*North American Journal of Fisheries Management* 18:31–45, 1998


# Simulating Migration Mortality of Atlantic Salmon Smolts in the Merrimack River

B. F. BLACKWELL,[1,2] G. GRIES, AND F. JUANES

*Department of Forestry and Wildlife Management, University of Massachusetts Amherst, Massachusetts 01003, USA*

K. D. FRIEDLAND

*National Marine Fisheries Service, Northeast Fisheries Science Center Woods Hole, Massachusetts 02543, USA*

L. W. STOLTE

*U.S. Fish and Wildlife Service, Office of the Central New England Anadromous Fish Coordinator 151 Broad Street, Nashua, New Hampshire 03063, USA*

J. F. MCKEON

*U.S. Fish and Wildlife Service, Office of Fishery Assistance Federal Building, Room 124, Laconia, New Hampshire 03246, USA*

*Abstract*.—Successful restoration of Atlantic salmon *Salmo salar* to New England rivers involves the identification and management of mortality sources at different life history stages. The purpose of this study was to examine the effects of mortality during migration on Atlantic salmon smolts exiting the Merrimack River. Our objective was to review data pertaining to smolt production, migration, passage at hydroelectric facilities, and predation in the Merrimack River and construct a simulation model of smolt migration. We constructed a migration model incorporating river-flow-based decision rules affecting migration rate, delay at dams, dam passage mortality, and migration mortality. Mean model estimates of in-river survival ranged from 0.7% to 23.5%. Estimated transit times generally increased in migration scenarios in which smolts began migration later in the season; beginning migration later in the season also resulted in lower in-river survival. The model was evaluated by comparing records of returns of two-seawinter adults to the Merrimack River to a likely range of marine survival rates. For 9 of 14 smolt years, model estimates for the number of smolts exiting the river were comparable with the range of smolt output necessary to achieve the corresponding adult returns. Model estimates of in-river survival that fell below the the lower threshold for 5 of the 14 smolt years could be explained in part by relatively high marine survival experienced by these cohorts. We argue that this model can have important applications in population assessment, river management, and salmon restoration.

In precolonial New England, at least 28 major rivers contained populations of Atlantic salmon *Salmo salar* (MacCrimmon and Gots 1979). The largest populations in New England were in the Connecticut, Merrimack, Androscoggin, Kennebec, and Penobscot rivers (USFWS 1989). Yet, by the end of the 19th Century, dam construction and overfishing had extirpated most of these populations (Moring 1987). Persistent habitat loss threatened the remaining Atlantic salmon runs throughout the first half of the 20th Century. However, over the last half century, cooperative efforts between state and federal conservation agencies have succeeded in revitalizing portions of the original spawning and nursery habitat, protecting remaining habitat, and improving passage facilities at dams (Baum 1983; Moring 1987; Stolte 1994).

Although conservation of freshwater habitat is critical, it is important to recognize that adult recruitment is affected not only by in-river survival of smolts but by at-sea events as well. The combination of effects was illustrated by Scarnecchia et al. (1989), who examined yields of Atlantic salmon from 59 Icelandic rivers relative to streamflows and sea and air temperatures. They found that yields fluctuated most in stocks that experienced variable spring and summer ocean temperatures, but seasonal streamflow also was an important explanatory variable. Friedland et al. (1993) reported that stocks from different loca-

[1] Corresponding author: nwrcsandusky@lrbcg.com
[2] Present address: U.S. Department of Agriculture, Animal and Plant Health Inspection Service, National Wildlife Research Center, 6100 Columbus Avenue, Sandusky, Ohio 44870, USA.

tions, and thus experiencing different migration obstacles and estuarine effects, exhibited coherence in the return rates for two-seawinter (2SW) adults. They concluded that broadscale effects during the postsmolt year regulated annual recruitment in this group of stocks. More specifically, rates of 1SW and 2SW returns are related to postsmolt growth, which is dependent upon environmental conditions at sea (Gudjonsson et al. 1995; Friedland and Haas 1996; Friedland et al. 1996).

Neighboring (and distant) stocks may have significantly different mean rates of return but show correlated year-to-year variability in return rate (Friedland et al. 1996). The correlation indicates a broadscale forcing function that acts on all stocks in the group; the differing mean return rates indicate that smolt survival during river and estuarine residencies varies among rivers. Such a coherence pattern can persist only if marine influences on survival dominate earlier influences and if marine effects are similar among stocks in a group. In the northeastern United States, return rates to some rivers remained nearly constant fractions of rates to neighboring rivers even after commercial marine fisheries for Atlantic salmon were closed (Friedland and Haas 1996). Thus, discrepancies in adult return rates among rivers imply differing rates of smolt emigration among rivers. The purpose of this study was to examine the effects of smolt loss in the Merrimack River during migration on the rate of smolts exiting the system. Our objective was to construct a simulation model of smolt migration based on a review of data on smolt production, migration, passage of hydroelectric dams, and predation in the Merrimack River.

## Methods

*Study area*.—The Merrimack River basin drains an area of 12,975 km$^2$, 76% of which is in central New Hampshire and the rest in northeastern Massachusetts (Stolte 1994). The Merrimack River has nine major tributaries, the largest of which, the Pemigewasset River, has five principal tributaries. Since 1975, restoration of Atlantic salmon in the Merrimack River has focused primarily on annual stockings of cultured fry during April and May. Over 60% of habitat suitable for smolt production in the Merrimack River basin is in the Pemigewasset River subbasin (Stolte 1994). From the mouth of the Pemigewasset to the mouth of the Merrimack (Figure 1), migrating smolts encounter seven hydropower facilities and one earthen flood control dam (Table 1). The Merrimack tributary

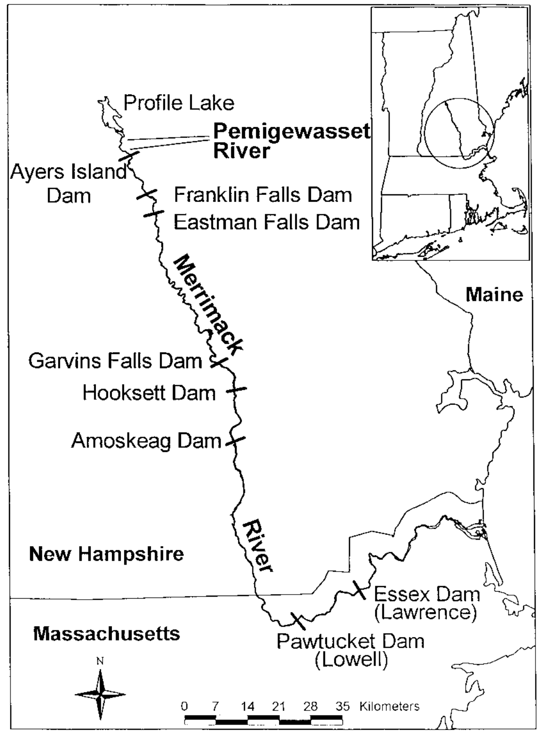


FIGURE 1.—Map of the main stem of the Merrimack River, showing location of dams.

system, apart from the Pemigewasset River, contains over 100 dams (Stolte 1994).

*Model construction*.—The number of smolts exiting a river obstructed by dams can be viewed, in its simplest form, as resulting from a sequence of survival functions associated with the number of smolts migrating past and between successive dams. We constructed a smolt migration model for the main stem of the Merrimack River consisting of river-flow-based decision rules affecting migration rate, mortality at time of dam passage, and site-specific mortality during migration between dams (Figure 2). Smolts began migration above the Ayers Island Dam (Figure 1), from which each individual was monitored relative to day (1 April–30 June) and location (e.g., dam or interval between dams) until it died or exited to the sea. Day and location were also used to assign the appropriate river flow. River flows (m$^3$/s) incorporated in decision rules reflected mean daily rates measured at the closest of three U.S. Geological Survey (USGS) gauges: above Ayers Island Dam, between Ayers Island and Eastman Falls dams, and in the lower Merrimack River at Lowell.

