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Anadromy in brown trout (*Salmo trutta*): A review of the relative roles of genes and environmental factors and the implications for management and conservation.

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ABSTRACT

While many brown trout (*Salmo trutta*) populations spend their entire life cycle in freshwater, especially as river-lake migrants or river residents, others show facultative anadromy. That is, some trout migrate to sea while other individuals of the same population remain within their natal river. Sea trout can give rise to resident offspring and *vice versa*, although there is a strong tendency to track the parental life history. Anadromy delivers better feeding and thus larger size, which results in higher fecundity in females, enhanced mate choice, and other reproductive benefits. River residence, more prevalent in males as anadromy conveys fewer benefits, can give higher survival and avoids the energy expenditure required by anadromy. Overall, the costs and benefits of anadromy versus residency, measured in terms of survival and reproduction, are finely balanced and small changes to the cost-benefit equation can lead to evolutionary changes in life history. The decision to be anadromous or resident is a quantitative threshold trait, controlled by multiple genes and environmental factors. The dichotomous nature of the trait is postulated to be the result of the

environmentally influenced physiological condition (e.g. energy status) relative to a genetically determined threshold. Anadromy ensues when an individual's condition fails to meet the threshold level, which varies between sexes and among individuals and populations. Environmental factors and genetic architecture may also directly influence life history, e.g., by altering gene expression. A strong genetic influence on the anadromy decision means that facultative anadromy can be altered by natural selection driven by changes such as differential exploitation, stocking with farm-reared brown trout, partial barriers to migration, and changes in climate, and freshwater and marine productivity, together with parasite, pathogen and predator abundance resulting in reduced marine survival and growth. Further studies of the factors determining life history choice, together with multiple population estimates of heritability and differential reproductive success (fitness), are required to understand fully the impact of natural and anthropogenic environmental changes on sea trout dynamics.

NOMENCLATURE

While many valid species names have been designated for distinct trout lineages and morphotypes (e.g. Ferguson, 2004; Kottelat & Freyhof, 2007), brown trout and *Salmo trutta* L. are still widely used as common and scientific species names for the native trout of Europe, western Asia and north Africa, and include both sea and freshwater life histories. However, it is common practice among anglers and managers to use the term brown trout only for non-anadromous trout, although it will be used here in the species context. Within brown trout, there are various alternative life histories in respect of migration, reproduction and feeding (Frost & Brown, 1967; Elliott, 1994; Klemetsen *et al.*, 2003). In formerly glaciated regions in NW Europe many populations have abandoned the anadromy of their postglacial colonist ancestors and have adopted a freshwater migratory or resident life history, including river-lake migration (adfluvial potamodromy), extensive migrations within rivers (fluvial potamodromy), river resident, and lake resident (Ferguson, 2006). Thus sea trout, where trout migrate to sea to feed before returning to their natal river to breed (anadromy), is just one extreme of a continuum of life histories, with some individuals pursuing more than one option within their lifetime. Many authors use the term 'freshwater resident' in the sense of river resident, while some incorrectly use it to include all freshwater forms including migratory ones, in spite of the fact that the dictionary definition of resident is "an animal that does not migrate". Because of this ambiguity, the term should not be used but river resident or lake resident specified as appropriate to account for important evolutionary differences in brown trout life history variation. Use of the general term 'migratory' has also led to some confusion with studies involving adfluvial migrants being incorrectly cited by others as referring to anadromy. Where there is likely to be confusion, the term 'migratory' should be qualified as above.

A major physiological difference between freshwater migration and anadromy is the changes required due to the different ionic strengths and osmolality experienced by sea trout. The distinction breaks down further in areas such as the Baltic Sea where salinity is around 0.1-0.2% in the far north and east compared to more than 3% in oceanic sea water (Encyclopedia of Earth). In the Baltic, fry and 0+ parr can migrate to the sea (Landergren, 2001) and spawning can occur in this brackish water (Landergren & Vallin, 1998). Similarly in the Burrishoole system (Western Ireland) parr migrate to the brackish Lough Furnace and appear to remain there, or in the estuary, before returning to freshwater as un-silvered trout (Poole *et al.*, 2006).

Adfluvial migration is probably similar in benefits to anadromy (see below) but lowers the relative costs. In regions such as Ireland and Scotland, with numerous freshwater lakes, an adfluvial life history for brown trout is estimated to be numerically the most common one, based on the relative abundance of such populations. Migration to lakes can occur where there is no barrier to anadromy and in many cases both adfluvial and anadromous life histories are present in the same catchment, with the adfluvial form often predominating (e.g. Poole *et al*., 2006). In Loch Lomond (Scotland), a large freshwater lake, carbon stable-isotope analysis showed that individual brown trout appear to repeatedly move between the lake and estuarine / marine environments (Etheridge *et al*., 2008), which concurs with angling reports of non-breeding sea trout of various sea ages in the lake (Balmaha Anglers). In this case there is only a short river (ca. 10 km) separating the loch and the River Clyde estuary. For rainbow trout (*Oncorhynchus mykiss* (Walbaum)), anadromy is also less common in river systems with large lakes (Kendall *et al*., 2015). Holecek & Scarnecchia (2013) regarded the switch in a rainbow trout population to an adfluvial life history as "exercising the next best option" when anadromy was prevented by dam construction.

Although a simple dichotomy between sea trout and freshwater trout belies the large temporal and spatial diversity of life history patterns in brown trout (Cucherousset *et al*., 2005), it does reflect the emphasis of many studies relevant to sea trout. Thus, this review concentrates on the factors responsible specifically for adopting an anadromous life history and mainly considers only the two extremes of sea trout, and trout which spend their entire life within their natal region of a river (river resident, hereafter simply 'resident'). Due to the limited studies on the genetics of anadromy in brown trout, this review draws from work on other species in the *Salmoninae* sub-family (salmonines), especially rainbow trout, where again the species name is often used to denote freshwater life histories and steelhead its anadromous form.

BACKGROUND BIOLOGY

This section does not attempt to provide a complete overview of sea trout biology but rather to deal only with those aspects relevant to discussions below. A more detailed review is given by Thorstad *et al*., (2016). Sea trout are found in western Europe from the River Miño (Caballero *et al*., 2013), which forms the northern border between Portugal and Spain, northwards to Scandinavia and the Cheshkaya Gulf in NW Russia, including Iceland and the Baltic Sea (Klemetsen *et al*., 2003), although natural stocks in Finnish rivers have largely

been lost (Kallio-Nyberg *et al*., 2010). Within this range sea trout biology varies considerably. Migration to sea as smolts varies from age 1+ in the southern part of the range to 9+ in the north with most smolts being 2+ and 3+ over large parts of the distribution area (Jonsson & L'Abée-Lund, 1993; Jonsson *et al*., 2001). The period spent at sea ranges from a few weeks (finnock) to eight years, with average sea residence times generally decreasing with increasing latitude (L'Abee-Lund *et al*., 1989). In Norway, where lakes are present in a catchment, overwintering by both post-spawning and immature sea trout is generally in freshwater (Klemetsen *et al*., 2003) although in small rivers with poor wintering conditions both juvenile and mature sea trout can feed at sea during the winter (Knutsen *et al*., 2004; Jensen & Rikardsen, 2012). Overwintering can occur in rivers other than the natal one and brown trout have been recorded wintering up to four times elsewhere before returning to the natal one for reproduction (Jensen *et al*., 2015). Where the winter is spent in freshwater, the seasonal migration to sea can be repeated annually (Jonsson, 1985; Elliott, 1994; Klemetsen *et al*., 2003) although former sea trout can subsequently adopt a freshwater life history, a phenomenon also known in rainbow trout (Null *et al*., 2013). In Dolly Varden (*Salvelinus malma* (Walbaum)) older, larger individuals cease to migrate (Bond *et al*., 2015). It is increasingly recognised that sea trout can spend a minority of their life at sea with the rest spent in lakes or rivers. Hodge *et al*., (2016) identified 38 life history categories at maturity in rainbow trout, these involving different combinations in patterns of movement between freshwater and the sea, age of maturity, and occurrence of repeat spawning.

Sea trout feed mainly in estuaries and coastal waters (Middlemas *et al*., 2009; Davidsen *et al*., 2014a) with most individuals in Norway staying within 100 km of the river mouth (Jonsson & Jonsson, 2005). However, tagged sea trout have crossed the North Sea from France to Scandinavia (Euzenat, 1999). It has been suggested that estuaries provide better feeding than rivers but with reduced likelihood of predation and reduced salinity compared to the open sea (Thorpe, 1994a), although fluctuating salinity may actually produce greater physiological stress than the higher, but more stable, salinity of sea water (Jensen & Rikardsen, 2012).

FACULTATIVE ANADROMY AND POPULATION STRUCTURING

In brown trout, there is a continuum from completely freshwater populations to completely anadromous ones (Jonsson & Jonsson, 2011). Many populations show facultative anadromy with some individuals migrating while other individuals remain resident within their natal river, sometimes referred to as 'partial migration' (Dellefors & Faremo, 1988; Jonsson & Jonsson, 1993), although 'partial' does not qualify the migration. Even for brown trout populations in close geographical proximity, the proportion of individuals showing anadromy can vary considerably (Jonsson & Jonsson, 2006a), which suggests that complex genetic and ecological factors influence the balance between anadromy and residency among populations (Kendall *et al*., 2015). Understanding the relative importance, and interplay, of the determinants of anadromy within facultatively anadromous populations is a fundamental requirement for their effective management. Increased life history diversity potentially decreases overall population fluctuations as a result of environmental changes, in an analogous fashion to the stabilising influence of asset diversification in a financial portfolio (Schindler *et al*., 2015).

