

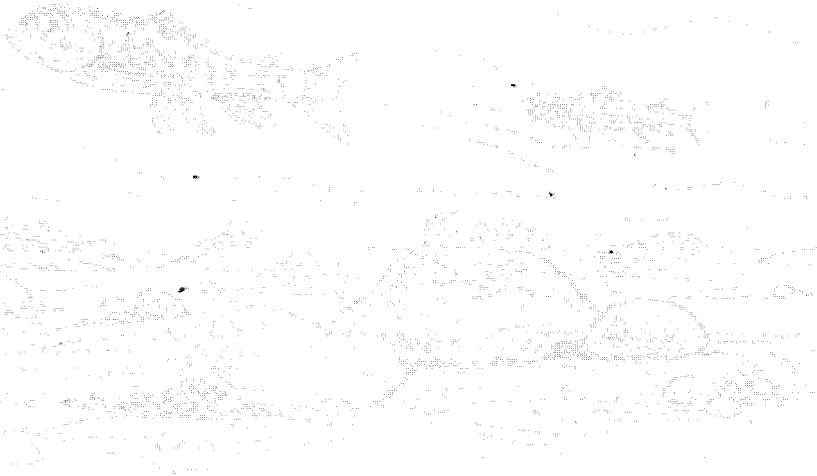
U.S. DEPARTMENT OF THE INTERIOR
NATIONAL BIOLOGICAL SERVICE

NATIONAL WETLANDS
RESEARCH CENTER LIBRARY
700 Cajundome Blvd.
Lafayette, LA. 70506-3152

BIOLOGICAL SCIENCE REPORT 3



HABITAT SUITABILITY
INDEX MODELS:
NONMIGRATORY
FRESHWATER LIFE
STAGES OF
ATLANTIC SALMON



QH
540
.U64
no.3
c.2

National Biological Service

Technical Report Series

The National Biological Service publishes four technical report series. Manuscripts are accepted from Department of the Interior employees or contractors, students and faculty associated with cooperative research units, and other persons whose work is sponsored by the Department. Manuscripts are received with the understanding that they are unpublished. Manuscripts receive anonymous peer review. The final decision to publish lies with the editor.

Series Descriptions

Technical Series

Biological Science Report ISSN 1081-292X

Highest quality of original-science, review, and inventories, which include *North American Fauna* and periodic status and trends reports. Each publication will be available on the electronic library server of the Information Transfer Center (ITC). Selected publications will be converted to CD-ROM and may be obtained from the Publications Unit or the National Technical Information Service.

Information and Technology Report ISSN 1081-2911

Series contains conference proceedings, syntheses, annotated bibliographies, new techniques, and other products.

Other Reports

National Biological Service Information Bulletin (formerly *Research Information Bulletin*)

Contains interim results of scientific studies. Hard copies of each bulletin are distributed to appropriate offices and stations throughout the department. Electronic copies are available from the ITC library server.

National Biological Service Open File Reports

An all-electronic series of reports is available as part of the Other Reports series, and may include pre-publication information or other material (data sets, Geographic Information System [GIS] maps not appropriate for hard-copy publication). Provisions are underway for hard-copy access and registration with the National Technical Information Service.

Editorial Staff

Information Transfer Center
1201 Oak Ridge Drive, Suite 200
Fort Collins, CO 80525-5589
Phone: (970) 223-9709
Fax: (970) 226-9455
CCMail: ITC@NBS.GOV

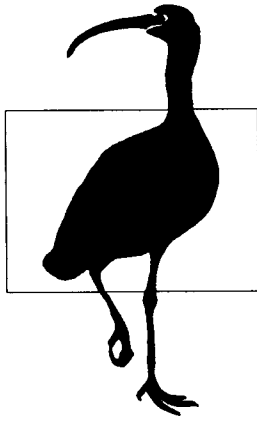
MANAGING EDITOR	Paul A. Opler
ASSISTANT BRANCH LEADER	Paul A. Vohs
SCIENCE EDITORS	Elizabeth D. Rockwell James R. Zuboy
TECHNICAL EDITORS	Jerry D. Cox Deborah K. Harris
VISUAL INFORMATION SPECIALIST	Constance M. Lemos
EDITORIAL ASSISTANT	Martha W. Nichols
EDITORIAL CLERK	Donna D. Tait
CLERK-TYPIST	Linda K. Bogard

Copies of this publication may be obtained from the Publications Unit, U.S. Fish and Wildlife Service, 1849 C Street, N.W., Mail Stop 130, Webb Building, Washington, D.C. 20240 (call 703-358-1711; FAX 703-358-2314), or may be purchased from the National Technical Information Service (NTIS), 5285 Port Royal Road, Springfield, Virginia 22161 (call toll free 1-800-553-6847).



Printed on recycled paper

611
210
1124
MD.3
1.2-



U.S. DEPARTMENT OF THE INTERIOR
NATIONAL BIOLOGICAL SERVICE
WASHINGTON, D.C. 20240

BIOLOGICAL SCIENCE REPORT 3
MAY 1995

HABITAT SUITABILITY
INDEX MODELS:
NONMIGRATORY
FRESHWATER LIFE
STAGES OF
ATLANTIC SALMON

By

Jon G. Stanley

and

Joan G. Trial

Preface

Information in this report is for impact assessment and habitat management. This Habitat Suitability Index (HSI) model for nonmigratory freshwater stages of Atlantic salmon is the third generation of a model that was developed originally from a review and synthesis of existing information on Atlantic salmon (Triel and Stanley 1984). We define a juvenile as either the fry or parr stage up to the time of transformation to the smolt. We also include model variables for the embryo stage. We report on how the model was modified based on field testing in Maine in 1984 and further evaluated by comparison of alternative model outputs with a long-term data base from Canada and habitat selection data gathered in Maine. Despite the testing that went into developing this HSI model, it is nevertheless a hypothesis of species-habitat interactions, not a statement of proven cause and effect. These interactions are presented as an index on a scale from 0 (unsuitable habitat) to 1 (optimally suitable habitat). Through further use of this HSI model in assessing habitat in relation to Atlantic salmon populations, this index can be further refined. The National Biological Service encourages model users to convey comments and suggestions that may help increase the utility and effectiveness of the model. A form is provided in the appendix for this purpose.

Contents

	Page
Preface	ii
Abstract	1
Habitat Use Information For Atlantic Salmon	1
General	1
Age, Growth, and Food	2
Reproduction	2
Specific Habitat Requirements	3
Habitat Suitability Index (HSI) Models	6
Applicability of the Models	6
Model Description	8
Suitability Index Graphs for Model Variables	8
Rationale and Assumptions for Suitability Indices (SI's)	13
Field Application of the Models	13
Interpreting Model Outputs	14
Sources of Additional Models	14
Acknowledgments	15
Cited References	15
Appendix. Model Evaluation Form	18

Habitat Suitability Index Models: Nonmigratory Freshwater Life Stages of Atlantic Salmon

by

Jon G. Stanley¹

*National Biological Service
Great Lakes Science Center
1451 Green Road
Ann Arbor, Michigan 48105*

and

Joan G. Trial

*Maine Department of Inland Fisheries and Wildlife
Fisheries Division
650 State Street
Bangor, Maine 04401*

Abstract. A Habitat Suitability Index model was developed by evaluating individual suitability indices of 17 environmental variables that have been shown to affect productivity or survival of nonmigratory freshwater life history stages of Atlantic salmon (*Salmo salar* L.). These stages included egg, embryo, fry, and parr but not smolt. During summer base flows, the most suitable habitats had temperatures of 16–19° C, oxygen percent saturation exceeding 60%, and pH between 5.5 and 6.8. The most suitable current velocity was 10–30 cm/s for fry and 10–40 cm/s for parr. The most suitable depth was 10–40 cm for fry and 20–50 cm for parr. The Habitat Suitability Index model is useful for evaluating stream habitat for production and survival of juvenile Atlantic salmon when these variables cannot practically be measured directly.

Key words: Atlantic salmon, ecology, habitat, water quality, substrate, streams, parr, spawning, habitat suitability index.

Habitat Use Information For Atlantic Salmon

General

The Atlantic salmon, *Salmo salar* L., inhabits the North Atlantic Ocean basin from Greenland to the Connecticut River of New England (Scott and Crossman 1973). In

Europe it ranges from Iceland to Portugal, including the Baltic Sea (Netboy 1974). Anadromous populations once migrated into most New England streams and the St. Lawrence River tributaries, including Lake Ontario and Lake Champlain. Dams, pollution, and overfishing have eliminated spawning runs over much of the Atlantic salmon's range in North America and Europe (Danie et al. 1984; Mills 1989; Thompson 1993). Landlocked populations in North America, on the other hand, were endemic to only a limited number of large lakes and watersheds but now occur in numerous lakes, especially in Maine, because of

¹ Present address: School of Natural Resources and Environment, University of Michigan, Ann Arbor, Michigan 48109-1115.

stocking (Warner and Havey 1985). The juveniles of anadromous parents can be distinguished from juveniles of landlocked populations, but the difference is not great enough to categorize any particular individual (Riley et al. 1989). Their habitat use in small streams is similar (Sayers 1990), and the Habitat Suitability Index (HSI) model in this report applies to both.

The Atlantic salmon has high social and economic value. The adults are harvested commercially on their feeding grounds off Greenland and southern Labrador, Canada, and they are caught in the recreational fishery during their migration as they reenter fresh water. The annual return of anadromous Atlantic salmon to U.S. streams is about 5,000 individuals; the number returning from year-to-year varies about five-fold (Rideout 1989). In Canada, the annual production potential is about 1.5 million large salmon and an equal number of grilse, which are young salmon that are returning to their native rivers to spawn after one winter at sea (Lear 1993).

Worldwide there are more than 350 recognized stocks of Atlantic salmon (Chadwick 1985). In general, each major river system has its own stock uniquely adapted to the local conditions (Thorpe 1988). In North America, the populations of Atlantic salmon are bolstered by stocking of hatchery fish (Rideout 1989). In some runs, more than 90% of the fish are from hatcheries. The juveniles are generally stocked when they are 1-year-old smolts ready to migrate to the sea. In the United States, the hatchery stock consists of seven different strains or developing strains reared at six federal and four state hatcheries (Kane 1989). The HSI model was developed for the stock of Atlantic salmon inhabiting streams in New England and the southern Canadian maritimes. Suitability indices (SI's) have been produced for Atlantic salmon in Newfoundland (Scruton and Gibson 1993), and a workshop to develop models was conducted in 1992.