The numbers of smolts migrating during 1980–

TABLE 1.—Dams on the main stem of the Merrimack River.

| Dam | River km[a] | Turbine capacity ($m^3/s$) | Fish passage facility[b] | |
|---|---|---|---|---|
| | | | Upstream | Downstream |
| Ayers Island | 210 | 46.2 | None | Spill gate |
| Franklin (flood control) | 196 | 72.8 | None | None |
| Eastman Falls | 188 | 140.0 | None | Bypass |
| Garvin Falls | 142 | 151.2 | None | Bypass |
| Hooksett | 132 | 42.0 | None | Bypass |
| Amoskeag | 119 | 140.0 | Vertical slot | Bypass |
| Pawtucket | 67 | 196.0 | Vertical slot | Bypass |
| Essex | 48 | 224.0 | Lift | Bypass |

[a] From the mouth of the Merrimack River.
[b] U.S. Fish and Wildlife Service, unpublished data.

1993 were derived from the combination of production estimates of age-1 parr at index sites within the Pemigewasset region of the Merrimack River (U.S. Fish and Wildlife Service, unpublished data) and the assumption of 65% overwinter survival (Symons 1979). Parr abundance was estimated by stratified sampling of Atlantic salmon habitats and equal-effort catch–removal by electrofishing. The majority of Atlantic salmon smolts in the Merrimack River begin migration at age 2 (USFWS 1989). Precision estimates for the number of smolts migrating per year were unavailable.

Smolt migration was started in the model according to river temperature cues patterned after observations made for Atlantic salmon populations in the region and elsewhere (McCleave 1978; Solomon 1978; Jonsson and Ruud-Hansen 1985; McMenemy and Kynard 1988; Jonsson et al. 1989). The exact temperature threshold appears to vary by river, but most smolt runs begin when water temperatures above 10°C are sustained. In arctic regions where temperatures vary little after the initial spring snowmelt, smolts migrate at lower temperatures under the influence of river flow (Österdahl 1969; Hesthagen and Garnås 1986). This type of migration response does not appear relevant to the Merrimack River stock. Therefore, from comparison with other temperate rivers in North America and Europe, we modeled the mode of the smolt migration as the first day after five consecutive days of water temperatures greater than or equal to 10°C. This decision is generally consistent with observations of McMenemy and Kynard (1988), who reported that migration of smolts in the Connecticut River extends from early April through mid-May. We modeled the balance of the run as a normal distribution over 21 d each year (Figure 2).

Lacking a complete river temperature time series for the study period, we relied on a correlated time series from a neighboring river system. We used mean daily river temperatures measured at the Connecticut Yankee generating station on the lower Connecticut River (Northeast Utilities, unpublished data). The usefulness of Connecticut River data for deriving a temperature-based migration modal date was evaluated by regressing mean daily river temperatures measured on the Merrimack at Ayers Island, Eastman Falls, and Garvin Falls dams on Connecticut River temperatures for the period 1 April–30 June 1990–1993 (Figure 3). Merrimack River temperatures were significantly ($P < 0.01$) correlated to Connecticut River temperatures and exhibited, as suspected, the greatest correspondence at the southernmost dam. The migration modal dates for the base or standard scenario were 1, 4, 9, 13, 7, and 3 May (1980–1985); 26 and 27 April (1986–1987); and 13, 4, 1, 3, and 10 May and 28 April (1988–1993).

*Migration parameters.*—Because of potential entrainment of smolts in headponds at Ayers Island and Eastman Falls dams (R. Dumore, Public Service of New Hampshire [PSNH], personal communication) we incorporated river-flow-based migration delays into the decision rules (Table 2). Decision rules defining smolt mortality during passage of the six uppermost dams and migration between those dams were based on observations of smolt route selection during dam passage and subsequent detection of surviving smolts at sites downstream (PSNH 1992). We assumed a linear relationship between observed mortalities due to passage of Ayers Island Dam and migration to Eastman Falls Dam and the associated rates of river flow (Table 2). Observational data relating passage and migration mortality to specific ranges of river flow at dams downstream of Ayers Island were unavailable. Instead, we assumed that passage mortalities at Eastman Falls (except under migration delay conditions), Garvin Falls, and

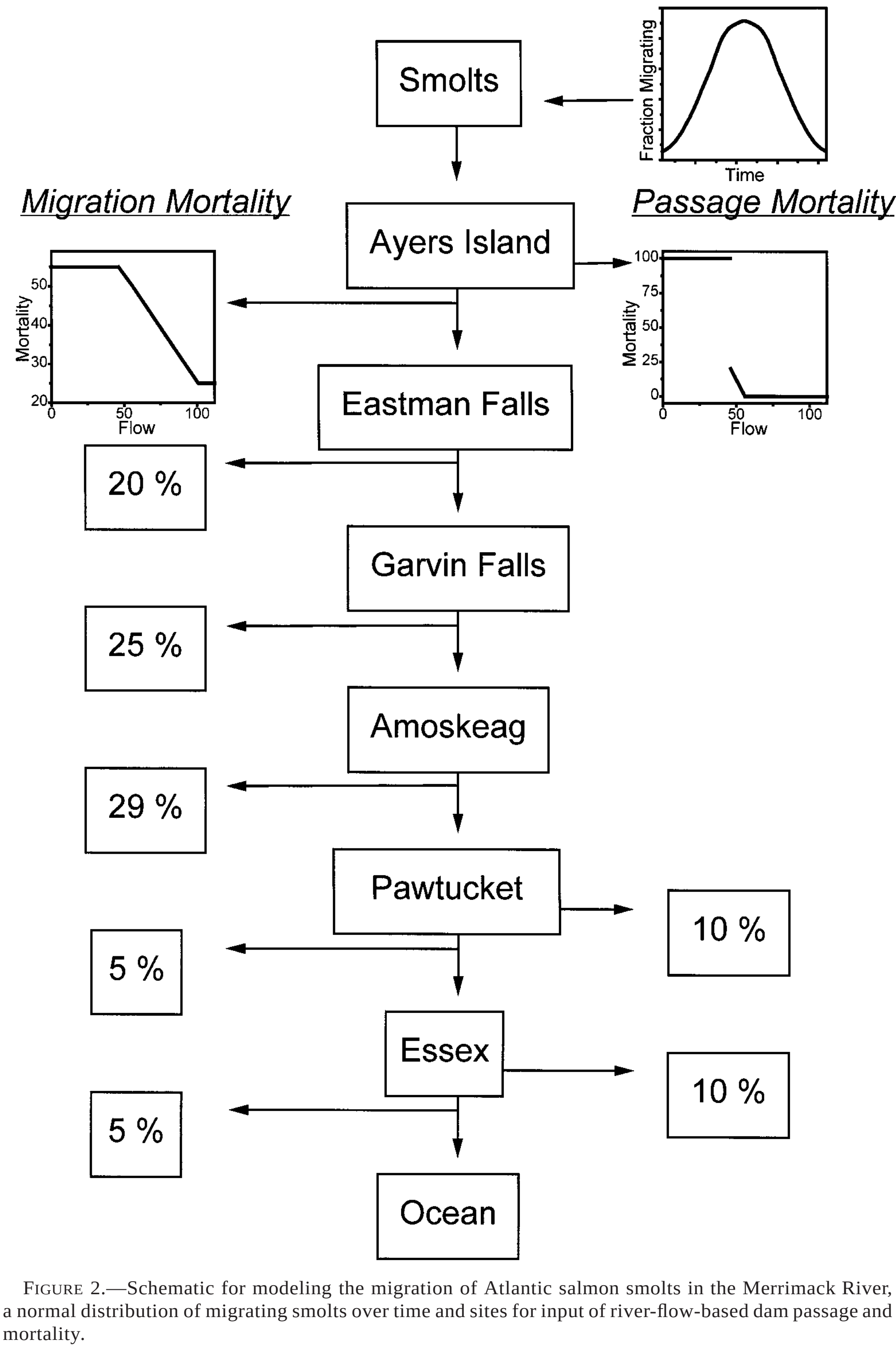


FIGURE 2.—Schematic for modeling the migration of Atlantic salmon smolts in the Merrimack River, including a normal distribution of migrating smolts over time and sites for input of river-flow-based dam passage and migration mortality.

