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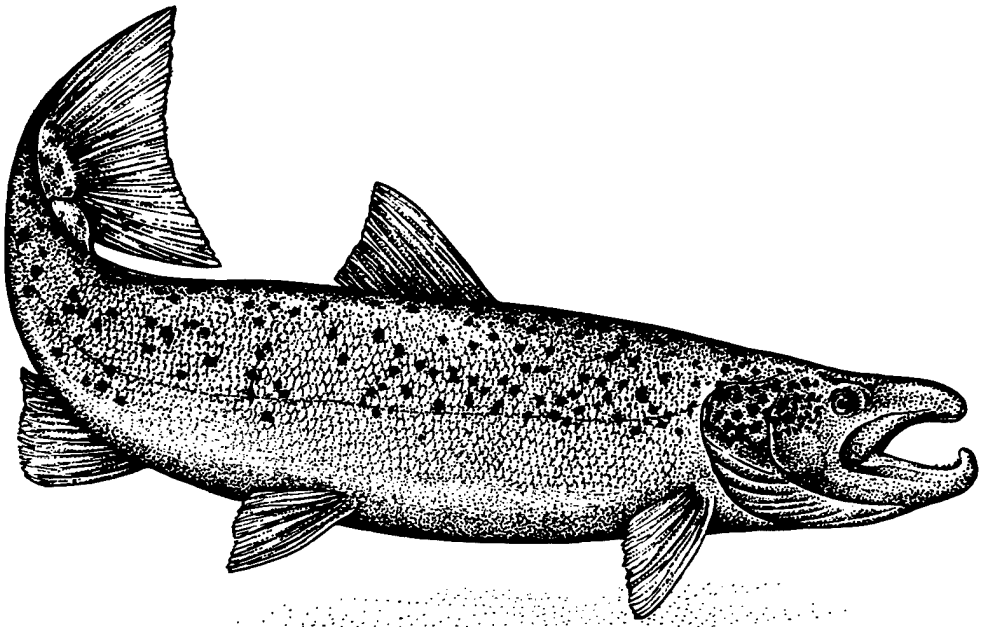
Age, Growth, and Mortality of Juvenile Atlantic Salmon in Streams: A Review



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Age, Growth, and Mortality of Juvenile Atlantic Salmon in Streams: A Review

by

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Age, Growth, and Mortality of Juvenile Atlantic Salmon in Streams: A Review

Introduction

Populations or stocks of sea-run Atlantic salmon (*Salmo salar*) are reproductively isolated. As a result of homing, adult salmon return to spawn in the same stream in which they were reared; however, these populations maintain genetic diversity through their diverse life history. The variability in age at smoltification, length of sea life before first spawning, and possibility of multiple or precocious spawning may allow a single year class of salmon to persist in a Canadian stream for up to 10 years (Saunders and Schom 1985). Hence, the effective population size is increased and genetic variability is maintained. Environmental determinants—temperature and flow regimes, predation, and food availability—have the potential for population-specific adaption of juvenile salmon to natal streams (Riddel and Leggett 1981). The combination of genetic and environmental determinants allows for the wide diversity found in naturally occurring Atlantic salmon stocks throughout the natural range.

This report summarizes published and unpublished knowledge of the age, growth, and sources of mortality in juvenile Atlantic salmon in streams. Though not intended to be a complete life history compendium, it is a synopsis of current data on this portion of the life cycle.

Life History

Spawning

Atlantic salmon require a freshwater environment for spawning and the development of early life stages (Jones 1959). The female constructs a nest or redd, which consists of several depressions 25 to 50 cm deep in the streambed (Cutting 1966). Each depression (or "egg pit") contains eggs after the fish finish (Leim and Scott 1966). The optimum location for a spawning redd is a shallow, gravelly area at the tail of a pool where the water velocity is increasing (Peterson 1978). Other locations may include the head of a pool (Scott and Crossman 1973), the downstream end of riffles (Danie et al. 1982), or areas near upwelling of ground water (Peterson 1978). The number of eggs carried by a female ranges from 2,000 to more than 10,000, depending mainly on the size of the fish. As a rule of thumb, anadromous females produce 1,500 to 1,800 eggs per kilogram of body weight (Danie et al. 1984). The male aligns himself with the female and fertilizes the eggs as they are being deposited into each pit (Jordan and Beland 1981). Some male parr become sexually mature and take an active part in fertilizing eggs (Myers 1984). The female covers the eggs with about 10 to 25 cm of gravel (Cutting 1966), which comes from the excavation of another egg pit just upstream. This process continues until spawning is completed (Danie et al. 1984).

Spawning usually occurs at temperatures less than 7°C (Decola 1970; Peterson et al. 1977; R. K. Sweeney, Fisheries and Oceans, Halifax, NS, personal communication). In five rivers of eastern Maine, spawning was at temperatures of 3 to 10.5°C (Jordan and Beland 1981). These stream temperatures correspond with egg deposition in rivers tributary to the Gulf of Maine during the period from mid-October to mid-November (Bigelow and Schroeder 1953); in Scotland spawning is usually in November to January (Egglishaw and Shackley 1977). Excellent reviews of salmon spawning habitat were documented by Knight and Greenwood (1981); McLaughlin (1986); and given by D. M. Kuzmeskus (U.S. Fish and Wildlife Service, Laconia, NH, personal communication).

Egg Development

Eggs remain in the redds until the following spring. Incubation periods vary, depending on temperature regimes. Eggs reach the "eyed stage" (when the eyes can be discerned clearly

through the shell) some weeks after fertilization. Leim and Scott (1966) cited an incubation period of 110 days at 3.9°C for hatchery eggs (Danie et al. 1984), and Peterson et al. (1977) determined an incubation period of 128 days at 4°C and 44 to 49 days at 10°C. In eastern Maine, hatching typically occurs in late April or early May, after 175 to 195 days of normal winter conditions (Jordan and Beland 1981). Hatching in Scotland occurs from March to April (Egglishaw and Shackley 1977). Temperatures between 0.5 and 9°C are considered adequate for normal egg development (Decola 1970). The optimal temperature for incubation is about 6°C (Peterson et al. 1977).

Larval Development

The newly hatched alevin or yolk-sac larva (the eleuthero-embryo of Allen and Ritter 1977), which is about 15-18 mm long, requires about 6 weeks to absorb its yolk sac while remaining buried in the gravel (Danie et al. 1984). The yolk sac is usually fully absorbed when the larvae reach a length of 25 mm (fry stage). Fry begin to forage for food even before they emerge from the substrate. In eastern Maine fry emerge between 19 May and 1 June (i.e., 3 to 5 weeks after hatching), when water temperatures are between 10 and 20°C (Jordan and Beland 1981). Gustafson-Marjanen (1982) observed that emergence was always at night. Emergence peaks from 12 June to 23 June in New Brunswick streams (Randall 1982) but in April and May in Scotland (Egglishaw and Shackley 1977). Similar early fry emergence was found by Jordan and Beland (1981) in Maine when redds were located on spring seepage.

Juvenile Development

After emergence, fry disperse and immediately establish territories (Allen 1940*a*; Kalleberg 1958; Mills 1964) in a mosaic of more or less separate territories throughout all suitable habitats of the streams. The young salmon are also displaced downstream by water flow.

Upon reaching a length of about 40 mm during the first summer, young salmon are called parr or fingerlings. They are found predominantly in riffles at sites where water velocity averages 50-60 cm/s. Symons and Heland (1978) found the highest densities of parr in diverse sections of the stream. Habitat preference of the parr depends on the size of the fish rather than on their age; a change occurs after the parr reach a total length (TL) of 6 to 7 cm (McLaughlin 1986).

