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Lake-specific variation in growth, migration timing and survival of juvenile sockeye salmon *Oncorhynchus nerka*: separating environmental from genetic influences

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Time series on juvenile life-history traits obtained from sockeye salmon *Oncorhynchus nerka* were analysed to assess lake-specific environmental influences on juvenile migration timing, size and survival of fish from a common gene pool. Every year for the past two decades, *O. nerka* have been spawned at a hatchery facility, and the progeny released into two lakes that differ in average summer temperatures, limnological attributes and growth opportunities. Juveniles reared in the warmer, more productive Crosswind Lake were larger and heavier as smolts compared to those from the cooler, less productive Summit Lake and had higher in-lake and subsequent marine survival. Crosswind Lake smolts migrated from the lake to sea slightly earlier in the season but the migration timing distributions overlapped considerably across years. Fry stocking density had a negative effect on smolt length for both lakes, and a negative effect on in-lake survival in Summit Lake. Taken together, the results revealed a strong effect of lake-rearing environment on the expression of life-history variation in *O. nerka*. The stocking of these lakes each year with juveniles from a single mixed-source population provided a large-scale reverse common-garden experiment, where the same gene pool was exposed to different environments, rather than the different gene pools in the same environment approach typical of evolutionary ecology studies. Other researchers are encouraged to seek and exploit similar serendipitous situations, which might allow environmental and genetic influences on ecologically important traits to be distinguished in natural or semi-natural settings.

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Key words: climate; common garden; life-history plasticity; salmon; smolt.

INTRODUCTION

A fundamental challenge in evolutionary ecology is to determine the degree to which phenotypic differentiation within and between populations can be attributed to genetic *v.* environmental sources of trait variation (Fox *et al.*, 2001). Phenotypic differences can reflect evolutionary divergence (genetic differences that accumulate over time) or phenotypic plasticity (developmental, physiological or behavioural responses by individuals to environmental cues and constraints). In both cases, environmental differences might be responsible for phenotypic divergence among populations, but

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the mechanisms are very different (evolution by natural selection involves genetic change, plasticity does not). Resolving these mechanisms is important not only to understand the evolutionary forces and environmental processes that have shaped phenotypic diversity but also to predict the adaptive potential of populations facing environmental change (Stockwell *et al.*, 2003; Gienapp *et al.*, 2008).

One way to distinguish genetic from environmental sources of phenotypic variation is to conduct so-called common-garden experiments, where individuals from two or more populations are reared and measured in a single environment. If phenotypic differences between populations persist in the common environment, this points to a genetic basis to trait differences (Kinnison *et al.*, 2001; McGinnity *et al.*, 2007; Fraser *et al.*, 2008). If, on the other hand, phenotypic differences disappear in the common environment, this suggests that differences observed in the wild stem from environmental rather than genetic sources of trait variation between populations. The reverse experiment can also be undertaken, whereby individuals from the same population (or series of populations) are exposed to and measured in different environments, when the specific goal is to quantify phenotypic plasticity (Pigliucci, 2001).

Pacific salmon *Oncorhynchus* spp. are characterized by strong among-population differences in morphological and life-history characters (Groot & Margolis, 1991; Quinn, 2005). Much of this intraspecific variation is thought to reflect reproductive isolation of populations that home to natal spawning sites and local adaptation to distinct breeding and rearing habitats (Taylor, 1991; Hendry *et al.*, 2000). Phenotypic plasticity also plays a role in population differentiation, and many commonly observed plastic life-history responses (*e.g.* earlier maturation in response to increased food availability, changes in adult migration timing in response to shifting oceanic and river cues) can have important fitness consequences (Hutchings, 2004; Hodgson *et al.*, 2006; Crozier *et al.*, 2008). The role of phenotypic plasticity in salmonid population dynamics is becoming even more relevant in light of potential effects of climate change (Crozier *et al.*, 2008). The ability to predict future population responses is hampered, however, by limited mechanistic understanding of how environmental factors influence key life-history attributes such as migration timing, growth trajectories and stage-specific survival rates.