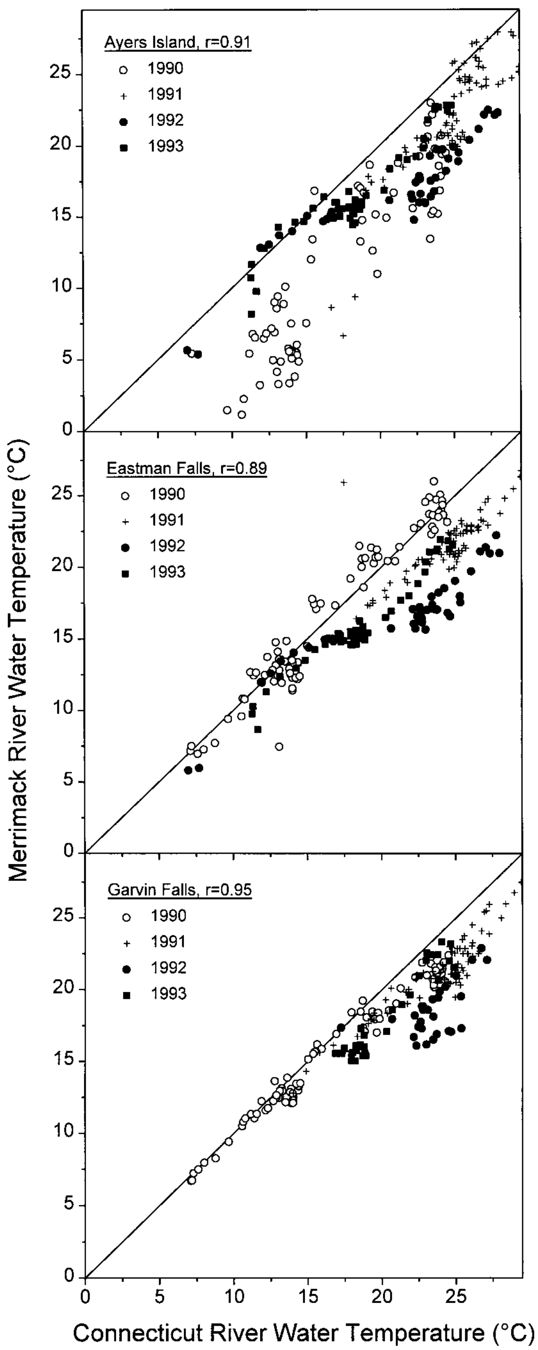


FIGURE 3.—Regression of water temperatures measured at three dams on the Merrimack River on water temperatures measured at the mouth of the Connecticut River.

Amoskeag dams were equal to zero and that migration mortalities (PSNH 1992) were fixed. Specific data for passage of Franklin Falls and Hooksett dams were not reported by PSNH; instead, these dams were included within migration intervals bounded by other dams (Figure 1). We note that the PSNH smolt movement data did not generate accurate estimates of survival because biases reflecting mortality from radio-tagging, tag malfunction, tag regurgitation, battery expiration, predation, and failure to migrate were not accounted for in the study design. Therefore, we assumed that the statistics for passage and migration success represented minimum estimates of survival.

At the two lowermost dams, Pawtucket and Essex, migration delays were incorporated because of the potential entrainment of smolts in canal systems (Consolidated Hydro., Inc., unpublished data; J. Warner, USFWS, personal communication). Further, we assumed that passage mortality reflected the combination of entrainment and turbine mortality. This mortality was set to a level of 10% (Table 2) after we inspected the facilities and conferred with passage experts (R. Iwanowicz, Massachusetts Division of Marine Fisheries, and Warner, personal communications). Also, although we had no data concerning smolt mortality in free-flowing areas of the lower Merrimack River, we assumed that migration mortality occurred between the Pawtucket and Essex dams and within the estuarine area below Essex Dam at levels of 5% (Table 2).

We assigned rates of migration relative to river flow and location in the river. Migration rates were based on unpublished observation of smolts in the Merrimack River itself indicating that transit of the system can take as little as 5 d and as many as 35 d (USFWS, unpublished data). From this bracketing of transit times, we developed linear relationships between migration rate and flow (Table 2). Migration rates used in this model are generally corroborated elsewhere. For example, Fried et al. (1978) reported a mean rate of travel of 22 km/d for hatchery-reared age-2 smolts released within the Penobscot River estuary. Spicer et al. (1995) found that age-1 smolts released approximately 91 km upstream from the mouth of the Penobscot River traveled at a mean rate of 3.7 km/d (range, 0.5–15.7 km/d). Finally, Fängstam (1993) reported a downstream displacement of less than 20 km/d for Baltic Atlantic salmon smolts at water velocities of 19.3–20.5 cm/s.

Survival during dam passage and migration between dams was determined by a comparison of

TABLE 2.—River-flow-based decision rules used in modeling the migration of Atlantic salmon smolts in the main stem of the Merrimack River.

| Location and river flow ($m^3/s$) | Parameter value |
|---|---|
| Ayers Island Dam | |
| Pemigewasset River flow | |
| <46.2 | The smolt is held for up to 10 d awaiting a higher river flow. After 10 d, passage mortality = 1.0 |
| 46.2 to <56.0 | Passage mortality = (river flow·−0.1019368) + 5.7084608 |
| ≥56.0 | Passage mortality = 0.0 |
| Migration to Eastman Falls Dam | |
| Pemigewasset River flow | |
| <46.2 | Migration mortality = 0.55 |
| 46.2 to <56.0 | Migration mortality = (river flow·−0.005103) + 0.7856151 |
| 56 to <100.8 | Migration mortality = (river flow·−0.0055804) + 0.8125 |
| ≥100.8 | Migration mortality = 0.25 |
| <46.2 | Migration rate = 10 km/d |
| 46.2 to <672.0 | Migration rate = (river flow·0.05194805) + 7.090909 |
| ≥672.0 | Migration rate = 42 km/d |
| Eastman Falls Dam | |
| Merrimack River flow above Eastman | |
| <72.8 | The smolt is held for up to 5 d awaiting a higher river flow. After 5 d, passage mortality = 1.0 |
| ≥72.8 | Passage mortality = 0.0 |
| Migration to Garvin Falls Dam | |
| Merrimack River flow above Eastman | Migration mortality = 0.20 at all flows |
| <46.2 | Migration rate = 10 km/d |
| 46.2 to <672.0 | Migration rate = (river flow·0.05194805) + 7.090909 |
| ≥672.0 | Migration rate = 42 km/d |
| Garvin Falls Dam | |
| Merrimack River flow above Eastman | Passage mortality = 0.0 at all flows |
| Migration to Amoskeag Dam | |
| Merrimack River flow above Eastman | Migration mortality = 0.25 at all flows |
| <46.2 | Migration rate = 10 km/d |
| 46.2 to <672.0 | Migration rate = (river flow·0.05194805) + 7.090909 |
| ≥672.0 | Migration rate = 42 km/d |
| Amoskeag Dam | |
| Merrimack River flow above Eastman | Passage mortality = 0.0 at all flows |
| Migration to Pawtucket Dam | |
| Merrimack River flow above Eastman | Migration mortality = 0.29 at all flows |
| <46.2 | Migration rate = 10 km/d |
| 46.2 to <672.0 | Migration rate = (river flow·0.05194805) + 7.090909 |
| ≥672.0 | Migration rate = 42 km/d |
| Pawtucket Dam | |
| Merrimack River flow at Lowell | |
| <196.0 | The smolt is held for up to 5 d awaiting a higher river flow. After 5 d, passage mortality = 1.0 |
| ≥196.0 | Passage mortality = 0.90 |
| Migration to Essex Dam | |
| Merrimack River flow at Lowell | Migration mortality = 0.05 at all flows |
| <46.2 | Migration rate = 10 km/d |
| 46.2 to <672.0 | Migration rate = (river flow· 0.05194805) + 7.090909 |
| ≥672.0 | Migration rate = 42 km/d |
| Essex Dam | |
| Merrimack River flow at Lowell | |
| <224.0 | The smolt is held for up to 5 d awaiting a higher river flow. After 5 d, passage mortality = 1.0 |
| ≥224.0 | Passage mortality = 0.10 |
| Migration to sea | |
| Merrimack River flow at Lowell | Migration mortality = 0.05 at all flows |
| <46.2 | Migration rate = 10 km/d |
| 46.2 to <672.0 | Migration rate = (river flow·0.05194805) + 7.090909 |
| ≥672.0 | Migration rate = 42 km/d |

