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Recommended Citation

Barber, B.L., Gibson, A.J., O'Malley, A.J. and Zydlewski, J. (2018), Does What Goes up Also Come Down? Using a Recruitment Model to Balance Alewife Nutrient Import and Export. Mar Coast Fish, 10: 236-254. https://doi.org/10.1002/mcf2.10021

ARTICLE

Does What Goes up Also Come Down? Using a Recruitment Model to Balance Alewife Nutrient Import and Export

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Abstract

Migrating adult Alewives *Alosa pseudoharengus* are a source of marine-derived nutrients on the East Coast of North America, importing nitrogen and phosphorus into freshwater habitats. Juvenile migrants subsequently transport freshwater-derived nutrients into the ocean. We developed a deterministic model to explore the theoretical nutrient dynamics of Alewife migrations at differing spawner abundances. Net nutrient balance was calculated relative to these abundances along the spawner–recruit curve. The ecological consequences of these subsidies in a particular watershed depend on the magnitude of adult escapement relative to the habitat's carrying capacity for juveniles. At low escapement levels and assuming complete habitat access, the number of recruits produced per spawner was high and juvenile nutrient export dominated. At high escapement levels, fewer recruits were produced per spawner because recruitment is density dependent. As a result, adult nutrient import dominated. At varying levels of freshwater productivity and fisheries mortality for upstream spawners, this trend remained the same while the magnitude of the endpoints changed. Productivity level was the major determinant of export, while fisheries mortality had the strongest effect on adult import. The dynamics of this nutrient trade-off are important for managers to consider as a recovering population will likely shift from net export to net import as escapement increases. This transition will be sensitive to both harvest rates and to fish passage efficacy at dams and other barriers.

In freshwater systems nitrogen and phosphorus concentrations are major determinants of primary production rates (Vanni 2002; Allan and Castillo 2007; Durand et al. 2011), and net community production can increase or decrease based on the relative availability of these nutrients. Anadromous species that migrate from the ocean into freshwater to spawn can affect resident communities by supplying pulsed inputs of energy and marine-derived nutrients that enter the food web through direct consumption of carcasses and gametes or indirectly through excretion (Bauer and Hoye 2014; Childress et al. 2014). This can be particularly important in temperate regions, where marine habitats are more productive than freshwater habitats and anadromous fish exhibit rapid growth in the ocean (Gross et al. 1988). While these inputs are important to the innate functioning of a system, the dynamics of import and export have not been fully explored.

Anadromous fish have complex interactions with their environment, and the ecological effects of these species on lake communities can be difficult to study because of the transient nature of their influence. In freshwater systems, nutrient limitations and responses to shifts in biologically available nitrogen and phosphorus are dynamic, changing spatially and temporally. Within a site, different plant and algal taxa have distinct nutrient requirements, often with the N:P ratio determining the dominant algal group (Klausmeier et al. 2004; Allan and Castillo 2007). Competition for allochthonous resources can therefore affect food web structure, influencing nutrient control through both bottom-up and top-down pathways (Huxel et al. 2002; Wood et al. 2016).

The influence of marine-derived nutrient input on freshwater systems has been explored in semelparous species, such as Pacific salmon *Oncorhynchus* spp., that leave carcasses in streams to decay (for reviews, see Cederholm et al. 1999; Naiman et al. 2002; Schindler et al. 2003). In the Columbia River watershed, Pacific salmon contribute roughly 3,000 metric tons of nitrogen and 360 metric tons of phosphorus per year (Moore and Schindler 2004). Carcasses and gametes are incorporated slowly throughout the season as they are broken down and nutrients become bioavailable. Such additions increase primary production (Richey et al. 1975; Cederholm et al. 1999), biofilm growth (Wipfli et al. 1998), macroinvertebrate density (Piorkowski 1995; Minakawa 1997; Wipfli et al. 1998), and fish growth (Bilby et al. 1996). Studies on other semelparous species, such as Sea Lamprey *Petromyzon marinus*, have demonstrated that the nutrient input released by carcasses is incorporated by stream macroinvertebrate and algal communities at a local scale (Guyette 2012; Weaver et al. 2016).