Offspring of sea trout and resident brown trout may show different life histories from their parents (Jonsson, 1982). Courter *et al.,* (2013) also found that female resident rainbow trout produced anadromous offspring that survived and returned to spawn. However there is often a strong tendency to track the parental life history (Jonsson, 1982). Studies using molecular genetic markers, such as allozymes, microsatellites and mitochondrial DNA (mtDNA), have failed to detect any genetic differentiation between samples of sea and resident brown trout obtained from exactly the same area of a river rather than adjacent ones, i.e. truly sympatric rather than parapatric populations (Hindar *et al*., 1991; Cross *et al*., 1992; Charles *et al*., 2005, 2006). Similar studies in rainbow trout have also failed to identify differentiation (Docker & Heath, 2003). However, in the absence of a high level of reproductive isolation, such effectively neutral markers would not be expected to reveal differentiation (Ferguson, 1994). It should be emphasised strongly that this lack of detectable genetic differentiation between anadromous and resident salmonines based on such markers does not imply that there is not a genetic basis to anadromy because heritable traits segregate within families and lineages without requiring reproductive isolation.

The consensus from studies carried out to date is that anadromous and resident conspecific salmonines can freely interbreed, though the extent of reproductive isolation varies among species. Jonsson (1985) and Schreiber & Diefenbach (2005) noted female sea trout and

resident male brown trout at the same spawning grounds and suggested that the unequal sex ratio (see below) led to resident males breeding with anadromous females. Similarly for brook charr (*Salvelinus fontinalis* (Mitchill)), Thériault *et al*. (2007) found that interbreeding was due to resident males mating with both resident and anadromous females. The sneaking behaviour of these small males prevents any genetic differentiation that could arise due to size-assortative mating (Dodson *et al*., 2013).

There are a few examples of genetic differentiation between sympatric anadromous and resident rainbow trout (Zimmerman & Reeves, 2000; Docker & Heath, 2003). In the first case, the apparent differentiation of the two forms was associated with spatial and temporal segregation of spawning activities (Zimmerman & Reeves, 2000), as was the genetic differentiation between resident and anadromous brook charr (Boula *et al*., 2002). In another situation (Narum *et al*., 2004), where genetic divergence between sympatric steelhead and resident rainbow occurred in one tributary of a river system but not in another, the genetic differentiation appeared to have resulted from stocking with a genetically distinct steelhead stock. At the other end of the continuum, anadromous sockeye salmon (*O. nerka*) and the non-anadromous form, known as kokanee, display a combination of reproductive isolating mechanisms and selection against hybrids that commonly results in significant genetic differences between the forms even when they are sympatric, despite some interbreeding (Foote *et al*., 1989; Wood & Foote, 1996).

Typically where genetic differentiation is detected between predominantly anadromous and principally resident brown trout populations within rivers there is a complete or partial upstream barrier to sea trout migration (e.g. Skaala & Nævdal, 1989). However, such allopatric genetic differentiation is typical of brown trout populations (Ferguson, 1989) and may simply represent independent evolution rather than being correlated with life history. Where populations exist above falls there is clearly strong selection against migration, as such migrants are lost from the population, resulting in genetic differences in respect of life history determinants as well (Thrower *et al*., 2004; Thrower & Hard, 2009).

In a few cases significant genetic differentiation has been reported between parapatric/ allopatric populations of both brown trout and rainbow trout where no physical barrier to interbreeding occurs. In the Glenarrif River (NE Ireland) significant allozyme and mtDNA differences were found between sea trout and resident trout samples taken ca. 1 km apart in the river (Fleming, 1983; unpublished studies cited in Ferguson, 2006). The resident trout sample was taken immediately below an upstream impassable waterfall and was genetically more similar to samples from above the fall than to the downstream sea trout sample. It

seems, therefore, that this resident population was formed by displaced individuals from above the falls, and has remained distinct through spatial or other reproductive isolation. Similar situations have been found for rainbow trout in small Californian rivers where above waterfalls residents sometimes descend over the falls. These remain near the base of the falls and form populations that are reproductively isolated from the below falls stocks (Pearse *et al*., 2009; Hayes *et al*., 2012). Berejikian *et al*., (2013) found that below barriers the proportions of resident rainbow trout were greater in the upper reaches, suggesting that above-barrier populations may be contributing to these resident populations through ongoing migration. Hayes *et al*., (2012) and Wilzbach *et al*., (2012) detected movement to reaches of the stream below a waterfall by a small proportion of rainbow trout tagged above it, with some detected near the entrance to the sea. In the Wilzbach *et al*., (2012) study some tagged individuals were also released 5 km downstream of the falls and, while most remained within a few hundred metres of the release site, a few moved downstream.

WHY IS ANADROMY FACULTATIVE IN BROWN TROUT AND SOME OTHER SALMONINES?

BENEFITS OF ANADROMY

Anadromy potentially offers many benefits to individuals continuing with this postglacial ancestral life history, while at the same time these are countered by ensuing costs (Rounsefell, 1958; Gross, 1987; Quinn & Myers, 2004; Brönmark *et al*., 2014) (summarised in Table 1). Thus anadromous and resident life histories show compromises between survival to first reproduction and the size and age at reproduction. Migration to the sea, where in temperate regions productivity and thus food availability is higher than in freshwater (Gross *et al*., 1988), results in larger size, higher fecundity and greater energy stores at reproduction (Fleming & Reynolds, 2004; Jonsson & Jonsson, 2006a). However, it delays maturity and lowers the probability of surviving to reproduce. While sexual maturation and the choice of anadromous life history are closely interconnected, they are also conflicting strategies that need to be considered together (Thorpe, 1994b; Thorpe & Metcalfe, 1998; Sloat *et al*., 2014).

BENEFITS OF RESIDENCY

Switching from anadromy to residency conveys many benefits, which can also be seen as the costs of anadromy. These include less risk of predation during migration and in the marine environment. In Denmark, as a result of predation by fish and birds, smolt mortality during passage through lakes and reservoirs is substantially higher than in rivers (Jepsen *et al*., 1998). Weirs for water offtake can also cause substantial mortalities and, together with predation, are the crucial factors responsible for smolt mortality in Danish rivers (Rasmussen, 2006). Predators may be attracted to concentrations of migrating smolts and adults (Wood, 1987a, b; Greenstreet *et al*., 1993; Hendry *et al*., 2004). The number of trout predators appears to be higher at sea than in fresh water, including lakes (Jonsson & Jonsson, 2004) and predation is a major mortality factor shortly after the smolts reach the sea (Dieperink *et al*., 2002).

In addition, residency avoids the energetic costs associated with migration. Increased mortality may result from energy depletion during upstream migration especially if there are waterfalls or other barriers that cause delays (Hendry *et al*., 2004). Bohlin *et al*., (2001) found a negative correlation between altitude and the extent of anadromy in Swedish trout populations, suggesting that anadromy is less common in populations where migration involves greater energy expenditure (Wood, 1995). However, altitude is also related to other factors such as water temperature and flow regimes that can have a proximate influence on migration (see below). Jonsson & Jonsson (2006b) found that the condition factor (i.e. mass / length ratio) of returning sea trout decreased as they migrated progressively inland.

SEX AND FACULTATIVE ANADROMY

Often within brown trout populations, with both sea trout and residents, there is a sex bias with typically females predominating among anadromous trout and males among residents (Jonsson, 1985; Dellefors & Faremo, 1988; Elliott, 1994). In 17 coastal rivers in Norway Jonsson *et al*. (2001) found that, on average, 50% of the males but only 4% of the females spawned as residents. In the Glynn River (N. Ireland), Fleming (1983) found that above a series of impassable waterfalls the sex ratio was not significantly different from equality. However, in the section below the waterfalls, of 248 mature resident trout only two were females (0.8%) but in 111 smolts and mature sea trout that were examined 104 (94%) were female. A sex ratio bias has also been observed in *O. mykiss* (Rundio *et al*., 2012).

A sex bias would be expected from the balance of benefits of the two life histories (Hendry *et al*., 2004). Thus, female reproductive success is generally limited by gamete production with a larger body size giving greater fecundity and egg size (Fleming, 1996; Quinn, 2005). Larger females can attract mates, acquire and defend better spawning sites in a wider range of substrate sizes, and excavate deeper nests (Fleming & Reynolds, 2004).

Compared with females, male reproductive success is typically limited by access to mates (Fleming, 1998) rather than gamete production since even small males can produce millions of sperm (Munkittrick & Moccia, 1987). While a larger size can be of benefit to males in attracting and defending mates, obtaining a large body size is less critical for male reproduction because instead of aggressive defence of females, a tactic typically displayed by larger anadromous males (Esteve, 2005), they can adopt a 'sneaking' tactic allowing successful egg fertilisation at a small size (Gross, 1985; Hutchings & Myers, 1988). Thus males more often mature as residents since they are less dependent on large body size for reproductive success and consequently mature across a much greater range of ages and sizes (Jonsson & Jonsson, 1993). Early maturity in males also results in reduced pre-reproductive mortality (Gross & Repka, 1998).