Small parr, 4 to 7 cm (TL) and usually age 0+, appear to prefer a substrate of gravel that is 1.6 to 6.4 cm in diameter, at stream depths of 10 to 15 cm (Symons and Heland 1978); similar habitats have been noted in rivers in New Hampshire (Knight 1981), Nova Scotia (R.K. Sweeney, Fisheries and Oceans, Halifax, NS, personal communication), and New Brunswick (Rimmer et al. 1984). Symons and Heland (1978) conducted experiments with underyearling salmon in laboratory streams having water depths of 5 to 27 cm. Most underyearlings selected depths of 5 to 9 cm until they were 6.5 cm (TL). At this size they began seeking deeper water.

Juvenile salmon exceeding 7 cm TL are designated large parr. The substrate selected by such parr seemingly depends on the size of the fish. Fish 8 to 9 cm long prefer a cobble-boulder substrate in which particle diameter exceeds 6.4 cm (Symons and Heland 1978). As the parr grow and exceed 9 cm, they appear to prefer larger substrate material (>25.6 cm diameter). Elson (1975), who examined habitat preferences of parr in the Pollett River, New Brunswick, found that yearling and older parr preferred cobble-rock (>15 cm diameter) habitat. The depth and velocity preferences of parr indicate that large parr (age 1 and older) prefer deeper habitat and higher velocities. The laboratory studies by Symons and Heland (1978) also showed that the percentage of juveniles that sought deeper water (≥30 cm) increased with increasing size.

Rimmer et al. (1983), who used snorkling gear to make visual observations of any changes in habitat preferences of parr during the summer-autumn transition in the Little Sevogle River, found that parr stayed close to summer locations—the only exceptions being large parr translocating from rock runs. However, when autumn temperatures declined to 10°C, the salmon parr used sheltered substrate chambers almost exclusively. Gibson (1978) observed that salmon parr showed a greater tendency than brook trout (*Salvelinus fontinalis*) to hide in crevices and

under rocks as temperatures decreased below 11°C. In a follow-up report, Rimmer et al. (1984) noted that small parr (fork length to 6.0 cm, age 0+) shifted to larger home stones in autumn. The mean home stone size was 6.6 cm in summer and 17.8 cm in autumn. Large parr preferred particle sizes more than 20 cm in diameter (1+, x = 20.9 cm; 2+, x = 24.4 cm). There was no significant change in the mean depth from summer to autumn (means, small parr 30-31 cm; large parr 31-32 cm); however, the range of depths significantly narrowed. More than 90% of the 0+ parr and more than 95% of the larger parr were found in water depths of 24 to 36 cm (maximum available depths were near 66 cm). In autumn, most parr preferred focal velocities averaging less than 10 cm/s (0+, 7.8 cm/s; 1+, 9.4; 2+, 7.1). Parr found in focal velocities of more than 10 cm/s were not in sheltered substrates.

Juvenile salmon of all classes have similar cool temperature requirements. They grow little at a temperature less than 7°C (Symons 1979). Power (1969) suggested that the effective growing season is determined by the number of days in which the temperature exceeds 6°C. Decola (1970) reported that parr tolerate temperatures to 27°C, at which time they seek cooler water. He reported incipient lethal temperatures for fingerlings to be 27.5-28.4°C at acclimation temperatures of 20°C (Fry 1947). The lethal temperature for juveniles is 32°C (Garside 1973). The optimal temperature range for normal growth of parr is between 15 and 19°C (Decola 1970), and optimal growth is at 16.6°C (Siginevich 1967), though some recent data may indicate the upper limit of the optimal range to be several degrees higher (A. E. Knight, U.S. Fish and Wildlife Service, Laconia, NH, unpublished data).

As parr grow, their territories increase in area (Warkowski and Thorpe 1979), forcing individuals to move to new territories (Kalleberg 1958) and pools (Rimmer et al. 1983). These movements sometimes result in migrations of relatively short distances, generally downstream (Bulleid 1973), though there has been evidence of upstream movement (Saunders and Gee 1964).

Studies by Rimmer et al. (1983) indicated that the use of pools by juvenile Atlantic salmon depends on age and size; 0+ parr (fork length to 6.0 cm) rarely were found in pools, whereas about 5% of age 1+ parr (5.0-10.0 cm) and about 15% of 2+ parr (7.5-13.0 cm) used pools throughout summer and autumn. Pool use increased with age. Saunders (1960) found that some Atlantic salmon parr used a pond in Ellerslie Brook, Prince Edward Island, as a rearing area. Ryan (1986) suggested that lake use by parr in Newfoundland resulted from relatively short migrations upstream or downstream in the presence of high stock densities in spawning areas; underyearlings remain in the fluvial river. Parr that enter lakes move into them in spring and remain until maturation or smoltification of precocious male parr (Hutchins 1986).

Hutchins (1986) concluded that the benefits of lake habitat in Newfoundland—abundance of food, decreased competition for space, lower energy cost in maintaining position, and the presence of overwinter habitat for large parr and presmolts—increased growth rates and produced better parr survival. The extensive use of lake habitat by parr may be a function of availability or may be confined to Newfoundland waters (Ryan 1986). Harris (1973) determined that, for British smolts, juveniles reared in lakes and ponds (compared with those reared under natural river conditions) grew faster, smolted at an earlier age, and showed a higher rate of survival to the smolt stage. Lake use by juvenile salmon offers a counterpoint to the accepted "classical" freshwater life history of salmon and should be investigated in other geographical regions.

In fall, many male parr become sexually mature (precocious parr). Precocious sexual development is common over the entire geographical range of the species and occurs in both natural and hatchery stocks (Dalley et al. 1983). From 12.3 to 100% of male parr mature precociously (Myers 1984). Dalley et al. (1983), who studied the sexual maturation of male parr in Newfoundland, found that the age of precocious males ranged from 1+ to the oldest parr in a stream. The mean length of precocious 1+ parr in a stream ranged from 72.6 to 116.1 mm, the shortest being 60 mm. Large parr mature earlier. The size threshold for precocious maturation is significantly lower than for smoltification (Bailey et al. 1980). Precocious parr are late to smoltify (Myers 1984), and collect in spawning areas, where they can fertilize a considerable fraction of spawned eggs. After fertilization, some precocious parr migrate to the sea as "spent" smolts in autumn, but some remain in

the river for at least 1 year (Myers 1984). Dalley et al. (1983) concluded that the observed higher mortality of male smolts results from decreases in condition of spent smolts that had allocated valuable energy reserves into reproductive products. Overwintering precocious males also incur a higher mortality, as well as increased exposure to predation the following year (Myers 1984).

Because of this precocious maturation and related heavy mortality, the females may significantly outnumber males in smolt runs (Birt and Green 1986). Myers (1984) estimated that 60% of the annual male salmon production was lost from the Little Condroy River, Newfoundland, due directly or indirectly to precocious male maturation. The age at sexual maturity of an Atlantic salmon stock is influenced by the natural mortality during each year at sea, as well as by the length and discharge volume of rivers and the average expected ocean temperatures (Scarnecchia 1983). Therefore, variation in the sexual maturation of male parr within a year class ensures a mixture of breeding stock (Refstie et al. 1977) and the insurance of the continuity of breeding stock (Saunders and Schom 1985).

Parr remain in the stream until they are 125-150 mm long, which may take up to 2-3 years in Gulf of Maine rivers (Bigelow and Schoeder 1953; Danie et al. 1984; Schaffer and Elson 1975). Egglishaw and Shackley (1977) reported that in Scottish streams, parr may remain for 1 to 4 years (usually 2 years) and reach 90-150 mm in length. Parr that fail to reach the critical length by spring or early summer in any one year do not transform into smolts until the following spring, regardless of subsequent growth (Refstie et al. 1977). Elson (1957) concluded that Atlantic salmon parr must reach a length of 10 cm in fall to smoltify during the following spring. Smolts from Canadian rivers average 13 to 18 cm in length (Dymond 1963). After the onset of smoltification, pronounced changes in physiology and behavior result in the initiation of the salmon's downstream journey to the sea.

