LETTER

Independent lineages in a common environment: the roles of determinism and contingency in shaping the migration timing of even- versus odd-year pink salmon over broad spatial and temporal scales

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Abstract

Studies of parallel evolution are seldom able to disentangle the influence of cryptic environmental variation from that of evolutionary history; whereas the unique life history of pink salmon (*Oncorhynchus gorbuscha*) presents an opportunity to do so. All pink salmon mature at age two and die after breeding. Hence, pink salmon bred in even years are completely reproductively isolated from those bred in odd years, even if the two lineages bred in same location. We used time series (mean = 7 years, maximum = 74 years) of paired even- and odd-year populations from 36 rivers spanning over 2000 km to explore parallelism in migration timing, a trait with a strong genetic basis. Migration timing was highly parallel, being determined almost entirely by local environmental differences among rivers. Interestingly, interannual changes in migration timing different somewhat between lineages. Overall, our findings indicate very strong determinism, with only a minor contribution of contingency.

Keywords

Contingency, convergent evolution, determinism, evolutionary history, migration timing, non-parallel evolution, parallel evolution, phenology, pink salmon, run timing.

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INTRODUCTION

The relative importance of deterministic natural selection versus contingent evolutionary history remains a major question in evolutionary biology (Blount *et al.* 2018). Parallel (or convergent) evolution, the repeated evolution of similar traits in similar habitats, provides evidence for a deterministic role of natural selection; yet even in natural systems considered to be classic examples of parallelism, outcomes typically involve substantial non-parallelism (Langerhans 2017; Oke *et al.* 2017; Bolnick *et al.* 2018). When non-parallelism is detected, its cause can be hard to determine (Travisano *et al.* 1995; Langerhans & DeWitt 2004). One reason is that the supposedly replicate environments – and presumed similar selection pressures – actually differ cryptically (e.g., Berner *et al.* 2008; Kaeuffer *et al.* 2012; Moore *et al.* 2016). Alternatively, past evolutionary events might generate cryptic genomic variation that makes different 'replicate' lineages respond differently to the same selective regime (Travisano *et al.* 1995; Langerhans & DeWitt 2004; Pfenninger *et al.* 2015; Blount *et al.* 2018).

The importance of these different contributions to non-parallelism can be assessed through 'replay experiments' in the sense of Gould's (1989) famous thought experiment of replaying the tape of life to see whether the new biosphere outcomes would differ from the contemporary biosphere (Blount *et al.* 2018). For instance, laboratory experiments can generate multiple replicate environments and replicate evolutionary lineages to assess the effects of each on evolutionary trajectories and end-points (Travisano *et al.* 1995; Langerhans & DeWitt 2004; Blount *et al.* 2018). Laboratory environments, however, are highly simplified and cannot address the extent to which cryptic environmental variation and cryptic evolutionary history shape parallel and non-parallel outcomes in nature. Hence, we also need to study natural replay experiments (Blount *et al.* 2018), such as introductions or range expansions (e.g., Reznick & Bryga 1987; Walsh & Reznick 2010; Kolbe *et al.* 2014), responses to environmental gradients (e.g., Nosil *et al.* 2002; Mahler *et al.* 2013; Stuart *et al.* 2017) or long-term surveys of responses to environmental change (e.g., Silvertown *et al.* 2006; Gardner *et al.* 2011). Such studies inform our understanding of the role of determinism versus contingency in shaping both current patterns of biodiversity and contemporary evolutionary responses to changing environments – most obviously climate change (Parmesan 2006). Yet in such natural 'experiments', it takes a very particular type of organism to allow a clear partitioning of the different

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contributions to determinism and contingency. We study just such an organism, which has two reproductively isolated lineages in a single species replicated across many locations across large environmental gradients.

Pink salmon, *Oncorhynchus gorbuscha* (Walbaum, 1792), is a semelparous species of Pacific salmon that, in their native range, matures at 2 years of age and dies shortly after breeding (Quinn 2018). As a result of this invariant maturation schedule, pink salmon breeding in even years (2000, 2002, 2004, etc.) versus odd years (2001, 2003, 2005, etc.) represent genetically distinct, temporally isolated lineages that do not interbreed, even if they breed in the same locations (Godfrey 1959; Aspinwall 1974; Hawkins *et al.* 2002; Beacham *et al.* 2012; Seeb *et al.* 2014). Considerable gene flow occurs among populations *within* lineages, but gene flow *between* lineages is exceedingly rare (Aspinwall 1974; Churikov & Gharrett 2002; Hawkins *et al.* 2002). Indeed, even-year North American populations are more closely related to even-year populations breeding more than 2000 km away in Asia, than they are to odd-year populations breeding in the same locations (Churikov & Gharrett 2002; Hawkins *et al.* 2002; Tarpey *et al.* 2017). In short, even- and odd-year pink salmon represent distinct evolutionary lineages that have been isolated from each other for thousands of generations that now breed in the same locations across a huge geographical range (Aspinwall 1974; Beacham *et al.* 1988; Churikov & Gharrett 2002; Limborg *et al.* 2014).