These patterns are readily studied in sockeye salmon *Oncorhynchus nerka* (Walbaum) because juveniles typically spend 1 or 2 years in nursery lakes before migrating to sea, and lacustrine conditions can have a large effect on juvenile growth, development and migratory behaviour. In *O. nerka*, the timing of juvenile seaward migration by smolts is thought to be strongly influenced by interannual and intra-annual variation in environmental conditions (Quinn *et al.*, 2009), although genetic differences among populations have been documented in Atlantic salmon *Salmo salar* L. (presumably reflecting adaptation; Orciari & Leonard, 1996; Nielsen *et al.*, 2001; Stewart *et al.*, 2006). In general, earlier downstream migrations are associated with warmer springs, which in northern lake systems coincide with earlier dates of ice-out (ice melting) in spring (Quinn, 2005). Smolt size in *O. nerka* is also strongly affected by variation in temperature and food availability within and between lakes (Burgner, 1987; Edmundson & Mazumder, 2001; Schindler *et al.*, 2005; Rich *et al.*, 2009). Timing of ocean entry and smolt size can affect early marine survival (Henderson & Cass, 1991; Koenings *et al.*, 1993; Achord *et al.*, 2007; Scheuerell *et al.*, 2009), and large smolt size can also lead to earlier age at maturity (Vøllestad *et al.*, 2004;

Quinn *et al.*, 2009). Environmental conditions experienced during the rearing phase can, therefore, affect fitness at later life stages *via* a range of mechanisms.

A SERENDIPITOUS REVERSE COMMON-GARDEN EXPERIMENT

Most studies of environmental modulation of life-history traits in salmonids and other fishes involve examining time series for correlations with biologically relevant environmental variables (Hartman *et al.*, 1982; Quinn & Adams, 1996; Roper & Scarnecchia, 1999; Byrne *et al.*, 2003; Achord *et al.*, 2007; Aprahamian *et al.*, 2008; Keefer *et al.*, 2008; Taylor, 2008). This type of correlational approach yields important insights but does not provide unambiguous evidence for phenotypic plasticity (*i.e.* direct or indirect effects of the environment on the physiology and behaviour of individuals). For instance, changes in the genetic or demographic composition of populations through time, also driven by environmental changes, could explain the correlations (Quinn *et al.*, 2006, 2007). Common-garden and reverse common-garden experiments can provide a more powerful way to distinguish genetic from environmental sources of phenotypic variation. Rarely, however, is it possible to experimentally dissect causes of phenotypic variation in a natural setting, most studies are conducted under controlled conditions in the laboratory, or under semi-natural field conditions, and are rarely temporally replicated (Carlson & Seamons, 2008).

Here, results from a long-term *O. nerka* enhancement programme in south-central Alaska, U.S.A., are reported, which for the present purposes provided a serendipitous, large-scale, ongoing natural experiment. *Oncorhynchus nerka* originating from a single natural population were spawned artificially each year and their embryos incubated at a stream-side facility. Emerging juvenile *O. nerka* were then released annually into three different rearing lakes not far from the hatchery, and data collected on timing of smolt migration, size and survival for two of these lakes on an annual basis. Despite geographic proximity, the two lakes differ considerably in average temperature, limnological attributes and growth opportunities for juvenile *O. nerka* (Table I). The lakes, however, provide little suitable spawning habitat, and so the transplanted populations have not been allowed to adapt to local conditions. Rather, each year the vast majority of returning adults are spawned at the hatchery, effectively re-mixing the gene pool each generation, and the resulting juveniles are dispersed to the lakes without regard to where their parents had reared. This operation provided a rare opportunity to explore lake-specific environmental influences on juvenile growth and migration timing, and their joint consequences for survival to adulthood. Thus, it is a *de facto* reverse common-garden experiment (*i.e.* same gene pool in different environments, rather than the traditional different gene pools in the same environment approach).

MATERIALS AND METHODS

GULKANA HATCHERY

The data used in this study were obtained from the Gulkana Hatchery, an ongoing *O. nerka* enhancement programme in the upper reaches of the Copper River basin, in south-central Alaska. Gulkana Hatchery, owned by the Alaska Department of Fish and Game (ADFG)

TABLE I. Summary of physical and limnological attributes of two study Alaskan lakes. All variable values, with the exception of June water temperatures, are based on values reported in Edmundson & Mazumder (2001). June water temperatures are averages across the period 6–19 June, with measurements taken at either 0000 or 0800 hours at the smolt traps