the mortality factor and a random variable. Each mortality factor, either fixed or flow dependent, was used as a threshold value and was compared to a uniform random number to determine whether a mortality occurred at that location. The date of each passage event was tracked for individual fish in order to incorporate the appropriate river flow, mortality parameter, delay time, and migration rate. Results represent the mean values of 200 realizations for each smolt year (1980–1993) and for each of five migration scenarios testing the temperature-derived modal migration date plus or minus 7 and 14 d.

*Model sensitivity and evaluation.*—Because passage and migration mortalities were arranged sequentially within the model (Figure 2), their effect on the proportion of smolts exiting the river was multiplicative. Thus, a change in the probability of mortality during passage of a particular dam or migration between dams produced (given exceptions created by randomly generated comparison values) a nearly equal change in the proportion of smolts surviving migration. However, by varying migration modal dates (i.e., the midpoint of the 21-d normal distribution of migrating smolts), we could vary the river flows encountered by smolts, which in turn affected the probability of mortality during dam passage and movement between dams. The sensitivity of the model to variation in modal migration date was assessed by shifting the date plus or minus 7 and 14 d, while other parameters were held constant.

To evaluate the decision rules incorporated in the migration model, we used records of 2SW adult returns to the Merrimack River for 1982–1995. State and federal agencies counted returning adults at the Essex Dam fish lift from early May through July and from mid-September through October each year. Included in records of returning adults were fish that were incidentally landed and killed by sport anglers downstream from Essex Dam. Scale samples were used to age returning adults. Typically, over 80% of adult returns to the Merrimack River were 2SW individuals (USFWS, unpublished data). We assumed that all 2SW returns originated from fry stocked in the Pemigewasset River. We validated the model by comparing the number of successful migrants from annual model runs to a range of smolts necessary to achieve the given numbers of 2SW returns, assuming a marine survival range of 0.5–5.0% (Bley and Moring 1988).

Because we assumed a normal distribution for the estimated number of migrating smolts for 1980–1993 and created decision rules that were based on river flow, we assessed the role of these variables in the recruitment of returning 2SW adults. We first regressed returns of 2SW salmon from the 1980–1993 smolt cohorts on the number of smolts beginning migration and the average of the mean daily river flows for May measured between Ayers Island and Eastman Fall dams. The independent variables were not transformed. Next, we calculated Pearson's product-moment correlation coefficient (Conover 1980) between the observed 2SW returns and the predicted values from the regression model ($\alpha = 0.05$).

## Results

### *Model Estimates*

For all annual simulations considered in this study, river flows within the headwaters of the Merrimack River directly affected smolt passage at Ayers Island Dam, the first dam on the main stem. During early May, river flows generally exceeded the turbine capacity (46.2 $m^3$/s) at Ayers Island Dam (Figure 4), a flow rate below which a migration delay was incorporated (Table 2). Further, for 12 of the 14 years, modal dates for the standard migration scenario fell within periods when river flow exceeded turbine capacity. However, with the exception of 1983–1984 and 1989–1990, river flows had decreased below the turbine capacity at Ayers Island Dam before the first week of June.

Over the range of migration scenarios simulated, the time required to complete migration, which also was affected by river flow, varied annually. For 8 of the 14 years, smolts migrating under the earliest-migration scenario (14 d before the standard migration modal date) were predicted to exit the river in less time (averaging $\leq$18 d) than smolts migrating under the other scenarios (Figure 5). Under the standard migration scenario, smolts migrating in 1984 and 1989 experienced the lowest transit times (averaging $<$14 d) but those migrating in 1981, 1985, and 1986 required the longest periods (25–27 d). Over all migration scenarios, smolts migrating in 1983, 1984, 1989, and 1990 had the smallest range of transit times (averaging 11–18 d). The largest range of transit times, across all migration scenarios, occurred in 1980, 1986, and 1992 (averaging 12–35 d). During years with marked decreases in river flows before and during June, particularly 1980, 1985, 1986, and 1992 (Figure 4), the mean time required to complete migration ranged from less than 12 d to approxi-

