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Long-term changes in rearing habitat and downstream movement by juvenile sockeye salmon (*Oncorhynchus nerka*) in an interconnected Alaska lake system

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Abstract – In some populations the phenomenon of partial migration develops where some individuals stay in a given habitat rather than move with the migratory component. Depending on the selective pressures, the individuals that stay may be larger, smaller or similar in size to those that move. Freshwater movements of juvenile sockeye salmon (*Oncorhynchus nerka* Walbaum) fry vary among and within populations, and can be complex, especially in interconnected lake systems. We examined variation of movement patterns by a sockeye salmon population in an interconnected lake system during a period of rapid natural habitat change and found that fry migrating downstream were shorter, had lower body condition, and were more likely ill and moribund compared with fish remaining in the lake. However, otolith microstructure measurements indicated that emigrants did not grow significantly slower than residents prior to downstream movement. We show that patterns (i.e., demography of migrants, timing of movement) of downstream movement have changed since the 1970s, corresponding to changes in rearing habitat. Our findings parallel the results with other salmonid species and are generally consistent with the paradigm that density-dependent interactions from declining habitat availability or quality result in the downstream movement of competitively inferior individuals, although the mechanisms governing downstream migration are unclear in this system.

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Introduction

Migration and shifts among habitats represent important periods in the life histories of many fish species (Lucas & Baras 2001) and may reflect proximate (Werner & Hall 1988; Dahlgren & Eggleston 2000) or ultimate causal mechanisms (Hendry et al. 2004). Patterns of movement among habitats vary dramatically in time and space; differ among species, conspecific populations, and individuals within populations (see e.g., Quinn & Brodeur 1991). Intrapopu-lation variability in migratory behaviour can result in a phenomenon where a subset of a migratory population remains in a particular habitat rather than moves. This phenomenon, termed partial migration, occurs across a wide range of organisms (reviewed by Dingle 1996) and has important ecological and evolutionary implications (see Jonsson & Jonsson 1993 for a review of partial migration in fishes). Genetic control over migratory behaviour has been identified in some species (birds: Berthold et al. 1990), although environmental conditions can also influence whether an

when they move in the season (i.e., they will be larger if moving later in the growing season, all other things being equal). Cumulative catch curves were constructed and the date of median downstream migration was compared among years using a multiple sample median test (Zar 1999). The test consists of tabulating for each year the number of fish caught above or below the grand median date (median of all data pooled). The resulting 2×6 contingency table was analysed by chi-square. For this and all statistical analyses we used $\alpha = 0.05$ to be indicative of significance.

Gear selectivity

We were cognizant of the potential for differences in gear selectivity to bias our results and we took this into consideration during all stages of the study. Selectivity by fyke nets has been reported by Breen & Ruetz (2006); however, this finding was based on work with nonsalmonid species in lakes rather than in flowing water. Ideally, sampling gear would be fished simultaneously to test for differences in size selectivity, but that is impractical because gear appropriate for sampling in lakes (i.e., beach seines and townets) cannot be effectively fished in a river. Nevertheless, several lines of evidence suggest that differences in gear were unlikely to have biased our results. First, Dolly Varden (*Salvelinus malma* Walbaum) and coho salmon smolts >100 mm were routinely caught, eliminating the possibility that the gear was incapable of capturing large fish. Second, following extensive sampling of downstream migrating sockeye salmon smolts, Burgner (1962) concluded that fyke nets like ours exhibited no selectivity on fish below 105 mm in flows of approximately 0.9 m·s^{-1}. Accordingly, our sites were in areas with relatively high velocity, always exceeding the maximum sustained swimming speed of juvenile sockeye (Carpenter 1987). Third, lengths of fish caught in fyke nets and screw traps were statistically similar thus indicating that the gear was capturing a representative sample of fish migrating downstream. Finally, any gear biases were assumed to be consistent among years because similar nets were fished in nearly identical locations.