	Summit Lake	Crosswind Lake
Physical attributes		
Location	63.06° N; 145.29° W	62.20° N; 146.00° W
Elevation (m)	914	644
Area (km ²)	10.1	38.2
Mean depth (m)	13	16
Maximum depth (m)	52	39
Volume (10 ⁶ m ³)	135	626
Limnological attributes		
Mean June temperature (° C)	6.2	12.9
Mean ice-out date (spring melt)	15 June	28 May
Chlorophyll <i>a</i> (mg l ⁻¹)	0.3	0.6
Zooplankton biomass (mg m ⁻²)	491	1200

and operated by the Prince William Sound Aquaculture Corporation, is the largest modern *O. nerka* incubation facility in the world, where *c.* 35 million eggs are taken annually. The hatchery contributes to a larger enhancement programme designed to augment natural *O. nerka* production in the basin, in response to declining abundance and heavy demand by commercial, personal use, subsistence and sports fisheries. The Gulkana Hatchery is located on the west bank of the Upper East Fork of the Gulkana River in the north-central portion of the Copper River basin (Fig. 1: 63° 04' N; 145° 30' W; vertical elevation: 921 m; 416 river km from the ocean). Historically, the Upper East Fork of the Gulkana River contributed significantly to total *O. nerka* production in the Copper River, but loss of spawning habitat in the 1960s and 1970s precipitated a marked decline in natural production in the region. In 1973, the first stream-side incubation unit was constructed at Gulkana Hatchery, and currently there are 134 plastic tote incubator units in production.

HATCHERY OPERATION AND STOCKING OF LAKES

The Gulkana incubation facility is located adjacent to a large spring aquifer, between Summit and Paxson Lakes (Fig. 1). The source of the springs is water from Summit Lake, which is force-filtered naturally through glacial moraine. Exceptional water quality, stable water temperatures (annual mean range of 2.5–5.0° C, despite extreme fluctuations in air temperature) and stable year-round flows provide an ideal location for stream-side incubators. *Oncorhynchus nerka* return in large numbers to spawn in gravel beds at aquifer springs near the hatchery. Adult fish are collected annually during natural spawning, from early September to mid-October, and spawned artificially at the hatchery. Gametes from two males and one female are mixed in separate buckets, and the fertilized eggs are transferred to large plastic tote incubators (following ADFG *O. nerka* hatchery spawning protocols). Embryos develop through the winter in these stream-side incubators, which simulate natural redds but provide a protected developmental environment. *Oncorhynchus nerka* fry emerge volitionally from the gravel in late spring and swim through outlet pipes into aluminium collection boxes. Egg-to-fry survival rates of *c.* 70% are achieved at the hatchery, greatly exceeding those typical of wild *O. nerka* (*c.* 13%; Quinn, 2005).

Fry are counted and then released *en masse* into one of three nursery lakes, Paxson Lake, located immediately downstream of the hatchery facility, Summit Lake (SL), located immediately upstream of the hatchery, and Crosswind Lake (CL), located on a tributary of the

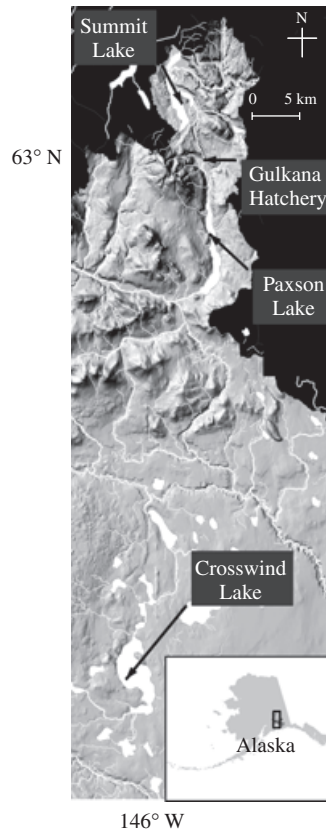


FIG. 1. Map of upper Copper River watershed, south-central Alaska, showing location of Gulkana Hatchery and Summit (SL) and Crosswind (CL) lakes.

West Fork of the Gulkana River, *c.* 100 km to the south and downstream of the hatchery (Fig. 1). Approximately 6 million fry each year are released on site; these fry migrate a short distance and rear in Paxson Lake. Since 1980, an average of *c.* 7.6 million fry per year have been transported by lorry and released into SL, while an annual average of *c.* 10 million fry have been transported by aircraft and released into CL, starting in 1987. For full details on hatchery operations and the enhancement programme, see Roberson & Holder (1987).

