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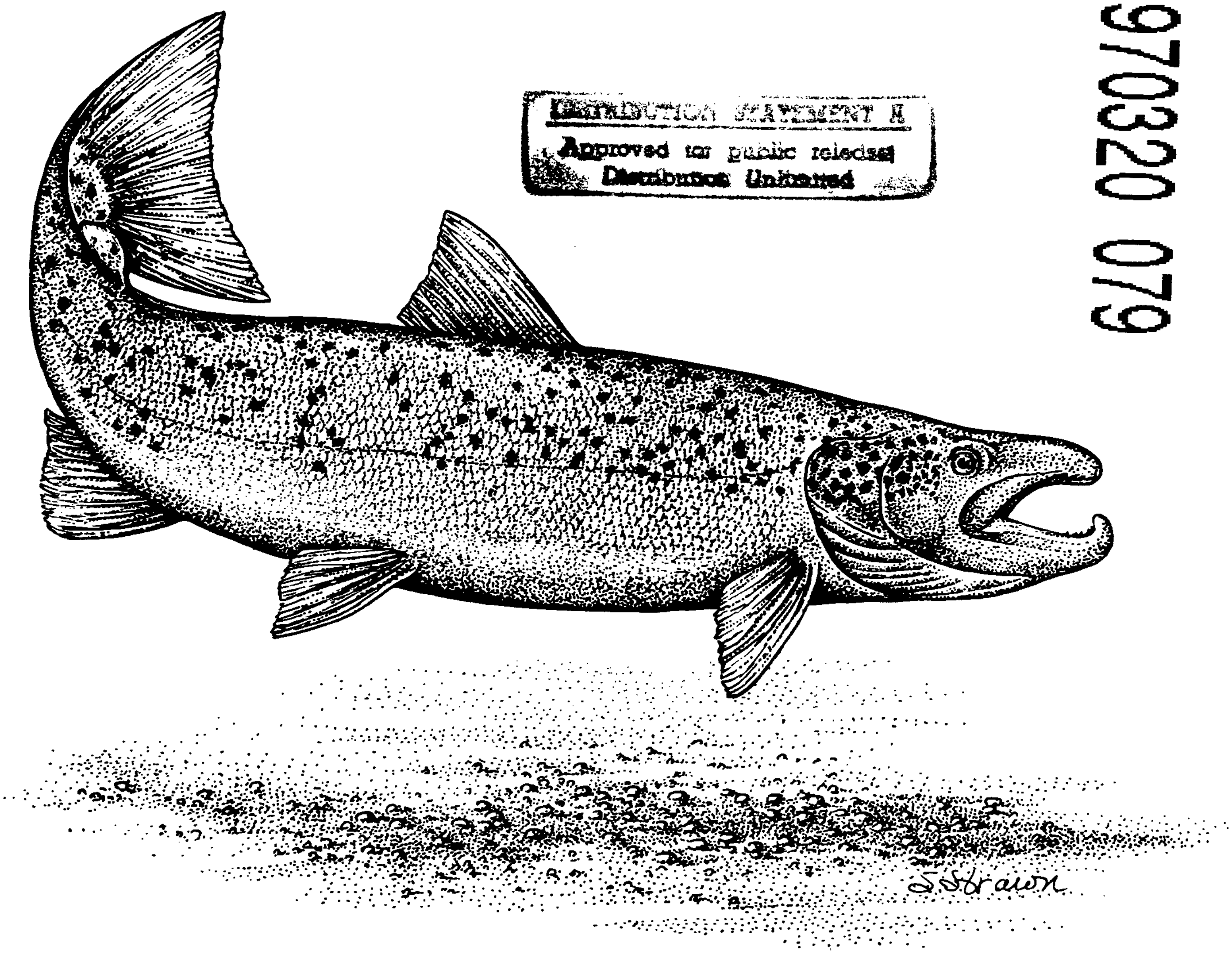
FRESHWATER AND OCEAN SURVIVAL OF ATLANTIC SALMON AND STEELHEAD: A SYNOPSIS



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Freshwater and Ocean Survival of Atlantic Salmon and Steelhead: A Synopsis

by

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Atlantic Salmon

Accurate values for survival of Atlantic salmon *(Salmo salar)* are necessary for effective management of the species, particularly in areas with active restoration efforts. The steelhead *(S. gairdneri)* is a species close to the Atlantic salmon, in both life history and taxonomy. Comparison of survival estimates at different life stages can be informative. The data available on survival in freshwater and saltwater is scattered among technical reports, scientific papers, and unpublished records.

This report summarizes much of this material in a comparative synopsis by life stages. Though not intended to be a complete life history compendium, it presents the available information in a single report.

Atlantic Salmon Terminology

Term	**Definition**
Ova	Eggs produced by female adult salmonids.
Green egg	A newly fertilized stage in the development of the salmon egg.
Eyed egg	A period in egg development where the salmon embryo's dark eye spots are clearly visible through the shell. Eggs can be handled and transported at this stage.
Alevin	Young salmon from hatching through absorption of yolk sac to independent feeding. Also known as sac fry.
Fry	Brief transitional stage from emergence to dispersal from the area of the redd. Duration of this stage is usually measured in days.
Parr	Stage initiated by dispersal from the redd. Parr markings (vertical bars, 9–11 each side) are discernible. These marks last until somewhat prior to migration to the sea, though fish in this latter stage are sometimes known as "pre-smolts."
0+ parr	Parr that are less than 1 year old, also known as: young-of-the-year, fry, underyearlings.
1+ parr	Parr that are in second summer or less than 2 years old. Also known as yearlings or small parr.
2+ parr	Parr that are in third summer or less than 3 years old. Also known as large parr.
3+ parr	Parr in their fourth summer.
Precocious Parr	Sexually mature male parr.
Pre-smolt	Parr that have commenced smoltification, that is, undergoing physiological changes prior to migration to the sea. Also known as silvery parr.
Smolt	An actively migrating juvenile salmon that has undergone the physiological changes to survive the transition from freshwater to saltwater. Smoltification is size dependent and migration occurs in spring.
Post-smolt	Stage during first year at sea from the time of departure from river to the end of first winter at sea.
Salmon	All adult fish regardless of age or state of sexual maturity. This stage begins after post-smolt period and ages are described according to the number of sea winters for feeding salmon.
Grilse	A one sea-winter salmon that returns to its natal river to spawn.
Kelt	A spawned-out or spent salmon found in the freshwater portion of a river system. Also known as a black salmon.

Post-kelt	A spent or spawned-out salmon that has returned to the marine environment. This stage ends when the fish regains the weight it lost during spawning.
Repeat spawners	Salmon that are returning to their natal streams on another spawning journey.
Bright salmon	This term refers to all fresh run salmon that enter their natal stream after spending time at sea. It is synonymous with maiden salmon.