Age, Growth, and Food

Juvenile Atlantic salmon grow relatively slowly in fresh water, whereas adults grow rapidly at sea. Juveniles may spend 2–3 years in fresh water to reach 125–150 mm length in New England and 4–8 years to reach 180 mm in Ungava Bay, Canada (Schaffer and Elson 1975). The young salmon grow fastest at temperatures of 15–19° C (DeCola 1970). The lower temperature limit of growth, which varies with nursery stream conditions, ranges from 5 to 10° C (Jensen and Johnsen 1986). Survival is positively correlated with water discharge from streams (Frenette et al. 1984; Gibson et al. 1993). Growth in fresh water also is limited by availability of food, interspecific and intraspecific competition, and a range of other factors. Growth is fastest in habitat with water velocities of about

30 cm/s, corresponding to the preferred habitat selected by parr (Heggenes and Borgstrom 1991).

Juvenile Atlantic salmon occupy stations in streams and feed on invertebrates drifting on the surface and in the water column (Bley 1987). The diet is variable, generally consisting of the larvae of mayflies, chironomids, caddisflies, blackflies, and stoneflies; annelids; and mollusks (Scott and Crossman 1973). Larger juveniles also eat the adult forms of aquatic insects and terrestrial insects. Food size varies in direct proportion to the size of the fish (Sosiak et al. 1979). Atlantic salmon are opportunistic feeders, readily changing their diet to the most abundant prey available.

After juveniles reach a total length of 125–150 mm, environmental stimuli trigger transformation into a smolt ready to migrate to sea (Danie et al. 1984). At the smolt stage, landlocked salmon migrate from streams into lakes (Warner and Havey 1985). Migration is keyed to environmental stimuli of rising water temperature, freshets, and photoperiod (Bley 1987). A few individuals in one population of landlocked Atlantic salmon migrated to lakes in autumn (Warner and Havey 1985).

Reproduction

Atlantic salmon spawn in fresh water during October and November when water temperatures reach 4.4–5.6° C (DeCola 1970). Eggs are deposited in redds dug by adult females at the downstream end of riffles where water percolates through the gravel or at upwellings of ground water. One or more males fertilizes the eggs as they are deposited, and the female then completes the redd by covering the eggs with 10–25 cm of gravel displaced from upstream. The eggs are slightly adhesive and stick to the substrate until they are covered.

The eggs incubate over winter buried in gravel. The incubation period varies with temperature. Eggs hatch after 175–195 days under normal winter conditions of Maine (Jordon and Beland 1981). The incubation time of 110 days cited by Leim and Scott (1966) was for a temperature of 3.9° C, typical of a hatchery drawing hypolimnetic water from a lake.

After hatching, the eleutheroembryos (alevin or yolk-sac larvae) remain buried in the gravel for about 6 weeks, until their yolk sac is depleted of nourishment. The resultant fry begin foraging while still in the substrate, then emerge at night from mid to late May in Maine (Gustafson-Marjanen 1982) and from late May to early June in Canada (Scott and Crossman 1973; Lear 1993). In one river in Finland, emergence was as late as July (Mills 1989). Survival from fertilization through hatching was 74%, and only 2% from fertilization through emergence (MacKenzie and Moring 1988). Chadwick (1982) found that the survival rate was depressed during a year when

winter air temperatures and water discharge were both low. After emergence, fry disperse, mostly downstream, and establish territories. Dispersal is highest at night (Crisp 1991).

Specific Habitat Requirements

During its anadromous life cycle, the Atlantic salmon completely changes its habitat from freshwater streams to the sea. This report emphasizes the freshwater segment of the life cycle. Atlantic salmon require cold, clear streams that flow freely to the ocean. Because many such streams in the northeastern United States and Canada arise in areas with granitic bedrock, they are subject to acidification. Atlantic salmon streams are generally well oxygenated, except in a few rivers receiving industrial or domestic pollutants. Impoundments on many rivers not only block migration but also create long reaches of still water that result in increased water temperatures. The environmental requirements of Atlantic salmon were thoroughly reviewed by Gibson (1993).

Water Temperature

Temperature is a key variable in determining habitat suitability for Atlantic salmon. All stages of the life cycle require cool temperatures. Spawning occurs between 4.4 and 10° C; the optimal temperature for fertilization and incubation is about 6° C (Danie et al. 1984). Development proceeds, but at a slower rate, at temperatures as low as -0.5° C (Peterson 1978). Incubation temperatures above 12° C cause direct mortality, whereas temperatures between 8 and 12° C may cause secondary mortality because of fungal infections (Garside 1973; DeCola 1975).

Newly hatched larvae are exposed to and tolerate rising water temperatures in spring. Although they have little opportunity for selecting temperature, if given a choice they will move to the coldest temperature available (Peterson and Metcalfe 1979). At about 250 degree-days after hatching, when the fry establish territories in streams, they prefer a temperature of 14° C. Juveniles (13–16 cm total length) select a temperature of 14.5° C (Trial and Stanley 1984). They need a growing season of about 100 days with stream temperatures above 6° C (Power 1969).

The optimal water temperature for growth and production—15 to 19° C (DeCola 1970)—seems to be slightly higher than the preferred temperature. Growth seemed to be fastest at 16.6° C (Siginevich 1967). In the laboratory, parr grew better at 13–19° C than at colder temperatures (Dwyer and Piper 1987). Young Atlantic salmon can tolerate temperatures up to 27° C for short periods but seek cooler water as these temperatures are approached (DeCola 1970). Juveniles withstand 32° C briefly (Huntsman 1942), and the lethal temperature under laboratory conditions is about 32° C (Garside 1973). Tolerance polygons

for first-year and yearling parr demonstrate that Atlantic salmon have the highest temperature limits for feeding (22.5° C) and survival (27.8° C) among brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and five species of Pacific salmon (Elliott 1991).

The information on temperature relationships from the literature was adequate for creating SI's for spawning temperatures, egg incubation, upper tolerances, and summer growth. The information was inadequate for developing models for cold lethal temperatures.

Dissolved Oxygen

Oxygen concentrations near saturation are needed for optimal development and growth. Embryo and larval development requires a minimum of 6 mg/L of dissolved oxygen (Elson 1975). Mortalities occur if embryos are exposed to oxygen concentrations of less than 6–7 mg/L (DeCola 1970). Juvenile salmon do not occur in streams in which dissolved oxygen regularly drops below 5 mg/L (Elson 1975). In the laboratory at 14.5° C, Atlantic salmon juveniles select the highest oxygen concentration available—7.5 mg/L or 72% saturation (Trial and Stanley 1984). At 15–16° C, lethal concentrations are 1.5 mg/L for juveniles during the first summer of life and 1.9 mg/L during the second year (DeCola 1970).

We converted all dissolved oxygen concentrations to units of saturation using standard tables to construct an SI for minimum summer values.

Acidity

The pH of salmon streams in granitic, sandy, or boggy areas may be depressed by melting snow or heavy rains that contain acid. Episodes of low pH are often accompanied by high concentrations of metal ions that leach from the soil, especially aluminum (Lacroix and Townsend 1987). Thus, toxicity may not be caused by acidity per se; nevertheless, pH may serve as a convenient indicator of water quality. For many areas in New England and the Canadian maritimes, organic compounds chelate aluminum. Rivers in Nova Scotia with a mean annual pH of less than 4.7 have lost their salmon runs; in rivers with pH between 4.7 and 5.0, runs declined, and in those with pH above 5.0, runs were normal (Watt et al. 1983). In these same streams, juveniles were most numerous where the mean annual pH was above 5.4, were much reduced between pH 4.7 and 5.0, and were absent below pH 4.7.

Eggs develop normally at pH 6.7 (Peterson et al. 1980). The embryo has a lower lethal level of about pH 3.5 during early cleavages and pH 3.1 just before hatching (Peterson et al. 1980). However, a pH of 4.0–5.5 delays hatching. A pH less than 5.0 inhibits enzymes necessary for hatching, and reproduction fails (Haines 1981). Yolksac fry in situ had 100% mortality at pH 5.1 with high aluminum and

65% mortality at pH 5.7 with lower aluminum (Norrgrén and Degerman 1993).

Juvenile Atlantic salmon are often exposed to low pH along with other stresses, such as swift water, toxic metals, and turbidity. The low pH causes edema of the gill lamella and may disrupt respiration and excretion at times when metabolic demands are high. In the laboratory, juveniles had a lower lethal pH of 4.0 after 28 days of exposure (Daye and Garside 1977, 1980). Concentrations of sodium, calcium, and chloride declined in the plasma after exposure to pH 4.6 but not at pH 5.0 or 5.5 (Farmer et al. 1989).

An SI was developed with this literature information in which frequency of acidic episodes and their intensity are key variables. Although aluminum and other metals are obviously important in the manifestation of acidic effects, we could not incorporate such information into a simple model. In general, HSI models do not consider toxic substances. The intent is for the models to predict the quality of habitat in the absence of specific contaminants and myriad other confounding factors.

Velocity

Atlantic salmon in fresh water require flowing water, although they will occupy slow-moving or lentic habitats (Einarsson et al. 1990; Cunjak 1992). Adults select spawning sites in riffles where the average velocity is about 50 cm/s (Elson 1975; Beland et al. 1982). The lower limit of velocity was 15–20 cm/s, and the upper limit was related to female size (e.g., a 50-cm female would be limited to velocity less than 100 cm/s; Crisp and Carling 1989).

Egg incubation requires upwelling of ground water or percolation of stream water through the gravel substrate, which is measured with a standard permeability test in which the rate of water dispersal from a pipe is determined. Permeabilities of 1.3–1.4 L/h are typical (Gustafson-Marjanen and Moring 1984).

Newly emerged fry occupy areas with current but select microhabitat with slower water. In an artificial stream, newly emerged fry dispersed fastest when in a low velocity of about 8 cm/s (Crisp 1991). More stayed in the stream at velocities of 25–70 cm/s, implying that the faster velocity was more suitable for fry. There was considerable variation in how velocity was measured, reported, and interpreted. The prevailing velocity may be as important as that where the juvenile actually rests. The mean velocity in the water column in areas preferred by first-year fish is 50–65 cm/s (Symons and Heland 1978). Knight et al. (1981) reported that the preferred habitat had a mean column velocity of 14 cm/s. The preferred mean column velocity was 10–31 cm/s in one Canadian stream and 10–46 cm/s in another (DeGraff and Bain 1986). Morantz et al. (1987) reported the mean column velocity in eight

Canadian streams to be 32 cm/s, and juveniles were absent in areas with a mean column velocity exceeding 120 cm/s. Fry were most abundant in stream sections where mean column velocity was less than 30 cm/s, but some fry were observed at mean column velocities up to 60 cm/s (Heggenes et al. 1990).