SUMMIT AND CROSSWIND LAKES: DIFFERENT REARING ENVIRONMENTS

Oncorhynchus nerka fry typically spend the first 1 or 2 years of their lives rearing in nursery lakes, where they grow slowly (relative to the growth they achieve subsequently in the ocean). In the early summer of their second or third year of life, juveniles undergo smolt transformation (Quinn, 2005). SL and CL provide different rearing environments for juvenile *O. nerka* (Table I). SL is a higher altitude, less productive lake that remains frozen for longer and is slower to heat up in early summer (when newly emerged *O. nerka* fry are growing fastest, and when smolts are preparing to leave). CL, in contrast, is a lower elevation, more productive lake that loses ice earlier and warms faster in early summer. Water temperature and zooplankton biomass are overriding factors controlling growth of *O. nerka* fry in lakes (Hyatt & Stockner, 1985; Edmundson & Mazumder, 2001): mean June temperatures in CL are twice those at SL and zooplankton biomass is greater by a factor of *c.* 2.45 (Table I).

DATA COLLECTION

Each year, emigrating smolts from SL and CL were captured for counting and measurement using a fyke-type tunnel net, deployed at the outlet of each lake. Smolt nets were put in place towards the end of May in advance of the first smolts migrating, and smolt sampling continued through until no more smolts were emigrating (typically the first week in July). Emigrating smolts were counted daily, and from these daily counts annual median emigration dates (the date by which 50% of the total migration had occurred each year) were calculated. Each year, 400–500 smolts (captured across the migration period) were also weighed and measured (fork length, L_F) at each lake. Fry-to-smolt survival was calculated as the number of emigrating smolts that year, divided by the number of fry released into the lake the previous summer. In both lakes, the vast majority of juveniles spend just one full year rearing in the lake (on average, *c.* 1.4% of smolts in SL and <0.4% of smolts in CL are age 2 years); this ratio was a sufficiently accurate measure of fry-to-smolt survival for the dominant smolt age class. Lake-specific smolt-to-adult survival rates could also be calculated for six cohort years (1990 to 1995), as samples of smolts from each lake were tagged with coded wire tags in these years (*c.* 12 000 tags were put out on average each year at CL and 14 000 at SL). Smolt-to-adult survival was calculated as the proportion of tagged emigrating smolts from each lake that were recovered 2 or 3 years later as mature adults on their upriver migration. Recoveries included fish caught in commercial and personal and subsistence fisheries, as well as in the escapement. To obtain accurate absolute survival estimates, an expansion factor would need to be applied to the recovery data to correct for incomplete sampling. Here, however, the interest was in testing for differences in relative smolt-to-adult survival between SL and CL so the raw (unexpanded) recovery data were used, on the assumption that returning fish from both lakes were equally likely to be caught in the fisheries (*i.e.* any differences in relative survival reflect natural mortality differences).

Water temperature was measured only irregularly at each lake, and there were many missing years within the time series. Air temperature data were therefore obtained from a nearby weather station at Gulkana airport (62.15° N; 145.45° W; elevation: 479 m; 100 km due south of Gulkana Hatchery; data obtained from the Alaskan Western Regional Climate Center: <http://www.wrcc.dri.edu/summary/Climsmak.html/>). Average May temperatures each year were used as a proxy for general climatic conditions at each lake (the weather station is located *c.* 37 km from CL and *c.* 105 km from SL), on the assumption that both lakes should be warmer in springs that are generally warm for the region.

HYPOTHESES

Based on previous studies and conventional wisdom on the ecology of *O. nerka* in lakes (Burgner, 1991; Quinn, 2005; Quinn *et al.*, 2009), the following predictions were made: (1) smolts should migrate earlier in the summer from CL than SL, because of the much warmer temperatures and earlier ice-out dates at CL. Within each lake, a negative relationship between annual migration dates and spring temperatures (as indexed by May air temperatures at Gulkana airport) was also predicted. (2) Smolts should be longer and heavier at CL, the warmer and more productive lake. (3) Fry-to-smolt survival should be higher at CL, because of the more favourable temperatures and growing conditions. (4) If CL smolts are larger, they should also have higher rates of survival to adulthood than SL smolts.

At SL, data exist on migration timing, smolt size and fry-to-smolt survival from 1981 to 2008, whereas at CL, data on the same variables only span the period 1992 to 2008. Because the goal was to directly compare these variables between lakes, only years in common were focussed on when conducting statistical tests and reporting lake-specific means \pm s.d. Likewise, for the comparison of smolt-to-adult survival rates, data were restricted to only those years in common (1990 to 1995). Paired *t*-tests were used to test for significant differences in annual median migration dates, average annual smolt L_F and masses, fry-to-smolt survival rates and smolt-to-adult survival rates. Paired *t*-tests were deemed appropriate as they account for common genotypes and common hatchery incubation conditions in each yearly cohort, which could vary from year to year. Fry density can influence growth rates and survival to the smolt stage (Burgner, 1987; Edmundson & Mazumder, 2001; Rich *et al.*, 2009), so models were also run including fry stocking density (the ln of the number of fry released the previous

year) as a covariate when testing for lake differences in timing, smolt L_F and fry-to-smolt survival.

