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Long-distance downstream movements by homing adult chinook salmon

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Unusually long downstream movements totalling several hundred kilometres to >1100 km were observed during upstream homing migrations of radio-tagged spring chinook salmon *Oncorhynchus tshawytscha* in the Columbia and Snake Rivers, U.S.A. Downstream migrants, identified by their repeated ascension and fallback over a series of large hydroelectric dams within the migration corridor, were primarily hatchery-origin males.

Key words: chinook salmon; downstream migration; hatchery; *Oncorhynchus*; radiotelemetry.

The environmental, reproductive, and genetic cues affecting upstream migration timing and upstream migration rates of adult anadromous salmonids (*Oncorhynchus* and *Salmo*) have been well documented (Banks, 1969; Burger *et al.*, 1985; Stewart *et al.*, 2002; Quinn *et al.*, 2002; Keefer *et al.*, 2004*a*,*b*). Downstream movements also occur during salmonid homing migrations, and have been reported on a scale of metres to tens of kilometres following fish handling (Bernard *et al.*, 1999; Mäkinen *et al.*, 2000), near migration obstacles (Gowans *et al.*, 1999) and on spawning grounds (Berman & Quinn, 1999; Økland *et al.*, 2001). Relatively little is known, however, about the extent of downstream movements or about how such behaviours affect migration success. The behaviours and traits of a group of salmonids with exceptionally long downstream movements during upstream homing migration within a regulated river system were investigated in the present study.

Results from a large, multi-year radiotelemetry study of thousands of adult salmonid migrations in the Columbia River basin (U.S.A., 46° N; 124° W; Fig. 1) indicate that substantial downstream movements may be much more frequent than previously described. Boggs *et al.* (2004) described widespread downstream movement by these fishes past hydroelectric dams, a behaviour termed 'fallback'. On average, 15–22% of the fishes from studied runs of chinook salmon *Oncorhynchus tshawytscha* (Walbaum) and steelhead

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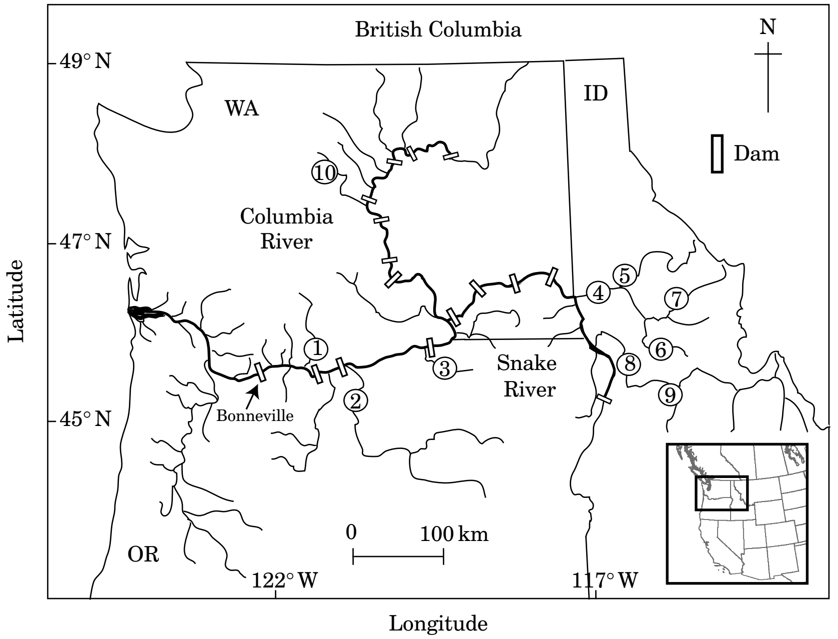

Fig. 1. Locations of the Columbia and Snake Rivers, major hydroelectric dams (□), the chinook salmon radio-tagging site (Bonneville Dam) and tributaries where successful study fish were last recorded: 1, Klickitat River; 2, Deschutes River; 3, Umatilla River; 4, Clearwater River; 5, North Fork Clearwater River; 6, South Fork Clearwater River; 7, Lochsa River; 8, Salmon River; 9, Rapid River; 10, Icicle River.

