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Contemporary divergence in migratory timing of naturalized populations of chinook salmon, *Oncorhynchus tshawytscha*, in New Zealand

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ABSTRACT

Hypotheses: Recently established populations, sharing common ancestry but facing different reproductive habitat seasonality, will genetically diverge in the timing of their reproductive migrations.

Organism: Exotic populations of chinook salmon (*Oncorhynchus tshawytscha*) established from common ancestors introduced to South Island of New Zealand between 1901 and 1907.

Site of experiments: Early rearing at Silverstream Hatchery, Waimakariri River, New Zealand, followed by release to sea, growth in coastal ocean, and return to freshwater.

Methods: We reared early- and late-spawned juveniles from two populations that differ in spawning time in the wild, and released those fish to mature at sea. We obtained dates of migratory return to freshwater, fish age, and experimental group identity from angler captures at river mouths. Analyses involved assessment of population, spawning date, and age at return effects for the current experiment, plus an expanded analysis of data from previous release experiments.

Results: After ~26 generations, the population that reproduces later in the wild now returns to freshwater an average of 18 days later than the early spawning population. This divergence is likely genetic, given the common-garden nature of our experimental design, and was apparent even after accounting for significant effects of age at return and marginal effects of initial spawning date.

Keywords: evolution, migration, phenology reproduction, salmon, timing.

INTRODUCTION

Seasonal patterns of migration and breeding are critical adaptations of animal populations that coordinate major life-cycle events of adults and their offspring with seasonally dependent processes (Bailey *et al.*, 2010; Bowlin *et al.*, 2010). Like many traits, migration and breeding

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are affected by phenotypically plastic responses to environmental stimuli and genetic adaptation to long-term conditions. Shifts in timing have been reported in many species in response to changing climate (Parmesan, 2006; Both, 2010). Migratory species appear to be particularly sensitive to disruptions of reproductive timing (Robinson *et al.*, 2009; Both, 2010), and such effects are an important component of conservation plans. However, the ability of species to accommodate alterations to seasonality, including effects of climate change, will depend on the evolutionary capacity of phenological traits (Bradshaw and Holzapfel, 2008; Gienapp *et al.*, 2008). Phenological attributes of populations may be especially important in the range expansion and adaptive radiation of indigenous and exotic species. Specifically, timing of breeding can contribute to reproductive isolation through local adaptation or phenotypic plasticity. Such isolation can then foster further local adaptation and divergence (Quinn *et al.*, 2000).

Pacific salmon, *Oncorhynchus* spp., and Atlantic salmon, *Salmo salar*, are model organisms for the study of phenology and adaptation. Maturing salmon migrate from distant oceanic feeding grounds to the mouths of rivers and then ascend to their natal spawning grounds to breed (Shearer, 1992; Quinn, 2005). Salmon populations vary greatly in the timing of migration and breeding (Brannon, 1987; Webb and McLay, 1996; Hodgson and Quinn, 2002), and these are defining traits for many populations (Ricker, 1972). Inter-annual variation in salmon migration timing may be correlated with environmental conditions (Keefer *et al.*, 2008), but timing seems to be less phenotypically plastic than in some other anadromous fishes such as American shad, *Alosa sapidissima* (Quinn and Adams, 1996), and alewife, *A. pseudoharengus* (Ellis and Vokoun, 2009). In addition, heritabilities for timing tend to be stronger in salmonids than they are for other life-history traits (Carlson and Seamons, 2008). Genetic control over return timing has been reported within salmon populations (Smoker *et al.*, 1998; Sato *et al.*, 2000) and directed selection can adjust the timing of breeding (Siitonen and Gall, 1989; Neira *et al.*, 2006). Understanding the genetic control over timing is important because this may determine the ways in which populations respond to altered selection regimes from climate change (Crozier *et al.*, 2008; Mathes *et al.*, 2010), exploitation in fisheries (Quinn *et al.*, 2007; Jepson *et al.*, 2010), and inadvertent selection during artificial propagation (Flagg *et al.*, 1995; Quinn *et al.*, 2002).