NATURAL SELECTION ON ANADROMY VERSUS RESIDENCY

Facultative anadromy and residency in brown trout and other salmonines can be explained as alternative tactics within a conditional strategy (Dodson *et al*., 2013; Sloat *et al*., 2014; Kendall *et al*., 2015); individuals within a population can adopt either tactic. Whichever tactic is more successful under particular environmental conditions will result in the individuals adopting that tactic leaving more offspring, that is, they will have higher Darwinian fitness (Gross, 1987; Brönmark *et al*., 2014). Taking into consideration that there is a partial genetic basis to variation in life history choice (see below), positive natural selection for one or other tactic (e.g. anadromy) will tend to increase the frequency of that tactic over generations. While the expected outcome is that populations would become fixed for one tactic, the relative benefits and costs can vary temporally as a consequence of diverse factors including different environmental conditions, population density and composition. These changes in the cost-benefit equation result in many populations displaying both life histories, to a greater or lesser degree (see Table 2). That is, fluctuating natural selection on alternative phenotypes is expected to lead to the evolution of flexible life history strategies such as facultative anadromy, provided that reliable environmental cues are available for individuals (see section

on Proximate Environmental Factors). It is also possible that frequency dependent selection plays a role where increased frequency of one life history could allow selection to favour the other until a balance is achieved (Hecht *et al.*, 2015). Thus, as the migratory fraction increases, the resident fish will have reduced competition for food. Similarly, the rarer male type may have a competitive advantage in spawning. It is worth noting that similar balancing selection mechanisms (e.g. fluctuating environments, frequency dependence, opposing selection between the sexes) are also likely to explain why some populations of brown trout are capable of producing either river residents or adfluvial migrants that use lakes (instead of the sea) to grow larger, or why yet other populations are characterised by more complex mixes of river residents, adfluvial migrants and sea trout. Variability in the extent of anadromy or migration within populations, and among geographically adjacent populations, would suggest that the relative benefits and costs are finely balanced and thus evolutionary changes may occur rapidly as a result of relatively small alterations to any of the underlying factors (see below for more detailed discussion).

If anadromy or residency is advantageous in particular situations, it would be expected that compensatory adaptations would occur to increase benefits relative to costs (Hendry *et al.*, 2004). Jonsson & Jonsson (2006b) found that sea trout body size, age at sexual maturity, relative fecundity, and the ratio of fecundity to egg mass increased with distance from the sea to the spawning grounds, consistent with the hypothesis that selection favours a larger body size when migratory costs are greater. Bernatchez & Dodson (1987) noted that anadromous salmonines that migrated longer distances were more efficient in energy use. Freshwater residents can have, although not invariably, larger ova than similar sized anadromous females (Jonsson & Jonsson, 1999) and increased survival of young may compensate to some extent for lower fecundity.

Due to greater survival, residents should be more likely to show multiple spawning (iteroparity) than anadromous fish and this can increase the total lifetime fecundity. In a rainbow trout population, although female residents produced on average 1400 eggs, compared with 3500 eggs for steelhead, most of residents spawned a second time whereas this was the case for less than 5% of steelhead (Schroeder & Smith, 1989). However, repeat spawning in sea trout would appear to be more common than in steelhead as, in a survey of 102 European populations, Jonsson & L'Abée-Lund (1993) found that the proportion of repeat breeders in sea trout was from 30% in northern rivers to 60% in southern ones. Individual sea trout have been recorded spawning up to 11 times (Harris & Milner, 2006).

COMPONENTS OF ANADROMY

It is important to recognise that anadromy consists of a number of distinct, but interlinked, consecutive components. In particular, it is important to differentiate between the genetic and environmental factors that drive the individual's choice of anadromy or residency and the subsequent downstream changes that take place as a consequence of this decision. Thus fundamental to facultative anadromy is the decision on whether to migrate or to remain as a resident in the river and mature. This decision may involve one or more 'decision windows', which may take place a considerable time before external evidence of migration occurs (Hecht *et al*., 2015; McKinney *et al*., 2015) in the form of the changes associated with smoltification, i.e. the changes that occur prior to and during downstream movement to the sea as smolts. Failure to recognise this distinction between the decision process and consequential smoltification has led to misinterpretation of some studies. Examining the changes in gene expression in individuals during smoltification primarily indicates those genes which determine the physiological and other changes outlined below.

In addition to smoltification other components of anadromy include migrations to and from the sea, which involve directed movement and precise navigation to reach appropriate feeding habitats and return to natal spawning grounds. Return migration to freshwater may be triggered by the onset of sexual maturation, although such return does not necessarily involve spawning and, as noted by Quinn *et al*., (2016), the delay between return migration and spawning is highly variable.

SMOLTIFICATION

Smoltification involves a set of changes prior to seaward migration (Hoar, 1988), with subsequent return to freshwater involving a reversal of these. Smoltification happens in response to environmental cues (McCormick *et al*., 1998; Jensen *et al*., 2012) with the brain being the main integrator of this information, and thus the main regulator of the process (McKinney *et al*., 2015). This occurs through interpretation of seasonal cycles, often via the effects of photoperiods on circadian rhythms ('biological clocks'), and through various hormones (Björnsson *et al*., 2011).

The most obvious external aspect of smoltification is the body colouration changes that are necessary for the different camouflage requirements of bottom dwelling life in a river compared to mid-water life in the sea. In rivers, dark backs and spotted sides allow fish to

blend with bottom rock and gravel patterns. Conversely, light bellies, silver sides, and dark backs help camouflage fish in a mid-water marine environment as they will not stand out against the background, irrespective of the direction from which they are viewed by predators. Similar silvering also occurs in some pelagic lake dwelling brown trout (Crozier & Ferguson, 1986; Olsson & Greenberg, 2004) as it is an adaptation for mid-water camouflage and is not specifically associated with anadromy. There are also changes in shape, which are likely associated with greater swimming efficiency, with the snout becoming more pointed, the body slimmer and more streamlined, and a lengthening of the caudal peduncle (Hard *et al.*, 1999).

Smoltification involves physiological and biochemical adjustments including changes in visual pigments, haemoglobin, olfactory sensitivity, buoyancy (swim bladder size), metabolism, and salinity tolerance (Dann *et al*., 2003; McCormick *et al*., 1998). Most of the ionic regulation is carried out by the gills and involves an increase in enzymes such as gill Na^+/K^+-ATPase together with a switch in its isozymes from $\alpha 1a$, which is most abundant in freshwater, to $\alpha 1b$, the dominant isozyme in seawater (McCormick *et al.*, 2009, 2013). Sea survival increases with smolt size possibly because they have better osmoregulation and are less vulnerable to predation (Klemetsen *et al*., 2003).

Studies at the smoltification stage are the earliest at which it is possible to externally differentiate migrants from residents within a population and many comparative studies on smolts and non-smolts have been undertaken for this practical reason. To examine earlier genetic and phenotypic changes between migrants and residents currently requires the establishment of offspring lines based on populations of predominantly migrant or resident life histories. Over the past century, rainbow trout throughout their natural range in western North America have been blocked from anadromy by construction of artificial barriers and by artificial translocations above natural barriers (Thrower *et al*., 2004; Phillis *et al*., 2014; Pearse *et al*., 2014). These multiple replicate 'selection experiments' have provided valuable material for the investigation of phenotypic and genetic differences between steelhead and resident rainbow trout.

DETERMINANTS OF THE ANADROMY / RESIDENCY DECISION

GENETIC FACTORS

It has been known for some time, from the results of rearing and translocation experiments, that there is a genetic foundation for the anadromy 'decision' in brown trout. Skrochowska (1969) released reared progeny of anadromous, resident and reciprocal hybrid parentage. Subsequent recaptures indicated a propensity for offspring to follow parental life history, with hybrids being intermediate. Jonsson (1982) reciprocally transplanted juvenile brown trout between an isolated lake containing a resident population and a lake downstream containing a sea trout population, the juvenile growth rates in both populations being similar. Subsequent downstream movement was more frequent in the anadromous rather than the resident trout irrespective of the lake of release.

As with brown trout, resident rainbow trout can produce anadromous offspring and *vice versa*. However, again the predominant pattern is for offspring to track the parental life history (Zimmerman & Reeves, 2000; Seamons *et al*., 2004; Zimmerman *et al*. 2009; Hayes *et al*., 2012). Overall, many genetic studies carried out on salmonines have confirmed that there is genetic variation for the propensity for facultative migration (reviewed by Kendall *et al*., 2015, with emphasis on rainbow trout) but with considerable developmental plasticity. Sex associated differences in anadromy within populations under communal environmental conditions are also a clear indicator of a genetic basis to life history.

Unfortunately, heritability estimates, i.e., the contribution of genetic variance to the variability of life history among individuals in a given population, have been determined in only a few studies. Thrower *et al*., (2004) bred pure and reciprocally-crossed lines of anadromous and resident rainbow trout from Sashin Creek (Alaska), the residents being from an above waterfalls population that had been artificially established from the anadromous stock 70 years previously. After two years in a common hatchery environment they found that narrow sense heritability (h^2 - additive genetic variance only) estimates for freshwater maturation and smolting were between 0.44 - 0.51 and 0.45 - 0.56 respectively. Hecht *et al*., (2015) found a modal h^2 estimate of 0.61 (0.39 - 0.77) for life history in the same hatchery lines but using a larger pedigree. They also found significant genetic correlations of life history with growth rate, size, condition factor, and morphological traits, which themselves showed moderate heritabilities. Heritability estimates (h^2) for anadromy in a natural population of brook charr were 0.52 - 0.56 (Thériault *et al*., 2007). All these heritability

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estimates are within the range of values reported for threshold traits (reviewed by Roff, 1996). While no heritability estimates have as yet been published for sea trout, the similarity of steelhead and brook charr estimates under very different environments and, in spite of the few populations examined, may suggest heritability of a similar magnitude, Thus, approximately half of the variability in life history among individuals within a population is likely to be due to additive genetic variance for this trait, with the remainder attributed to non-additive genetic variance, parental effects and environmental influences. However, it is very important to acknowledge that heritability estimates are specific to the population and particular environmental conditions examined. Therefore, explicit estimates are required for a range of brown trout populations under different conditions before credence is given to any estimate. What is clear, however, is that there are both strong genetic and strong environmental influences on facultative anadromy within salmonine populations.