The velocity in microhabitats selected by fish was less than the mean column velocity. The mean velocity in the microhabitat where fry hold was 17 cm/s in one stream and 5 cm/s in another (Trial and Stanley 1984). In Canadian streams, fry preferred 0–5 cm/s in one stream and 17–21 cm/s in another (DeGraff and Bain 1986). The mean velocity where fry held position was 12 cm/s; most selected velocities of 5–19 cm/s (Morantz et al. 1987). Gibson (1993) reported that the mean velocity where fry held position was 13 cm/s in riffles and pools. In the laboratory, the velocity where fry can no longer hold position was 150 cm/s at 6–8° C and 190 cm/s at 12–14° C (Heggenes and Traaen 1988). Trial and Stanley (1984) reported that 3-month-old Atlantic salmon could maintain position in a flow tank in a velocity of 50 cm/s at 16° C and pH 4.5–6.0. Below pH 4.0, however, they were unable to maintain position in velocities faster than 42 cm/s. Even in this flow tank, the fry were able to find pockets with currents that were 60–70% of those measured.

Competition between size groups is reduced by habitat segregation (Gibson et al. 1993). Yearling Atlantic salmon parr have about the same velocity preferences as fry. The older and larger parr take the best territories, usually in midstream. Habitat selection toward the middle of the stream was evident from measuring where parr occurred relative to the shore—18 fish were 0–0.2 m from shore, 121 were 0.3–0.7 m from shore, and 266 were 0.8–1.5 m from shore (Hesthagen 1988). In some streams fry prefer riffles and parr prefer runs (Tremblay et al. 1993). As juveniles grow, they are able to cope with the faster water and thus benefit from more drifting food (Morantz et al. 1987). They minimize energy expended on swimming by utilizing low-velocity areas, hiding among rocks in riffles and darting into the swifter current only to feed. The most favorable territories in some streams were in faster water, in others slower, possibly because of other factors, such as cover. Trial and Stanley (1984) reported that the velocity in the microhabitat occupied by yearling parr in one stream was 9 cm/s, which was slower than in the areas occupied by fry, and 6.5 cm/s in another stream, which was faster than in areas occupied by fry.

The gradients of streams where juvenile salmon occur range from 2 to 12 m/km (Elson 1975). In rivers in Nova Scotia, the highest densities of parr were at a gradient of 1.2–1.4% (Amiro 1993). Such gradients generate mean column and microhabitat velocities within the preferred ranges for fry and parr. Knight et al. (1981) found that

yearlings occupied stations where the mean velocity was 14 cm/s. Based on distribution in one stream, most parr preferred a mean column velocity of 10–24 cm/s; in another stream, parr preferred 16–57 cm/s (Degraff and Bain 1986). The mean column velocity selected by small parr (about 85 mm long) was 40 cm/s and by large parr (about 120 mm) 35 cm/s (Morantz et al. 1987). Gibson (1993) reported, however, that small (6–10 cm) and large parr (>10 cm) were located at a mean velocity of 20 cm/s in riffles. In pools, however, small parr selected velocity of 6 cm/s and large parr 13 cm/s. The most preferred holding velocity of parr was 0–5 cm/s in one stream and 16–21 cm/s in another (Degraff and Bain 1986). Large parr were found in velocities of 22 cm/s but preferred velocities of 10–20 cm/s (Morantz et al. 1987). Larger parr occupied microhabitats with velocities of 0–25 cm/s in streams with mean velocity of overlying water of 0–75 cm/s (Heggenes et al. 1991).

In fall, 2-year-old juvenile Atlantic salmon moved from the riffle area of streams into slower water, where they remain during winter, whereas 1-year-old juveniles did not move (Rimmer et al. 1984). Huntingford et al. (1988) found, however, that all fish sought areas of low flow in fall. In winter, parr hide under rocks in riffle areas with overlying velocities of 38–46 cm/s (Cunjak 1988). Parr destined to become smolts the following year selected faster currents in an artificial stream than did parr destined to remain in fresh water for 2 years (Huntingford et al. 1988).

Suitability indices were developed for velocities measured at 0.6 of total depth of the water column or below. The lower portion of the water column is where the fish spend most of their time, and velocity at 0.6 of the total depth approximates the average velocity for the water column (Hamilton and Bergersen 1984). We had insufficient velocity data to develop a fall or winter SI for velocity.

Depth

Spawning sites are selected at the tails of pools that are near the beginning of riffles. The depth depends on the size of the stream and the size of the fish. A 50-cm female requires depths of 10–40 cm (Crisp and Carling 1989). In Maine rivers, the average depth over spawning redds was 40 cm (Beland et al. 1982); in New Brunswick, it was 20 cm (Peterson 1978).

After hatching, fry disperse and establish territories. Fry establish residence in shallower water nearer shore. The depths where fry reside in each stream are related to stream morphology, which determines the depth of near-shore areas at low flows. Thus, average depth selected by fry will vary among streams. Knight et al. (1981) reported that fry habitat in New England streams averaged 25 cm deep (range 9–39 cm). In Maine, fry preferred water 34 cm deep in one stream and 27 cm in another (Trial and Stanley 1984). In Canada, for 62 sites on New Brunswick streams and rivers where fry

were abundant, mean depth ranged from 10 to 31 cm (Francis 1980). The preferred depths for fry in one stream in Newfoundland were 13–25 cm and in another, 20–60 cm (DeGraff and Bain 1986). In Newfoundland, fry occurred at 17 cm depth in riffles and 32 cm in pools (Gibson 1993). In eight streams in Nova Scotia and New Brunswick, the average depth used by fry was 35 cm; most individuals were found between 20 and 40 cm (Morantz et al. 1987). In a Norwegian stream, fry were mostly in water less than 60 cm deep (Heggenes et al. 1990). In England, in water less than 20 cm deep, fry outnumbered parr, whereas in water deeper than 20 cm, parr were more abundant (Kennedy and Strange 1986). In another English stream, the number of fry was positively correlated with depth up to 20 cm and inversely correlated with depth greater than 20 cm (Egglisshaw and Shackley 1985).

Parr seem to prefer deeper water than fry (Gibson 1993; Gibson et al. 1993), which is usually found midstream. Selection within streams is affected by availability of deep water with suitable velocities related to stream morphology. As with fry, the average depth selected by parr varies among streams and therefore among studies. The mean depth of preferred areas for parr in one New England stream was 29 cm (Knight et al. 1981), 49 cm in another, and 33 cm in a third (Trial and Stanley 1984). In some Canadian streams, parr preferred depths of only 10–15 cm (Symons and Heland 1978), whereas in two other streams, preferred depths were 22–42 cm and 14–48 cm (DeGraff and Bain 1986). The range of depths preferred by parr differed in eight Canadian streams; most occurred between 30 and 60 cm (mean 47 cm; Morantz et al. 1987). In Newfoundland, small parr (6–10 cm) were found in 22 cm of water in riffles and 42 cm in pools (Gibson 1993). Large parr (>10 cm) used slightly deeper areas, 24 cm in riffles and 57 cm in pools. In Europe, yearlings were most abundant at a depth of 35 to 40 cm in one stream (Kennedy and Strange 1986) and deeper than 25 cm in another (Egglisshaw and Shackley 1985). Most yearling or older parr occupied habitats with depths less than 90 cm (Heggenes et al. 1990). Larger parr used depths between 25 and 85 cm, but a few were in water deeper than 100 cm (Heggenes et al. 1991).

Suitability indices were developed for depth over spawning areas and at summer low flows for fry and parr. We had insufficient data to develop a winter SI for depth over redds. However, because most fish descend into the substrate in winter, we believe that the summer depth SI's for fry and parr are also applicable to winter low flows. In winter, parr occupy riffles in water 41–49 cm deep (Cunjak 1988).

Substrate, Sediment, and Turbidity

Adults select spawning sites at the tails of pools that have substrate composition reflecting sorting by the swift currents

that move over this habitat. In Peterson's (1978) study, the particle size composition was 0–3% fine sand (0.06–0.5 mm), 10–15% coarse sand (>0.5–2.2 mm), 40–50% pebble (>2.2–22 mm), and 40–60% cobble (>22–256 mm). Spawners preferred gravel of 20–30 mm diameter (Crisp and Carling 1989). The substrate composition of the redds of landlocked Atlantic salmon included higher percentages of intermediate-size particles (Warner 1963). The landlocked fish, which are smaller than the sea-run fish, may not be capable of moving the larger particles.

Because juvenile salmon occur in the riffle area of streams, they are likely to be found above substrate containing sand, gravel, and cobble rather than silt. In one stream, Atlantic salmon fry selected a substrate classified as 4.8, based on an index in which 3 represents fines and detritus; 4, sand; 5, gravel; and 6, cobble (Trial and Stanley 1984). In two Canadian streams, the most preferred substrate had an index of 4.5–5.5 for fry and parr (DeGraff and Bain 1986). In eight other Canadian streams, this index was 5.6 for fry, 5.9 for small parr, and 6.4 for large parr, indicating selection of a coarser substrate as juveniles grow (Morantz et al. 1987). During their first year, juveniles preferred gravel substrate (16–64 mm), whereas yearling parr preferred a boulder and rubble substrate where diameters were greater than 260 mm (Symons and Heland 1978). Gibson (1993) concluded that fry are most common where there is a pebbly bottom, and parr over coarser substrate. In a Norwegian stream, fry were observed over a gravel to boulder substrate, and parr occupied a wider range of substrate types (Heggenes et al. 1990).

Depth, velocity, and substrate are interdependent. Substrate is related to velocity, and velocity is affected by depth. It is difficult to determine whether juveniles, as they grow, select larger substrates, faster velocities, or deeper areas with similar substrate and velocity. However, all variables seem to be differentially selected by fry and parr. Our SI's were constructed so that pebble-size substrates were best for fry and cobble substrates best for parr.

Sedimentation into the spaces between pebbles and cobble interferes with the use of this space as shelter for young Atlantic salmon and decreases their survival rate in summer (McCrimmon 1954). In winter, siltation and suspended debris within the substrate are also important because fish hide in spaces under rocks (Cunjak 1988). Such sedimentation obviously also affects benthic production and reproductive success.