Egg-to-Alevin Survival

There is a distinct lack of studies on the survival of Atlantic salmon eggs from deposition to pre-emergent fry (alevins) in naturally occurring anadromous salmon populations. In studying landlocked salmon redds, Warner (1963) reported an egg survival to the eyed stage of 93.2%. Shearer (1961) planted "green" eggs in slatted perspex boxes buried to a depth of 50 cm in the gravel of the River Dee, Scotland. Egg survival to the hatching stage was estimated by subtracting the number of dead eggs and alevins remaining in the boxes from the known number of eggs buried. Survival ranged from 84.8% to 90.9%. In a similar experiment, Stewart (1963) reported that only 8.0% of eggs planted in Vibert boxes survived. This may have been due to improper implanting procedures, since there was evidence of heavy silting and erosion of the artificial redds. Gustafson-Marjanen (1982) found survivals of 0.9%, 3.3%, and 7.2% from eyed egg stage to emergence in artificially constructed redds and estimated survivals of 5.8%, 6.1%, and 6.4% in natural redds.

In the hatchery, typical survival of green eggs to swim-up stage (when yolk sac is absorbed) is 90% (Craig Brook National Hatchery, East Orland, ME), though this is highly variable. Mortality of pre-emergent fry living in the substrate is not known; however Danie et al. (1984) suggest it could be as high as 95%; that is, 5% survival. MacKenzie (1985) confirmed this, finding survival through hatching averaged 74%, but average survival at emergence was only 2%.

Survival at the post-hatching or larval stages of Atlantic salmon exhibit a density dependent pattern; that is, mortality at these stages is directly correlated with egg deposition densities (Symons 1979). Water quality (silt load, pH, and dissolved oxygen content) and stream bed movement can influence this pattern.

Egg to Emergent Fry Survival

In numerous studies (Table 1), the survival of deposited eggs to fry in Atlantic salmon has ranged from 0.42% (Stewart 1963) to 80% (Brunet 1980). In Maine, typical survival from natural redds appears to be 15%–35% (Jordan and Beland 1981). Studies of natural production (Meister 1962; Elson 1975) based survival rates on potential egg deposition, which is an estimate derived from the number and fecundity of surviving upstream female migrants. Actual egg deposition may be less due to angling and poaching (Symons 1979). Meister (1962) estimated egg deposition at 226 per 100 yd^2 in 1955 and 293 per 100 yd^2 in 1956. By the summers of the following years, he reported standing crops of young-of-the-year salmon of 20 per 100-square yard unit and 33 per unit (1956 and 1957, respectively). This corresponded to an egg-to-fry survival of 8%–9% for the eggs deposited in 1955 and 11.3% for those in 1956. Elson (1975), who studied Atlantic salmon in the Pollett River, NB, reported fry survivals of 1.7% and 8.0% over a range of estimated potential egg deposition of 121,800 to 3,506,900 (resulting in densities of 28 to 806 per 100 yd^2). Symons (1979) suggested that these survivals may be too low since the survival to age 1 was greater than 100% in 4 out of 8 cases. Actual egg deposition estimates in the Miramichi River, New Brunswick (Elson 1975), produced a mean egg deposition of 136+ 16 index (N/100 yd^2) with mean survivals to the underyearling stage of 17.6%.

Egg to fry survival in Newfoundland streams was influenced by winter temperatures and changes in water level described by Chadwick (1982) in the equation:

$$N_{fry}/N_{eggs} = 68.07 + 1.89\,X - 0.005\,Y$$

where X = the lowest mean monthly temperature (°C) and Y = the difference between the November mean discharge and the lowest winter mean monthly discharge (l/sec.). Ottaway and Clarke (1981) found high mortality rates for fry during emergence and dispersion.

Hatchery plants of eggs have produced similar egg to fry survivals. Egglishaw and Shackley

(1980) found this survival to range from 11.1% to 14.8% for eggs planted in perspex boxes in the gravel of the Fender Burn, Scotland. Planting "green" eggs in the River Bush, Northern Ireland, produced a much lower egg to fry survival than planting "eyed" eggs (1.4% vs. 10.3%) at densities of 6.2 per square meter (Kennedy and Strange 1981). There was evidence of winter flood scouring to which the longer developing green eggs would be exposed. Stream gradient was also important in the survival of the eyed eggs to fry (Kennedy and Strange 1984). Of eggs planted in a stream with a stream gradient of 1:22, only 6.8% produced fry by the summer of the following year while egg to fry survival of 17.5% was reported in a stream with a 1:35 gradient. Further investigation showed that the egg-to-fry survival was 37.1% in a section of the 1:35 gradient stream where all fish had been removed. Kennedy and Strange (1980) found survivals of 17.5% to 18.7% for the "eyed" egg-to-fry stage planted in a trout stream in Ireland. However, when older salmon parr were present, this survival was reduced from 10.3% to 8.8%.

While planted eyed eggs can have a survival to advanced fry of 50%–80% (Brunet 1980), the overwinter temperature and flow regimes, and the presence of predators and/or competitors can substantially reduce this survival in nature.

Table 1. Estimates of survival from egg to fry for Atlantic salmon (ranges in parentheses).

Source	Location	% Survival	Comments
Meister (1962)	Cove Brook, Maine	(8.8–11.4)	PED[a] = 226/100 yd^2 (est.) = 293/100 yd (est.)
Elson (1975)	Pollett River, New Brunswick	(1.7–8.0)	Range of PED (est.) 121,000–3,506,900
	Miramichi, New Brunswick	17.6	VED[b] = 136± 16/100 yd^2
Egglishaw and Shackley (1980)	Fender Burn, Scotland	(11.1–14.8)	Planted in perspex boxes
Brunet (1980)	River Nivelle, France	(50.0–80.0)	Eyed eggs of Danish or Scottish origin to yolk sac-less fry
Kennedy and Strange (1980)	River Bush, N. Ireland	(17.5–18.7)	With trout and no salmon
		(8.8–10.3)	With both trout and salmon
Kennedy and Strange (1981)	River Bush, N. Ireland	10.3	Eyed ova stocked at 6.2/m^2
		1.4	Green ova Evidence of winter flood scouring
Jordan and Beland (1981)	Maine	25.0 (15–35)	Mean of survival from natural redds in several rivers
Kennedy and Strange (1984)	River Bush, N. Ireland	17.5	SG[c] = 1:35
		37.1	All fish removed
		6.8	SG[c] = 1.22; all stocked at 6.2 eyed ova/m^2

[a] PED = Potential egg deposition
[b] VED = Virtual egg deposition
[c] SG = Stream gradient

Fry to Underyearling Survival

There is little information available relating to survival of the emergent fry to the underyearling (0+ parr) stage in natural populations. However, numerous experiments with stocked hatchery fry in streams have shown that survival during this life stage ranged from 0.8% to 46% (Table 2).

Stewart (1963) found that for five rivers in Lancaster, plantings of fed salmon fry showed higher survival to the end of the first growing season than did unfed fry (8.8% and 1.73%, respectively). Feeding fry before release may increase the salmon production of a marginally acceptable salmon river. There is some evidence of interstitial feeding of alevins in gravel before emergence (Gustafson-Marjanen 1982; Danie et al. 1984).

Cote and Pomerleau (1985) studied factors influencing Atlantic salmon fry survival in the Sainte-Anne-des-Monts River, Quebec. They found most variable losses of unfed fry of 28%–95% (i.e., survival of 5%–72%) occurred during the first 40 to 80 days after stocking. Low river water temperature (<10°C) and low fry weight were identified as important factors affecting survival at this stage.

