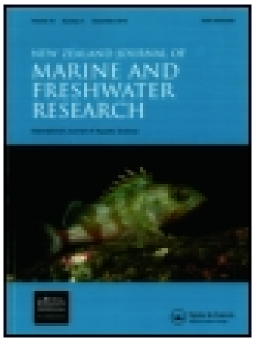

New Zealand Journal of Marine and Freshwater Research

ISSN: 0028-8330 (Print) 1175-8805 (Online) Journal homepage: http://www.tandfonline.com/loi/tnzm20

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New Zealand Journal of Marine and Freshwater Research, 1995: Vol. 29: 257–269
0028–8330/95/2902–0257 $2.50/0

Spawning migrations and reproduction of landlocked sockeye salmon (*Oncorhynchus nerka*) in the Waitaki catchment, New Zealand

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Abstract The spawning migrations of landlocked sockeye salmon (*Oncorhynchus nerka*) within the Waitaki catchment from 1975 to 1992 are described. In late February and early March an overlapping succession of spawning runs, consisting of fish of different origins and ages, spawned in cool (8–12°C) spring-fed tributaries of lakes Ohau and Benmore. The size, age, and sex compositions of the runs were highly variable. Mature fish ranged in age from 2 to 5 years and in length from 138 to 462 mm. Redds were constructed in gravel (15–30 mm diam.) in water 0.15–0.50 m deep, flowing at 0.20–0.50 m s^{-1}. Runs increased during the 1970s, reaching a peak number of over 18 000 in 1979. Dam construction that was completed in late 1979 blocked spawning migrations from Lake Benmore to Lake Ohau; spawning runs are now fewer than 100 fish per annum and may be insufficient to maintain the wild stock. Attempts to increase the spawning runs by liberating hatchery-reared juveniles and by the transfer of mature fish into warm (14–19°C) rain-fed streams have failed, possibly because of the premature emergence of fry in mid winter.

Keywords sockeye salmon; *Oncorhynchus nerka*; spawning migrations; Waitaki River; hydro-electric development

M94032
Received 11 July 1994; accepted 8 March 1995

INTRODUCTION

The sockeye salmon (*Oncorhynchus nerka*) stock in New Zealand originated from a single introduction from British Columbia in 1901 (Scott 1984). Fry were released into tributaries of Lake Ohau in the Waitaki catchment in the South Island of New Zealand (Fig. 1) and a landlocked population developed here. Mature fish spawn in Larch Stream, at the head of Lake Ohau, and fish rear in this lake and in hydrolakes situated down stream (Fig. 1) (Hardy 1969; Flain 1971; Keillor 1975). No salmon have been recorded from Lake Tekapo, only one from Lake Pukaki and no other wild populations have become established in New Zealand.

In recent years hydro-electric power developments have had major impacts on salmon spawning migrations. Since 1980, fish migrating from Lake Benmore to Lake Ohau were blocked first by a weir on the Ohau River and in later years by the Ruataniwha Dam. In an attempt to establish new spawning runs, over 14 000 hatchery-reared fry and juveniles have been released into Lake Benmore and 16 400 mature wild fish (salvaged from Larch Stream in 1979 and from below the Ruataniwha Dam in 1982) were released into its tributaries (Graynoth 1979; Hawke 1982).

In 1975, studies were initiated to determine the ecology of sockeye salmon in New Zealand and their potential value in aquaculture, as a sports fish, or as forage for trout (Graynoth & Hawke 1985; Graynoth et al. 1986; Graynoth 1987). The principal aim of the present paper is to describe their spawning grounds, spawning runs, and reproduction primarily using data collected from Larch Stream. Secondary aims are to evaluate the influence of hydro-electric power development and other factors on the stock and determine how they differ from kokanee, the genetically distinct form of sockeye salmon resident in northern hemisphere lakes.

