REVIEW

Extent and scale of local adaptation in salmonid fishes: review and meta-analysis

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What is the extent and scale of local adaptation (LA)? How quickly does LA arise? And what is its underlying molecular basis? Our review and meta-analysis on salmonid fishes estimates the frequency of LA to be ∼55–70%, with local populations having a 1.2 times average fitness advantage relative to foreign populations or to their performance in new environments. Salmonid LA is evident at a variety of spatial scales (for example, few km to > 1000 km) and can manifest itself quickly (6–30 generations). As the geographic scale between populations increases, LA is generally more frequent and stronger. Yet the extent of LA in salmonids does not appear to differ from that in other assessed taxa. Moreover, the frequency with which foreign salmonid populations outperform local populations (∼23–35%) suggests that drift, gene flow and plasticity often limit or mediate LA. The relatively few studies based on candidate gene and genomewide analyses have identified footprints of selection at both small and large geographical scales, likely reflecting the specific functional properties of loci and the associated selection regimes (for example, local niche partitioning, pathogens, parasites, photoperiodicity and seasonal timing). The molecular basis of LA in salmonids is still largely unknown, but differential expression at the same few genes is implicated in the convergent evolution of certain phenotypes. Collectively, future research will benefit from an integration of classical and molecular approaches to understand: (i) species differences and how they originate, (ii) variation in adaptation across scales, life stages, population sizes and environmental gradients, and (iii) evolutionary responses to human activities.

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Introduction

Environmental heterogeneity across the geographic range of species should exert local selective pressures that act to maximize individual fitness within specific environments. This process is known as local adaptation (LA) wherein individuals of a local population exhibit higher fitness in their local environment compared with individuals from a different population and environment (Box 1; Kawecki and Ebert, 2004). The state of becoming locally adapted, however, is not an inevitable outcome even where different selective pressures operate. Selection can be counteracted by gene flow or rendered less efficient by genetic drift (Wright, 1931), frequent extinction and recolonization may impede the process towards LA (Levins, 1968), and the intensity or direction of selection in relation to environmental heterogeneity may vary temporally, favouring generalist genotypes and/or phenotypic plasticity over LA *per se* (Bradshaw, 1965). Consequently, conditions predicted to result in LA include: low gene flow (from low dispersal or high habitat fidelity), greater spatial than temporal variation

in selection, small or negligible fluctuations in habitat quality and/or where costs or constraints to plasticity exist (Kawecki and Ebert, 2004).

Consideration of LA has a long-standing tradition in well-studied salmonid fishes, which include salmon, trout, charr, whitefishes and graylings (Ricker, 1972; Taylor, 1991; Adkison, 1995; Garcia de Leaniz et al., 2007). Salmonids are highly structured spatially because of their natal homing and frequently low dispersal between habitat patches (Quinn, 2005), trait differentiation among populations is often associated with local environmental features (Taylor, 1991), most phenotypic traits have a heritable component (Carlson and Seamons, 2008), and trait differences can translate into individual fitness differences (Garcia de Leaniz et al., 2007). These observations, along with the failure of many historical transplants of salmonids within their native ranges (Withler, 1982; Federenko and Shepherd, 1986) have resulted in a chief paradigm of salmonid biology that populations are adapted to their local environments. Despite this paradigm, the extent and scale of salmonid LA remains poorly characterized, as does its molecular basis. Furthermore, the vast majority of evidence in support of the salmonid LA paradigm is only circumstantial and indirect.

Understanding what drives the extent and scale of LA in salmonids is important for several reasons. The study

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Box 1 Criteria for demonstrating local adaptation

(a) Populations must exhibit different fitness across different environments.

(b) A population must exhibit higher fitness in its 'local' environment (or under experimental conditions resembling those of the 'local' environment) compared with 'foreign' populations in the same environment (the 'local vs foreign' criterion). There has been some controversy regarding whether LA should also be defined as individuals exhibit higher fitness in their own environment compared with a different environment ('home vs away'). Ideally, both 'local vs foreign' and 'home vs away' criteria should be fulfilled to provide evidence for local adaptation. However, we concur with Kawecki and Ebert, 2004 that 'local vs foreign' should be the main criterion, as it directly addresses the issue of divergent selection. In contrast, the 'home vs away' criterion could be fulfilled if population A performs better in environment A than in environment B, and population B performs better in environment B than in environment A, even if population A performs better than population B in both environments, thereby not strictly fulfilling a criterion of LA.

(c) It must be demonstrated that fitness differences among populations have a heritable basis: maternal effects, phenotypic plasticity, previous experience effects and experimental artifacts must be ruled out or controlled for. In the case of applying molecular tools, population differences at the loci or genes in question must also be shown to be because of selection as opposed to genetic drift. This can be done either by specific tests for selection for example, (Storz, 2005), or an extrinsic hypothesis that states a mechanism between variation at traits and genes, and local environmental variables (Joost et al., 2007). Genome scans should include a statement of a mechanism between loci subject to selection and environmental variables in order to rule out type 1 error. Parallelism in patterns should be tested to more firmly assess the role of selection acting on outlier loci.

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of extensive geographic variation within salmonids can be exploited to better understand LA's significance as a fundamental element of evolutionary change (Hendry and Stearns, 2004), including speciation (Behnke, 1972; Bernatchez et al., 2010). In addition, understanding LA is central to determining how quickly, and to what extent, particular salmonid populations will respond to habitat alterations (Haugen et al., 2008), climate change (Crozier et al., 2008), fisheries- or farming-induced evolution (Hutchings and Fraser, 2008) and interactions with hatchery- or captive-reared counterparts (Araki et al., 2008; Fraser, 2008). Quantifying the extent and scale of LA is also increasingly important to the definition and application of conservation units within species for legal protection, including 'distinct population segments' under the US Endangered Species Act (Waples, 1991) and 'designatable units' under Canada's Species at Risk Act (Green, 2005). Even in the absence of formal legal recognition of intraspecific conservation units, a consideration of the scale and extent of LA can be important in proactive conservation prioritization (Taylor et al., 2011) or in restoration programs (Ricker, 1972; Hendry et al., 2003). Indeed, the failure of many restoration programs within the native ranges of Pacific salmon has been suggested to partly result from inadequate adaptive 'matching' of translocated populations to their new environments (Allendorf and Waples, 1996). Functional gene-associated molecular markers are one example of how locally adapted populations might be identified and used in restoration or even aquaculture development projects (Bonin and Bernatchez, 2009).

Many approaches and tools can be used to study adaptation (reviewed extensively in Endler, 1986; Reznick and Travis, 1996; Kawecki and Ebert, 2004; see also Garcia de Leaniz et al., 2007 for an excellent discussion relating to salmonids). Owing to their different properties, however, they do not all yield the same kind of information on LA, nor are they necessarily equally capable of demonstrating the existence of LA (Endler, 1986; Garcia de Leaniz et al., 2007). Namely, reciprocal transplant experiments, translocations and common-garden field experiments offer the most tractable means to demonstrate conclusively the existence of LA. In particular, the former two can be used to determine the magnitude by which fitness varies across populations and environments. Yet interpretations of LA with these approaches can still be challenging if

study animals incur post-release stress or if maternal effects are not accounted for (Kawecki and Ebert, 2004). It can also be difficult to decipher the exact or potential selective agents, traits or genes implicated in LA with these approaches, in contrast to studies at the phenotypic or molecular level (Garcia de Leaniz et al., 2007). These latter studies may also reveal information on the likely scale or speed of LA if they are done in concert with a consideration of local environmental features, common-garden laboratory experiments, and/or after translocations or known environmental perturbations.

What then, do existing empirical studies suggest about the extent and scale of LA in salmonids? A first objective of this review is to address this question quantitatively using meta-analysis. We then summarise empirical studies that shed light on two other important elements of salmonid LA: its (i) potential speed and (ii) molecular basis. For (i), we found only one study in the wild that included a measure of fitness (Unwin et al., 2003), so we also review relevant literature on the rate of phenotypic and molecular change in salmonids following known environmental perturbations and translocations. For (ii), no studies on salmonids, as yet, have translated variation at the molecular level to fitness differences among populations that fulfilled LA criteria. We thus consider what molecular approaches have revealed about the potential selective agents or specific traits implicated in putative salmonid LA, the likely extent or scale of LA and the molecular basis of LA. The main impetus for our objectives was to integrate information on LA collected over several decades on salmonids using a variety of approaches and tools. The role of phenotypic plasticity in mediating salmonid LA, another important consideration, is considered by Hutchings (2011).