In reciprocal common garden experiments involving steelhead from two populations, Doctor *et al*., (2014) demonstrated that both genetics and temperature play an important role in determining growth rate, condition-factor, and proportion of age-1 smolts in steelhead. Broad-sense heritabilities (H^2 – all genetic variance) for the two populations at different times of year and for these three traits, ranged as follows: 0.49 – 0.60; 0.07 – 0.59; 0.69 – 0.77.

Studies of the molecular genetic basis of anadromy have identified several gene markers and chromosome regions associated with alternative life histories in rainbow trout (Nichols *et al*., 2008; Martínez *et al*., 2011; Narum *et al*., 2011; Hecht *et al*., 2012). Pearse *et al*., (2014) showed that a large region of one rainbow trout chromosome, Omy5, was strongly associated with life history in 13 resident (above a barrier) and 8 anadromous populations. The genes in this region appear to be tightly linked, possibly as the result of a chromosomal inversion or other rearrangement limiting recombination. The common genetic basis for life-history variation in a geographically varied set of populations probably results from strong parallel natural selection acting on one or more genes in this region that influence life history traits. This study supports previous suggestions (Nichols *et al*., 2008; Hale *et al*., 2013) that this gene group on Omy5 represents a 'master control region' influencing rainbow trout life history.

In a key study involving the offspring of wild anadromous and resident rainbow trout from Sashin Creek reared under common hatchery conditions for one year, McKinney *et al*. (2015) found differential gene expression in the brain between these lines for 1982 genes (7% of genes examined). Differences between anadromous and resident offspring were detected from hatching onwards with the greatest number of gene differences being found at eight

months of age, more than a year before obvious external appearance of smolt transformation. Patterns of gene expression during development differed between males and females, which may reflect the fact that males in the resident population mature earlier than females (McKinney *et al*., 2015). Genes showing differential expression included those involved with light sensitivity, circadian biological rhythms, growth, morphology, and olfactory imprinting, the latter being important in homing. A caveat to the use of the offspring of allopatric anadromous and resident trout is that aspects other than life history traits (including traits correlated with the anadromy decision, such as growth rate) may differ as a result of evolutionary divergence, although their recent common ancestry (c70 years) should minimise this.

PROXIMATE ENVIRONMENTAL FACTORS

Many studies have shown that environmental influences, including those during embryo development within the egg (Jonsson & Jonsson, 2014a), collectively determine a trout's developmental and physiological state (i.e. 'condition'), which has a proximate influence on the decision on whether to migrate or remain resident. Key aspects of condition potentially include size, growth rate, and 'energy status' including lipid levels and standard metabolic rate (see references below).

Size and growth rate of migrants are the aspects of condition most easily, and thus commonly, measured in association with life history. However, the relationship is complicated by time of measurement relative to emigration time, sex, age, temperature, and potentially genetic background. For example, size at smoltification may not reflect size at decision time perhaps a year earlier (Acolas *et al*., 2012; Beakes *et al*., 2010; Sloat, 2013; McKinney *et al*., 2015). In the meantime residents may have diverted energy from growth to sexual maturation. Conversely, as survival at sea is size dependent (Klemetsen *et al*., 2003), pre-migrants may have accelerated growth during this period. Also, emigration may occur over several successive years for the same cohort. Not surprisingly then, the relationship of size and growth to life history has varied (in both sign and magnitude) among studies and appears to be population specific to some extent. Body size in a brook charr population was correlated with age of migration (Thériault & Dodson, 2003), with smaller fish at age 1+ delaying migration to age 2+; however, larger 1+ fish that migrated were no different in size to 1+ fish that remained resident (Thériault & Dodson, 2003). Thériault *et al*., (2007) subsequently reported, for the same population, a negative correlation between the size of age

1+ parr and their propensity to remain in the river at that age, but these 'residents' likely included fish that would have migrated at age 2+. These results suggest that, at least for facultatively anadromous brook charr, the smallest 1+ parr are constrained from smoltifying, but this does not necessarily imply that size at age 1+ is the actual cue that triggers anadromy or residency; although it may be correlated with the true physiological cue.

Failure to account for sex of the juveniles, and even their parents, can make it difficult to evaluate effects of size and growth on migration in some studies. Males from resident rainbow trout mothers matured at smaller sizes than those from anadromous mothers (Berejikian *et al*., 2014). McMillan *et al*., (2012) found no difference in size between migrant and resident rainbow trout unless males and females were examined separately.

Some studies have found large size and fast growth associated with migration while others have found the opposite, suggesting that any relationship between life history and size is purely coincidental correlation. Jonsson (1985) found that the largest and fastest growing juveniles became anadromous while those with medium growth rates became residents, and the slowest growing individuals became sea trout but at an older age. Hecht *et al*., (2015) found a significant correlation between life history and condition factor with steelhead migrants showing a lower mean condition factor than residents at 12, 15 and 24 months post-fertilisation, the last being at smoltification. This indicates that the life history decision was taken during the first year of life in this experimental population derived from Sashin Creek steelhead and residents.

Various studies suggest that brown trout become migratory due to energy limitation in natal rivers. Accordingly they remain in the river until growth starts to level off (i.e. they approach asymptotic body size), at which point they either mature or migrate to better feeding areas (Jonsson & Jonsson, 1993). It has been suggested that population asymptotic size, especially for females, is one of the best predictors of life history (Sloat & Reeves, 2014). That is, if only a small size can ultimately be reached in the river then migration occurs. Increased juvenile density can result in increased competition for food and space resulting in fewer fish reaching the necessary condition to mature as residents (Jonsson & Jonsson, 1993). Hence food limitation may be a significant factor. O'Neal & Stanford (2011) found that resident brown trout dominated in smaller tributary rivers of the Rio Grande in Patagonia, where invertebrate biomass was two to three times higher than in larger tributaries. The latter either supported a mix of anadromous and resident individuals or were dominated by anadromous fish. Marco-Rius *et al*., (2013) found strong evidence for positive density dependence determining anadromy in brown trout with migrants maximising growth

by moving into the sea. It is also important to acknowledge that food quality, i.e. energy value, may be as important as food quantity (Kendall *et al*., 2015).

Olsson *et al*., (2006) transplanted offspring of adfluvial brown trout between two sections of a river with different fish densities. Adfluvial migratory behaviour developed in the river section with high trout density and low specific growth rate, whereas residency developed in the section with the converse situation. Cucherousset *et al*., (2005) found that life history traits varied among brown trout cohorts due to environmental variability and that trout with higher metabolic needs were more likely to migrate. Wysujack *et al*., (2009) fed hatchery-reared offspring of adfluvial brown trout from the same population at three different levels and found that low food availability, which was associated with low growth rates, increased the proportion of migrants: more so for females than males. Although the trout were from migratory parents, at the lowest food level 17% were residents and at the highest 42%. Jones *et al*., (2015) provided hatchery trout, derived from an adfluvial stock, either high or low food provisions in the autumn, winter or spring prior to release in the spring and found that spring food reduction caused increased smolting. However, they do not indicate whether those that did not smolt did so when older. This issue is shared by several published studies, including those citing Atlantic salmon studies, which are more about the age of smolting rather than the migration / residency decision.

Van Leeuwen *et al*., (2015) reared brown trout offspring of allopatric (different tributaries of River Tweed) river-resident and anadromous parents for seven months under high-, mid-, or low-food availability. They were then made to compete for feeding territories in a semi-natural river channel. Parental migration trait had a significant effect on dominance status in territorial interactions; offspring of anadromous fish dominated equivalent sized offspring of residents, but only when both were reared under the intermediate food regime. The results suggest that the inherited migratory tendency of the offspring interacts with the environmental conditions to influence competition for feeding territories and thus the probability of migration.

Metabolism, rather than actual growth or size, may be important in determining life history. Individuals that eventually become anadromous often have higher metabolic rates as parr, and thus become energy constrained sooner than those that become residents and metabolic rate differences can have a genetic basis (Sloat & Reeves, 2014) Greater metabolic costs can lead to lower energy efficiency and reduced lipid storage, the latter being an important component in maturation (McMillan *et al*., 2012). Forseth *et al*., (1999) found that faster growing adfluvial brown trout became migratory earlier, albeit at a smaller body size

than slower growing individuals which migrated one year later. Migrants maintained higher metabolic rates and were energetically constrained (i.e. growth rate could not be sustained) at a younger age by limited food resources in the river. Under conditions of limited food availability, fish with lower metabolism will meet their metabolic requirements easier, a tendency that should lead to residency. Future migrants in brook charr also exhibit lower growth efficiencies and higher associated metabolic costs than future residents (Morinville & Rasmussen, 2003). Lipid storage, the major source of energy for maturation (Tocher, 2003) may likewise be a good predictor of life history. In rainbow trout, McMillan *et al*., (2012) found that larger males with higher lipid levels had a greater probability of maturing as residents at age 1+.

Temperature appears to be a key factor in the migratory decision (Brannon *et al*., 2004; Sloat & Reeves, 2014), with both absolute temperature and variation in temperature being important (Kendall *et al*., 2015). Temperature is clearly linked to food availability, feeding activity, metabolism and lipid storage, and may also have a direct influence as a stressor on the migratory decision (Sogard *et al*., 2012). McMillan *et al*., (2012) found an inverse relationship between individual condition and water temperature as growth was greater in warmer streams while whole body lipid content was higher in cooler streams. This observation suggests one possible mechanism whereby temperature can influence life history. In a common garden experiment at different temperatures, Sloat & Reeves (2014) found that individuals of both sexes with the fastest growth, within their respective temperature treatments, had a greater probability of freshwater maturation (i.e. residency), but higher temperatures resulted in decreased freshwater maturation despite significantly increasing growth.