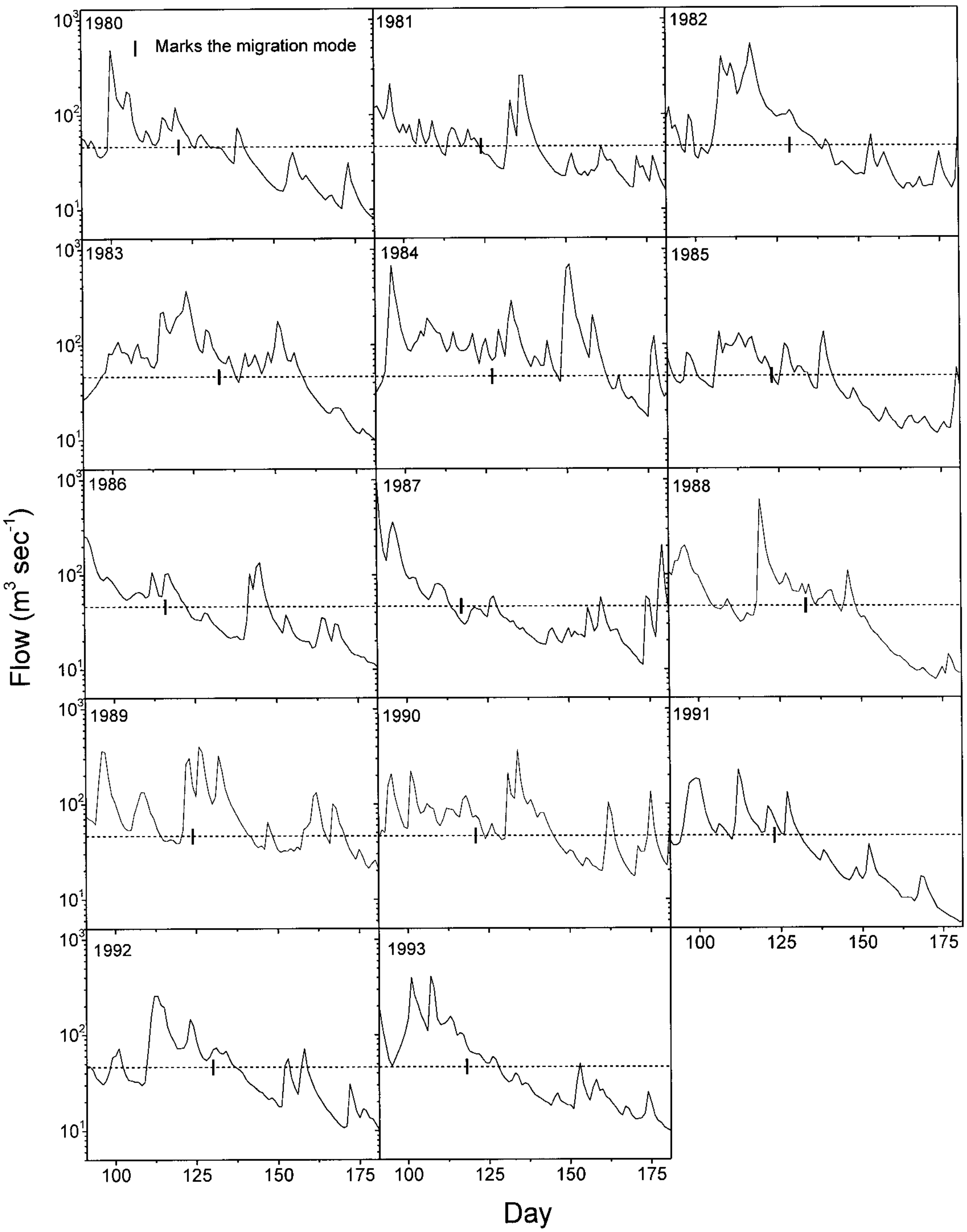


FIGURE 4.—Rates of river flow above Ayers Island Dam in the headwaters of the Merrimack River from 1 April (day 90 of the year) to 30 June. The broken horizontal line represents turbine capacity (46.2 m$^3$/d) at the dam, a rate below which migrating Atlantic salmon smolts were assumed to be delayed for lack of spill. The vertical hatch mark represents the standard migration modal date, the midpoint of the simulated 21-d migration period. Migration was normally distributed about the mode, which was set at the first day after five consecutive days of water temperatures greater than or equal to 10°C.

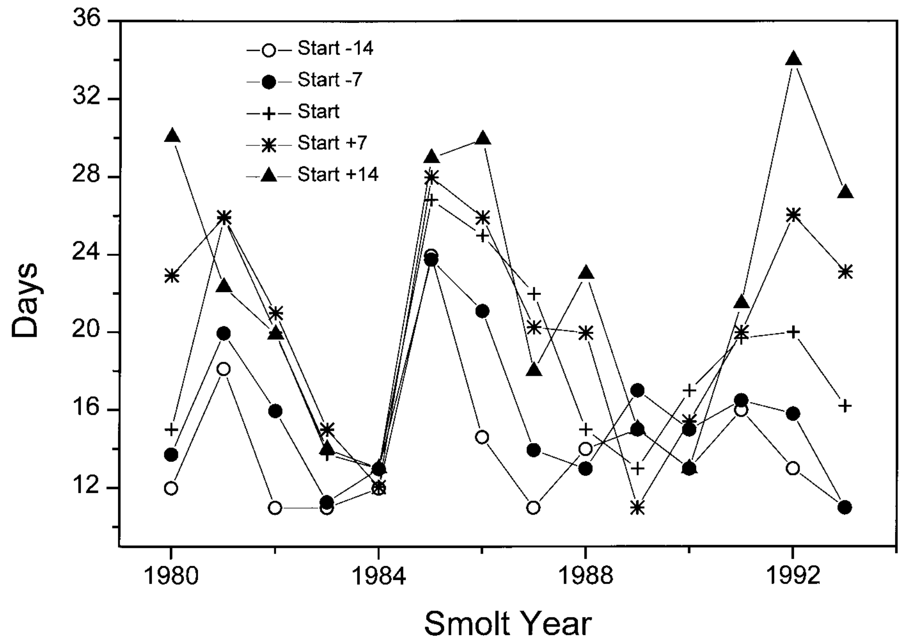


FIGURE 5.—Estimates of the mean number of days required by Atlantic salmon smolts to complete migration from the headwaters to the mouth of the Merrimack River for five migration modal dates: 14 or 7 d before the standard migration modal date (''start''), on the standard modal date, and 7 or 14 d after the standard modal date.

mately 35 d. Under the latest-migration scenario (i.e., the standard modal date plus 14 d), transit time averaged approximately 29–35 d.

Mean rates of in-river survival varied little except under the later-migration scenarios. Yearly in-river survival rate averaged 0.7–23.5% over the range of years and migration scenarios simulated (Figure 6). The highest rates of mean in-river survival (22.5–23.5%) occurred within the earliest migration scenario, while the largest range of mean survival rates (0.7–23.1%) were for smolts beginning migration 14 d after the standard modal date. Under the standard migration scenario, survival averaged 19.4–23.3%. During 1985–1988 and 1991–1993, years in which survival averaged 3.2–23.0% under the later two later-migration scenarios, smolts experienced late-season river flows that were low or decreasing rapidly relative to turbine capacity at Ayers Island Dam (Figure 4). In contrast, during 1983–1984 and 1989–1990, years when late-season river flows were generally at or above the turbine capacity at Ayers Island Dam through May, survival decreased only slightly with later-migration scenarios. Survival during 1980–1982 averaged 16.6–20.1% under the latest-migration scenario, although river flows decreased below the Ayers Island turbine capacity before the end of May.

### *Model Evaluation*

The number of surviving smolts required to achieve a 0.5–5.0% rate of 2SW return varied depending on the number of 2SW adults used to back-calculate the smolt cohort size range. For example, in 1980 the threshold extended from 40 to 400 smolts; in 1989 the range was 5,080–84,667 smolts (Figure 7). For 9 of the 14 years, the estimated number of smolts surviving the in-river migration was sufficient to achieve rates of adult returns falling within the 0.5–5.0% range. Further, with the exception of 4 of the 9 years (1987, 1988, 1991, and 1993), the number of surviving smolts across all migration simulations was within the threshold range. However, the number of smolts surviving migration under the scenario of the standard modal date plus 7 d (1987) or plus 14 d (1987, 1988, 1991, and 1993) fell below the minimum threshold value. For 1981 and 1983–1986, the number of surviving smolts (averaging 135–436) under all migration scenarios fell below the 0.5–5.0% threshold range (760–28,333 smolts).

Finally, the two main variables in the model, the number of smolts beginning migration and river flow, together proved to be critical components in the production of returning adults (Table 3). Although neither variable was uniformly distributed

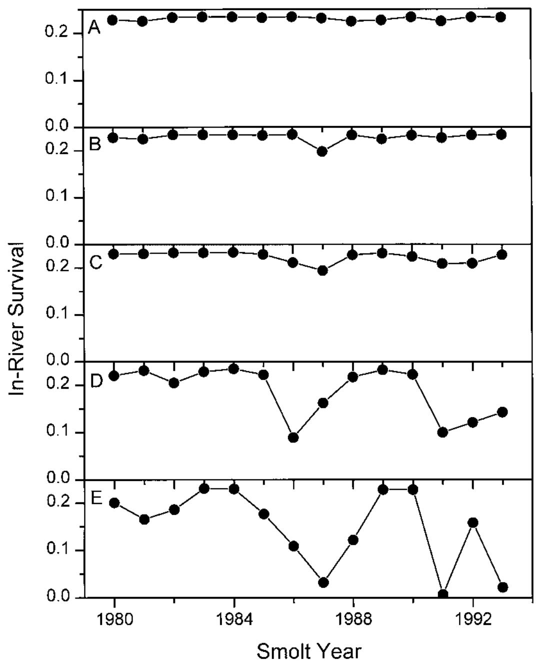


FIGURE 6.—Estimates of the mean rate of in-river survival of Atlantic salmon smolts migrating from the headwaters to the mouth of the Merrimack River for migration modal dates **(A)** 14 d before, **(B)** 7 d before, **(C)** on, **(D)** 7 d after, and **(E)** 14 d after the standard migration modal date.