The extent and scale of LA

Meta-analysis and quantitative survey of fitness data

We reviewed the primary and secondary literature for available data on the extent and scale of LA in salmonids. Our meta-analysis considered two LA criteria, 'local vs foreign' and 'home vs away' (Box 1). For these criteria, we found a total of 15 and 11 studies, respectively, conducted on five species and at one or multiple life stages, for a total of 48 and 45 interpopulation compar-

Table 1 Summary of salmonid fitness data related to the 'local vs foreign' criterion of local adaptation

Species	Fitness measure	Life stage	Comp[a]	Fitness, local vs foreign			Reference
				>	=	<	
Studies in the wild							
AS	Survival (adult recovery rate)	Egg to adult return	2	2	—	—	Garcia de Leaniz *et al.*, 1989
AS	Survival	Fertilized egg to hatch	2	1	1	—	Donaghy and Verspoor, 1997
AS	Survival (adult recovery rate)	Eyed egg to adult return	1	1	—	—	McGinnity *et al.*, 2004
AS	Survival (recapture rates)	Fry to age 0+in freshwater	6	—	6	—	Houde *et al.*, 2010
CS	Survival (adult recovery rate)	Fry to adult return	1	1	—	—	Brannon and Hershberger, 1984
CS	Survival (adult recovery rate)	Fry (6 months) to adult return	2	2	—	—	Unwin *et al.*, 2003
CS	Survival (adult recovery rate)	Early juvenile to adult return	2	1	—	1	Bagatell *et al.*, 1981a
CS	Survival (adult recovery rate)	Early juvenile to adult return	2	1	—	1	Fuss *et al.*, 1981
CO	Survival (adult recovery rate)	Early juvenile to adult return	5[b]	4	—	1	Bagatell *et al.*, 1980
CO	Survival (adult recovery rate)	Early juvenile to adult return	6[b]	2	—	4	Bagatell *et al.*, 1981b
CO	Survival (adult recovery rate)	Early juvenile to adult return	4[b]	1	2	1	Bagatell *et al.*, 1981c
CO	Survival (adult recovery rate)	Early juvenile to adult return	5[b]	2	1	2	Fuss and Rasch, 1981
CO	Survival (adult recovery rate)	Smolt to adult return	4[b]	1	3	—	Dann and Smoker, 2010
MS	Survival (adult recovery rate)	Smolt to adult return	4[b]	4	—	—	Mayama *et al.*, 1989
BT	Survival (tag return rate)	Smolt to adult	2	1	—	1	Bartel *et al.*, 2001
Laboratory studies							
AS	Survival (pH)	Alevin to 69 days post-hatch	2	1	1	—	Fraser *et al.*, 2008
CS	Survival (temperature)	Fertilized egg to emergence	4	1	3	—	Beacham and Murray, 1989
CO	Survival (salinity tolerance)	Juvenile	1	1	—	—	Kreeger, 1995
CS	Survival (water chemistry)	Eyed egg to yolk absorption	2	—	2	—	Evans *et al.*, 2010
CO	Survival (pathogen resistance)	Juvenile	2	2	—	—	Hemmingsen *et al.*, 1986
CO	Survival (pathogen resistance)	Juvenile	1	1	—	—	Bower *et al.*, 1995
SS	Survival (temperature)	Fertilized egg to emergence	2	1	1	—	Beacham and Murray, 1989
SS	Survival (pathogen resistance)	Juvenile	1	1	—	—	Bower *et al.*, 1995
SS	Survival (temperature)	Fertilized eggs to emergence	2	—	2	—	Hendry *et al.*, 1998
CH	Survival (temperature)	Fertilized eggs to emergence	4	1	2	1	Beacham and Murray, 1986
RT	Survival (pathogen resistance)	Juvenile	1	1	—	—	Buchanan *et al.*, 1983
EG	Survival (temperature)	Hatch to emergence	6	6	—	—	Haugen and Vollestad, 2000

Abbreviations: AC, Arctic charr (*Salvelinus alpinus*); AS, Atlantic salmon (*Salmo salar*); BC, Brook charr (*Salvelinus fontinalis*); BT, Brown trout (*Salmo trutta*); CH, Chum salmon (*Oncorhynchus keta*); CO, Coho salmon (*Oncorhynchus kisutch*); CS, Chinook salmon (*Oncorhynchus tshawtyscha*); EG, European grayling (*Thymallus thymallus*); LC, Lake charr (*Salvelinus namaycush*); LW, Lake whitefish (*Coregonus clupeaformis*); MS, Masou salmon (*Oncorhynchus masou*); PS, Pacific salmon, general (*Oncorhynchus* spp.); RT, Rainbow trout (*Oncorhynchus mykiss*); SS, Sockeye salmon/kokanee (*Oncorhynchus nerka*).
[a]Comp = number of comparisons. Of the comparisons in each study, '>' represents the number where statistically the local population performed better than the foreign population, '=' represents the number where there was no difference between local and foreign population fitness and '<' represents the number where the foreign population performed better than the local population.
[b]Replicated twice for two interpopulation comparisons.

isons (Tables 1, 2 and Supplementary Table S1). Note that, we only considered studies that (i) measured fitness components (for example, survival and reproductive success) or (ii) measured reasonable proxies of fitness components (for example, putative survival from recovery rates); to date, studies in the wild fulfilling LA criteria have only provided data for (ii), with one exception (Donaghy and Verspoor, 1997). Studies also had to account for any differences in age-at-maturity between populations when comparing survival on the basis of adult recapture rates, to make such comparisons valid ones. Too few studies on different species precluded separate species assessments.

We first calculated the effect size of the relative proportion of recaptured 'local' and 'foreign' fish in each study using the log odds ratio (Lipsey and Wilson, 2001). We standardized our data using the following equation:

$$\mathrm{ES_{LOR}} = \log_e \left[\frac{p_{recapture\ population\ A}}{1 - p_{recapture\ population\ A}} \right] - \log_e$$

$$\times \left[\frac{p_{recapture\ population\ B}}{1 - p_{recapture\ population\ B}} \right]$$

where ES_{LOR} was the effect size of the log odds ratio, $p_{recapture\ population\ A}$ was the proportion of recaptured local fish and $p_{recapture\ population\ B}$ was the proportion of recaptured foreign fish. A positive effect size would indicate that local fish survived better than foreign fish, whereas a negative effect size would indicate the opposite trend. We used the same method for studies involving the 'home vs away' criterion, but did not compare the two LA criteria because many interpopulation comparisons did not overlap between them (Tables 1, 2 and Supplementary Table S1). In the few comparisons with zero recaptures, we added 0.5 to these cells for analysis following Lipsey and Wilson (2001). For each effect size, we calculated an error term (SE_{LOR}) using the following equation:

$$\mathrm{SE_{LOR}} = $$

$$\sqrt{\frac{1}{n_{\text{recaptures pop A}}} + \frac{1}{1 - n_{\text{recaptures pop A}}} + \frac{1}{n_{\text{recaptures pop B}}} + \frac{1}{1 - n_{\text{recaptures pop B}}}}$$

Table 2 Summary of salmonid fitness data related to the 'home vs away' criterion of local adaptation

Species	Fitness measure	Life stage	Comp[a]	Fitness, Home vs Away			Reference
				>	=	<	
Studies in the wild							
AS	Survival (adult recovery rate)	Smolt to adult return	15[b]	9	6	—	Ritter, 1975
AS	Survival (adult recovery rate)	Smolt to adult return	5[c]	5	—	—	Jonasson, 1996
AS	Survival	Fertilized egg to hatch	2	1	1	—	Donaghy and Verspoor, 1997
AS	Survival (recapture rates)	Fry to age 0+ in freshwater	6	—	6	—	Houde et al., 2010
CS	Survival (adult recovery rate)	Fry (5–8 g) to adult return	2	—	—	2	Hancock and Marshall, 1985
CS	Survival (adult recovery rate)	Fry (5–6 g) to adult return	3	2	1	—	Federenko and Shepherd, 1986
CO	Survival (adult recovery rate)	Early juvenile to adult return	2	1	—	1	Bagatell et al., 1980
CO	Survival (adult recovery rate)	Early juvenile to adult return	1	1	—	—	Bagatell et al., 1981b
CO	Survival (adult recovery rate)	Early juvenile to adult return	3	3	—	—	Fuss and Rasch, 1981
MS	Survival (adult recovery rate)	Smolt to adult return	4[d]	4	—	—	Mayama et al., 1989
BT	Survival (tag return rate)	Smolt to adult	2	1	—	1	Bartel et al., 2001
Laboratory studies							
AS	Survival (pH)	Alevin to 69 days post-hatch	2	1	1		Fraser et al., 2008
CS	Survival (water chemistry)	Eyed egg to yolk absorption	2	—	2	—	Evans et al., 2010
SS	Survival (temperature)	Fertilized egg to emergence	6	4	2	—	Beacham and Murray, 1989
SS	Survival (temperature)	Fertilized eggs to emergence	2	—	2	—	Hendry et al., 1998
CH	Survival (temperature)	Fertilized eggs to emergence	4	3	—	1	Beacham and Murray, 1986
EG	Survival (temperature)	Hatch to emergence	6	4	2	—	Haugen and Vollestad, 2000