All of the anadromous fish species that were historically present along the northeastern coast of North America are severely depressed compared with historic numbers (Saunders et al. 2006). Of these species, Alewives *Alosa pseudoharengus* are currently the most abundant and have the highest potential for population restoration. Alewives exhibit a north–south gradient in life history traits, with high rates of iteroparity occurring throughout New England watersheds (Bozeman and Van der Avyle 1989). Alewives have a high reproductive potential, and a small number of returning adults can produce a large number of offspring (Gibson and Myers 2003a). Density-dependent processes limit the number of recruits that a given habitat can produce such that the number of recruits will plateau regardless of additional spawners (Gibson and Myers 2003a). Thus density-dependent production of juvenile Alewives, as illustrated by a spawner–recruit curve, can be a major determinant of net nutrient flow. A population with low spawner density will deliver fewer nutrients but have a higher per capita rate of juvenile production that would drive greater export, resulting in a negative net nutrient flow (Moore and Schindler 2004; West et al. 2010).

As spawner biomass increases, upstream nutrient transport is expected to increase in proportion to spawner biomass. As the habitat available for juvenile Alewives is more fully utilized, nutrient export is also expected to continue to increase. In this dynamic, however, the rate of export per capita must decrease as juvenile abundance approaches carrying capacity. Thus, as spawner abundance increases, a shift to a net positive nutrient influx might be expected (Nislow et al. 2004). West et al. (2010) demonstrated this trend when estimating phosphorus dynamics during recovery of an Alewife population in a small pond (9.4 ha) in Connecticut. Based on a measured low juvenile survival rate (6.39 juveniles/spawner), they modeled net export to be negligible. However, when they based their calculations on a higher hypothetical rate (63.9 juveniles/spawner), they found that phosphorus export dominated until escapement reached roughly 6,500 adults, after which import became large enough to outweigh juvenile export. Thus, the net nutrient exchange is sensitive to both population size and to survival parameters.

For Alewife populations, excretion may be the most influential input (West et al. 2010) because inorganic forms of nutrients are available for immediate uptake by primary producers. Smaller fish have higher mass-specific nutrient excretion rates, meaning Alewives could contribute a higher nutrient load to a site per unit biomass through excretion than Atlantic Salmon *Salmo salar* (Twining et al. 2017). Alosines also likely produce more nitrogen through excretion and more phosphorus through gametes and carcasses (Twining et al. 2017). Adult nutrient import to freshwater systems is coincident with increased freshwater aquatic community metabolism early in the year (Levi et al. 2013; Samways and Cunjak 2015).

Even if the autumnal juvenile exodus results in a net zero nutrient gain or loss for the system, this pulse of nutrients would boost primary productivity in the spring when other sources of input are limited.

Previous studies have modeled the net nutrient balance of Alewife populations and have estimated recruitment for specific lakes and streams, but the inputs used were site-specific (Durbin et al. 1979; Walters et al. 2009; West et al. 2010), which hinders the direct comparison of the results. Variability in spawner escapement, mortality rates, and input pathways led to a wide range in annual estimates. Walters et al. (2009) used a high spawner density (4–8 spawners/m^2) and a low mortality (0.1%) and used excretion and carcasses as the primary source of nitrogen and phosphorus as the study site was a small stream. Mortality was higher for studies conducted in lake habitats as nutrient sources were primarily attributed to carcass and gamete inputs. Both Durbin et al. (1979) and West et al. (2010) used lower spawning density (0.9 spawners/m^2 and 0.3 spawners/m^2, respectively) and higher mortality rates (37.5% and 56%, respectively). These different scenarios resulted in a range of nitrogen input from 63.6 mg·m^{-2}·y^{-1} to 2,700 mg·m^{-2}·y^{-1} and phosphorus input from 7.4 mg·m^{-2}·y^{-1} to 430 mg·m^{-2}·y^{-1}. Even when comparing the two lake studies, input calculations varied as they used the same estimate of phosphorus concentration for carcasses but different estimates for excretion and gametes. Both Durbin et al. (1979) and West et al. (2010) calculated juvenile export but concluded it was negligible when compared with adult delivery given the escapement levels relevant to their system at the time of study.