Atlantic salmon typically occur in clear streams and depend on transparent water for site-feeding. Turbidities of 40 nephelometric turbidity units (NTU) or less are considered to represent clear water that is highly suitable for feeding. Survival of fry and parr was highest in stream segments with the lowest base turbidities (McCrimmon 1954). As turbidities increase to 100 NTU, progressive

interference with sight feeding and growth is possible. In the laboratory, coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss*) grew fastest in clear water; growth was inhibited at 45–50 NTU (Sigler et al. 1984). In some tests, 38–49 NTU did not inhibit growth, and in other tests turbidity as low as 25 NTU inhibited growth. When coho salmon were exposed to turbidities of 30 and 60 NTU, territoriality deteriorated and prey capture rates declined (Berg and Northcote 1985). Coho salmon avoided turbidity of 70 NTU (Bisson and Bilby 1982). Episodes of high turbidity seem to do no harm, and turbidity alone correlated poorly with effects of suspended sediments on fish (Newcombe and MacDonald 1991). Relatively low turbidities over long periods caused reduced feeding in several species of salmonids (Newcombe and MacDonald 1991). Turbidities exceeding 1,150 standard units, measured with a photometer during fall freshets, did not injure or kill Atlantic salmon fry or parr (McCrimmon 1954).

The SI for turbidity was based on effects on other species of salmonids, primarily as reported in the review by Newcombe and MacDonald (1991).

Habitat Suitability Index (HSI) Models

Applicability of the Models

Potential users of the HSI model for Atlantic salmon can have confidence in applying the model in habitats where the model was developed and tested. Considerable effort has gone into validating the model, especially for the more important variables. The model is equally applicable to anadromous and landlocked populations of juvenile Atlantic salmon. We recommend the use of this HSI model to help formulate expert opinion on habitat quality. However, we caution that the model is a hypothesis describing a simplified version of complex interrelationships within a seasonally dynamic environment. In addition, the model concerns a species with shifting habitat requirements, complex behaviors, and a long life cycle. Furthermore, this HSI model does not consider toxic chemicals, which if present may limit the application to predicting what habitat quality would be if the contaminant were removed.

Geographical Area

The HSI model was designed for Atlantic salmon in streams of New England and the Canadian maritimes of temperate North America. The model applies to embryos, fry, and parr in streams and to adults only in regard to the selection of spawning sites. European populations share many of the same characteristics as the North American populations, and the model could probably be applied to European populations with little modification.

Season

The water quality, fry, and parr components of the HSI model are designed to evaluate the summer habitat of juvenile Atlantic salmon during base flow, when the extent of the available habitat is limited. The reproductive component obviously applies during the fall period. Winter habitat may be particularly important to the survival of Atlantic salmon; for example, low winter discharge significantly affects juvenile survival (Gibson and Myers 1988). Except for temperature and ice, the habitat occupied by juveniles differs only slightly from summer habitat (Rimmer et al. 1984; Cunjak 1988). Although survival is correlated with winter air temperatures and water levels (Chadwick 1982), no measurements link specific winter conditions to embryo or juvenile survival.

Habitat Types

The HSI model applies to embryos and juveniles in freshwater, riverine (lotic) habitat. The model describes the area where spawning and egg incubation occur, as well as nearby nursery areas for juveniles. The model does not consider the lake and marine feeding grounds of adults or any habitat characteristics critical to successful downstream or upstream migration in estuaries or freshwater streams. The model has the most validity when applied to the streams in which it was tested or to similar streams. Tests were done in streams ranging from small brooks to the mainstem of major rivers, such as the St. John River in New Brunswick.

Minimum Habitat Area

In HSI models, the minimum habitat area usually includes egg incubation areas, nursery and juvenile feeding grounds, and adult feeding grounds. For Atlantic salmon, the usual definition of minimum habitat area does not apply because the habitats for the different life stages usually are not contiguous. Of critical importance to Atlantic salmon populations is free passage between the different habitats, unobstructed by dams or interception by excessive fisheries.

The area of habitat used by Atlantic salmon varies considerably. Some stocks of landlocked Atlantic salmon exist within a single river system in which spawning, nursery, and feeding areas are within a few kilometers of each other, for example, the West Branch of the Penobscot River in Maine (Warner and Havey 1985). At the opposite extreme, some populations have nursery grounds in small streams in Portugal, and the adults feed in Arctic waters off the coast of Baffin Island in North America (Netboy 1974). The minimum habitat area for the juvenile life stages is poorly defined, in part because little information is published on distances for the dispersion of fry and parr. Dispersal occurs rapidly in spring as fry emerge from the redd and move predominantly downstream (McKenzie and Moring 1988; Gustafson-Greenwood and Moring

1990). Parr then disperse gradually over the summer to occupy all suitable stream habitats. In winter, older parr move from the riffles in streams into slower waters (Rimmer et al. 1984). Dispersal was faster for parr planted in deep, slow water than for parr planted in their preferred habitat of fast-moving water (Heggenes and Borgstrom 1991). For most of these dispersal phases, the extent of movements is unknown.

Verification Level

Originally, the SI's and HSI model presented here were derived from literature values and initially tested in Maine streams (Trial and Stanley 1984; Trial et al. 1984). Suitability indices for water depth, velocity, and substrate were independently developed and tested in Canadian streams (Morantz et al. 1987). A third test for validation was done in Maine streams (Trial 1989). A fourth test was done in which Trial (1989) analyzed data collected in New Brunswick by Francis (1980) and Trial (1989). Recently, SI's developed for Newfoundland rivers were tested and found to consistently predict standing crop of fry (Scruton and Gibson 1993).

Trial (1989) formulated four alternative HSI models based on an evaluation of SI's related to velocity, substrate, and depth. Two of the HSI models used SI's from Morantz et al. (1987) from the fry and parr components, and two used SI's from Trial and Stanley (1984). Trial (1989) determined the goodness of fit between the measured variables for habitat selected by juveniles and the SI values. In other words, the cumulative frequency distribution (CFD) of suitability based on habitat selection by fish was compared with the hypothetical CFD. This process was done stepwise for individual SI's and the life stage component indices produced from either the product of the three SI's or their geometric mean. Trial's (1989) test of fry and parr components indicated that the CFD from the SI's in Trial and Stanley (1984) and Morantz et al. (1987) had a more gradual rise to 100% than the CFD from her data on fry in Maine streams. The apparent lack of fit of the components was expected because the SI's were overestimates of the optimal range of each habitat variable (Trial 1989).

In a second test, Trial (1989) found that the joint probabilities and geometric means for the fry component index were correlated with the density of fry. The two ways of calculating component indices did not affect the ranking of the sites—the ranks of the alternative component indices were correlated with the rank of fry density at 16 sites. In contrast, none of the parr component models correlated with parr densities, probably because other variables, such as cover, were important. For total numbers of juveniles, three of the four HSI models were correlated with population density, and only the model based on joint probability and the SI's by Morantz et al. (1987) was not correlated.

These tests of HSI models verified the HSI approach toward evaluating habitat and validated some of the SI's, especially for the water velocity, depth, and substrate of fry. These tests measured density, abundance, or site selection as an indicator of carrying capacity. In general, the microhabitat used within any one stream was narrower than predicted by the models, whereas the range of habitats used among streams was predicted accurately. Scruton and Gibson (1993) noted that SI's are more useful if derived from macrohabitat measurements (e.g., stream width) rather than microhabitat (e.g., variables measured at location of individual fish).

In tests of HSI models by Trial (1989), the reproductive component was based on water quality and stream order. Thus, the complete reproductive component, which consists of variables for depth, velocity, spawning temperature, incubation temperature in winter, stream order, and dominant substrate (Trial and Stanley 1984), was not tested adequately.

The models tested by Trial (1989) did not include food availability because of the difficulty in sampling food abundance for an animal with opportunistic feeding habits. A surrogate measure for food might be possible, based on variables related to the productivity of food of salmonids, such as alkalinity and conductivity (McFadden and Cooper 1962; Cooper and Scherer 1967).

Model Description

The implicit assumption of HSI models is that habitat with high HSI values has high carrying capacity and high productivity potential. These models were developed to predict the effects of environmental changes by relating environmental conditions to carrying capacity (U.S. Fish and Wildlife Service 1981). The aquatic and fish species HSI models provide a systematic method for evaluating projects that may alter the habitat of indicator species.

Life Stage Component Indices

The previously published model (Trial and Stanley 1984) defined parr component suitability as the geometric mean of the SI's for velocity, depth, and substrate. A geometric mean increases the most when the individual variable with the lowest value is increased. In contrast, an arithmetic mean changes the same amount for a fixed amount of increase in a single variable, regardless of which variable is increased. We describe component models in which the quality of holding or redd sites is based on multiplication of three variables (velocity, depth, and substrate) with values on a scale of 0 to 1.0. If the SI for a variable is considered to be a probability of habitat utility, then the component suitability would be a product of the individual variable values. We believe this "joint probability" approach for combining velocity, depth, and substrate suitabilities is biologically

most conservative approach for modeling life stage suitabilities. Because there was no difference in the statistical fit of component indices calculated using the joint probability or the geometric mean (Trial 1989), we chose to use the model that is easiest to use. Bain and Robinson (1988) expressed concern that numerous variables in a geometric mean would result in an unrealistic degree of compensation for the lowest values. Therefore, we used a joint probability approach to calculate component indices.

Water Quality

The water quality component was modeled by a minimum value. Fry (1971) and Brett (1979) recommended this model for limiting and lethal factors. The water quality component in Trial and Stanley's (1984) model consisted of water temperature, pH, turbidity, and minimum oxygen. This component was not correlated with observed densities for fry or parr (Trial 1989). Because the two temperature variables, maximum and average temperature, were within the tolerance range for juvenile Atlantic salmon at all sites, the component index did not discriminate differences. However, temperature might profoundly affect biomass or growth rate, should these be used as end point measurements for testing component indices. Growth of juvenile salmon is highly dependent on temperature (Egglisshaw and Shackley 1985).

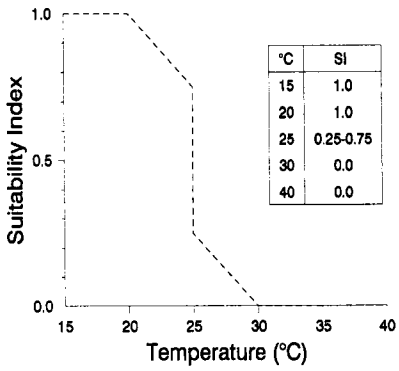
Suitability Index Graphs for Model Variables

The SI for each variable, as a function of the environmental range for that variable, is shown graphically in this section. Habitat suitability indices can be computed with the following SI's, which we modified from Trial and Stanley (1984), based on new literature and Trial (1989). Trial (1989) discussed the assumptions associated with constructing the SI's, and assumptions are also discussed in sections below.

