1999; Beakes *et al.*, 2010). Several studies have shown that the incidence of migratory phenotypes and the variance in body size and other traits correlated with migratory behaviour is under genetic control (Table 3). Although quantitative genetic parameters have not been estimated specifically for the physiological traits involved in these threshold mechanisms, these results allow us to speculate that such traits are also characterized by genetic variation.

The observation of significant genetic variance in these traits may contribute to explain the contradiction among studies regarding the role that body size and growth play in the development of migratory phenotypes. For example, it could be argued that the physiological conditions to trigger migration differ across the geographical distribution of salmonids, such that these trends are the outcome of natural selection. This hypothesis, however, requires further testing.

(2) Multiple threshold mechanisms for AMTs?

The decision to migrate or to suspend migration and mature early at smaller body sizes may involve more than a single threshold mechanism signalling two alternative developmental pathways, as illustrated with studies on the life-history variation of the Atlantic salmon. The decision to migrate does not occur at the same time as the decision to mature and remain in fresh water, indicating the existence of more than one sensitive time during ontogeny when these life-history pathways may be activated (Thorpe *et al.*, 1998; Páez, Bernatchez & Dodson, 2011a; Rossignol, Dodson & Guderley, 2011). Furthermore, some data also reveal that anadromy may be achieved through at least two

developmental pathways characterized by very different growth rates (Letcher & Gries, 2003). In a common rearing experiment, Páez *et al.* (2011b) and Rossignol *et al.* (2011) identified three alternative developmental pathways (Fig. 1). Consistent with the observations of Metcalfe (1998), individuals with body lengths greater than approximately 85 mm by the winter of their first year of life grew very rapidly and became the largest smolt (forming the upper modal group of body sizes; Fig. 1). Males and females below this size formed the lower modal group of body sizes, becoming either mature male parr or smolt (Fig. 1). An analysis of variance in body mass and length among the upper modal group smolt, lower modal group smolt and lower modal group mature parr (Rossignol *et al.*, 2011, D. J. Páez, in preparation) revealed significant differences between all groups in January and April, with mean mature parr mass and length intermediate between that of upper modal group smolt and lower modal group smolt in both months. In July, there was no statistical difference between the mean mass and length of lower modal group smolt and that of lower modal group mature parr. In November, the mean body mass and length of lower modal group mature parr was significantly lower than that of upper and lower modal group smolt. Therefore, in the initial stages of the adoption of these tactics, mature parr growth is intermediate between that of upper and lower modal group smolt, subsequently declining because of maturation. Similar observations have been recorded in the field for brown trout in a Norwegian lake (Jonsson & Jonsson, 2011, p. 234). For both males and females, the fastest growing individuals smolted at the youngest age. Slower growing fish matured sexually as resident trout whereas even slower growing fish smolted 1 year later.

Thus, two consecutive threshold mechanisms associated with AMTs seem to occur in some salmonids (Fig. 2). The accelerated developmental pathway of Atlantic salmon observed in the laboratory does not appear to involve a threshold mechanism for maturation and residency. Fish recruiting to this rapid developmental pathway tend to be females and develop the anadromous life style. Fish recruiting to the slower developmental pathway tend to be males and are exposed to a second threshold mechanism to adopt either early maturity or to smolt later. Smolting in this developmental pathway is then related to slower growth and smaller size (Bailey, Saunders & Buzeta, 1980; Thorpe & Morgan, 1980; Heggenes & Metcalfe, 1991; Skilbrei & Heino, 2011). Anadromy may thus be achieved through two alternative developmental pathways.

The contradiction among studies about the effect of growth on the probability of AMTs is to some extent caused by the use of laboratory-based studies that involve major modifications to environmental variables that may alter developmental phenology. In nature, however, contradictory observations may arise from spatial and seasonal variations in growth rate. In the Atlantic salmon example, if low annual growth precludes the development of the upper modal growth group, sampling would be limited to the lower modal group and we would conclude that mature parr

Table 3. Studies reporting significant heritability estimates for the development of alternative migratory tactics and associated liability traits.

Species	Field (F) or laboratory (L) study; sib structure (full-sib = FS, half-sib = HS); number of male (M) and female (F) progenitors	Trait measured	Evidence of genetic variation h^2 – narrow sense heritability	References
Atlantic salmon <i>Salmo salar</i>	L; FS; 53M and F	Incidence of precocious maturity <i>versus</i> immaturity in males	Significant differences between four pure populations and hybrids	Piché <i>et al.</i> (2008)
	L; FS; 120F, 113M	Incidence of early <i>versus</i> delayed migrants	Significant differences between two populations	Nicieza <i>et al.</i> (1994b)
	L; HS; 47F, 52M. Study conducted over 5 years	Incidence of smoltification	$h^2 = 0.16 \pm 0.05$. ANOVA, greater variance between than within populations	Refsic <i>et al.</i> (1977)
	L; HS; 14M, 4F	Average body length (mm) of mature parr Average body mass (g) of early migrants	$h^2 = 0.25 \pm 0.14$ $h^2 = 0.33 \pm 0.15$	Páez <i>et al.</i> (2011a).
		Timing of early sexual maturity in male parr	$h^2 = 0.31 \pm 0.19$	D. Páez, L. Bernatchez & J.J. Dodson, unpublished data
		Incidence of early <i>versus</i> delayed migration	$h^2 = 0.77 \pm 0.33$	Páez <i>et al.</i> (2011b)
Brook charr <i>Salvelinus fontinalis</i>	F; FS; 89–91M and F	Incidence of migration vs residency Body length (mm) at capture	$h^2 = 0.52–0.56$ $h^2 = 0.44–0.50$	Thériault <i>et al.</i> (2007)
Chinook salmon <i>Oncorhynchus tshawytscha</i>	L; HS; 12M, 3F	Incidence of Jacks vs non-Jacks	$h^2 = 0.54 \pm 0.23$	Thériault <i>et al.</i> (2007) Heath <i>et al.</i> (1994)
	L and F; HS; 36M, 72F	Timing of return to spawning grounds Timing of sexual maturation Body mass	$h^2 = 1.26 \pm 0.4$ $h^2 = 1.06 \pm 0.42$ $h^2 = 0.59 \pm 0.02$ $h^2 = 0.59 \pm 0.03$	Quinn, Kinnison & Unwin (2001) Quinn <i>et al.</i> (2001) Martyniuk <i>et al.</i> (2003)
Rainbow trout <i>Oncorhynchus mykiss</i>	Two-generational pedigree using two domesticated strains: Paternal generation: HS, 4M, 60F. Subsequent generation: diallele lots consisting of 94 pure-strain families and 38 hybrid families	Condition factor Incidence of precocious maturation	$h^2 = 0.35 \pm 0.04$	Martyniuk <i>et al.</i> (2003) Martyniuk <i>et al.</i> (2003)

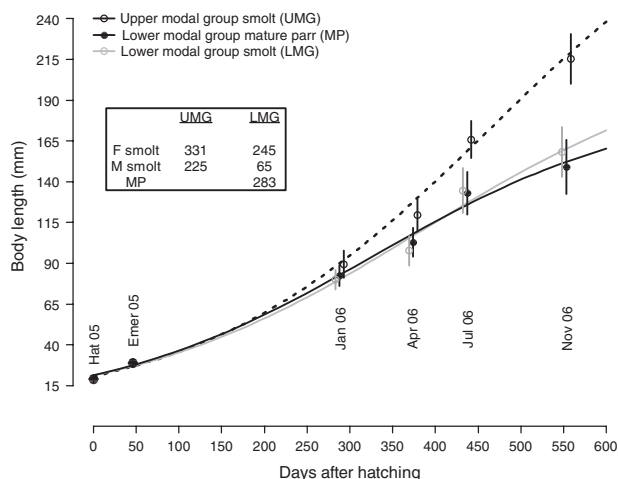


Fig. 1. Divergent growth trajectories of individually tagged juvenile salmon raised in the laboratory from hatching in 2005 until the end of the experiment in November 2006 (see Páez *et al.*, 2011a, b for experimental design). The curves (based on a logistic growth function) represent the growth trajectories of the upper modal group (UMG), and the lower modal group (LMG) as identified in November 2006. Mature male parr (MP) belong to the LMG but their growth trajectory is presented separately. Labels within the figure represent dates when measurements of standard length and mass were obtained (Hat 05, hatching 2005; Emer 05, emergence 2005). Data points are mean lengths and error bars are standard deviations. The box contains male (immature and mature) and female sample sizes of UMG and LMG growth trajectories.

initially grow faster than the smolts of the same age class. In years or locations with good growth opportunities, more fish could recruit to the upper modal growth group and we would conclude that smolts grow faster than mature parr.

However, this hypothesis cannot explain the observation in at least one population of Atlantic salmon, where exceptionally fast growth resulted in the maturation of male parr during the first summer of life, many months prior to the first opportunity for migration to sea (e.g. Letcher & Terrick, 1998). Furthermore, mature males in the autumn are sometimes capable of migrating to sea the following spring (Myers, 1984; Letcher & Gries, 2003) such that the decision to reproduce as mature parr in the fall does not necessarily preclude subsequent migration. It thus appears that additional developmental pathways may be activated under exceptional environmental conditions.

(3) The additional effect of age on the expression of AMTs

It is important to recognize that the effect of body size on the probability of migration depends on individual age (Hutchings & Myers, 1994). For example, in brook charr, migration first occurs at the age of 1+ (i.e., greater than 1 but less than 2 years of age) and emigrants are among the bigger, most metabolically active juvenile fish (Morinville & Rasmussen, 2003). However, emigration also occurs at

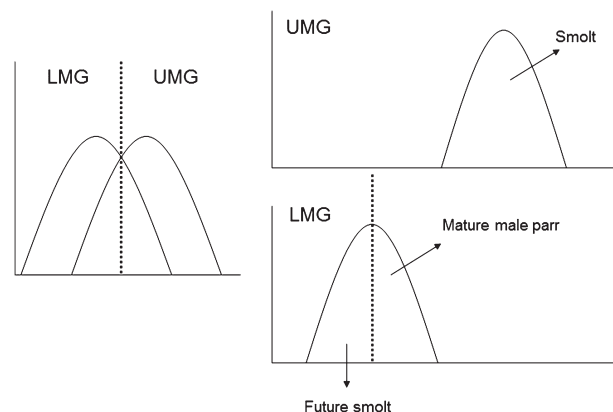


Fig. 2. The consecutive threshold mechanisms proposed to explain the development of alternative migratory tactics in Atlantic salmon, as observed in the laboratory. The x -axis represents the proxy for the liability trait (e.g. body size), the y -axis, frequency. An initial threshold mechanism (dotted line denotes threshold value) leads to two developmental pathways and a bimodal size distribution. UMG, upper modal growth group; LMG, lower modal growth group. The UMG developmental pathway does not appear to involve a threshold mechanism for maturation and residency. Fish recruiting to this rapid developmental pathway (female biased), are destined for the anadromous lifestyle. Fish recruiting to the LMG developmental pathway (male biased) will be exposed to another threshold mechanism (dotted line denotes threshold value) to adopt either early maturity or to smolt at a smaller size. These events take place at different times during development such that different phenotypes appear at different ages. Smolting and migration may thus be triggered by at least two different threshold mechanisms and two threshold sizes.

the age of 2+. In this case, emigrants are among the smallest juvenile fish remaining in fresh water. The largest 2+ juveniles remain resident in fresh water to spawn the following year (Thériault & Dodson, 2003). This suggests that the trade-off between survival and fecundity as a function of body size is altered as the age of maturity is approached. In the specific case studied by Thériault & Dodson (2003), residency and hence a greater probability of survival to reproduction appears to be favored among the biggest juveniles of the older age class whereas migration, and its concomitant increase in fecundity and competitive ability (due to the larger body size of anadromous migrants (Fleming & Gross, 1994)) is favored among the biggest fish of the younger age class (Thériault *et al.*, 2008).