The two lineages of pink salmon using the same breeding area should experience the same average selective regime, especially as they apparently also occupy the same regions in the ocean before returning to breed in fresh water (Radchenko *et al.* 2018). Although important abiotic and biotic environmental variables in fresh water and the ocean (e.g., temperature, precipitation, prey availability, predators, and parasites) vary across years (Quinn 2018), none of these variables should differ consistently between even and odd years for a given location. Hence, in a completely deterministic world, no adaptive phenotypic differences would be expected between the lineages at a given breeding location. However, differences have long been reported (Godfrey 1959; Ricker 1962, 1981), suggesting that the two lineages could respond differently to the same environmental variables. The same could be true for ongoing environmental change. Pink salmon run timing in south-eastern Alaska has been getting earlier in recent years, seemingly in response to climate change (Taylor 2008; Kovach *et al.* 2012, 2013, 2015), but even- and odd-year lineages might vary in their responses.

In pink salmon, strong parallelism (similar phenotypes within rivers, regardless of lineage) would suggest a deterministic role of natural selection, whereas substantial deviations from parallelism would suggest an important contribution of contingent evolutionary history. Previous work hints that either outcome could be possible. At the genomic level, recent analyses of the two lineages across three locations from Washington State to Alaska have found strong signatures of both parallel and non-parallel evolution (Limborg *et al.* 2014; Seeb *et al.* 2014). At the phenotypic level, adult body size varies among rivers; yet within rivers the odd-year lineage is sometimes larger bodied than the even-year lineage (Godfrey 1959;

Beacham & Murray 1985; Beacham *et al.* 1988). However, for robust inferences about *evolution*, we need a trait that has an exceptionally strong genetic basis – as opposed to body size, which is strongly influenced by environmental effects.

An excellent candidate trait is the timing of the annual return migration from the ocean to fresh water (henceforth 'run timing'). As with other salmonids (Quinn *et al.* 2016), run timing in pink salmon is highly heritable, with estimates of narrow sense heritabilities typically in the range of 0.2–1.4 (Smoker *et al.* 1998; Dickerson *et al.* 2005; Carlson & Seamons 2008). The trait also shows considerable evidence of adaptive divergence among populations in different environments, such as cold versus warm water (Taylor 1980; Smoker *et al.* 1998; Carlson & Seamons 2008; Gharrett *et al.* 2013). Early studies by Skud (1958), Merrell (1962), Aro & Shepard (1967), and Helle (1970) suggested differences in run timing between even- and odd-year lineages of pink salmon in some instances; however, the topic has not been recently or comprehensively examined, nor has this trait been used to evaluate parallel evolution.

Our overarching goal was to determine the relative contributions of current environments and evolutionary history to parallel and non-parallel patterns of variation in pink salmon run timing across a broad spatial (from 55° to 63° N) and temporal (from 1926 to 2016) scale. First, we used variance partitioning to assess the relative contributions of evolutionary history (lineage), environment (river of origin), and their interaction to observed variation in run timing. Second, we evaluated the extent to which a broad proxy for environmental variation among locations (latitude) explains the parallel spatial variation. Third, we considered whether recent temporal environmental variation across years (e.g., climate warming) influences parallel or non-parallel phenotypic changes in contemporary time.

MATERIALS AND METHODS

We reviewed published literature and government reports to find studies reporting pink salmon run timing for individual rivers. We also queried online government databases (Alaska Department of Fish and Game [ADF&G] commercial fish count data search tool, online at: http://www.adfg.alaska.gov/sf/FishCounts; Fisheries and Oceans Canada [DFO] 'WAVES' catalogue and search tool, online at: http://waves-vagues.dfo-mpo.gc.ca), and contacted agencies and hatcheries that might collect relevant data. We limited our analysis to rivers with at least 2 years of data from both even and odd years. Overall, data on 36 rivers were collected, ranging from 1925 to 2016 and from British Columbia, Canada, to Alaska, USA (Fig. 1, Table S1).