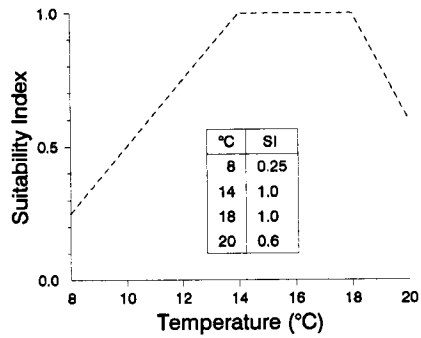
Field use of these SI's requires measurements of key environmental variables. Methods for sampling habitat are described in detail in Terrell et al. (1982), along with some shortcuts applicable to less rigorous studies. A multimillion dollar project with great potential for widespread damage might warrant a full-scale study with multiyear sampling. A local project with probable minimal impact might require only a single visit to the site during summer base flow. Users must decide on the level of sampling required but should not compromise on the methods recommended by Terrell et al. (1982). Alternative methods for gathering data on individual variables were discussed by Hamilton and Bergersen (1984). As with the overall sampling plan, the method selected to measure a variable may be dictated by the scope of the project.

Water Quality Component

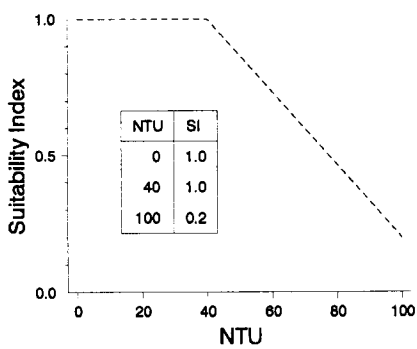
V1: Mean maximum daily water temperature for the warmest contiguous 3-day period of summer during base flow, preferably taken from a continuous temperature record (i.e., hydrothermograph).



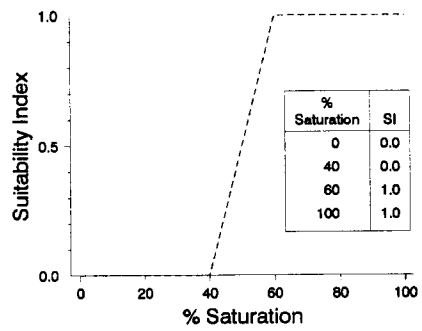
V2: Mean water temperature for the growing season or summer, preferably taken with a hydrothermograph.



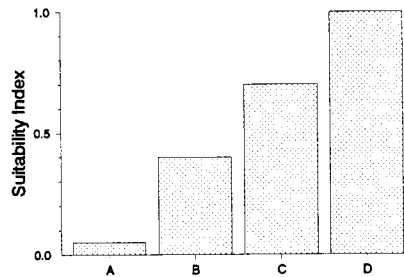
V3: Mean turbidity based on monthly measurements over as much of the year as possible.



V4: Mean minimum daily oxygen saturation for the 3-day period with the lowest percent saturation during the summer, ideally monitored continuously.



V5: Minimum pH - The frequency at which critical pH levels are reached, as measured during episodes of acid runoff over 3-day periods.

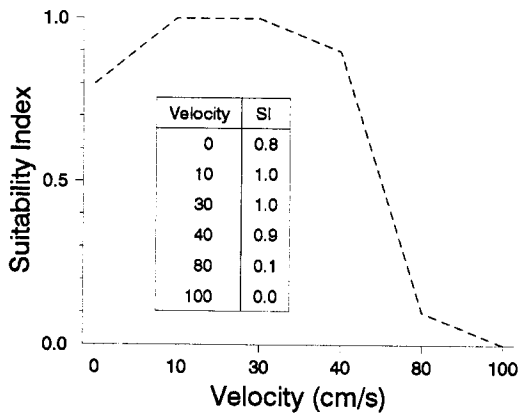


pH Category	Description	S.I.
A	pH below 4.0 at least once annually	0.05
B	pH 4.0 to 5.5 at least once annually	0.40
C	pH occasionally falls below 5.5 but never below 5.0	0.70
D	pH always 5.5 to 6.8	1.00

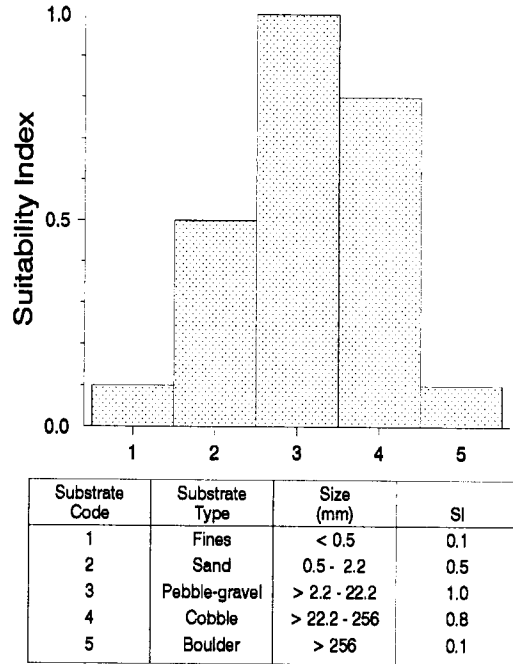
Fry Component

If mean stream depth is greater than 50 cm, divide the stream into fourths. Because fry occur mostly in the shallower sections, average the variables for the two shallowest fourths of the section to arrive at a mean value for each SI of the fry component. In streams shallower than 50 cm, simply average the entire stream.

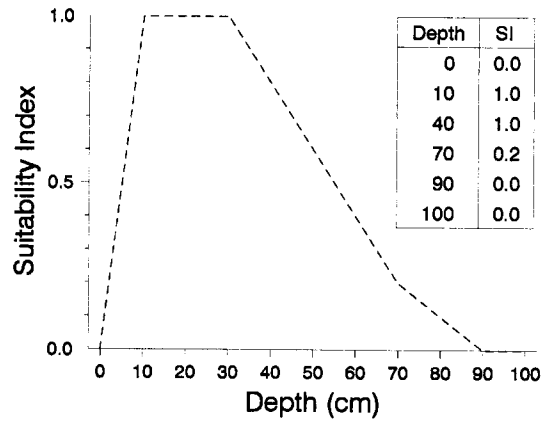
V6: Mean column velocity for fry during base summer flow. Measuring at a point 0.6 x total depth from the surface approximates mean column velocity.



V7: Dominant substrate for fry.



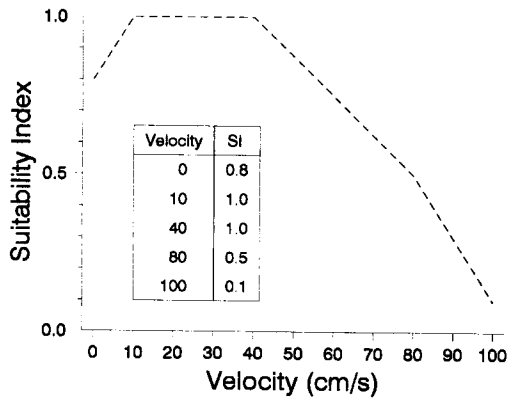
V8: Mean depth for fry during base summer flow.



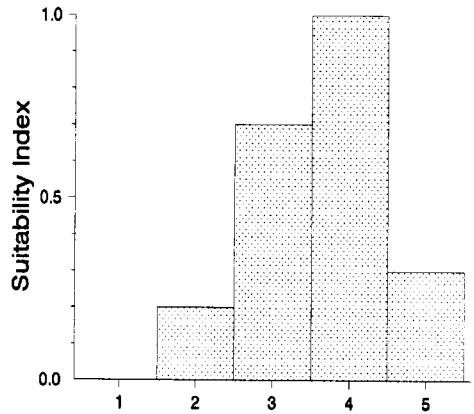
Parr Component

If mean stream depth is over 50 cm, divide the stream into fourths, and average the variables in the two deepest fourths to arrive at the mean value for each SI. In streams shallower than 50 cm, use the mean values for the entire stream.

V9: Mean column velocity for parr during base summer flows.

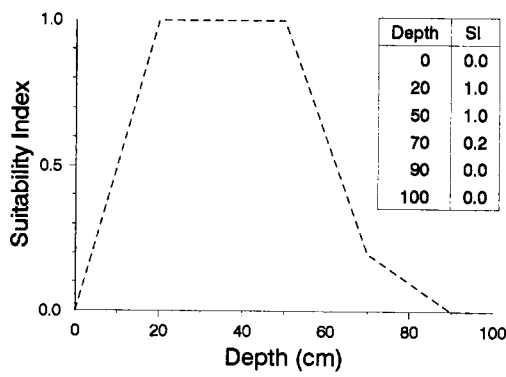


V10: Dominant substrate for parr.



Substrate Code	Substrate Type	Size (mm)	SI
1	Fines	< 0.5	0.0
2	Sand	0.5 - 2.2	0.2
3	Pebble-gravel	> 2.2 - 22.2	0.7
4	Cobble	> 22.2 - 256	1.0
5	Boulder	> 256	0.3

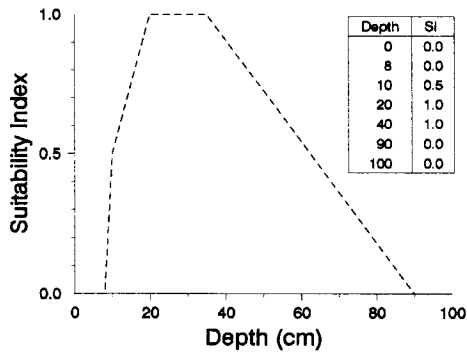
V11: Mean depth for parr during base summer flows.



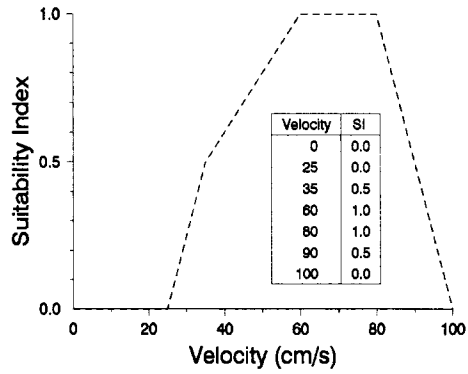
Reproductive Component

Evaluate at the head or tail of pools only if the substrate material is > 2.2 to 256 mm in diameter and water is at least 15 cm deep. The best time to conduct the field work would be in the fall, when Atlantic salmon are selecting spawning areas. Otherwise, attempt to estimate fall conditions by historical information on seasonal variation.