Abbreviations: AC, Arctic charr (*Salvelinus alpinus*); AS, Atlantic salmon (*Salmo salar*); BC, Brook charr (*Salvelinus fontinalis*); BT, Brown trout (*Salmo trutta*); CH, Chum salmon (*Oncorhynchus keta*); CO, Coho salmon (*Oncorhynchus kisutch*); CS, Chinook salmon (*Oncorhynchus tshawtyscha*); EG, European grayling (*Thymallus thymallus*); LC, Lake charr (*Salvelinus namaycush*); LW, Lake whitefish (*Coregonus clupeaformis*); MS, Masou salmon (*Oncorhynchus masou*); PS, Pacific salmon, general (*Oncorhynchus* spp.); RT, Rainbow trout (*Oncorhynchus mykiss*); SS, Sockeye salmon/kokanee (*Oncorhynchus nerka*).
[a]Comp = number of comparisons. Of the comparisons in each study, '>' represents the number where statistically the home population performed better in the home environment than when away, '=' represents the number where there was no difference between home and away fitness, and '<' represents the number where the home population performed better when away. Species codes are found in Table 1.
[b]Replicated twice for four interpopulation comparisons.
[c]Replicated three times for one interpopulation comparison and twice for another interpopulation comparison.
[d]Replicated twice for two interpopulation comparisons.

The weights (w_{LOR}) associated with each effect size estimate were then calculated using:

$$w_{LOR} = \frac{1}{SE^2_{LOR}}$$

We used ES_{LOR} as the dependent variable in our meta-analysis, and w_{LOR} was included to weight each effect size to account for differences in sample size across studies. We were interested not only in the overall effect size but also in the degree to which effect size may be influenced by geographic distance, or whether the study was peer-reviewed on the basis of the metric of originating from the primary vs secondary literature. We thus included these variables as fixed effects in our linear mixed-effects models, and study as a random effect to account for any within-study bias. Implicit in models incorporating geographic distance was that this was a reasonable proxy of the extent to which populations were exposed to differing local selective pressures.

Our approach to the analysis was twofold. First, we assessed whether there was a significant overall effect size for comparisons involving 'local vs foreign' and 'home vs away' criteria. This was done by testing for a significant intercept in our mixed-effects models. Second, we investigated whether our fixed effects had any influence on the magnitude of the effect size estimates. We began with a full model including an interaction between geographic distance and peer review, and reduced models in a stepwise manner. We used maximum likelihood to allow for comparison between

models incorporating different fixed effects, and compared model fit using both Akaike's Information Criterion and log likelihood ratio tests. Geographic distance was *ln* transformed because of the broad range of distances among studies. All analyses were carried out using the *lme* function in S-Plus 6.1 (Insightful Corp., Seattle, WA, USA).

The possibility of publication bias of positive results was assessed by (i) producing and visualizing funnel plots of the standard error of the log odds ratio (SE_{LOR}) vs the log odds ratio effect size (ES_{LOR}) (Light and Pillemer, 1984; Supplementary Material) and by (ii) formally assessing whether peer review had any influence on effect size in a combined dataset of both LA criteria in our mixed effects models.

To quantify the extent of LA across studies in the wild, we determined the overall proportion of statistically significant interpopulation comparisons wherein 'local vs foreign' or 'home vs away' criteria were accepted vs when they were rejected. When statistical significance was not assessed for comparisons in the original study, we used Fisher's exact tests to assess statistical significance on the raw data. Owing to the overall limited number of data points for our analyses, and the limited statistical power for detecting fitness differences in some studies (for example, Ritter, 1975), we also calculated the proportion of comparisons where the 'local' or 'home' population fitness relative to the 'foreign' or 'away' population exceeded one. We repeated these same assessments with an inclusion of laboratory studies,

which added 11 new studies (Tables 1, 2 and Supplementary Table S1). To be included in these analyses, laboratory studies had to provide clear information on known environmental differences between salmonid populations that were testable under common environmental conditions. Such studies clearly do not adequately typify the natural environment, so they were excluded in our formal meta-analysis. There are, however, many conservation situations in salmonids where studies in the wild are not permissible and decision making may depend on results from lab studies (for example, Fraser *et al.*, 2010). Lab studies may also confirm the relative importance of particular traits implicated in putative LA. We did not, however, compare the extent of salmonid LA in wild relative to lab studies, because the two categories of study, thus far, have been largely conducted at different life stages (Table 1 and 2 and Supplementary Table S1).

Fitness data—Results and Discussion

Meta-analysis: We found a significant, positive overall effect size for both local–foreign ($t_{33} = 2.60$, $P = 0.014$; Figure 1a) and home–away criteria ($t_{34} = 2.21$, $P = 0.034$; Figure 1b). This suggested that local populations outperform foreign populations in their home environment, and that survival is higher in home environments relative to being transplanted to different environments. In addition, we found an effect of geographic distance for both LA criteria (Figure 1), although this effect was more pronounced for home–away comparisons, and it depended on the type of model comparison that is used (Supplementary Table S2). We did not find a significant influence of peer review for local–foreign comparisons. While there was some indication that including peer review in the model improved model fit for home–away comparisons, this effect disappeared when geographic distance was included (Supplementary Figure S1; Supplementary Table S2). Funnel plots revealed no asymmetric distributions caused by publication bias. That is, there was no evidence that bottom left-hand sides of the plots were biased towards non peer-reviewed works or contained no data; on the contrary, peer-reviewed studies reported negative results (Supplementary Figure S1).

Extent of LA

Over all statistically significant interpopulation comparisons involving studies in the wild, 77.3% (51 of 66 comparisons) were in favour of the local or home salmonid population (Table 3). Across all 93 significant and nonsignificant comparisons in the wild, the local/ home population had, on average, 1.20 times higher fitness (median = 1.44) over foreign populations or relative to being away, although with considerable variability (range: 6.46 times less to 37.9 times more the average fitness) (Supplementary Table S1). With the inclusion of lab studies, 82.3% of statistically significant comparisons (79 of 96) were in favour of the local/home population, and the average local/home fitness advantage across all 143 comparisons was 1.23 times (median = 1.36 times). In the 47 comparisons with no statistical significance, there was no trend for fitness to be greater (that is, exceed a ratio of 1:1) in the local or home population (wild and lab studies, respectively, local–foreign: 6/13 and 4/11 comparisons towards the local population; home–away:
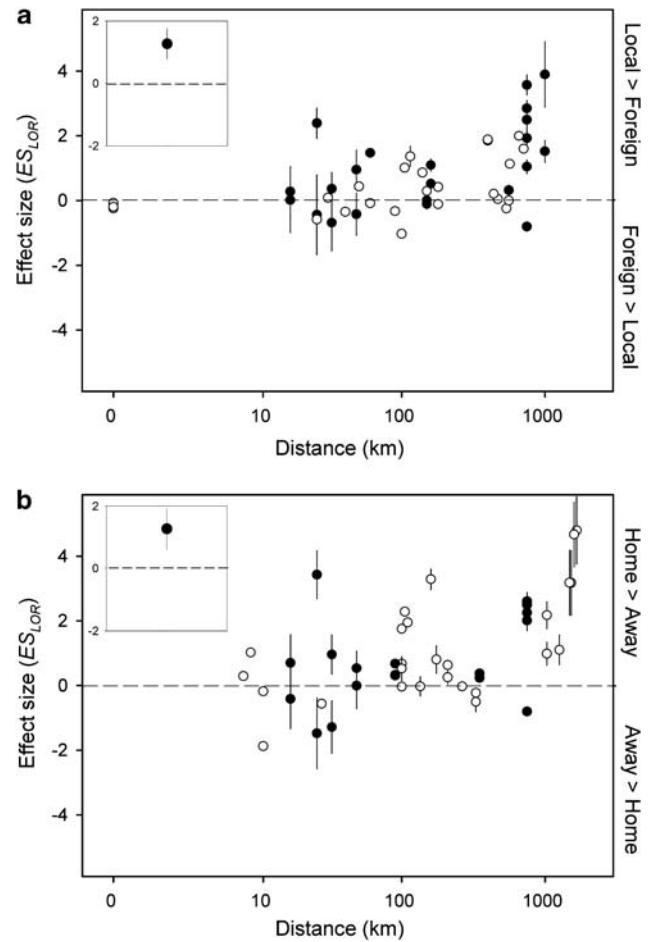