Results

Between 1971 and 2006, 118,258 sockeye salmon fry were captured leaving Black Lake. Approximately 15% of the captured fish were sampled for length; 9896 sockeye salmon fry were measured from Black Lake and 7407 from the Black River (Table 2). In each of 6 years, mean size differed between residents and emigrants (ANOVA, $P<0.001$, Fig. 3). When the fish were pooled over the whole season emigrants were
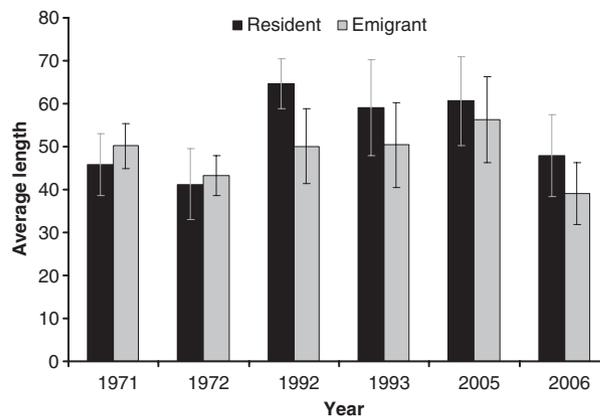

Fig. 3. Average length (±SD) of resident and emigrant sockeye salmon fry in Black Lake Alaska during 1971, 1972, 1992, 1993, 2005 and 2006. Differences in length between resident and emigrant fish were significantly different (ANOVA, $P < 0.05$) within a given year.

significantly larger than resident fish in the 1970s and smaller than resident fish beginning in 1992 (Fig. 3). Patterns in size differences between emigrants and residents also differed between the beginning and the end of the season in the 1970s, although high variation in sample sizes among sampling periods makes strong conclusions difficult. In general, during June and July of 1971 and 1972 emigrants tended to be larger than residents but in August and September emigrants were smaller on average. In contrast, in 1992, 1993, 2005 and 2006 emigrants were typically smaller than residents on average throughout the season (Table 3). Additionally, the average size of sockeye salmon from the Black Lake population, particularly lake residents, increased from a minimum size of 42 ± 8 mm in 1972 to a maximum of 64 ± 6 mm in 1992 (Fig. 3).

Emigrants tended to be lighter than residents for a given length, especially at large and small lengths (Fig. 4). Residuals from OLS fit to log-transformed pooled length–weight data confirmed this observation; emigrants were lighter for their length than residents in both 2005 and 2006 (emigrants $\bar{X} = -0.027$, residents $\bar{X} = 0.018$; t-test, $P < 0.001$). Differences in body condition between residents and emigrants were consistent with the disparity in occurrence of unhealthy (presumably diseased) individuals. No unhealthy resident fish were observed in Black Lake during 2005 or 2006 but 7.5% and 2.1%, respectively, of downstream migrants were visually ill in these years, as indicated by the presence of dark colouration, bulging eyes and fungus on the gills. Interestingly, the occurrence of unhealthy fish increased throughout the season. For example, during June unhealthy individuals represented <<1% of the catch, increasing to approximately 20% of the catch in August in both years. This pattern and magnitude of unhealthy fish

Table 3. Sample size (*N*), mean length (±SD) of lake resident and downstream emigrant sockeye salmon fry in the Chignik Lake system, Alaska, during the summer of 1971–2006.

Year	Migrant status	Month									
		May		June		July		August		September	
		N	Mean (±SD)	*N*	Mean (±SD)	*N*	Mean (±SD)	*N*	Mean (±SD)	*N*	Mean (±SD)
1971	Resident	0	N/A	289	35 ± 3*	1451	46 ± 6*	540	52 ± 6*	0	N/A
	Emigrant	0	N/A	6	42 ± 5*	805	51 ± 6*	823	50 ± 5*	0	N/A
1972	Resident	0	N/A	524	33 ± 3	1076	36 ± 4*	921	43 ± 4	727	53 ± 5*
	Emigrant	0	N/A	3	33 ± 4	89	45 ± 5*	931	43 ± 4	41	46 ± 5*
1992	Resident	0	N/A	0	N/A	0	N/A	494	64 ± 6*	0	N/A
	Emigrant	476	31 ± 2	902	37 ± 4	196	45 ± 7	35	50 ± 8*	0	N/A
1993	Resident	0	N/A	267	47 ± 7	154	52 ± 7	367	63 ± 7*	265	69 ± 6*
	Emigrant	60	38 ± 3	487	47 ± 7	311	54 ± 10	168	57 ± 9*	37	57 ± 7*
2005	Resident	0	N/A	401	55 ± 5	291	61 ± 6*	160	70 ± 9*	39	74 ± 6*
	Emigrant	0	N/A	313	54 ± 5	406	57 ± 8*	269	57 ± 11*	26	68 ± 8*
2006	Resident	206	37 ± 4*	479	39 ± 5*	501	48 ± 6*	744	56 ± 6*	0	N/A
	Emigrant	166	33 ± 3*	597	38 ± 5*	139	43 ± 8*	121	51 ± 6*	0	N/A