Oncorhynchus mykiss (Walbaum) fell back over at least one dam during migration (Boggs *et al.*, 2004). Most fishes that fell back at a dam did so one to two times during migration, apparently in response to dam operations, river environment, or spawning site locations (*i.e.* fishes fell back at dams upstream from natal tributaries). A much smaller number of fishes fell back multiple times and at multiple dams, and this behaviour often included downstream movements of hundreds of kilometres. Long-distance movements were most frequent among spring-run chinook salmon, and migration details for a sub-sample of fish from this run are given.

Over 7 study years (1996–2003), migration histories were reconstructed for 4892 spring-run adult chinook salmon using data from an extensive array of radiotelemetry sites. All chinook salmon were collected at Bonneville Dam on the Columbia River (river kilometre 235) during April and May, where they were anaesthetized and received uniquely coded intragastric radio transmitters. After recovery and release downstream, chinook salmon were monitored as they migrated upstream past as many as nine dams, through reservoirs, and to spawning sites up to 1500 km from the Pacific Ocean (Fig. 1). Between 115 and 335 underwater and aerial antennas were deployed each year to record fish movements at seven to 10 major hydroelectric dams as well as in reservoirs and major tributaries (Boggs *et al.*, 2004; Keefer *et al.*, 2004*a*,*c*). This monitoring configuration allowed detection of almost all dam passage and fallback events by chinook salmon, as well as up- and downstream movements between dams and other monitoring sites.

To identify chinook salmon with long-distance downstream movement, all migration histories were searched for multiple fallback events at dams because this behaviour clearly indicated retrograde movement. A total of 33 fish (0·7%) had seven or more fallbacks at dams, and this group was further analysed. Seven was arbitrarily selected as the cutoff to facilitate presentation of the most extreme cases, while still providing an adequate sample. In total, 3842 fish (78·5%) did not fall back over a dam, 907 (18·5%) fell back one to three times, and 110 (2·2%) fell back four to six times. The 33 fish with seven or more fallbacks were 67% male (based on physical characteristics) and 85% had fin clips indicating hatchery origin; mean ± S.D. fork length, L_F, was 80 ± 6 cm (range = 70–96 cm). By comparison, 53% of the full sample was male, 44% had hatchery fin clips, and mean ± S.D. L_F was 77 ± 8 cm (range = 51–125 cm). Seventy-three per cent (24 of 33) of the sub-sample returned to hatcheries or spawning tributaries and were considered successful migrants. Successful chinook salmon returned to the Clearwater (10 fish), Deschutes (eight), Salmon (three), Klickitat (one), Umatilla (one) and Icicle (one) River basins (Fig. 1). The nine (27%) unsuccessful fish were last recorded at Columbia River dams or in reservoirs and had unknown fate.

Cumulative mean ± S.D. downstream movements by the 24 successful migrants were 528 ± 195 km (range = 245–1181 km). The 24 were predominantly male (71%) and of hatchery origin (79%), much like the initial sub-sample of 33. On average, the 24 fish made 14 ascents of Columbia River and Snake River dams and fell back over dams nine times before reaching potential spawning sites (Table I). Some fell back over multiple dams in succession with no recorded upstream movements, resulting in protracted downstream movements that were often >200 km (Fig. 2). The single longest downstream movement by a successful fish (403 km) was by a male chinook salmon that returned to Dworshak National Fish Hatchery on the Clearwater River [Fig. 2(a)]. This fish had cumulative downstream movements of 1181 km (Table I).

Cumulative mean ± S.D. downstream movements by the nine unsuccessful migrants were 379 ± 129 km (range = 137–538 km), significantly shorter than for successful fish (two-tailed *t*-test, $P < 0·05$). Unsuccessful fish also averaged slightly fewer dam ascents (10) and fallback events (eight) than successful fish, but these differences were non-significant (*t*-tests, $P > 0·10$). About 75% of all fallback events were at one of the three Columbia River dams closest to the ocean, with the largest proportion (32%) recorded at Bonneville Dam. Most first fallbacks by both successful (92%, 22 of 24) and unsuccessful (67%, six of nine) migrants were also at one of the three lower dams, and these first fallback locations appeared to be random with respect to final fish location. Within year, there was no evidence of synchronous downstream movement.