Further environmental factors associated with the migration/residence decision include water flow rate, although again the relationship is complex. Female residency in rainbow trout increased with decreasing mean annual flow (Mills *et al*., 2012), possibly because lower water conditions are unsuitable for spawning of larger steelhead females. Conversely, Berejikian *et al*., (2013) found that steelhead were more prevalent in rivers with low flows and high temperatures. These latter factors likely operate more as indirect agents of natural selection, however, rather than as proximate drivers of individual decisions.

Expected survival in the natal river measured over the long term, which is likely determined by a combination of the factors outlined above, clearly influences what life histories should evolve there; for example, low expected survival should select for higher rates of anadromy on average. Year-to-year variation in survival in the natal river, or

variation in survival across river microhabitats, may also correlate with temporal or spatial variation in anadromy within a given river, with individual parr in theory capable of basing their migratory decisions on some projection of their likely survival prospects should they not migrate (e.g. using current physiological condition as a proximal cue). However, while low survival may result in more juveniles selecting anadromy, it may not actually produce more migrants because fewer juveniles survive to the smolt stage (Railsback *et al.*, 2014).

A major unanswered question concerns the extent to which correlations between 'environmental' variables (defined broadly to include aspects such as individual condition) and the anadromy/residency decision reflect adaptive responses of individuals to predictive cues, versus non-adaptive, unavoidable constraints. For example, do individual parr use their own condition as a cue to adaptively choose one tactic over the other, or are they simply constrained to migrate when in poor condition? It seems logical that migrating to better feeding grounds when in poor condition is a 'good choice', but testing this rigorously would require quantification of how the lifetime fitness of individuals adopting either tactic varies as a function of the putative cue (e.g. parr condition during a decision window) they ostensibly use to choose one option over the other (Tomkins & Hazel, 2007). If choosing anadromy over residency when in low condition results in higher overall lifetime reproductive success on average, and *vice versa* when in high condition, this would be strong evidence that facultative anadromy represents adaptive plasticity. Interestingly, theory suggests that at evolutionary equilibrium (i.e. when the population has converged on a stable balance of tactic frequencies), the mean fitness of anadromous versus resident individuals need not be equal (i.e. the condition switch point for choosing anadromy over residency need not correspond with the condition value at which the fitness functions cross, although it might) (Tomkins & Hazel, 2007).

PARENTAL FACTORS

Parental effects, especially maternal ones, can be both genetically and environmentally induced, as well as resulting from unique gene-environment interactions. A maternal environmental effect, for example, refers to situations where environmental factors (e.g. feeding opportunities) affect some aspect of the mother's phenotype (e.g. her body size), which in turn affects the life histories of her offspring. A maternal genetic effect occurs when maternal genotype affects offspring phenotypes independently of the genes she passes on to them; for example, genetically large mothers may invest in larger eggs and the resulting

offspring may be more likely to adopt one or other life history tactic – not because they inherited their mother's genes for large body size, but because they hatched from large eggs. Indeed, egg size affects survival and growth of juveniles, particularly in the early stages of life (Einum & Fleming, 1995; Kamler, 2005). Resident trout co-occurring with sea trout have larger eggs than corresponding resident only populations (Olofsson & Mosegaard, 1999). Jonsson & Jonsson (2006a) argue that this larger egg size of resident brown trout compared to sea trout of similar body size may enable the young to compete with sea trout. Although few studies have so far been undertaken, epigenetic changes in the parental genomes induced by environmental conditions, especially during early development, can be transmitted to their offspring (Burton & Metcalfe, 2014). In a study of Atlantic salmon (*Salmo salar* L.), Burton *et al*. (2013) found that maternal influences on juvenile performance could be related to the environment experienced by the mother as a juvenile, as well as to her condition at the time of breeding. Jonsson & Jonsson (2016) found that the egg size in Atlantic salmon offspring, and thus yolk availability to alevin grand-offspring, is influenced by the temperature experienced by the mother during the last two months of egg maturation.

Berejikian *et al*., (2014) found that variation in the expression of residency or anadromy in both male and female rainbow trout was strongly influenced by maternal life history. Female offspring produced by anadromous mothers rarely expressed residency (2%), while the percentage of maturing male parr produced by anadromous mothers was much higher (41%) across a diversity of freshwater habitats. Both male and female parr that were produced by resident mothers were significantly more likely to show residency than the offspring of anadromous mothers. In an experimental stocking programme with brown trout, Marco-Rius *et al*., (2013) found a greater sea trout return from sea with crosses involving anadromous males, but no maternal effect was observed. In cases where the sex of the offspring is unknown, distinguishing such parental effects from sex-specific patterns of gene inheritance or expression is challenging, however.

INTEGRATING GENETIC AND ENVIRONMENTAL FACTORS IN THE ANADROMY / RESIDENCY DECISION

As outlined above, there are genetic, environmental and parental influences on the life history decision in facultatively anadromous salmonines. Thus facultative anadromy is a classic quantitative trait controlled by multiple genes with the manifestation dependent on interactions between this genetic architecture and environmental factors. However, unlike

continuous quantitative traits, the life history decision is one of discrete options controlled by a threshold. Thus, at the decision window an individual can decide to migrate, mature as a resident, or defer the migratory / residence decision until a later time, resulting in migration occurring at different ages. While several threshold models have been proposed, an environmentally-cued genetic threshold (ET) model (based on Tompkins & Hazel, 2007) is compatible with much of what is known about the life history decision in facultatively anadromous salmonines (Kendall *et al*., 2015). Although it may not be the precise and only mechanism involved (see below), a consideration of it provides a useful framework to understand how genetic and environmental influences operating via a threshold could result in the alternative tactics of migration or residency. If an individual's condition (for example, size, recent growth rate, lipid level) exceeds a genetically determined threshold value at a 'decision window' it will remain in the river and mature there. If it does not, it will become a sea trout, delaying maturation until a larger size (Figure 1). In practice, at least two decision windows may be necessary to account for some observations (Satterthwaite *et al*., 2009; Dodson *et al*., 2013). Information on condition is possibly translated into a physiological signal via hormonal changes (McCormick, 2009).

Under the ET model, individuals within a population have different thresholds values in respect of condition cues. These values are likely to be continuous and follow a normal distribution within the population, as is typical of other quantitative traits (Tomkins & Hazel, 2007). Variation in threshold values means that the proportion of individuals expressing anadromy versus residency depends on both the distribution of variation in thresholds and the distribution of the condition of individuals in the population at the time. The distribution of tactics within a population can change in the short term as a consequence of environmentally induced changes in condition. Evolutionary changes can arise through variations in the mean distribution of thresholds up or down, as an outcome of the environmental conditions acting as agents of selection in determining relative reproductive success of life history strategies. Accordingly if the success of anadromy is reduced due, e.g., to poorer feeding or survival at sea, then selection will result in a lowering of mean condition-threshold values, resulting in more resident fish (see below for more detailed discussion).

Threshold values vary between sexes in response to differential selection (Sloat *et al*., 2014) (Figure 2). Hence males are likely to have lower condition threshold values than females, i.e. they are less likely to be anadromous. This in turn implies that either some of the genes affecting the threshold(s) are linked to sex-determining genes, or they exhibit sex-dependent expression patterns. Thresholds also vary among populations resulting in

population-specific norms of reaction between condition and the decision to migrate or remain freshwater (Quinn *et al*., 2009). Populations with a lower incidence of anadromy would also have lower mean threshold values than populations with a higher incidence. In addition, populations differ in the likelihood of their individuals achieving the condition-threshold, and this may fluctuate from year-to-year depending on environmental conditions.

Baerwald *et al*., (2015) indicated that differential DNA methylation at gene regulatory elements may be an important molecular mechanism allowing interactions between an organism and its environment to determine life history. They propose that life history may be at least partially controlled by an epigenetic response threshold involving an integration of parentally inherited factors, environmental factors and developmental history. Interactions among these factors can influence life history choice dependent on whether the threshold is achieved or not.

Genes may directly influence the occurrence of anadromy, as in obligate anadromous species, irrespective of environmental influences. However, it could be that apparently obligate anadromous populations were once facultatively anadromous, but subsequently evolved very high condition thresholds such that they no longer produce residents in that environment. This raises the intriguing possibility that residency, or other freshwater life histories, could re-emerge, as a result of changing environmental conditions at sea, in populations that are obligatively anadromous at present.

The fact that genetic, environmental, and parental factors are inextricably, and complexly, linked in determining life history (Figure 3) means that they cannot be considered separately in either empirical or mathematical modelling studies. Not surprisingly where only specific aspects have been looked at in isolation, the findings are often inconsistent with other data. Significant genetic variance in traits, such as size, growth rate, metabolic rate, and age of smoltification, may in part explain the contradiction among studies regarding the role that these traits play in the life history decision (Dodson *et al*., 2013; Doctor *et al*., 2014; Hecht *et al*., 2015). Thus studies of condition and life history have often being carried out against variable genetic backgrounds where both intra-population and inter-population variability in the genetic propensity for life history occurs. It is generally well recognised that examining genetic differences between populations or other groups requires studies to be carried out in communal environmental conditions (common garden experiments), with reciprocal hybrids to control for parental effects. However, it seems less widely appreciated that investigating the influence of varying environments requires either common gene pool experiments or reciprocal transfers of pure and hybrid stocks among the environments being tested.