In addition to the downstream movement of smolts in the spring, many pre-smolt and non-anadromous (landlocked) fish move downstream during fall, winter, and spring (Calderwood 1906; Meister 1962; Mills 1964; Chapman and Bjornn 1969; Thorpe and Morgan 1978). In addition, some upstream movement of juvenile salmonids often occurs in spring and early summer (Bjornn 1971; Bulleid 1973). These movements of non-smolts have been attributed to innate behavior, lack of suitable winter cover (Chapman and Bjornn 1969; Bustard and Narver 1975), a decrease in food supply (Symons 1971), changes in aggressive behavior (Chapman 1962; Symons 1968, 1971), or to spawning activity of precocious mature males (Buck and Youngston 1979). These non-smolt migrations usually do not account for movement into the sea or, if they do, such movement is inconsequential to the life history of most populations of anadromous Atlantic salmon (Ruggles 1980). These non-smolt seaward movements probably represent fish surplus to the carrying capacity of the freshwater habitat.

Transformation from Parr to Smolt

The change from a stream-dwelling parr to a migrating smolt is accompanied by marked changes in appearance. Parr have characteristic parr marks, are brightly colored, and blend with their background in cryptic fashion (Jones 1959). Smolts are slimmer and more streamlined, have a longer tail with a deeper fork, and are silvery in appearance. These physical changes are reflected in weight-length relation or coefficient of condition (Hoar 1939), and by the increase in the amount of layers beneath the scales and in the dermis adjacent to the muscle (Hoar 1976; McCormick et al. 1985). Both guanine and hypoxanthine occur in these layers and the guanine:hypoxanthine ratio increases during smolting (Johnston and Eales 1967). Johnston and Eales (1970) reported that size may also play a factor in the speed at which salmon took on a silvery appearance.

Along with morphological changes during the parr-to-smolt metamorphosis, biochemical and physiological changes are also occurring. There is a decrease in total body lipids (Hoar 1939; Fessler and Wagner 1969; Farmer et al. 1977) and certain enzymes change, accompanied by a loss of glycogen from the liver (Hoar 1965; Baggerman 1960; Saunders and Henderson 1970; Wendt and Saunders 1973; Hoars 1976). Smolts are more buoyant than non-smolts. Although these changes are well documented, their biological significance remains speculative (Hoar 1976).

The gill enzyme, Na^+K^+ATPase, plays an important role in the maintenance of proper salt and water balance in anadromous fishes. This enzyme catalyzes the derivation of energy for active transport of salts for fish in sea water (Parry 1960, 1966; Maetz 1971). An increase in the production of Na^+K^+ATPase accompanies the parr-smolt transformation while the smolt is still in fresh water (Saunders and Henderson 1978). The changes that occur as the salmon parr transform into smolts apparently prepare the juvenile salmon for life in the sea. After the onset of smoltification, pronounced changes in behavior, such as the loss of rheotactic response and replacement of territorial behavior with schooling behavior, result in the initiation of the salmon's downstream migration to the sea (Kalleberg 1958; Hoar 1976).

This metamorphosis appears to be precisely timed to prepare the fish for seaward migration and for adaption to life in the sea (Ruggles 1980). It occurs only in spring (Saunders and Henderson 1970; Komourdjian et al. 1976) and is a result of increasing day length and water temperature, and possibly other environmental factors (Hoar 1976; Youngson et al. 1983). If migration to the sea does not occur, the smolt again become parr and lose their ability to survive in salt water (Lundquist and Fridberg 1982); however, the smolt features reappear the following spring (Evropeitseva 1957; Kock 1968; Hoar 1976). Thus, the salmon must reach the sea through a time window that may remain open for only a relatively short period, and which appears to be a critical factor in determining subsequent survival of both hatchery and wild smolts (Durkin et al. 1970; Ebel et al. 1973; Raymond et al. 1975).

The key environmental stimulus triggering seaward migration of smolts is probably a period of rising water temperature; migration peaks at water temperatures of 10°C or higher (White 1939; Elson 1962; Mills 1964; Jessop 1975; Bagliniere 1976; Fried 1977; Solomon 1978). Melnikova (1970) observed that smolting and migration were earlier when the average water temperatures were higher than normal in preceding months. In the Thurso River, Scotland, Allen (1944) reported that spring emigration of smolts was triggered by freshets and a rise in water temperature from 4.5 to 5.5°C. In tracking experiments in the Penobscot River, Maine (Fried et al. 1978), and the Merrimack River, New Hampshire (Knight et al. 1979), investigators found that emigration began after water temperatures reached 5°C. Full migratory behavior occurred at temperatures exceeding 9-10°C, and peak seaward movement was closely associated with increased water flows. Huntsman (1945) also stated that freshets induce emigration of smolts in the Margave River, Nova Scotia.

Some authors (Osterdahl 1969; Mason 1975) have suggested that several other environmental stimuli may be important in triggering smolt migration: photo-periodism (Hoar 1976); light intensity (Osterdahl 1969); light transition stimulus (Richardson and McCleave 1974), which results in a failure of the rheotactic response (Huntsman 1952); or alteration in locomotor activity patterns (Richardson and McCleave 1974) due to a diel rhythm in oxygen consumption in smolts, peaking at midday and midnight (Power 1959). The increased demand for oxygen at these times would reduce the scope of activity accordingly, and hence the ability to maintain position in the stream.

The spring smolt emigration occurs over a period of 30 days (Ruggles 1980). Peak daily movements are variable in different river systems. Bakshtansky et al. (1977) concluded that the dynamics of emigration in the Poye and Sayana rivers were influenced strongly by their defensive responses to the predatory activity patterns of northern pike (*Esox lucius*). The pike had difficulty in capturing smolts in sunny weather, when light ripples on the shallow water surface coincided with periods of smolt migration (Bakshtanksy et al. 1977). Thorpe and Morgan (1978) found similar diurnal emigrations for rivers in high latitudes; however, their review concluded that seaward migration is generally nocturnal, being most intense about 2 h after sunset. Fried et al. (1978) concluded that peak movements were at dawn and dusk. Ruggles (1980) suggested that the timing of smolt migrations is influenced by natural selection and that both day and nighttime emigrations occur (Bakshtansky et al. 1979).

Laboratory and field observations of smolts have indicated that during the freshwater phase of seaward migration, the following may occur: passive downstream movement (Jones 1959; Fried et al. 1978); active

downstream movement (White and Huntsman 1938; Kalleberg 1958; Stasko et al. 1973); and holding position against the current (White and Huntsman 1938; Stasko et al. 1973). Danie et al. (1984) suggested that smolts orient downstream in riffles and low-velocity stream sections but upstream in swift currents. In general, migrating smolts passively drift in the main current of the stream away from the shoreline—that is, in areas of maximum flow (Ruggles 1980; Danie et al. 1984). Bakshtansky et al. (1979) observed that hatchery-produced smolts tended to migrate closer to the bottom than did wild smolts, and that the hatchery fish preferred areas of slower current. These movement patterns can continue until the smolts encounter water of at least 20°/oo salinity in estuarine waters (Fried 1977).

Migration rates for smolts are highly variable. Knight et al. (1979), using radio-telemetry techniques, found smolts to migrate at a rate of 7.2 to 28 km/day in the Merrimack River, New Hampshire; Semple (1971) reported that hatchery smolts migrated at an average rate of 17 km/day when released in the St. John River system, New Brunswick; Allen (1944) observed rates of 0.2 to 6.0 km/day for smolts in an English river; at East River Sheet Harbour, Nova Scotia, smolts moved downstream at 1.9 to 2.9 km/day (Semple 1979); and Mills (1964) reported average rates of 0.4 to 2.04 km/day for different groups of fish in different years in a small Scottish river. Slower migration rates were observed in slower flowing reaches of the river. Solomon (1978) found the rate of downstream smolt movement to be slower than the average flow rate of the river. In general, the rate of migration appears to be slower in small than in large streams (Ruggles 1980). Fried (1977), using ultrasonic telemetry transmitters, measured the rate of smolt migration through the Penobscot River estuary in Maine. He recorded travel times of 29.4 to 44.5 h (mean 37.1 h) from the head of tide to 35 km seaward (about 22 km/day). The entire 57-km journey from fresh water to seawater took less than 48 h (Fried et al. 1978).