Most data came from daily counts at fences and weirs, structures that partially control upstream salmon migration to allow for accurate enumeration of salmon prior to spawning. For consistency, we excluded data from studies that counted fish at other stages in their migration, such as test fisheries in marine waters or aerial surveys of breeding grounds. A potential confounding issue with using weir data is that the distance upstream from the ocean differed among rivers, so the relative importance of marine and riverine conditions might differ (see
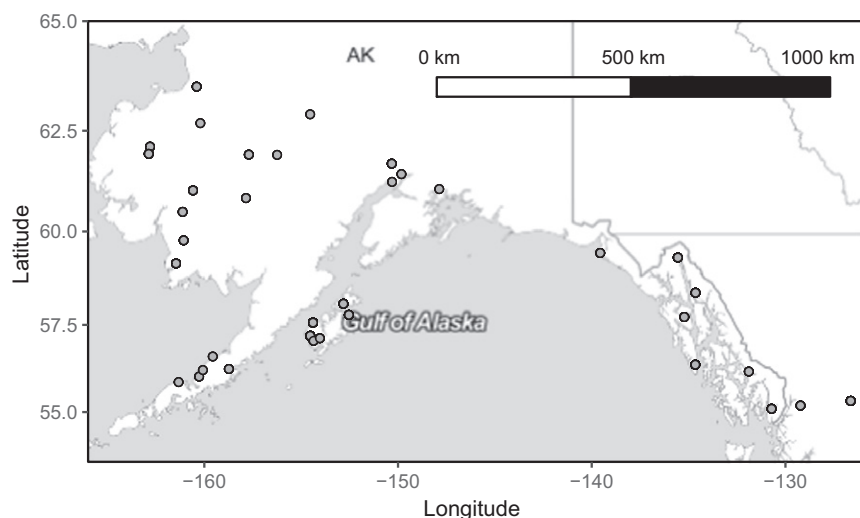
Figure 1 Map of the study area, including southern Alaska and northern British Columbia, with rivers included in the analysis shown as grey circles. This map was created in the package ggmap (Kahle & Wickham, 2013) in R (R Development Core Team, 2012), using data downloaded from Google.

Hodgson *et al.* 2006). However, most pink salmon populations breed near the coast (Heard 1991) shortly after completing their migration into fresh water, so the timing of migration and breeding tend to be similar in pink salmon (Quinn *et al.* 2016). Weir placement along rivers likely reflects the biology of each system; rivers with longer migration distances tend to have weirs farther upstream. Nonetheless, in the supplemental information we include an analysis of the influence of migration distance on run timing, which reveals that migration distance has only a very minor effect on run timing that is likely due to a strong correlation between migration distance and latitude.

Run timing data were typically reported as daily counts of upstream migrants but reports of median return date were also considered. To directly compare these two types of data, and to obtain an easily comparable metric across rivers, we fit normal distributions to daily count data to estimate median date of return. In some cases, the daily records had missing data due to flooding events, late installation or early removal of the counting fence or weir (especially those primarily installed to count other species), or other unexpected events; therefore, fitting a curve to these data allowed a more accurate estimate of return date than a simple empirical measure, such as the date by which 50% of the total annual count had migrated past the weir. Normal distributions were fit to daily count data by minimising the negative log-likelihood of the model given the data, using the package *bbmle* (Bolker & R Development Core Team 2016). Observation error was assumed to be Poisson distributed, as the data represent counts of individual pink salmon over a daily sampling time interval. Lack of fit was evaluated visually and years for which the data were too sparse (or for which fit was judged to be spurious, irrespective of the actual run timing) were discarded. These data were typically for years in which no peak in arrival occurred, often due to early weir removal or too few individuals returning. Rivers with fewer than 2 years in each lineage after removing years with poor fits were excluded

from analysis. After this extensive quality control, we retained data from 36 rivers, ranging from 4 to 69 years in each (mean of 7 years, Table S1).

Variance partitioning

To determine the relative contributions of evolutionary history (lineage), environment (river), and their interaction to run timing phenotypes, we conducted variance partitioning and analysis of variance (ANOVA) using the *car* package (Fox & Weisberg 2011). Significance was tested at an alpha level of 0.05 using type III sums of squares (due to the presence of a significant interaction term) and effect sizes were estimated as η^2 (SS_{effect}/SS_{total}) using the package *heplots* (Fox *et al.,* 2007). Median date of return was the response variable. Lineage (even or odd) and river were both fixed factors. Although river could have been a random factor, its specification as a fixed factor allows us to directly compare effect sizes between the evolutionary history and environment proxies (e.g., Langerhans & DeWitt 2004; Langerhans *et al.* 2006).

General additive models for environmental effects

The freshwater temperature regimes to which embryos are exposed during development vary spatially and temporally over our dataset and seem likely to influence parallelism in run timing. We analysed freshwater temperature effects, as well as long-term and lineage-specific changes in run timing, using linear models and generalised additive models (GAMs).