In New Hampshire, fry planting at various densities done over several years on the Baker (Greenwood 1981) and Mad (Knight et al. 1982) rivers showed mean survival of fry to 0+ parr of 21.3% and 25%, respectively. This probably represents a typical survival in productive streams with the presence of predators.

Table 2. Estimates of survival from fry to 0+ parr stage for Atlantic salmon (ranges in parentheses).

Source	Location	% Survival	Comments
MacCrimmon (1954)	Duffin Creek, Ontario	12.7 (10.7–14.6)	34,780 fry (June). Mean of plantings: 1 fry/yd; no previous salmon stocks, low trap efficiency minimum estimate
Stewart (1963)	Means five rivers in Lancaster, U.K.	1.73	2,000 unfed fry at 2/yd.
		8.80	61,000 fed fry at 5–14/yd.
Mills (1969)	Three tributaries of River Bran, Scotland	(1.3–23.3)	unfed fry stocked at: 3.43–15.52/m^2 over 5 years.
		(0.8–12.9)	3.0-12.73/m^2 over 5 years.
		(1.3–30.3)	1.7-5.5/m^2 over 4 years.
Egglishaw and Shackley (1980)	Fender Burn, Scotland	(9.4–31.0)	2,859-31,638 fry stocked in 2.8 km of stream, range over 7 years
Greenwood (1981)	Baker River, New Hampshire	12.3 (15.3–25.8)	mean over 3 years. swim up fry stocked at 16–78/100m^2 ($\bar{x} = 39$)
Knight et al. (1982)	Mad River, New Hampshire	25 (11–46)	mean over 5 years swim up fry stocked at 12.3–25.3/100m^2
Kennedy and Strange (1984)	River Bush, N. Ireland	16.7	swim up fry stocked at 6.2/m^2
Cote and Pomerleau (1985)	Quebec	(5–72)	unfed fry stocked at 160/100 m^2 over 5 years.

Survival of Underyearlings to Yearling Parr

In the stream environment, estimates of survival from 0+ parr to 1+ parr are less variable and tend to be much higher than fry to 0+ parr survival for the same streams (Table 3). Ranges for this survival are from 18% to 88% for parr which were survivors of a previous planting of eggs or fry. Notable exceptions to these survivals are reported by Brunet (1980) and Cote and Pomerleau (1985). Brunet (1980) summarized underyearling to yearling survival of fry releases in French lakes in the River Neville watershed, and found values up to 90%. This high survival may be due to an elimination of density dependent mortality in lakes and a decrease in predation due to parr size. Cote and Pomerleau (1985) found that stocking of fry at 160/100 m^2 in a Quebec River produced high mortality of 1+ parr (69% to 99%), a function of parr population density. They recommended a reduction in stocking density to 40–60/100 m^3 and maximal dispersion of fry during release. From egg plantings in Northern Ireland, Kennedy and Strange (1980) found increased 0+ parr to 1+ parr survival in a stream where the gradient was 1:35 compared to parr in a stream where the gradient was 1:22. These survivals were 31.7% and 14.3%, respectively.

In studies where mean survivals over several years were calculated, Egglishaw and Shackley (1980) and Knight et al. (1982) found similar, mean underyearling-to-yearling survival of 50% (51% and 45%, respectively) which agrees well with estimates of wild parr by Meister (1962): 41.4% and 59.4%. This should be the target survival rate by fisheries managers for this life stage.

Table 3. Estimates of survival from 0+ parr to 1+ for Atlantic salmon (ranges in parentheses).

Source	Location	% Survival	Comments
MacCrimmon (1954)	Ontario	70.7	from fed fry planted at 1/yd the previous year.
Meister (1962)	Maine	59.4	
Egglishaw and Shackley (1980)	Scotland	51.0 (22–88)	
Kennedy and Strange (1980)	N. Ireland	31.7 14.3	SG[a] 1:35 SG[a] 1:22
Brunet (1980)	France	up to 90	fry planted in lakes at assumed low densities
Knight et al. (1982)	New Hampshire	45.0 (18–64)	
Cote and Pomerleau (1985)	Quebec	1–31	range from 5 years of fry stocking at 160/100 m^2

[a] Stream gradient.

Fry to Yearling Parr Survival

Most estimates of survival of fry to 1+ parr are from fry release studies (Table 4). With the exception of one case reported by Knight et al. (1982) as 30%, survival estimates range from 3.3% to 13.3%. However, he found the mean from 5 years of stocking at various densities was 11.5%. There is evidence that wild production of salmon parr from fry can show survival of up to 38% (Dickson and MacCrimmon 1982), significantly higher than survival of hatchery fry (8% to 12%).

Table 4. Estimates of survival from fry to 1+parr for Atlantic salmon (ranges in parentheses).

Source	Location	% Survival	Comments
MacCrimmon (1954)	Ontario	9.2 (9.0–9.2)	
Stewart (1963)	Lancaster, U.K.	3.6	mean from 5 rivers, stocked at 7,800 fed fry stocked at density of 13/yd
Greenwood (1981)	New Hampshire	7.2 (3.3–13.3)	mean over 2 years with an average stocking density of $39/100m^2$ (16-78)
Knight et al. (1982)	New Hampshire	11.5 (4–30)	mean over 5 years with a stocking density of $12.3–25.3/100m^2$
Dickson and MacCrimmon (1982) and Elson (1975)	Pollett River, New Brunswick	(8.0–12.0)	unfed hatchery fry
		38.0	wild fry

Egg to Parr Survival

Natural salmon production of underyearling parr ranges from 4.7% to 14% using potential egg deposition estimates (Table 5). After the cessation of successive yearly spraying of fenitrothion, Elson et al. (1973) reported 21% survival from egg to underyearling stage. This may have resulted from decreased density of older parr due to insecticide spraying. Later, egg depositions were characterized by lower survival to 0+ parr. Plantings of hatchery eggs in the gravel have produced even lower egg to underyearling survival, ranging from 0.42% to 2.0% (various studies).

This differential survival between natural and planted egg to parr is evident as the salmon reach age 1+. Meister (1962) found this survival to be 2.03% in Cove Brook, Maine, while Elson (1957) found it to be as high as 8.0% in the Pollett River, NB. In the British Isles, Shearer (1961) found egg to yearling survival to range from 0.08% to 0.46% for salmon ova planted over 3 years. Stewart (1963) found the mean survival of egg to 1+ parr from five rivers in Lancashire to be 0.55% when eggs were planted at 26/yd^2 of river. These lower survivals of planted salmon eggs are probably due to increased mortality from planting through the first summer of life and may be the result of poor selection of artificial redd sites and improper planting of eggs.

Elson (1957) found the survival to 2+ parr to 4.0% and 6.0% from estimated potential egg depositions of 0.72 and 0.39 eggs/yd^2, respectively. Studies giving actual percentages for this survival are noticeably lacking in the literature; however, Evans et al. (1985) assumed a 20% survival from underyearling to 2+ parr in a model of salmon production based on 6 years of egg planting in the Little Codroy River, Newfoundland. A.E. Knight (U.S. Fish Wildlife Service, Laconia, NH, personnal communication) found that survival from 1+ parr to 2+ parr was 70% in the Mad River, New Hampshire. This survival may be as low as 25.4% due to mortality and downstream migration of 2+ smolts (Meister 1962).