Smolt movement in estuaries depends on the characteristics of the estuary (Clarke 1981). Smolts may travel in the direction of water flow during ebb and flood tides (Fried et al. 1978), or swim seaward during flood tides (Danie et al. 1984). Stock-specified sun compass orientation and tidal transport are responsible for smolt movement out of the estuary. Movement is parallel to current direction in deep water whereas sun compass orientation dominates in shallow water (Clarke 1981). McInerney (1964) reported that salmon show a temporal progression of changes in salinity preference that would aid the smolt's navigation of unfamiliar, spacious estuaries through the existing salinity gradients.

Impoundments can delay or restrict smolt downstream migration. Migration is delayed in hatchery and wild fish released above or in lakes. Hansen et al. (1984) suggested that lack of current velocity in the surface lake flow prevented smolts relying on passive displacement to move quickly to the lake outlet. Delay in lakes or impoundments can lead to sexual maturity in landlocked salmon and precocious parr (Birt and Green 1986), desmoltification in large autumn parr (Evropeitseva 1957; Saunders 1969), and "lost" parr (Hansen et al. 1984). Indirectly, the delay in migration may increase migratory mortality due to increased susceptibility to lake predators or impaired osmotic capacities of smolts (Saunders 1960). Kennedy and Strange (1982) considered intraspecific competition for space between salmon parr and fry to be a critical regulating factor affecting fry survival.

In a review of young salmonids of various lengths, Allen (1969) concluded that there was a positive linear relation between average area required by individual fish and fish length, when both were plotted on logarithmic scales.

Growth and Feeding

Growth

Growth of Atlantic salmon is influenced by both genetic and environmental factors. Embryo size and weight are determined by egg size, which is influenced by the size and physiological condition of the female (Kazakov 1981). Egg diameter increases with the age of the fish and the length of time the fish feed in the ocean (Danie et al. 1984). Egg size also varies within individual females, depending on the position of the eggs in the

ovary (Kazakov 1981). In hatchery fish, the development of bimodality in the length frequency distribution of sibling salmon is a function of egg size and nutrition.

Freshwater growth of fry and parr is relatively slow. Salmon fry obtain maximum growth in July and grow little if any after September (Randall and Paim 1982; Lund and Heggberget 1985). This slow growth is reflected in weight and length relations. Hoar (1939) found that newly emerged fry are relatively slim (mean condition factor = 0.89), but quickly thicken during the first 4 weeks of stream life (mean condition factor = 1.00). The coefficient of condition remains constant (or declines) throughout the year. He also concluded parr condition factor rose progressively from 1.00 to 1.17 with increasing size. In New England streams, it may take 2 to 3 years to reach a 125-150 mm fork length (Knight and Greenwood 1982; Danie et al. 1984); in Ungave Bay, it may take 4 to 8 years for a salmon to reach 180 mm (Power 1969; Schaffer and Elson 1975). Danie et al. (1984) stated that 1+ parr may reach 150-175 mm and that 2+ parr of 210 mm can be seen in productive Maine streams

Normal growth of parr occurs at water temperatures of 15-19°C (Decola 1970), or possibly several degrees higher (A. E. Knight, U.S. Fish and Wildlife Service, Laconia, NH, unpublished data). Optimal temperature for growth is at 16.6°C (Siginevich 1967). Faster growing parr and younger smolts are associated with waters having diurnal peaks of 22 to 25°C (Elson 1975). Egglishaw (1969) concluded that growth ceases at 5 to 7°C. However, in a review of Atlantic salmon growth at extreme climates, Jensen and Johnsen (1986) found that the lowest temperature for growth varies with nursery stream temperature conditions. Thus, for the Matamek River in Quebec (Gibson 1978) and the Little Sevogle River, New Brunswick (Rimmer et al. 1983), the apparent lowest temperature for growth is 9-10°C, whereas Power (1981) stated that 5.6 to 6°C was the lowest temperature of growth in the Ugava Bay region. The "normal" lower limit for growth appears to be about 7°C (Symons 1979; Jensen and Johnsen 1986).

There is evidence that photoperiod influences growth (Lundqvist 1980). Sexually immature male and female Atlantic salmon grew faster when exposed to a light:dark ratio of 20:4 than when exposed to a natural light:dark ratio of 6:18. However, sexually maturing male parr grew slower in the 20:4 photoperiod region but ripened earlier when exposed to the natural photoperiod. There is much more work to be done on this aspect of salmon growth.

The time at which Atlantic salmon become smolts is determined by size, not age (Refstie et al. 1977). The parr-smolt transformation generally occurs during the season after the salmon reaches a length of 10 cm (Elson 1957). However, recent evidence suggests that fish only 8 cm long may migrate as smolts when there has been a longer growing season, as in some rivers in Connecticut (R. D. Orgiari, Conn. Dep. Environ. Prot., Harwinton, CT, unpublished data). This transformation is accompanied by a decrease in condition factor. Hoar (1939) found a 4% decrease in the coefficient of condition (K) as the range of values dropped from 0.99-1.30 (average 1.16) to 0.74-0.90 (average 0.86). He concluded that the decrease in K (loss of weight) was due to a decrease in the amount of fat bodies and a corresponding increase in length. Normal smolt lengths are 13 to 18 cm (Jensen and Johnsen 1986). Downstream salmon migrants are actively feeding and growing during this stage in the life history (Ruggles 1980). Several authors have reported that both size and age composition of salmon smolts decrease during the migrating season (Allen 1944; Osterdahl 1969; Bagliniere 1976). Smolts forced to remain in the river do not increase their weight or grow as well as salmon that reach the sea (Hoar 1939). This is in contrast to landlocked salmon, which can grow at rates similar to those of sea-run grilse (Cuerrier 1983).

In extreme conditions, Jensen and Johnsen (1986) stated that Atlantic salmon populations have adopted two different strategies. When the sea temperature limits salmon distribution (rivers in northern Canada and USSR), populations are characterized by a large resident river population, higher percentage of precocious male parr, larger smolts, and smolt runs consisting primarily of females. Alternatively, when river temperature is limiting, salmon populations produce smaller smolts and a sex ratio closer to 1:1.

Population density also affects growth and survival (Danie et al. 1984). Lund and Heggberget (1985) concluded that growth rate is

inversely proportional to salmon population density when food is limiting, and this is evident for all age groups. Growth of stocked fry was significantly lower in the presence of older resident salmonids than for fry planted in a section of an upland river cleared of competitors (Kennedy and Strange 1986). Dickson and MacCrimmon (1982), who conducted stream tank experiments with underyearling wild salmon, wild brook trout, and hatchery-reared Atlantic salmon, found that daily increases in fork length were greater when salmon of either type were with brook trout than when they were with other salmon. For mixed populations of wild and hatchery-reared salmon, however, both types showed a lower daily gain in length than when alone. For two New Brunswick streams, Randall (1982) stated that salmon fry growth was greatest at sites where salmon densities were lowest. When brook trout were removed from an area of a Quebec boreal river, growth of 2+ salmon parr increased but that of 1+ parr did not (Gibson and Dickson 1984). Growth of juvenile salmon is little affected by the presence or absence of coarse fish such as shiners, dace, and suckers (Symons 1979), but is typically enhanced when hatchery or wild salmon fry are stocked in fishless areas of nursery streams (Bulleid 1973; Gibson and Dickson 1984).

The growth of Atlantic salmon is reflected in scales. Fry begin to grow scales when they are 24 (Ken 1961) to 30 mm (Danie et al. 1984) long—first along the lateral line at the central and posterior parts of the body. As in growth rings on a tree, broad bands form on the scale during rapid growth (spring and summer) and narrow bands during slow growth (autumn and winter). These bands are used to determine the age and growth of individuals. From scales taken from just behind the dorsal fin and between the lateral line and dorsal margin, Ken (1961) derived the scale-to-length equation:

$$L = 2.40 + 12.90\,s + 1.22\,s^2$$

where L is fork length in centimeters and s is anterior scale radius in millimeters for Miramichi fisheries.