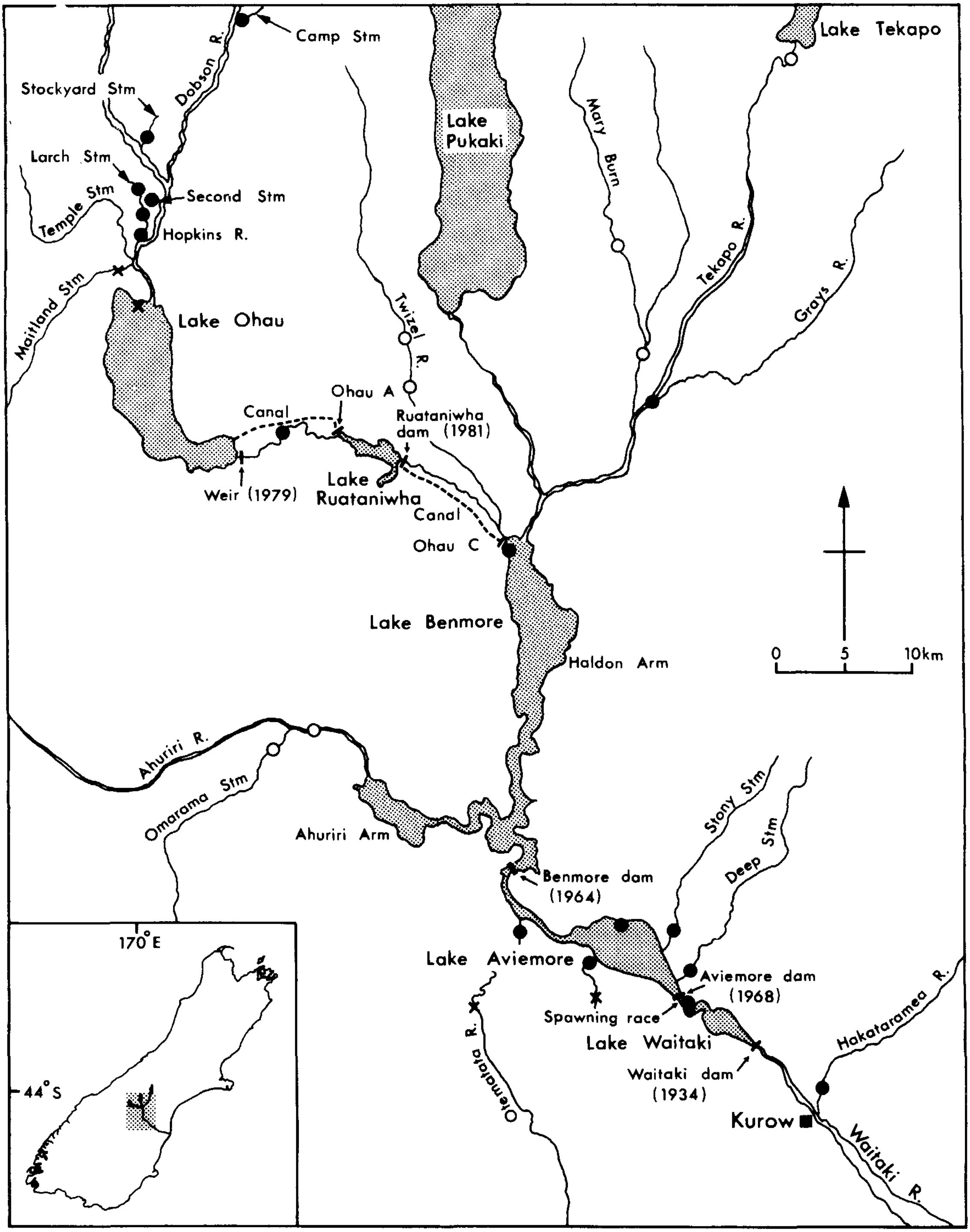

Fig. 1 Map of the Waitaki River catchment, South Island, New Zealand, showing the sockeye spawning areas and rearing lakes. •, spawning ground 1970–92, o, 1979 and 1982 liberations of adult fish and fry; ×, additional spawning ground before 1970 (C. J. Hardy & M. Keillor unpubl. data)

STUDY AREA

Larch Stream is spring-fed and joins the Hopkins River, 5 km upstream from Lake Ohau (Fig. 1). It is 5.3 km in length, with an average width of 5.5 m, has a gentle gradient (1 : 900) and a mean flow of 1.3 $m^3 s^{-1}$. Pools range in depth from 0.6 to 1.5 m and riffles from 0.25 to 0.70 m and their velocity from 0.3 to 1.0 m s^{-1}. In March water temperatures average 10.1°C (range 8.2–12.1°C) and then decline to 7°C in July. The stream bed is composed of rounded gravels, sand, and clay. Scattered weed beds of *Myriophyllum* spp. and *Potamogeton* spp. are common. The stream contains a diverse population of macroinvertebrates and three species of native fish (*Anguilla dieffenbachii, Gobiomorphus breviceps*, and *Galaxias brevipinnis*). Adult rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) migrate into the stream to spawn, and juvenile trout are abundant in spring and summer.

Salmon also spawn in several small streams (< 1 $m^3 s^{-1}$ mean annual flow) entering the Hopkins River, such as "Second" Stream and Stockyard Stream (Fig. 1) and two unnamed streams near Ohau A and Ohau C power stations. These spring-fed streams all contain cool (about 12°C), clear water, abundant macrophyte beds, and limited amounts of spawning gravel.

The large rivers in the Waitaki catchment, such as the Ahuriri and Hopkins Rivers, have unstable, braided river beds which are unsuitable for salmon spawning. They contain warm water during March (14–19°C) but are generally colder (4°C) during mid winter (July and August) than Larch Stream (Mosley 1982; pers. obs.). Small rain-fed tributaries such as Stony Stream and Mary Burn (Fig. 1) contain patches of suitable spawning gravel but are also relatively warm in March and cold in mid winter.

Lake Ohau is a large (area 54 km^2), deep (mean depth 74 m) oligotrophic lake of glacial origin with a long (580 d) residence time (Graynoth et al. 1986; Graynoth 1987). Lake Benmore and the other hydro-electric lakes vary in area from 5 to 69 km^2 and are more productive and shallower (mean depths 7–28 m) than Lake Ohau with shorter residence times.

METHODS

Field work

To determine the distribution of spawning grounds and the abundance of salmon, foot surveys were undertaken each year from 1975 to 1992. The main spawning streams (Fig. 1) were examined weekly whereas less important areas were surveyed only once. Information was also collected on fish appearance, length, sex, and age composition. To check all spawning areas had been identified, 230 km of tributaries and lake beaches were scrutinised from a helicopter in March 1978.

From 1976 to 1985, and in 1992, the spawning runs into Larch Stream were monitored by maintaining a trap at its confluence with the Hopkins River from late February/early March to late March/early April. Each day, fish were counted, sexed, and fork length (FL) was recorded to the nearest mm. Only a few of the larger mature males had extended snouts (kypes) and lengths were not adjusted to compensate for this feature. Mature fish from lakes Ohau and Benmore entered Larch Stream and were separated by differences in size, colour, and otolith patterns (Graynoth 1987). Spent fish and carcasses which drifted down stream to the trap were collected daily and their length, sex, and number of residual ova were recorded. Stream water levels and temperatures were recorded daily.

The total number of fish spawning in Larch Stream was calculated by adding pre-trap, spawning survey counts to trap catches and to estimates of the remnant run after the trap was removed. Spawning survey counts (2–9 per annum) were used to estimate runs in years when it was not trapped (1975, 1986–91).

Changes in stock abundance in the Waitaki catchment were assessed from Larch Stream estimates and from spawning survey counts elsewhere. From 1980 onwards, salmon migrating up the Ohau River were blocked by the Ruataniwha Dam. Stock numbers were estimated from surveys in the residual river and tailraces, and from salvage records.