Overall, body size may be considered an adequate proxy for the liability trait controlling the decision to migrate in salmonids. However, the threshold body size values signaling migration probably vary as a function of growth rate, age class and previous reproductive state. Individuals may reach the same phenotypic outcome (anadromy, residency) after surpassing very different threshold body sizes. Furthermore, individual age may interact with body size to modify the probability of the alternative phenotypes and this may vary according to the species studied. Such variability may thus contribute to the apparent contradictions in the literature

concerning the relationship between AMTs and body size.

IV. GENETIC VARIATION AND THE PHYSIOLOGY OF AMTs

The development of AMTs in salmonids depends on the action of many genes influencing individual physiological condition (the liability) and their sensitivity (both physiological and genetic) to environmental variables. Clear evidence for this is provided by the analysis of quantitative trait loci (QTL) in two species. In rainbow/steelhead trout, a small number of QTL contribute greatly to variation in several smolting-related traits (Nichols *et al.*, 2008). In Atlantic salmon, a large proportion of the variation in body mass and condition factor is controlled by a few QTL with relatively large effects (Reid *et al.*, 2005). These authors also identified chromosomal regions that appear to show conserved QTL effects on body mass in rainbow trout and Arctic charr. The fact that multiple single-trait QTL have been found to explain the variation of several traits linked to AMTs is consistent with the hypothesis that AMTs have a polygenic basis.

(1) The genetic control of AMTs

As introduced above, several studies have shown a significant heritable component in the development of alternative migratory tactics, mainly by documenting the heritability of liability traits (Table 3). The values so obtained generally conform to the range of heritability estimates reported for threshold traits (reviewed in Roff, 1996), where approximately one-half of the phenotypic variation can be attributed to additive genetic variance. Thus, migratory tactics have considerable potential to respond to selection and evolve (Heath, Fox & Heath, 1999; Garant, Dodson & Bernatchez, 2003; Perry *et al.*, 2004; Garcia de Leaniz *et al.*, 2007; Páez *et al.*, 2010, 2011a, b) (Table 3). Using related individuals obtained from the St. Marguerite River, Quebec, Canada, produced from a half-sib pedigree design and raised in a common garden experiment, Páez *et al.* (2011b) demonstrated a significant heritability estimate for the incidence of upper and lower modal size groups of immature juvenile salmon (Table 3). This genetic variation was also evident in the threshold body sizes that marked the divergence between the lower and upper modal groups (Fig. 3). It thus appears that, at least in Atlantic salmon, significant additive genetic variance exists for body size at migration. Further evidence for the capacity of these traits to evolve has been shown by comparing the AMTs produced by raising individuals from different populations under common conditions, and through reciprocal transplantation experiments (e.g. Stewart, Middlemas & Youngson, 2006; Piché *et al.*, 2008). For example, (Nicieza, Reyes-Gavilán & Braña, 1994b) observed, in a common rearing experiment, significant differences in the incidence of upper and lower

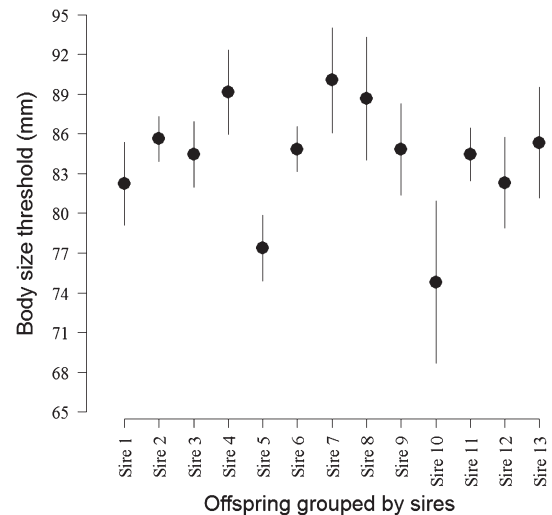


Fig. 3. Significant variation among the sire groups of Atlantic salmon in the body size marking the divergence in growth trajectories between the lower and upper modal groups of the experiment reported in Páez *et al.* (2011b). Whiskers represent 95% confidence intervals. Significant variation in estimated threshold levels suggests additive genetic variance for the propensity to smolt and migrate.

modal body length groups in juvenile Atlantic salmon from a Scottish river and a more southerly river in Spain.

(2) Threshold traits and switching mechanisms

In threshold traits such as AMTs, the continuous value of the liability trait must be translated into a signal that will activate development into a discontinuous migratory tactic. Very little is known about the proximal mechanisms mediating the activity of the AMT's developmental switch in salmonids, although it has been proposed that information on size/growth is translated into a physiological signal such as a hormone titre that acts as an integrator of developmental and environmental change (McCormick, 2009). Based on what is known in invertebrates, the most likely mechanism includes a change in concentrations of one or several hormones during development (Nijhout, 1999; Emlen, 2000; West-Eberhard, 2003). These hormones activate cellular processes leading to a specific developmental course and often affect multiple traits in a coordinated manner. In invertebrates, hormones have been found to differ in their concentration or timing of secretion during the development of threshold traits. In addition, artificial manipulation of hormone levels has resulted in different developmental courses, for traits as diverse as alternative reproductive morphs in male horned beetles (*Onthophagus taurus*) (Emlen & Nijhout, 1999), wing polymorphism in crickets (*Gryllus* spp.) (Zera, 2003) and seasonal morphs in butterflies (*Bicyclus anynana*) (Oostra *et al.*, 2011). In salmonids, the value of liability traits underlying AMTs is also likely to be translated into physiological information through shifts in hormonal concentrations or

in the timing of hormonal peaks. Concentrations of several hormones are known to increase months before or at the onset of smolting in salmonids. Pleiotropic effects of these hormones could explain the phenotypic changes, which must occur in a cohesive fashion to produce a functional migrating individual. Candidates include (but are not limited to) growth hormone, which controls the value of the liability trait (size/growth) and is also involved in the smolting process by enhancing the capacity to face a saltwater challenge (Dickhoff *et al.*, 1997) as well as growth-hormone-releasing hormone, the neuropeptide that stimulates the release of growth hormone, that has also been directly implicated in downstream swimming behaviour (Ojima & Iwata, 2010). Circulating levels of insulin-like growth factor (IGF), a peptidic hormone also implicated in growth, increase months before smolting (McCormick *et al.*, 2007) resulting in greater salinity tolerance (McCormick, 1996). Another candidate is cortisol, a glucocorticoid hormone involved in the stress response with numerous energy-related functions that is also implicated in behaviour in salmonids (Gilmour, Dibattista & Thomas, 2005) and saltwater tolerance (McCormick *et al.*, 2007). Recent work in salmonids has shown that the corticotropin-releasing factor, which is also part of the hormonal stress response cascade, can have direct effects on downstream swimming behaviour (Clements & Schreck, 2004; Ojima & Iwata, 2010) and locomotor activity (Carpenter *et al.*, 2007). Finally, thyroid hormone has been involved in downstream swimming behaviour and in the lowering of aggressiveness in smolts (Iwata, 1995; Hutchison & Iwata, 1998; Specker *et al.*, 2000). The control of thyroid hormone activity by specific enzymes (e.g. deiodinase) may also be involved (Specker *et al.*, 2000). Nonetheless, as divergence in phenotypes associated with AMTs are detectable many months in advance in some cases (Thorpe *et al.*, 1989 1998; Páez *et al.*, 2011a; Fig. 1), studies determining the endocrine state of individuals during this early stage of divergence and how they relate to the development of AMTs are needed. The threshold value may also be represented by the individual's sensitivity to these physiological messages, through different levels of receptors, their sensitivity to the hormonal message, or the timing of their expression in a given tissue. Recent molecular work has shown that thyroid hormone receptors vary in expression levels during the development of the migrant phenotype (Harada *et al.*, 2008), potentially affecting the sensitivity to this hormone.

Different thresholds have been found between individuals/populations in salmonids for threshold traits such as early sexual maturity (Aubin-Horth & Dodson, 2004; Baum *et al.*, 2004; Aubin-Horth *et al.*, 2006; Piché *et al.*, 2008; Páez *et al.*, 2011a) and migration (Nicieza *et al.*, 1994b; Páez *et al.*, 2011b). It could be hypothesized that these different thresholds result from inter-individual variation in the sensitivity to physiological messages translating the value of the liability trait. Thus, investigating inter-individual variation in hormone receptor levels at a specific time point prior to smolt development or the hormone-affinity of that

receptor in populations that differ in their thresholds would potentially provide important insights into the nature of their variation.

(3) Evolutionary potential of AMTs

Once development activates phenotypic divergence *via* threshold traits, the genetic and phenotypic correlation between traits in the alternative tactics may become small, thus unlinking the response to selection of the alternative tactics and facilitating the phenotypic evolution of alternative life histories in their own directions (Roff, 1996). The decoupling of developmental pathways involves the expression of genes specific to a particular morph and has been a central hypothesis in the evolution of plasticity (Snell-Rood *et al.*, 2010). As such, alternative tactics may evolve to their phenotypic optimum without being affected by correlated effects if genetic correlations for a given trait are small (Lande, 1979).

Genomic-scale brain transcription differences between resident and migrant Atlantic salmon of the same cohort have been quantified in a wild population (Aubin-Horth, Letcher & Hoffmann, 2009). These authors sampled wild individuals in the spring that were either migrating or residing in fresh water for another year. At this time, differences in morphology, growth rate and colouration had appeared, yet migratory behaviour had not commenced. The analysis of the expression patterns of more than 1800 genes uncovered differences between migrants and residents in the brain expression of 144 genes. These genes were associated with various biological functions including behaviour, metabolism and growth, as well as learning and memory (Aubin-Horth *et al.*, 2009). Based on a comparison of the genes differentially expressed between mature sneaker males and immature males of Atlantic salmon (Aubin-Horth *et al.*, 2005), a set of genes was differentially expressed in both life-history transitions, suggesting the possibility that these genes are co-regulated by one or a few key master regulators. Similarly, changes in gene expression in multiple tissues observed between parr and smolt ready to migrate were assessed in hatchery-raised fish (Seear *et al.*, 2010). They found genes that were differentially expressed in specific tissues, while one gene (a translation elongation factor) was differentially regulated in brain, gills and kidney. These authors also found that gills showed the highest number of differentially expressed genes related to biological functions central in the developmental switch to a migrant phenotype, including growth, metabolism, oxygen transport and osmoregulation. Far more work is required to understand fully the genetic, molecular and developmental basis of tactic formation and to test the hypothesis that sets of genes differentially expressed during life-history transitions are co-regulated by one or a few key master regulators (Aubin-Horth *et al.*, 2009). Furthermore, work on the functional implications of these differential gene expression patterns is needed. Quantitative genetic studies of the genetic correlations among common traits measured in alternative tactics could further allow us to understand whether the activation of these

contrasting developmental pathways decouples or dissociates the evolutionary capacity of these traits (West-Eberhard, 2003).

V. LOCAL ADAPTATION AND BIOGEOGRAPHIC PATTERNS OF AMTS

A major challenge to the theory concerning alternative traits and developmental thresholds lies in providing a coherent theory to explain the tremendous diversity of intraspecific life-history pathways in salmonid fishes. Two prominent biogeographical gradients in the incidence of alternative migratory strategies in salmonids encompass much of this variation: increasing residency with altitude or distance upstream, and increasing anadromy at higher latitudes. Whether these gradients reflect either strict local adaptation or phenotypic plasticity (adaptive or not) is not clear.