Survival to 3+ parr is not well documented since smoltification and downstream migration usually occur before this life stage over most of the geographical range of Atlantic salmon. Interesting studies of salmon populations which are exceptions to this are discussed by Power (1969) and Jensen and Johnsen (1986). In Cove Brook, Maine, Meister (1962) found survival of 2+ parr to 3+ parr to be only 4.3% for one year class. Many of the fish had migrated downstream.

Symons (1979) estimated low, medium, and high annual survival rates for juvenile Atlantic salmon: 28%, 41%, and 44%, respectively. For older parr (1+ or older), annual survival is 57%. The major limiting factors are competition for territory (Allen 1969), especially if food is limiting, and predation (MacCrimmon 1954).

Fry To Smolt Survival

In the literature, fry to smolt survival estimates are based on hatchery fry plantings. In these studies, typical survival rates range from about 1% to 12% (Table 6). Fry to smolt survival may be a function of juvenile survival from predation and, for larger parr less susceptible to predation, competition for space.

Harris (1973) reported a five-fold increase in fry-to-smolt survival (0.25% to 1.7%) when trout and

Table 5. Estimates of survival from egg to parr for Atlantic salmon (ranges in parentheses).

Source	Location	% Survival to 0+	% Survival to 1+	% Survival to 2+	Comments
Elson (1957)	New Brunswick		6.0 8.0	6.0 4.0	PED [a] = 0.39 eggs/yd^2 PED = 0.72 eggs/yd^2
Shearer (1961)	Scotland	(1.7–2.0)	(0.08–0.46)		113,000–128,000 ova planted over 3 years in perspex boxes.
Meister (1962)	Maine	5.3 4.7	2.03		PED = 63,000 (est.) PED = 81,750 (est.)
Stewart (1963)	Lancashire, U.K.;	0.42	0.55		15,000 ova at 25/yd^2
	means from five rivers				66,000 ova at 26/yd^2
Elson et al. (1973)	New Brunswick		21 14 5		PED = 57/100 yd^2 PED = 47/100 yd^2 PED = 160/100 yd^2; years free of fentitrothion spraying.

[a] PED = Potential egg deposition.

eel predators were controlled. However, Elson (1962) found no significant differences in fry to smolt survival when predatory birds were controlled. He concluded that factors other than predation limited smolt production in the Pollett River (e.g., parr density).

Interestingly, the lowest and highest estimates of fry-to-smolt survivals come from lake-reared smolt studies in the British Isles (Pedley and Jones 1978). These survival estimates (0.01% and 35.0%) were interpreted as being due to heavy predation in lake environments and the increased carrying capacity in lakes, respectively. Harris (1973) determined that lake-reared smolts of all ages could typically be produced with fry-to-smolt survivals of 5% to 15%.

Increased fry to smolt survival could probably be attained by timing the fry release to avoid the heaviest predation, planting larger fry, and releasing fry at densities which will not limit the older parr and smolt stages. Thus streams should be thoroughly investigated and monitored before and during restoration programs.

Egg to Smolt Survival

Estimates of egg to smolt survival from both natural production and plantings range from 0.38% to 3.2% (Table 7). As with fry-to-smolt survival, egg-to-smolt survival is probably a function of juvenile mortality of the overwintering eggs which is a result of density–independent environmental factors (scouring, low water, silting, etc.).

Symons (1979) suggested that egg-to-smolt survival can range from less than 1% (4+ or older

Table 6. Estimates of survival from fry to smolt for Atlantic salmon (ranges in parentheses).

Source	Location	% Survival	Comments
MacCrimmon (1954)	Ontario	3.0	34,780 fry (June) at 1/yd²; mean of 3 plantings
Elson (1957)	New Brunswick	2.57	925,000 YOY[a] at 2.13/yd²
		9.52	240,000 YOY at 0.55/yd²
		12.38	65,000 YOY at 0.15/yd²
Elson (1962)	New Brunswick	(2.0–12.0)	predators uncontrolled, 0.03–0.57 YOY/yd²
		(5.9–9.8)	predators controlled, YOY at 0.57/yd²
Mills (1964)	River Bran, Scotland	2.4	estimated production from 750,000; unfed fry
		3.1	estimated production from 550,000 unfed fry.
Harris (1973)	Cottage River, U.K.	0.25	predation uncontrolled
		1.7	predation controlled (40,000 fed fry)
Egglishaw and Shackley (1977)	Ireland	(1.0–3.0)	
Pedley and Jones (1978)	British Isles	(0.01–35.0)	fry planted in lakes at densities of 0.25–1.49/m²

[a] YOY = Young-of-the-year (underyearlings, fry).

smolts at low juvenile survival rates) to 11% (1+ smolts at high juvenile survival rates). Rarely does one find a 11% egg-to-smolt survival in nature. In fact, Meister (1962) found only 8.9% survival of 1+ parr to 2+ and 3+ smolts (5.3% survival of 0+ parr to smolt).

Elson (1962) found that percentage survival to smolt decreases with smolt age (0.96%–1.44% for 2+ smolts versus 0.38%–0.58% for 3+ smolts) in the Pollett River, New Brunswick. However, in the Northwest Miramichi River, egg to 3+ smolt survival was 2.4% when virtual egg deposition was at an optimum value of 61/100 m^2 (Paloheimo and Elson 1974).

Ultimately, the limiting factor in Atlantic salmon smolt production (and, hence, egg-to-smolt survival) could be smolt density. In an ideal salmon stream, average annual smolt production should not exceed 6 smolts/100 m^2 (Elson 1975). Meister (1962) found that in Cove Brook, Maine, naturally spawning salmon populations produced 5–6 smolts per 100 yd^2 unit. However, Symons (1979) suggested that the average smolt production can reach 10.2/100 m^2 in productive streams.

Downstream Survival

As the Atlantic salmon undergoes smoltification, it commences a migration downstream into the sea where it will mature and become an adult salmon. During this migration, it is subject to different environmental conditions and thus specific sources of mortality. The effects of water temperature, dissolved oxygen, pollution, pH, and predation during this migratory life stage have been reviewed by Bley (1987). The most significant sources of smolt mortality are impoundments and downstream obstructions (i.e., dams).

Mortality due to free fall over dams and natural falls is likely if the velocity of the fish exceeds 15 m/s on impact with the water (Danie et al. 1984). This velocity is reached by smolts falling a vertical distance of 27 m when the discharge is 0.4/m^3/s (Sweeney and Rutherford 1981). However, smolts may survive a free fall of at least 90 m if an adequate plunge pool is present (Ruggles 1980). Salmonid survival rates for both Kaplan and Francis turbines range from 0% to 100% (mean range: 50% to 95%), the highest survival occurring at the point of highest turbine efficiency (Bell et al. 1967).

Artificial and natural impoundments may present a variety of problems to migrating fish. The stratification and lack of current in lakes and reservoirs can delay and trap fish (Foerster 1937; Saunders 1960; Raleigh and Ebel 1967). These delays prolong exposure of smolts to predation, and disease organisms (Ruggles 1980). The surviving trapped smolts sometimes resume their seaward migration the following spring (Munro 1965). However, if this doesn't happen, the smolts may lose their migratory tendency and ability to survive the transition to salt water.