Mean lengths, within a year and month, that differ (anova, *P* < 0.05) among residents and emigrants are denoted with an asterisk.
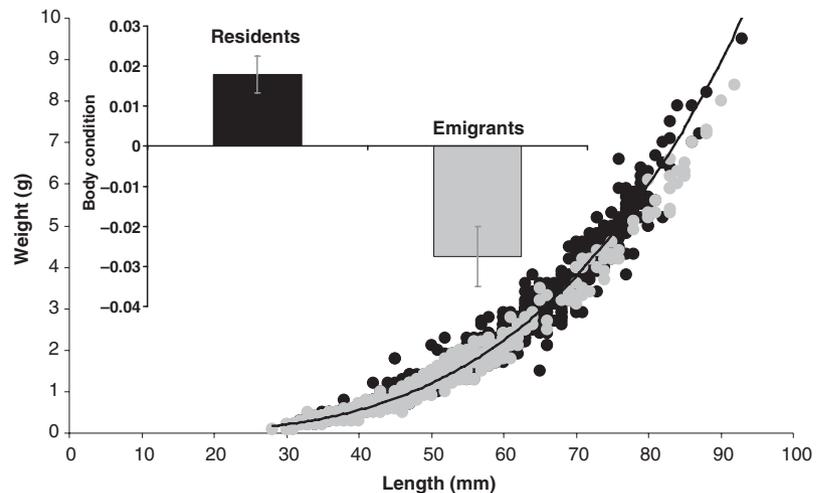

Fig. 4. Length–weight relationship and average body condition (inset, residuals from log length–weight data, see Materials and methods section) between resident (black bars and points) and emigrant (grey bars and points) sockeye salmon fry in Black Lake, Alaska, during 2005–2006. Error bars represent one standard deviation.

occurrence was also observed in 1993 (Ruggerone 1994), but were not mentioned in historical reports or datasets (e.g., Parr 1972).

Results of otolith microstructure indicated that emigrants and residents did not differ in mean specific growth rates (*t*-test, *P* = 0.13). The high level of variation and small sample sizes limited our ability to detect differences but other evidence suggested a growth advantage by residents. By subtracting the age of a fish (in days) from the date of collection we calculated the date of emergence for resident and emigrant fish. Emigrants emerged into the lake environment and began feeding significantly earlier (averages: 9 June vs. 24 June) than resident fish (*t*-test, *P* < 0.001). Fish that entered the lake early tended to grow more slowly than individuals that entered later in the season (*P* < 0.001, Fig. 5); emergence date explained approximately a third of the variation in growth (r^2 = 0.32). This was partic-

ularly interesting because the size of an individual did not depend on age (OLS, *F* = 4.13, *P* = 0.45, r^2 = 0.045) or emergence date (OLS, *F* = 0.004, *P* = 0.835, r^2 = 0.000).

Within Black Lake we found that the average length of sockeye salmon fry tended to decrease with proximity to the lake's outlet (Fig. 6). This relationship was significant in 2006 (OLS, *F* = 15.1, r^2 = 0.79, *P* = 0.017) but not 2005 (OLS, *F* = 2.3, r^2 = 0.37, *P* = 0.20). Extensive sampling of the pelagic area of the lake in 1993 indicated a similar pattern of declining size from the western area (49.5 ± 0.6 mm) of Black Lake towards the outlet (36.8 ± 0.4 mm) of the lake (Ruggerone 1994).

Finally, downstream migration, as inferred from date of median cumulative catch, occurred earlier in the season in recent years than in the past: 3 August 1971, 14 August 1972, 23 June 1992, 22 July 1993, 19 July 2005 and 11 June 2006 (Fig. 7). The difference in