EFFECTS OF SIZE AND TIME OF RELEASE ON SEAWARD MIGRATION OF SPRING CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*

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ABSTRACT

Juvenile spring chinook salmon, *Oncorhynchus tshawytscha*, from Round Butte Hatchery on the Deschutes River, Oregon, were released monthly into a 3.7 km fish ladder. Fish released into the ladder from February to May migrated through the ladder in mid-May in both 1977 and 1978. Fish released after mid-May migrated through the ladder within 2 weeks after release. The extent of migration decreased progressively in fish released after 15 June. The migration was presumably photoperiod dependent, although temperature may have acted both as a releasing factor for migration and as a stimulus for growth. In the fish ladder, size of the fish remained constant over a 3-week migration period, suggesting that larger fish migrated before smaller fish. After a migration of 213 km, fish captured at the Dalles Dam had very large apparent growth rates, suggesting that larger fish were faster migrants.

Maximum survival of juvenile salmonids after release from hatcheries is dependent upon their rapid migration to the sea (Raymond 1979). Delays in this seaward migration may subject the juveniles to starvation and stress which rapidly deplete their numbers (Miller 1952, 1958). Residual hatchery juveniles in a river often have an impact on wild stocks of fish through piscivory (Sholes and Hallock 1979) and competition for food (Chapman 1966). Rapid migration of hatchery juveniles ensures maximum survival to adulthood with minimal interaction with wild stocks.

Timing and duration of the physiological conditions which result in migratory behavior are still relatively unknown. Timing of seaward migration in juvenile salmonids depends upon a number of environmental factors, including photoperiod (Wagner 1974), temperature (Solomon 1978), water flow (Mains and Smith 1964), and fish size (Wagner 1974). The interrelationships between these are not well understood, but the available data suggest that these relationships may be complex. Hoar (1958) and Baggerman (1960) have postulated that these environmental factors act as "releasers" which, in conjunction with a physiological readiness to migrate, trigger overt migrational behavior.

In most river systems, the relative influence of such factors is estimated by extensive sampling programs which use multivariate analysis of the data. Control of environmental variables in such a system is not possible. Furthermore, the size of many river systems prevents an unbiased sampling of juveniles during migration. It is difficult, therefore, to obtain reliable estimates of the size of fish at migration, the timing of migration, and the influence of the environment on that timing.

In the present study, an unused fish ladder provided a relatively constant environment for migration of juvenile spring chinook salmon, *Oncorhynchus tshawytscha*, over a 3.7 km distance. Serial releases of hatchery-reared juveniles into this system permitted an investigation of the timing of seaward migration, the duration of the migration tendency of the juveniles, and the relationship of several environmental variables to seaward migration.

METHODS

Study Area

The study area included the lower 175 km of the Deschutes River, Oreg., and the lower Columbia River from its confluence with the Deschutes River to the Dalles Dam (Fig. 1).

Rearing Conditions

Progeny from spring chinook salmon spawned at

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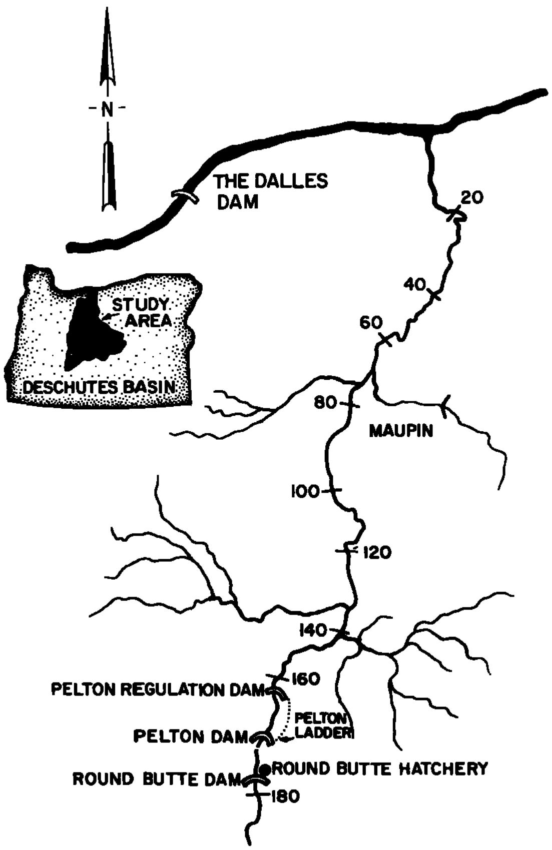

FIGURE 1.—Map of the lower 175 km of the Deschutes River and its confluence with the Columbia River. Numbers refer to kilometers from the mouth of the Deschutes River.