RESULTS

Differences between the two lakes in smolt migration dates, smolt size, fry-to-smolt survival and smolt-to-adult survival are summarized in Table II. As predicted, annual median smolt migration dates were on average slightly earlier at CL compared to SL (12 June *v.* 16 June, respectively). The distributions of annual median dates overlapped considerably, however (Fig. 2), and the difference was marginally non-significant (two-tailed paired *t*-test: $t = 1.74$, d.f. = 15, $P > 0.05$). $\text{Log}_e(\text{ln})$ fry density did not have a significant effect on migration timing in either lake (SL: $t = 0.29$, d.f. = 14, $P > 0.05$; CL: $t = 0.69$, d.f. = 14, $P > 0.05$), and the lake effect remained marginally non-significant when ln fry density was included in the analysis of timing differences (lake effect: $F_{1,29} = 3.78$, $P > 0.05$, overall model $r^2 = 0.12$).

Across years within SL, there was a weak negative relationship between migration dates and average May air temperatures (*i.e.* later migration in colder years) across the period 1981 to 2008 (slope = -1.30 ± 0.75 days °C⁻¹; $F_{1,24} = 3.00$, $P > 0.05$). At CL, there was no significant relationship between migration dates and average May air temperatures, across the period 1993 to 2008 (slope = -0.85 ± 1.13 days °C⁻¹; $F_{1,14} = 0.56$, $P > 0.05$). The migration timing response to temperature did not differ between lakes (data from both lakes analysed together using ANCOVA: lake × temperature interaction term, $F_{1,38} = 0.12$, $P > 0.05$, overall model $r^2 = 0.17$).

Smolts were, on average, longer at CL (mean of average annual $L_F = 102.00 \pm 5.87$ mm) compared to SL (mean of average annual $L_F = 94.78 \pm 6.02$ mm; two-tailed paired *t*-test: $t = 5.027$, d.f. = 16, $P < 0.001$), and heavier (mean of average annual masses at CL = 9.78 ± 3.13 g, mean at SL = 7.09 ± 1.59 g; $t = 5.769$, d.f. = 16, $P < 0.001$; Fig. 3). Ln fry density had a significant negative effect on smolt L_F (slope = -3.76 ± 1.75 ; $F_{1,30} = 4.64$, $P < 0.05$) when included in the

TABLE II. Summary of differences between Summit and Crosswind Lakes (Alaska) in *Oncorhynchus nerka* average annual smolt migration timing, smolt size, fry-to-smolt survival and smolt-to-adult survival

Variable	Mean ± s.d.		Years	<i>t</i> value	<i>P</i>
	Summit Lake	Crosswind Lake			
Migration date	June 16 ± 6 days	June 12 ± 6 days	1993–2008	1.739	>0.05
Smolt L_F	94.78 ± 6.02 mm	102.00 ± 5.87 mm	1992–2008	5.027	<0.001
Smolt mass	7.09 ± 1.59 g	9.78 ± 3.13 g	1992–2008	5.769	<0.001
Fry-to-smolt survival	6.34 ± 4.69%	12.77 ± 6.42%	1992–2008	3.622	<0.01
Smolt-to-adult survival*	0.69 ± 0.09%	2.17 ± 0.41%	1990–1995	4.30	<0.01

*Based on unexpanded total recovery data, it should not be taken as an estimate of absolute marine survival for *O. nerka* from each lake, rather an index of relative survival.

L_F , fork length.

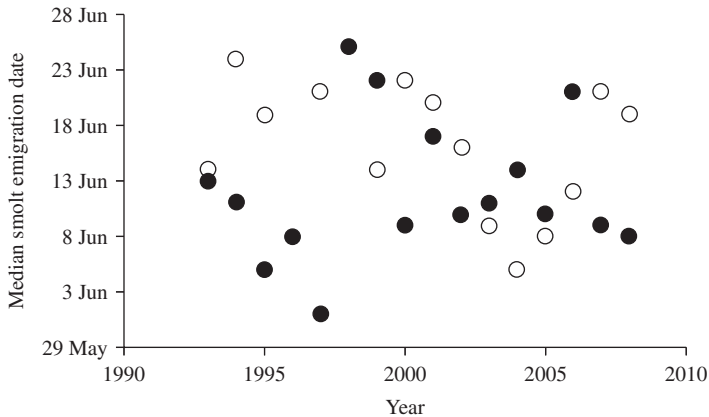


FIG. 2. Annual median *Oncorhynchus nerka* smolt migration dates at Summit (○) and Crosswind (●) Lakes.