Visual observations were made on salmon distribution within the spawning streams. Water depths and velocities were measured 0.12 m above stream bed at 137 redds in Larch Stream and at 12 redds in Stony Stream in March 1979. Four redds in Larch Stream were excavated to determine the size of spawning gravels and depths to which ova were buried. To determine the potential spawning habitat available for salmon, water depths, velocities, and substrate composition were measured in 8–10 cross-sectional transects along selected reaches of Larch, Temple, and Maitland Streams in 1981. The development and survival of ova and alevins in the gravels of Larch Stream, Omarama Stream, and the Mary Burn was measured from March to May 1979 using the methods of Hobbs (1937).

Laboratory methods

Otoliths were examined to determine age, growth, and the lake of origin of mature fish (Graynoth 1987). Growth rates are higher in Lake Benmore than Lake Ohau and were used to determine the age at which fish moved down stream. Fish ages are described using the Gilbert & Rich notation (Foerster 1968) whereby the age at which fish migrated down stream from Lake Ohau is identified by a subscript (Graynoth 1987).

Fecundity was determined by counting the eggs contained in 113 two- to five-year-old mature females collected at the Larch Stream trap from 1976 to 1978, and in 16 two-year-old females reared at Glenariffe Hatchery. To assess the completeness of egg deposition, residual eggs were counted in 71 dead spent females.

RESULTS

Distribution and size of the spawning runs

Larch Stream was the most heavily utilised spawning stream and about 98% of the salmon spawned here (Table 1 and 2). Larch Stream runs averaged 13 000 during 1976–79, declined to 1600 during 1980–86 and were nil from 1987 to 1991. In 1992 only 85 fish were trapped and fewer than 14 000 eggs were available for deposition in redds.

Small runs entered other spring-fed tributaries of Lake Ohau and irregular runs occurred elsewhere. Salmon occasionally spawned in tributaries of Lake Benmore. In 1978, 204 fish spawned in two spring-fed drains at the Ohau A tailrace construction site (Table 1 and 3) and from 1988 to 1992 up to 1100 fish spawned in spring-fed streams and ponds near Ohau C power station (Table 1 and 3). Small numbers of mature salmon spawned in tributaries of Lake Ruataniwha after it was filled in April 1982. The spawning runs into

Table 1 Estimated spawning runs of sockeye salmon in the Waitaki River system from 1975 to 1992. These are minimal estimates and refer to the locality where the fish were first observed or captured. Excludes mature fish transferred to tributaries of Lake Benmore in 1979 and 1982. –, no survey.

	Lake Ohau			Lake Benmore		Lake Aviemore		Lake Waitaki, Aviemore Spawning Race	
Year	Larch Stream	"Second" Stream	Other tribs.[1]	Ohau River[2]	Other tribs.	Beaches	Tribs.[3]		Total (minimum)
1975	6	0	0	–	–	–	0	0	6
1976	5254	48	4	–	–	17	0	0	5323
1977	16 246	210	113	–	–	30	88	100	16 787
1978	13 595	50	61	204	0	5	13	12	13 940
1979	18 223	270	–	–	0	30	77	3	18 603
1980	250	–	–	11	0	–	–	3	264
1981	1400	15	0	0	0	–	18	0	1433
1982	3743	125	147	8855†	0	–	8	17	12 895
1983	700	1	–	4	2	–	8	2	717
1984	374	–	–	0	1	–	0	0	375
1985	2728	993	20	421	0	–	–	–	4162
1986	2100‡	65	–	100	0	–	–	0	2265
1987	0	–	–	80	0	–	0	–	80
1988	0	–	–	1100	–	–	0	0	1100
1989	0	0	–	135	7	–	–	0	142
1990	0	–	–	54	–	–	0	0	54
1991	0	0	–	5	–	–	–	0	5
1992	85	0	0	20	–	–	0	11	116

[1]Stockyard Stream, Camp Stream
[2]Ohau River includes the Ohau River, Ohau A and C power station area, and Lake Ruataniwha
[3]Deep Creek, Stony Stream
†fish salvaged below the Ruataniwha Dam
‡estimate – based on a single partial spawning survey

tributaries of Lake Aviemore and into the Aviemore Spawning Race have also been small, variable in size, and have declined in recent years (Table 1).

Larch Stream spawning runs

From 1975 to 1979, spawning runs into Larch Stream comprised an overlapping succession of different sex and age classes of fish from Lakes Benmore and Ohau. From 1980 onwards only fish from Lake Ohau were present as the migration from Lake Benmore was blocked by hydro-electric power development. As a result there were substantial annual variations in numbers of fish spawning and in the length-frequency distribution, sex ratio, and age composition of the fish present (Table 2).

Spawning migration into Larch Stream extended from mid February to early April (Fig. 2), with a mean date of entry of 6 March (n = 20, s.d. = 5 d). Run duration ranged from 9 to 48 days, the mid-point of each run generally occurring one or two days earlier than the mean date of entry.

Table 2 Lake of origin, age class, sex, and mean FL of fish in the Larch Stream spawning runs 1976–92. No sockeye salmon were seen in spawning surveys from 1987 to 1991. ? indicates estimate based on a single spawning survey and a sample of 24 fish seine-netted. –, no data.

			Fish in each year class								Mean fork length (mm) of each year class			
			Total number				Proportion of males (%)							
Year	Lake of origin	Size of run	2	3	4	5	2	3	4	5	2	3	4	5
1976	Ohau	3160	0	2964	196	0	–	92	48	–	–	197	237	–
	Benmore	2094	66	1973	55	0	–	52	–	–	254	259	293	–
1977	Ohau	7770	0	0	7656	114	–	–	65	–	–	–	282	–
	Benmore	8476	0	404	8072	0	–	63	28	–	–	298	344	–
1978	Ohau	1348	0	0	116	1232	–	–	39	59	–	–	330	326
	Benmore	12247	11802	0	0	445	90	–	–	62	236	–	–	450
1979	Ohau	591	396	145	50	0	99	63	0	–	139	220	–	–
	Benmore	17632	4590	13042	0	0	78	14	–	–	208	322	–	–
1980	Ohau	250	0	250	0	0	–	97	–	–	–	200	–	–
1981	Ohau	1400	814	317	269	0	96	72	90	–	175	210	218	–
1982	Ohau	3743	0	3743	0	0	–	75	–	–	–	226	–	–
1983	Ohau	700	2	2	696	0	–	–	76	–	–	–	288	–
1984	Ohau	374	238	135	0	1	91	62	–	–	232	309	–	–
1985	Ohau	2728	0	2726	2	0	–	59	–	–	–	295	–	–
1986	Ohau	2100?	300	1600	200	0	100	50	50	–	198	309	–	–
1992	Ohau	85	0	85	0	0	–	53	–	–	–	276	–	–

Table 3 Percentage composition by lake of origin, age class, sex, and the mean FL of fish in the spawning runs into tributaries of the hydro lakes and Hakataramea River. –, no data. Males: all ages combined.