The timing of salmon breeding is closely linked to the temperature regimes experienced by developing embryos; salmon should breed at a population-specific 'optimum' that allows for appropriate timing of juvenile emergence (Sheridan 1962; Brannon 1987; Hodgson & Quinn 2002). In general, the higher the latitude, the colder the temperatures experienced by embryos, and the earlier adults breed (Brannon 1987; Hodgson & Quinn 2002; Brannon *et al.* 2004). Given that

incubation temperature is not known for the specific breeding locations of each population, nor were freshwater temperature measurements available for most rivers, we used the latitude of the weir, or if this information was not available, the latitude of the mouth of the river (10/36 cases) as a proxy. However, because we have only a single river at each latitude, these two factors are highly collinear and could not be included in the same model (e.g., including a random effect of river with a fixed effect of latitude would mean each level of the random effect has no variation or replication, making it non-estimable). For this reason, we fit the model described below twice, once with river included as a fixed factor and once with latitude included as a covariate.

To incorporate spatial and temporal effects into our models, we first included the same linear fixed effects as in the variance partitioning methods: river, lineage, and a river-by-lineage interaction. We detected evidence of nonlinearity through time, so we added a year-by-lineage as a nonlinear factor smoothed interaction, which allowed each lineage to be treated as independent time series. We used the 'GCV.Cp' smoothing parameter estimation method in package *mgcv* (Wood 2004, 2006, 2011) to cross-validate for the optimal amount of smoothing. We tested for spatial and temporal autocorrelation by including a smoothed latitude by longitude interaction and autocorrelated error term in our models, neither of which was supported by the data. As mentioned above, the same model also re-fit with latitude as a covariate in the place of river because both terms cannot be included in the same model. Finally, we took two steps to confirm that our results were not influenced by statistical artefacts from including short time series or tributaries from the same watershed. First, we re-fit our models to a subset of river-specific time series that included 10 or more years of data. Second, we re-fit our models to include only the single longest time series from each watershed, which resulted in the removal of two Yukon River tributaries and five Kuskokwim River tributaries. In all cases, the results remained the same, thus confirming that heterogeneity in time series duration and watershed structure did not influence model results; see supplemental information.

To estimate effect sizes for GAM parameters, we calculated the proportion of variance explained by each fixed effect by dropping that effect from the model and comparing the R^2 of the new model to the R^2 of the full model. We calculated R^2 following Xu (2003); but using the adjusted R^2 from the function 'summary.gam' gave equivalent results. All analyses were performed in the R statistical language (R Development Core Team 2012).

RESULTS

Variance partitioning

Most of the variation in pink salmon run timing was due to the environment (river: $\eta^2 = 0.779$, $F_{35,652} = 30.3$, $P < 0.0001$), whereas evolutionary history had no effect (lineage: $\eta^2 = 0.0004$, $F_{1,652} = 1.56$, $P = 0.21$). However, a significant river-by-lineage interaction indicated that, although neither lineage was consistently earlier, even- and odd-year lineages sometimes differed in timing within a river ($\eta^2 = 0.022$, $F_{35,652} = 2.10$, $P = 0.0003$; Fig. 2). We conclude
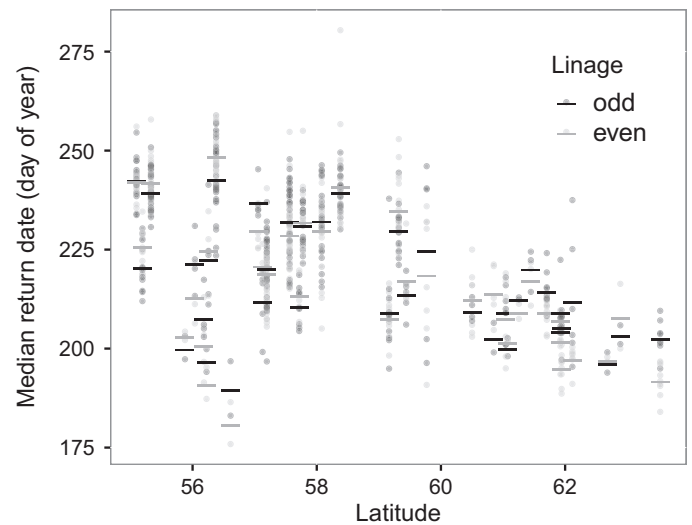

Figure 2 Pink salmon return date by latitude. In general, the median return date for even-year (dark grey circles) and odd-year (light grey circles) pink salmon is earlier in the year at higher latitudes, but individual rivers at similar latitudes vary markedly in their run timing. Each latitude represents a single river and each data point represents the median date of return for that river in a given year. The average (across years) median return date for each lineage in each river shown as horizontal lines.

that run timing is predominantly shaped by environmental differences among rivers, with only a minor contribution of evolutionary history.