These previous efforts highlight the wide variability seen in Alewife populations related to estimates of spawner density and mortality rates. While they focused on nutrient dynamics related to an established spawning run, many questions remain with respect to how deviations in population input affect restoration and population growth. We explored how variation in Alewife population levels could theoretically affect nitrogen and phosphorus dynamics related to adult import and juvenile export. To answer this, we developed a deterministic population dynamics model that was linked to estimates of nutrient import by adults and export by juveniles. We then used this model to explore how nutrient dynamics would be expected (1) to differ as a function of spawner abundance, (2) to change through the process of population growth, (3) to vary among watersheds with different carrying capacities, and (4) to vary with different levels of in-river fishing mortality.

METHODS

Model overview.— The model developed for this study included two main components: (1) population dynamics and (2) nutrient import and export. Several examples of age-structure population models have been developed specifically for Alewife (Gibson and Myers 2003a; ASMFC 2012), but these do not estimate juvenile abundance directly and so could not be used to calculate export. For the population component, fish were moved through the life cycle using a stepwise annual progression. Stocks in the ocean entered freshwater to spawn and produce juveniles. A proportion of these survived to "graduate" into juveniles that then became part of the ocean population, completing the cycle (Figure 1). This deterministic model did not include any measure of environmental stochasticity, and the population was assumed to be unimpacted in order to explore fundamental patterns in nutrient dynamics.

Forward-projecting population model.— The forward-projecting population model consisted of a series of equations for each life history stage. Egg production for a given year t, $N_{eggs,t}$, is calculated using the number of females that survived to spawn multiplied by the fecundity relationship as below:

$$N_{eggs,t} = \sum_{a=3}^{8} [S_t(e^{-0.25M_{spawn}})0.5]F_a,$$

where S_t is the total number of fish in the spawning population in year t (described below), M_{Spawn} is the instantaneous rate of mortality (annual) associated with the spawning run, prorated for 3 months (or 0.25 years), 0.5 is the assumed female : male ratio, and F_a is the fecundity
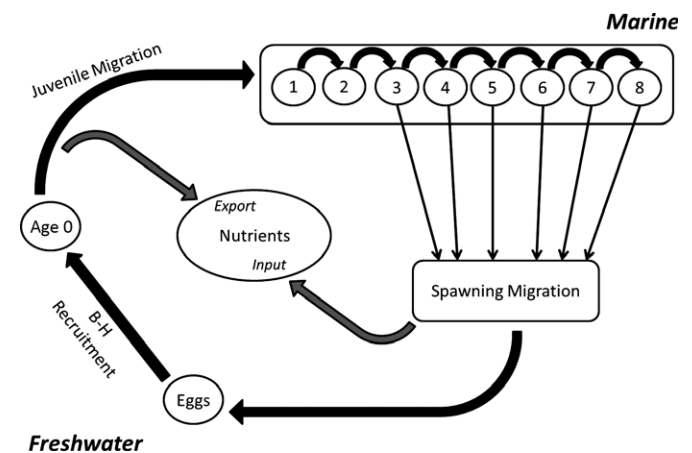
FIGURE 1. Basic structure of deterministic Alewife population model. For each annual time step, fish in the ocean population that are ages 2–7 mature and enter the spawning run. These fish move into spawning habitat where they lay eggs that hatch, with survival to age 0 determined by a Beverton–Holt (B–H) spawner–recruit curve. Nutrient dynamics are calculated in the model through adult import (carcasses, gametes, excretion) and age-0 nutrient export.

relationship (Table 1). For this model, mortality associated with the spawning run was assumed to occur before spawning such that only females that survived contributed to egg production.

The number of juveniles produced in a year-class was modeled as a density-dependent process, which was characterized using a spawner–recruit (SR) relationship. The choice of SR curve can affect the dynamics of the recruitment rate as the spawning population increases, which can in turn affect net nutrient balance through time (Elliott 1985; Needle 2002; Subbey et al. 2014). There are many different types of SR curves used in fish population modeling (Hilborn and Walters 1992), and the Ricker curve has been used to explore the Alewife SR relationship (Tommasi et al. 2015). However, the Beverton–Holt curve was used for this model because Gibson (2004) found that it provided a better fit to the data for eight Alewife populations in the northern part of their population range than did the Ricker curve and

that the data available for these populations were not sufficient to fit a three-parameter model. The Beverton–Holt curve was used to model a density-dependent relationship in the population model by tying egg production to juvenile production (J_t) as follows:

$$J_t = \frac{\alpha N_{eggs,t}}{1 + \dfrac{\alpha N_{eggs,t}}{R_{asy}}}.$$

Here, juvenile abundance was calculated for year t based on the total number of eggs for year t ($N_{eggs,t}$), the asymptotic recruitment level (R_{asy}), and the maximum number of juveniles given the average fecundity per unit mass at the origin of the SR relationship (α).