Several interrelated factors may help explain these long-distance downstream movements. First, anadromous fishes in the Columbia River basin migrate in an environment transformed by hydroelectric development. Homing adults from upper basin stocks must pass as many as nine large hydroelectric dams and reservoirs to reach spawning sites, encountering multiple fisheries, dam operations that can affect passage and survival (Boggs *et al.*, 2004; Keefer *et al.*, 2005),

TABLE I. Migration details for 33 radio-tagged spring chinook salmon that fell back at dams seven or more times in the Columbia and Snake Rivers, 1996–2003. Presence of fin clip indicated hatchery origin. Letters in parentheses refer to fish described in Fig. 2

					Cumulative migration distance (rkm)		
Fate	Sex	Fin clip	Year	Total dam passages up (down)	Downstream	Upstream	Total
Clearwater[1(a)]	M	yes	1997	24 (16)	1181	1992	3173
Clearwater[1(b)]	M	yes	1997	22 (14)	838	1649	2487
NF Clearwater[2(d)]	M	yes	2003	20 (12)	739	1593	2332
Clearwater[1]	M	yes	2002	17 (9)	645	1517	2162
Salmon[3]	M	yes	2000	16 (8)	629	1541	2170
Rapid[2]	M	yes	2001	15 (7)	623	1594	2217
Clearwater[1(c)]	F	no	2003	17 (9)	622	1436	2058
Deschutes[3]	M	no	1996	13 (11)	574	902	1476
Deschutes[2]	M	yes	1997	9 (7)	560	959	1519
Unsuccessful	F	yes	1998	14 (11)	538	1005	1543
Deschutes[3]	M	yes	1998	13 (11)	528	924	1452
Deschutes[2]	F	yes	1997	9 (7)	525	922	1447
Unsuccessful	M	yes	1998	9 (8)	517	752	1269
Rapid[1]	M	yes	2000	17 (9)	512	1492	2004
SF Clearwater[3]	F	yes	2002	15 (7)	503	1369	1872
Deschutes[2]	F	yes	2000	9 (7)	499	896	1395
Unsuccessful	M	yes	1997	11 (8)	490	957	1447
Clearwater[3]	M	yes	2000	18 (10)	485	1238	1723
Unsuccessful	F	yes	2001	9 (9)	475	707	1182
Clearwater[1]	M	no	1997	16 (8)	474	1285	1759
Clearwater[3]	F	no	1996	15 (7)	393	1196	1589
Deschutes[3]	F	yes	1997	10 (8)	381	777	1158
Deschutes[1]	M	yes	1997	9 (7)	371	864	1235
Unsuccessful	M	yes	2000	15 (8)	369	1098	1467
Deschutes[1]	M	yes	1998	9 (7)	361	855	1216
Icicle[3]	M	no	1997	14 (7)	356	1154	1510
Unsuccessful	M	yes	2001	7 (7)	347	579	926
Umatilla[2]	F	yes	2003	10 (7)	314	779	1093
Lochsa[1]	M	yes	1998	16 (8)	312	1327	1639
Unsuccessful	M	yes	1998	9 (7)	286	613	899
Unsuccessful	F	yes	1997	9 (7)	251	596	847
Klickitat[3]	M	yes	1998	10 (9)	245	600	845
Unsuccessful	F	yes	2000	11 (7)	137	641	778

[1]Hatchery or fish trap.
[2]Fishery.
[3]Unknown.

and widely variable environmental conditions. Some of the observed downstream movements may have been a function of fishes searching for cues from natal sites within this transformed system. Second, increased production of hatchery salmonids may contribute to fishes wandering and searching