					Age class (year)					Mean length (mm)		
Lake of origin	Year	Location netted	Max. no. counted	No. sampled	2	3	4	5	Males (%)	2	3	4
Ruataniwha	1985	Ohau A	400	27	0	100	0	0	30	–	359	–
	1992	Lake	17	17	–	–	–	–	–	–	252	–
Benmore	1978	Ohau A	200	12	92	0	0	8	58	317	–	–
	1982	Ruataniwha Dam	8855	158	0	100	0	0	53	–	297	–
	1988	Ohau C	1100	31	0	100	0	0	16	–	321	–
	1989	Ohau C	135	35	0	100	0	0	20	–	326	–
	1990	Ohau C	54	54	91	9	0	0	54	232	355	–
Aviemore	1976	Beaches	17	15	0	100	0	0	33	–	283	–
	1977	Stony River	50	23	4	4	92	0	0	–	–	389
Waitaki	1977	Spawning race	100	26	0	13	87	0	38	–	323	337
	1977	Hakataramea River	20	11	0	9	91	0	0	–	–	332
	1978	Spawning race	12	7	0	0	100	0	–	–	–	408

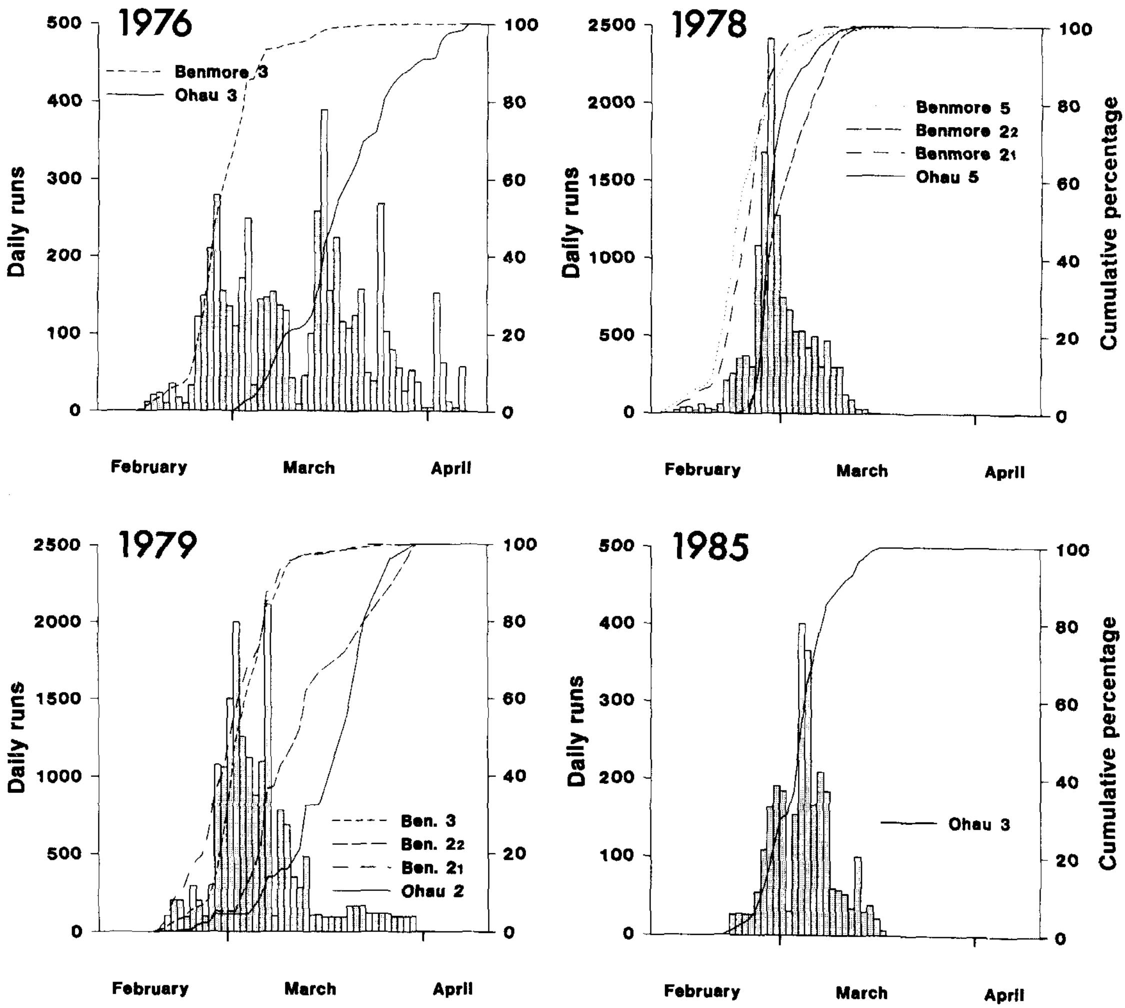

Fig. 2 Timing of representative spawning runs into Larch Stream. Timing of the spawning run before 6 March 1976 was estimated using data from 1979.

Run timing depended on the size of the fish in the run. Mean date of entry (D = day of the year) was negatively correlated with the mean FL of fish in the run (D = 87.8 – 0.084 FL, $n = 21$, $r = 0.76$, $P < 0.001$). Within each spawning run, mean FL decreased with time, at rates ranging from –0.04 to –2.3 mm d^{-1}. The percentage of females trapped increased during most spawning runs, females entering the stream on average 1.9 days later than males (range 0 to 5.4 days, $n = 16$ runs). Moon phase and Larch Stream water temperatures and flows had no detectable influence on the daily catches at the Larch Stream trap.