(Figure 8A), the residuals were not correlated with the predicted values ($r = 0.20$, $P = 0.153$). Further, there was a significant ($P < 0.002$) correlation between the observed numbers of 2SW adult returns (1982–1995) to the Merrimack River and the numbers predicted from the regression model (Figure 8B).

## Discussion

*Model Construction*

The migration model developed in this study is a basic representation of the factors affecting the mortality of smolts during emigration from the Pemigewasset region of the Merrimack River basin. Parameterization of the model was a direct interpretation of the primary data describing fish passage and emigration on the river, thus it represents a first step to modeling this system. Because the data were in the form of tagged performance studies of fish in the river, more complex interactions were not included. Data on the exact nature of predation on smolts in the river is unavailable. Thus, to explicity incorporate predation models, such as encounter rate functions, would be an inappropriate extension of the data at this time. However, as new information is contributed, this model will provide a framework into which more detailed and site-specific submodels can be incorporated to better estimate in-river survival of migrating smolts.

The migration model can be improved with precision estimates of smolt production in the headwaters of the Merrimack River, which would result in better estimates of the number of migrating smolts. Working on a tributary to the Connecticut River, Orciari et al. (1994) found density effects on growth of yearling parr and, subsequently, increased overwinter mortality. They attributed their findings to competition for substrate chambers as water temperatures dropped in the fall. Because density and environmental factors might affect smolt production in the Merrimack, the assumption of a constant overwinter mortality rate would appear unrealistic. Currently, the effects of parr density, early winter floods, and overwinter mortality of age-1 parr as related to the production of age-2 smolts in the Merrimack River have not been assessed.

The model also can be refined by fully specifying the effects of river flow on migration success of smolts. The effects of river flow and obstruction on the migration of anadromous fish are well documented (Ruggles and Watt 1975; Raymond 1979, 1988; Williams and Matthews 1995). For example, Hvidsten and Hansen (1988) demonstrated a positive and significant relationship between total adult recapture rate and maximum river flow at time of smolt release in the rivers Surna and Gaula, Norway. Hvidsten and Johnsen (1993) and Hvidsten et al. (1995) reported that the magnitude of river flow, as well as increased flow, affected the initiation of smolt migration and shoal formation. These studies showed that shoal formation during periods of increased water discharge resulted in increased survival of both hatchery and wild smolts and subsequent adult returns. In the present model, only the upper dam and interval between Ayers Island and Eastman Falls dams were calibrated with river-flow-dependent data. Although river flow and the number of smolts migrating explained a significant amount of the variation in 2SW returns to the Merrimack, our model validations suggest that flow was insufficiently accounted for as a site-specific variable affecting the number of smolt migrants.

River flows used in this study were not specific for each dam because records of water discharge (the volume of water released via spill and through

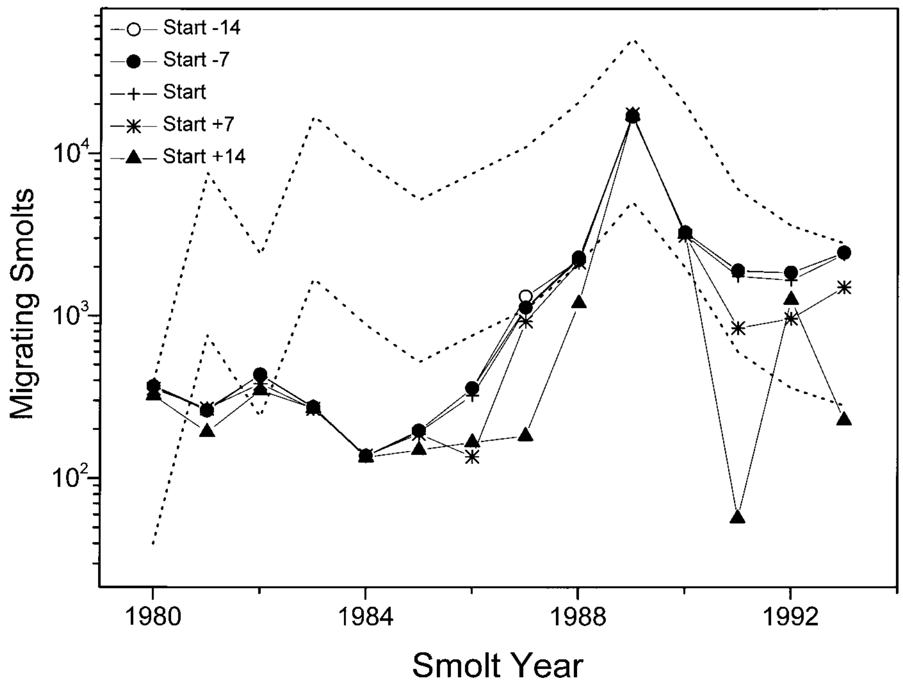


FIGURE 7.—Estimates of the mean number of Atlantic salmon smolts surviving migration from the headwaters to the mouth of the Merrimack River under early-, standard, and late-migration scenarios. The broken lines denote the ranges of surviving smolts necessary to achieve 0.5–5.0% at-sea survival over two seawinters.

the turbines) over the smolt migration period, which might differ from actual river flow, were unavailable. Further, we incorporated river-flow-related trends in passage mortality at Ayers Island Dam only. However, the combined effects of river flow and passage opportunities at dams affected annual variation in model estimates of transit time between migration scenarios (Figure 5). Ruggles and Watt (1975) and Raymond (1979) stressed that prolonged delay in passage of dams increases exposure time of anadromous fish to predators and disease. Further, prolonged migration periods expose smolts to increasing river temperatures and loss of physiological smolt characters (e.g., gill $Na^+$, $K^+$-ATPase activity) which might result in decreased survival, growth, and swimming performance in seawater (McCormick et al. 1997).

TABLE 3.—Analysis of variance statistics for the regression of observed number of two-seawinter (2SW) Atlantic salmon returning to the Merrimack River during 1982–1995 on number of smolts beginning migration 2 years previously and average mean river flow between Ayers Island and Eastman Falls dams during May in the outmigration year.[a]

| Source of variation | df | Sum of squares | Mean square | $F$ | Significance $F$ |
|---|---|---|---|---|---|
| Regression | 2 | 42,644 | 21,322 | 39.56 | 9.464E−06 |
| Residual | 11 | 5,929 | 539 | | |
| Total | 13 | 48,573 | | | |

[a] The regression was: number of 2SW adults = −17.8066 + 0.002204(number of smolts) + 0.243952(flow, $m^3/s$); multiple $R$ = 0.94; $R^2$ = 0.88; adjusted $R^2$ = 0.86; SE = 23.22; $N$ = 14. For the intercept, SE = 16.28, $t$ = −1.094, and $P$ = 0.297. For the smolt coefficient, SE = 0.0004, $t$ = 5.654, and $P < 0.001$. For the flow coefficient, SE = 0.0802, $t$ = 3.043, and $P < 0.012$.