Figure 1 Log odds ratio effect size (ES_{LOR}) plotted against geographic distance (km) for (**a**) local vs foreign comparisons and (**b**) home vs away comparisons involving salmonids. The dashed line represents zero effects and open circles denote studies that were not from the primary literature; closed circles represent primary literature studies. Inset graphs are overall effect sizes and error bars represent SE_{LOR}. Data are from the studies listed in Tables 1 and 2; complete details of the data are found in Supplementary Table S1.

Table 3 Summary statistics for local–foreign and home–away criteria of local adaptation in salmonids

Criterion	Local	No diff.	Foreign/ Away	Total number of comparisons
Local vs Foreign				
Studies in the wild	24	13	11	48
Laboratory studies	16	11	1	28
Combined	40	24	12	76
Home vs away				
Studies in the wild	27	14	4	45
Laboratory studies	12	9	1	22
Combined	39	23	5	67
Both criteria				
Studies in the wild	51	27	15	93
Laboratory studies	28	20	2	50
Combined	79	47	17	143

The table reports the total number of interpopulation comparisons wherein either (i) the local/home or foreign/away population had a statistically significant fitness advantage or (ii) there was no statistical difference ('No difference').

5/14 and 6/9 comparisons towards the home population) (Supplementary Table S1).

Collectively, and depending on the conservativeness of the assessment, the extent of salmonid LA ranged from 54.8 to 69.9%. First, assuming that all nonsignificant comparisons did not reflect LA, the local/home population had greater fitness than the foreign population or when 'away' in 55.2% of comparisons (79 of 143) or in 54.8% of comparisons (51 of 93) for studies in the wild only (Table 3). Second, assuming that any comparison reflected LA if the local-foreign or home-away fitness ratio exceeded one (Figure 1 and Supplementary Table S1), the extent of LA was 69.9 (100 of 143 comparisons) or 66.7% (62 of 93 comparisons) for studies in the wild only.

In summary, based on quantitative measures that could be compared with other studies, the estimates on the extent of LA reported here support that salmonids do not differ in their frequency of LA relative to plants ('local vs foreign' comparisons only: 67.1 (51 of 76 comparisons) vs 71% (740 or 1042 comparisons) from Leimu and Fischer, 2008, Fisher's Exact test, $P = 0.78$) or other assessed taxa, mainly plants and invertebrates (67.1 (51 of 76 comparisons) vs 65% (505 of 777 comparisons) from Hereford, 2009, $P = 0.92$).

The frequency with which foreign populations outperformed local populations (22.9–35.4%; Table 3) also suggests that this is not a rare occurrence in salmonids. A lack of fulfillment of LA criteria does not definitively preclude the existence of LA; for instance, temporal variation in selection or gene flow could result in local and foreign populations exhibiting similar fitness at the time of comparison. Yet this result is intriguing because salmonids are expected to adapt quickly to their local environments (see section on the speed of LA below). It implies that other factors, specifically genetic drift, gene flow and phenotypic plasticity, often affect salmonid LA (Travisano et al., 1995; Hereford, 2009). Why these factors may or may not hinder LA in particular population systems represents an understudied element of salmonid research.

Geographic scale of LA

LA was evident in salmonids at a variety of spatial scales (Figure 1), from several kilometres in European grayling, Thymallus thymallus (Haugen and Vollestad, 2000) to >1000 km in Atlantic salmon, Salmo salar (Ritter, 1975). In addition, as suggested by previous authors (Ritter, 1975; Reisenbichler, 1988), LA generally became stronger as the geographic scale increased at which 'local vs foreign' or 'home vs away' comparisons were made (Figure 1).

A salient feature of this review, however, is that there may be greater variability in the magnitude of LA in salmonids at geographic scales of ⩽100–200 km (Figure 1). At ⩽100 km, for example, a considerable proportion of foreign–local fitness ratios exceeded one (47.1% (16 of 34); 60.0% (12 of 20), excluding lab studies) or local populations performed equally well or better when 'away' than when 'home' (32.4% (11 of 34); 40.0% (8 of 20), excluding lab studies). In other words, at successive 200 km intervals from 0–200 km to 400–600 km, the percentage of comparisons consistent with fulfilling LA in each interval increased (62.8, 76.0 and 80.0%); beyond 600 km, it increased to 92.3% (Figure 1 and Supplementary Table S1). Therefore, although

geographically distant salmonid populations are almost unanimously exposed to very different selective regimes, those between more geographically proximate populations can be similar or different.

Other aspects of the 'scale' of LA

An additional aspect of the 'scale' of LA that we considered was fitness trade-offs. If being adapted to one environment results in maladaptation in another environment, population pairs raised in each others environments should always perform better in their home environment (Kawecki and Ebert, 2004; Hereford, 2009). Only four salmonid studies in the wild have assessed both local–foreign and home–away criteria (Supplementary Table S1); statistically-speaking, the local population always performed better in its home environment in only two of seven comparisons. Nonetheless, a relationship between geographic distance and fitness for each LA criterion (Figure 1) suggests that trade-offs associated with LA do exist in salmonids, and that they are more likely at larger spatial scales where greater differences in environmental features are expected. Alternatively, because isolation by distance typically characterizes genetic differentiation among anadromous populations, gene flow between distant populations is more restricted and therefore less likely to counteract the effect of selection driving LA.

Two aspects of the 'scale' of LA, which we did not consider were (i) whether LA was more or less prominent in salmonids depending on the life stage and (ii) 'adaptation-by-time' (temporal adaptation within the same environment). For (i), generalities await further study because most studies of wild fish have been done on later life stages and most laboratory studies have been restricted to early life stages only. We also urge that potential adaptation to the marine phase of anadromous salmonid lifecycles (Box 2) continues to be an overlooked issue for salmonid conservation (Taylor, 1991). For (ii), Hendry and Day (2005) discussed the theory behind the evolution of 'adaptation-by-time', and there are several examples of spring/summer/winter breeding runs within rivers in some salmonids, which may represent this phenomenon (for example, Waples et al., 2004). In fact, a few data points from our quantitative survey may reflect such temporal adaptation rather than spatial adaptation (Bagatell et al., 1980; Hendry et al., 1998; Beacham and Murray, 1986). Further distinguishing between temporal and spatial adaptation might help to reveal additional insights into the 'scale' of salmonid LA.

Fitness data caveats

No comparisons in our meta-analysis came from nonanadromous populations, so our conclusions are most relevant to anadromous populations. Moreover, all 12 data points from lab studies of nonanadromous populations were derived from one study (Haugen and Vollestad, 2000). Potentially greater spatial and temporal isolation in the habitats that nonanadromous populations inhabit could more readily favour LA than in anadromous populations. Indeed, at neutral genetic markers, nonanadromous populations generally exhibit greater levels of genetic differentiation (F_{ST}) than anadromous populations (DeWoody and Avise, 2000). Conversely, the life histories of nonanadromous popula-

Box 2   Potential for local adaptation to the marine phase in anadromous salmonids

The seemingly homogeneous marine environment suggests that LA likely occurs at larger spatial scales than in freshwater. Survival in freshwater (egg-to-smolt) is often lower than in seawater (smolt-to-adult), so selective pressures also have a potentially greater influence on 'freshwater' than 'marine' adaptation. Thus, some authors suggest that most salmonid LA relates to selective pressures in freshwater (Quinn, 2005; Garcia de Leaniz et al., 2007). Yet marine areas differ in productivity, salinity, temperature, current regimes, prey items, seasonality and predators, as do marine estuaries. Furthermore, both highly varying migration distances (to and from feeding grounds) and persistent spatiotemporal differences in marine distributions have been found between populations of several salmonids (e.g. Svardson and Fagerstroem, 1982; Healey, 1983; Jessop, 1986; Weitkamp et al., 1995). The latter have been shown to be genetically-determined in some cases, where F1 hybrids exhibited intermediate distributions relative to parental populations (Brannon and Hershberger, 1984; Kallio-Nyberg et al., 2000).