Round Butte Hatchery (river km 175 from the Columbia River) in 1976 and 1977 were used for experiments in 1977 and 1978, respectively. Eggs from 1976 brood fish were incubated in Heath[4] incubators in 10°C spring water, and the resulting fry were reared in raceways using the same water source. Eggs from 1977 brood fish were divided into two groups. One group was reared under conditions as described above and referred to as "fast-reared". The second group of eggs was incubated in Heath incubators in spring water chilled to 5°-6°C. The resulting fry were transferred to raceways and reared in 7°-8°C tail-race water from Round Butte Dam. After 2 mo, the group was transferred to 10°C spring water and reared there until release. This group was referred to as "slow-reared" and was released in March 1979 as yearlings.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

In May and June, production lots of fast-reared spring chinook juveniles were released into the Deschutes River below Pelton Regulation Dam. At this time, experimental groups were transferred to oval fiber glass ponds supplied with 10°C spring water at 9.5 l/s. In May 1977, 5,600 fast-reared spring chinook juveniles (average fork length 10.0 cm) were transferred to a fiber glass pond and reared there through June 1978. In late March 1978, 2,500 fast-reared fish (average fork length 8.5 cm) were transferred to a fiber glass pond and reared there through August.

All fish were reared under a natural photoperiod and fed to repletion daily with Oregon Moist Pellet.

Seaward Migration

Migratory behavior of the spring chinook salmon was assessed by the release and recapture of hatchery-reared juveniles from two groups. Migration tendency of the experimental groups was assessed by monthly release of about 200 fish into the upper end of Pelton ladder during 1977 and 1978 (Fig. 1). The ladder is 3.7 km long and is constructed with concrete walls and bottom except for a 1.1 km central section which is a natural stream channel. It is supplied with water from Lake Simtustus (directly above Pelton Dam) at a constant flow rate of 1,130 l/s. Maximum depth of the ladder is 2.1 m. The ladder is closed by revolving screens at both the upper and lower ends. A trap located at the lower end of the ladder was used to capture migrants. Temperature of the water at the lower end of the ladder was measured by a thermograph placed near the trap.

Fish from the various experimental groups were identified upon recapture in the trap at the lower end of the ladder by unique combinations of polystyrene dye (Phinney et al. 1967) and fin clips. The trap was checked 5 d a week during May and June and 2 d a week during the remainder of the year. Fish captured in the trap were considered migrants while those remaining in the ladder following the date of peak recapture were assumed to be residuals. Fork lengths and marks of each migrant were recorded upon capture. In January 1978, the ladder was drained and all residual fish from the 1977 studies were removed before the 1978 releases.

The second group of hatchery-reared fish used for assessment of migration were production lots of fast-reared juvenile chinook released into the Deschutes River immediately below Pelton Regulation Dam (river km 161). These fish were marked with coded wire tags (Jefferts et al. 1963). In 1977, 62,000 fast-reared fish were released on 2 May and 73,000 fast-reared fish were released on 3 June. These fish averaged 9.7 cm and 11.2 cm FL, respectively. On 31 May 1978, 121,000 fast-reared fish, which had been graded according to fork length, were released in two groups of 95,000 and 26,000 fish to test the effects of size on migration and survival to adulthood. These fish averaged 10.9 and 11.8 cm FL, respectively. Downstream movement in both years was monitored in the Columbia River at the Dalles Dam (52 km downstream from the mouth of the Deschutes River) by gatewell sampling conducted by the National Marine Fisheries Service and the Oregon Department of Fish and Wildlife. Sampling was conducted 5 d a week throughout May and June. Juveniles originating at Round Butte Hatchery were identified by analysis of coded wire tags.