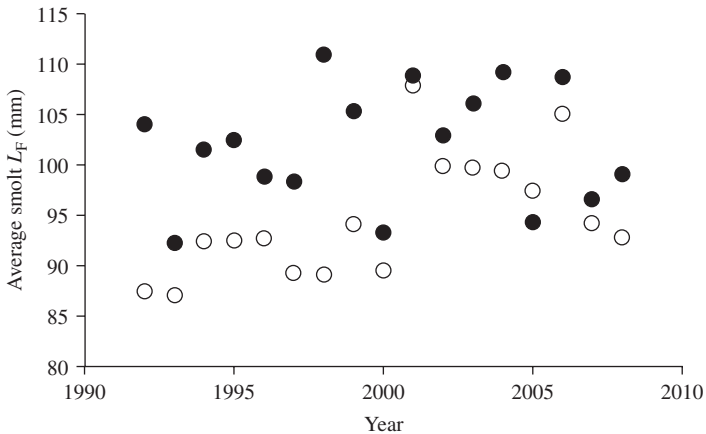


FIG. 3. Average *Oncorhynchus nerka* smolt fork length (L_F) at Summit (○) and Crosswind (●) Lakes, across the period 1992 to 2008: the years in common for each time series.

model, but the independent lake effect remained highly significant ($F_{1,30} = 17.35$, $P < 0.001$, overall model $r^2 = 0.42$; lake \times ln fry density interaction: $P > 0.05$). Similarly, ln fry density had a marginally non-significant negative effect on smolt mass (slope = -1.40 ± 0.77 , $F_{1,30} = 3.34$, $P > 0.05$), but the independent lake effect remained highly significant ($F_{1,30} = 19.48$, $P < 0.001$, overall model $r^2 = 0.43$, lake \times ln fry density interaction: $P > 0.05$).

Fry-to-smolt survival was higher at CL (mean survival at CL = $12.77 \pm 6.42\%$, mean at SL = $6.34 \pm 4.69\%$; two-tailed paired t -test: $t = 3.62$, d.f. = 16, $P < 0.01$; Fig. 4). Ln fry density had a significant negative effect on fry-to-smolt survival in SL ($t = -3.18$, d.f. = 14, $P < 0.01$) but not in CL ($t = 1.24$, d.f. = 15, $P > 0.05$). The independent lake effect remained significant when this interaction between ln fry density and lake was taken into account in the model (lake effect: $F_{1,29} = 11.99$, $P < 0.01$, overall model $r^2 = 0.40$, lake \times ln fry density interaction: $P < 0.05$).

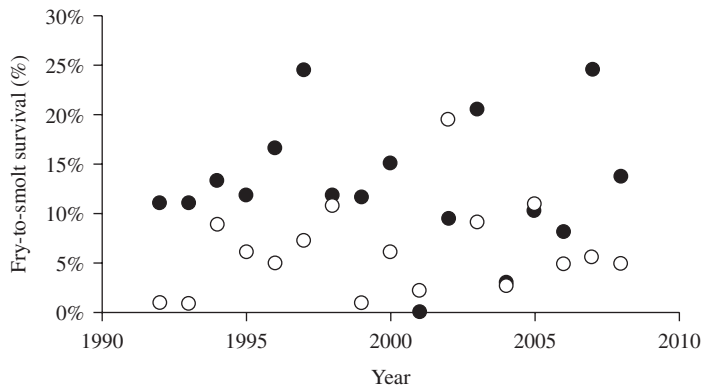


FIG. 4. Average *Oncorhynchus nerka* fry-to-smolt survival each year at Summit (O) and Crosswind (●) Lakes across the period 1992 to 2008.

Smolt-to-adult survival was higher for fish that reared in CL (mean \pm s.d. relative survival at CL = $2.17 \pm 0.41\%$, mean \pm s.d. at SL = $0.69 \pm 0.09\%$; two-tailed paired t -test: $t = 4.30$, d.f. = 5, $P < 0.01$).