(1) Altitudinal gradients

A number of studies has demonstrated that the anadromous tactic in populations exhibiting AMTs tends to diminish with altitude and/or distance upstream and that anadromous individuals preferentially occupy the lower reaches of their nursery rivers. For instance, in two independent studies, the incidence of early maturity among the male parr of Atlantic salmon was correlated with altitude (Baum *et al.*, 2004) or distance upstream (Aubin-Horth *et al.*, 2006), suggesting a causative relationship between residency and the fluvial gradient. In both cases, parr of a given age and size were more likely to be sexually mature and hence resident if located further upstream or at higher altitudes. In brown trout, the recruitment of anadromous populations declined with altitude relative to that of resident populations illustrating a cost of migration that is positively correlated with altitude (Bohlin, Pettersson & Degerman, 2001). In chinook salmon, precocious male maturation and freshwater residency is characteristic only of the stream-type (spring-run) phenotype that is typical of northern-latitude populations and headwater tributary populations in temperate North America (Healey, 1991). The prevalence of resident phenotypes in the upper reaches and headwaters of rivers has also been documented in brook charr (Curry, 2005) and Dolly Varden (Armstrong & Morrow, 1980). Genetic analyses of steelhead/rainbow trout from multiple tributaries of a drainage revealed that high-elevation sites are principally occupied by the resident phenotype (rainbow trout) and high gradients and barriers act to limit the anadromous form (steelhead) to low-elevation sites (Narum *et al.*, 2008).

These observations may reflect population-specific evolutionarily stable states (ESS) that result in the local adaptation of tactic frequency. Under negative frequency-dependent selection, changes in the fitness functions of either or both alternative tactics will change the relative abundance of tactics at which the average tactic fitness is equal (i.e. at which the ESS is found) (Hutchings & Myers,

1994; Brockman & Taborsky, 2008). Given the evidence for additive genetic variance for the liability trait and threshold mechanisms, selection may thus act to shift tactic frequencies to these equilibrium values.

The decline in anadromy relative to residency with increasing altitude or distance upstream is consistent with the hypothesis that increased migratory costs incurred during the upstream migration result in a lower fitness function of the migrant *versus* the resident tactic. Migratory costs may include mortality related to energy expenditures during the upstream migration (Dodson, 1997; Jonsson & Jonsson, 2006) and an increasing probability of losing access to upstream or higher elevation spawning grounds due to low discharge (stranding) and/or high summer temperatures encountered during the migration (Aubin-Horth *et al.*, 2006). If the fitness of the migrant male phenotype declines due to survival selection (Endler, 1986) or an increased probability of exclusion from the spawning grounds, then the reproductive success of residents may always exceed that of migrants regardless of condition. As a result, frequency-dependent selection may either completely remove the migratory phenotype from the population or shift the ESS to a new equilibrium value.

Although selection on fecundity and competition among females are hypothesized to favour a large body size (Fleming & Gross, 1994), this advantage may be mitigated if, as previously discussed, spawning grounds in small tributary streams are inaccessible to larger anadromous females. Thus, female resident phenotypes would be expected to develop in cases of extreme selection against the anadromous phenotype either due to mortality or the inability to reach spawning grounds. The many cases that document the development of land-locked populations above impassable barriers to migration, whether natural (e.g. rainbow trout: Kostow, 2003) or artificial (e.g. white-spotted charr *Salvelinus leucomaenis*: Yamamoto *et al.*, 2004), represent an extreme situation whereby downstream migrants cannot return to spawning sites, culling the migratory phenotype from the population.

(2) Latitudinal gradients

Many salmonid species share a latitudinal pattern of AMTs characterized by residency in the extreme south of the range, with populations restricted to high-altitude sites, female anadromy throughout most of the range and increasing male anadromy to the north. Many populations at low latitudes are faced with critically high water temperatures in the lower reaches of rivers and appear to be confined to thermal refuges found at higher altitudes (Table 4). This latitudinal gradient is to some extent the result of the altitudinal gradient discussed above. As downstream areas at the southerly limits of distribution are too warm, anadromous fish must migrate to higher altitudes to ensure an appropriate rearing habitat for their offspring. As discussed in Section V.1, the reproductive success of residents may exceed that of migrants such that frequency-dependent selection no longer acts to maintain the alternative phenotypes. Natural

Table 4. Examples of salmonid species exhibiting latitudinal gradients in alternative migratory tactics: residency in the extreme south of their range, with some populations restricted to high-altitude sites; female anadromy throughout most of the range; and male anadromy increasing to the north of their distributional range.

Species	Region	Pattern	References
Dolly Varden <i>Salvelinus malma</i>	Japanese archipelago	Lower limits of their distribution extend to sea level in the north of their range, restricted to more than 140 m above sea level at the southern margin of their range	Nakano, Kitano & Maekawa (1996) and Maekawa & Nakano (2002)
White-spotted charr <i>Salvelinus leucomaensis</i>	Honshu north to Nabarin Cape, Russia	Lower limits of altitudinal distribution steadily increase from sea level in the north to 450 m at the southern margin of their range	Nakano <i>et al.</i> (1996) and Yamamoto <i>et al.</i> (1999)
Masu salmon <i>Oncorhynchus masou</i>	Japanese archipelago	Proportion of anadromous males declines in the southern part of their range	Kato (1991) and Tsukamoto <i>et al.</i> (2009)
Arctic charr <i>Salvelinus alpinus</i>	Atlantic coasts	Non-anadromous forms predominate in the southern part of their distribution	Doucett <i>et al.</i> (1999)
Brown trout <i>Salmo trutta</i>	Iberian peninsula	Anadromy less common at the southern limit of their distribution as increased water temperatures restrict populations closer to the headwaters	Antunes <i>et al.</i> (2006)
Brook charr <i>Salvelinus fontinalis</i>	North America	Most-southerly populations of brook charr are non-anadromous; incidence of anadromy increasing to the north ^a	Castric & Bernatchez (2003)
Rainbow trout/steelhead <i>Oncorhynchus mykiss</i>	Kamchatka peninsula	Predominantly resident in the south and anadromous in the most northern rivers	McPhee <i>et al.</i> (2007)

^aHistorical observations indicate that anadromy in the southern part of the range has been extirpated in recent times (B. Letcher, personal communication).

selection then culls the anadromous strategy from the most southerly populations and they become spatially restricted to high-altitude temperature refuges.

However, it seems that other mechanisms are required to explain the decline in frequency of the resident phenotype in more northerly populations. The food availability hypothesis (Gross, Coleman & McDowall, 1988) emphasizes the importance of food intake and growth for fitness and proposes that anadromy is favoured at high latitudes where marine productivity is greater than freshwater productivity. The hypothesis was originally formulated to explain the difference in the latitudinal distribution of anadromy (predominant at higher latitudes) and its inverse biological phenomenon, catadromy (predominant at lower latitudes where freshwater productivity exceeds that of marine waters). This hypothesis has subsequently been used to explain intraspecific differences in the incidence of anadromy and residency across the rather limited latitudinal ranges characterizing the distribution of anadromous fishes (principally salmonids) in the northern hemisphere (e.g. masu salmon: Tsukamoto *et al.*, 2009). However, given the high productivity of estuaries and coastal areas in the northern hemisphere, salmonid migration to estuarine habitats should always be favoured if anadromy is uniquely the result of selection for increased food intake and growth. It appears that other variables must be involved to explain the gradient in the frequency of the resident phenotype across the distributional range of many salmonid fishes.

An increase in anadromy may also be related to an increase in freshwater mortality (Thériault *et al.*, 2008;

Jonsson & Jonsson, 2011). There are several potential sources of increased mortality at high latitudes. Short growing seasons and low productivity require high-latitude fish to store sufficient lipids to survive the long winter months. Longer and more severe winters may cause higher energy-selective mortality in the north (Finstad *et al.*, 2010). In addition, greater vulnerability to predation and reduced longevity may arise as a result of the maximisation of energy intake and growth rate during the brief growing seasons at high latitudes (Lankford, Billerbeck & Conover, 2001). Salmonids exhibit higher than normal growth rates and replenish energy reserves after periods of food shortage or unfavourable temperatures (Jonsson & Jonsson, 2011). Such compensatory growth is associated with a reduction in longevity and may be more prevalent in colder, harsher northern rivers. Some observations from Atlantic salmon suggest that high-latitude populations have a higher growth capacity than their low-latitude conspecifics (Nicieza, Reiriz & Braña, 1994a). Such countergradient selection involves acquisition trade-offs, whereby an increase in foraging rates results in an increase in mortality (Angilletta *et al.*, 2003). However, the evidence for such countergradient selection in the growth of salmon and brown trout is contradictory, with some studies either failing to support this hypothesis or providing alternative explanations for observed differences in growth rate (e.g. Jonsson *et al.*, 2001a; Finstad & Jonsson, 2012). Nevertheless, moving to more productive coastal and marine habitats could increase the average fitness of the anadromous phenotype relative to the resident phenotype if foraging in high-latitude fresh waters

involves increased mortality rates, but this hypothesis remains to be tested. In such cases, frequency-dependent selection may either completely remove the resident phenotype from the population or shift the ESS to a new equilibrium value.

VI. WHAT'S NEXT?

(1) Testing the frequency-dependence model

Negative frequency-dependent selection, though advocated as the main mechanism maintaining AMTs and ARTs in a population, has seldom been demonstrated in natural populations [but see Berejikian *et al.* (2010) for chinook salmon]. For this process to occur, the reproductive success of a tactic should vary inversely with the frequency of individuals following it. Whether this implies equal average fitness of the alternative phenotypes at an evolutionarily stable state or equal fitness of the alternative phenotypes at the threshold remains a contested question (Charnov, 1993; Gross, 1996; Shuster & Wade, 2003; Tomkins & Hazel, 2007). Under pure frequency-dependent selection, when condition does not influence the choice of developmental pathway, selection adjusts the frequency of the alternative phenotypes to equalize average fitness (Charnov, 1993). Under conditional selection, as typified by the status-dependent selection hypothesis (Gross, 1996), selection favours the threshold value at which the fitness of the alternative phenotypes are equal (the evolutionarily stable strategy switch point; Gross, 1996). The average fitness of the alternative phenotypes are thus not necessarily equal, a position that is considered untenable by Shuster & Wade (2003). We thus need studies that not only demonstrate frequency-dependent selection, but also establish whether alternative migratory tactics provide equal or unequal average fitness. Unfortunately, such experiments are logistically challenging to conduct. A precise measure of tactic fitness requires knowledge of individuals that reproduce and those that fail to reproduce as underestimation of the variance in reproductive success may lead to different conclusions about tactic fitness (Shuster & Wade, 2003). Estimations of relative or absolute reproductive success of the individuals that reproduce have been greatly facilitated by our capacity to reconstruct the genetic relationships between individuals through genotyping (e.g. Garant *et al.*, 2003; Thériault *et al.*, 2007). However, estimation of the number of individuals that fail to reproduce is problematic because failing to detect offspring genotypes does not necessarily mean that they do not exist in nature. Failure to detect some genotypes may simply be due to restrictions in sampling efforts. Greater sampling efforts have been made in some species of Pacific salmonids (Thériault, Moyer & Banks, 2010) and future work should aim at devising long-term sampling strategies to test the hypothesis of frequency-dependent selection and the equality (or lack thereof) of fitness in the alternative phenotypes.