Apparent Growth Rates

Apparent growth rates in Pelton ladder and in the Deschutes River were calculated from the size of the juveniles released into the ladder or the river and the size and time at which they were recaptured. Actual growth rates could not be measured, because selective mortality of small fish or migration of larger ones could not be estimated. Differences in fork lengths were tested for significance at the 95% confidence level using Student's t test.

RESULTS

Timing of Migration

Maximum migration of chinook salmon juveniles released in February and March into Pelton ladder occurred between mid-May and the first of June in both 1977 and 1978. There was little migration in these groups before or after this 4-wk period (Tables 1, 2). Fish released in April showed two peaks in migration. A large percentage of the fish moved through the ladder within 2 wk after release, while a second peak of migration occurred during the last 2 wk of May. Fish released in early May also had a large percent migration within 2 wk after release, but the greatest percent migration occurred during the first 2 wk in June. When chinook salmon juveniles were released from June to November, most of the fish moved through the ladder within 7 d after release. The maximum percent migration within 7 d after release occurred in fish released in early June 1977 (Fig. 2) and in mid-June 1978 (Fig. 3). Fish released in August and at later times had reduced migration and had a higher tendency to become residual (Tables 1, 2). Migration of slow-reared fish released into Pelton ladder from May to August 1978 was less than half that of fast-reared fish released at the same time (Fig. 3B).

Daily migrations of two groups released in February and March 1978 were compared with those from 8 May to 8 June. Movement of both groups was coincidental throughout this period (Fig. 4), suggesting that environmental factors such as temperature influenced migration tendency. Temperatures in the ladder varied seasonally due to solar warming (Fig. 5). Maximum temperatures of 17°C were attained in August 1977 and in July and August 1978. Temperatures in both years exceeded 13 °C by June, suggesting a possible temperature threshold for migration. While the relationship between migration and temperature was very poor (correlation coefficient, $R^2 = 0.074$), there may have been a tendency for peaks in seaward migration to occur 1-2 d after transient increases in temperature (Fig. 4).

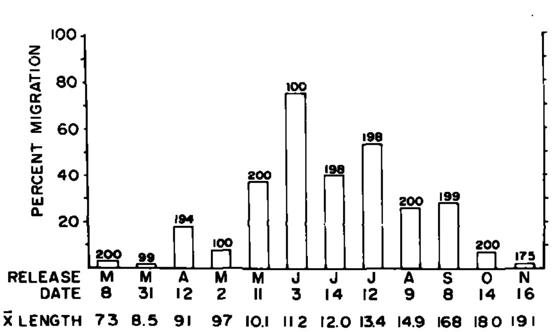

FIGURE 2.—Percentage seaward migration within 7 d following release for each group of fast-reared spring chinook salmon released into Pelton ladder in 1977. Above each bar is the number of fish released. Lengths are means of samples of 30 fish taken from the population at the time of release.

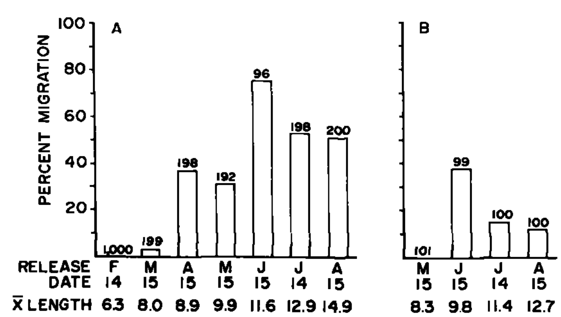

FIGURE 3.—Percentage seaward migration within 7 d following release for each group of spring chinook salmon released into Pelton ladder in 1978. A) Fast-reared chinook salmon. B) Slow-reared chinook salmon. Above each bar is the number of fish released. Lengths are means of samples of 30 fish taken from the population at the time of release.

TABLE 1.—Percentage downstream migration for fast-reared spring chinook salmon released into the Pelton ladder in 1977.