General additive models for environmental effects

General additive models confirmed that environment had by far the strongest effect on run timing (proportion of variance explained = 0.651, $F_{35} = 27.4$, $P < 0.0001$), but also revealed some interesting nuances. Most notably, formally considering temporal variation in run timing by including a nonlinear smoothed year-by-lineage interaction revealed different patterns for the two lineages (proportion of variance explained = 0.015, $F = 2.71$, $P < 0.0001$, Fig. 3a). Specifically, odd-year pink salmon showed greater variation in their long-term run timing trend than did even-year pink salmon (Fig. 3b). Consistent with the earlier ANOVA, neither lineage was earlier overall (proportion of variance explained = 0.019, $F_1 = 0.069$, $P = 0.793$), but a significant river-by-lineage interaction suggested that lineage differences were more important in some rivers than in others (proportion of variance explained = 0.020, $F_{35} = 1.94$, $P = 0.001$).

We next replaced the categorical 'river' with the continuous 'latitude' as a linear predictor and re-ran the above GAM. In this case, latitude (like river before) explained a much larger proportion of the variation in run timing (proportion of variance explained = 0.267, $F_1 = 131$, $P < 0.0001$) than did the other terms in the model, including the lineage effect (proportion of variance explained = 0.002, $F_1 = 0.097$, $P = 0.755$). In general, pink salmon at higher latitudes returned earlier than pink salmon at lower latitudes (Fig. 2; coefficient for latitude = −8.28). As in the GAM that included river, the lineages
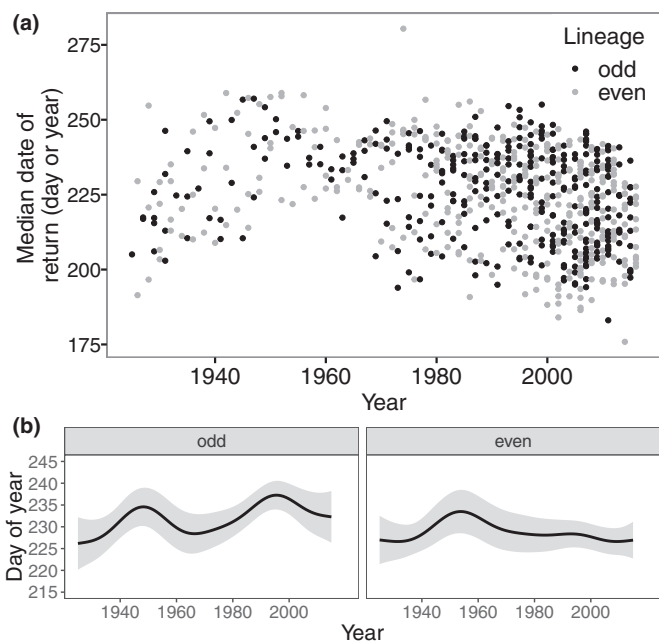
Figure 3 Pink salmon run timing shows complex patterns through time. (a) Median date of return (as day of year) indicated that, in general, both lineages shifted towards later return dates until around the 1950s, and since then have been shifting earlier. Each data point represents the median date of return for a single river in a single even (light grey circle) or odd (dark grey circle) year. (b) The general additive model (GAM) more precisely revealed that odd-year and even-year lineages show different patterns through time, shown here as the conditional partial plot for the year-by-lineage interaction smoother. To facilitate interpretation, year smoothers (the variable of interest) are shown with all other variables held constant at their median value or most common value (i.e., longest time series, Karluk River). No river-by-year-by-run interaction was included so the smoothers for all rivers show the same pattern (though intercepts may shift earlier or later depending on local phenotypes).

differed in their patterns through time (proportion of variance explained = 0.069, $F = 4.38$, $P < 0.0001$), although the latitude-by-lineage interaction was not significant (proportion of variance explained = 0.002, $F_1 = 2.75$, $P = 0.097$). Overall, the GAM that included latitude was far less informative and explained far less of the deviance (adjusted $R^2 = 0.421$) than did the earlier GAM that included river (adjusted $R^2 = 0.794$). The lower explanatory power of latitude than river suggests that although latitudinal patterns in run timing are present, environmental factors at the local river scale play a more important role in determining run timing. For this reason, we focus most of our discussion on the GAM that included river rather than latitude.