Efforts have been made to derive equations that estimate biomass and production of Atlantic salmon streams. Gibson and Dickson (1984) concluded that the changes in size of salmon were related to changes in population density in an area of a Quebec boreal river according to the following linear equations:

$$1+\text{ parr } Y = 0.026 + 0.005X$$

$$2+\text{ parr } Y = 2.377 + 0.013X$$

where Y is biomass (kg/ha) and X is density (No/ha). Production (P) of juvenile salmon can be estimated from the mean biomass (B) for all year classes present in a "typical" Welsh stream (Gee et al. 1978) with the following formula:

$$P = 2.5\,B^{0.91}$$

Ranges for the exponent and coefficient were 0.73 to 1.24 and -1.91 to -3.05 respectively. The higher values appeared in spring and summer.

Growth rate equations also have been developed from empirical data. Andrews (1965), using 1951 data from the Ganger River system in Newfoundland, derived the following age-length relation for one of the best salmon-producing areas in Newfoundland:

$$Y = 20.2\,X + 48.4$$

where Y = fork length in mm and X = age in years. According to Egglishaw and Shackley (1977) the size of 0+ salmon in a Scottish river depended on the length of the growing season, which is determined by emergence time, degree days above 0°C, and population density (numbers/m^2). The relation of fork length (FL) to population density (N) and degree days (D) is given by the following equation:

$$FL = 17.152 - 2.800\,N + 0.0194D$$

No significant relation between length of 1+ salmon and their population density could be established.

The result of the interaction of these genetic and environmental factors is seen in the variety of growth rates geographically, as well as within the same stream (Symons 1979). Lund and Heggberget (1985) stated that within-stream differences in growth could be due to the environment outside the stream (agricultural activity), fish population structure (densities and species interactions), water quality (temperature and chemical properties), or different kinds (abundance) of food. They concluded that the growth of underyearling salmon in a small Norwegian

stream was influenced most by stream temperature and growth of older fish was influenced most by population density and food.

Growth Rate and Weight-Length Relation

Riddell and Leggett (1981) described the between-population difference in growth rate between two rivers in New Brunswick, using the following formula:

$$\text{Log}_{10}\ \text{LT cm} = 0.00034\ \text{d} - 0.095\ \text{flow} + 0.0504\ \text{P.} - 0.003\ \text{T°C} + 0.045\ \text{diet} + 0.7982$$

where LT is fork length (cm), d is age (years), and P. is a dummy variable. Flow rate was the most significant factor affecting growth rate and was negatively correlated with length. The weight-length relation was less responsive to environmental variation (temperature was the only sensitive variable).

$$\text{Log}_{10}\ \text{WT} = 2.9904\ \log_{10}\ \text{LT} + 0.0044\ \text{T°C} - 2.0034$$

where WT is weight (grams). They also found that daily growth increments consistently decrease with age. Riddell and Leggett (1981) concluded that the highest growth rates occur in temperate waters—0.39 mm/day; however, in northern Labrador, where the growing season is very short, growth rates of 0.9 mm/day have been reported.

Feeding

Juvenile Atlantic salmon remain relatively stationary in the stream and feed on invertebrate drift. The act of feeding includes visual location of prey and subsequent capture and ingestion. Typically, the food organisms available to stream-dwelling fish are divided into the following categories: substrate (benthic), surface (terrestrial), and suspended (benthic and terrestrial). Wankowski and Thorpe (1979) in SCUBA observations of salmon in Scotland, described salmon feeding behavior that consisted of direct capture, head-jerk, and surface (water and substrate) feeding. Their diet consists chiefly of immature forms of mayflies (Emphemeroptera), stoneflies (Plecoptera), chironomids (Diptera), caddisflies (Trichoptera), blackflies (Diptera), beetles (Coleoptera), and dragonflies (Odonata); aquatic annelids; crustaceans; and mollusks. Food availability, not food abundance, is the primary factor controlling what is or is not ingested (Williams 1981). In addition to proximal and temporal availability, the shape, size, color, and mobility of food items determine whether or not it is ingested (Kislalioglu and Gibson 1976; Rimmer and Power 1978). Sosiak et al. (1979) stated that there is a direct relation between food size and salmon size.

If Atlantic salmon alevins ever feed on interstitial stream invertebrates, it seldom occurs (Williams 1981). The first diets of fry include emerging chironomids (and caddisflies) from the surface, and blackfly larvae and preemergent stoneflies and beetle larvae from the bottom. Allen (1940*a*), working on streams in the north of England and Scotland, found that alevins most frequently selected chironomid and mayfly larvae, although stonefly nymphs dominated the benthos. In contrast, fish 2.5-3.0 cm long in the River Suldolslagen, Norway, also ate stonefly larvae in June (Lillehammer 1973). Planktonic crustaceans were the most common food items in August and September, when they were the most numerous. In another Norwegian study, 62-67% of the summer diet of 0+ parr consisted of Ephemeroptera (mayfly) larvae (Lund and Heggberget 1985).

In older parr, food selection is size-dependent. Lund and Heggberget (1985) found that mayfly larvae and both larval and adult water beetles (Coleoptera) composed the major food items for yearling parr. The diet of 2+ parr was primarily of terrestrial origin (54%); water beetles were less important food items. In New Brunswick, smaller wild yearlings consumed more true flies (Diptera) whereas larger hatchery yearlings ate a greater proportion of dragonfly nymphs (Sosiak et al. 1979). These investigators also stated that wild parr generally had a greater degree of fullness, ingested larger amounts and types of organisms, and fed more often from the surface and bottom than did hatchery parr. Hatchery parr acted as a different species, in that they inhabited a different microhabitat and had less diverse prey "searching images" than did wild parr.

Riddell and Leggett (1981) found that overwintering parr feed even when water

temperatures are 0-1°C. Parr stomachs held stoneflies (Nemouridae); however, assimilation efficiencies have not been measured for juvenile salmon in this temperature regime.

Smolts actively feed and grow during downstream migration (Ruggles 1980). The major food items appear to be crustaceans and winged insects. Specific studies for feeding of Atlantic salmon smolts are lacking.

Sources of Mortality

Temperature

Water temperature is a key factor influencing the geographical range of Atlantic salmon (MacCrimmon and Gots 1979). The fish require relatively low temperatures throughout life (Danie et al. 1984). The optimum temperature of egg incubation is about 6°C (Peterson et al. 1977). Temperatures of 7°C are tolerated, but temperatures above 12°C increase egg mortality (Danie et al. 1984). Indirect increases of egg mortality, due to a higher incidence of fungal infection, may occur at temperatures of 8 to 12°C (Garside 1973). Newly hatched alevins select the lowest temperatures available (Danie et al. 1984).

Growth of juvenile salmon is optimal at 16.6°C (Siginevich 1967); normal growth and production occur at temperatures of 15-19°C (Decola 1970)—though the upper limit may be higher (A. E. Knight, U.S. Fish and Wildlife Service, Laconia, NH, unpublished data)—and the fish may tolerate temperatures up to 27°C before they seek cooler water. Salmon mortality at high temperatures is a function of the temperature to which the parr were acclimated. Decola (1970) stated that, at an acclimation temperature of 13°C, 50% mortality of parr occurs within 6 h at 26.7°C. Alabaster and Downing (1967) found that juveniles acclimated to 16.7°C had an incipient lethal temperature of 25.2°C, and Fry (1947) concluded that the incipient lethal temperature limit was 28.5°C when fish were acclimated to 25°C. Huntsman (1942) found that salmon could withstand temperatures of 32°C for brief periods. The ultimate upper lethal temperature for juveniles appears to be about 32°C (Garside 1973). MacCrimmon (1954) stated that planted salmon fry were eliminated from sections of streams characterized by lethal temperatures.