Capture dates	Release date: $\overline{X}$ length (cm): n:	8 Mar. 7.2 200	31 Mar. 8.5 99	12 Apr. 9.1 194	2 May 9.7 100	11 May 10.2 200	3 June 11.2 100	14 June 12.0 198	12 July 13.4 198	9 Aug. 14.9 200	9 Sept. 16.8 199	15 Oct. 18.0 200	16 Nov. 19.1 175
3/1-3/15		3.5											
3/16-3/31		1.0											
4/1-4/15		1.0	1.0	17.5									
4/16-4/30		0.0	0.0	0.5									
5/1-5/15		1.5	1.0	3.0	9.0	37.0							
5/16-5/31		34.5	42.0	27.0	19.0	5.5							
6/1-6/15		8.0	16.0	18.0	37.0	35.5	78.0	7.0					
6/16-6/30		0.0	1.0	0.5	6.0	3.0	4.0	35.0					
7/1-7/15		0.5	0.0	0.0	0.0	0.5	1.0	2.0	40.0				
7/16-7/31		0.5	0.0	0.0	1.0	0.0	0.0	0.5	18.5				
8/1-8/15		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	26.0			
8/16-8/31		0.0	0.0	0.5	0.0	0.0	1.0	1.0	0.5	7.5			
9/1-9/15		0.0	0.0	0.0	1.0	0.0	1.0	3.5	0.5	2.0	29.0		
9/16-9/30		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	3.0		
10/1-10/15		0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
10/16-10/31		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.5	
11/1-11/15		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
11/16-11/30		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.5	2.5	5.0
12/1-12/15		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	1.5	0.5
12/16-12/31		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1/1-1/15		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	1.5	1.0
Total percentage migration		50.5	61.0	62.0	73.0	81.5	85.0	49.0	60.0	37.0	36.0	13.0	6.5
Percent residuals		0.0	0.0	0.0	2.0	0.0	0.0	0.0	2.0	14.5	31.5	43.5	55.0
Total percentage recovered		50.5	61.0	62.0	75.0	81.5	85.0	49.0	62.0	51.5	67.5	56.5	61.5

TABLE 2.—Percentage downstream migration over semimonthly intervals for fast-reared spring chinook salmon released into the Pelton ladder in 1978.

Capture dates	Release date: $\overline{X}$ length (cm): n:	14 Feb. 6.3 1,000	15 Mar. 8.0 199	15 Apr. 8.9 198	15 May 9.9 192	15 June 11.6 96	14 July 12.9 192	15 Aug. 14.9 200
2/15-2/28		0.1						
3/1-3/15		0.0						
3/16-3/31		0.0	3.0					
4/1-4/15		0.0	0.0					
4/16-4/30		0.1	1.0	37.0				
5/1-5/15		17.3	8.0	2.5				
5/16-5/31		64.8	62.8	32.8	41.7			
6/1-6/15		3.8	8.5	12.0	33.8			
6/16-6/30		1.7	0.0	1.0	3.1	77.0		
7/1-7/15		0.5	0.0	0.0	0.0	0.0		
7/16-7/31		1.3	1.0	0.0	0.0	2.0	55.0	
8/1-8/15		0.0	0.0	0.0	0.0	0.0	0.5	
8/16-8/31		0.7	0.0	0.0	0.5	1.0	0.5	54.5
9/1-9/15		2.2	0.5	0.0	2.5	1.0	2.5	5.0
Total percent migration		92.5	84.8	85.3	81.6	81.0	58.5	59.5

Recovery of Released Fish

In 1978, the greatest recovery of fish liberated into Pelton ladder (92.5%) was from the large group of 1,000 fish released on 14 February (Table 2). From 81.0 to 85.3% of the fish released from 15 March through 15 June were recovered. Only 58.5 and 59.5% of the fish released on 14 July and 15 August, respectively, were recovered in the trap as migrants. Presumably the remainder were residuals in the ladder.