(2) Local adaptation and phenotypic plasticity

The current phenotypic variation in the expression of AMTs depends on both genetic and environmental variation (Hutchings & Morris, 1985; Jonsson & Jonsson, 1993; Hendry *et al.*, 2004). Knowledge of the relative contribution of genetic *versus* environmental variation is fundamental to our understanding of the response of populations to environmental change in both the short and the long term. To our knowledge however, there are no rigorous experimental investigations of whether phenotypic variation in AMTs arises from local adaptation. Variation in the incidence of different migratory phenotypes over latitudinal gradients is well known (see Section V.2). In addition, latitudinal variation in various life-history characteristics (particularly in the age and size of smolting and emigration) is recognized in anadromous Atlantic salmon (Metcalf & Thorpe, 1990), brown trout (L'Abée-Lund *et al.*, 1989) and white-spotted charr (Yamamoto, Morita & Goto, 1999). Transplant experiments are needed to test whether such variation reflects local adaptation. At the intrapopulation level, a transplant experiment involving white-spotted charr demonstrated that the relationship between fish body size and the probability of becoming mature at a given age exhibited plasticity. Despite a common genetic origin of the fish, threshold values for maturity differed among groups transplanted to sites that differed in river width and temperature (Morita, Tsubi & Nagasawa, 2009). How this plasticity affects reproductive success and fitness remains to be demonstrated.

Although an increasing number of studies is providing evidence to demonstrate local adaptation in salmonids (e.g. Atlantic salmon: Garcia de Leaniz *et al.*, 2007), it may be less prevalent than has been traditionally assumed for the family (Fraser *et al.*, 2011). An interesting corollary to the quest for proof of local adaptation concerns the degree to which plasticity provides equal fitness in populations exposed to a variety of environmental settings. This question has two components. First, does plasticity of both the liability trait and the threshold mechanism produce different proportions of the alternative migratory tactics in different environmental settings? Secondly, does such plasticity equalize average fitness across environments? Answering these questions could provide insight into the resilience of anadromous populations to the changing temperature and hydrological regimes associated with a warming climate. Given the extraordinary intraspecific variation in AMTs documented in salmonids to date (Table 1), we suspect high levels of plasticity to be the norm. Nevertheless, given the importance of additive genetic variance in characterising liability traits and AMTs, some level of local adaptation is to be expected if selection is acting differentially across spatial scales. However, the scales and conditions under which locally adapted plasticity evolves remain to be demonstrated.

The nature of alternative migratory tactics possibly determines the ability of many salmonid populations to respond relatively rapidly to environmental change. Although strong directional selection may move the phenotypic proportion of one migratory tactic towards

fixation, it is unable to erode much of the genetic variation, which remains 'hidden' by virtue of the threshold nature of the trait (Roff, 1996). If selection pressures change, this hidden variation could be exposed and a response in the reverse direction can be achieved. This may be responsible for the expression of anadromy in apparently freshwater populations following transplantation to novel environments (e.g. Pascual *et al.*, 2001). Although some understanding of the genetic basis associated with AMTs has been achieved, very little is known about the intensity of selection (if any) occurring in the natural habitats of salmonids. Evidently, this information is essential to understand the capacity for evolution in these species.

(3) Threshold traits and switching mechanisms

Very little is known about the proximal mechanisms mediating the activity of the AMTs developmental switch in salmonids. To quantify molecular changes that happen prior to the development of the migrant phenotype, a clear and complete description of the various life stages that lead to migration must first be outlined. For example, this has been done in detail for hormonal titres in hatchery-raised Atlantic salmon (reviewed in Björnsson, Stefansson & McCormick, 2011). Time series using hormone titres as markers of developmental stage in conjunction with the quantification of how gene expression changes at different stages along alternative developmental pathways could then be performed. Correlations between gene expression and developmental stage are the first step in defining the molecular and hormonal mechanisms leading to AMTs (Giger *et al.*, 2006; Aubin-Horth *et al.* 2009).

The hypothesis that sets of genes differentially expressed during life-history transitions are co-regulated by one or a few key master regulators (Aubin-Horth *et al.*, 2009) needs to be tested. A regulator such as a steroid hormone receptor (which acts as a transcription factor) could have a pleiotropic effect and control the expression of several genes during the development of the migrant phenotype. We hypothesize that such a regulator may act to translate the liability trait into a physiological signal. The initial studies of (Aubin-Horth *et al.*, 2009) and Secar *et al.* (2010), outlined above (Section IV.2) point the way to understanding which biological functions are affected and which tissues are remodelled, in addition to providing candidate genes to pursue in detail. Studies on hormonal cascades involved in some aspects of migration (outlined in Section IV.2) have also provided prime candidates. The next step will be to perform more detailed time series to define which changes in gene expression instigate the physiological changes leading to AMTs and which changes are the consequences of the physiology of the newly activated phenotype (e.g. tissue metabolic capacities: Rossignol *et al.*, 2011). The manipulation of genes and hormones (using genetic and pharmacological tools) that are altered during the development of AMTs will also provide information on the causation mechanisms and extend correlational studies. Advances in the molecular tools available for different salmonid species will aid in this

endeavour. It has been shown recently that developmental plasticity expressed in the form of alternative life histories may also be controlled by epigenetic mechanisms, such as differential methylation of DNA, leading to long-term changes in gene expression (Kucharski *et al.*, 2008; Morán & Pérez-Figueroa, 2011; reviewed in Aubin-Horth & Renn, 2009). The inclusion of these molecular mechanisms in the study of proximal causes of AMTs will potentially provide important additional information on how developmental and environmental changes are integrated and turned into alternative migratory tactics.

(4) Beyond salmonids

Although we have limited this discussion to salmonid species, the phenomenon of partial migration appears to be taxonomically widespread among fishes, being observed in moronids, cyprinids, gasterosteids and gadids (Pálsson & Thorsteinsson, 2003; Kitamura *et al.*, 2006; Brodersen *et al.*, 2008; Kerr, Secor & Piccoli, 2009). For example, a portion of a population of the estuarine-dependent white perch (*Morone americana*) resides in the natal freshwater habitat whereas another portion migrates downstream to exploit the brackish waters of the upper estuary (Kerr *et al.*, 2009). In addition, there is ample evidence that a diversity of migratory tactics exist within catadromous anguillid eels (Daverat *et al.*, 2006; McCleave & Edeline, 2009). Whether all of these examples are true alternative phenotypes remains to be demonstrated, but the large number of reported cases of partial migration provides many biological models for the objectives summarized above.

Given that the phenomenon of partial migration extends far beyond fish, we may also ask if the concepts discussed here may be generally applicable across all cases of partial migration, independent of taxonomic identity. Threshold models of migration have been used to describe the inheritance and evolution of the incidence of partial migration in birds (Pulido, Berthold & van Noordwijk, 1996; Pulido, 2011) and the distribution and inheritance of macroptery in insects, which is correlated with migration tendency (Roff & Fairbairn, 2007). Studies of partial migration in birds, insects and salmonids have contributed significantly to the development of the threshold model of quantitative genetics. However, not all cases of partial migration can be studied within the context of threshold traits. The literature on partial migration recognizes three different patterns: non-breeding partial migration, whereby residents and migrants share a breeding habitat but spend the non-breeding season apart; breeding partial migration where residents and migrants share a non-breeding habitat but breed apart; and skipped breeding partial migration, whereby residents and migrants are apart during the breeding season, but since migration is required for reproduction only migrant individuals reproduce (Shaw & Levin, 2011). In breeding partial migration, the genetic segregation of resident and migratory phenotypes would effectively prevent gene flow between the phenotypes and thus preclude a role for alternative developmental pathways and their threshold

traits. Thus, only non-breeding and skipped breeding partial migration may be considered within the theoretical context developed here. Future studies in a variety of taxa would benefit greatly from testing the frequency-dependent selection hypothesis, establishing the relative importance of phenotypic plasticity in explaining geographical variation in migratory behaviour and identifying the physiological and genetic basis of the switching mechanisms responsible for AMTs.

VII. CONCLUSIONS

(1) Alternative migratory tactics (AMTs) in salmonid fishes co-exist within populations and all individuals may potentially adopt any of the alternative phenotypes. As AMTs occur within populations of interbreeding individuals, tactics may be mediated by individual sensitivity to threshold values along a liability trait characterized by genetic variation.

(2) Genetic divergence between AMTs may occur infrequently if the different phenotypes segregate spawning activities. Such segregation may be driven by female salmonids reducing intrasexual competition by selecting different oviposition sites based on their body size.

(3) Body size is an adequate proxy for the liability trait controlling the decision to migrate in salmonids. However, the threshold body size values signaling migration vary as a function of growth, age class and previous reproductive state. Individuals may thus achieve the same phenotypic outcome (anadromy or residency) through different developmental pathways.

(4) The incidence of migratory phenotypes and the variance in body size and other traits correlated with migratory behaviour is under polygenic control. Heritability estimates reveal that approximately one-half of the phenotypic variation can be attributed to additive genetic variance. Migratory tactics thus have considerable potential to respond to selection and evolve.

(5) Very little is known about the proximal mechanisms mediating the activity of the AMT's developmental switch in salmonids, although it has been proposed that information on size/growth is translated into a physiological signal such as hormone titre that acts as an integrator of developmental and environmental change.

(6) The decoupling of developmental pathways involves the expression of genes specific to a particular morph. As such, alternative tactics may evolve to their phenotypic optimum without being affected by correlated effects. Further work on genetic correlations between tactics is needed to test this hypothesis.

(7) Many salmonid species share common altitudinal (anadromy diminishes upstream) and latitudinal patterns (residency in the extreme south of the range, with populations restricted to high-altitude sites; female anadromy throughout most of the range; and increasing male anadromy to the north), possibly reflecting population-specific evolutionarily

stable states (ESS) that result in the local adaptation of tactic frequency.

(8) Future research opportunities include testing the frequency-dependent selection hypothesis, establishing the relative importance of phenotypic plasticity in explaining some geographic gradients in migratory behaviour, and identifying the physiological and genetic basis of the switching mechanisms responsible for AMTs.

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IX. REFERENCES

- ADAMS, B. K. (2007). *Migratory strategies of Atlantic salmon (Salmo salar) of Newfoundland and Labrador*. PhD Thesis: Dalhousie University.
- ANGILLET, M. J., WILSON, R. S., NAVAS, C. A. & JAMES, R. S. (2003). Trade-offs and the evolution of thermal reaction norms. *Trends in Ecology and Evolution* **18**, 234–240.
- ANTUNES, A., FARIA, R., JOHNSON, W. E., GUYOMARD, R. & ALEXANDRINO, P. (2006). Life on the edge: the long-term persistence and contrasting spatial genetic structure of distinct brown trout life histories at their ecological limits. *Journal of Heredity* **97**, 193–205.
- ARAI, T. & MORITA, K. (2005). Evidence of multiple migrations between freshwater and marine habitats of *Salvelinus leucomaenis*. *Journal of Fish Biology* **66**, 888–895.
- ARMSTRONG, R. H. & MORROW, J. E. (1980). The dolly varden. In *Charrs: Salmonid Fishes of the Genus Salvelinus* (ed. E. K. BALON), pp. 99–140. Dr. W. Junk Publishers, The Hague.
- AUBIN-HORTH, N., BOURQUE, J.-F., DAIGLE, G., HEDGER, R. D. & DODSON, J. J. (2006). Longitudinal gradients in threshold sizes for alternative male life history tactics in a population of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 2067–2075.
- AUBIN-HORTH, N. & DODSON, J. J. (2004). Influence of individual body size and variable thresholds on the incidence of a sneaker male reproductive tactic in Atlantic salmon. *Evolution* **58**, 136–144.
- AUBIN-HORTH, N., LANDRY, C. R., LETCHER, B. H. & HOFMANN, H. A. (2005). Alternative life histories shape brain gene expression profiles in males of the same population. *Proceedings of the Royal Society of London B* **272**, 1655–1662.
- AUBIN-HORTH, N., LETCHER, B. & HOFMANN, H. A. (2009). Gene-expression signatures of Atlantic salmon's plastic life cycle. *General and Comparative Endocrinology* **163**, 278–284.
- AUBIN-HORTH, N. & RENN, S. C. (2009). Genomic reaction norms: using integrative biology to understand molecular mechanisms of phenotypic plasticity. *Molecular Ecology* **18**, 3763–3780.
- BACON, P. J., PALMER, S. C. F., MACLEAN, J. C., SMITH, G. W., WHYTE, B. D. M., GURNEY, W. S. C. & YOUNGSON, A. F. (2009). Empirical analyses of the length,