Historical introductions can provide semi-natural experiments to assess the evolutionary potential of species in contemporary time (Hendry and Kinnison, 1999; Kinnison and Hendry, 2001). Chinook salmon, *O. tshawytscha*, brought to the South Island of New Zealand (NZ) at the beginning of the twentieth century, provide one of the best documented and extensively studied systems of such population divergence in contemporary time (Quinn *et al.*, 2001). We previously reported experimental evidence that two extant populations of NZ chinook salmon differed in the timing of return migration and breeding even though they were recently derived from a common ancestral source (Quinn *et al.*, 2000). The present paper reports the results of further experiments using one of those and a third population to investigate the extent of genetic control over return timing for populations with very different breeding times. Specifically, we tested the hypothesis that individuals from populations that tend to differ in breeding date would, if bred in captivity and released to sea, show similar differences when they returned. We further hypothesized that individuals within each population that were bred early would produce offspring that returned earlier than those bred later in the same season. Finally, in many Pacific salmon populations, the larger or older individuals return earlier in the year than smaller ones (Quinn, 2005), so we examined the data for evidence of this phenotypic effect as well as the influences of population and parental spawning date. This factor is important because age at maturity also evolves in

newly established populations (Quinn and Unwin, 1993; Kinnison *et al.*, 2011), so differences in timing *per se* need to be distinguished from changes linked to altered age composition. The current study thus provides important insights into the generality and capacity for divergence in timing and its interaction with divergence in other traits.

METHODS AND MATERIALS

All anadromous chinook salmon in New Zealand were established when representatives from the fall-run Battle Creek population, in the Sacramento River system of California (Quinn *et al.*, 1996; O'Malley *et al.*, 2007), were brought to the Waitaki River system (Fig. 1) between 1901 and 1907 (McDowall, 1994). Spawning salmon were observed in a tributary of the Waitaki system (the Hakataramea River) within a few years, and within 10 years in the other large, glacier-fed rivers on the east coast of the South Island where spawning occurs today. Analyses of population structure based on DNA microsatellite variation indicated that salmon in different drainages now show some reproductive isolation (Kinnison *et al.*, 2002; O'Malley *et al.*, 2007), consistent with the high degree of philopatry in the species.

Our study involved an experimental comparison between the Glenariffe Stream and Poulter River populations. Glenariffe Stream, a stable, spring-fed tributary, joins the Rakaia River 100 km above its mouth at an altitude of 430 m. The Poulter River, a 30-km