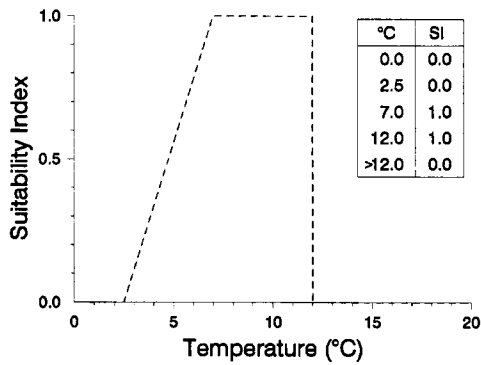
V12: Mean depth for reproduction at spawning time.



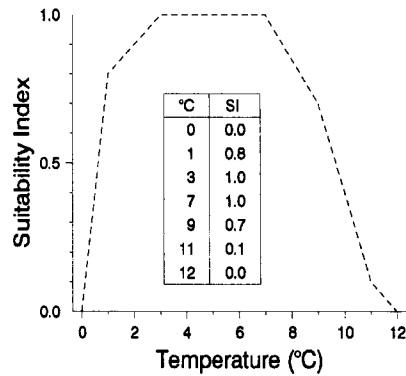
V13: Mean column velocity for reproduction during fall, or at flow conditions approximating those occurring during fall.



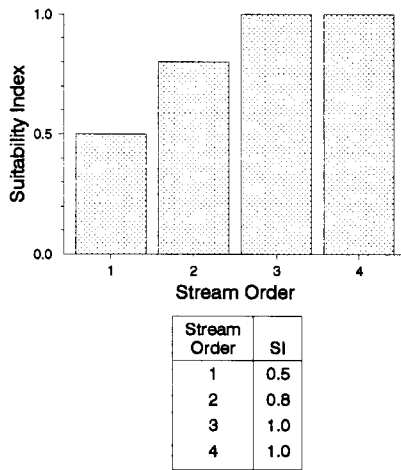
V14: Spawning temperature - If water temperature reaches then declines below 12°C in late October and early November, SI=1.0. Spawning will follow the date that water temperature reaches and maintains a temperature between 12° and 7°C.



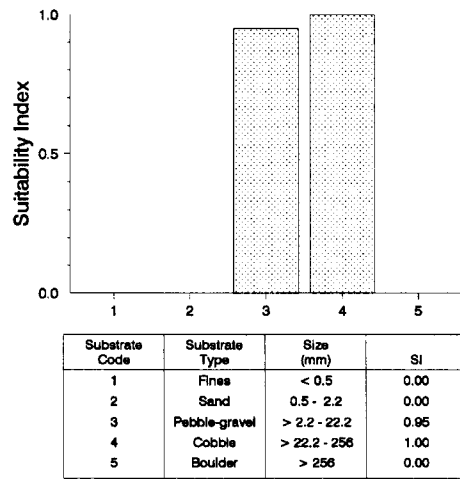
V15: Embryo incubation temperature - Average maximum daily temperature for the warmest 2-day period between November 15 and May 1, preferably taken with a hydrothermograph left in the stream over winter.



V16: Stream order, based on stream branches having permanent water flow.



V17: Dominant substrate for spawning and embryo incubation.



HSI Determination

Water Quality Component

$$CWQ = \text{lowest of } V1, V2, V3, V4, \text{ or } V5$$

Fry Component

$$CFry = V6 \times V7 \times V8$$

Parr Component

$$CParr = V9 \times V10 \times V11$$

Reproductive Component

$$CR = \text{lowest of } V14, V15, V16, \text{ or } V17$$

Habitat Suitability Index

$$HSI = (CWQ \times CFry \times CParr \times CR)$$

Some environmental situations might alter the appropriateness of the HSI approach. For example, the presence of aluminum in combination with high acidity may affect survival. Users may modify SI's based on local conditions, carefully documenting the rationale for the changes. Likewise, the structure of the component and final HSI model may be modified.

Rationale and Assumptions for Suitability Indices (SI's)

The SI's for Atlantic salmon represent the relation between habitat variables and the population density of fry and parr in freshwater streams; population density is assumed to indicate stream productivity. Another assumption is that animals select suitable habitats, when available, that enhance individual survival. Optimal habitat has a suitability value of 1.0. Where optimal habitat is unavailable or already fully occupied, the number of survivors in suboptimal habitat indicates habitat suitability (with a value less than 1.0). Suitability indices are proportional to population density, which is determined by distribution and survival of the species. The mean value of a habitat variable indicates habitat suitability for the area where the measurement was taken.

We assumed that contaminants are absent. If contaminants occur in the stream and their effects can be documented, then the user might assign an HSI of zero. Alternatively, the HSI might be calculated as if no contaminant were present, with a qualification added that this is the value if pollution remediation were implemented.

While we recognize that competition between species and between life stages might be important, competition is not modeled. The HSI model is based on physical factors only. The HSI value is stated as if competition were absent.

The velocity that Trial (1989) reported was measured where fish were actually located, which was usually less than the average column velocity. Morantz et al. (1987) and DeGraff and Bain (1986) measured mean velocity of the water column and the velocity selected by each individual. In both papers, the SI's developed for velocities selected by

fry and parr had suitability of 1.0 for a more restricted range of velocities than SI's for mean column velocity. Similarly, Rimmer et al. (1984) found that velocities selected by fry and parr were lower than velocities in the overlying water. We recommend measuring column velocity at 0.6 of the depth (i.e., at a point 60% of the way from the surface of the water column to the bed of the stream).

Field Application of the Models

For the mean maximum daily temperature for the warmest contiguous 3-day period of summer (V1), the SI was based on maximum summer temperatures of streams with Atlantic salmon populations and upper incipient lethal temperatures. The significance of maximum temperature is confounded because juvenile Atlantic salmon avoid high temperatures. The 3-day period of exposure corresponds to lethal exposure periods of some laboratory experiments. We recommend that hydrothermographs be placed in streams being evaluated. If hydrothermographs are not available, visit the stream during periods of hot weather to get daily temperatures.

Embryo incubation temperature (V15) was based on the acute lethal temperatures for Atlantic salmon eggs and embryos. The period of exposure reported in the literature varied from 24 to 72 h. Thus, some consideration of the duration of lethal temperature was included in the variable label. The ideal way to measure this variable would be to place hydrothermographs in or near the redds over winter. Without the equipment, the user may have to measure stream temperatures, guessing at the times, based on episodes of warm weather (probably in spring). The mean temperature (V2) should be for the growing season or summer—again we recommend a hydrothermograph. In addition, remember that V14 is the temperature during spawning and that if water temperatures reach, then decline below 12° C in late October and early November, spawning will follow when temperatures are between 12° and 7° C.

Calculate mean turbidity (V3) by month over as much of the year as possible. High turbidity during freshets is not as important as chronic exposure, which has a sustained inhibiting effect on feeding. The months during the growing season are most important. If available turbidity data are expressed as concentrations of suspended sediments (C) in mg/L, convert to NTU units with the formula $NTU = 10 + 0.178 C$ (Sigler et al. 1984).

Mean minimum oxygen saturation (V4) was based on acute tolerances of Atlantic salmon to low dissolved oxygen concentrations at several temperatures and the average conditions of streams that have populations. If low percent saturation of oxygen persisted for no more than 1 day, then the suitability of the habitat would be higher than if oxygen was low for an extended period. We recommend taking daily

measurements in the early morning on a cloudy day during the warmest summer periods. A recording oxygen probe in the stream would be ideal.

Minimum pH (V5) was based on the acute lethal pH for Atlantic salmon eggs and embryos. The period of exposure reported in the literature varied from 24 to 72 h. Thus, some consideration of the duration of lethal pH was included in the variable label. In addition, V5 includes consideration of frequency of low pH events. Other variables, such as aluminum, affect survival to acid exposure—users are encouraged to modify the SI if appropriate data are available for specific sites.

The area and time for calculating the mean for several of the variables were stated in Terrell et al. (1982), but we will repeat them to avoid confusion. We recommend that measurements be made at five transects, 10 m apart, across the stream. Establish the position of the first transect at random, such as at the position where a ball lands. Measure current, depth, and substrate at 1-m intervals across the stream, or at 0.25, 0.5, and 0.75 of the width if streams are less than 2 m wide. For spawning riffles, take a measurement at the head, tail, and center of the riffle. Bottom substrate is calculated by summing the linear amount of each type.

Lack of suitable water quality at a site or in a river system can limit the distribution of the species. The disappearance of Atlantic salmon from European and Canadian rivers coincident with decreased pH is evidence of a limiting factor (Haines 1981; Watt et al. 1983). Thus, the water quality component was included in the HSI as potentially limiting. However, habitats for all life stages are not necessary at each site for reproducing populations because interspersed habitats may provide for all of the species' needs. The Atlantic salmon's life cycle requires that some habitats exist within the drainage for each riverine life stage. The model user must be aware of the mix of different qualities of life stage habitats within the study area and drainage. Calculating a species HSI that combines all life stage components into one index obscures information but may be needed in an assessment. Thus, the model includes component indices for water quality, reproduction, fry, and parr and a formula for the species HSI.

Interpreting Model Outputs

There are numerous possible applications of the HSI model for Atlantic salmon. Potential users might differ widely in their understanding of the premises and limitations of the model. Only the most naive would take it "off the shelf," make a few measurements in a target habitat, and attempt to make far-reaching conclusions. Experts on life history and biology should be able to use the model in the more realistic context described below.

The HSI should be treated as a linear index to the carrying capacity of the particular habitat—the higher the HSI value, the more fish the habitat should be able to support. However, only physical and chemical characteristics of a habitat are considered. Biological interactions and the effect of barriers are ignored. Predation, human harvest, competition, and nutrition are not considered, even though they would obviously affect survival, density, or carrying capacity. For Atlantic salmon, habitat is often uninhabited because dams block access. Nevertheless, the model could assign a high HSI, indicating the potential to support salmon spawning if there were no barriers.