The population of immature fish in the ocean was divided into age-classes between age-0 and age-8 fish, each with an associated instantaneous mortality rate (annual) for fish in the ocean, M_{ocean}, and a probability of

TABLE 1. Population inputs used in the Alewife model, including those taken from the literature and those estimated from the St. Croix Milltown trap Alewife data (Fisheries and Oceans Canada et al. 1981–2016).

Parameter	Value	Description	Data source
Forward-projecting population model			
M_T	0.85	Instantaneous natural mortality rate	Gibson (2004), ASMFC 2012
M_{spawn}	2.391	Instantaneous mortality rate, ages 3–8	Kissil (1974), Durbin et al. (1979)
M_{ocean}	0.648	Instantaneous mortality rate, ages 0–8	Iteratively calculated
φ	0.95	Probability of spawning, ages 3–8	Bailey and Zydlewski (2013)
F_a	$y = bx - c$	Fecundity relationship	Fisheries and Oceans Canada et al. (1981–2016)
$\tilde{R}_{asy}$	51.4	Asymptotic recruitment level (t/km^2)	Gibson (2004)
$\tilde{\alpha}$	2.96	Log maximum lifetime reproductive rate	Gibson (2004)
m_3	0.35	Maturity between age 2 and age 3	Gibson and Myers (2003a)
m_4	0.51	Maturity between age 3 and age 4	Gibson and Myers (2003a)
m_5	0.96	Maturity between age 4 and age 5	Gibson and Myers (2003a)
m_6–m_8	1.0	Maturity from age 6 to age 8	Gibson and Myers (2003a)
Parameter value derivation			
α	0.0015	Lifetime reproductive rate	Gibson (2004)
	0.0017	10th percentile	
	0.0022	90th percentile	
R_{asy}	3,283	Asymptotic recruitment level (age 0/acre)	J. Gibson (unpublished data)
	1,917	10th percentile	
	5,626	90th percentile	
b	871.72	Fecundity slope	Fisheries and Oceans Canada et al. (1981–2016)
c	50,916	Fecundity intercept	Fisheries and Oceans Canada et al. (1981–2016)
W_3	0.144	Mass age 3 (kg)	Fisheries and Oceans Canada et al. (1981–2016)
W_4	0.186	Mass age 4 (kg)	Fisheries and Oceans Canada et al. (1981–2016)
W_5	0.209	Mass age 5 (kg)	Fisheries and Oceans Canada et al. (1981–2016)
W_6	0.244	Mass age 6 (kg)	Fisheries and Oceans Canada et al. (1981–2016)
W_7	0.277	Mass age 7 (kg)	Fisheries and Oceans Canada et al. (1981–2016)
W_8	0.353	Mass age 8 (kg)	Fisheries and Oceans Canada et al. (1981–2016)

maturing at that age, m_a (Table 1). The ocean population was linked to juvenile production in freshwater by setting the number of age-0 fish in the ocean population in year t, $O_{0,t}$, equal to the number of juveniles produced in that year:

$$O_{0,t} = J_t.$$

The abundance of immature fish in other age-classes was calculated by projecting the abundance forward using the mortality rates and maturity probabilities:

$$O_{a+1,t+1} = O_{a,t}e^{-M_{Ocean}}(1 - m_{a+1}).$$

Immature fish between age-2 and age-7 also had a probability of maturing, which allowed them to enter the spawning run the next year (ages 3–8), with survival occurring between spawning year-classes. For age a and year t, first-time spawners ($S_{a+1,t+1,0}$) and repeat spawners ($S_{a+1,t+1,p+1}$) that spawned p times previously were calculated as follows:

$$S_{a+1,t+1,0} = O_{a,t}e^{-M_{Ocean}}(m_{a+1}),$$
$$S_{a+1,t+1,p+1} = \varphi S_{a,t,p}e^{-(0.75M_{ocean}+0.25M_{spawn})} + (1-\varphi)S_{a,t,p}e^{-M_{ocean}}.$$

Each year-class had an associated probability of spawning (φ), which was separate from the probability of maturing and allowed those individuals that did not successfully spawn to return to the ocean.