GENETIC AND ENVIRONMENTAL INFLUENCES ON OTHER COMPONENTS OF ANADROMY

Once the decision to migrate has been made then several downstream consequential events occur. While there is clear evidence for both genetic and environmental influences on the anadromy decision, to what extent are the other components heritable and to what degree is variation in these the result of environmentally induced plasticity? Note, however, that these are not mutually exclusive alternatives as the degree of plasticity in given traits itself can be heritable. As with the decision to migrate, each of these components is also likely to involve interacting genetic and environmental factors. Furthermore, natural selection is likely to operate to maximise Darwinian fitness in each case. Thus these further components of anadromy may evolve under the action of selection and resultant, 'more efficient', anadromy may compensate for some of the costs involved in this life history as noted above.

GENETIC CORRELATES OF SMOLTIFICATION

Results from crosses between sympatric adfluvial kokanee and anadromous sockeye salmon (*O. nerka* (Walbaum)) indicated that there is a genetic basis for the propensity to undergo smolting (Foote *et al*., 1992). Hybrids between the two forms were intermediate in osmoregulatory ability in seawater, suggesting that the propensity for smoltification is the result of additive genetic variance at multiple genes. While the ecology and physiology of smoltification is well understood in salmonine fishes, relatively little was known of the genetic and molecular regulatory mechanisms underlying this process until recently. Two main molecular genomics approaches have been used to compare smolts and residents. The first comprises studies of gene expression, i.e. which genes are differentially active in the two life histories. The second involves determining genes or groups of genes (chromosome regions) that are correlated with life history through mapping quantitative trait loci (QTL) and genome wide association studies (GWAS). As emphasised above, while such studies are informative with regard to the genetic control of smoltification, they do not indicate why or how the smoltification is initiated in the first place, i.e. the decision to migrate.

Giger *et al*., (2006) found shared differences in the genes expressed between smolts and resident brown trout from various European populations irrespective of their geographical

and phylogenetic background, thus indicating common genetic pathways related to smoltification. Subsequently, Giger *et al*., (2008) found that 21% of a random sample of screened genes were differentially expressed, which would suggest that many genes are involved in smoltification, or are indirectly affected by the process, in keeping with the genome wide distribution of gene associations found in later studies. Many other studies have shown gene expression differences, especially in the gills, between smolts and resident salmonines (e.g., Boulet *et al*., 2012; Robertson & McCormick, 2012; Garrett, 2013; Hecht *et al*., 2014; Sutherland *et al*., 2014). Genes that have been found to be differentially expressed relate, in most cases, to known physiological differences between smolts and residents, i.e., those associated with circadian rhythmicity, growth, osmoregulation, metabolism, protein breakdown, innate immunity, and sexual maturation. Differences in one of the genes, *transaldolase* 1, which is involved in lipid metabolism and is expressed at a lower level in smolts, can be detected over three months prior to migration (Amstutz *et al*., 2006).

QTL and gene markers correlated with smoltification traits in rainbow trout have been found on many chromosomes, including Omy5 as outlined above and Omy12 (Nichols *et al*., 2008; Hecht *et al*., 2012, 2013; Hale *et al*., 2013; Pearse *et al*., 2014). In a QTL analysis of osmoregulatory capacity in resident rainbow trout, Le Bras *et al*., (2011) identified three QTL on Omy12 for traits associated with seawater adaptability. Hecht *et al*., (2012) found the largest number of smoltification QTL associated with *Omy*12. Similarly, Hecht *et al*., (2013) in a genome wide association study found associations between anadromy and this chromosome. Just as a gene region on Omy5 may act as a master switch for the life history decision so the genes on Omy12 may control smoltification in steelhead.

As noted above, one possible pathway through which environmentally induced phenotypic plasticity could be linked to variation in life history is epigenetic regulation determining which genes are expressed or silenced. One common mechanism for this is gene methylation, by which methyl groups are attached to the DNA preventing gene expression. Different genome-wide methylation patterns between hatchery freshwater controls and seawater transferred brown trout have been identified suggesting that epigenetic mechanisms may be involved, at least partially, in gene activation or deactivation during smoltification (Morán *et al*., 2013). Baerwald *et al*., (2015), using F_2 siblings produced from a cross between steelhead and resident Sashin Creek rainbow trout reared in a common environment, detected 57 highly significant differentially methylated regions (DMRs) between smolts and resident juveniles. Many of the DMRs encode proteins with activity relevant to

smoltification, including circadian rhythms and protein kinase activity: an enzyme to which a multitude of functions have been attributed.

INHERITED MIGRATION PATTERNS AND HOMING

Juvenile steelhead, without prior migratory experience, responded to magnetic fields at the latitudinal boundaries of their ocean range with oriented swimming that would lead them towards appropriate foraging grounds (Putman *et al*., 2014a). Environmental factors could still play an important role if fish calibrate their responses relative to the local magnetic field in which they develop. Two Chinook salmon (*Oncorhynchus tshawytscha* (Walbaum)) populations and their hybrids reared under identical conditions differed in their oceanic distribution, and hybrids displayed an intermediate distribution relative to the two pure populations (Quinn *et al*., 2011). Subsequently Chinook salmon were shown to use an inherited magnetic map that facilitates navigation during their oceanic migration (Putman *et al*., 2014b). Similar mechanisms may exist for other salmonines; and there are many other examples of populations from the same river having different distributions at sea (e.g., Sharma & Quinn, 2012).

Hatchery-reared sea trout from different populations showed distinct migration pathways when released from common sites in the Baltic (Svärdson & Fagerström, 1982; Kallio-Nyberg *et al*., 2002) and natural sea trout populations differed in their distribution at sea (Jonsson & Jonsson, 2014b), indicating at least a partial genetic basis for their migratory behaviour. Jonsson & Jonsson (2014b) noted a higher straying rate of some hatchery reared stocks from populations distant to the river of release compared to more local stocks, which indicates that homing is partly inherited.

Little is known of the factors controlling the timing of sea trout return from the sea, an aspect showing considerable variation within and among populations (Quinn *et al*., 2016). Many Norwegian populations have been shown to overwinter in freshwater (Klemetsen *et al*., 2003) and may simply be a direct physiological response to the greater difficulty of ionic regulation in cold water. Unlike Atlantic salmon, return to freshwater in sea trout is not necessarily accompanied by sexual maturation, a phenomenon also known in steelhead (Hodge *et al*., 2014), although this may be the driving force in many cases. It is not known if timing of maturation at sea is connected to the original freshwater mature or migrate decision or whether these are independent aspects of the anadromous life history.

Timing of maturation in brown trout is a quantitative trait (Palm & Ryman, 1999). While age at sexual maturity in salmonines has a moderate heritability (Dodson *et al*., 2013), it is phenotypically plastic. In Atlantic salmon, a single genome region under natural selection has been associated with age of maturity (Ayllon *et al*., 2015; Barson *et al*., 2015). Interestingly one of the genes in this region has previously been found to be associated with the timing of puberty in humans, suggesting a conserved mechanism for timing of maturation in vertebrates. It would seem highly likely then that the same gene region may control time of maturity in brown trout.

MANAGEMENT AND CONSERVATION IMPLICATIONS OF A GENETIC BASIS TO ANADROMY

A strong genetic component to the anadromy decision in brown trout means the trait can be changed by (i.e. can evolve as a result of) natural selection. Due to the large heritabilities for growth, size and morphological traits, these characters also have substantial evolutionary potential (Hecht *et al*., 2015). However, the significant genetic correlation between traits, including life history, means that they do not evolve independently but as a suite of interlinked characters. This genetic covariance means that the response of life history to selection cannot be examined in isolation from these other traits (Hecht *et al*., 2015).

Facultative anadromy is the result of a balance between the benefits and costs of life history traits and these are expected to vary spatially and temporally with changes in environmental conditions, including those imposed by anthropogenic actions and climate changes (Kendall *et al*., 2015). Environmental changes can result in: (1) a proximate effect

through changing individual condition and thus the likelihood of migration; and (2) ultimate evolutionary changes to the genetic make-up including the threshold for migration, as a consequence of changes in the relative reproductive success of anadromous and resident trout. For example, reduction in the number of spawning sea trout could have a direct impact on the extent of anadromy as well as an evolutionary one. Thus reduced spawning would result in an overall reduction in juvenile density, which, as discussed above, may favour residency. In the longer term a reduced benefit to anadromy will lower the threshold for residency. The main environmental and anthropogenic changes likely to result in genetic changes are outlined below. A full consideration of the topic would require a dedicated review (see, for example, Thorstad *et al*., 2016 for a fuller treatment).

Negative changes to marine survival and feeding, and to survival and energy expenditure during migrations, will result in genetic changes in favour of residency (Hendry *et al*., 2004). Marine survival and, in some situations, growth may decline as the outcome of predicted climate changes resulting in changes in food availability (see below), increased predation (Friedland *et al*., 2012), and exploitation by commercial nets, either directly or as a by-product of netting for other fishes, both of sea trout and their prey, as well as their predators. A major problem in some areas is infestations of sea lice (*Lepeophtheirus salmonis*) associated with Atlantic salmon farming, which have led to reduced marine survival and changes associated with migration, growth, physiology and reproduction (Skaala *et al*., 2014; Thorstad *et al*., 2015). Model projections by Satterthwaite *et al*., (2009) for steelhead suggest that when sea survival rates were reduced by some 50%, anadromy no longer occurred, although the extent of the reduction required was population specific (Satterthwaite *et al*., 2010). Taranger *et al*.. (2015) noted that within 15 km of salmon farms in Norway sea lice levels are sufficiently high to result in 50% - 100% mortality of sea trout. Poole *et al*. (2006) found that in the Burrishoole system the mean return rate of smolts as finnock (.0SW maidens) in the years 1988-98 was one third of that prior to 1988, finnock being the predominant returning age class in this system. Sea lice emanating from salmon farms were implicated in this decline. It is not known whether the subsequent decline in sea trout smolts was the result of lower marine survival acting through natural selection to reduce anadromy or whether this decrease was the result of lowering of juvenile density due to depressed egg deposition. However, the fact that, even prior to the collapse, sea trout contributed less than 20% of the total egg deposition in the system would suggest a heritable rather than a direct density-dependent response (Poole *et al*., 2006).