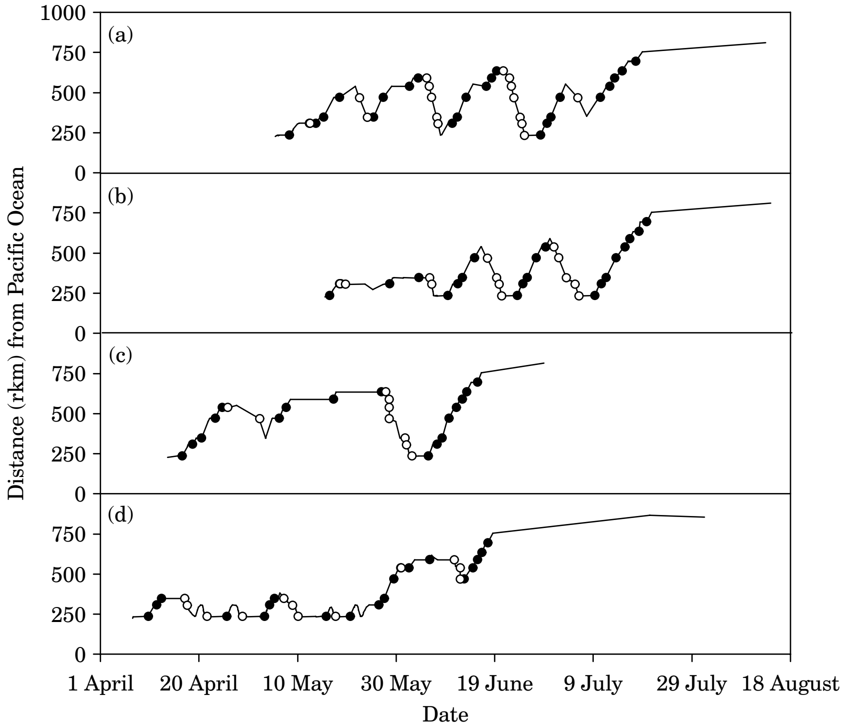

FIG. 2. Migration tracks, including dam passages (●) and downstream fallbacks over dams (○), for (a)–(b) four radio-tagged spring chinook salmon (see Table I). All fish were released downstream from Bonneville Dam and returned to the Clearwater River. Some passage and fallback symbols overlap.

behaviours, as homing by hatchery fishes can be less precise than by wild fishes (McIsaac & Quinn, 1988; Quinn, 1993). Third, some downstream movement may be attributable directly to inter-basin straying, a behaviour associated with both male salmonids (Hard & Heard, 1999) and hatchery fishes (Quinn, 1993). It was not possible to assess straying by the study sub-sample, but Snake River and upper Columbia River chinook salmon routinely stray into lower river tributaries, and particularly into the large Deschutes River (C. Peery, unpubl. data). Fourth, many Columbia basin salmonids are transported downstream as juveniles to mitigate mortality risks associated with dams and reservoirs, and this management strategy has been tied to elevated fallback rates and reduced adult homing (Bugert *et al.*, 1997; Chapman *et al.*, 1997). Downstream movements by the study fish are consistent with disorientation or homing impairments, some of which may be attributable to imprinting interruptions for transported fishes (Pascual *et al.*, 1995). Origin and transportation histories were unknown for all but four (two successful, two unsuccessful) of the 33 chinook salmon in the study sub-sample: these four were transported from the Snake River as juveniles. It is plausible that a combination of these factors and others (*i.e.* handling of adults during tagging, sexual maturation status or migration timing) contributed to the observed behaviours.

These observations highlight the remarkable energetic reserves available to some long-distance adult salmonid migrants. Unfortunately, no data on reproductive success at spawning sites were available, and the question of how long-distance downstream movements affect overall reproductive success remains to be answered. There is compelling evidence that fallback at Columbia and Snake River dams reduces adult escapement to spawning areas for several chinook salmon and steelhead runs (Keefer *et al*., 2005), and it is intuitive that multiple fallbacks may incur additional energetic and reproductive costs. Separating the costs of fallback and reascension at dams from the energetic costs of long-distance downstream movements, however, will be difficult within the developed Columbia River system. Closer examination of downstream movement by adult salmonids in undeveloped systems may help identify whether the behaviour is a natural aspect of homing resulting from past selection pressures or is primarily a product of a highly altered environment and associated salmonid management strategies.

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