Mature salmon ranged in length from 110 to 515 mm (Fig. 3), although most fish ranged from 200 to 360 mm. The smallest fish were 2-year-old males from Lake Ohau, which in 1979 averaged 139 mm, and the largest were 5-year-olds from Lake Benmore, which averaged 462 mm in 1978. Annual variations in length frequency were caused by differences in the age composition and growth rates of fish present. Before 1980, fast growing fish from Lake Benmore were a major component of the run together with slower growing fish from Lake Ohau (Table 2). From 1983 onwards Lake Ohau residents grew faster, mean FL of 3-year-olds increasing from 212 to 297 mm ($P < 0.001$) (Table 2, unpubl. data 1973 run).

The sex composition of the spawning runs also varied between years (Table 2). In 1980–84 the Larch Stream runs were dominated by males (75–97% of the total run) but in 1979 females were most abundant (68%). Males generally matured at an earlier age than females (Table 4); 92% (range 78–99%) of the 2-year-olds were males compared with 63% (14–97%) of the 3-year-olds and 49% (0–90%) of the 4-year-olds (Table 2).

Mature salmon ranged from 2 to 5 years old (Tables 2 and 3). Salmon resident in Lake Benmore usually matured at 2 or 3 years old (average 2.76) whereas fish from Lake Ohau matured at age 3 or 4 (average 3.19: Table 4). There was evidence for a triennial cycle with a strong 1973 year class and large runs of 3-year-old fish spawning in or destined for Larch Stream in 1976, 1979, 1982, and 1985 (Table 2).

The influence of growth rates and parental age on the proportion of fish maturing at age 2 and older was examined using data on the 1973, 1976–79, and 1982 year classes (Table 4). In a multiple regression equation the percentage maturing at age 2 was positively correlated both with their mean length as yearlings (1+) and with their parents' age (males $n = 12$, $r^2 = 0.67$, $P < 0.05$, females $n = 10$, $r^2 = 0.80$, $P < 0.01$, excluding four weak year classes of <100 fish). The cumulative percentage of fish spawning at ages ≤ 3 and ≤ 4 years old was also positively correlated with their mean length as yearlings. Growth rates beyond age 1 had no statistically significant influence on the age at which fish matured. Therefore fish which grew rapidly as juveniles matured earlier and at maturity were often similar in size to slow-growing, late-maturing fish (Fig. 3 and Table 4).

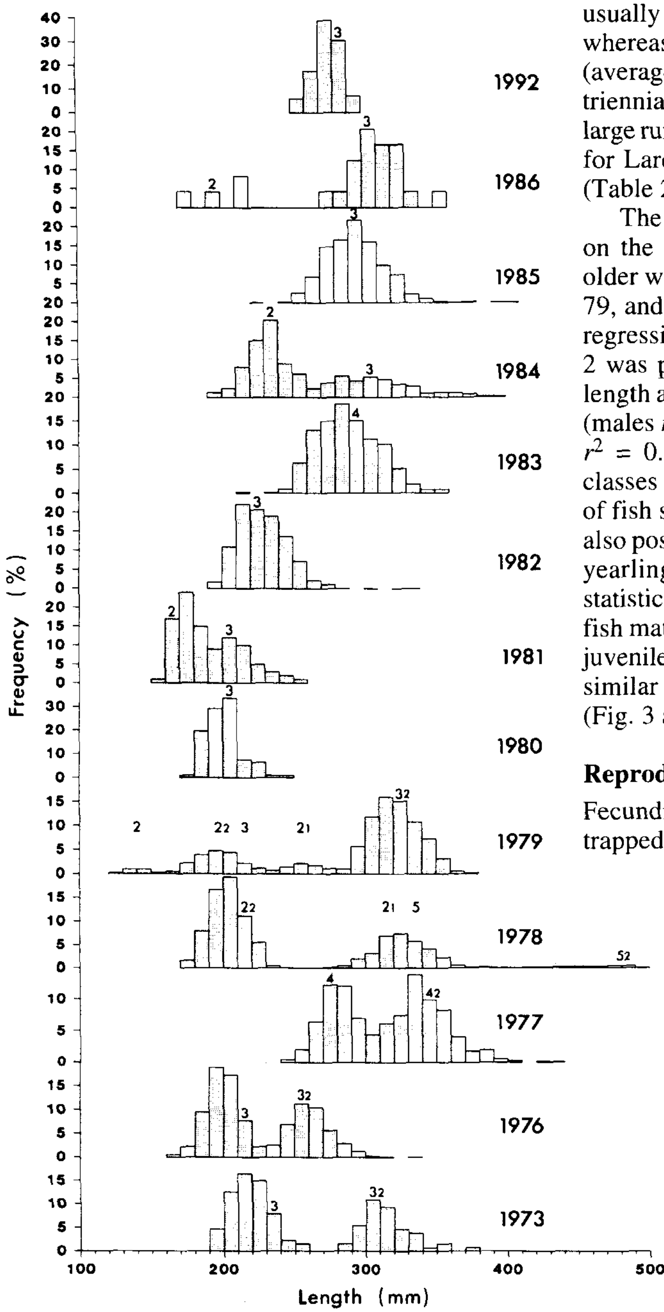

Fig. 3 Length frequency of spawning sockeye salmon in Larch Stream 1973–92. 1973 data (C. J. Hardy unpubl. data). Subscript refers to age fish migrated down stream from Lake Ohau.

Reproduction

Fecundity (F) for 3- to 5-year-old mature females, trapped from 1976 to 1978, ranged from 95 to

1554 (Fig. 4). Fecundity was strongly correlated with FL: ln (F) = 2.291 ln (FL) – 7.040 (r = 0.86, n = 107). Two-year-old females, either trapped in Larch Stream or reared at Glenariffe Hatchery, contained 195 to 2755 eggs and were more fecund for their length than older fish (Fig. 4):
ln (F) = 2.557 ln (FL) – 7.867 (n = 22, r = 0.98). Residual ova counts from spent females ranged from 0 to 73 with a mean of 7.