Though we assumed that migration mortality includes predation, we were unable to specify the contribution to overall mortality at each dam or interval between dams. Despite the absence of specific predation rate data for the Merrimack River, the nature of predation on juvenile salmonids is becoming more fully described. On some European rivers smolt losses to predation exceed 20% (Larsson 1985; Hvidsten and Møkkelgjerd 1987). Reitan et al. (1987) reported that predation by gulls *Larus* spp. on smolts in the River Eira, Norway, was negatively correlated with recapture rate of adults. Researchers working on the Columbia River, Oregon–Washington, identified predation by resident fish as causing mortality equal to or higher than that attributed to dam passage (Rieman et al. 1991). Blackwell and Krohn (1997) reported that double-crested cormorants *Phalacrocorax auritus*

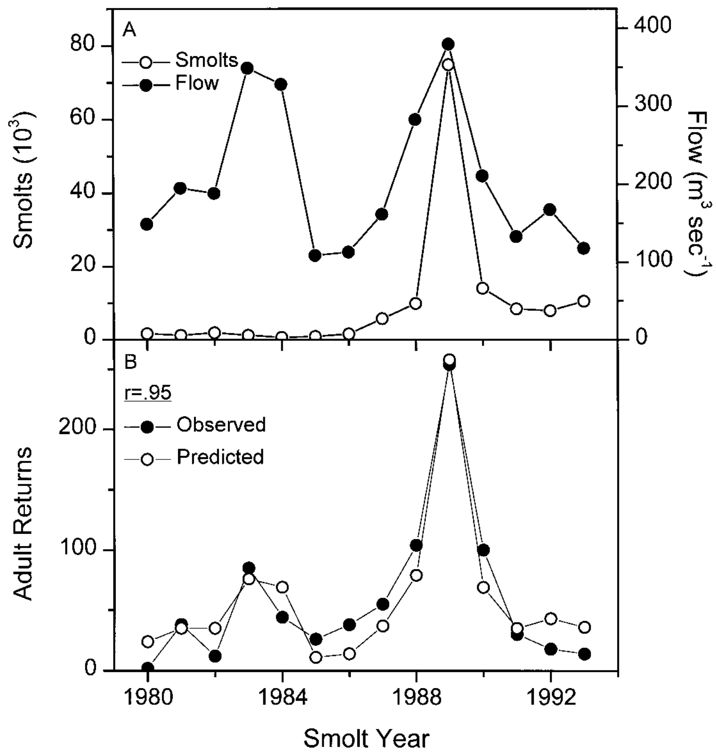


FIGURE 8.—**(A)** The number of Atlantic salmon smolts migrating in the Merrimack River during 1980–1993 as related to river flow and **(B)** the observed number of two-seawinter Atlantic salmon returning to the Merrimack River versus the predicted number resulting from a regression of two-seawinter Atlantic salmon returns on the number of smolts beginning migration and the average mean river flow during May, measured between Ayers Island and Eastman Falls dams.

that used the Penobscot River selectively foraged in areas adjacent to main-stem dams during May, the period of smolt migration. Moreover, of the prey items recovered from stomachs of double-crested cormorants collected during May in areas adjacent to dams and in free-flowing sections of the Penobscot River, smolts were among the two most important prey species (Blackwell et al. 1997). These and other reports will provide the basis of future model modifications that partition mortality between predation and other sources.

*Model Evaluation*

Though new information concerning smolt migration in the Merrimack would improve estimates of in-river survival, it was necessary to validate the estimates under the current migration parameters. Bley and Moring (1988) reported marine survival rates of 0.2–5.7% for wild and hatchery-reared smolts entering a commercial marine fishery. More recently, Friedland et al. (1996) reported a return rate (including in-river mortality) for 2SW Penobscot River Atlantic salmon of 0.20–1.27%. Return rates of 2SW adults from the Connecticut River (also including in-river mortality) ranged from 0.03% to 0.51%. Multiplying the range of model mean yearly in-river survival estimates by 0.5–5.0% yielded a composite survival range of 0.003–1.18%. Thus, given model estimates of in-river survival and the assumption of 0.5–5.0% marine survival, composite survival for migrating smolts in the Merrimack River overlapped survival estimates for the Penobscot and bounded those for the Connecticut. Moreover, if all returning 2SW Atlantic salmon (1982–1995) were not of Pemigewasset origin, the smolt output necessary for adult recruitment, given 0.5–5.0% marine survival, is decreased.

However, if marine survival ranges from 0.5% to 5.0% and all returning 2SW Atlantic salmon were of Pemigewasset origin, then the model underestimated in-river survival for smolt years 1981 and 1983–1986 (Figure 7). Possible reasons for the underestimates include the distribution of mi-

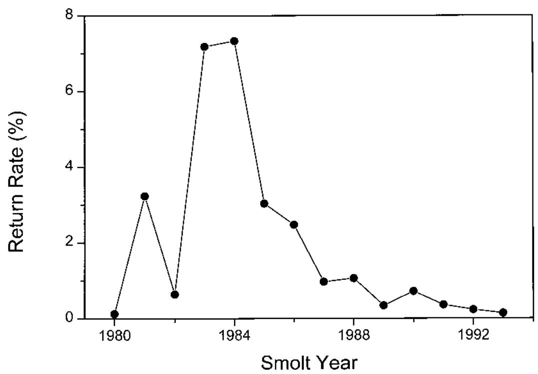


FIGURE 9.—The rate of return (relative to estimated smolt production) of two-seawinter Atlantic salmon to the Merrimack River.

grating smolts and the parameterization of river-flow effects at each dam. As independent variables, both factors explained a significant amount of the variance associated with annual returns of 2SW fish to the Merrimack River (Figure 8). Another reason for the underestimates might be migration success parameters that reflected the behavior of the hatchery-reared smolts used by PSNH. Smolts produced from stocked fry, being better adapted to riverine conditions (Moring et al. 1995), might exhibit greater migration success. Finally, the possibility of improved marine survival due to variability in climatic conditions at sea must be considered. The rates of 2SW returns (returning adults/estimated number of smolts produced) for these smolt cohorts peaked relative to other years (Figure 9). Evidence of improved marine survival for individuals from these smolt cohorts is also indicated by records of adult returns to neighboring New England rivers (Friedland et al. 1993, 1996).

Thus, although factors affecting survival during the marine phase of Atlantic salmon life history cannot be dismissed as unimportant, the combination of multiple obstructions to migration, a managed flow regime on most New England Atlantic salmon rivers, and in-river predation indicates that mortality before smolts reach the marine system might be substantial. Given that over 60% of nursery habitat in the Merrimack River system lies above eight main-stem dams, utilities and managers must continue to work cooperatively in developing adequate measures to insure successful migration. Realistic modeling of rates of smolt emigration and subsequent passage of dams requires multiple sampling stations where frequent measurements of river flow, rates of smolt migration, and estimates of smolt survival can be obtained. We suggest that future work be directed toward improvements in the monitoring of smolt migration, measuring sources of in-river mortality, and the further development of predictive models that allow evaluation of proposed management strategies.

## Acknowledgments

Funding for this study was provided by the National Oceanic and Atmospheric Administration, National Marine Fisheries Service, through the Cooperative Marine Education and Research Program (CMER) at the University of Massachusetts, Amherst. We thank J. McLaughlin and R. Dumore of PSNH for their cooperation and help with parameterization of the model. J. Boreman, CMER, and R. Dumore, PSNH, provided helpful reviews of the manuscript. Also, we thank C. Campbell, of the University of Massacheusetts, Amherst, for constructing the map of the study area.

## References

Baum, E. T. 1983. The Penobscot River. An Atlantic salmon river management report. Maine Atlantic Sea-Run Salmon Commission, Bangor.

Blackwell, B. F., and W. B. Krohn. 1997. Spring foraging distribution and habitat selection by double-crested cormorants on the Penobscot River, Maine. Colonial Waterbirds 20:66–76.

Blackwell, B. F., W. B. Krohn, N. R. Dube, and A. J. Godin. 1997. Spring prey use by double-crested cormorants on the Penobscot River, Maine. Colonial Waterbirds 20:77–86.