Annual mortality rates were used in several population equations, and total natural mortality for mature spawners was split into ocean mortality (M_{ocean}) and spawning mortality (M_{spawn}) in order to estimate carcass nutrient inputs. The instantaneous natural mortality rate for adults was reported as 1 by Gibson and Myers (2003a) and an average rate of 0.7 was reported by the ASMFC (2012), and so an instantaneous rate of 0.85 was used in this study. A range of interval spawning mortality was reported in both Kissil (1974) and Durbin et al. (1979). The average of those reported values (45%) was used to calculate an instantaneous spawning mortality rate (annual). The contribution from the ocean mortality to overall natural mortality was then calculated based on defined total mortality and spawning mortality rates (Table 1). Ocean mortality was iteratively adjusted based on age-class proportions and probabilities of spawning such that the product of interval survivals (based on M_{ocean} and M_{spawn}) reflected the total interval mortality rate (based on an instantaneous M of 0.85). The term M_{ocean} was applied as an annual rate to both immature fish and the small percentage of individuals that did not successfully enter the river to spawn ($1 - \varphi$). Only the ocean mortality rate was used to project their abundance

forward, whereas a higher mortality rate associated with spawning, M_{spawn}, was included for fish that spawned successfully. The term M_{ocean} was prorated to 9 months and M_{spawn} to 3 months to reflect the timing of the Alewife spawning run.

The total number of fish in the spawning population in year t (S_t) was calculated as follows:

$$S_t = \sum_{a,p} S_{a,t,p}\varphi.$$

The number of spawners was used to calculate egg production, thereby closing the loop for calculating population dynamics associated with each portion of the Alewife life history.

Parameter value derivation.— The equations in the forward-projecting population model required the derivation of multiple parameters. We based the Alewife population for this "Model River" on data from the St. Croix watershed, which forms the northeast border between Maine and New Brunswick. Morphometric information collected from the St. Croix River (1981–2016) was used as inputs for mass and fecundity (Table 1; Fisheries and Oceans Canada et al. 1981–2016). For mass-at-age calculations, an average mass was calculated for each age-class combining males and females. Maturity rates were averaged from Gibson and Myers (2003a; Table 1). Spawner–recruit parameter derivation was taken from the Alewife model developed by Gibson (2004) based on multiple Alewife populations in northeastern North America. Parameters of the SR curve were adjusted based on the habitat amount, which for this study was set arbitrarily at 4.047×10^6 m^2 or 1,000 acres. So while the underlying population information was taken from the St. Croix River, the model results presented here are for a theoretical "Model River."

Four parameters were used in the calculation of the egg deposition from the number of spawners. The probability of spawning was kept constant for all ages at 95%, the sex ratio was assumed to be 50%, and spawning mortality was imposed over a 3-month period as described above. Fecundity slope and intercept were calculated using a linear regression with an average mass-at-age value and corresponding average gonad mass-at-age value recorded from the St. Croix River (Fisheries and Oceans Canada et al. 1981–2016). For each female with a recorded ovary mass, the total egg mass was calculated by subtracting a spawned gonad mass from an unspawned gonad mass with the assumption that the former represented the mass of just the organ itself. The spawned gonad mass was an average from 14 downstream migrants from the St. Croix River. A total egg count for each fish was then calculated by multiplying the total egg mass by 7,890 eggs/g (Kissil 1974). This resulted in an average of ~130,000 eggs per

female (range = 5,050–305,659 eggs). The total number of eggs per fish then was regressed against mass to generate average egg production for each age-class. This was done to account for differences in fecundity with the age of the fish when calculating the total number of eggs produced in a given year. A linear regression function provided the best fit to the data ($R^2 = 0.66$; fecundity = $bx − c$, where $b = 871.72$, x = mass, and $c = 50,916$) when compared with exponential ($R^2 = 0.4711$), logarithmic ($R^2 = 0.63$), and power functions ($R^2 = 0.51$), though the differences were small.