In Larch Stream, salmon spawned principally in riffles, at tails of pools and along stream margins. The distribution of spawners depended on the size of the spawning runs, flow conditions, and substrates. During a large run in 1977, densities ranged from 0.3 fish m^{-2} in the lower reaches and minor tributaries to 0.9 fish m^{-2} in the middle reaches of the stream. Spawning gravels ranged from fine (5–10 mm diam.) gravels mixed with sand to coarse (25–90 mm diam.) gravels mixed with cobbles. Redds were dug in water ranging from 0.13 to 0.95 m in depth and from 0 to 0.66 m s^{-1} in velocity. Suitability-of-use curves (Glova 1982) showed that salmon selected water depths of 0.30 m (range 0.15–0.50 m) and velocities of 0.35 m s^{-1} (0.20–0.50 m s^{-1}). Salmon occasionally spawned in still water around the shorelines of Lake Aviemore and along the margins of ponds near Ohau A and C.

Estimates of ova deposited in Larch Stream ranged from nil to 4.3 million (1977). Deposition rates dropped drastically, from 1.4 million p.a. before 1980 to fewer than 100 000 p.a. afterwards.

Table 4 Age at maturity of various year classes of sockeye salmon reared in Lake Ohau, Lake Benmore, and hatcheries (Graynoth & Hawke 1985). Benmore subscript indicates year of downstream migration to Lake Benmore.

Year class	Location reared	Sex	No.	Spawning (%) at age 2	3	4	5	Mean age	FL* Age=1+	Parent's age
1973	Ohau	M	8491	1	32	59	9	3.75	93	3
		F	3461	1	7	77	15	4.05	90	3
	$Benmore_{1-3}$	M	3697	3	28	62	7	3.74	101	3
		F	6993	1	13	83	2	3.86	96	3
1976	Ohau	M	92	0	100	0	0	3.00	106	3
		F	53	0	100	0	0	3.00	106	3
	$Benmore_1$	M	2806	82	18	0	0	2.18	182	3
		F	3127	30	70	0	0	2.70	175	3
	$Benmore_2$	M	9626	86	14	0	0	2.14	124	3
		F	9285	3	97	0	0	2.97	126	3
1977	Ohau	M	880	45	28	28	0	2.83	94	4
		F	35	6	20	74	0	3.69	90	4
	$Benmore_1$	M	980	96	4	0	0	2.04	176	4
		F	552	43	57	0	0	2.57	164	4
	$Benmore_2$	M	3080	85	8	7	0	2.22	101	4
		F	4313	18	41	40	0	3.22	97	4
	Hatchery	M	29	79	21	0	0	2.21	170	4
		F	26	81	19	0	0	2.19	170	4
1978	Ohau	M	229	0	100	0	0	3.00	99	2.84
		F	88	0	100	0	0	3.00	99	2.84
1979	Ohau	M	4111	19	68	13	0	2.94	125	2.65
		F	1143	3	82	15	0	3.12	125	2.65
1982	Ohau	M	1829	12	88	0	0	2.88	120	3
		F	1126	2	98	0	0	2.98	117	3
	Hatchery	M	2184	97	3	0	0	2.02	261	3
		F	1493	61	39	0	0	2.39	261	3
All	Ohau	M	6	13	69	17	1	3.07	106	3.08
		F	6	2	68	28	2	3.31	105	3.08
	Benmore	M	5	70	14	14	1	2.46	137	3.4
		F	5	19	56	25	0	3.06	132	3.4

*Fork length at age 1+ (Graynoth 1987)

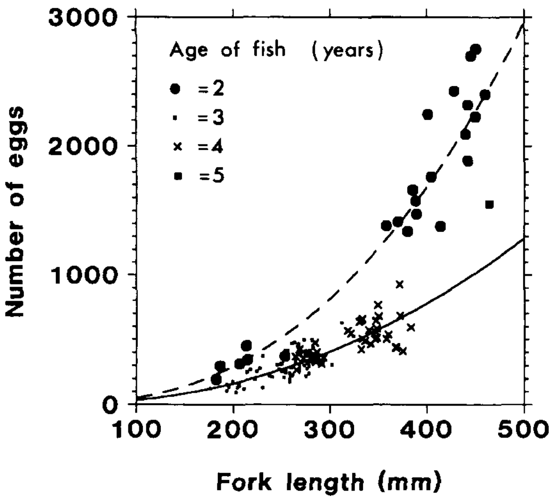

Fig. 4 Relationship between fork length and fecundity for 2-year-old wild and hatchery-reared sockeye and also for 3- to 5-year-old wild fish.

Survival rates from ova to adult for the 11 year classes for which there was adequate data ranged from 0.1% to 8% (1976) with a mean of 1.5%.

Ova incubation rates varied between streams (Table 5). In the Mary Burn all ova were eyed by the end of March 1979 and the majority had hatched by the end of April. By the end of May, alevins were present in redds in all three streams studied. In mid June 1988, free-swimming fry (26–29 mm) were present in a spring-fed (7°C) stream near Ohau C and in early July 1978 in a stream near Ohau A (9.5°C). In mid September 1977, fry were seen throughout Larch Stream but by February fry and underyearlings had left Larch Stream and migrated to Lake Ohau.

Lake of residence of juvenile and adult fish

A high percentage of the adult fish entering Larch Stream reared as juveniles in Lake Ohau before migrating down stream to Lake Benmore (Table 6). Numbers of juveniles out-migrating from Lake Ohau were estimated from the returns of mature fish (Table 2) assuming an annual survival rate of 63% for yearling and older fish (Ricker 1962; Hoelscher et al. 1990). On average 84% of females and 61% of males of the 1973–79 year classes migrated down stream as juveniles from Lake Ohau to Lake Benmore (Table 6). Over 96% of the 1976 year class migrated compared with fewer than 60% of the 1973 year class. Most fish migrated as yearlings (1+) (Table 6). The 1+ and 2+ migrants overlapped in back-calculated lengths (Graynoth 1987) with resident fish but were on average 7 mm longer (Table 6).