In 1977, recovery of both migrants and nonmigrants from all groups was lower than in 1978 (Table 1), although the extent of migration of fish released near the time of maximum migration tendency on 11 May and 3 June was 81.5 and 85%, respectively, similar to that observed for most release groups in 1978. Few residual chinook salmon from releases before August 1977 were found when the ladder was drained in January 1978. Nonmigrant fish were recaptured in increasing numbers from releases from 12 July on.

Size and Growth Relationships

Growth rates of juvenile chinook salmon reared at Round Butte Hatchery were 0.046 and 0.058 cm/d

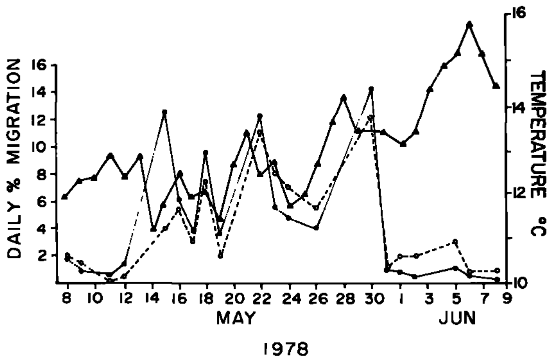

FIGURE 4.—Daily percent seaward migration from 8 May to 8 June for groups released 14 February (solid circles) and 15 March (open circles). Temperature (triangles) is the average daily temperature.

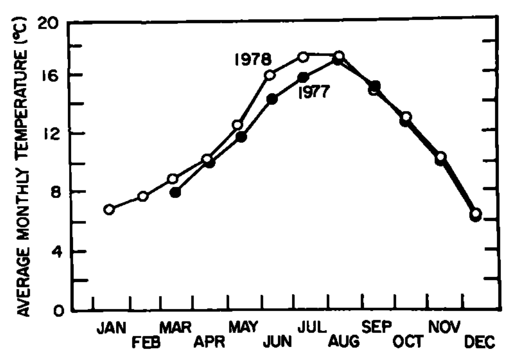

FIGURE 5.—Average monthly temperature in Pelton ladder in 1977 (solid circles) and 1978 (open circles).

for fast-reared fish in 1977 and 1978, respectively. Slow-reared fish in 1978 grew at 0.043 cm/d. Apparent growth rates of fish placed in Pelton ladder varied from 0.034 to 0.124 cm/d (Table 3). These apparent growth rates increased in later introductions, reflecting the increasing water temperature of the ladder (Fig. 5).

There was no evidence for differences in migration timing by fish of different sizes. Fork lengths of fish recaptured in the trap within a few days of release were usually not significantly different ($P > 0.05$) from those of fish at release (Table 4). However, fish recaptured from the large group of juveniles released on 14 February 1978 were similar over a 3-wk period (Table 5), suggesting that faster growing fish were migrating more rapidly that slower growing fish.

Apparent growth rates of marked spring chinook juveniles released below Pelton Regulation Dam in 1977 were calculated from fork lengths of recaptured fish at the Dalles Dam, after a migration distance of 213 km (Table 6). This apparent growth rate is nearly twice that of fish reared at Round Butte Hatchery.

TABLE 3.—Apparent growth rates of juvenile chinook salmon released into Pelton ladder, 1977 and 1978.

	Release date	Average recapture date	Apparent growth rate (cm/d)
1977	3/8	5/24	0.078
	4/12	6/1	0.081
	5/2	5/28	0.124
	5/11	6/4	0.120
Hatchery	—	—	0.048
1978	2/14	5/27	0.034
	3/15	5/20	0.071
	4/15	5/26	0.097
	5/15	6/7	0.097
Hatchery	—	—	0.046

TABLE 4.—Fork lengths of juvenile chinook salmon at time of release into Pelton ladder and at time of recapture, 1977 and 1978. Values are means ± standard errors. Number of samples is given in parentheses.