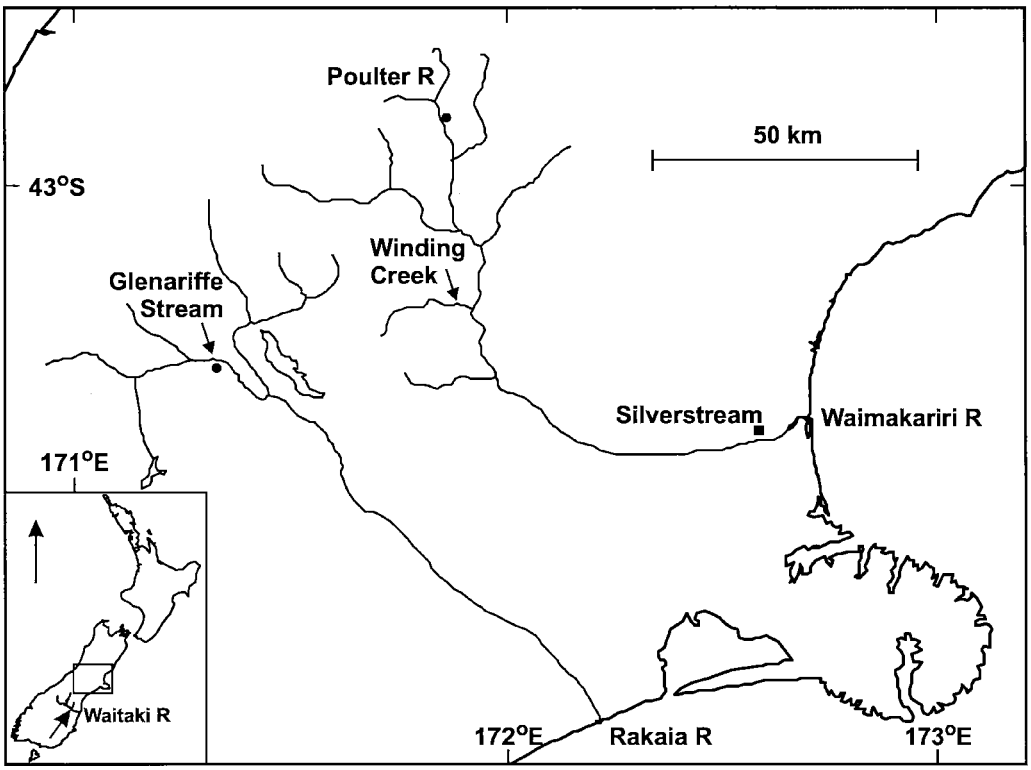

Fig. 1. Map of New Zealand (insert) showing the sources of chinook salmon and the locations of the experimental facilities used in the study of migration timing.

long rain- and snow-fed stream, joins the Waimakariri River 95 km above its mouth (Fig. 1). Long-term, precise records are not available, due to the remote spawning location of the Poulter population, but periodic efforts to sample these populations have indicated that the Poulter River population breeds about 2–3 weeks later at peak and is composed primarily of fish that spend a full year in freshwater prior to seaward migration, whereas more of the Glenariffe Stream fish leave in their first year of life (Unwin *et al.*, 2000).

We established full-sib families of Glenariffe and Poulter origin in May (autumn) 1997 by spawning fish from one or both populations on three different dates, approximating the peak of spawning in Glenariffe Stream (1 May, 14 families), late spawning in Glenariffe Stream and peak spawning in the Poulter River (18 May, 14 Glenariffe families and 12 Poulter families), and late spawning in the Poulter River (29 May, 7 families).

An average of 2900 ova from each female were fertilized with milt from one male from the same population and then transported to and incubated at the Silverstream Hatchery near the mouth of the Waimakariri River. These fish were reared at Silverstream, tagged with coded wire to identify each release group and population, and released to sea on 3 August 1998. Mean group weights at this time were as follows: Glenariffe fish spawned on 1 May = 62.3 g; those spawned on 18 May = 96.7 g; Poulter fish spawned on 18 May = 84.7 g; those spawned on 29 May = 77.8 g. We used date of capture by anglers in the Waimakariri River sports fishery to characterize variation in return timing. Adult salmon migrating to Silverstream are available to anglers only within the 3–4 km tidal section of the lower Waimakariri River, so the date of capture was a surrogate for date of entry to freshwater.

We examined the data using a combination of unpaired *t*-tests for specific comparisons and analysis of variance (ANOVA) incorporating population, age, and spawning date effects, plus the two-way interactions between factors. Spawning date was treated as a continuous covariate, whereas population and age were treated as fixed factors. We also conducted further analyses using comparable data from an earlier experiment (Quinn *et al.*, 2000) in which brood year 1994 and 1995 chinook salmon were released from both Silverstream and Glenariffe Stream hatcheries. Reanalysis and inclusion of these data allowed us to examine possible differences in return timing associated with different brood years, different release sites, different return sites, and earlier breeding dates.