All models represent simplifications of complex systems. The purpose of HSI models is to help predict the responses of key species to development projects or management practices. These models may be useful for presenting simple alternatives to managers so that rational decisions can be made with data gathered at modest costs. The HSI model approach has been widely accepted because it provides a rational approach for evaluation of habitat that does not depend solely on the opinion of experts. We prefer that our model be used by experts as an aid to systematically applying their knowledge to complex problems.

Sources of Additional Models

The National Biological Service, Midcontinent Ecological Science Center, in Fort Collins, Colorado, maintains a library of SI's for use with the Instream Flow Incremental Methodology.

The Canadian Department of Fisheries and Oceans, St. John's, Newfoundland, has developed SI's to evaluate habitat for the various freshwater life stages of Atlantic salmon in Newfoundland (Scruton and Gibson 1993), and a workshop was held in 1992 to develop a model. The SI's were based on data on the density of juvenile Atlantic salmon and on the habitat from 242 stations on 18 rivers on the island of Newfoundland. Suitability indices consistently predicted densities of fry based on important habitat variables. Suitability indices were most useful if based on macrohabitat measurements of stream dimensions and characteristics rather than on the microhabitat for the location of individual fish.

The U.S. Army Corps of Engineers has developed an Aquatic Habitat Appraisal Guide, based on the Habitat Evaluation Procedures, using 16 habitat variables and HSI scores.

Two other National Biological Service ecological science centers (located in Leetown, West Virginia, and Columbia, Missouri) are evaluating habitat requirements for adult Atlantic salmon and developing an improved approach for evaluating water quality requirements.

Acknowledgments

We thank James W. Terrell, Jeanette Carpenter, and Henry E. Booke for reviewing earlier drafts of this manuscript. Jeanette Carpenter produced the final SI graphs.

Cited References

- Amiro, P. G. 1993. Habitat measurement and population estimation of juvenile Atlantic salmon (*Salmo salar*). Pages 81–97 in R. J. Gibson and R. E. Cutting, editors. Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Canadian Special Publication in Fisheries and Aquatic Sciences Number 118.
- Bain, M., and C. L. Robinson. 1988. Structure, performance, and assumptions of riverine Habitat Suitability Index models. Alabama Cooperative Fisheries and Wildlife Research Unit. Aquatic Resources Research Series 88-3. Auburn, Ala. 20 pp.
- Beland, K. F., R. M. Jordan, and A. L. Meister. 1982. Water depth and velocity preferences of spawning Atlantic salmon in Maine rivers. *North American Journal of Fisheries Management* 2:11–13.
- Berg, L., and T. G. Northcote. 1985. Changes in territorial, gill-flaring, and feeding behavior in juvenile coho salmon (*Oncorhynchus kisutch*) following short-term pulses of suspended sediment. *Journal of the Fisheries Research Board of Canada* 42:1410–1417.
- Bisson, P. A., and R. E. Bilby. 1982. Avoidance of suspended sediment by juvenile coho salmon. *North American Journal of Fisheries Management* 2:371–374.
- Bley, P. W. 1987. Age, growth, and mortality of juvenile Atlantic salmon in streams: A review. U.S. Fish and Wildlife Service Biological Report 87(4). 25 pp.
- Brett, J. R. 1979. Environmental factors and growth. Pages 599–675 in W. S. Hoar, D. J. Randall and J. R. Brett, editors. *Fish physiology*, Volume VIII. Bioenergetics and growth. Academic Press, New York.
- Chadwick, E. M. P. 1982. Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1496–1501.
- Chadwick, E. M. P. 1985. Fundamental research problems in the management of Atlantic salmon, *Salmo salar* L., in Atlantic Canada. *Journal of Fish Biology* 27A:9–25.
- Cooper, E. L., and R. C. Scherer. 1967. Annual production of brook trout (*Salvelinus fontinalis*) in fertile and infertile streams of Pennsylvania. *Pennsylvania Academy of Science Proceedings* 41:65–70.
- Crisp, D. T. 1991. Stream channel experiments on downstream movement of recently emerged trout, *Salmo trutta* L., and salmon, *S. salar* L.—III. Effects of developmental stage and day and night upon dispersal. *Journal of Fish Biology* 39:371–381.
- Crisp, D. T., and P. A. Carling. 1989. Observations on siting, dimensions and structure of salmonid redds. *Journal of Fish Biology* 34:119–134.
- Cunjak, R. A. 1988. Behavior and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. *Canadian Journal of Fisheries and Aquatic Sciences* 45:2156–2160.
- Cunjak, R. A. 1992. Comparative feeding, growth and movements of Atlantic salmon (*Salmo salar*) parr from riverine and estuarine environments. *Ecology of Freshwater Fish* 1:26–34.
- Danie, D. S., J. G. Trial, and J. G. Stanley. 1984. Species profiles: Life histories and environmental requirements of coastal fish and invertebrates (North Atlantic)—Atlantic salmon. U.S. Fish and Wildlife Service FWS/OBS-82/11.22. U.S. Army Corps of Engineers TR EL-82-4. 19 pp.
- Daye, P. G., and E. T. Garside. 1977. Lower lethal levels of pH for embryos and alevins of Atlantic salmon, *Salmo salar* L. *Canadian Journal of Zoology* 55:1504–1508.
- Daye, P. G., and E. T. Garside. 1980. Development, survival, and structural alterations of embryos and alevins of Atlantic salmon, *Salmo salar* L., continuously exposed to alkaline levels of pH from fertilization. *Canadian Journal of Zoology* 58:369–377.
- DeCola, J. N. 1970. Water quality requirements for Atlantic salmon. U.S. Department of the Interior Federal Water Quality Administration, Northeast Region, Boston, Mass. 42 pp.
- DeCola, J. N. 1975. Atlantic salmon restoration and the question of water quality. *International Atlantic Salmon Foundation Special Publication Series* 6:24–28.
- DeGraff, D. A., and L. H. Bain. 1986. Habitat use by and preferences of juvenile Atlantic salmon in two Newfoundland rivers. *Transactions of the American Fisheries Society* 115:671–681.
- Dwyer, W. P., and R. G. Piper. 1987. Atlantic salmon growth efficiency as affected by temperature. *Progressive Fish-Culturist* 49:57–59.
- Egglisshaw, H. J., and P. E. Shackley. 1985. Factors governing the production of juvenile Atlantic salmon in Scottish streams. *Journal of Fish Biology* 27A:27–33.
- Einarsson, S. M., D. H. Mills, and V. Johannsson. 1990. Utilization of fluvial and lacustrine habitat by anadromous Atlantic salmon, *Salmo salar* L., in an Iceland watershed. *Fisheries Research* 10:53–71.
- Elliott, J. M. 1991. Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshwater Biology* 25:61–70.
- Elson, P. F. 1975. Atlantic salmon rivers, smolt production and optimal spawning: An overview of natural production. *International Atlantic Salmon Foundation Special Publication Series* 6:96–119.
- Farmer, G. J., R. L. Saunders, T. R. Goff, C. E. Johnston, and E. B. Henderson. 1989. Some physiological responses of Atlantic salmon (*Salmo salar*) exposed to soft, acidic water during smolting. *Aquaculture* 82:229–244.
- Francis, A. A. 1980. Densities of juvenile Atlantic salmon and other species, and related data from electroseining studies in the Saint John River system, 1968–78. *Canadian Data Report on Fisheries and Aquatic Sciences Number* 178. 95 pp.
- Frenette, M., M. Caron, P. Julien, and R. J. Gibson. 1984. Interaction entre le débit et les populations de tacons (*Salmo salar*) de la rivière Matamec, Québec. *Canadian Journal of Fisheries and Aquatic Sciences* 41:954–963.