These sources of mortality for downstream migrants contribute to 5% to 100% mortality in smolts (Ruggles 1980). Mills (1964) described a loss due to angling and predation of only 5% in smolts migrating through three reservoirs, whereas the predation loss was as high as 85% for smolts passing through an impoundment and dam in Loch Luichart, Scotland (Menzies and Pentelow 1965). The potential loss of Atlantic salmon smolts as they passed over two dams in the Merrimack River, Massachusetts, was estimated at 17% (A.E. Knight, U.S. Fish and Wildlife Service, Laconia, NH, personal communication). Watt (1986) found the average downstream migration survival for the St. Croix River, Maine, was 48%. For five other rivers in Maine, downstream migration survival estimates ranged from 77.3% to 89.2%, depending on type and number of hydroelectric projects (A.E. Knight, personal communication).

Due to the wide variability in rivers of factors affecting the mortality of Atlantic salmon smolts migrating to the sea, each river considered for restoration or study should be investigated thoroughly to establish survival estimates.

Post-smolt Survival

In numerous studies of Atlantic salmon from smolt stage to return as adult salmon, the estimated survival has ranged from 0% to 20% (Table 8). While the return survival may be specific to a stock of salmon (Ryman 1970) or even to a river (Kanis et al. 1976), some trends can be found.

Studies involving recaptures assume that recovery of marked fish may be a function of survivability of the salmon after release (Ryman 1970). Generally, investigators have found that the percentage of hatchery smolts returning are significantly lower than for wild smolts from the same river systems. In Ireland, Piggins (1979) concluded that 3.6 wild smolts returned for every 1 hatchery smolt. Isakson (1979) also found similar results in Iceland (2.8 wild: 1 hatchery smolt). In the western

Atlantic, Baum (1983) found a range of sea survivals for Green Lake smolts to be 0.24%–1.39%, while Watt (1986) estimated wild smolt survival to adult as 3% to 8%.

An experiment to improve hatchery smolt viability in the sea by training hatchery smolts in stream tanks showed some improvement in sea survival (Wendt and Saunders 1973), but it was not a significant improvement. However, there was significantly lower mortality during handling, transport, and release of the trained smolts as compared to the untrained smolts.

Age 2+ smolts seem to have a higher sea survival than either 1+ or older smolts, though this may be a reflection of size. Faster growing 1+ smolts may be an economically feasible alternative to rearing 2+ smolts, since there is not a great difference in smolt-to-returning adult survival if the smolt size is comparable (Harris 1973; Peterson 1973). Smolts of age 3+ or older may elect to stay at sea rather than return to their natal stream to spawn (Chadwick et al. 1978).

The Atlantic salmon fishery is heavily exploited on both sides of the Atlantic. There is evidence that the farther the salmon must travel in the sea, the lower the adult returns to the home river (Watt 1986). This may explain the north-south gradient in declining smolt to returning adult survivals (Table 8). Also, this may explain the higher percentage of adult returns in so called Baltic (Northern European) salmon.

Knowledge of the marine phase of the Atlantic salmon life history is sparse (Thorpe 1980). Thus, the Atlantic Ocean is treated as a classical "black box," where rough guesses of the numbers of juvenile fish entering the sea and the unknown carrying capacity for the sea make predictions of adult returns based only on empirical data sketchy at best.

It should be noted that Atlantic salmon adults returning to the river environment are again subjected to many of the same potential sources of mortality as were downstream running smolts. In Maine, the estimated upstream survival of spawning adults ranges from 6% to 9%, depending on the number and type of hydroelectric projects (A.E.

Table 7. Estimates of survival from egg-to-smolt for Atlantic salmon (ranges in parentheses).

Source	Location	% Survival	Comments
Meister (1962)	Maine	1.1	PED[a]=63,000 (est.)
Elson (1962)	New Brunswick	(0.96–1.44)	survival to 2+ smolt
		(0.38–0.58)	survival to 3+ smolt
Paloheimo and Elson (1974)	Northwest Miramichi River, New Brunswick	1.9	mean VED[b] = 32/100 m^2
		2.4	62
		1.2	81
		0.8	120
		0.6	176
			age 3+ smolt
Gray and Conrad (1974)	Nova Scotia	(0.59–2.24)	egg deposition; 35,520 to 199,200
Piggins (1980)	Ireland	0.52	mean over 5 years
		(0.39–0.89)	
Chadwick (1982)	Newfoundland	3.6	for each stream
		3.2	
Buck and Hay (1984)	Scotland	2.1	200,000 ova at 3.4/m^2

[a] PED = potential egg deposition

[b] VED = virtual egg deposition (0.75 x PED).

Knight, U.S. Fish and Wildlife Service, personal communication). Elson (1962) assumed a 25% reduction in potential egg deposition to virtual egg deposition due to removal of spawners by angling.

Thus, the survival from smolt to spawning adult may only range from 0.35% to 1.5% (A.E. Knight, personal communication) for western Atlantic rivers. The actual survival would be based on whether the smolts were of wild or hatchery origin, time spent in riverine environment (if other than hatchery smolts are used, that is, egg, fry, or parr), distance of downstream migration, distance of sea migration, and level of exploitation during all life stages.

In contrast to Pacific salmon, Atlantic salmon do not die after spawning. Many spent fish survive the winter in freshwater and resume feeding. Chadwick et al. (1978) found that grilse-to-kelt survival ranged from 29% to 88% with the average survival being 63% for a Newfoundland river. Apparently, mortality is high when the kelts enter saltwater (Danie et al. 1984). However, actual survival rates have not been estimated. Fish that survive and migrate to oceanic feeding grounds can become repeat spawners. These repeat spawners can be a significant portion of the smolt run in any year and may be up to 10% of surviving spawners (A.E. Knight, U.S. Fish and Wildlife Service, Laconia, NH, personal communication). Much more research needs to be done on this stage of Atlantic salmon life history.

Table 8. Estimates of ocean survival for Atlantic Salmon to return of adults (ranges in parentheses).

Source	Location	% Recovery	Comments
Carlin (1962)	Sweden	(8.6–17.3) (0.0–10.95)	wild smolts hatchery smolts (returns from commercial fishery)
Elson (1957)	Five Canadian rivers	(8.0–1.5)	mean over 9 years; of different workers
Meister (1962)	Cove Brook, Maine	2.95	natural escapement and return: no tagging
Murray (1968)	Little Codroy River, Newfoundland	2.29	"adjusted possible returns;" includes estimate of commercial catch
Österdahl (1964)	Richlean, Sweden	(18.0–19.4)	hatchery smolt releases in 3 different tributaries
Österdahl (1969)	Sweden	(19.5–25.6) (5.9–13.2)	"wild" returns hatchery smolt release
Shearer (1971)	North Esk, Scotland	(2.5–5.7) (0.2–1.7)	wild smolts hatchery smolts (returns from commercial fishery)
Peterson (1973)	Ontario	(14.7–19.4) (17.6–21.3)	1+ smolts 2+ smolts (returns to date)