Perhaps most importantly, adaptations to marine and freshwater environments are probably inseparably linked. Collective phenotypic differentiation between migratory populations is often difficult to understand without considering it in the context of the entire lifecycle (e.g. Fraser and Bernatchez, 2005). Further inclusion of the marine environment in salmonid LA research is timely because oceanic changes are implicated in the declines or extirpation of some salmonid population groups (e.g. COSEWIC 2006). Such research may also help to reveal why escaped farmed salmonids can outcompete wild salmonids in freshwater stages but then fare poorly in the ocean (see McGinnity et al., 2003), or why nonanadromous salmonids have had greater overall success when introduced to nonnative environments than anadromous ones (e.g. Utter, 2004; Quinn, 2005).

tions (for example, no migrations between freshwater and marine habitats) and other aspects such as lower population sizes might slow down or impede LA.

It also cannot be ruled out that apparent survival differences in some cases may reflect other entities such as different migrations at sea when sampling was conducted/completed (for example, Bartel et al., 2001). Furthermore, many studies, particularly those predating the 1990s, either did not explicitly account for maternal effects or rearing/transfer/release effects, or details were not available to assess whether such effects were negligible in influencing study results (but see Bagatell et al., 1981a, b c). Where applicable, our analysis also assumed that the potential fitness effects of hatchery rearing were equal across the populations being compared (see Fraser, 2008).

Finally, most studies assessed only one or a few components of fitness, usually just survival or a proxy of survival, and they rarely evaluated lifetime success. This was unsurprising because of the logistical constraints of conducting long-term studies on salmonids, but it prevented some potentially very useful analyses. For example, we are unaware of any research on salmonids that has examined whether the extent of being locally adapted confers higher mating success, despite theoretical predictions (Correia et al., 2010). One must therefore be cognizant that salmonid LA (for example, ability to swim upstream to a distant spawning ground) might not necessarily translate into perceptible differences in mating success. More importantly, the apparent lack of LA in some studies could be a result of incomplete fitness surrogates (see Hereford, 2009). Conflicting selection pressures on survival vs reproduction, or at different life stages, might have made it difficult to detect LA.

Overall, as more LA studies are conducted on salmonids, similar or extended quantitative surveys could be carried out to account for potential effects on the extent and scale of LA of separate species, life history types (anadromous, resident, lake migratory and so on), varying population sizes, particular life stages, different environmental gradients and/or varying geographic scales.

Extent and scale of LA inferred from phenotypic/ molecular approaches

We found six chief phenotypic/molecular approaches that have been used to detect natural selection in salmonids, and to relate this to either putative selective agents, specific traits implicated in putative LA, and/or the likely extent and scale of LA (Table 4). We did not review each approach quantitatively because too few studies have been conducted on salmonids for some approaches. Others are discussed elsewhere (Approach IV, see 'Speed of LA' below), whereas others have only been used sparingly at the within-population level (Approaches V, VI). We thus focused more on what Approaches I–III revealed about salmonid LA. Collectively, they provided compelling evidence that LA may be prevalent and may occur at a variety of spatiotemporal scales (and traits), notwithstanding the caveat that detecting true LA with these approaches is either very difficult or impossible (Endler, 1986; Garcia de Leaniz et al., 2007; Table 4).

Agents of and traits under selection

Abiotic or biotic environmental factors that may act as selective agents in salmonids include temperature, photoperiod, surface geology, water chemistry, river hydrology, migration distance, pathogens, parasites, prey, predators and interspecific competitors. Trait or gene variation that is potentially coupled with these selective agents (whether genetically based or inferred to be genetically based) is extensive and will not be exhaustively reviewed here. It extends to all aspects of phenotype, including behaviour, life history, phenology, morphology and physiology (reviewed extensively in Taylor, 1991; Garcia de Leaniz et al., 2007; see also examples included in Table 4).

A key question then is: which traits might be more likely to exhibit LA in salmonids? This is obviously difficult to discern, for the functions of individual traits and their potential link to fitness are most often inseparably linked with other traits (Gould and Lewontin, 1979). Furthermore, very few salmonid studies have experimentally manipulated single traits to measure consequences for fitness (Table 4, also a common trend in studies of LA across taxa: Kawecki and Ebert 2004). If the common-garden laboratory experiments conducted on putative selective agents in salmonids are any indication, an example of particularly strong LA may be pathogen resistance (Supplementary Table S1). For instance, populations of several species of Pacific salmon (*Oncorhynchus* spp.) inhabiting the Columbia River

Table 4 Summary of main approaches (using phenotypic, genetic and/or environmental data) that have been used for detecting natural selection in salmonids and relating this to putative selective agents, specific traits implicated in putative LA, or the likely extent or scale of LA

Approach, general hypothesis	Salmonid examples, traits/genes involved	Reference
I. Correlation with environmental factors		
(a) 'Divergence with gene flow'/landscape genetics-negative association between the extent of phenotypic or habitat differentiation and the amount of gene flow between populations	Trophic ecology and habitat use: AC, LW	1,2
	Habitat or life-history and population structure: AS	3,4
	Breeding/non-breeding habitat features, migration distance: BC	5
	Nonbreeding habitat spatial segregation: AS	6
	Breeding habitat features, reproductive traits: SS	7
(b) Clines selection invoked to explain clinal variation at phenotypic traits (best if corroborated by multiple traits)	Migration timing, spawning time: SS, CO	8,9
	Growth and maturation of precocial males: MS	10
(c) Countergradient variation selection invoked to explain expression of the same phenotype across an environmental gradient	Production and use of carotenoids in migratory and nonmigratory forms: SS	11
	Growth in relation to passage time and digestion rate: BT	
(d) 'Phenotype-environment associations'—a demonstrable genetic basis of trait differentiation, differential gene expression or phenotypic plasticity, and a link with environmental/habitat factors	Single phenotypic traits (many), for example: reviewed in PS, AS	13,14
	Integrative: behavioural, life history, morphological: LW, AS	15,16
	Transcriptomics: differential gene expression among populations or life-history types, related to physiological, metabolic and immune function: LW, AS	17–20
	Genomic basis of anadromous salinity tolerance	21,22
(e) Tests of parallel evolution-independent evolution of the same phenotypes or gene expression in unrelated populations living in similar environments suggests a role for divergent selection in population differentiation	Parallel evolution of life history traits and gene expression between benthic and limnetic population pairs: LW	17,18,23
	Parallel evolution of nonmigratory forms: SS	24
	Parallel evolution of run-timing: CS	25
II. Deviations from neutral expectations		
(a) F_{ST} vs Q_{ST} greater genetic differentiation at quantitative traits (Q_{ST}) than at neutral genetic markers (F_{ST}) suggests a role for divergent selection in population differentiation. Other cases: $Q_{ST} = F_{ST}$ -selection cannot be disentangled from drift $Q_{ST} < F_{ST}$ -stabilizing selection in population differentiation	Embryonic traits: anadromous, resident, lake migratory BT	26
	Embryonic traits and juvenile growth traits: BC, EG, CO	27–29
	Swimming behaviour, growth, morphology: LW	30
	Early-late history traits: CS	31
(b) Single candidate gene approaches greater genetic differentiation at candidate genes potentially exposed to selection relative to selectively neutral genes suggests a role for divergent selection in population differentiation. Alternatively, clinal patterns that cannot be ascribed to neutral processes (for example. corroborated by analysis of neutral loci not showing clinal variation)	Allele frequencies at MEP-2 × temperature, and latitude: AS	32,33
	MHC allelic diversity: AS, SS, BT, RT, CS	34–44
	MHC allelic diversity × temperature, and latitude: AS	36
	Clock gene loci: CS, CO	45,46
	Salinity tolerance: BT	47
	TAP polymorphisms: BT	48
	Transferrin, somatolactin and p53 genes: CS	49
	Tansaldolase gene expression: BT	50
	Growth hormones 1&2, transferrin, immunoglobin: CS	51
	EST-linked microsatellites, comparing immune related versus nonimmune related genes: AS	52
(c) Genome scans—role of selection invoked based on outlier loci, that is, loci at which genetic differentiation deviates from expectations of neutrality	EST-linked and anonymous microsatellites: BT	53
	Amplified fragment length polymorphisms (AFLP): LW	54
	Expressed sequence tag (EST) -linked microsatellites: AS	55
	Transcriptomic scan of recently diverged subpopulations: AS	56
III. Integrative genomics approaches (for example QTL+transcriptomics/SNPs)		
Combining different approaches and targeting several functional and biological levels to investigate the molecular basis of LA	Putative adaptive divergence between benthic and limnetic niches: LW	57,58
	Putative adaptive divergence (genes associated with lipid synthesis and immunity function) between benthic and pelagic niches using RNA-seq and qPCR: LC	59
IV. Perturbation of natural populations		
Trait distributions (or gene frequencies) change relative to before the perturbation due to selection:		
(a) Introductions into new environments (translocations)	CS, SS, EG, AS	60–62,56
(b) Artificially-induced changes to populations or their habitats (eg. experimental manipulations of traits or selective agents)	Early life history traits: AS; body morphology: BT	63,64
(c) Temporary or seasonal environmental shifts (natural/human induced)	Evolution following installation of a fish ladder: BT	65
V. Cohort analysis		
Significant relationship between demography and trait values	Body size, age-specific survival and fitness: BC	66