Fish continued to migrate down stream from Lake Ohau to Lakes Benmore and Ruataniwha in the 1980s and 1990s. For example, most of the 1985 and 1986 year classes migrated down stream to Lake Benmore and spawned as 3-year-old fish at Ohau C in 1988 and 1989 (Table 2 and 3 and otolith examination).

DISCUSSION

Distribution and size of spawning runs

Larch Stream is the only stream to have consistently supported large spawning runs of salmon. From

Table 5 Water temperatures and the development and survival of ova and alevins in sockeye redds during 1979. Ova were deposited between 22 and 28 February in Mary Burn, between 1 and 2 March in the Omarama Stream, and late February and March in Larch Stream.

Stream	Date	No. of egg and alevins examined	Dead (%)	Pre-eyed (%)	Eyed (%)	Alevins (%)	Mean monthly temperature (°C)
Mary Burn	29 Mar	170	32	0	68	0	14.0
	26 Apr	170	35	0	10	55	9.4
	24 May	35	34	0	0	66	6.5
Omarama	29 Mar	150	12	23	65	0	12.3
	26 Apr	72	12	0	88	0	9.9
	24 May	67	22	0	0	78	5.7
Larch	29 Mar	–	–	–	–	–	8.8
	26 Apr	–	–	–	–	–	8.0
	24 May	83	13	0	2	84	7.1

1975 to 1986 other streams contained fish similar in appearance and age composition to those spawning in Larch Stream and were probably strays from this source. Although thousands of mature fish were transferred into other rivers and streams to initiate new runs, none were established. Larch Stream appears to be critical to the survival of the wild stock in New Zealand.

There are several possible reasons for the pre-eminence of Larch Stream. Firstly, it contains a large area of stable flood-protected spawning gravel whereas most other local rivers and streams have unstable cobble beds which move during floods. As it is spring fed it also contains cool water in autumn and relatively warm water over winter. In the Mary Burn and other streams, cold winter temperatures may be a limiting factor. In Canada, sockeye salmon ova develop slowly over winter at temperatures of about 3°C (Brannon 1987). Fry emergence occurs in spring (May), and is synchronised with increases in water temperatures, stream flows, and food supplies (Foerster 1968; Brannon 1987). In New Zealand, water temperatures are higher in autumn and early winter; ova and alevins develop quicker and fry emerge prematurely in mid winter (June and July). Fry in Larch Stream and other warm spring-fed streams (c. 7°C) may have a better survival than in colder streams and rivers (c. 4°C). Fry in warm streams may migrate more quickly and over a shorter time span than those in colder waters (Brannon 1967), or if resident feed more actively and have better survival (Bilton & Robins 1973).

From 50 to 75% of anadromous sockeye salmon fry are eaten by predators (Foerster 1968) and predation on Larch Stream outmigrant fry could be less than in other locations. As Larch Stream is within 5 km of Lake Ohau, more fry may reach the lake than from more distant streams such as the Mary Burn, which is 20 km from Lake Benmore. Lake Ohau also may be a more suitable rearing lake than Lakes Aviemore and Waitaki, where fry may be lost down stream through the turbines because of the strong current and short water residence time.

Larch Stream is clearly the major spawning stream because of the extent and quality of its spawning gravels, stable flows and water temperatures, minimal predation on out-migrant fry, and because Lake Ohau is suitable for rearing juvenile and adult fish.

The largest spawning runs into Larch Stream occurred in the 1970s, when most fish reared in Lake Benmore. These fish grew quicker, matured earlier, and were more fecund than fish resident in Lake Ohau. Their life history was similar to that of their anadromous ancestors—rearing for 1 year in Lake Ohau before migrating down stream to rear in a more productive environment. Since 1980, these migratory fish have been unable to return to spawn because of power developments and as a result the Larch Stream runs have declined substantially. It is hypothesised that the percentage of fish with a genetic tendency to migrate (see Ricker 1940, 1972) increased substantially when Lake Benmore was formed because of their early maturity and greater fecundity. Since 1980, the remaining small runs of fish from Lake Ohau have not increased in size, probably because female fish still have a genetic tendency to migrate down

Table 6 Estimated number of juvenile sockeye salmon present in Lake Ohau during spring (September-November) and the number and size of fish migrating down stream to Lake Benmore. M, male; F, female; –, no data; ?, small sample.

Age of fish	Year class	Total numbers (1000s)		% migrating		Mean length (mm) Residents		Mean length (mm) Migrants	
		M	F	M	F	M	F	M	F
0+	1973	54	50	3	4	–	–	–	–
	1976	25	36	17	5	–	–	–	–
	1977	11	16	17	8	–	–	–	–
1+	1973	33	31	10	56	93	90	99	95
	1976	13	22	97	96	99?	126?	129	136
	1977	6	10	73	99	101	100?	102	101?
	1979	20	14	63	84	123	125	132	134
2+	1973	19	9	19	18	149	143	154	148

stream, and possibly because small runs, and their progeny, could be more susceptible to predation than large runs (Ward & Larkin 1964). (The migrating adults were eaten by trout, longfinned eels, black cormorants, gulls and harrier hawks.) This could explain why the run into Larch Stream has not recovered and has declined to almost nil recently.

There is no indication that changes in the Lake Ohau or Larch Stream environments are responsible for the decline in the stock. Apart from occasional floods from the adjacent Hopkins River there have been no major physical or chemical changes in Larch Stream. The only biological change has been the commercial harvesting of eels from 1979 onwards which should have improved the survival of adults and fry.