- weight, and condition of adult Atlantic salmon on return to the Scottish coast between 1963 and 2006. *ICES Journal of Marine Science* **66**, 844–859.
- BAILEY, J. K., SAUNDERS, R. L. & BUZETA, M. I. (1980). Influence of parental smolt age and sea age on growth and smolting of hatchery-reared Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 1379–1386.
- BAUM, D., LAUGHTON, R., ARMSTRONG, J. & METCALFE, N. (2004). Altitudinal relationship between growth and maturation rate in salmon parr. *Journal of Animal Ecology* **73**, 253–260.
- BEAKES, M. P., SATTERTHWAITE, W. H., COLLINS, E. M., SWANK, D. R., MERZ, J. E., TITUS, R. G., SOGARD, S. M. & MANGEL, M. (2010). Smolt transformation in two California steelhead populations: effects of temporal variability in growth. *Transactions of the American Fisheries Society* **139**, 1263–1275.
- BECKMAN, B. R. & DICKHOFF, W. W. (1998). Plasticity of smolting in spring Chinook salmon: relation to growth and insulin-like growth factor-I. *Journal of Fish Biology* **53**, 808–826.
- BEREJIKIAN, B. A., VAN DOORNIK, D. M., ENDICOTT, R. C., HOFFNAGLE, T. L., TEZAK, E. P., MOORE, M. E. & ATKINS, J. (2010). Mating success of alternative male phenotypes and evidence for frequency-dependent selection in Chinook salmon, *Oncorhynchus tshawytscha*. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 1933–1941.
- VAN DEN BERGHE, E. P. & GROSS, M. R. (1989). Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 204–206.
- BJÖRNSSON, B. T., STEFANSSON, S. O. & MCCORMICK, S. D. (2011). Environmental endocrinology of salmon smoltification. *General and Comparative Endocrinology* **15**, 290–298.
- BOHLIN, T., PETTERSSON, J. & DEGERMAN, E. (2001). Population density of migratory and resident brown trout (*Salmo trutta*) in relation to altitude: evidence for a migration cost. *Journal of Animal Ecology* **70**, 112–121.
- BOULA, D., CASTRIC, V., BERNATCHEZ, L. & AUDET, C. (2002). Physiological, endocrine and genetic bases of anadromy in the brook charr, *Salvelinus fontinalis*, of the Laval River (Québec, Canada). *Environmental Biology of Fishes* **64**, 229–242.
- BRECKMAN, S. J. & CORBETT, S. C. (2005). Extent of anadromy in bull trout and implications for conservation of a threatened species. *North American Journal of Fisheries Management* **25**, 1073–1081.
- BROCKMAN, H. J. & TABORSKY, M. (2008). Alternative reproductive tactics and the evolution of alternative allocation phenotypes. In *Alternative Reproductive Tactics: An Integrative Approach* (eds R. F. OLIVEIRA, M. TABORSKY and H. J. BROCKMAN), pp. 25–51. Cambridge University Press, Cambridge.
- BRODERSEN, J., NILSSON, P. A., HANSSON, L. A., SKOV, C. & BRONMARK, C. (2008). Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology* **89**, 1195–1200.
- BURGNER, R. L. (1991). Life history of Sockeye salmon (*Oncorhynchus nerka*). In *Pacific Salmon Life Histories* (eds C. GROOT and L. MARGOLIS), pp. 1–118. UBC Press, Vancouver.
- BUSBY, P. J., WAINWRIGHT, T. C., BRYANT, G. J., LIERHEIMER, L. J., WAPLES, R. S., WAKNITZ, F. W. & LAGOMARSINO, I. V. (1996). Status review of west coast steelhead from Washington, Idaho, Oregon and California. NOAA Technical Memorandum NMFS-NWFSC-27.
- CARPENTER, R. E., WATT, M. J., FORSTER, G. L., ØVERLI, Ø., BOCKHOLT, C., RENNER, K. J. & SUMMERS, C. H. (2007). Corticotropin releasing factor induces anxiogenic locomotion in trout and alters serotonergic and dopaminergic activity. *Hormones and Behavior* **52**, 600–611.
- CASTRIC, V. & BERNATCHEZ, L. (2003). The rise and fall of isolation by distance in the anadromous brook charr (*Salvelinus fontinalis* Mitchell). *Genetics* **163**, 983–996.
- CHAPMAN, B. B., BRÖNNMARK, C., NILSSON, J.-Å. & HANSSON, L.-Å. (2011). The ecology and evolution of partial migration. *Oikos* **120**, 1764–1775.
- CHARLES, K., GUYOMARD, R., HOYHEIM, B., OMBREDANE, D. & BAGLINIÈRE, J.-L. (2005). Lack of genetic differentiation between anadromous and non-anadromous sympatric trout in a Normandy population. *Aquatic Living Resources* **18**, 65–69.
- CHARLES, K., ROUSSEL, J.-M., LEBEL, J.-M. & BAGLINIÈRE, J.-L. (2006). Genetic differentiation between anadromous and freshwater resident brown trout (*Salmo trutta* L.): insights obtained from stable isotope analysis. *Ecology of Freshwater Fish* **15**, 255–263.
- CHARNOV, E. (1993). Life-history invariants: some explorations of symmetry in evolutionary ecology. In *Ecology and Evolution*, 128p. Oxford University Press, Oxford.
- CHRISTIE, M. R., MARINE, M. L. & BLOUIN, M. S. (2011). Who are the missing parents? Grand-parentage analysis identifies multiple sources of gene flow into a wild population. *Molecular Ecology* **20**, 1263–1276.
- CLEMENTS, S. & SCHRECK, C. B. (2004). Central administration of corticotropin-releasing hormone alters downstream movement in an artificial stream in juvenile chinook salmon (*Oncorhynchus tshawytscha*). *General and Comparative Endocrinology* **137**, 1–8.
- CLUTTON-BROCK, T. (2009). Sexual selection in females. *Animal Behaviour* **77**, 3–11.
- CRAIG, J. K. & FOOTE, C. J. (2001). Countergradient variation and secondary sexual colour: phenotypic convergence promotes genetic divergence in carotenoid use between sympatric anadromous and nonanadromous morphs of Sockeye salmon (*Oncorhynchus nerka*). *Evolution* **55**, 380–391.
- CRAIG, J. K., FOOTE, C. J. & WOOD, C. C. (2005). Countergradient variation in carotenoid use between sympatric morphs of sockeye salmon (*Oncorhynchus nerka*) exposes non-anadromous hybrids in the wild by their mismatched spawning colour. *Biological Journal of the Linnean Society* **84**, 287–305.
- CUCHEROUSSET, J., OMBREDANE, D., CHARLES, K., MARCHAND, F. & BAGLINIÈRE, J.-L. (2005). A continuum of life history tactics in a brown trout (*Salmo trutta*) population. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 1600–1610.
- CURRY, R. A. (2005). Assessing the reproductive contribution of sympatric anadromous and freshwater-resident brook trout. *Journal of Fish Biology* **66**, 741–747.
- DAVERAT, F., LIMBURG, K., THIBAUT, I., SHIAO, J.-C., DODSON, J. J., CARON, F., TZENG, W.-N., IIZUKA, Y. & WICKSTÖM, H. (2006). Plasticity of habitat use in temperate eel species. *Marine Ecology Progress Series* **308**, 231–241.
- DELLEFORS, C. & FAREMO, U. (1988). Early sexual maturation in males of wild sea trout, *Salmo trutta* L., inhibits smoltification. *Journal of Fish Biology* **33**, 741–749.
- DICKHOFF, W. W., BECKMAN, B. R., LARSEN, D. A., DUAN, C. & MORIYAMA, S. (1997). The role of growth in endocrine regulation of salmon smoltification. *Fish Physiology and Biochemistry* **17**, 231–236.
- DODSON, J. J. (1997). Fish migration: an evolutionary perspective. In *Behavioral Ecology of Teleost Fishes* (ed. J.-G. GODIN), pp. 10–36. Oxford University Press, Oxford.
- DOUCETT, R. R., POWER, M., POWER, G., CARON, F. & REIST, J. D. (1999). Evidence for anadromy in a southern relic population of Arctic charr from North America. *Journal of Fish Biology* **55**, 84–93.
- ELLIOTT, J. M. (1994). *Quantitative Ecology and the Brown Trout*. Oxford University Press, New York.
- ELSON, P. F. (1957). The importance of size in the change from parr to smolt in Atlantic salmon. *Canadian Fish Culturist* **21**, 1–6.
- EMLEN, D. J. (2000). Integrating development with evolution: a case study with beetle horns. *BioScience* **50**, 403–418.
- EMLEN, D. J. (2008). The evolution of animal weapons. *Annual Review of Ecology and Systematics* **21**, 1227–1235.
- EMLEN, D. J. & NIJHOUT, H. F. (1999). Hormonal control of male horn length dimorphism in the horned beetle *Onthophagus taurus*. *Journal of Insect Physiology* **45**, 45–53.
- EMLEN, D. J. & NIJHOUT, H. F. (2000). The development and evolution of exaggerated morphologies in insects. *Annual Review of Entomology* **45**, 661–708.
- ENDLER, J. A. (1986). *Natural Selection in the Wild*. Princeton University Press, Princeton, NJ.
- ESSINGTON, T. E., SORESENSEN, P. W. & PARON, D. G. (1998). High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 2310–2316.
- ESTEVE, M. (2005). Observations of spawning behaviour in Salmoninae: *Salmo*, *Oncorhynchus* and *Salvelinus*. *Reviews in Fish Biology and Fisheries* **15**, 1–21.
- FALCONER, D. S. & MACKAY, T. F. C. (1996). *Quantitative Genetics*. Fourth Edition. Pearson Education Ltd, Essex.
- FINSTAD, A. G., BERG, O. K., FORSETH, T., UGEDAL, O., TOR, F. & NÆSJE, T. F. (2010). Adaptive winter survival strategies: defended energy levels in juvenile Atlantic salmon along a latitudinal gradient. *Proceedings of the Royal Society of London B* **277**, 1113–1120.
- FINSTAD, A. G. & JONSSON, B. (2012). Effect of incubation temperature on growth performance in Atlantic salmon. *Marine Ecology Progress Series* **454**, 75–82.
- FLEMING, I. & GROSS, M. R. (1994). Breeding competition in a Pacific salmon (Coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. *Evolution* **48**, 637–657.
- FOERSTER, R. E. & RICKER, W. E. (1953). The coho salmon of Cultus Lake and Switzer Creek. *Journal of the Fisheries Research Board of Canada* **10**, 293–319.
- FOOTE, C. J., BROWN, G. S. & HAWRYSHYN, C. W. (2004). Female colour and male choice in sockeye salmon: implications for the phenotypic convergence of anadromous and nonanadromous morphs. *Animal Behaviour* **67**, 69–83.
- FOOTE, C. J., BROWN, G. S. & WOOD, C. S. (1997). Spawning success of males using alternative tactics in sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1785–1795.
- FOOTE, C. J. & LARKIN, P. A. (1988). The role of male choice in the assortative mating of sockeye salmon and kokanee, the anadromous and nonanadromous forms of *Oncorhynchus nerka*. *Behaviour* **106**, 43–62.
- FORSETH, T., NÆSJE, T. F., JONSSON, B. & HARSAGER, K. (1999). Juvenile migration in brown trout: a consequence of energetic state. *Journal of Animal Ecology* **68**, 783–793.
- FRASER, D. J., WEIR, L. K., BERNATCHEZ, L., HANSEN, M. M. & TAYLOR, E. B. (2011). Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. *Heredity* **106**, 404–420.
- GARANT, D., DODSON, J. J. & BERNATCHEZ, L. (2003). Differential reproductive success and heritability of alternative reproductive tactics in wild Atlantic salmon. *Evolution* **57**, 1133–1141.
- GARCIA DE LEANIZ, C., FLEMING, I. A., EINUM, S., VERSPOOR, E., JORDAN, W. C., CONSUEGRA, S., AUBIN-HORTH, N., LAJUS, D., LETCHER, B. H., YOUNGSON, A. F., WEBB, J. H., VOLLESTAD, L. A., VILLANUEVA, B., FERGUSON, A. & QUINN, T. P. (2007). A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. *Biological Reviews* **82**, 173–211.