DISCUSSION

Run timing in pink salmon shows strong parallelism. That is, local river-specific environmental differences shape run timing to the extent that two reproductively isolated lineages (even and odd) of the same species evolve very similar phenotypes within each river and often very different phenotypes in different rivers. Strong divergent selection among rivers has thus generally overwhelmed any legacy of past evolutionary history, leading to strong determinism in spatial variation in an

important adaptive trait. In addition to this strong spatial parallelism, the different lineages show some differences in their long-term changes in run timing. Although they are relatively minor compared to the strong determinism among rivers, these contingent responses are interesting from a global climate change perspective. Overall, run timing is strongly deterministic, especially across space, with an interesting hint of contingency, especially across years.

These general conclusions make sense given the biology of the study species. In particular, the strong effect of local river on salmon life history timing is known to reflect local environmental conditions. For instance, previous studies of pink salmon (Sheridan 1962), sockeye salmon (*O. nerka* (Walbaum, 1792); Brannon 1987; Hodgson & Quinn 2002; Lisi *et al.* 2013), and Chinook salmon (*O. tshawytscha* (Walbaum, 1792); Brannon *et al.* 2004) show that populations breed earlier in rivers where embryos incubate in colder water. A broad-scale predictor of incubation temperature (as well as other environmental factors) should be latitude (Hodgson & Quinn 2002; Beechie *et al.* 2008). In our study, however, latitude as a continuous predictor variable explained considerably less of the variation in run timing than did river as a categorical predictor variable, indicating that local environmental differences among rivers have stronger effects on trait variation than do large-scale, latitudinal gradients. Indeed, previous work has documented fine-scale variation in run timing across salmon populations due to very local geomorphological attributes (Sheridan 1962; Brannon 1987; Lisi *et al.* 2013; Kovach *et al.* 2015). Our study shows that these local factors strongly and deterministically shape current trait values in pink salmon despite the thousands of generations of isolation between the two lineages (Aspinwall 1974; Churikov & Gharrett 2002; Tarpey *et al.* 2017).

Parallelism

Early studies reported some differences in run timing between odd- and even-year pink salmon in the same river(s) (Skud 1958; Merrell 1962; Aro & Shepard 1967; Helle 1970). We confirmed that such differences between lineages do occur in some rivers, but that – overall – local environmental conditions were the predominant driver of run timing variation. For traits other than run timing, even greater differences between the even- and odd-year lineages have been suggested, including in body mass (e.g., Godfrey 1959; Bilton 1973; Ricker 1981), body length (Bilton 1973; Beacham & Murray 1985; Beacham *et al.* 1988), body shape (Beacham 1985), developmental rates (Beacham *et al.* 1988) and gill raker number (Beacham 1985). Thus, perhaps run timing shows stronger spatial parallelism than do other traits in pink salmon, although confirming this expectation must await formal analyses of parallelism for more traits. If run timing turns out to be exceptionally parallel in relation to those other traits, then selection on run timing is likely more consistent within rivers and more divergent among rivers than is selection on other traits. The next step then would be to determine why, with candidate reasons being the high heritability of run timing (Smoker *et al.* 1998; Dickerson *et al.* 2005; Carlson & Seamons 2008) and the high fitness costs of migrating too early

or too late (Smoker *et al.* 1998; Quinn 2018; Tillotson *et al.* 2018).

The parallelism we documented for pink salmon was strong in comparison with parallelism reported for phenotypic traits in other fishes. For instance, meta-analyses have reported R^2 for the fixed effect of habitat type from linear models fit on population means (Langerhans 2017; Oke *et al.* 2017). Employing this method for pink salmon run timing gives an R^2 of 0.78 for the effect of river (habitat) – although direct comparison might not be optimal because the meta-analyses grouped populations by a given habitat 'type', such as lake versus stream, benthic versus limnetic, or high predation versus low predation. Only the unique life history of pink salmon (odd- and even -year lineages in the same rivers) allowed the use of specific locations (rivers), as opposed to habitat type (Oke *et al.* 2017), as the fixed effect for assessing parallelism. However, taking the R^2 comparison at face value, 0.78 is much higher than the mean R^2 across all traits for live bearing fishes (0.41 ± 0.29 SD: Langerhans 2017) and for fishes in general (0.46 ± 0.32 SD: Oke *et al.* 2017). Yet, pink salmon run timing does not stand alone: parallelism as strong or stronger was observed in 14% of traits examined by Langerhans (2017) and 19% of traits examined by Oke *et al.* (2017). For example, $R^2 \geq 0.90$ was calcuated for gill raker number in multiple species. Much like run timing in pink salmon, gill raker number typically shows very high heritability (e.g., Hagen 1973; Rogers & Bernatchez 2006; Glazer *et al.* 2014) and the fitness costs of deviations from the apparent optimum are likely high (Kahilainen *et al.* 2011).