Dissolved Oxygen

Dissolved oxygen concentrations should be at or near saturation for optimum growth and development of Atlantic salmon (Doudoroff and Shumway 1970); good development requires at least 6 mg/l (Elson 1975), and higher values up to 10 mg/l are ideal. Oxygen consumption differs among fish of different sex, age, and weight (Danie et al. 1984). Embryos require oxygen levels of 6-7 mg/l (Decola 1970) whereas alevins may be even more sensitive to oxygen concentrations less than 6 mg/l (Lacroix 1985). Lethal concentrations are about 1.1 mg/l for age 0+ parr and 2.3 mg/l for age 1+ parr tested at the same water temperatures. The respiration of adult Atlantic salmon is depressed at oxygen concentrations below 4.5-5.0 mg/l (Kazakov and Khalyapina 1981). Streams with dissolved oxygen concentrations below 5 mg/l are not usually inhabited by salmon (Danie et al. 1984).

pH

Fluctuation in pH of water is an important limiting factor for the freshwater environment of the Atlantic salmon (Peterson et al. 1980). Tolerance to low pH varies among different life stages and ages (Danie et al. 1984). High mortality of eggs and alevins has been attributed to low pH, which is characteristic of snowmelt and heavy fall rains (Power 1981; Haines and Akielaszek 1984). Normal egg development occurs at pH 6.6-6.8 (Danie et al. 1984); hatching is delayed or prevented at pH 4.0-5.5. Lacroix (1985) found that hatching success for acidic Atlantic Canadian streams was directly proportional to pH values between 4.5 and 5.0. A pH of 5.0 or lower affects eggs by degradation of the enzymes responsible for movement of the embryo within the egg, without which hatching is impossible (Haines 1981). The value at which 50% of the eggs survive (LD_{50}) appeared to be pH 4.7 in field studies but is 3.9 to about 4.5 in laboratory studies (Lacroix et al. 1985). The

lower lethal pH for embryos is about 3.5 during early cleavage and about 3.1 just before hatching (Danie et al. 1984). Little work has been done on susceptibility of preemergent fry to low pH; although Lacroix (1985) suggested that preemergent alevins are more sensitive than eggs to low pH.

Death at low pH for free-swimming stages of Atlantic salmon is attributed to dysfunction of ion regulation (hydrogen ion toxicity), asphyxiation, and elevation of metal concentrations (aluminum toxicity). Exposure to low pH causes edema between outer gill lamellar cells and gill tissue, disrupting respiration and excretion (Danie et al. 1984). Indirect pH-related mortality of juveniles may occur at low pH as the abundance and variety of prey food decreases (Power 1981). Alevins subjected to low pH at 7 days and parr at 28 days after hatching had a lower lethal limit of about pH 4.0 (Daye and Garside 1977, 1980). Lacroix et al. (1985) found that the most pH-sensitive period for salmon occurred during the transition of alevins to exogenous feeding (after emergence) where the lethal pH was about 4.5. In Norway, salmon have disappeared from streams of pH less than 5.5 through recruitment failure (Lacroix et al. 1985). Watt et al. (1983) reported that, in Nova Scotia streams, juveniles were most numerous at mean annual pH above 5.4, much reduced between 4.7 and 5.0, and absent below 4.7

Depth and Velocity

The availability of appropriate stream habitat is important in freshwater life history stages of Atlantic salmon. The optimum stream habitat for spawning is a gravel tail of a pool with a hydraulic head produced by a riffle or a steeper gradient below the pool (Danie et al. 1984). Salmon fry less than 7 cm long (underyearlings) are found in depths of 9 to 39 cm (Francis 1980; Knight et al. 1981) and in water velocities of 1.8 to 32 cm/s (mean 14 cm/s) (Knight et al. 1981). Parr, age 1+ and older salmon (7 cm long), seem to prefer water 10-40 cm deep (Danie et al. 1984) and water velocities of 14-32 cm/s (mean 20 cm/s) (Knight et al. 1981). Larger fish appear to prefer deeper waters and faster velocities (Kennedy and Strange 1982). Atlantic salmon prefer stream gradients of 2 to 12 m/km (Elson 1975).

The proportion of eggs that result in the production of fry is influenced by winter water levels (Chadwick 1982). During the transition of alevins to free-swimming fry, salmonids are highly vulnerable to sudden increases in water velocity that result in downstream displacement (Ottaway and Clarke 1981), especially in the presence of older and larger parr. Older parr defend territories and attack other parr of similar size entering the defended zone (Wankowski and Thorpe 1979). This competition for territory may limit the number of fish in the stream population (Danie et al. 1984). The rapid change in water levels as a result of hydroelectrical production can lead to stranding and death of underyearling salmon (Hvidsten 1985). During the downstream migration of Atlantic salmon smolts, the occurrence of lakes and impoundments can indirectly cause mortality by delaying the smolt progress and increasing the time during which fish are exposed to predation, pollution, and disease (Ruggles 1980).

Parasitism and Disease

The freshwater life stages of Atlantic salmon are subject to a wide variety of parasites and disease (Jones 1959; Hoffman 1967). Generally, salmon are affected by fungi, protozoans, flukes (Trematoda), tapeworms (Cestoda), roundworms (Nematoda), leeches (Annelida), crustaceans, and thorny-headed worms (Acanthocephala; Hoffman 1967; Sandeman and Pippy 1967). They can be found in all life stages of salmon, determined by the mode of infection and pathology; however, some parasites are found only in certain organs or tissues (Hoffman 1967). Under hatchery conditions, parasitism can range from low but detectable infections causing no overt problems to chronic, annually occurring diseases causing heavy mortalities.

Although surveys have determined the incident of parasitic disease organisms in the wild (Sandeman and Pippy 1967; McCarthy 1974; Hare and Burt 1975; Heggberget and Johnsen 1982; Aho and Kennedy 1984), there has been no estimation of mortality in the wild. However, some generalities have been made. Parasites of Atlantic salmon can be host specific (salmon are a necessary vector in

the organism's life cycle) or infections may be incidental. For some parasites, infection is possible only when the salmon is under stress: a "weakness parasite." In the wild, salmon can be stressed when subjected to high water temperatures, reduced water flows, and pollution (Heggberget and Johnsen 1982). In salmon populations where the incidence of infection increases with age of juveniles, that disease might directly limit the size of the population (Aho and Kennedy 1984). A more probable effect of the parasite infection observed in the wild is to reduce the fitness of the fish so that they are more vulnerable to other sources of mortality such as saprolegniasis, caused by the fungus *Saprolegnia* (McCarthy 1974; Heggberget and Johnsen 1982), or furunculosis (A. E. Knight, U.S. Fish and Wildlife Service, Laconia, NH, personal communication)—the only documented sources of mortality by disease in the wild for New England.

Predation

Juvenile Atlantic salmon are eaten by a variety of predators during their development in freshwater (Leim and Scott 1966; Harris 1973; Scott and Crossman 1973). Natural mortality in streams is generally a function of spatial or nutritional factors (Larson 1985).

Underyearling Atlantic salmon are vulnerable to predation by a number of predaceous fishes: the eels *Anguilla anguilla* and *A. rostrata* (Godfrey 1957; Elson 1967; Gray 1969), northern pike and the chain pickerel *Esox niger* (Barr 1962), brook trout (Symons 1974), brown trout *Salmo trutta*, and older Atlantic salmon. Bird predators (with the possible exception of the belted kingfisher) do not appear to affect the fry population (Huntsman 1941). Leeches sometimes damage a significant portion of the fry population (Harris 1973).

The larger salmon parr are still susceptible to fish predation (Jacobson and Jarvi 1976), although bird predation may become more important (Huntsman 1941). Mergansers, herons, and gulls have been reported to eat salmon parr (White 1939).