- GIGER, T., EXCOFFIER, L., DAY, P. J. R., CHAMPIGNELLE, A., HANSEN, M. M., POWELL, R. & LARGIADÈR, C. R. (2006). Life history shapes gene expression in salmonids. *Current Biology* **16**, R281–R282.
- GILMOUR, K. M., DIBATTISTA, J. D. & THOMAS, J. B. (2005). Physiological causes and consequences of social status in salmonid fish. *Integrated Comparative Biology* **45**, 263–73.
- GROSS, M. R. (1996). Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution* **11**, 92–98.
- GROSS, M. R., COLEMAN, R. M. & McDOWALL, R. M. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science* **239**, 1291–1293.
- GULSETH, O. A. & NILSSEN, K. J. (2001). Life-history traits of charr, *Salvelinus alpinus*, from a high Arctic watercourse on Svalbard. *Arctic* **54**, 1–11.
- GWO, J.-C., HSU, T.-H., LIN, K.-H. & CHOU, Y.-C. (2008). Genetic relationship among four subspecies of cherry salmon (*Oncorhynchus masou*) inferred using AFLP. *Molecular Phylogenetics and Evolution* **48**, 776–781.
- HARADA, M., YOSHINAGA, T., OJIMA, D. & IWATA, M. (2008). cDNA cloning and expression analysis of thyroid hormone receptor in the coho salmon *Oncorhynchus kisutch* during smoltification. *General and Comparative Endocrinology* **155**, 658–667.
- HEALEY, M. C. (1991). Life history of chinook salmon. In *Pacific Salmon Life Histories* (eds C. GROOT & L. MARGOLIS), pp. 311–394. UBC Press, Vancouver.
- HEATH, D. D., BETTLES, C. M., JAMIESON, S., STASIAK, I. & DOCKER, M. F. (2008). Genetic differentiation among sympatric migratory and resident life history forms of rainbow trout in British Columbia. *Transactions of the American Fisheries Society* **137**, 1268–1277.
- HEATH, D. D., DEVLIN, R. H., HEATH, J. W. & IWAMA, G. K. (1994). Genetic, environmental and interaction effects on the incidence of jacking in *Oncorhynchus tshawytscha* (chinook salmon). *Heredity* **72**, 146–154.
- HEATH, D. D., FOX, C. W. & HEATH, J. W. (1999). Maternal effects on offspring size: variation through early development of chinook salmon. *Evolution* **53**, 1605–1611.
- HEGGENES, J. & METCALFE, N. B. (1991). Bimodal size distributions in wild juvenile Atlantic salmon populations and their relationship with age at smolt migration. *Journal of Fish Biology* **39**, 905–907.
- HENDRY, A. P., BOHLIN, T., JONSSON, B. & BERG, O. K. (2004). To sea or not to sea? Anadromy versus non-anadromy in salmonids. In *Evolution Illuminated: Salmon and Their Relatives* (eds A. P. HENDRY & S. C. STEARNS), pp. 92–125. Oxford University Press, Oxford.
- HINDAR, K., JONSSON, B., RYMAN, N. & STAHL, G. (1991). Genetic relationships among landlocked, resident, and anadromous brown trout, *Salmo trutta* L. *Heredity* **66**, 83–91.
- HIRATA, T., GOTO, A. & YAMAZAKI, F. (1988). Individual growth and smoltification of juvenile masu salmon, *Oncorhynchus masou* Brevoort, under rearing conditions. *Journal of Fish Biology* **32**, 77–84.
- HOMEL, K., BUDY, P., PFENDER, M. E., WHITESEL, T. A. & MOCK, K. (2008). Evaluating genetic structure among resident and migratory forms of bull trout (*Salvelinus confluentus*) in Northeast Oregon. *Ecology of Freshwater Fish* **17**, 465–474.
- HUTCHINGS, J. A. (1986). Lakeward migration by juvenile Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 732–741.
- HUTCHINGS, J. A. & JONES, M. E. B. (1998). Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 22–47.
- HUTCHINGS, J. A. & MORRIS, D. W. (1985). The influence of phylogeny, size and behaviour on patterns of covariation in salmonid life histories. *Oikos* **45**, 118–124.
- HUTCHINGS, J. A. & MYERS, R. A. (1987). Escalation of an asymmetric contest: mortality resulting from mate competition in Atlantic salmon, *Salmo salar*. *Canadian Journal of Zoology* **65**, 766–768.
- HUTCHINGS, J. A. & MYERS, R. A. (1994). The evolution of alternative mating strategies in variable environments. *Evolutionary Ecology* **8**, 256–268.
- HUTCHISON, M. J. & IWATA, M. (1998). Effect of thyroxine on the decrease of aggressive behaviour of four salmonids during the parr-smolt transformation. *Aquaculture* **168**, 169–175.
- IWATA, M. (1995). Downstream migratory behavior of salmonids and its relationship with cortisol and thyroid hormones: a review. *Aquaculture* **135**, 131–139.
- JOHNSON, J. R., BAUMSTEIGER, J., ZYDLEWSKI, J., HUDSON, J. M. & ARDREN, W. (2010). Evidence of panmixia between sympatric life history forms of coastal cutthroat trout in two lower Columbia River tributaries. *North American Journal of Fisheries Management* **30**, 691–701.
- JONSSON, B., FORSETH, T., JENSEN, A. J. & NAESJE, T. F. (2001a). Thermal performance of juvenile Atlantic salmon *Salmo salar* L. *Functional Ecology* **15**, 701–711.
- JONSSON, B. & HINDAR, K. (1982). Reproductive strategy of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, Western Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1404–1413.
- JONSSON, B. & JONSSON, N. (1993). Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* **3**, 348–365.
- JONSSON, B. & JONSSON, N. (2006). Life history effects of migratory costs in anadromous brown trout. *Journal of Fish Biology* **69**, 860–869.
- JONSSON, B. & JONSSON, N. (2011). *Ecology of Atlantic Salmon and Brown Trout: Habitat As a Template for Life Histories, Fish & Fisheries Series, Volume 33*. Springer, New York.
- JONSSON, B., JONSSON, N., BRODTKORB, E. & INGEBRIGTSEN, P.-J. (2001b). Life-history traits of brown trout vary with the size of small streams. *Functional Ecology* **15**, 310–317.
- KAERIYAMA, M. & UEDA, H. (1998). Life history strategy and migration pattern of juvenile sockeye (*O. nerka*) and chum salmon (*O. keta*) in Japan: a review. *North Pacific Anadromous Fish Commission Bulletin* **1**, 163–171.
- KATO, F. (1991). Life histories of Masu and Amago salmon (*Oncorhynchus masou* and *Oncorhynchus rhodurus*). In *Pacific Salmon Life Histories* (eds C. GROOT & L. MARGOLIS), pp. 447–520. UBC Press, Vancouver.
- KERR, L. A., SECOR, D. H. & PICCOLI, P. M. (2009). Partial migration of fishes as exemplified by the estuarine-dependent white perch. *Fisheries* **34**, 114–123.
- KITAMURA, T., KUME, M., TAKAHASHI, H. & GOTO, A. (2006). Juvenile bimodal length distribution and sea-run migration of the lower modal group in the Pacific Ocean form of three-spined stickleback. *Journal of Fish Biology* **69**, 1245–1250.
- KLEMETSEN, A., AMUNDSEN, P.-A., DEMPSON, J. B., JONSSON, B., JONSSON, N., O'CONNELL, M. F. & MORTENSEN, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* L.: a review of aspects of their life histories. *Ecology of Freshwater Fish* **12**, 1–59.
- KONDOLF, G. M. & WOLMAN, M. G. (1993). The sizes of salmonid spawning gravels. *Water Resources Research* **29**, 2275–2285.
- KOSTOW, K. (2003). Factors that influence evolutionarily significant unit boundaries and status assessment in a highly polymorphic species, *Oncorhynchus mykiss*, in the Columbia basin. Oregon Department of Fish and Wildlife Information Report #2003-04. Oregon Department of Fish and Wildlife, Fish Division, Portland.
- KRISTINSSON, J. B., SAUNDERS, R. L. & WIGGS, A. J. (1985). Growth dynamics during the development of bimodal length-frequency distribution in juvenile Atlantic salmon (*Salmo salar* L.). *Aquaculture* **45**, 1–20.
- KUCHARSKI, R., MALESZKA, J., FORET, S. & MALESZKA, R. (2008). Nutritional control of reproductive status in Honeybees via DNA methylation. *Science* **319**, 1827–1830.
- L'ABÉE-LUND, J. H., JONSSON, B., JENSEN, A. J., SAETTEM, L. M., HEGGBERGET, T. G., JOHNSEN, B. O. & NAESJE, T. F. (1989). Latitudinal variation in life-history characteristics of sea-run migrant brown trout *Salmo trutta*. *Journal of Animal Ecology* **58**, 525–542.
- LANDE, R. (1979). Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* **33**, 402–416.
- LANKFORD, T. E., BILLERBECK, J. M. & CONOVER, D. O. (2001). Evolution of intrinsic growth and energy acquisition rates II. Trade-offs with vulnerability to predation in *Menidia menidia*. *Evolution* **55**, 1873–1881.
- LENORMAND, S., DODSON, J. J. & MÉNARD, A. (2004). Seasonal and ontogenetic patterns in the migration of anadromous brook charr (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 54–67.
- LETCHER, B. H. & GRIES, G. (2003). Effects of life history variation on size and growth in stream-dwelling Atlantic salmon. *Journal of Fish Biology* **62**, 97–114.
- LETCHER, B. H. & TERRICK, T. D. (1998). Maturation of male age-0 Atlantic salmon following a massive, localized flood. *Journal of Fish Biology* **53**, 1243–1252.
- MAEKAWA, K. & NAKANO, S. (2002). Latitudinal trends in adult body size of Dolly Vardon, with special reference to the food availability hypothesis. *Population Ecology* **44**, 17–22.
- MARTYNIUK, C. J., PERRY, G. M. L., MOGAHADAM, M. M., FERGUSON, M. M. & DANZMANN, R. G. (2003). The genetic architecture of correlations among growth-related traits and male age at maturation in rainbow trout. *Journal of Fish Biology* **63**, 746–764.
- MCCLEAVE, J. D. & EDELINE, E. (2009). Diadromy as a conditional strategy: patterns and drivers of eel movements in continental habitats. In *Challenges for Diadromous Fishes in a Dynamic Global Environment* (eds A. J. HARO, K. L. SMITH, R. A. RULIFSON, C. M. MOFFITT, R. J. KLAUDA, M. J. DADSWELL, R. A. CUNJAK, J. E. COOPER, K. L. BEAL & T. S. AVERY), pp. 97–120. American Fisheries Society, Symposium 69, Bethesda.
- MCCORMICK, S. D. (1996). Effects of growth hormone and insulin-like growth factor I on salinity tolerance and gill Na⁺, K⁺-ATPase in Atlantic salmon (*Salmo salar*): interaction with cortisol. *General and Comparative Endocrinology* **101**, 3–11.
- MCCORMICK, S. D. (2009). Evolution of the hormonal control of animal performance: insights from the seaward migration of salmon. *Integrative and Comparative Biology* **49**, 408–422.
- MCCORMICK, S. D. & NAIMAN, R. J. (1984). Some determinants of maturation in brook trout, *Salvelinus fontinalis*. *Aquaculture* **43**, 269–278.
- MCCORMICK, S. D., SHRIMPTON, J. M., MORIYAMA, S. & BJÖRNSSON, B. T. (2007). Differential hormonal responses of Atlantic salmon parr and smolt to increased daylength: a possible developmental basis for smolting. *Aquaculture* **273**, 337–344.
- MCPHAIL, J. D. & BAXTER, J. S. (1996). A review of Bull Trout (*Salvelinus confluentus*) life-history and habitat use in relation to compensation and improvement opportunities. Fisheries Management Report No. 104. Department of Zoology, University of British Columbia, Vancouver.
- MCPHEE, M. V., UTTER, F., STANFORD, J. A., KUZISHCHIN, K. V., SAVVAITOVA, K. A., PAVLOV, D. S. & ALLENDORF, F. W. (2007). Population structure and partial anadromy in *Oncorhynchus mykiss* from Kamchatka: relevance for conservation strategies around the Pacific Rim. *Ecology of Freshwater Fish* **16**, 539–547.