These results and comparisons support a hypothesis that parallelism will be strongest for traits with two properties. First, selection should be strongly stabilising within habitats and strongly divergent among habitats. In other words, environmental variability should be low (and therefore a single narrow fitness peak) within a habitat relative to among habitats; and the cost to individuals whose phenotype differs from the optimum therefore should be high. Indeed, theory predicts that adaptive divergence, adaptive radiation, and speciation should be strongest on adaptive landscapes that are 'rugged' – with multiple, steep fitness peaks separated by deep and wide valleys, although not so deep as to prevent adaptation to new peaks (Schluter 2000; Arnold *et al.* 2001; Hendry 2017). Second, the trait should have a strong genetic – as opposed to plastic – basis. This facet of the hypothesis might not seem straightforward from a theoretical perspective, because plastic responses also could lead to similar phenotypes in similar environments (Oke *et al.* 2016). However, the first facet of the hypothesis (strong divergent selection among habitats) is expected to favour genetic (as opposed to plastic) divergence (Hendry 2016). Thus, parallelism of traits – and a strong genetic basis for those traits – might both be consequences of strong and predictable divergent selection – as opposed to a strong genetic basis for a trait being a cause of strong parallelism.

Temporal trends

Selection varies not only in space but also in time (Siepielski *et al.* 2013), yet very few studies have considered parallelism through time (Bolnick *et al.* 2018). Our data allowed us to ask: to what extent do the two different lineages show similar responses to environments that are changing over time? In these data, a significant year-by-lineage interaction indicated that even- and odd-year pink salmon showed somewhat different average interannual trends in run timing. Specifically, the odd-year lineage has recently (post 1960s) trended toward later run timing, whereas the even-year lineage has trended toward earlier run timing (Fig. 3). Although these temporal differences between lineages explained far less of the overall variation in run timing than did spatial variation shared by the lineages, they remain interesting from the perspective of global climate change.

Extensive research on phenotypic responses to climate change has revealed that diverse taxa have advanced their phenology (timing of seasonal activities) with remarkable consistency. That is, although *rates* of change vary among populations and taxa, the vast majority of populations and species share a 'fingerprint' of recent advances in spring/summer phenological timing (Walther *et al.* 2002; Parmesan & Yohe 2003; Poloczanska *et al.* 2013). Previous location-specific observations from south-eastern Alaska also show that pink salmon are migrating earlier (Taylor 2008; Kovach *et al.* 2013, 2015). However, GAMs revealed that the two lineages of pink salmon showed relative similar temporal changes in run timing until the 1970s, and then showed divergent responses until the 1990s, with odd-year lineages migrating increasingly later and even-year lineages migrating increasingly earlier (Fig. 3b). The shared trend towards earlier migration in both lineages is relatively recent, starting in about 1995. Moreover, temporal trends continue to differ substantially among rivers (Fig. 4). Our results therefore suggest that – perhaps in analogy with fingerprints – no two responses to global change are identical, being instead characterised by considerable variation among lineages and locations. Indeed, other studies have revealed similar variation (e.g., Primack *et al.* 2009; Diez *et al.* 2012).

The causality of the temporal patterns – and variation in them – cannot be discerned from our data; yet the considerable variability in temporal patterns among rivers and lineages supports the assertion that phenological responses to climate change are highly context-dependent (Primack *et al.* 2009; Diez *et al.* 2012; Kovach *et al.* 2015). Environmental variation is, of course, a major driver of non-parallelism (Bolnick *et al.* 2018), so it is perhaps not surprising that responses to environmental change will depend on subtle differences in the local environment. In addition to these recognised effects of local environments mediating the effects of shared regional climates, our data show an additional moderating (contingent) effect of different evolutionary lineages. These contingent responses to shared environmental trends could reflect a number of hypothesised reasons for non-parallelism, such as correlated traits, different histories, different population sizes or different genomic architectures (Travisano *et al.* 1995; Kaeuffer *et al.* 2012; Bolnick *et al.* 2018).