DISCUSSION

Broad differences in the nursery–lake environment of *O. nerka* resulted in substantial differences in smolt size and survival (both in-lake and at-sea) and subtle differences in smolt migration timing. These are all key traits affecting individual fitness and population productivity in salmonids (Henderson & Cass, 1991; Koenings *et al.*, 1993; Quinn, 2005; Achord *et al.*, 2007; Scheuerell *et al.*, 2009). The annual stocking of two starkly contrasting lakes (one cold and oligotrophic, the other warmer and more productive) with fry originating from a single panmictic spawning population effectively allowed an examination of lake-specific expression of juvenile phenotypes. Genetic differences were controlled because each year returning adults were spawned at the hatchery, and resulting progeny were dispersed to each lake without regard for where their parents had reared. A small fraction of returning adults attempt to spawn at each lake (*e.g.* at Gunn Creek, an inlet stream to Summit Lake) but are mostly unsuccessful, thus the vast majority of juveniles in each lake are hatchery produced (Roberson & Holder, 1987). Embryos also experienced the same developmental conditions at the hatchery, so there were no initial differences in fry phenotypes with respect to destined rearing lake (size at emergence, *e.g.* can affect early survival of juvenile salmonids; Einum & Fleming, 2000; Quinn, 2005). This repeated reverse common garden is a potentially more powerful approach to separate environmental from genetic influences on phenotypes than the more convenient alternative, taking fish from a single source population and introducing them (once) into different sites. In this latter case, each population might be evolving differences as well as showing phenotypic plasticity to changing environmental conditions (Haugen, 2000), and the distinction might be difficult to determine.

Small differences in smolt migration timing were observed between lakes. Median smolt migration dates were, on average, 4 days earlier at CL (12 June) compared

to SL (16 June). Slightly earlier smolt migration at CL probably reflects warmer spring and summer water temperatures at that lake: CL becomes ice-free earlier in the spring (average ice-out date 28 May), and by mid-June is typically twice as warm as SL (average ice-out date 15 June; Table I). For lake-rearing *O. nerka* populations, the timing of the annual smolt migration is generally later in northern lakes, which freeze during the winter months, than it is further south (where lakes may or may not freeze) (Burgner, 1991). There is considerable variation, however, among lakes at similar latitudes, even within the same river system (Peven, 1987). Within lakes, migration is typically earlier after or during a warm spring (Quinn, 2005). There was weak evidence for such a relationship at SL across years, and no evidence for a negative relationship at CL. The measure of summer climatic conditions at each lake, however, was a broad-scale proxy (mean May air temperature at nearby Gulkana airport), which might have been too coarse to explain timing patterns at finer spatial (and perhaps also temporal) scales important to *O. nerka*.

In addition to temperature effects, smolt age and size influence timing, with older, larger smolts often migrating earlier than younger smolts, or smaller smolts of the same age (Quinn, 2005). At both CL and SL, the vast majority of juveniles smolt after one full year rearing in the lake, and there is minimal interannual variation in age structure. Smolts at CL, however, are noticeably larger than at SL (Table II and Fig. 3), which might partially explain the earlier migration there. Regardless of size and temperature differences, migration dates at each lake overlapped considerably (Fig. 2), suggesting other factors might be responsible for interannual variation in timing. Somewhat unexpectedly, the time series were not correlated with each other ($r = -0.03$, $P > 0.05$), indicating that timing differences across years were not being driven by regionally homogeneous climate factors, which might have affected physical conditions at each lake differently (Rogers & Schindler, 2008).

The ecological and physiological mechanisms underpinning environmental modulation of juvenile migration behaviour in salmonids are complex and still somewhat unclear (Beckman *et al.*, 2003, 2007). In general, photoperiod is the primary external driver for the smolt transformation process, interacting with internal endocrine rhythms (Dickhoff & Sullivan, 1987). This assures that the fish will enter marine waters at a generally appropriate time of year, given long-term average conditions, but migration timing plasticity is generally thought to be of adaptive value. The optimal time window for smolts to enter salt water probably varies considerably on an interannual basis, with fluctuations in physical conditions, food supply and predators in the nearshore environment affecting survival and growth (Hartman *et al.*, 1967; Koenings *et al.*, 1993; Willette *et al.*, 2001; Achord *et al.*, 2007; Scheuerell *et al.*, 2009). If conditions in fresh water and the marine environment covary, migrating juveniles might be able to use freshwater cues such as lake temperatures to time their migration to coincide with the optimum period for ocean entry. If migration timing plasticity in this population indeed evolved to allow juveniles to enter the ocean at the right time, then SL fish might be responding maladaptively to the much lower temperatures and thereby migrating too late, which might contribute to their reduced marine survival. Conditions at CL, however, are more similar to those at Paxson Lake. Thus, presuming that the norm of reaction for the source population evolved in response to prevailing conditions at Paxson Lake, the innate plastic responses exhibited by CL juveniles are probably more adaptive in that environmental context

(e.g. CL smolts migrating earlier in response to warmer lake temperatures may enter the ocean at the right time) compared to at SL.