- METCALFE, N. B. (1998). The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 93–103.
- METCALFE, N. B. & THORPE, J. E. (1990). Determinants of geographical variation in the age of seaward migrating salmon *Salmo salar*. *Journal of Animal Ecology* **59**, 135–145.
- MOGEN, J. T. & KAEDING, L. R. (2005). Identification and characterisation of migratory and non-migratory bull trout populations in the St. Mary R. drainage, Montana. *Transactions of the American Fisheries Society* **134**, 841–852.
- MORÁN, P. & PÉREZ-FIGUEROA, A. (2011). Methylation changes associated with early maturation stages in the Atlantic salmon. *BMC Genetics* **12**, 86.
- MORBAY, Y. E. & HENDRY, A. P. (2008). Adaptation of salmonids to spawning habitats. In *Salmonid Spawning Habitat in Rivers: Physical Controls, Biological Responses, and Approaches to Remediation* (eds D. A. SEAR & P. DEVRIS), pp. 15–36. American Fisheries Society, Bethesda, MD Symposium 65.
- MORBAY, Y. E. & YDENBURG, R. C. (2003). Timing games in the reproductive phenology of female Pacific salmon (*Oncorhynchus* spp.). *American Naturalist* **161**, 284–298.
- MORINVILLE, G. R. & RASMUSSEN, J. B. (2003). Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 401–410.
- MORITA, K. & NAGASAWA, T. (2009). Latitudinal variation in the growth and variation of masu salmon (*Oncorhynchus masu*) parr. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 955–965.
- MORITA, K., TSUBI, J. & NAGASAWA, T. (2009). Plasticity in probabilistic reaction norms for maturation in a salmonid fish. *Biology Letters* **5**, 628–631.
- MYERS, R. A. (1984). Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 1349–1353.
- NAKANO, S., KITANO, F. & MAEKAWA, K. (1996). Potential fragmentation and loss of the thermal habitats for charrs in the Japanese archipelago due to climatic warming. *Freshwater Biology* **36**, 711–722.
- NARUM, S. R., CONTOR, C., TALBOT, A. & POWELL, M. S. (2004). Genetic divergence of sympatric resident and anadromous forms of *Oncorhynchus mykiss* in the Walla Walla River, USA. *Journal of Fish Biology* **65**(2), 471–488.
- NARUM, S. R., ZENDT, J. S., GRAVES, D. & SHARP, W. R. (2008). Influence of landscape on resident and anadromous life history types of *Oncorhynchus mykiss*. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 1013–1023.
- NICHOLS, K. M., EDO, A. F., WHEELER, P. A. & THORGAARD, G. H. (2008). The genetic basis of smoltification-related traits in *Oncorhynchus mykiss*. *Genetics* **179**, 1559–1575.
- NICIEZA, A. G., REIRIZ, L. & BRAÑA, F. (1994a). Variation in digestive performance between geographically disjunct populations of Atlantic salmon: countergradient in passage time and digestion rate. *Oecologia* **99**, 243–251.
- NICIEZA, A. G., REYES-GAVILÁN, F. G. & BRAÑA, F. (1994b). Differentiation in juvenile growth and bimodality patterns between northern and southern populations of Atlantic salmon (*Salmo salar* L.). *Canadian Journal of Zoology* **72**, 1603–1610.
- NIJHOUT, H. F. (1999). Control mechanisms of polyphenic development in insects. *Bioscience* **49**, 181–192.
- NORDENG, H. (1983). Solution to the “char problem” based on Arctic char (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 1372–1387.
- OJIMA, D. & IWATA, M. (2010). Central administration of growth hormone-releasing hormone and corticotropin-releasing hormone stimulate downstream movement and thyroxine secretion in fall-smolting coho salmon (*Oncorhynchus kisutch*). *General and Comparative Endocrinology* **168**, 82–87.
- ØKLAND, F., JONSSON, B., JENSEN, A. J. & HANSEN, L. P. (1993). Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon. *Journal of Fish Biology* **42**, 541–550.
- OLSEN, J. B., WUTTIG, K., FLEMING, D., KRETSCHMER, E. J. & WENBURG, J. K. (2006). Evidence of partial anadromy and resident-form dispersal bias on a fine scale in populations of *Oncorhynchus mykiss*. *Conservation Genetics* **7**, 613–619.
- OLSSON, I. C., GREENBURG, L. A., BERGMAN, E. & WYSUJACK, K. (2006). Environmentally induced migration: the importance of food. *Ecology Letters* **9**, 645–651.
- OOSTRA, V., DE JONG, M. A., INVERGO, B. M., KESBEKE, F., WENDE, F., BRAKEFIELD, P. M. & ZWAAN, B. J. (2011). Translating environmental gradients into discontinuous reaction norms via hormone signaling in a polyphenic butterfly. *Proceedings of the Royal Society of London B* **278**, 789–797.
- ORLAY, W., JOHNSON, O. W., RUCKELSHAUS, M. H., GRANT, W. S., WAKNITZ, F. W., GARRETT, A. M., BRYANT, G. J., NEELY, K. & HARD, J. J. (1999). Status review of coastal cutthroat trout from Washington, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-37.
- PÁEZ, D. J., BERNATCHEZ, L. & DODSON, J. J. (2011a). The genetic basis of alternative life-histories in the Atlantic salmon I. The evolutionary potential of the sneaker reproductive tactic in males. *Proceedings of the Royal Society of London B* **278**, 2150–2158.
- PÁEZ, D. J., BRISSON-BONENFANT, C., ROSSIGNOL, O., GUDERLEY, H. E., BERNATCHEZ, L. & DODSON, J. J. (2011b). Alternative developmental pathways and the propensity to migrate: a case study in the Atlantic salmon. *Journal of Evolutionary Biology* **24**, 245–255.
- PÁEZ, D. J., MORRISSEY, M., BERNATCHEZ, L. & DODSON, J. J. (2010). The genetic basis of early-life morphological traits and their relation to alternative male reproductive tactics in Atlantic salmon. *Journal of Evolutionary Biology* **23**, 757–768.
- PÁLSSON, O. K. & THORSTEINSSON, V. (2003). Migration patterns, ambient temperature, and growth of Icelandic cod (*Gadus morhua*): evidence from storage tag data. *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 1409–1423.
- PASCUAL, M. A., BENTZEN, P., RIVA ROSSI, C. M., MACKAY, G., KINNISON, M. & WALKER, R. (2001). First documented case of anadromy in a population of introduced rainbow trout in Patagonia, Argentina. *Transactions of the American Fisheries Society* **130**, 53–67.
- PEARSE, D. E., HAYES, S. A., BOND, M. H., HANSON, C. V., ANDERSON, E. C., MACFARLANE, R. B. & GARZA, J. C. (2009). Over the falls? Rapid evolution of ecotypic differentiation in steelhead/ rainbow trout (*Oncorhynchus mykiss*). *Journal of Heredity* **100**(100), 515–525.
- PEARSONS, T. N., JOHNSON, C. L., JAMES, B. B. & TEMPLE, G. M. (2009). Abundance and distribution of precociously mature male spring Chinook salmon of hatchery and natural origin in the Yakima River. *North American Journal of Fisheries Management* **29**, 778–790.
- PERRY, G. M. L., TARTE, P., CROISETIERE, S., BELHUMEUR, P. & BERNATCHEZ, L. (2004). Genetic variance and covariance for 0+ brook charr (*Salvelinus fontinalis*) weight and survival time of furunculosis (*Aeromonas salmonicida*) exposure. *Aquaculture* **235**, 263–271.
- PICHÉ, J., HUTCHINGS, J. A. & BLANCHARD, W. (2008). Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*. *Proceedings of the Royal Society of London B* **275**, 1571–1575.
- POWER, G. (1980). The brook charr, *Salvelinus fontinalis*. In *Charrs, Salmonid Fishes of the Genus Salvelinus* (ed. E. K. BALON), pp. 141–203. Dr W. Junk Publishers, The Hague.
- POWER, G. (1981). Stock characteristics and catches of Atlantic salmon (*Salmo salar*) in Quebec, and Newfoundland and Labrador in relation to environmental variables. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1601–1611.
- PULIDO, F. (2011). Evolutionary genetics of partial migration – the threshold model of migration revisited. *Oikos* **120**, 1776–1783.
- PULIDO, F., BERTHOLD, P. & VAN NOORDWIJK, A. J. (1996). Frequency of migrants and migratory activity are genetically correlated in a bird population: evolutionary implications. *Proceedings of the National Academy of Sciences of the United States of America* **93**, 14642–14647.
- QUINN, T. P. (2005). *The Behaviour and Ecology of Pacific Salmon and Trout*. University of Washington Press, Seattle.
- QUINN, T. P., KINNISON, M. T. & UNWIN, M. J. (2001). Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* **112–113**, 493–513.
- REFSTIE, T., STEINE, T. A. & GJERDREM, T. (1977). Selection experiments with salmon. II. Proportion of Atlantic salmon smoltifying at 1 year of age. *Aquaculture* **10**, 231–242.
- REID, D. P., SZANTO, A., GLEBE, B. D., DANZMANN, R. G. & FERGUSON, M. M. (2005). QTL for body weight and condition factor in Atlantic salmon (*Salmo salar*): comparative analysis with rainbow trout (*Oncorhynchus mykiss*) and Arctic charr (*Salvelinus alpinus*). *Heredity* **94**, 166–172.
- RICE, S. & CHURCH, M. (1998). Grain size along two gravel-bed rivers: statistical variation, spatial pattern and sedimentary links. *Earth Surface Processes and Landforms* **23**, 345–363.
- RIKARDSEN, A. H. & ELLIOTT, J. M. (2000). Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in North Norway. *Journal of Fish Biology* **56**, 328–346.
- ROFF, D. A. (1996). The evolution of threshold traits in animals. *Quarterly Review of Biology* **71**, 3–35.
- ROFF, D. A. (1997). *Evolutionary Quantitative Genetics*. Chapman & Hall, New York.
- ROFF, D. A. & FAIRBAIRN, D. J. (2007). The evolution and genetics of migration in insects. *Bioscience* **57**, 155–164.
- ROSSIGNOL, O., DODSON, J. J. & GUDERLEY, H. (2011). Relationship between metabolism, sex and reproductive tactics in young Atlantic salmon. *Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology* **159**, 82–91.
- ROWE, D. K. & THORPE, J. E. (1990). Differences in growth between maturing and non-maturing male Atlantic salmon *Salmo salar* L. parr. *Journal of Fish Biology* **36**, 643–658.
- ROWE, D. K., THORPE, J. E. & SHANKS, A. M. (1991). Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 405–413.
- SANDERCOCK, F. K. (1991). Life-history of coho salmon. In *Pacific Salmon Life Histories* (eds C. GROOT & L. MARGOLIS), pp. 395–446. UBC Press, Vancouver.
- SHUSTER, S. M. & WADE, M. J. (1991). Equal mating success among male reproductive strategies in a marine isopod. *Nature* **350**, 606–610.
- SHUSTER, S. M. & WADE, M. J. (2003). *Mating Systems and Strategies*. Princeton University Press, Princeton.