RESULTS

Of the salmon released to the sea from the 1997 Poulter–Glenariffe experiment, 135 returned and were recovered by anglers who reported the capture date (Poulter: $n = 31$; Glenariffe: $n = 114$; see Table 1). Mean date of entry was 18 days earlier for Glenariffe fish (23 February) compared with Poulter fish (13 March) ($t_{133} = 3.75$, $P < 0.001$). Fish from the Poulter group spawned on 18 May returned significantly later than those from the Glenariffe group spawned on the same day ($t_{56} = 2.11$, $P = 0.02$). In addition to the effect of population, older salmon tended to return earlier in the year than younger ones of the same population (Table 2). ANOVA with population, age, and spawning date as factors revealed no significant interaction terms ($P > 0.21$), so they were not included in the final model. That model indicated significant effects of population ($F_{1,131} = 7.62$, $P = 0.007$) and age at return ($F_{1,131} = 15.29$, $P < 0.001$) but not a significant effect of spawning date ($F_{1,313} = 0.10$, $P = 0.748$). There was also no significant variation in timing of return as a function of the

Table 1. Summary statistics on the mean day of the year in which maturing chinook salmon were captured in recreational fisheries

Population	Spawning date	Release site	Mean day of the year	s.d.	Sample size
Glenariffe	22 April 1994	Glenariffe	9 February	32.9	75
Glenariffe	22 April 1994	Silverstream	8 February	31.6	37
Glenariffe	30 April 1995	Glenariffe	12 February	30.5	40
Glenariffe	1 May 1997	Silverstream	22 February	24.5	67
Glenariffe	18 May 1997	Silverstream	23 February	25.3	37
Poulter	18 May 1997	Silverstream	9 March	23.8	21
Poulter	29 May 1997	Silverstream	19 March	9.0	10

Note: The populations, dates when the salmon had been spawned, and their release location are indicated. Data from the 1994 spawning events were re-analysed from Quinn *et al.* (2000).

Table 2. Mean day of the year in which maturing chinook salmon were captured in recreational fisheries as a function of their age, for two experimental populations (spawning dates in a given year combined)

		Age at return (years)		
Population	Brood year	2	3	4
Glenariffe	1994	16 February ($n = 11$)	10 February ($n = 79$)	31 January ($n = 21$)
	1995	8 March ($n = 8$)	10 February ($n = 22$)	30 January ($n = 10$)
	1997	7 March ($n = 22$)	19 February ($n = 80$)	20 January ($n = 2$)
Glenariffe total		2 March ($n = 41$)	14 February ($n = 181$)	30 January ($n = 33$)
Poulter	1997	26 March ($n = 8$)	8 March ($n = 22$)	24 February ($n = 1$)

Note: Data from the 1994 and 1995 spawning events were re-analysed from Quinn *et al.* (2000).

river to which the fish returned ($F_{1,130} = 0.18$, $P = 0.667$), and addition of this factor did not change other model inferences.

We then conducted ANOVA on the larger data set, including the 1994 and 1995 releases of Glenariffe Stream salmon from Silverstream and Glenariffe Stream, using population, age, spawning date, and brood year as covariates, plus all two-way interactions. None of the interactions was significant ($P > 0.19$) and so they were not included in the full model. Timing of recovery was a function of population ($F_{1,281} = 5.07$, $P = 0.025$) and age ($F_{1,281} = 16.41$, $P < 0.001$) but neither brood year ($F_{2,281} = 0.96$, $P = 0.382$) nor spawning date ($F_{1,281} = 0.10$, $P = 0.751$) had a significant effect. When brood year was omitted (as not significant), an effect of spawning date was detected ($F_{1,283} = 4.44$, $P = 0.036$). Timing of recovery was not affected by release location ($F_{1,280} = 0.08$, $P = 0.777$) or river of recovery ($F_{5,276} = 1.93$, $P = 0.089$) when one or the other was added to a model that included population, age, spawning date, and brood year.

DISCUSSION

The earlier return of Glenariffe Stream fish relative to their Poulter River counterparts was consistent with expectations because natural spawning by chinook salmon in Glenariffe Stream is earlier than in the Poulter River (Unwin *et al.*, 2000). Other populations within New Zealand differ in mean dates of entry into freshwater and spawning (Quinn and Unwin, 1993), and differences between Glenariffe and Hakataramea populations persisted under experimental conditions (Quinn *et al.*, 2000).