Juvenile production involved an estimate of density-dependent survival using a Beverton–Holt SR relationship. Two parameters were derived for this equation in addition to egg deposition: R_{asy} and α, neither of which are available for the St. Croix River Alewife population. These two parameters were both calculated from the results of a meta-analysis of the dynamics of Alewives based on 8 populations in the northern part of their distribution ranging from Rhode Island to Nova Scotia (Gibson 2004). Following the approaches of Myers et al. (1999, 2001), Gibson (2004) standardized the data prior to analysis in order to produce probability distributions for the maximum lifetime reproductive rate ($\tilde{\alpha}$) and the asymptotic recruitment levels in terms of the spawning population size ($\tilde{R}_{asy}$). For his analysis, Gibson defined the age of recruitment as age 3. For our analysis, the relationship was rescaled from age-3 recruits and spawning stock biomass to juveniles and egg production in order to calculate nutrient parameters. The term R_{asy} was the asymptotic recruitment level in terms of the number of juveniles and was calculated as follows:

$$R_{asy} = \frac{\frac{\tilde{R}_{asy}}{SPR_{F=0}}}{\left(e^{-M_{ocean}\times3}\right)}.$$

The term M_{ocean} was multiplied by 3 because the age of recruitment was defined as 3 years in Gibson's meta-analysis (2004). The term ($\tilde{R}_{asy}$) was divided by the spawning biomass per recruit (SPR) in the absence of fishing mortality ($SPR_{F=0}$). This value represented the rate at which age-3 recruits produce spawners throughout their lives (Gibson 2004) and can be calculated for a specific population as follows:

$$SPR_{F=0} = \sum_{a=3}^{8} SS_a W_a,$$

where SS_a = the spawning stock for a given age-class and W_a = the average mass for each age-class. Each year-class contribution reflected (1) probability of maturity, (2) cumulative adult mortality, and (3) juvenile mortality such that

$$SS_3 = m_3$$

$$SS_4 = SS_3 e^{-M_{adult}} + (1 − m_3)e^{-M_{juv}}m_4$$

$$.$$

$$.$$

$$SS_8 = SS_7 e^{-M_{adult}} + (1 − m_3)(1 − m_4)(1 − m_5)(1 − m_6)$$
$$\times (1 − m_7)e^{-5M_{juv}}m_8,$$

where M_{adult} = the instantaneous mortality rate of mature fish, M_{juv} = the instantaneous mortality rate of immature fish, and m_a = the probability that immature fish alive at age a will mature at that age (Gibson 2004; Table 1). For this paper, an average SPR was used from Gibson's meta-analysis ($SPR_{F=0} = 0.357$ kg/recruit; Gibson 2004).

The alpha value (α) is the slope of the origin for the SR curve and was calculated similarly. Gibson (2004) provided a probability distribution for the maximum lifetime reproductive rate ($\tilde{\alpha}$), expressed in units of spawners per spawner, which was first divided by SPR in the absence of fishing mortality to calculate the number of age-3 recruits per unit spawner biomass and then by $M_{ocean} \times 3$ to convert the units of recruitment to the number of juvenile fish as follows:

$$\alpha = \frac{\frac{\tilde{\alpha}}{SPR_{F=0}}}{\left(e^{-M_{ocean}\times3}\right)}.$$

A second standardization was required to change from units of spawner biomass to the number of eggs. Spawning stock biomass in year t, SSB_t, was calculated for each year of the model based on the number of fish in the spawning population as follows:

$$SSB_t = \sum_{a=3}^{8} \sum_{p=1}^{5} S_{a,t,p} W_a,$$

where for each year t, $S_{a,t,p}$ is the number of fish of age a that have spawned p times and W_a is the mass at age a (Gibson and Myers 2003b). The model was run with a habitat size of 4.047×10^6 m^2 for 300 years (to ensure population stabilization), and outputs then were used to iteratively estimate the α value that described the slope at the origin of the SR curve that related juvenile recruitment from total egg production.