Date of release	Mean fork length at release (cm)	Date of recapture	Mean fork length at recapture (cm)
1978:			
2/14	6.5±0.1 (60)	5/15-6/9	13.4±0.1 (245)
3/15	8.2±0.1 (30)	5/16-5/24	13.0±0.1 (81)
4/15	9.0±0.1 (100)	5/22-5/31	13.0±0.2 (42)
5/15	10.1±0.1 (29)	6/5-6/9	12.3±0.1 (54)
6/15	11.3±0.1 (30)	6/16	11.9±0.1 (30)
7/14	13.7±0.1 (30)	7/17	13.2±0.2 (30)
8/15	15.1±0.3 (30)	8/16	15.5±0.4 (9)
9/15	17.1±0.3 (28)	9/18	17.2±0.2 (30)
1977			
3/8	7.5±0.1 (30)	5/24	13.5±0.1 (25)
3/31	8.5±0.1 (30)	5/24-5/28	13.5±0.1 (26)
4/12	9.4±0.1 (30)	6/1	13.4±0.1 (26)
5/2	9.7±0.1 (30)	5/28	12.9±0.1 (7)
5/11	9.9±0.1 (29)	5/12-6/4	11.7±0.1 (61)
6/3	11.2±0.1 (30)	6/3	11.4±0.1 (25)
6/14	12.0±0.1 (30)	6/17	12.3±0.1 (30)
7/12	13.5±0.1 (60)	7/15	13.9±0.1 (28)
8/9	15.1±0.2 (88)	8/15	16.1±0.2 (20)
9/9	16.7±0.2 (88)	9/9-9/13	16.8±0.2 (42)
10/15	17.5±0.5 (30)	10/17	18.4±0.4 (15)

TABLE 5.—Mean fork lengths of juvenile spring chinook salmon recovered in 1978 after release into Pelton ladder on 14 February 1978. Values are means ± standard errors. Number of samples is given in parentheses.

Date of recovery	Fork length (cm)
2/17	6.7±0.1 (30)
5/15	12.8±0.1 (30)
5/16	13.2±0.1 (30)
5/18	13.1±0.1 (30)
5/22	13.4±0.1 (30)
5/24	13.2±0.1 (30)
5/30	13.9±0.1 (30)
6/1	13.5±0.2 (19)
6/5	13.6±0.1 (21)
6/9	11.2±0.1 (25)

TABLE 6.—Fork lengths and apparent growth rates of juvenile spring chinook salmon recaptured at the Dalles Dam after release into the Deschutes River, 1977. Fork lengths are means ± standard errors for the number of samples shown in parentheses.

Recapture date	Fork length (cm)	Apparent growth rate (cm/d)
2 May release (9.7±0.1 cm fork length)		
5/27	11.6±0.2 (12)	0.075
6/3	12.2±0.1 (19)	0.078
6/7	12.2±0.1 (22)	0.077
6/8	12.2±0.1 (21)	0.076
3 June release (11.2±0.1 cm fork length)		
6/7	11.9±0.1 (23)	0.168
6/8	11.8±0.1 (30)	0.120

DISCUSSION

Determination of the migratory characteristics of juvenile chinook salmon during smolting has been complicated by the variety of migratory behaviors displayed by the juveniles. Some fry migrate from tributaries shortly after emergence from the gravel (Reimers 1973; Ewing et al. 1980), but there is little evidence that the fry move into the estuary at that time (Schluchter and Lichatowich 1977). In some stocks, a general movement of fish through the river occurs during the fall of the first year (Reimers 1973) with a majority of the fish entering the ocean during the fall of the first year (Reimers 1973; Schluchter and Lichatowich 1977; Buckman and Ewing 1982). In other stocks, seaward movement occurs primarily in the following spring when the fish are more than 1 yr old (Mains and Smith 1964; Diamond and Pribble 1978; Raymond 1979). Krcma and Raleigh (1970) reported migration of juvenile chinook salmon into Brownlee Reservoir (Snake River, Idaho) in fall and spring for 2 consecutive years. The migration pattern seems to depend upon stock, size, and rearing conditions and may be highly variable. It is therefore important in the culture of various stocks of juvenile chinook salmon to determine the timing of maximum migration tendency.