Bley, P. W., and J. R. Moring. 1988. Freshwater and ocean survival of Atlantic salmon and steelhead: a synopsis. U.S. Fish and Wildlife Service, Biological Report 88(9).

Conover, W. J. 1980. Practical nonparametric statistics, 2nd edition. Wiley, New York.

Fängstam, H. 1993. Individual downstream swimming speed during the natural smolting period among young of Baltic salmon (*Salmo salar*). Canadian Journal of Zoology 71:1782–1786.

Fried, S. M., J. D. McCleave, and G. W. LaBar. 1978. Seaward migration of hatchery-reared Atlantic salmon, *Salmo salar*, smolts in the Penobscot River estuary, Maine: riverine movements. Journal of the Fisheries Research Board of Canada 35:76–87.

Friedland, K. D., and R. E. Haas. 1996. Marine post-smolt growth and age at maturity of Atlantic salmon. Journal of Fish Biology 48:1–15.

Friedland, K. D., R. E. Haas, and T. F. Sheehan. 1996. Post-smolt growth, maturation, and survival of two stocks of Atlantic salmon. Fishery Bulletin 94:654–663.

Friedland, K. D., D. G. Reddin, and J. F. Kocik. 1993. Marine survival of North American and European

Atlantic salmon: effects of growth and environment. ICES (International Council for the Exploration of the Sea), Journal of Marine Science 50:481–492.

Gudjonsson, S., S. M. Einarsson, Th. Antonsson, and G. Gudbergsson. 1995. Relation of grilse to salmon ratio to environmental changes in several wild stocks of Atlantic salmon (*Salmo salar*) in Iceland. Canadian Journal of Fisheries and Aquatic Sciences 52:1385–1398.

Hesthagen, T., and E. Garnås. 1986. Migration of Atlantic salmon smolts in River Orkla, central Norway, in relation to management of a hydroelectric station. North American Journal of Fisheries Management 6:376–382.

Hvidsten, N. A., and L. P. Hansen. 1988. Increased recapture rate of adult Atlantic salmon, *Salmo salar* L., stocked as smolts at high water discharge. Journal of Fish Biology 32:153–154.

Hvidsten, N. A., A. J. Jensen, H. Vivås, Ø. Bakke, and T. G. Heggberget. 1995. Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction. Nordic Journal of Freshwater Research 70:38–48.

Hvidsten, N. A., and B. O. Johnsen. 1993. Increased recapture rate of adult Atlantic salmon released as smolts into large shoals of wild smolts in the River Orkla, Norway. North American Journal of Fisheries Management 13:272–276.

Hvidsten, N. A., and P. I. Møkkelgjerd. 1987. Predation on salmon smolts, *Salmo salar* L., in the estuary of the River Surna, Norway. Journal of Fish Biology 30:273–280.

Jonsson, B., N. Jonsson, and J. Ruud-Hansen. 1989. Downstream displacement and life history variables of Arctic char. Physiology and Ecology Japan, Special 1:93–105.

Jonsson, B., and J. Ruud-Hansen. 1985. Water temperature as the primary influence on timing seaward migrations of Atlantic salmon (*Salmo salar*) smolts. Canadian Journal of Fisheries and Aquatic Sciences 42:593–595.

Larsson, P. O. 1985. Predation on migrating smolts as a regulating factor in Baltic salmon, *Salmo salar* L., populations. Journal of Fish Biology 26:391–397.

MacCrimmon, H. R., and D. L. Gots. 1979. World distribution of Atlantic salmon. Journal of the Fisheries Research Board of Canada 36:442–457.

McCleave, J. D. 1978. Rhythmic aspects of estuarine migration of hatchery-reared Atlantic salmon (*Salmo salar*) smolts. Journal of Fish Biology 12:559–570.

McCormick, S. D., J. M. Shrimpton, and J. D. Zydlewski. 1997. Temperature effects on osmoregulatory physiology of juvenile anadromous fish. Society for Experimental Biology Seminar Series 61: 279–301.

McMenemy, J. R., and B. Kynard. 1988. Use of inclined-plane traps to study movement and survival of Atlantic salmon smolts in the Connecticut River. North American Journal of Fisheries Management 8:481–488.

Moring, J. R. 1987. Restoration of Atlantic salmon to Maine: overcoming physical and biological problems in the estuary. Pages 3129–3140 *in* O. T. Magoon, and five coeditors. Proceedings of Coastal Zone 1987, the fifth symposium on coastal and ocean management Seattle, Washington. American Society of Civil Engineers, New York.

Moring, J. R., J. Marancik, and F. Griffiths. 1995. Changes in stocking strategies for Atlantic salmon restoration and rehabilitation in Maine, 1871–1993. Pages 38–46 *in* H. L. Schramm and R. G. Piper, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society, Symposium 15, Bethesda, Maryland.

Orciari, R. D., G. H. Leonard, and D. J. Mysling. 1994. Survival, growth, and smolt production of Atlantic salmon stocked as fry in a southern New England stream. North American Journal of Fisheries Management 14:588–606.

Österdahl, L. 1969. The smolt run of a small Swedish river. Pages 205–215 *in* T. G. Northcote, editor. Salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.

PSNH (Public Service of New Hampshire, Inc.). 1992. Downstream migration of Atlantic salmon smolts at Public Service of New Hampshire hydroelectric stations on the Merrimack and Pemigewasset rivers 1989–1990. Final report to the Policy and Technical Committees for Anadromous Fishery Management of the Merrimack River, Manchester, New Hampshire.

Raymond, H. L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. Transactions of the American Fisheries Society 108: 505–529.

Raymond, H. L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer Chinook salmon and steelhead in the Columbia River basin. North American Journal of Fisheries Management 8:1–24.

Reitan, O., N. A. Hvidsten, and L. P. Hansen. 1987. Bird predation on hatchery reared Atlantic salmon smolts, *Salmo salar* L., released in the River Eira, Norway. Fauna Norvegica, Series A 8:35–38.

Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:448–458.

Ruggles, C. P., and W. D. Watt. 1975. Ecological changes due to hydroelectric development on the Saint John River. Journal of the Fisheries Research Board of Canada 32:161–170.

Scarnecchia, D. L., Á. Ísaksson, and S. E. White. 1989. Oceanic and riverine influences on variations in yield among Icelandic stocks of Atlantic salmon. Transactions of the American Fisheries Society 118: 482–494.

Solomon, D. J. 1978. Some observations on salmon

smolt migration in a chalkstream. Journal of Fish Biology 12:571–574.
Spicer, A. V., J. R. Moring, and J. G. Trial. 1995. Downstream migratory behavior of hatchery-reared, radio-tagged Atlantic salmon (*Salmo salar*) smolts in the Penobscot River, Maine, USA. Fisheries Research 23:255–266.
Stolte, L. W. 1994. Atlantic salmon restoration in the Merrimack River basin. Pages 22–35 *in* S. Calabi and A. Stout, editors. Proceedings of the New England Atlantic salmon management conference: a hard look at some tough issues, April 22–23, Danvers, Massachusetts. New England Salmon Association, Newburyport, Massachusetts.
Symons, P. E. K. 1979. Estimated escapement of Atlantic salmon (*Salmo salar*) for maximum smolt production in rivers of different productivity. Journal of the Fisheries Research Board of Canada 36:132–140.
USFWS (U.S. Fish and Wildlife Service). 1989. Atlantic salmon restoration in New England: final environmental impact statement 1989–2021. U.S. Fish and Wildlife Service, Region 5, Newton, Corner, Massachusetts.
Williams, J. G., and G. M. Matthews. 1995. A review of flow and survival relationships for spring and summer chinook salmon, *Oncorhynchus tshawytscha*, from the Snake River Basin. Fishery Bulletin 93:732–740.

Received August 14, 1996
Accepted May 19, 1997