Table 4 Continued

Approach, general hypothesis	Salmonid examples, traits/genes involved	Reference
VI. Age or life stage analysis		
Selection results in differences in trait or gene frequency distributions between age classes or life stages	AS	67

Abbreviations: AC, Arctic charr (*Salvelinus alpinus*); AS, Atlantic salmon (*Salmo salar*); BC, Brook charr (*Salvelinus fontinalis*); BT, Brown trout (*Salmo trutta*); CH, Chum salmon (*Oncorhynchus keta*); CO, Coho salmon (*Oncorhynchus kisutch*); CS, Chinook salmon (*Oncorhynchus tshawytscha*); EG, European grayling (*Thymallus thymallus*); LC, Lake charr (*Salvelinus namaycush*); LW, Lake whitefish (*Coregonus clupeaformis*); MS, Masou salmon (*Oncorhynchus masou*); PS, Pacific salmon, general (*Oncorhynchus* spp.); RT, Rainbow trout (*Oncorhynchus mykiss*); SS, Sockeye salmon/kokanee (*Oncorhynchus nerka*).
Main sources from which the approaches have been derived or modified: Endler, 1986; Conover and Schultz, 1995; Schluter, 2000; Merila and Crnokrak, 2001; Bernatchez, 2004; Beaumont and Balding, 2004. Ref = reference. Species codes are found in Table 1.
References: 1, Gislason *et al.*, 1999; 2, Lu and Bernatchez, 1999); 3, Vaha *et al.*, 2007; 4, Dionne *et al.*, 2008; 5, Fraser and Bernatchez, 2005; 6, Potvin and Bernatchez, 2001; 7, Wood and Foote, 1996; 8, examples in Quinn, 2005; 9, Spence and Hall, 2010; 10, Morita and Nagasawa, 2010; 11, Craig and Foote, 2001; 12, Nicieza *et al.*, 1994; 13, Taylor, 1991; 14, Garcia de Leaniz *et al.*, 2007; 15, Bernatchez, 2004; 16, Fraser *et al.*, 2010; 17, Derome *et al.*, 2006; 18, St-Cyr *et al.*, 2008; 19, Normandeau *et al.*, 2009; 20, Tymchuk *et al.*, 2010; 21, Giger *et al.*, 2006; 22, Giger *et al.*, 2008; 23, Nolte *et al.*, 2009; 24, Taylor *et al.*, 1996; 25, Waples *et al.*, 2004; 26, Jensen *et al.*, 2008a; 27, Perry *et al.*, 2005; 28, Koskinen *et al.*, 2002; 29, McClelland and Naish, 2007; 30, Rogers *et al.*, 2002; 31, Kinnison *et al.*, 2008; 32, Jordan and Youngson, 1991; 33, Jordan *et al.*, 2005; 34, Landry and Bernatchez, 2001; 35, Consuegra *et al.*, 2005; 36, Dionne *et al.*, 2007; 37, Consuegra and Garcia de Leaniz, 2008; 38, Dionne *et al.*, 2009; 39, Miller *et al.*, 2001; 40, Campos *et al.*, 2006; 41, Hansen *et al.*, 2007; 42, Aguilar and Garza, 2006; 43, Evans and Neff, 2009; 44, Turner *et al.*, 2009; 45, O'Malley *et al.*, 2007; 46, O'Malley *et al.*, 2010; 47, Larsen *et al.*, 2008; 48, Jensen *et al.*, 2008b; 49, Ford, 2000; 50, Amstutz *et al.*, 2006; 51, Heath *et al.*, 2006; 52, Tonteri *et al.*, 2010; 53, Hansen *et al.*, 2010; 54, Campbell and Bernatchez 2004; 55, Vasemagi *et al.*, 2005; 56, Roberge *et al.*, 2007; 57, Rogers and Bernatchez, 2007; 58, Bernatchez *et al.*, 2010; 59, Goetz *et al.*, 2010; 60, Hendry *et al.*, 2000; 61, Haugen and Vollestad, 2000; 62, Kinnison *et al.*, 2008; 63, Einum and Fleming, 2000; 64, Pakkasmaa and Piironen, 2001; 65, Haugen *et al.*, 2008; 66, Morrissey and Ferguson, 2009; 67, McGinnity *et al.*, 2004.

drainage have evolved sympatrically with the parasite *Ceratomyxa shasta* and are far more resistant to bacterial infection than allopatric populations (for example, Buchanan *et al.*, 1983; Hemmingsen *et al.*, 1986). Another case of potentially strong salmonid LA involves the migratory behaviour of newly emerged fry. In many salmonids, innate differences in compass-orientation behaviour between outlet and inlet stream populations correspond to specializations in movement from incubation areas to habitats favourable to feeding and growth (for example, Raleigh, 1971; Kelso *et al.*, 1981). Similarly, traits associated with photoperiodicity (for example, run-timing and spawning time) and hydrology or migration distance (for example, body morphology and swimming performance) may also be under particularly strong selective pressures across different salmonids (Taylor, 1991; Garcia de Leaniz *et al.*, 2007). The application of particular phenotypic molecular approaches discussed below provides an indirect test of determining which traits are most likely under divergent selection (for example, Q_{ST}–F_{ST}), and thus which may be mediating LA.

Approach I
The most common approach applied to studying salmonid LA has been to correlate differentiation at the phenotypic or molecular level with environmental factors in various ways (Approach I and Table 4). For example, several studies have explicitly tested the 'divergence-with-gene flow' model and all found results consistent with its prediction (Table 4). A variety of phenotypic traits and environmental or habitat features throughout the lifecycle were considered. Most studies were conducted on trophically- or migration-differentiated sympatric populations inhabiting post-glacial lakes. Putative LA ranged from smaller geographic scales (that is, the same breeding habitats; Wood and Foote, 1996), to a few kilometres (Gislason *et al.*, 1999; Lu *et al.*, 1999), and to a 'regional' scale of 25–100 km, encompassing multiple populations occupying different

rivers (Potvin and Bernatchez, 2001; Fraser and Bernatchez, 2005). The scale of putative LA in two landscape genetic studies on anadromous Atlantic salmon populations was also variable. It ranged from distances of ⩽20–⩾100 km between mainstem, headwater and tributary populations within a large river system (Vaha *et al.*, 2007), to distances up to several hundred kilometres between regional groups of ecologically- and genetically-related populations occupying separate rivers (Dionne *et al.*, 2008). Several studies have also shown clinal (latitudinal) variation in phenological or life history traits (for example, run-timing and age-at-maturity) in relation to temperature or day length (Table 4). Usually, the role of selection in differentiation was invoked at the scale of 100s to 1000s of kilometers in these studies. Finally, parallel evolution across multiple lakes of the same genetically-based phenotypic differentiation (and in one case gene transcription) has been observed at scales of just a few kilometres between ecotypes occupying distinct, adjacent ecological niches (Table 4).