Nutrient model.— The second component of the model calculated nutrient import and export. We assumed that adults were not feeding while in freshwater so that nutrient import was solely from the marine environment. Total nitrogen or phosphorus inputs (I_t) were calculated for year t based on total carcass inputs (C_t), total gametes

produced by both males and females (G_t), and total excretion rates (E_t) for year t as follows:

$$I_t = C_t + G_t + E_t.$$

Carcasses.— Total carcass input for each year t (C_t) was calculated using separate nitrogen and phosphorus values for somatic and gonad tissues, which differ in elemental composition (Durbin et al. 1979), with the assumption that if Alewives die, they die before spawning. For both tissue types, total wet mass from carcass inputs was calculated for year t using separate mass-at-age values for males and females:

$$C_t = C_{Somatic,f,t} + C_{Somatic,m,t} + C_{Ovaries,t} + C_{Testes,t},$$

where $C_{Somatic,f}$ = the female somatic input, $C_{Somatic,m}$ = the male somatic input, $C_{Ovaries}$ = the ovary input, and C_{Testes} = the testes input. Male and female mass-at-age, ovary mass-at-age, and testes mass-at-age values were calculated using data collected from the St. Croix River (Fisheries and Oceans Canada et al. 1981–2016; Table 2). For this dataset, 563 fish were aged using scales and corresponding gonad weighs were recorded (306 females and 257 males). For each individual fish, gonad mass was subtracted from total mass to calculate somatic mass. These were averaged by age-class and sex to calculate somatic input, and total carcass input was calculated as follows:

$$
\begin{aligned}
C_{Somatic,f,t} &= \{\Sigma_{a=3}^{8}[S_{a,t}(1 - e^{-0.25M_{spawn}})0.5]W_{Somatic,f,a}\} \\
&\quad \times DW_{Somatic}n_{Somatic},
\end{aligned}
$$

$$
\begin{aligned}
C_{Somatic,m,t} &= \{\Sigma_{a=3}^{8}[S_{a,t}(1 - e^{-0.25M_{spawn}})0.5]W_{Somatic,m,a}\} \\
&\quad \times DW_{Somatic}n_{Somatic},
\end{aligned}
$$

$$
\begin{aligned}
C_{Ovaries,t} &= \{\Sigma_{a=3}^{8}[S_{a,t}(1 - e^{-0.25M_{spawn}})0.5]W_{Ovaries,a}\} \\
&\quad \times DW_{Ovaries}n_{Ovaries},
\end{aligned}
$$

$$
\begin{aligned}
C_{Testes,t} &= \{\Sigma_{a=3}^{8}[S_{a,t}(1 - e^{-0.25M_{spawn}})0.5]W_{Testes,a}\} \\
&\quad \times DW_{Testes}n_{Testes},
\end{aligned}
$$

where $S_{a,t}$ = the number of spawners at age a for year t, M_{spawn} = the instantaneous mortality rate due to spawning calculated for 3 months (0.25 years), $W_{Somatic,f,a}$ = the average somatic mass of females age a, $W_{Somatic,m,a}$ = the average somatic mass of males age a, $DW_{Somatic}$ = the wet mass to dry mass conversion for somatic tissue, $n_{Somatic}$ = the percent dry mass content of nitrogen or phosphorus for somatic tissue, $W_{Ovaries,a}$ = the average ovary mass for age a, $DW_{Ovaries}$ = the wet mass to dry mass conversion for ovaries, $n_{Ovaries}$ = the percent dry mass content of nitrogen or phosphorus for ovaries, $W_{Testes,a}$ = the average testes mass for age a, DW_{Testes} =

the wet mass to dry mass conversion for testes, and n_{Testes} = the percent dry mass content of nitrogen or phosphorus for testes (Durbin et al. 1979).

Gametes.— Total gamete contribution for year t (G_t) was calculated separately from carcass gamete contribution to account for the difference between spent and unspent gonad mass. Gamete contribution included sperm input ($G_{Sperm,a,t}$) and egg input ($G_{Eggs,a,t}$) for age-class a in year t as follows:

$$G_t = G_{Sperm,a,t} + G_{Eggs,a,t}.$$

Total female gonad mass was calculated as the age-specific ovary mass of inbound females minus the average ovary mass for outbound females so that only the spawned egg mass was included (Table 2). For male gamete contribution, total wet mass of sperm input for age-class a ($W_{Spent,a}$) was calculated by subtracting spawned testes mass from unspawned testes mass (Fisheries and Oceans Canada et al. 1981–2016). Unspawned (inbound) testes mass was determined by age-class, but spawned (outbound) testes mass was an average that combined age-classes because only 33 individuals were sampled (Table 2).