Source	Location	% Recovery	Comments
Wendt and Saunders (1973)	Heden, Sweden	(0.43–13.13) (2.10–11.75)	untrained hatchery smolts trained hatchery smolts. Ranges from four releases
Harris (1973)	Burrishoole, U.K.	3.75 2.08	2+ hatchery smolts 1+ hatchery smolts (means from Higgins data)
Gray and Conrad (1974)	East River, Sheet Harbour, Nova Scotia	(0.84–4.91) (0.56–7.29)	smolt to 1 sea year salmon by brood year ranges from 5 years of returns
Chadwick et al. (1978)	West Arm Brook, Newfoundland	12 6 3	3+ smolt releases 4+ smolt releases 5+ smolt releases (all returns as grilse; no tagging)
Gibson (1979)	Matamek River, Quebec	1.5	
Piggins (1980)	Ireland	(12.7–4.4)	declining due to heavily exploited fishery; mostly grilse
Egglishaw et al. (1981)	Scotland	(5–20)	
Beland et al. (1982)	Dennys River, Maine	(3–5)	smolt to 2 sea-year salmon
Baum (1983)	Maine	(0.70–1.39)	Green Lake Hatchery smolts
Larsson (1984)	Sweden	12.5	hatchery smolts; 210,000 reports of 1.7 million tagged
Watt (1986)	St. John River, Nova Scotia	(5–8)	tagging and fish trap counts
Watt (1986)	Narraguagus River, Maine	(3–5)	

Steelhead

Introduction

There are numerous influences on survival of steelhead *(Salmo gairdneri)*, some inherent to the species and environment, and some related to influences of man, such as dams, harvest, and use of hatchery fish to supplement wild populations. Hatchery fish have higher survival and growth than wild fish in a hatchery situation but, in streams, wild fish generally have higher survival (Reisenbichler and McIntyre 1977). Perhaps the most complete analysis of survival from eyed egg to adult return was the long-term study of Bjornn (1978). Most studies, however, deal with a specific stage of life. In summarizing survival in fresh water and saltwater, we have primarily restricted data to anadromous stocks of the Pacific coast, even though non-endemic populations are now firmly established in the Great Lakes and certain other inland areas. We have summarized pertinent survival data from the text in Appendix Table 1.

Life History: Comparison with Atlantic Salmon

In terms of genetics, habitat requirements, size and growth, and life cycle, steelhead, the anadromous variety of rainbow trout, is the closest species to the sea-run Atlantic salmon. In its natural range, the steelhead is found from central California to the Bering Sea waters off Alaska. It has been introduced widely across the United States and Canada, most notably in the Great Lakes. One major difference between life histories of sea-run Atlantic salmon and steelhead is that Atlantic salmon generally have one upstream migration and spawning period each year, while there are two distinct forms of steelhead. Summer-run steelhead, or "summer steelhead," migrate upstream during spring and summer as immature fish and do not mature and spawn until the following spring. Winter-run steelhead, or "winter steelhead," migrate upstream in late fall and winter, spawning in late winter to early fall (Smith 1968; Chilcote et al. 1980). There is the opportunity in some waters for inter-breeding between the two races and, traditionally, steelhead ascended the major rivers of the Pacific coast during almost every month.

Hatchery stocks of winter steelhead may spawn earlier than wild stocks (December through February versus late March to early May). Many natural runs of steelhead are supplemented with hatchery stocks in California, Oregon, Washington, British Columbia, and, to a lesser extent, Alaska. In 1983, approximately 28 million steelhead smolts and fry were stocked in the Pacific coastal waters (Moring 1986). In many popular rivers, hatchery stocking is extremely important in maintaining existing runs of steelhead. For example, an estimated 97% of the 7,400 steelhead landed in 1977 by anglers on the Alsea River, Oregon, were of hatchery origin, and 75% to 80% of the fish in many Oregon rivers are of hatchery origin (Moring 1986).

Atlantic salmon runs in the United States are primarily supported by hatchery stocking. There are some wild fish in Maine, and many more in Canadian waters, but hatchery stocking is critical for most runs of Atlantic salmon in the United States and important in many areas for steelhead.

Another difference between the two species is incubation time. While eggs of Atlantic salmon may incubate from late autumn to April (Bley 1987), eggs of steelhead hatch in 4 to 7 weeks (Pauley et al. 1986). Whereas Atlantic salmon alevins may remain in the gravel for 4 to 6 weeks (Danie et al. 1984), steelhead alevins become free swimming in 3 to 7 days (Pauley et al. 1986), although Shapovalov (1937) found longer alevin periods during some limited experiments.

Time of residence in streams can also be slightly different between the two species. Most Atlantic salmon spend 2 years in freshwater before migrating to sea. Steelhead spend 2 to 3 years in freshwater, but hatchery fish may only spend 1 year (Pauley et al. 1986). With the heating of water in Atlantic salmon hatcheries, many salmon are released as 1-year-old smolts.

Finally, there is a component of the returning population of some Pacific coast rivers, notably the Klamath and Mad rivers in California, and the Rogue River in Oregon, that are known as "half pounders." These small steelhead return to the river 2 to 4 months after smolt emigration, and an estimated 97% of the smolts released in the Rogue River initially return as "half pounders" (Everest 1973).

Intergravel Survival

Fertilization success is similar between the different races and non-migratory rainbow trout. Approximately 97.5% of deposited eggs are fertilized

(Briggs 1953; Shapovalov and Taft 1954). Shapovalov (1937) conducted experiments related to hatching success of steelhead in experimental troughs in California. He found survival from egg deposition to emergence in two experiments was 30% and 80%. Survival of a control batch of eggs in a basket, not requiring emergence through gravel, was similar—82%. In later experiments, Shapovalov and Taft (1954) concluded that, under ideal conditions, survival-to-emergence averages 80%–90%. Sheppard (1972) summarized available information at that time and concluded that, under favorable conditions, survival to emergence averages 65% to 85%. In a series of experiments from 1962 to 1967, Bjornn (1978) determined survival from eyed egg stage to emergence ranged from 40% to 94% in gravel incubation channels.

Phillips et al. (1975) conducted experiments in Oregon relating intergravel survival of steelhead to sediment levels in gravel. Mean survival was highest (99%) in gravel containing no sediment fines (<3 mm), and was lowest (18%) in gravel containing 70% sediment fines. These results were similar to those obtained by Bjornn (1969).

Most recently, studies from 1976 to 1984 at the Snow Creek Research Station have shown a much lower value for survival-to-emergence for winter steelhead. Yearly values ranged from 12% to 30%, with a mean of 20% (T. Johnson and R. Cooper, Washington Department of Game, Port Townsend, WA, personnel communication and unpublished data).

Survival of Fry and Fingerlings

Information on survival of pre-smolt juveniles in streams is quite limited. Burns (1971) estimated that June-to-October survival of young-of-the-year salmonids in a California stream was only 27%, ranging from 20% to 29%. Age 1 and older juveniles survived at a higher rate during this same summer–fall period: 56%, with a survival range of 34% to 94%. Bjornn (1978) estimated only 10% to 20% first summer survival for steelhead in Big Springs Creek, Idaho, and 6% to 41% survival in the second summer after the fish moved into the Lemhi River. Allen (1986) found first summer survival of 6% to 24%, first winter survival of 26% to 70%, and second summer survival of 3% to 7.5% in four years of studies in the East Fork of the North Fork, Mad River, California. He also presented a good summary of physical and biological factors affecting in-stream mortality of steelhead.