- SEEAR, P. J., CARMICHAEL, S. N., TALBOT, R., TAGGART, J. B., BRON, J. E. & SWEENEY, G. E. (2010). Differential gene expression during smoltification of Atlantic salmon (*Salmo salar* L.): a first large-scale microarray study. *Marine Biotechnology* **12**, 126–140.
- SHAW, A. K. & LEVIN, S. A. (2011). To breed or not to breed: a model of partial migration. *Oikos* **120**, 1871–1879.
- SKILBREI, O. T. (1991). Importance of threshold length and photoperiod for the development of bimodal length-frequency distribution in Atlantic Salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 2163–2172.
- SKILBREI, O. T. & HEINO, M. (2011). Reduced daylength stimulates size-dependent precocious maturity in 0+ male Atlantic salmon parr. *Aquaculture* **311**, 168–174.
- SNELL-ROOD, E. C., CASH, A., HAN, M. V., KIJIMOTO, T., ANDREWS, J. & MOCZEK, A. P. (2010). Developmental decoupling of alternative phenotypes: insights from the transcriptomes of horn-polyphenic beetles. *Evolution* **65**, 231–245.
- SPECKER, J. L., EALES, J. G., TAGAWA, M. & TYLER, W. A. I. I. (2000). Parr-smolt transformation in Atlantic salmon: thyroid hormone deiodination in liver and brain and endocrine correlates of change in rheotactic behavior. *Canadian Journal of Zoology* **78**, 696–705.
- STEWART, D. C., MIDDLEMAS, S. J. & YOUNGSON, A. F. (2006). Population structuring in Atlantic salmon (*Salmo salar*): evidence of genetic influence on the timing of smolt migration in sub-catchment stocks. *Ecology of Freshwater Fish* **15**, 552–558.
- TABORSKY, M. (2008). Alternative reproductive tactics in fish. In *Alternative Reproductive Tactics: An Integrative Approach* (eds R. F. OLIVEIRA, M. TABORSKY and H. J. BROCKMAN), pp. 251–299. Cambridge University Press, Cambridge.
- THÉRIAULT, V. & DODSON, J. J. (2003). The role of size in determining anadromy or residency in brook charr (*Salvelinus fontinalis*). *Journal of Fish Biology* **63**, 1–16.
- THÉRIAULT, V., DUNLOP, E., DIECKMAN, U., BERNATCHEZ, L. & DODSON, J. J. (2008). The impact of fishing-induced mortality on the evolution of alternative life-history tactics in brook charr. *Evolutionary Applications* **1**, 409–423.
- THÉRIAULT, V., GARANT, D., BERNATCHEZ, L. & DODSON, J. J. (2007). Heritability of life history tactics and genetic correlation with body size in a natural population of brook charr (*Salvelinus fontinalis*). *Journal of Evolutionary Biology* **20**, 2266–2277.
- THÉRIAULT, V., MOYER, G. R. & BANKS, M. A. (2010). Survival and life history characteristics among wild and hatchery coho salmon (*Oncorhynchus kisutch*) returns: how do unfed fry differ from smolt releases? *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 486–497.
- THORPE, J. E. (1977). Bimodal distribution of length of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. *Journal of Fish Biology* **11**, 175–184.
- THORPE, J. E., ADAMS, C. E., MILES, M. S. & KEAY, D. S. (1989). Some influences of photoperiod and temperature on opportunity for growth in juvenile Atlantic salmon, *Salmo salar* L. *Aquaculture* **82**, 119–126.
- THORPE, J. E., MANGEL, M., METCALFE, N. B. & HUNTINGFORD, F. A. (1998). Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology* **12**, 581–599.
- THORPE, J. E. & MORGAN, R. I. G. (1980). Growth-rate and smolting-rate of progeny of male Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology* **17**, 451–459.
- TITUS, R. G. & MOSEGAARD, H. (1992). Fluctuating recruitment and variable life history of migratory brown trout, *Salmo trutta* L., in a small, unstable stream. *Journal of Fish Biology* **41**, 239–255.
- TOMKINS, J. L. & HAZEL, W. (2007). The status of the conditional evolutionarily stable strategy. *Trends in Ecology and Evolution* **22**, 522–528.
- TROTTER, P. C. (1989). Coastal Cutthroat Trout: a life-history compendium. *Transactions of the American Fisheries Society* **118**, 463–473.
- TSIGER, V. V., SKIRIN, V. B., KRUPYANKO, N. I., MASHKIN, M. A. & SEMENCHENKO, A. Y. (1994). Life history forms of male masu salmon (*Oncorhynchus masou*) in South Primor'e, Russia. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 197–288.
- TSUKAMOTO, K., MILLER, M. J., KOTAKE, A., AOYAMA, J. & UCHIDA, K. (2009). The origin of fish migration: the random escapement hypothesis. In *Challenges for Diadromous Fishes in a Dynamic Global Environment* (eds A. J. HARO, K. L. SMITH, R. A. RULIFSON, C. M. MOFFITT, R. J. KLAUDA, M. J. DADSWELL, R. A. CUNJAK, J. E. COOPER, K. L. BEAL and T. S. AVERY), pp. 45–62. American Fisheries Society, Symposium 69, Bethesda.
- UTRILLA, C. G. & LOBON-CERVIA, J. (1999). Life-history patterns in a southern population of Atlantic salmon. *Journal of Fish Biology* **55**, 68–83.
- VUORINEN, J. & BERG, O. K. (1989). Genetic divergence of anadromous and non-anadromous Atlantic salmon (*Salmo salar*) in the River Namsen, Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 406–409.
- WEST-EBERHARD, M. J. (2003). *Developmental Plasticity and Evolution*. Oxford University Press, New York.
- WOOD, C. C., BICKHAM, J. W., NELSON, R. J., FOOTE, C. J. & PATTON, J. C. (2008). Recurrent evolution of life history ecotypes in sockeye salmon: implications for conservation and future evolution. *Evolutionary Applications* **1**, 207–221.
- WOOD, C. C. & FOOTE, C. J. (1996). Evidence for sympatric genetic divergence of anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). *Evolution* **50**, 1265–1279.
- WOOD, C. C., FOOTE, C. J. & RUTHERFORD, D. T. (1999). Ecological interactions between juveniles of reproductively isolated anadromous and non-anadromous morphs of sockeye salmon *Oncorhynchus nerka*, sharing the same nursery lake. *Environmental Biology of Fishes* **54**, 161–173.
- WYSUJACK, K., GREENBERG, L. A., BERGMAN, E. & OLSSON, I. C. (2009). The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. *Ecology of Freshwater Fish* **18**, 52–59.
- YAMAMOTO, S. & MORITA, K. (2002). Interpopulation comparison of size and age at smolting of white-spotted charr, *Salvelinus leucomaenis*. *Ecology of Freshwater Fish* **11**, 281–284.
- YAMAMOTO, S., MORITA, K. & GOTO, A. (1999). Geographic variations in life-history characteristics of white-spotted charr (*Salvelinus leucomaenis*). *Canadian Journal of Zoology* **77**, 871–878.
- YAMAMOTO, S., MORITA, K., KOIZUMI, I. & MAEKAWA, K. (2004). Genetic differentiation of white-spotted charr (*Salvelinus leucomaenis*) populations after habitat fragmentation: spatial–temporal changes in gene frequencies. *Conservation Genetics* **5**, 529–538.
- YAMAMOTO, S. & NAKANO, S. (1996). Growth and development of a bimodal length-frequency distribution during smolting in a wild population of white-spotted charr in northern Japan. *Journal of Fish Biology* **48**, 68–79.
- ZERA, A. J. (2003). The endocrine regulation of wing polymorphism in insects: state of the art, recent surprises, and future directions. *Integrated Comparative Biology* **43**, 607–616.
- ZIMMERMAN, C. & REEVES, G. (2002). Identification of steelhead and resident rainbow trout progeny in the Deschutes River, Oregon, revealed with otolith microchemistry. *Transactions of the American Fisheries Society* **131**, 986–993.

X. APPENDIX 1: TERMINOLOGICAL CLARIFICATION OF THRESHOLD TRAITS, MECHANISMS AND VALUES

A threshold trait is a phenotypic trait that appears in a limited number of discrete states. A threshold trait is genetically determined by the additive effects of numerous genes rather than by the action of one or few genes. To understand the occurrence of threshold traits, the threshold model of quantitative genetics assumes the existence of an underlying trait, the liability, that is normally distributed and under polygenic control. In this model, categorical phenotypes occur because individuals with large values of the liability exceed a threshold value, producing one phenotype, whereas individuals that do not exceed the threshold value produce the alternative phenotype. The liability may be composite in nature, integrating the effects of all the traits that influence the expression of the categorical phenotypes (Roff, 1997).

A general characteristic underlying the expression of alternative phenotypes is the occurrence of a threshold mechanism responsible for signalling alternative developmental pathways. Such a switching mechanism is a process that sets a specific developmental course (which may be fixed or reversible throughout the life cycle). Such threshold mechanisms may be visualised as an electrical switch composed of a contact that can be connected to either of two other contacts leading to either of two pathways. There is no default setting, as development must continue along either one or the other pathway.

Threshold mechanisms are not strictly equivalent to the definition of threshold values used in current models of alternative phenotypes. Threshold values are interpreted as the value of the liability trait (or rather its proxy) at which individuals found below and above it develop alternative phenotypes. Therefore, the threshold value delimits the proportion of individuals displaying alternative phenotypes

in the population (Roff, 1996; Tomkins & Hazel, 2007). Its position depends on the observed incidences of alternative phenotypes. For example, in salmonids, logistic regression techniques are often used to express the threshold body size which best discriminates alternative life histories (e.g. Aubin-Horth *et al.*, 2005; Piché *et al.*, 2008; Páez *et al.*, 2011*b*). However, the calculation of the threshold value using these techniques depends entirely on the observed incidences of alternative phenotypes as the threshold value of the “trait” is calculated by solving the logistic equation.

$$\text{logit}(p_i) = \beta_0 + \beta_1 \cdot l_i. \quad (\text{A1})$$

Here, p_i is the probability of the alternative tactic i with body length l_i (which is the proxy for the liability trait), β_0 and β_1 are the intercept and slope of this linear model. Thus, calculation of the threshold body size [$\text{logit}(p_i) = 0$] is given by:

$$\text{Threshold} = -\beta_0/\beta_1. \quad (\text{A2})$$

Threshold body size is often equated with an incidence of 50% (e.g. Piché *et al.*, 2008). Examination of the relationship between the threshold values and the incidence of a phenotype shows that when the liability positively affects the incidence of a phenotype (e.g. larger body size favours migration), the higher the incidence of migrants, the smaller the calculated threshold value (G. Daigle, personal communication). Threshold values inferred from logistic regression analyses are thus simply a mathematical function of the relative frequencies of alternative phenotypes observed at some point in time. Threshold values of the liability trait that are inferred from the frequency of individuals adopting alternative phenotypes may be well ‘downstream’ in a developmental sense of the threshold mechanism activating different developmental pathways.

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