Predator control can lead to dramatic increases in smolt production (White 1939). Elson (1962) concluded that smolt production increased fivefold when fish-eating birds were controlled. A sixfold increase in fry to smolt survival was documented for a small stream in Ireland when trout and eel populations were reduced (Rogers 1968). But Huntsman (1941) found only a 120% increase in smolts when bird control was effected. He cautioned that predator control may lead to increased presence of competitors (older salmon) and predators (salmon and trout), which would act unfavorably on younger fish and leave the long-term effect of predator control in doubt.

During the downstream migration of smolts and large parr, predation leads to absolute mortality (density-independent, depensatory) and apparently can cause heavy fluctuations in Atlantic salmon recruitment (Larsson 1985). In fact, the observed behavior relating to seasonal and diel timing of the smolt migration is probably partly a response to predatory pressure (Ruggles 1980). Major smolt predators include northern pike and brown trout (Mills 1964); burbot (*Lota lota*) and eels (Larsson 1985); chain pickerel (Barr 1962); gulls and mergansers (Lindroth 1955; Mills 1964); the double-crested cormorant *Phalacrocorax auritus*, the mink *Mustela vison*, and the otter *Lutra lutra* (Ruggles 1980); and in Swedish estuaries, the pollock *Gadus pallachius* (Larsson 1985).

Mills (1964) estimated that 10% of the total smolt migration from a Scottish salmon river was consumed by northern pike. He also reported an instance where two mergansers shot on the river contained 30 to 32 tags from hatchery-reared smolts released only 3 days before. In Maine, as many as 55 smolt tags were recovered from individual cormorant stomachs, accumulated in 4 days or less (Cormorant Study Committee 1982). During May 1985, of 149 cormorant collected on the Machias and Penobscot rivers, Maine, all but 2 contained 1 to 8 smolts (N. Dubé, Maine Atlantic Sea Run Salmon Comm., Bangor, ME, personal communication). In three Swedish rivers, Larsson (1985) reported that 35 to 70% of the smolt run was lost through predation. Survival was better when the downstream migration distance was shorter. If the smolt migration is delayed as a result of impoundments, smolt mortality may increase due to the longer exposure to predators (Ruggles 1980). Observed differences between wild and hatchery fish in behavior, and the physiological condition of wild and hatchery

smolts, were believed to account for differences in smolt survival in Russia (Bakshtansky et al. 1979). In Maine, the presence or absence of buffer fish (an alternative food source for cormorants) determines the success of hatchery smolt plantings in evading bird predation (A.E. Knight, U.S. Fish and Wildlife Service, Laconia, NH, personal communication). Smolt predation is believed to determine the effectiveness of salmon smolt plantings in many rivers (Larsson 1977, 1985).

Downstream Migration

Atlantic salmon smolts and, to some extent, large pre-smolt parr, represent a transition from one life-history stage to another. The downstream migration presents unique sources of mortality for these fish. Ruggles (1980), in a review of salmon downstream migration, concluded that any one or a combination of the following unnatural conditions can result in the extinction of exposed anadromous salmonoid populations: (a) passage over spillways, (b) passage through turbines, (c) passage through impoundments, (d) exposure to atmospheric gas supersaturation, (e) exposure to pollutants, and (f) vulnerability to angling.

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). When discharge is 0.4 m^3/s, this velocity is reached by smolts falling a vertical distance of 27 m (Sweeny and Rutherford 1981). However, Ruggles (1980) concluded that smolts may withstand a free fall of at least 90 m.

Salmonid survival rates for both Kaplan and Francis turbines range from zero to 100% (mean range, 50 to 95%), the highest survival occurring at the point of highest turbine efficiency (Bell et al. 1967). Turbine-induced injuries represent a discriminate stress to the exposed population, and survival is not usually reduced in fish that survive passage through turbines without physical injury (Ruggles 1980).

Artificial (and natural) impoundments may present a variety of problems to downstream migrating fish. The stratification and lack of current in lakes and reservoirs can delay or trap smolts (Foerster 1937; Saunders 1960; Raleigh and Ebel 1967). Delays in reservoirs prolong the exposure of smolts to predation (Ruggles 1980). Mills (1964) described a loss to fish 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). Trapped juveniles may be restricted to marginal habitats between zones of high temperature in the epilimnion and low oxygen in the hypolimnion of the impoundment, resulting in high mortalities due to stress and prolonged exposure to pollution and disease organisms (Ruggles 1980). The surviving smolts sometimes resume their seaward migration in the following spring (Munro 1965).

Fish maintained in water supersaturated with air reach equilibrium with the gases dissolved in water. These gases, especially nitrogen, tend to equilibrate to the atmosphere (Lindroth 1957), and cause gas-bubble disease in juvenile salmonids at about 110% air saturation (Harvey and Cooper 1962; Rucker 1972). In terms of inflicting mortality to downstream salmon migrants, air entrapment occurring below natural falls and hydroelectric dams with plunge basins is a significant feature (Ruggles 1980). Juvenile migrants subjected to 120% air saturation in the field suffer substantial mortality after 20 days exposure (Ruggles 1980). Supersaturated water may remain supersaturated because it tends to run in deeper regions of a river and is recharged at downstream water falls (MacDonald and Hyatt 1973). Injury caused by sublethal periods of exposure to supersaturation is reversible if the juvenile is returned to normally saturated water (Ruggles 1980).

These sources of mortality for downstream migrants can lead to reductions in the smolt run of 5 to 100% (Ruggles 1980). Each river should be investigated thoroughly to estimate the survival of migrating smolts.

Pollution

Pollution of rivers and estuaries is an increasing hazard to juvenile Atlantic salmon in their present geographical range. In North America, increasing industrialization and economic growth have

been accompanied by change of water quality in salmon habitats (Elson et al. 1973).

Forest spraying in Maine, New Brunswick, and Quebec to control spruce budworm (*Choristoneura fumiferana*) and in Newfoundland to control the hemlock looper (*Lambdina fiscellaria*) has resulted in various insecticides being used in salmon nursery habitat. Mortality of young salmon held in cages placed in streams sprayed with DDT was high soon after the spraying (Kerswill and Edwards 1967). In New Brunswick streams, underyearlings, small parr, and large parr were only 2-10%, 30%, and 50% as abundant, respectively, in areas sprayed with DDT as in areas never subjected to spraying (Elson 1967). There was a substantial reduction as far as 24 km downstream from the lower spray boundaries. Besides killing young fish, DDT forest sprays reduce the number of aquatic insects, the food of juveniles (Ide 1967; Keenleyside 1967). Other incipient effects on salmon include increased parr mortality in cold (5°C) water (Anderson 1971; Elson et al. 1973) and changes in behavior—especially avoidance and sheltering from predators (Elson 1974). Dimond et al. (1971) reported that DDT persisted in sprayed streams for at least 10 years.

Phosphamidon spraying resulted in no reduction in stream fish populations (Elson et al. 1973), and aquatic insects were not seriously affected (Grant 1967). Fenitrothion, an organophosphate insecticide replacement for DDT, is relatively non-persistent in the environment (Yule and Duffy 1971) and has comparatively low lethality to young salmon; the 24-h LD_{50} was 7.4 mg/l (Wildish et al. 1971), and the incipient lethal level was about 1 mg/l (Zitko et al. 1970). Fenitrothion can depress invertebrate populations, but there is little or no evidence of direct mortality of juvenile salmon. There is some evidence of sub-lethal effects of fenitrothion (Elson et al. 1973): evacuation of sprayed streams by parr increased their vulnerability to capture by large brook trout, and a downward shift in selected temperature. Sub-lethal exposure of juveniles to other organophosphates has led to spinal and vertebral abnormalities and hemorrhaging (Wells and Cowan 1982). Hatfield and Anderson (1972) reported an increased vulnerability of juvenile salmon to predation after their exposure to insecticides.