- Fry, E. F. J. 1971. The effect of environmental factors on the physiology of fish. Pages 1–98 in W. S. Hoar and D. J. Randall, editors. Fish physiology. Vol. 6. Environmental relations and behavior. Academic Press, New York.
- Garside, E. T. 1973. Ultimate upper lethal temperature of Atlantic salmon, *Salmo salar*. Canadian Journal Zoology 51:898–900.
- Gibson, R. J. 1993. The Atlantic salmon in fresh water: Spawning, rearing and production. Reviews in Fish Biology and Fisheries 3:39–73.
- Gibson, R. J., and R. A. Myers. 1988. Influence of seasonal river discharge on survival of juvenile Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences 45:344–348.
- Gibson, R. J., D. E. Stansbury, R. R. Whalen, and K. G. Hillier. 1993. Relative habitat use, and inter-specific and intra-specific competition of brook trout (*Salvelinus fontinalis*) and juvenile Atlantic salmon (*Salmo salar*) in some Newfoundland rivers. Pages 53–69 in R. J. Gibson and R. E. Cutting, editors. Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Canadian Special Publication in Fisheries and Aquatic Sciences Number 118.
- Gustafson-Marjanen, K. I. 1982. Atlantic salmon (*Salmo salar* L.) fry emergence: Success, timing, distribution. M.S. thesis, University of Maine, Orono. 72 pp.
- Gustafson-Greenwood, K. I., and J. R. Moring. 1990. Territory size and distribution of newly-emerged Atlantic salmon (*Salmo salar*). Hydrobiologia 206:125–131.
- Gustafson-Marjanen, K. A., and J. R. Moring. 1984. Construction of artificial redds for evaluating survival of Atlantic salmon eggs and alevins. North American Journal of Fisheries Management 4:455–456.
- Haines, T. A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: A review. Transactions of the American Fisheries Society 110:669–707.
- Hamilton, K., and E. P. Bergersen. 1985. Methods to estimate aquatic habitat variables. Colorado State University, Ft. Collins. 260 pp.
- Heggenes, J., and R. Borgstrom. 1991. Effect of habitat types on survival, spatial distribution and production of an allopatric cohort of Atlantic salmon, *Salmo salar* L., under conditions of low competition. Journal of Fish Biology 38:267–280.
- Heggenes, J., Å. Brabrand, and S. J. Saltveit. 1990. Comparison of three methods for studies of stream habitat use by young brown trout and Atlantic salmon. Transactions of the American Fisheries Society 119:101–111.
- Heggenes, J., Å. Brabrand, and S. J. Saltveit. 1991. Microhabitat use by brown trout, *Salmo trutta* L. and Atlantic salmon, *S. salar* L., in a stream: A comparative study of underwater and river bank observations. Journal of Fish Biology 38:259–266.
- Heggenes, J., and T. Traaen. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. Journal of Fish Biology 32:717–727.
- Hesthagen, T. 1988. Movements of brown trout, *Salmo trutta*, and juvenile Atlantic salmon, *Salmo salar*, in a coastal stream in northern Norway. Journal of Fish Biology 32:639–653.
- Huntingford, F. A., N. B. Metcalfe, and J. E. Thorpe. 1988. Choice of feeding station in Atlantic salmon, *Salmo salar*, parr: Effects of predation risk, season and life history strategy. Journal of Fish Biology 33:917–924.
- Huntsman, A. G. 1942. Death of salmon and trout with high temperature. Journal of the Fisheries Research Board of Canada 5:485–501.
- Jensen, A. J., and B. O. Johnsen. 1986. Different adaptation strategies of Atlantic salmon (*Salmo salar*) populations to extreme climates with special reference to some cold Norwegian rivers. Canadian Journal of Fisheries and Aquatic Sciences 43:980–984.
- Jordan, R. M., and K. F. Beland. 1981. Atlantic salmon spawning survey and evaluation of spawning success. Atlantic Sea-Run Salmon Commission, Augusta, Maine. AFS-20-R. 25 pp.
- Kane, T. R. 1989. Atlantic salmon brood stock records. Pages 30–31 in H. L. Kincaid and J. G. Stanley, editors. Atlantic salmon brood stock management and breeding handbook. U.S. Fish and Wildlife Service Biological Report 89(12).
- Kennedy, G. J. A., and C. D. Strange. 1986. The effects of intra- and inter-specific competition on the distribution of stocked juvenile Atlantic salmon, *Salmo salar* L., in relation to depth and gradient in an upland trout, *Salmo trutta* L., stream. Journal of Fish Biology 29:199–214.
- Knight, A. E., G. Marancik, and J. C. Greenwood. 1981. Atlantic salmon production potential of the Mad River, New Hampshire 1975–1980. U.S. Fish and Wildlife Service, Laconia, N.H. 14 pp.
- Lacroix, G. L., and D. R. Townsend. 1987. Responses of juvenile Atlantic salmon (*Salmo salar*) to episodic increases in acidity of Nova Scotia rivers. Canadian Journal of Fisheries and Aquatic Sciences 44:1475–1484.
- Leim, A. H., and W. B. Scott. 1966. Fishes of the Atlantic coast of Canada. Bulletin of the Fisheries Research Board of Canada Number 155. 485 pp.
- Lear, W. H. 1993. The management of Canadian Atlantic salmon fisheries. Pages 151–176 in L. S. Parsons and W. H. Lear, editors. Perspectives on Canadian marine fisheries management. National Research Council of Canada, Ottawa, Ont.
- MacKenzie, C., and J. R. Moring. 1988. Estimating survival of Atlantic salmon during the intragravel period. North American Journal of Fisheries Management 8:45–49.
- McCrimmon, H. R. 1954. Stream studies on planted Atlantic salmon. Journal of the Fisheries Research Board of Canada 11:362–403.
- McFadden, J. T., and E. L. Cooper. 1962. An ecological comparison of six populations of brown trout (*Salmo trutta*). Transactions of the American Fisheries Society 91:53–62.
- Mills, D. 1989. Ecology and management of Atlantic salmon. Chapman and Hall, London and New York. 351 pp.
- Morantz, D. L., R. K. Sweeney, C. S. Shirvell, and D. A. Longard. 1987. Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 44:120–129.
- Netboy, A. 1974. The salmon: Their fight for survival. Houghton-Mifflin Company. Boston, Mass. 594 pp.
- Newcombe, C. P., and D. D. MacDonald. 1991. Effects of suspended sediments on aquatic ecosystems. North American Journal of Fisheries Management 11:72–82.

- Norrgren, L., and E. Degerman. 1993. Effects of different water qualities on the early development of Atlantic salmon and brown trout exposed in situ. *Ambio* 22:213-218.
- Peterson, R. H. 1978. Physical characteristics of Atlantic salmon spawning gravel in some New Brunswick, Canada, streams. Canadian Fisheries and Marine Service Technical Report Number 785. iv + 28 pp.
- Peterson, R. H., P. G. Daye, and J. L. Metcalfe. 1980. Inhibition of Atlantic salmon (*Salmo salar*) hatching at low pH. *Canadian Journal of Fisheries and Aquatic Sciences* 37:770-774.
- Peterson, R. H., and J. L. Metcalfe. 1979. Responses of Atlantic salmon alevins to temperature gradients. *Canadian Journal of Zoology* 57:1424-1430.
- Power, G. 1969. The salmon of Ungava Bay. Arctic Institute of North America Technical Report Number 22. Calgary, Alberta. 72 pp.
- Rideout, S. 1989. History of the Atlantic salmon restoration program. Pages 1-4 in H. L. Kincaid and J. G. Stanley, editors. Atlantic salmon brood stock management and breeding handbook. U.S. Fish and Wildlife Service Biological Report 89(12).
- Riley, S. C., G. Power, and P. E. Ihssen. 1989. Meristic and morphometric variation in parr of ouananiche and anadromous Atlantic salmon from rivers along the north shore of the Gulf of St. Lawrence. *Transactions of the American Fisheries Society* 118:515-522.
- Rimmer, D. M., U. Paim, and R. L. Saunders. 1984. Changes in the selection of microhabitat by juvenile Atlantic salmon (*Salmo salar*) at summer-autumn transition in a small river. *Canadian Journal of Fisheries and Aquatic Sciences* 41:469-475.
- Sayers, R. E., Jr. 1990. Habitat use patterns of native brook trout and stocked Atlantic salmon: Inter-specific competition and salmon restoration. Ph.D. thesis, University of Maine, Orono. 125 pp.
- Schaffer, W. M., and P. F. Elson. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. *Ecology* 56:577-590.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bulletin of the Fisheries Research Board of Canada Number 184. iv + 996 pp.
- Scruton, D. A., and R. J. Gibson. 1993. The development of habitat suitability curves for juvenile Atlantic salmon (*Salmo salar*) in riverine habitat in insular Newfoundland, Canada. Pages 149-161 in R. J. Gibson and R. E. Cutting, editors. Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Canadian Special Publication in Fisheries and Aquatic Sciences Number 118.
- Siginevich, G. P. 1967. Nature of the relationship between increase in size of Baltic salmon fry and the water temperature. *Gidrobiologicheskii Zhurnal* 3:43-48. Fisheries Research Board of Canada Translation Series Number 952. 14 pp.
- Sigler, J. W., T. C. Bjornn, and F. H. Everest. 1984. Effects of chronic turbidity on density and growth of steelhead and coho salmon. *Transactions of the American Fisheries Society* 113:142-150.
- Sosiak, A. J., R. G. Randall, and J. A. McKenzie. 1979. Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams. *Journal of the Fisheries Research Board of Canada* 36:1408-1412.
- Symons, P. E. K., and M. Heland. 1978. Stream habitats and behavioral interactions of underyearling and yearling Atlantic salmon (*Salmo salar*). *Journal of the Fisheries Research Board of Canada* 35:175-183.
- Terrell, J. W., T. E. McMahon, P. D. Inskip, R. F. Raleigh, and K. L. Williamson. 1982. Habitat Suitability Index models: Appendix A. Guidelines for riverine and lacustrine applications of fish HSI models with the Habitat Evaluation Procedures. U.S. Fish and Wildlife Service FWS/OBS-82/10.A. 54 pp.
- Thompson, D. 1993. Status of the Atlantic salmon, *Salmo salar* L., its distribution and the threats to natural populations. Pages 303-306 in J.G. Cloud and G.H. Thorgaard, editors. Genetic conservation of salmonid fishes. Plenum Press, New York and London.
- Thorpe, J. E. 1988. Salmon enhancement: Stock discreteness and choice of material for stocking. Pages 373-388 in D. Mills and D. Piggins, editors. Atlantic salmon, planning for the future. Timber Press, Portland, Ore.
- Tremblay, G., F. Caron, R. Verdon, and M. Lessard. 1993. Influence des parametres hydromorphologiques sur l'utilisation de l'habitat par les juveniles du Saumon atlantique (*Salmo salar*). Pages 127-137 in R. J. Gibson and R. E. Cutting, editors. Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Canadian Special Publication in Fisheries and Aquatic Sciences Number 118.
- Trial, J. G. 1989. Testing habitat models for blacknose dace and Atlantic salmon. Ph.D. thesis, University of Maine, Orono. 129 pp.
- Trial, J. G., and J. G. Stanley. 1984. Calibrating effects of acidity on Atlantic salmon for use in habitat suitability models. Completion Report A-054-ME. Land and Water Resources Center, University of Maine, Orono. 37 pp.
- Trial, J. G., C. S. Wade, and J. G. Stanley. 1984. HSI models for northeastern fishes. Pages 17-56 in J. W. Terrell, editor. Proceedings of a workshop on fish Habitat Suitability Index models. U.S. Fish and Wildlife Service Biological Report 85(6).
- U.S. Fish and Wildlife Service. 1981. Standards for the development of Habitat Suitability Index models. 103 ESM. U.S. Fish and Wildlife Service, Division of Ecological Services, Washington, D.C. 168 pp.
- Warner, K. 1963. Natural spawning success of landlocked salmon, *Salmo salar*. *Transactions of the American Fisheries Society* 92:161-164.
- Warner, K., and K. A. Havey. 1985. Life history, ecology and management of Maine landlocked salmon (*Salmo salar*). Maine Department of Inland Fisheries and Wildlife. Augusta. 127 pp.
- Watt, W. D., C. D. Scott, and W. J. White. 1983. Evidence of acidification of some Nova Scotian rivers and its impact on Atlantic salmon, *Salmo salar*. *Journal of the Fisheries Research Board of Canada* 40:462-473.

Appendix. Model Evaluation Form

The habitat suitability index (HSI) model for juvenile Atlantic salmon is intended for use in the habitat evaluation procedures (HEP) developed by the U.S. Fish and Wildlife Service. This model for nonmigratory freshwater stages of Atlantic salmon is the third generation of a model that was developed originally from a review and synthesis of existing information on Atlantic salmon. The model was modified based on field testing in Maine in 1984 and further evaluated by comparison of alternative model outputs with a long-term data base from Canada and habitat selection data gathered in Maine. Despite the testing of this HSI model, further improvement and revision could result in an even better and more useful model. Please complete this form following application or review of the model. Feel free to include additional information that may be of use to either a model developer or model user. We also would appreciate information on model testing, modification, and application, as well as copies of modified models or test results. Please return this form to

Landscape and Habitat Analysis Section
National Biological Service
Midcontinent Ecological Science Center
4512 McMurry Avenue
Fort Collins, CO 80525-3400

Thank you for your assistance.