Approach II
A second major approach used assesses whether greater genetic differentiation occurs at traits/or genes potentially exposed to selection relative to selectively neutral genes, or alternatively whether specific candidate loci are correlated with environmental features not ascribed to neutral differentiation (Approach II). For instance, all six salmonid studies comparing genetic differentiation at neutral molecular markers (F_{ST}) and quantitative traits (Q_{ST}) found that average Q_{ST} exceeded F_{ST} over a total of eight interpopulation comparisons, though not at all (20–60%) individual traits examined, and generally only early life traits were studied (Table 4). These differences were detected between populations separated by a few to 100 km. The approach has also been used to infer the most likely traits implicated in LA. In juvenile 'dwarf' and 'normal' lake whitefish (*Coregonus clupeaformis*) that occupy

limnetic and benthic habitats across multiple lakes, Rogers et al. (2002) found that Q_{ST} significantly exceeded F_{ST} for two of three swimming behaviour traits, one of four meristic traits (gill rakers), but zero of 10 morphological traits. Thus far, however, the ways in which F_{ST}–Q_{ST} comparisons have been implemented in salmonids have a number of caveats meriting further attention (for example, see Hendry, 2002; Whitlock, 2008).

Single candidate gene studies have also provided insight into the potential scale of salmonid LA, especially Major Histocompatibility complex (MHC) studies owing to potentially strong indications of immunity-related selection at MHC alleles and the capability to link such variation to selective agents in nature (for example, pathogens and parasites; Garrigan and Hedrick, 2003). Pathogens and parasites in riverine environments are generally assumed to be widespread across large geographical scales but to have highly heterogeneous distributions at microgeographical scales (Bakke and Harris, 1998). The presence of specific pathogens and parasites can also change drastically even over short time spans causing both spatially and temporally fluctuating selection (Garrigan and Hedrick, 2003). Thus, diversifying selection at MHC loci is expected to occur at small geographical scales and shift over time.

Results from several salmonid studies of variation at MHC-related loci generally concur with this prediction. Evidence for selection at MHC loci has been found at microgeographical scales (within a few kilometres), and with no general tendency of LA to increase with geographical distance, at least at the scale of a few hundred kilometres (Landry and Bernatchez, 2001; Miller et al., 2001; Aguilar and Garza, 2006; Jensen et al., 2008a). Fewer studies have investigated patterns of temporal selection, with some finding either temporally stable or fluctuating selection (Miller et al., 2001; Coughlan et al., 2006; Hansen et al., 2007; Jensen et al., 2008b). Nevertheless, a study comparing MHC Class II diversity in Atlantic salmon with bacterial diversity and temperature regimes in rivers along a North-South axis also suggests macrogeographical patterns of LA (Dionne et al., 2007). Positive relationships were found between MHC allelic diversity and, temperature or bacterial diversity, presumably reflecting selective responses to richer pathogen faunas in warmer water. Hence, putative LA at MHC loci can be viewed as a hierarchical process with different dynamics acting on different geographical scales. Yet a similar study on chinook salmon (Oncorhynchus tshawytscha) found no evidence for any MHC alleles to confer bacterial resistance (Evans and Neff 2009). Further research is merited to discern complexities related to the role of pathogen communities in the evolution of salmonid host LA.

Circadian (for example, CLOCK) genes have also recently attracted interest because of their role in photoperiodicity and determination of seasonal timing (phenology) (Lowrey and Takahashi 2004). For these loci, LA might be expected to occur at macrogeographical scales and mostly along a North-South axis as the photoperiod corresponding to the optimal timing of major life-history events will differ considerably along this axis (for example, adult or juvenile migration timing). A clinal pattern of CLOCK gene variation in chinook salmon populations along >4000 km of Pacific coastline supports these predictions (O'Malley and Banks, 2008).

Genome scans screen large numbers of loci (100–1000s) to estimate the number and proportion of loci linked to genes under selection ('outlier' loci deviating from neutrality). In salmonids, this method has been used to test the hypothesis that divergent selection is implicated in the diversification of populations at several spatial scales (Table 4). For instance, lake whitefish ecotypes inhabiting limnetic ('dwarf') and benthic ('normal') niches across multiple small lakes exhibited 14 outlier loci (of 440 amplified fragment lengh polymorphism (AFLP) loci screened). Among these loci, six exhibited parallel patterns of divergence across ecotype pairs and they were associated with mapped quantitative trait loci (QTL) (mainly linked to growth) (Campbell and Bernatchez, 2004; Rogers and Bernatchez, 2007). Among eight Atlantic salmon populations originating from different spatial scales and with different life histories (anadromous and nonanadromous), Vasemagi et al. (2005) found that more outlier loci were detected at larger geographic scales than smaller ones (25 vs 9, of 95 genomic and expressed sequence tag-derived mini- and microsatellites loci screened). Overall, however, the causal link between such outlier loci, phenotypic traits under selection and fitness remains hypothetical, and in some cases outlier tests can fail to detect loci under selection (Michel et al., 2010). Future such research on salmonids could also benefit from integrating geographical information systems and genome scans to assess putative associations with environmental variables (see Meier et al., 2011; Joost et al., 2007).

Collectively, studies applying Approach II reveal quite different spatial scales of selection and potential LA, corresponding to spatial variation of the associated selection regimes. Hence, similar to results based on fitness data, there appears to be no single spatial scale at which LA occurs; it depends on the specific traits/genes, their functional role and the specific selection regimes.

Approach III
This approach combines methods at several levels of organization (for example, variation at the DNA, gene expression and phenotypic levels) towards understanding the molecular basis of trait adaptation (Table 4). An illustrative salmonid example comes from pairs of dwarf and normal lake whitefish inhabiting multiple small lakes. First, a joint comparison of phenotypic and genome wide transcriptomic differentiation identified the phenotypic (including physiological) traits most likely to be adaptive and hence those meriting further investigation for understanding the molecular basis of adaptation (reviewed in Bernatchez et al., 2010). Then the integrative use of linkage, phenotypic (pQTL) and gene expression (eQTL) mapping revealed the genetic architecture of these same phenotypic traits (Rogers and Bernatchez, 2007; Whiteley et al., 2008). Finally, combined pQTL and eQTL mapping revealed numerous candidate markers resisting the homogenizing effects of gene flow, hence, those genomic regions for which the influence of natural selection in the wild could be methodically tested (Bernatchez et al., 2010). Outlier genomic regions were mainly associated with growth or swimming behaviour, or gene expression associated with these functions (for example, protein synthesis and energy metabolism).

Table 5 Studies focusing on the speed of adaptation in salmonid fishes, and the major phenotypic/gene expression changes associated with putative adaptation

Example	G	Phenotypic or gene expression changes	Reference
Natural colonization			
SS	100	Adult body morphology, egg mass	Pavey et al., 2010
Introductions			
SS	14	Breeding environment features: temperature, flow, migratory vigour	Hendry et al., 2000; Hendry, 2001
EG	10–22	Breeding environment temperatures; embryo developmental rates	Haugen and Vollestad, 2000; Kavanagh et al., 2010; Koskinen et al., 2002
CS	30	Breeding environment features: temperature, flow, migratory vigour	Kinnison, et al., 2001, 2008)
AS	6	Precocial male maturity size threshold, oxidant defense, thyroid hormone metabolism, defense against viral infections, ribosomal RNA processing, transcription regulation, and bacteriolytic function	Aubin-Horth et al., 2006; Roberge et al., 2007
Adaptation to captivity			
RT	1[a]	Not determined	Araki et al., 2007
RT	1[a]	Not determined	Caroffino et al., 2008
RT	2[a]	Not determined	Araki et al., 2009
Fisheries-induced evolution			
AS, PS	6–10	Smaller size-at-maturity	Ricker, 1981; Quinn et al., 2006
SS	7–9	Earlier run-timing	Quinn et al., 2007
EG	10–22	Earlier age-at-maturity	Haugen, 2000
Evolution following fish ladder			
BT	6–7	Size-at-smolting, size-at-maturity	Haugen et al., 2008
Evolution to hydropower dams			
CS	15–20	Age-at-smolting (subyearling to yearling)	Williams et al., 2008

Abbreviations: AC, Arctic charr (*Salvelinus alpinus*); AS, Atlantic salmon (*Salmo salar*); BC, Brook charr (*Salvelinus fontinalis*); BT, Brown trout (*Salmo trutta*); CH, Chum salmon (*Oncorhynchus keta*); CO, Coho salmon (*Oncorhynchus kisutch*); CS, Chinook salmon (*Oncorhynchus tshawtyscha*); EG, European grayling (*Thymallus thymallus*); LC, Lake charr (*Salvelinus namaycush*); LW, Lake whitefish (*Coregonus clupeaformis*); MS, Masou salmon (*Oncorhynchus masou*); PS, Pacific salmon, general (*Oncorhynchus* spp.); RT, Rainbow trout (*Oncorhynchus mykiss*); SS, Sockeye salmon/kokanee (*Oncorhynchus nerka*).
G = numbers of generations; Ref = reference; species codes are found in Table 1.