In the present study, the major migration of fish released early into Pelton ladder occurred in mid-May. Fish from the same brood released into the Deschutes River at about this time were found to migrate 213 km to the Dalles Dam within 7 d, suggesting that the migrational behavior was seaward directed (Hart et al. 1981). It is difficult to confirm in the Deschutes River that the release of fish into Pelton ladder 1 mo before the time of maximal migration tends to increase the time during which the fish will migrate. Release of the fish 1 mo later than the time of maximal migration tends to decrease the time for migration. It is important to note that it is not necessary to release the fish early to insure that all migrate to sea. Releases late in the migration period were recovered to the same extent as those released earlier. Migration tendency seems to be retained for some time, even though the fish are not permitted to begin migration. These results suggest that late releases hasten the seaward migration, thus removing the populations of hatchery fish quickly from the river system and affording maximum protection to the wild stocks.

Those groups released later than July were recaptured in the trap in decreasing numbers (Tables 1, 2). In 1977, nonmigrant fish were recaptured in increasing numbers from releases after 12 July (Table 1). This result indicates that the decrease in numbers of fish recaptured at the trap was due to decreased migration tendency and not due to increased mortalities at the higher water temperatures.

A major advantage of utilizing a closed system such as the Pelton ladder for studies of migration was that fish populations and flows could be effectively controlled. Variables which remained uncontrolled included photoperiod, lunar periodicity, temperature, and food supply. Of these, photoperiod seems the most important in stimulating seaward migration. Previous studies utilizing a closed system for studying seaward migration of steelhead trout, *Salmo gairdneri*, (Zaugg and Wagner 1973; Wagner 1974) and coho salmon, *Ocorhynchus kisutch*, (Lorz and McPherson 1976) also concluded that photoperiod was an important factor affecting the timing of seaward migration.

Lunar phase has been suggested to affect the onset of migration, based on the correlation between peaks in plasma thyroxine levels and lunar phase (Grau et al. 1981). Assuming maximal migration occurred on 22 May in both 1977 and 1978, this date corresponded to the time of a new moon in 1977 and that of a full moon in 1978. These brief data do not support the hypothesis that the migration is influenced by the lunar phase.

Temperature may have had a dual influence on migration. Temperature has been suggested as a releasing factor for salmon migration (Hoar 1958; Baggerman 1960), but we were unable to show a statistical relationship between daily migration and average daily temperature (Fig. 4).

Temperature also serves to increase growth rates in salmonids in the presence of abundant food supplies. Wagner (1974) suggested that a critical size was required in steelhead if migration were to take place. The importance of size on migration of spring chinook salmon can be seen by comparing the extent of migration of the slow- and fast-reared fish in 1978 (Fig 3). The slow-reared fish may have failed to migrate because they did not reach a critical size and/or growth rate by the appropriate photoperiod. Migration from Pelton ladder seemed to occur as fish reached a particular size, since during a 3-wk period of migration, there was no difference in average fork length of the fish recaptured (Table 5). From estimated growth rates (Table 3), fish at the end of the migration period might be expected to be nearly 2 cm larger than those at the beginning. This influence of size on migration could be best demonstrated in fish recaptured at the Dalles Dam after a migration distance of 213 km. Apparent growth rates were much higher than that of fish reared at Round Butte Hatchery, suggesting that a selection for larger fish occurs during the long migration distance.

A major concern in utilizing a closed system for studying seaward migration is the importance of aggressive behavior by resident fish toward newly introduced fish. Chapman (1962) found that aggressive behavior of resident fish may be partly responsible for emigration of fish introduced into the system. Aggressive behavior may have caused the rapid movement immediately following release for the March and April release groups in both 1977 and 1978. Further movement of these fish was not observed until May. Alternatively, migration in these fish immediately after release may have been due to disorientation of the fish upon release and a passive drifting downstream with the current. Fish released earliest into Pelton ladder migrated first in both 1977 and 1978.

The importance of determining appropriate times for hatchery releases of spring chinook salmon in order to obtain maximum seaward migration is demonstrated by the short time during which maximum migration occurred (Tables 1, 2). In both 1977 and 1978 peak migration occurred within a period of a few weeks. Releases made on either side of this time period exhibited decreased migratory activity. The use of model systems, such as the Pelton ladder, to determine when peak migration occurs can benefit hatchery programs by suggesting sizes and times for release of salmonids which maximize seaward migration.

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