More recently, Leider et al. (1986) looked at migratory pre-smolts moving from a tributary stream into the Kalama River, Washington. The actual survival estimates were a reflection of downstream recaptures of marked fish, so precise survival values are somewhat obscured, but the authors concluded that survival of such migratory pre-smolts was a reflection of rearing habitat downstream. These results were similar to those of Tredger (1980) who estimated that 69% of the smolts of a main stem river—Nicola River, British Columbia—were derived from fry and age-1 steelhead from a tributary stream.

Bjornn (1978) measured survival from the fry stage to downstream migration as yearling fish in Idaho. From 1962 to 1973, survival ranged from 0.4% to 3.8% in Big Springs Creek and the Lemhi River.

Perhaps the most accurate data on survival at this stage comes from studies of winter steelhead at the Snow Creek Research Station, Washington, from 1976 to 1984 (T. Johnson and R. Cooper, Snow Creek Research Station, Port Townsend, WA, personnel communication and unpublished data). Survival from emergence to smolt stage averaged 8.3% in wild fish (range of 3.4% to 16.2%), and 8.2% in hatchery-reared fish (range of 3.4% to 16.2%). The same data sets indicated overall survival from egg deposition to smolt stage averaged 1.6% in wild fish and 1.5% in fish of hatchery origin (Johnson and Cooper, unpublished data).

The actual density of stocked fish can inversely affect fry survival. Hume and Parkinson (1984) stocked fry in Lynn Creek, British Columbia, and found that survival to the fall age 1+ parr stage ranged from 17% (high density) to 26% (low density) for the 1980 age group. Low densities here refer to 0.14 fry/m^2 and high densities to 1.9 fry/m^2. For the 1981 age group, survival ranged from 5% for medium and high densities (0.68 to 18% for low densities (0.13 fry/m^2). Although the authors did estimate fry-to-smolt survival rates, there were errors in the smolt trap estimates, and retesting is necessary.

Post-Smolt Survival

The most information available on survival of steelhead deals with the life stage following smolt stocking or migration to the time of adult return. It is extremely difficult to isolate the mortality percentage related exclusively to marine survival from the mortality associated with downstream migration of smolts and upstream migration of adults. Survival estimates for this stage, nonetheless, are often the easiest to obtain, requiring simply stocking known numbers of smolts and having a mechanism (either a trap and/or effective creel survey) to count returning adults.

Hallock et al. (1961) summarized a series of experimental releases in California and concluded that an average of 2% of the fish released as yearlings eventually returned as adults. Part of the mortality included in this figure was from sport fishermen catching steelhead as legal-sized rainbow trout soon after the opening of trout season in the spring. Moring (1976) and Buchanan and Moring (1986) provided some indication of the extent of such mortality on juvenile steelhead by anglers. In studies from 1974 to 1976, 36% to 57% of the total catch of all fishes in Foster Reservoir, Oregon, were of steelhead delayed by a dam on their outmigration. Between 19,500 and 22,800 steelhead smolts were taken annually by anglers seeking rainbow trout in and above this relatively small 494-ha reservoir.

During the downstream migration by smolts, steelhead undergo a gradual smoltification process. Bjornn et al. (1979) found that, if the normal migration timing is interrupted by trapping and downstream trucking to bypass dams, steelhead may not be true "smolts" upon being placed into saltwater. The closer the site of migration interruption to the site of release, the higher the mortality of fish placed in saltwater areas. Many of the hatchery fish released in rivers in Idaho had fungus infections. The eventual mortality of such fish when trucked to saltwater areas was even higher—up to 91%—because of fungal infections (Bjornn et al. 1979).

Several studies have tried to define optimal size at release for steelhead smolts. Sheppard (1972) summarized several of these studies and concluded that smolt-to-returning-adult survival is about 2.5% for small, 1-year old trout, 6% for 2-year old trout, and 18% for 3-year old trout (Shapovalov 1967).

Wagner conducted a series of experiments in the 1950s and 1960s on aspects of steelhead movements in the Alsea River, Oregon, also demonstrating a higher rate of return for steelhead released at the largest size—12.1/kg (Wagner et al. 1963). Survival from smolt to adult return for 1956–1959 release groups ranged from 0% to 10.0%, depending on the size at release. Most return rates were less than 1.2%.

Wagner (1966, 1968) also showed that the liberation technique for hatchery fish does not statistically affect smolt to adult survival rates. For 1963, 1964, and 1965 groups, 3.9%, 9.2%, and 5.4%, respectively, of the fish survived as adults when allowed to move from the raceways voluntarily. Survival for groups intentionally stocked in the Alsea River in the same years was 4.4%, 10.9% and 4.5%. Wagner (1969) also indicated that stocking location may play a role in smolt-to-adult return survival. Steelhead released in the upper Alsea River had a return survival of 6.0% (1964 release group) and 1.6% (1965 release group). Smolts released in the lower river had survivals of 3.5% and 2.3%. Similar experiments in the Wilson River indicated survival rates of 3.1% and 1.7% for fish stocked in the upper river in 1964 and 1965; 5.7% and 1.5% for fish stocked in the middle river; and 7.0% and 3.3% for fish stocked in the lower river.

Unpublished data from 6 years of complete data at the Snow Creek Research Station indicated smolt-to-adult survival rates of wild fish ranged from 2.4% to 12.4%, averaging 7.3% for the 1978 to 1983 release groups (R. Cooper, T.Johnson, Washington Department Game, Port Townsend, WA, personal communication). Similarly, post-smolt survival of steelhead in the Keough River, BC, was 8%, 12%, and 15% for 1977, 1978, and 1979 release years, respectively (Slaney, in Matthews 1983); the differences were probably a reflection of release size (8 g, 48 g, and 50 g average size of smolts, respectively). In general, smolt-to-adult survival of hatchery fish averaged about 5%, while that of wild steelhead averaged about 13% (B. Ward and P. Slaney, unpublished data; Hume and Parkinson 1984). Some very limited data by Everest (1973) for the Rogue River, Oregon, show return rates of 0% to 25.3% depending on release site and size, but the individual sample sizes were quite low. In a 10-year study in Idaho, Bjornn (1978) found smolt-to-adult survival ranged from 0.5% to 2.2%.

The rearing regime can also influence smolt-to-adult survival. Bjornn and Ringe (1984*b*) found that, since 1980, survival percentage has been higher at Dworshak National Fish Hatchery, Idaho, for fish released as 1-year-old smolts compared to the "normal" 2-year-old smolts. Subjecting fish to thermal shock (4–10° C after rearing in 15°C water) prior to release also appears to increase return rates (Bjornn and Ringe 1984*a*)

Mortality due to sport or commercial fishing is highly variable between river systems and between years, and is reflected in the limited smolt-to-adult survival rates conducted by investigators. In Oregon and Washington in the mid-1950's, for example, commercial and sport fisheries removed between 19% and 26% of the winter steelhead returning to the Columbia River (Korn 1961). But, comparison of figures for the impact of angling and/or commercial fishing are probably unrealistic because of variations in management regulations, recent Indian catch settlements in the courts (Clark 1985), elimination of intentional commercial catches by non-Indians in many areas, and other factors.