The results of the 1997 brood year experiment can be compared with those from our previous study on migration and spawning timing of NZ chinook salmon (Quinn *et al.*, 2000). In that study, Glenariffe Stream salmon that spawned on 22 April 1994 had mean angler capture dates of 8 February (Silverstream release) and 9 February (Glenariffe release). Those that spawned on 30 April 1995 and were released from Glenariffe had a mean capture date of 12 February. Thus the mean recovery dates of Glenariffe fish observed in the 1997 brood year experiment (22 and 23 February) were later than had been seen in previous experiments. Later recovery dates are consistent with the fact that these fish had been spawned from parents that matured later in the season than those in the 1994 and 1995 experiments. By implication, the 1997 experiment may have underestimated the difference in timing between the Glenariffe and Poulter populations. However, ANOVA indicated a significant effect of spawning date on timing – beyond the effects of age and population – only when brood year was omitted as a factor.

Despite the possible effects of variation in river conditions and angler activity on the distribution of catches, we detected no differences in recovery dates among years, and there were no differences among release or return sites. These findings indicate that the timing of return was very robust with respect to diverse environmental factors. Importantly, there was no observer bias because the return of salmon tags by anglers was 'blind' with respect to our study and the difference between Poulter and Glenariffe fish was seen in all three return years (i.e. fish of ages 2, 3, and 4).

The effect of age on return time was hypothesized in advance owing to its presence in the data from the two previous experiments with Glenariffe fish, and is often seen in Pacific salmon (Quinn, 2005) and Atlantic salmon populations (Shearer, 1990). The reasons why older salmon might return earlier in the season than younger ones include: (1) more rapid swimming by larger fish, assuming they leave oceanic feeding grounds at the same time; (2) greater benefits to smaller (younger) fish in staying at sea longer in the season to grow more than fish that are already large; and (3) size selection in spawning females, associated with competition for spawning territory and nest protection, which may encourage smaller females to defer spawning until later in the season (Steen and Quinn, 1999; Doctor and Quinn, 2009). Regardless of the process, it is interesting that this phenotypic effect was strongly evident in addition to the other effects on return date seen in this study.

We were not able to explore the specific inheritance factors controlling migration timing but our common-garden rearing and release approach makes it likely that population differences in timing reflect heritable divergence. Similarly, analogous divergence patterns are also seen in the native range of Pacific salmon, where water temperature experienced during incubation affects the evolution of spawning dates (Brannon, 1987). Specifically, populations spawning in warmer water tend to spawn later than those spawning in cooler water. Adult migration timing is sometimes closely linked to spawning timing (i.e. the fish spawn soon after they enter freshwater) but in many Pacific (Hodgson and Quinn, 2002) and also Atlantic

salmon (*Salmo salar*) populations (Shearer, 1990), fish enter freshwater many months (sometimes nearly a year) before spawning. This phenomenon has not been fully investigated but some combination of flow and temperature experienced by migrating adults is likely involved in the evolution of migration timing (Brannon *et al.*, 2004). Consequently, changes in thermal and flow regimes, as has been occurring and may continue to occur in the future (Mantua *et al.*, 2010), may be an important factor in the evolution of migration timing within the range of salmon (Martins *et al.*, 2011).

In addition to the implications for salmon in their native range, our results shed light on the evolution of introduced populations in general, including possible trajectories of newly established salmon populations elsewhere in the southern hemisphere (Ciancio *et al.*, 2005). Specifically, rapid heritable divergence in phenological traits such as migration and spawning timing can accelerate differentiation in other traits by enhancing reproductive isolation between groups, as breeding individuals would be separated in both space and time. Colonization is facilitated by high immigration rates, so reproductive isolation is needed to counter the homogenizing effects of gene flow that might otherwise impede local adaptation (Garant *et al.*, 2007). Phenological divergence in NZ salmon has been accompanied by divergence in many other traits, such as egg size, morphology, age at maturity, and growth rates (Kinnison *et al.*, 2001, 2003; Quinn *et al.*, 2000, 2001). Consequently, NZ chinook salmon populations adapted to local migratory conditions have substantially greater lifetime survival and egg production than genotypes from New Zealand after less than a century of divergence (Kinnison *et al.*, 2008).

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