Implications

Differing evolutionary histories represent a potential source of non-parallelism that is very difficult to fully quantify outside
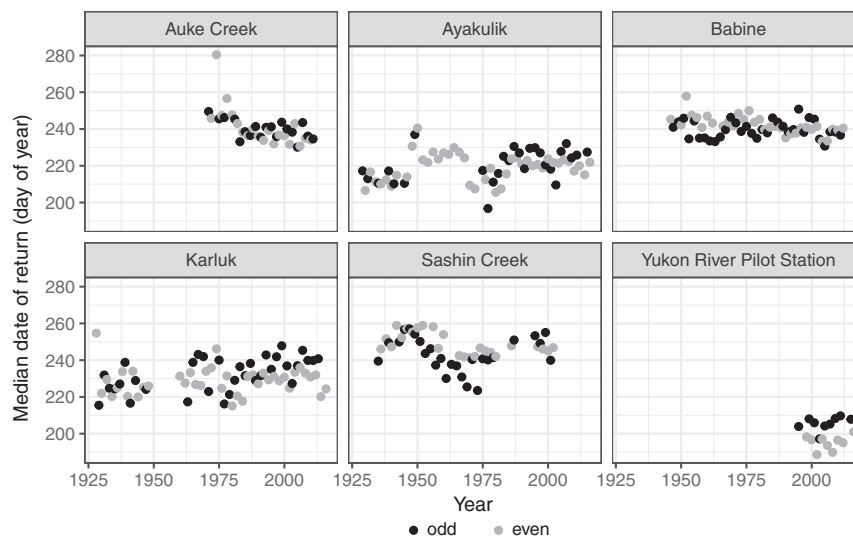
Figure 4 Median date of return (as day of year) shows highly variable patterns through time among rivers. Run time is shifting earlier in some rivers, such as Auke Creek, but not others, such as Karluk. Shown here are six examples of rivers from various areas with long data records: Auke (Southeast AK, 37 years), Ayakulik (Kodiak, AK, 68 years), Babine (Northern BC, 65 years), Karluk (Kodiak, AK, 74 years), Sashin (Southeast AK, 51 years), Yukon (Norton Sound, AK, 16 years).

of the laboratory. Our main goal was to determine the relative contributions of current environments and evolutionary history in shaping the parallel and non-parallel phenotypes of a study species with replicated lineages sharing the same breeding habitats. For run timing in pink salmon, our results suggest that parallel responses to local selective pressures predominate, shaping strong spatial phenotypic parallelism. These inferences are particularly robust because the strict 2-year life cycle of pink salmon allows us to consider two reproductively isolated conspecific lineages in multiple common environments across a wide environmental and spatial gradient.

Although our results suggest only a minor role of evolutionary history in shaping the overall patterns of phenotypic (non)parallelism across the landscape, the generality of this result among species is unclear. Our study falls towards the strongly parallel end of the continuum of parallelism observed in nature: that is, most traits in fishes show lower levels of parallelism (Langerhans 2017; Oke *et al*. 2017). Is this generally weak parallelism in other traits caused by evolutionary history, or simply a failure to fully account for the effects of unrecognised variation in natural selection among seemingly similar habitats? The fact that some highly parallel traits are evident, even in study systems that show generally moderate parallelism, might suggest that contingency is an unlikely culprit for non-parallelism. Yet the very nature of contingency could lead to differing legacies of evolutionary history in different areas of the genome. By this logic, contingency could result in non-parallelism in some traits but not others – even despite similar habitat-specific selective regimes. For example, in sulphide-adapted *Poecilia mexicana* populations, contingency has led to unique evolutionary trajectories at the molecular level despite very similar apparent selective regimes, whereas traits measured at higher levels of biological organisation show stronger parallelism (Pfenninger *et al*. 2015).

Similar studies that consider contingent histories using genomic methods and also the extent of parallelism in phenotypic traits would be an excellent next step in advancing our understanding of the roles determinism and contingency play in parallel evolution.

Another useful advance would be to expand the approach adopted in our study to other study systems by carefully selecting 'replicate' populations in identical (or nearly so) wild environments. For example, several studies have considered multiple species arrayed across the same environmental gradient in the same locations (e.g., Stireman *et al*. 2005; Rosenblum & Harmon 2010; Raeymaekers *et al*. 2017). Alternatively, studies can focus more attentively on quantitatively measuring environmental features that might cause spatial variation in selection among populations in a common habitat type. For instance, Stuart *et al*. (2017) showed that some deviations from parallelism between lake and stream stickleback could be explained by quantitative variation in habitat features. These and other recent studies formally assessing (non)parallelism and identifying its causes show great potential to increase our understanding of the explanatory power of both deterministic selection and historical contingency.

AUTHOR CONTRIBUTIONS

KBO, APH, and TPQ conceived of and designed the study. KBO collected data, KBO and CJC performed analyses. KBO lead writing and all authors contributed significantly to revising and editing the manuscript.

DATA AVAILABILITY STATEMENT

The majority of the data used in this study was collected from publicly available datasets. A compiled dataset is available on Dryad (https://doi.org/10.5061/dryad.n8k0mq1).

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