The year-to-year variability of ocean survival is a factor that has been little studied. Mathews (1983) provided an excellent summary of the factors influencing ocean survival rates of anadromous salmonids. Yet, isolating the strictly marine mortality component of the overall smolt-to-adult return rate is extremely difficult and has been essentially undocumented.

Other Influences on Survival

In addition to natural influences on freshwater and ocean survival of steelhead and the variable influences of angling and commercial netting by Indian tribes, there are other influences on survival, many related to management practices or man-made structures.

In areas with numerous large dams on a river system, such as the Columbia River, incidence of gas bubble disease may still have a significant impact on survival of outmigrant smolts. Ebel (1971) estimated 15% mortality of juvenile steelhead (1970 Dworshak Hatchery release group) at Ice Harbor Dam and a subsequent 90% mortality at McNary Dam due to gas bubble disease.

If fish, either smolts or returning adults, are trapped and then trucked around dams, other changes in survival rates can occur—often positive. Ebel et al. (1973) found that mortality from handling, marking, and transporting was approximately 5%. But, the authors also found significantly lower return survival of steelhead smolts hauled in trucks for 7 h versus smolts hauled for only 1 h. Downstream survival of such transported steelhead was four times higher than non-transported (1.3% and 0.4%, respectively). Non-transported fish were released above Ice Harbor Dam, transported fish were taken to below John Day Dam, and fish were recaptured (sample of all migrating smolts) at The Dalles Dam. Some of the mortality may have been due to gas bubble disease.

Cramer (1981) and Buchanan and Moring (1986) demonstrated that summer steelhead have well-defined homing abilities, even when adults are displaced upstream or downstream. In a study of steelhead in seven streams in California, Taft and Shapovalov (1938) found only 0% to 2.1% straying of fish between streams. Thus, survival estimates made for post-smolt trout do reflect most of the true numbers of returning adults. Use of certain artificial imprinting chemicals, such as morpholine, has been shown to further enhance this high degree of homing (Cooper and Scholz 1976).

This homing behavior can be a disadvantage to returning adult steelhead. When dams interfere with the normal return to release sites, or if fish are transported upstream from dams to provide spawning populations or angling experiences, many will recycle back through dams to release sites below dams. Buchanan and Moring (1986) showed that, of trapped adult summer steelhead released in the forebay and the head of Foster Reservoir, Oregon, 41% to 52% recycled back through the turbines, suffering high mortality.

When dams have properly designed adult fish passage facilities, mortalities of migrating steelhead can be limited. Wagner and Ingram (1973) estimated only a 0.1% trap mortality or less at Foster and Green Peter dams, Oregon. If a dam does not have proper downstream fish passage facilities for kelts, such as at Foster Dam, few kelts will survive to return and spawn: minimum rates of 22% to 41% mortality (Wagner and Ingram 1973). After modifications to the Green Peter Dam downstream passage facilities, mortalities of winter steelhead trout smolts ranged from 0.3% to 1.8% during 1968–1971. Downstream passage mortality at Foster Dam was much higher: 7% to 69%. Survival was highest for smolts released before April, and declined rapidly for May or June releases (Wagner and Ingram 1973.).

Hooking mortality is another variable that depends on angling pressure, gear restrictions, etc. Reingold (1975) found that hooking, playing the fish to exhaustion, then transporting the fish downstream did not significantly affect the homing rate compared to control groups, except for one group released 80 km downstream. Similarly, disease resistance is often a function of strain, and disease mortality in steelhead can be related to delays in downstream fish passage at dams and other factors (Sanders et al. 1970). For example, in a series of experiments by Buchanan et al. (1983), the Siletz strain of steelhead suffered 100% mortality when exposed to warm Willamette River water containing the pathogen *Ceratomyxa shasta*. Other strains suffered less mortality: as little as 2%–37% in the Deschutes strain.

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Appendix

Table 1. Summary of survival values for different life stages of steelhead. Refer to text for details.

Stage and location	% Survival	References
Egg to emergence		
California	30 and 80	Shapovalov (1937)
Oregon	18–99	Phillips et al. (1975)
Washington	20	Snow Cr. Res. Stn.[a]
Idaho	40–95[b]	Bjornn (1978)
Varied	65–85	Sheppard (1972)
Egg to smolt		
Washington	1.5 (hatchery)	Snow Cr. Res. Stn.[a]
Washington	1.6 (wild)	Snow Cr. Res. Stn.[a]
Emergence to smolt		
Washington	8.2 (hatchery)	Snow Cr. Res. Stn.[a]
Washington	8.3 (wild)	Snow Cr. Res. Stn.[a]
Idaho	0.4–3.8	Bjornn (1978)
Fry - fingerling		
California	27[c]	Burns (1971)
California	56[d]	Burns (1971)
Idaho	10–20[e]	Bjornn (1978)
Idaho	6–41[f]	Bjornn (1978)
California	6–42[e]	Allen (1986)
British Columbia	5–26[e]	Hume and Parkinson (1984)
Smolt to adult return		
California	2[g]	Hallock et al. (1961)
California	2.1–18	Shapovalov (1967)
Oregon	0–10	Wagner et al. (1963)
Oregon	3.9–9.2[h]	Wagner (1968)
Oregon	4.4–10.9[i]	Wagner (1968)
Oregon	1.6–6.0[j]	Wagner (1969)
Oregon	2.3–3.5[k]	Wagner (1969)
Oregon	1.7–3.1[j]	Wagner (1969)
Oregon	1.5–5.7[l]	Wagner (1969)
Oregon	3.3–7.0[k]	Wagner (1969)
Washington	7.3	Snow Cr. Res. Stn.[a]
British Columbia	8–12	Slaney (Mathews 1983)
British Columbia	13 (wild)	Hume and Parkinson (1984)
British Columbia	5 (hatchery)	Hume and Parkinson (1984)
Idaho	0.5–2.2	Bjornn (1978)
Specific conditions		
Washington	10–85[m]	Ebel (1971)
Washington	95[n]	Ebel et al. (1973)
Washington	0.4[o]–1.3[p]	Ebel et al. (1973)

Appendix Table 1. *Continued.*

Stage and location	% Survival	References
Oregon	59–78[q]	Wagner and Ingram (1973)
Oregon	98.2–99.7[m]	Wagner and Ingram (1973)
Oregon	7–61[r]	

[a] Unpublished data (R. Cooper, T. Johnson, Snow Creek Research Station, Washington Dep. Game, 8574 Highway 101, Port Townsend, WA 98368, personal communication).

[b] Eyed egg stage to emergence.

[c] Young-of-the-year.

[d] Age 1 and older.

[e] First summer.

[f] Second summer.

[g] Released as yearlings.

[h] Voluntary release groups.

[i] Forced release groups.

[j] Upper river releases.

[k] Lower river releases.

[l] Middle river releases.

[m] Downstream passage at dam.

[n] Trucking survival.

[o] Trucked.

[p] Not trucked.

[q] Kelts passing downstream at dam.

[r] Downstream passage at dam without passage facilities.

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The survival of both Atlantic salmon and steelhead is described for each of their life history stages and all of the pertinent literature is reviewed. A comparison shows the steelhead, the anadromous variety of the rainbow trout, is the closest to the sea-run Atlantic salmon in terms of genetics, habitat requirements, size and growth, and life cycle.

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