Spawning migrations

Sockeye salmon in New Zealand spawn in early autumn as do their Canadian ancestors. Spawning in Larch Stream, from late February to late March, coincides almost exactly with the dates when ova were collected in Canada (27 August to 22 September 1901). The mean date of entry of fish into Larch Stream (6 March) also compares closely to present-day runs into one of the ancestral streams (Scotch Creek), which peak on 4 September (Brannon 1987). In New Zealand, spawning and reproduction might be more successful if the spawning migration could be delayed until May or June because water temperatures would be cooler and fry would emerge in spring. However sockeye salmon have precisely timed spawning runs which have evolved for optimum fry emergence timing in different environments (Brannon 1987) and which are largely under genetic control—remaining unchanged when salmon are transferred to new environments (Ricker 1972). Therefore even if sockeye salmon were transferred elsewhere within New Zealand, they would probably continue to spawn from late February to late March and it may take generations for this timing to change.

Although age at maturity of salmon in New Zealand was closely correlated with juvenile growth rates, it seems unlikely that early maturing fish had a genetic disposition to grow faster, as is the case with Atlantic salmon (Thorpe et al. 1983). Fish from Lake Ohau reared in hatcheries grew rapidly and matured earlier than their genetically identical relatives in Lake Ohau (Graynoth & Hawke 1985). Also rapid juvenile growth is strongly correlated with and leads to early maturity in anadromous sockeye salmon and kokanee (Seeley & McCammon 1963; Foerster 1968; Bilton 1971; Peterman 1985).

The variation in sex composition was caused by the presence of strong year classes and the tendency for males to mature before females. The lack of females from 1980 to 1984 was probably caused by their tendency to migrate down stream, and dams preventing their return as adults. However there were always sufficient males present for successful reproduction. For example, in 1979 the lack of 3_2 males was compensated for by high numbers of 2_2 and 2_1 males. Few unspent ripe females were seen and successful reproduction in sockeye salmon can occur when the percentage of males is as low as 6% (Foerster 1968).

In New Zealand, 2-year-old fish were more fecund, at a given length, than older and slower-growing fish, possibly because they contained smaller ova. In 1978, fast-growing 2_1-year-olds from Lake Benmore had smaller ova than slow-growing 5-year-old fish from Lake Ohau (from visual observations and photographs), even though the fish were of the same length (mean 327 and 319 mm FL, respectively). Fast-growing hatchery-reared fish also have smaller ova than wild fish (Graynoth & Hawke 1985; pers. obs.).

Comparison with kokanee

New Zealand sockeye salmon mature earlier, at a wider range of sizes, but are less abundant than most populations of kokanee elsewhere. They mature mainly at 2–4 years old and are younger than their 4-year anadromous ancestors (Department of Marine and Fisheries 1902; Foerster 1968) and most populations of kokanee. Most kokanee stocks also mature at age 4, although some mature at 3 and others at 5 (Bjornn 1961; Seeley & McCammon 1966).

New Zealand salmon have a wider range of sizes at maturity than most stocks of kokanee, mainly because of the variation in growth rates and consequent age at maturity. Two-year-old males from Lake Ohau in 1979 averaged 139 mm FL and are the smallest mature kokanee or residual anadromous sockeye salmon (Ricker 1938) ever reported. Lake Ohau salmon were smaller than most kokanee and were similar in size to those in Lake Pend Orielle (Whitt 1958) and Priest Lake (Bjornn 1961). Fish resident in the hydrolakes were average to large in size, although smaller than kokanee in Kootenay Lake (Northcote 1973) and Lake Tahoe (Cordone et al. 1971).

The spawning runs in New Zealand are much smaller than those elsewhere (Northcote 1973; Hoelscher et al. 1990), possibly because the scarcity of zooplankton in Lake Ohau (Graynoth et al. 1986) may reduce the survival and abundance of juvenile fish (Foerster 1968; Northcote 1973; Hoelscher et al. 1990). Other reasons for the smaller runs include the absence of suitable spawning tributaries in the hydrolakes and the adverse impacts of hydro-electric power developments on the Ohau River.

Other differences from kokanee include the lack of colouration and other secondary spawning characteristics in most mature fish (Hardy 1969; unpubl. data), the absence of gill and intestinal parasites and diseases (T. G. Northcote pers. comm.; Boustead 1980) and the downstream migration of yearlings (Ricker 1940, 1972).

Current status and potential in New Zealand

The decline in the Larch Stream spawning runs raises concern about the future of the fish in New Zealand. As only 40 females entered Larch Stream in 1992 and as no mature fish were seen anywhere in March 1993 and 1994 (G. Hughes pers. comm.), the wild stock must be very small. However, thousands of fish are being reared in at least five salmon hatcheries and farms and surplus fish were used to restock Lake Ohau in 1993 and 1994. Unfortunately these hatchery fish may lack genetic variety as most, if not all, originated from 59 three-year-olds trapped in Larch Stream in 1982 (Graynoth & Hawke 1985). It is difficult to import fresh genetic stock into New Zealand because of the widespread occurrence of exotic viral and bacterial diseases elsewhere (Boustead 1980). Nevertheless to maintain wild stocks, hatchery-reared ova and fry should continue to be stocked in Larch Stream and it would also be beneficial to improve the spawning grounds at Ohau C.

The results of this study suggest it will be difficult to establish new spawning runs in most other New Zealand lakes because sockeye salmon require spring-fed, stable spawning streams for successful reproduction and because the juveniles have a tendency to migrate down stream out of the rearing lake. Lakes where salmon could become established and reach large sizes (Graynoth 1987) seem quite limited and include those with intermittent or no outlets such as Lakes Lyndon and Middleton and those with larger lakes situated down stream such as Lake Poerua.

ACKNOWLEDGMENTS

I thank the staff of the Fisheries Research Division and Freshwater Fisheries Centre of the Ministry of Agriculture and Fisheries (MAF) who assisted with the field programme. Field staff of the Waitaki Valley Acclimatisation Society and Dr D. Scott of the University of Otago undertook spawning surveys and made early records available. Dr T. P. Quinn, C.L. Hopkins, and M. J. Unwin reviewed and improved the manuscript and the project was funded by MAF, Department of Conservation, New Zealand Fish and Game Council, and Foundation for Research, Science and Technology (Contracts CO 1236, CO 1322).

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