The speed of LA

Studies following translocations, known environmental perturbations or trait manipulations offer the best available approaches for assessing how fast LA might evolve (Tables 4 and 5). Introduced salmonids can show evidence for phenotypic or gene expression differentiation associated with local environmental features and even restricted gene flow after 6–30 generations; in one case, the evolution of such differentiation from a common source population resulted in a 1.7–2.9 times greater fitness (survival) advantage to the local population after 30 generations (Unwin et al., 2003). Changes to selective regimes following the implementation of fish ladders or hydroelectric dams can result in phenotypic or life-history change within 6–15 generations. Adaptation to captivity, through either a relaxation of natural selective pressures or changes to them, can arise in salmonids even after one or two generations, resulting in fitness reductions of up to 40% per generation in one species (Table 5). Fisheries-induced evolution in the form of life-history change within several generations is also highly suspected in salmonids (Table 5). Heritabilities estimated from some of these works (typically $h^2 = 0.2$–0.4; see Carlson and Seamons, 2008) and likely selection differentials (for example, Williams et al., 2008) imply that there was ample opportunity for selection to operate

quickly. What is largely unknown from these studies is the degree to which study populations had approached local phenotypic optima. Selection should be strongest and the speed of adaptation fastest just following human manipulations or disturbances, followed by a more gradual levelling off and a shift to stabilizing selection as new adaptive peaks are approached (Stockwell et al., 2003; Haugen et al., 2008). At least in the case of introduced sockeye salmon (O. nerka), the local phenotypic optimum for body depth differences between beach and river males may have been reached within 14 generations as the relative difference between the two forms was similar to that normally observed between native populations (Hendry, 2001).

The molecular basis of LA

Our knowledge of the molecular basis of salmonid LA is still rudimentary in part because most phenotypic traits in salmonids are affected by many segregating loci as well as a large amount of nongenetic variability. Furthermore, the whole genome duplication event in salmonids that occurred some 60 million years ago (Allendorf and Thorgaard, 1984) makes it difficult to decipher ortholog from paralog genes, which poses an additional constraint for the development identifying particular loci that may be implicated in LA (for

example, 'true' single-nucleotide polymorphisms; Hayes *et al.*, 2007). Another challenge is that a solid theoretical and analytical framework is currently lacking to identify the role of natural selection in driving LA at the gene expression level. Consequently, we are unaware of any salmonid study that, as yet, has established a causal link between molecular variation and fitness variation in terms of reproductive success and/or survival. But even if the exact genes implicated in salmonid LA remain unknown, questions regarding the molecular basis of LA can be resolved with more recent approaches (see Approach III above).

First, what is the genetic architecture of traits that are under selection: are few loci of large effect implicated in LA, or does LA involve many loci of small effect? Between dwarf and normal whitefish over four independent lakes, only a small proportion of screened loci (AFLP: 1.4–3.2% of 440; single-nucleotide polymorphisms: 1.5% of 6,094) showed evidence of restricted gene flow relative to neutral expectations, suggesting they may be largely implicated in the divergence of the two forms (Campbell and Bernatchez, 2004; Renaut *et al.*, 2010). Rogers and Bernatchez (2005) also reported that 8 of 27 QTL linked to growth may be implicated in dwarf–normal adaptive divergence, of which only two QTL showed parallel reductions of gene flow over the four lakes. This again suggested that only a small proportion of genes may be implicated in LA. Nevertheless, for a host of reasons, current approaches for detecting outlier loci may be biased towards finding genes of large effect (for example, Michel *et al.*, 2010). More importantly, although salmonid studies have found that a few principle traits differ because of a few genes, it is very likely that many traits influence fitness differences between populations inhabiting different environments. Hence, in most cases, many genes of small or moderate effect undoubtedly underlie such fitness differences (see Michel *et al.*, 2010; Schluter *et al.*, 2010).

Second, do cases of parallel evolution of LA in salmonids involve the same genes or different ones? In dwarf and normal lake whitefish several hundred genes (approximately 11–15% of the total number of expressed genes) were differentially expressed between pairs in each of four lakes, but nearly 100 genes showed a parallel pattern of expression both in the lab and in the wild (discussed in Bernatchez *et al.*, 2010). Limnetic 'dwarfs' consistently showed significant overexpression of genes associated with survival through enhanced activity (energy metabolism, muscle contraction, homeostasis, lipid metabolism and detoxification). Genes associated with growth (protein synthesis, cell cycle and cell growth) were generally upregulated more so in the benthic 'normals'. Overall, LA in this case appears to involve a differential trade-off between growth, correlated fecundity and survival, which is mediated through the higher energetic cost of occupying the limnetic niche. Again, LA in lake whitefish also occurs at an exceptionally small spatial scale (different adjacent habitats within the same lakes).

A second case comes from the studies of Giger *et al.*, 2006, 2008). They found that migratory and non-migratory brown trout (*Salmo trutta*) sampled from independent, replicated vicinities consistently showed differential expression at several genes, but no differences were detected within life-history types. Intrigu-ingly, these genes may be consistently involved in preconditioning to seawater within anadromous populations, as similar patterns of expression were observed in both anadromous brown trout and anadromous Atlantic salmon (although the studies were based on wild-caught fish).

Eventually, it will be feasible to obtain genome scale insights into natural variation in salmonids through comparative sequencing of thousands of individual genomes from individual species (Tautz *et al.*, 2010). Combined QTL mapping and genome scans should also help to establish a firmer link between the strength of selection acting on different genomic regions and its consequences for LA. Alternatively, across populations, one could genotype many 1000s of single-nucleotide polymorphisms in a large number of phenotypically-diverse individuals to perform whole-genome association mapping in nature, thereby circumventing the need to first conduct linkage mapping from families reared in controlled conditions (Slate *et al.*, 2009). Overall, the speed of genomic data generation will soon outstrip the capacity of data analysis given current computational resources. Yet even once computational power is solved, the power offered by new generations of genomic tools for understanding LA will only be commensurate with: (i) the pertinence of questions being asked, (ii) the theoretical framework into which these questions are imbedded, (iii) the strength of the study design and (iv) integration with more 'classical' approaches of LA (for example, reciprocal transplants and translocations).

Conclusion

Although our review confirms that LA is prominent within salmonid species (~55–70% of the time), we demonstrate that it may be less prevalent than has been traditionally assumed, and no different in frequency relative to other assessed taxa. Our review also reiterates that empirical data on salmonid LA remain sparse. Although salmonid LA occurs at a wide range of scales and, hence, is undoubtedly linked to these species' persistence (Waples, 1991), productivity (Schindler *et al.*, 2010) and roles in community dynamics (Carlson *et al.*, 2011), it is generally not as frequent or strong at smaller geographic scales. Salmonid LA also exists at both larger and smaller geographic scales than at the 'one river' level, the scale that has been traditionally accepted in the literature. A key research direction will continue to be the assessment of the extent and the scale of potential human-induced maladaptation (through climate and habitat alternations, fisheries, aquaculture, hatcheries, captive breeding and so on), as well as its consequences for salmonid evolution and persistence. Clarifying the magnitude of LA and fitness trade-offs in relation to geographic scale could also be very useful for optimising future species restoration efforts, including reintroductions and the maintenance of genetic variation within captive populations through artificial gene flow. Finally, only through an integrative approach that establishes a causal link between the molecular and phenotypic level will it be possible to understand the causes of diversity within salmonids. Owing to the resource demands of such endeavours, now more than ever it is imperative that greater collaboration between disciplines be undertaken.

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Conflict of interest

The authors declare no conflict of interest.

Acknowledgements

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