Conversely, if conditions in the natal river become completely inhospitable (e.g. high temperature, low flow, low food availability) at certain times of the year the resident life history will be eliminated (Satterthwaite *et al*., 2010). However, in simulations that varied growth and survival only, Railsback *et al*., (2014) showed that as a result of variation among habitats and individuals, the extent of anadromy within a population changed gradually instead of shifting abruptly.

Changes in survival of both downstream and upstream migrants and in the energy costs of migration can occur for a number of reasons. Changes in water flow as a result of changes in precipitation and water abstraction can delay migration thus increasing the exposure to predators and energy expenditure. These effects can be increased by partial barriers to upstream migration due to water offtake and hydroelectric weirs. It should be emphasised that even where such barriers do not prevent upstream migration, they can increase the costs of facultative anadromy relative to residency. Sandlund & Jonsson (2016) reported that, following the construction of a hydroelectric power station and consequent reduced water flow, fluvial trout had ceased to migrate from a tributary to the main river due to reduced habitat quality in terms of food and shelter, which appeared to have removed the growth benefit previously associated with migration.

In many rivers more angling attention is given to sea trout than resident trout resulting in greater exploitation of the former. Since sea trout produce relatively more eggs than residents, this differential exploitation is magnified. Thériault *et al*., (2008) present a theoretical model of how increased harvesting of anadromous of brook charr reduces the probability of migration. Since cessation of fishing pressure does not produce as strong selection pressures in the opposite direction, recovery is likely to take much longer (Conover, 2000; Law, 2000).

Predicted climate changes are likely to impact on life history choice. The expected climate change in Western Europe is for warmer conditions with increased rainfall resulting in greater river flows (Harrod *et al*., 2009). Temperature increase in the sea is predicted to reduce primary productivity (Piou & Prévost, 2012) and thus potentially reduce food availability for sea trout although the impact is likely to vary throughout the latitudinal range. Conversely, temperature increase may reduce the need for overwintering in freshwater in the more northern regions. As noted above, both temperature and flow rate impact on anadromy and thus changes in sea trout distribution and biological characteristics are likely to occur (reviewed by Jonsson & Jonsson, 2009). Warmer conditions and a longer feeding period,

together with freshwater enrichment, may increase freshwater growth rates with a consequent decrease in anadromy (Finstad & Hein, 2012).

Stocking with fertile domesticated brown trout strains could result in a decrease in the genetic potential for anadromy in wild populations (Ferguson, 2007). Ruzzante *et al*., (2004) found that although domesticated trout, which had been stocked into rivers, produced smolts, these experienced high mortality at sea and were therefore largely absent in returning spawners. This suggests that genetic changes during domestication have reduced the ability to survive in the sea and the authors conclude that sea trout of domesticated origin are unlikely to reproduce to any significant extent. As discussed above, there is a genetic propensity for the ability to carry out ionic and osmoregulation at sea, which is independent of the actual seaward migration and the two aspects should not be confused. However, stocked domesticated brown trout that remain in freshwater have been shown to breed successfully (Hansen *et al*., 2000) and hence may lead to an increase in the proportion of freshwater trout relative to sea trout. Hatchery-produced steelhead smolts from residents above a barrier had substantially lower marine survival rates than similar smolts from the anadromous founder population below the barrier, indicating strong selection against aspects of anadromy in the above-barrier population over approximately 70 years (Thrower & Hard, 2009). The main farm strains of brown trout have been isolated from wild stocks for more than twice that time and were originally mainly derived from the adfluvial populations in Loch Leven, Scotland (Ferguson, 2007). An experimental study in Norway (Jonsson & Jonsson, 2014b) indicated that wild sea trout survived better than most hatchery produced trout, and that trout originating from populations distant to the river of release survived less well than those of local origin.

Stocking with farm-reared brown trout, or the hatchery-reared offspring of non-native brown trout, also reduces the reproductive success of wild populations through interbreeding with the stocked fish (reviewed by Ferguson, 2007); which would reduce population density thus favouring residency. Stocking with domesticated strains of farmed brown trout, other than sterile triploids, in areas with self-sustaining populations is no longer permitted in England and Wales as of 2015 (Environment Agency, 2014) and will be phased out in Scotland by 2020 (Scottish Government, 2015). However, such stocking is still permitted in other jurisdictions.

Stocking with hatchery-reared offspring of sea trout parents obtained from the same river as being stocked (supportive breeding) is widely practised in the countries surrounding the Baltic Sea. However, even if no genetic changes occur, hatchery-rearing can alter the

physiological condition of the trout thus changing their likelihood of migration (Davidsen *et al*., 2014b). In an experimental stocking programme, Marco-Rius *et al*., (2013) found that that planting artificially fertilized eggs in nursery areas of the river, together with the selection of anadromous males as brood stock, and mate pairs with higher similarity at the MHC class II B-gene locus, increased the return of sea trout.

FUTURE PERSPECTIVES

Studies on the determinants of anadromy in brown trout, especially genetic aspects, lag substantially behind those on rainbow trout; although, even for the latter, Kendal *et al*., (2015) consider that available information has many limitations. However, given the considerable similarities of facultative anadromy in the two species, rainbow trout genetic studies can act as a springboard enabling rapid progress to be made in respect of brown trout. Key aspects which need to be tackled are those essential to understanding and enabling predictive modelling of the impact of changing environmental conditions on anadromy and how lost or depleted anadromous populations can be restored. Fundamental to this is the estimation of heritability of anadromy and relative Darwinian fitness of alternative life histories in a range of populations of different phylogeographic origins and biological characteristics (Ferguson, 2006). In particular, theory suggests that in order to predict changing selection on environmentally-cued threshold traits we need to be able to measure (a) the frequency distribution of cue (e.g. condition) values and how this is affected by environmental change, and (b) how the fitness of each tactic varies as a function of the cue (Tomkins & Hazel, 2007). Heritability estimates of the various factors (e.g. growth, metabolic rate, lipid storage) contributing to individual condition are also required together with the genetic covariance of these and anadromy. In addition, detailed investigation of the genetic factors controlling the life history decision is required. It is emphasised that such studies need to target early developmental stages, as this is when the 'decision window(s)' occurs, and not focus on smolts, which are a downstream consequence of the decision. This will require making use of experimental lines derived from above (resident) and below (anadromous) barrier populations together with innovative approaches to predict the future life histories of individual fish at an early developmental stage.

Detailed studies of the influence of environmental factors on anadromy in brown trout are also required, including juvenile density, food availability, water temperature, water flow, and difficulty (cost) of migration. Variation in condition among populations as a result of

variation in these factors, and how individuals respond to this, requires examination. Similar recommendations in respect of rainbow trout have been advocated by Kendall *et al*., (2015) and that review should be consulted for a more detailed exposition.

As there is clear evidence of a density dependent aspect to facultative anadromy it should be instructive to artificially manipulate juvenile densities. This could be done using eggs or fry of sterile triploid farm trout, which would obviate the potential problems of genetic changes due to interbreeding noted above (Ferguson, 2007). The aim of this stocking would not be for the stocked fish to produce sea trout themselves but to increase the juvenile trout density thus potentially 'pushing' the wild trout to migrate.

Examination of issues affecting marine survival and growth is fundamental to full life cycle understanding. Experimental studies of environmental factors must be undertaken in the context of controlling for genetic variability as outlined above. Most studies to date of sea trout have been undertaken on a few river systems. However, there is requirement for investigation of relative frequency of life histories in a much larger number of rivers, together with detailed biotic and abiotic measurements and associated riverscape features. Detailed study is also required of the interaction between anadromous and the various freshwater life histories especially in view of the current understanding that these are interchangeable and do not have a rigid separation.

Studies of parental influences on life history and epigenetic modifications can serve to elucidate how genetic and environmental influences interact. Although investigations of the inheritance of environmentally induced epigenetic modifications are at an early stage (Burton & Metcalfe, 2014), studies of such inheritance are likely to be fundamentally important in understanding life history choice, as well as the impact of environmental changes in general.

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Table 1. Potential benefits of anadromy and river residency in brown trout. Based on information in: Gross et al., 1987; Elliott, 1994; Fleming, 1996, 1998; Jonsson & Jonsson, 1999; Fleming & Reynolds, 2004; Hendry et al., 2004; Jonsson & Jonsson, 2006. Note that the benefits of one tactic can be regarded as the 'costs' of the other.

Benefits of anadromy

- Migration to more stable marine environment avoids harsh abiotic or biotic conditions in river.
- Better feeding at sea than in rivers and thus faster growth, reaching larger size.
- As growth occurs, larger food items such as fish become accessible, increasing growth further.
- Larger size results in:
    - Being able to swim / hold position against higher current velocities;
    - Wider choice of spawning gravels, for females.
    - Better dominance in competition and female choice during mating, for males.
    - Eggs being buried deeper thereby reducing risk of washout and overcutting by smaller resident females.
    - Indirect effects to traits such as mortality rate, age at maturity, fecundity and egg mass.
    - Larger eggs, which produce larger offspring with better competitive ability and higher survival.