As expected, given the warmer summer temperatures and higher zooplankton biomass, CL smolts were significantly longer and heavier than SL fish (Table II and Fig. 3). Brett (1971) showed that the relationship between growth and temperature is dome shaped for juvenile *O. nerka*, with an optimal intermediate temperature for growth, but that maximal growth can be achieved at lower temperatures when food is less available. As well as exerting direct effects on growth rates, temperature can also influence growth indirectly through zooplankton availability (Burgner, 1987; Edmundson & Mazumder, 2001), although the relative strengths of density-independent and density-dependent temperature effects can vary among lakes (Edmundson & Mazumder, 2001; Schindler *et al.*, 2005; Rich *et al.*, 2009). The slightly stronger negative relationship between fry density (numbers stocked) and smolt size at SL compared to CL suggests that while food limitation might be important in both lakes at high fry densities, these effects might be modulated by temperature.

Edmundson & Mazumder (2001) analysed limnological and biological data from 36 Alaskan lakes, including both CL and SL. Across these lakes, average May to October zooplankton biomass was 515 mg m^{-2} (range 22–2233 mg m^{-2}). Average zooplankton biomass at SL was 491 mg m^{-2} (Table I), and typical of Alaskan lakes in general. Zooplankton biomass at CL, in contrast, was over twice (1200 mg m^{-2}) that at SL, which along with the higher summer temperatures explains why *O. nerka* smolts there are much larger (Table II). Compared to other Alaskan lakes, however, smolts from both CL and SL are relatively large: mean L_F across the 36 Alaskan lakes analysed by Edmundson & Mazumder (2001) was 87 mm, whereas CL smolts averaged 102 mm and SL smolts averaged 95 mm (this study). Thus, while growth conditions for juvenile *O. nerka* at CL are better than at SL, conditions at both lakes are good compared to most Alaskan lakes, which probably explains why the vast majority of juveniles at CL and SL can smolt after only 1 year of lake rearing.

Finally, there were large differences in both in-lake survival and marine survival between CL and SL. The greater fry-to-smolt survival rates at CL (Table II) were not unexpected, given the higher food (zooplankton) availability and warmer temperatures, though the other ecological features of the lakes such as predators presumably play a role as well. Fry density had a significant negative effect on fry-to-smolt survival in SL but not in CL, suggesting that stocking densities at SL might have been approaching carrying capacity in some years. There were also significant differences in smolt-to-adult survival, although smolts from both lakes face a similar migration to the ocean, presumably encounter similar conditions *en route* and presumably also exhibit similar distributions at sea (and encounter similar oceanic conditions once they move offshore). Smolt size differences are probably responsible, as timing differences were relatively subtle and seem unlikely to explain the substantial discrepancy in survival. Koenings *et al.* (1993) found that smolt L_F had a consistently strong effect on smolt-to-adult survival across populations, explaining c. 30% of the variation, and latitude explaining a further 21% (survival rates are higher for northern populations). The size effect they documented was non-linear, however, survival increased by 0.3–0.5% per mm up to c. 90–100 mm, but above that there was no further effect of larger size. Following previous findings by Hartt (1980), Koenings *et al.* (1993) suggested this non-linearity might reflect habitat segregation

of smolts in the marine environment, with larger smolts (>100 mm) tending to emigrate directly offshore, and smaller smolts remaining in the nearshore environment for longer. CL smolts are on the upper end of this size distribution, and this may explain their higher marine survival.

In conclusion, differences in the lake-rearing environment of juvenile *O. nerka* resulted in substantial phenotypic and survival differences between smolts from each lake. Early life environmental influences can affect survival in the ocean phase of the life history of *O. nerka*. Other researchers are encouraged to seek and exploit similar serendipitous reverse common-garden situations, which might allow environmental and genetic effects on ecologically important traits to be disentangled in natural or semi-natural settings.

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