Industrial effluent has a varied effect on juvenile Atlantic salmon. Some effluents from wood treatment plants and sawmills contain a complex mixture of creosote, pentachlorophenol, and other fungicides and polynuclear aromatic hydrocarbons (Zitko et al. 1969; Elson et al. 1972). The effluent is toxic to salmon, the lethal threshold being 0.5-3 mg/l Juvenile salmon can detect and avoid such mixtures at low concentrations (Zitko et al. 1969), thus not interfering with salmon emigration (Elson et al. 1972). However, some phenols do not produce consistent avoidance behavior, even at lethal concentrations (Sprague and Drury 1969).

Pulp and paper mills contribute pollutants of two categories (Elson et al. 1973): chemical wastes toxic to aquatic life, and those having little direct toxic effect but creating heavy oxygen demand. Toxic wastes—including detergents, chlorine and kraft mill effluents—damage chemoreceptors (Sprague and Drury 1969) and olfactory receptors (Sutterlin and Sutterlin 1971), thus precluding avoidance of attraction during migration. Chlorine elicited avoidance at 0.01 mg/l but not at higher, lethal concentrations of 0.1 mg/l or more. Organic material with high oxygen demand can deplete oxygen in salmon streams, especially in those with dams (Elson et al. 1973). At a swimming speed of 55 cm/s, smolts stopped swimming when oxygen concentrations dropped to 4.5 mg/l, or 50% air saturation (Elson et al. 1973).

Heavy (base) metal mining can produce effluents toxic to juvenile salmon. In New Brunswick and Newfoundland, extensive mine development for the extraction of copper, zinc, and associated heavy metals has led to significant impacts on salmon populations (Elson et al. 1973). Sprague et al. (1965) found lethal thresholds of about 20 mg/l for salmon parr to 48 mg/l for copper and 600 mg/l water hardness (as calcium carbonate). In combination, the effect of the two heavy base metal ions was additive. Concentrated humic compounds can decrease the acute toxicity of cupric ions. Carson and Carson (1972) found incipient lethal levels of copper to be 27 mg/l with no humic acid present and 170 mg/l with 10 mg/l humic acid. The toxicity of zinc was not similarly affected. Sublethal levels of copper-zinc pollution, in association with high water temperature, can reduce aquatic insect numbers (Sprague et al. 1965) and indirectly

increase the vulnerability of juvenile salmon to epidemic attack by an indigenous (and ubiquitous) pathogen—the bacterium *Aeromonas liquifaciens* (Pippy and Hare 1969). Levels or mercury (present in the form of methyl mercury) in juvenile Atlantic salmon are only about 0.1 mg/l (Elson et al. 1973) and do not endanger the species. Ray (1978) found that parr accumulate lead (as methylated lead) in spine, liver, and kidney tissue as they grow older. This accumulation can lead to black tails, spinal curvature, and neurological damage, which results in reduced growth at sublethal lead levels of 0.03 mg/l.

As a result of industrial processes, many chlorinated hydrocarbons are present in the environment. One of the most studied, polychlorinated biphenyl (PCB), can cause mortalities in salmon eggs at 0.6-1.9 mg/g wet weight (Anderson and Everhart 1966).

In spite of numerous papers on acute and chronic toxicity of chlorinated hydrocarbon pesticides to fish, there is still much to be done to establish the relation that is necessary for toxicological and ecological interpretation of the biological effects of pesticides and for the assessment of their impacts at observed environmental levels (Elson et al. 1973).

Most fish mortality arising from the use of agricultural chemicals is attributed to accidental spillage (Rudd 1964; Elson et al. 1973). Saunders (1969) found severe mortalities among juvenile Atlantic salmon of all ages after accidental spillage of a spray containing the fungicide nabam (disodium ethylene bidithiocarbonate) and the chlorinated hydrocarbon insecticide endrin. Surviving salmon descended unseasonably from the stream in summer and showed other abnormal behavior. Agricultural chemicals also reach streams through runoff (Smith 1959). These substances—pesticides, silt (Saunders and Smith 1965), herbicides (Elson et al. 1972), and highway de-icing salts—can, either singly or in combination, reduce fish production (Elson et al. 1973). MacCrimmon (1954) concluded that turbidity did not affect juvenile salmon survival. However, heavy silt loads sometimes prevent successful egg hatching and fry emergence (Mills 1973). Herbicides appear to be much less toxic than many insecticides, though sublethal levels of herbicides can cause vertebral dysplasia, behavioral abnormalities, and increased susceptibility to fungal attack and mortality (Wells and Cowan 1982). Highway de-icing salts sometimes contain additives such as sodium ferrocyanide, which releases cyanide during photodecomposition (Hanes et al. 1970). As in industrial chemical pollution, considerable works needs to be done to understand the biological and ecological influences of these agricultural chemicals.

Density, Production, and Survival

Population densities of juvenile Atlantic salmon of all ages in a stream depend on the carrying (holding) capacity of the stream for each age class. From the preceding discussion, carrying capacity of a river system is influenced by climatic conditions, type and abundance of food available, densities of competing fish species, and the amount and suitability of nursery habitat (water depth and flow, substrate, and water quality). Symons (1979) asserted that the carrying capacity of a river can be estimated from three sets of data: survival rates from egg to smolt; growth rates to smolt stage (smolt ages); and space requirements of young salmon at all stages between fry and smolt. There is a range of survival rates through the life stages (eggs, fry, parr, and smolt) of Atlantic salmon within which any naturally maintained population is likely to remain.

Estimates of survival from egg to emergent fry range from 91% (Shearer 1961) to 5% (Danie et al. 1984). In Maine, typical survival from natural redds appears to be 15-35% (A. E. Knight, U.S. Fish and Wildlife Service, Laconia, NH, personal communication). Egg-to-emergent fry survivals may be negatively correlated with egg deposition densities (Symons 1979), and influenced by water quality (especially silt load) and stream-bed movement (Kennedy 1984). In Newfoundland streams, egg-to-fry survival was influenced by winter temperatures and change in water levels, described by Chadwick (1982) in the equation: N fry/N eggs = 68.07 + 1.89 X - 0.005Y, where X = the lowest mean monthly temperature (°C) and Y = the difference between November mean discharge and the lowest mean monthly discharge in winter. By late summer, age 0+ parr densities of $<50/100m^2$ to $370/100m^2$ are typical (Elson 1975; Francis 1980; Danie et al. 1984). The

higher densities of young salmon are found in streams with few competitors, including older parr (Symons and Heland 1978; Kennedy and Strange 1982).

Symons (1978) estimated annual juvenile Atlantic salmon survival rates of 28%, 41%, 44% and 57% for low, medium, high, and older parr (1+ or older), respectively. The major limiting factors during these life history stages are competition for territory (Allen 1969), especially if food is limiting, and predation (MacCrimmon 1954). In New Brunswick streams, parr abundance is usually <15/100 m^2 but may be as high as 62/100 m^2 in a few streams (Francis 1980). Power (1973) estimated the number of presmolt salmon to be from 15 to 101/100 m^2 in Finnish rivers.

Symons (1979) also estimated that the juvenile to smolt survival ranged from 35% to 55% for 1+ smolts and 65% for older smolts. Juvenile to smolt survival may be primarily a function of predation. Therefore, egg-to-smolt survival can range from less than 1% (4+ or older smolts at low juvenile survival rates) to 11% (1+ smolts at high juvenile survival rates). Harris (1973) found a similar range in percent survival to smolts (0.25-12.38) in a review of studies from various European and North American rivers. He also determined that lake-reared smolts could be produced at even higher survival rates (maximum 35% for 3+ smolts, but typically between 5% and 15% for smolts of all ages). In an ideal salmon stream, average annual smolt production should not exceed 6 smolts/100 m^2 (Elson 1975). However, Symons (1979) suggested that the average smolt production can reach 10.2/100 m^2 in productive streams. Though these figures are generally based on natural populations, it should be noted that many smolt runs in restoration rivers in the United States must negotiate hydroelectric dams (with and without downstream passage facilities), thus often adding significant additional mortality during the smolt migration period.

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