Benefits of river residency

- Higher survival due to:
    - Less risk of predation during migration and at sea.
    - Avoidance of parasites and diseases which are more abundant at sea.
    - Less chance of capture by humans.
- Higher survival increases chance of iteroparity.
- Avoids energetic costs of migration and physiological changes required for moving from freshwater to sea.
- Able to gain access to spawning areas in small tributary rivers.
- Avoids straying and being unable to find a suitable breeding site.

- If accompanied by earlier maturity than anadromy, residency yields reduced generation time (and all else being equal, 'faster' life histories outcompete 'slower' life histories).

Table 2. Non-mutually exclusive hypotheses to explain why balancing selection may maintain a mix of anadromous and resident tactics in a population, rather than only one.

1. Ecological conditions vary across time

Explanation: If the relative fitness of anadromous and resident individuals varies through time, temporally fluctuating selection may favour the capacity of individuals to produce either type via phenotypic plasticity (where individuals 'choose' their tactic based on cues) or bet-hedging (where tactics develop randomly).

Examples: In some years, or for some cohorts, relative growth and survival benefits at sea may outweigh those in the river, but in other years, the reverse may be true. Thus, neither tactic outcompetes the other in the long-run.

2. Ecological conditions vary across space

Explanation: If the relative fitness of anadromous and resident tactics varies across habitat types within a single freely interbreeding population, this may select for individuals that are capable of producing either tactic (via plasticity or bet-hedging)

Examples: Fry that rear in more productive parts of the river, or that obtain better feeding territories, may be better off remaining resident and maturing early, whereas fry that rear in lower-energy environments may gain more by becoming anadromous. Smaller tributaries or spawning areas with smaller gravels may select for smaller resident females, whereas larger tributaries or areas with larger gravels may favour larger anadromous females (if going to sea is the only way to get big). A relatively small amount of gene flow among habitats/tributaries within rivers will still be enough to prevent genetic differentiation.

3. Frequency dependence favours a stable mix of tactics

Explanation: Smaller resident males may 'sneak' more fertilisations when rare, whereas larger anadromous males may obtain more fertilisations on average when small resident males are most abundant. This mechanism can act to stabilise tactic frequencies at some intermediate value or, in theory, could lead to constant cycling of tactic frequencies.

Examples: Early maturing resident males have a spawning advantage relative to anadromous males only when rare.

4. Sexually-antagonistic selection maintains genetic variation in anadromy

Explanation: The evolutionary interests of males and females may be in conflict, such that genes that increase the propensity for anadromy are selected for in females but against in males. This then maintains genetic variation in the propensity for anadromy.

Examples: Females carrying genes for higher condition-thresholds are more likely to be anadromous, which increases their reproductive success, but their sons may then inherit these same genes and hence also become anadromous, which may be less optimal for males than residency. Such 'sexual conflict' may mean that neither tactic has superior fitness overall (averaged across males and females), hence both co-exist.

5. **Heterozygote advantage favours the maintenance of genetic variation in anadromy**

Explanation: For a given genetic locus affecting the propensity for anadromy, two or more alleles (different copies of the same gene) can be maintained in the population if heterozygotes (individuals with two different copies) have higher fitness than homozygotes (individuals with two identical copies).

Example: Heterozygous parents may produce a mix of anadromous and resident offspring, whereas homozygous parents might produce more of one type than the other. If selection on average favours some intermediate threshold for anadromy, heterozygotes may have a long-term fitness advantage over homozygotes. This mechanism could partially explain why genetic variation in anadromy thresholds is maintained, but by itself does not explain why an intermediate degree of anadromy is favoured (although the other hypotheses might).

Figure 1. Illustration of how the genetically determined condition threshold can determine the life history adopted. The y-axis here represents some measure of physiological condition that triggers residency when it exceeds the hypothesised genetic threshold, or anadromy if not.
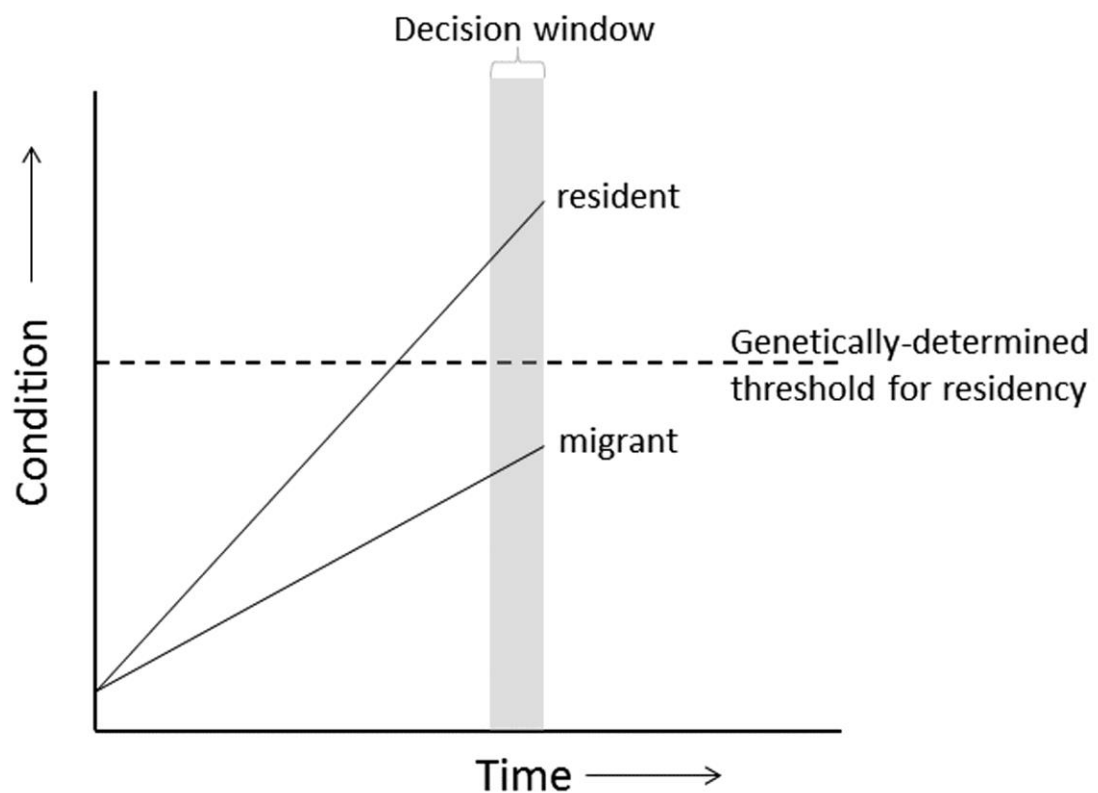
Figure 2. Possible distributions of condition threshold values in males (A) and females (B), or two populations with lower (A) and higher (B) propensities for anadromy. A single point along the x-axis here corresponds to a single threshold value, e.g. the dashed line in Fig.1.
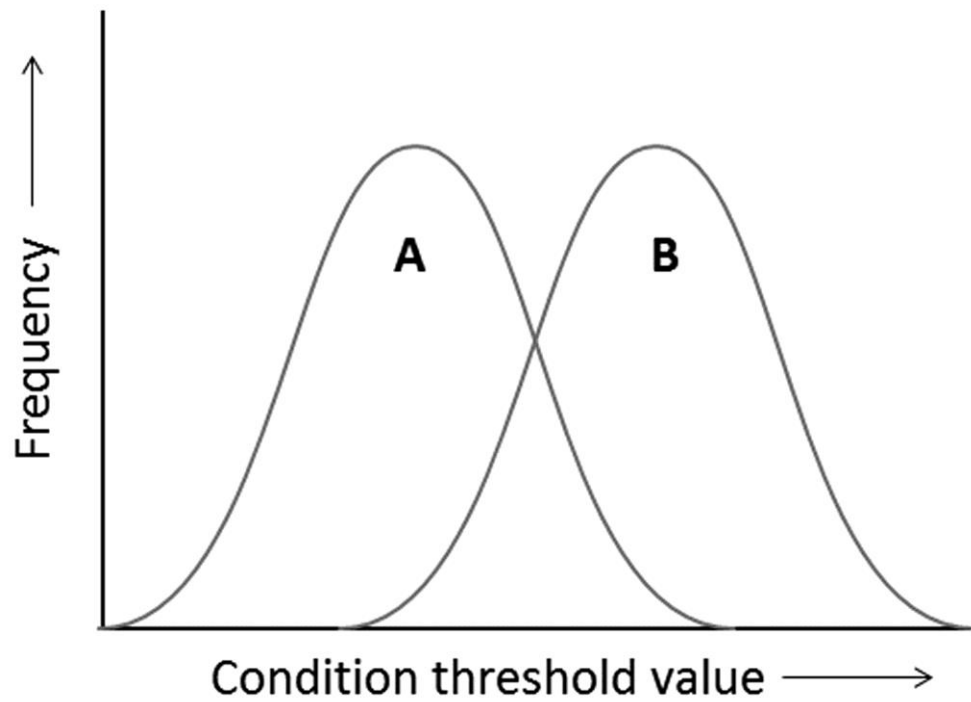
Figure 3. Summary of how genetic, environmental and parental factors could interact to determine the life history and how evolutionary changes to life history could result from environmental changes that alter the relative reproductive success of the two tactics.