The total contribution from sperm and eggs were calculated separately using the following equations:

$$
\begin{aligned}
G_{Sperm,a,t} &= \sum_{a=3}^{8}\{[S_{a,t}(e^{-0.25M_{spawn}})p_{a,t}0.5]W_{Spent,a}\} \\
&\quad \times DW_{Testes}n_{Testes},
\end{aligned}
$$

$$
G_{Eggs,a,t} = \sum_{a=3}^{8} N_{Eggs,a,t}W_{Egg}DW_{Eggs}n_{Eggs}.
$$

Here, the total wet mass of sperm input is calculated using the number of surviving male spawners in year t and age a times the weight of spent testes for each age-class. Total egg contribution involved $N_{Eggs,a,t}$ = the number of eggs from age-class a for year t and W_{Egg} = the average mass of 1 egg (0.1267 mg; Kissil 1974). Both sperm and egg contributions were then multiplied by a separate wet mass to dry mass conversion (DW) and the nitrogen or phosphorus percent dry mass content of each respective tissue (n) based on Durbin et al. (1979).

Excretion.— Total excretion inputs (E_t) were estimated for year t based on the number of fish that successfully entered the spawning habitat as well as an estimate of residence time as follows:

$$E_t = RT(E_n24\,\text{h})SSB_t,$$

where RT is the residence time of spawning adults, E_n is the excretion rate of 24.71 µg N or 2.17 µg P $\times$ g wet fish mass$^{-1}\cdot$h^{-1} (Post and Walters 2009) multiplied by 24 h to calculate a daily input, and SSB_t is the spawning stock

TABLE 2. Nutrient inputs used in the Alewife model. Data sources are indicated in the footnotes. Mass is in grams unless otherwise indicated. Values in parentheses are the number of fish sampled from each age-class, and DW/WW is the dry mass to wet mass conversion. Values given in columns labelled 3–8 indicate age-specific values. Values in bold italics were used for all age-classes.

Measurement	Age					
	3	4	5	6	7	8
Carcass						
Female carcass mass[a]	129 (2)	171 (204)	189 (195)	247 (38)	277 (5)	311 (1)
Male carcass mass[a]	131 (10)	161 (212)	177 (171)	199 (32)	212 (3)	
Carcass DW/WW[b]	*0.288*					
N content (% dry mass)[b]	*0.0866*					
P content (% dry mass)[b]	*0.0147*					
Gametes						
Prespawn ovary mass[a]	15 (1)	18 (142)	21 (128)	29 (26)	31 (4)	43 (1)
Change in ovary mass[a]	11 (1)	14 (142)	17 (128)	25 (26)	27 (4)	39 (1)
Prespawn testes mass[a]	6 (3)	6.8 (139)	9.3 (90)	10 (17)	11.8 (2)	
Change in testes mass[a]	4.5 (3)	5.2 (139)	7.7 (90)	8.5 (17)	10.2 (4)	
Postspawn ovary mass[a]	*4 (13)*					
Postspawn testes mass[a]	*1.6 (33)*					
Ovary DW/WW[b]	*0.295*					
Ovary N content (% dry mass)[b]	*0.115*					
Ovary P content (% dry mass)[b]	*0.0112*					
Testes DW/WW[b]	*0.249*					
Testes N content (% dry mass)[b]	*0.137*					
Testes P content (% dry mass)[b]	*0.0354*					
Excretion						
N rate (µg/g wet mass/hour)[c]	*24.71*					
P rate (µg/g wet mass/hour)[c]	*2.17*					
Age-0 export						
N content (g N/g wet mass)[b]	*0.02735*					
P content (g P/g wet mass)[d]	*0.0058*					
Age-0 mass[e]	*3.5*					

[a] Fisheries and Oceans Canada et al. (1981–2016).
[b] Durbin et al. (1979).
[c] Post and Walters (2009).
[d] West et al. (2010).
[e] Havey (1973).

biomass in year t. A residence time of 14 d in the river was used for each individual regardless of water temperature at the time of entry (Kissil 1974; West et al. 2010). While this may be a conservative estimate, this level of nutrient input is consistent with previous Alewife studies (Post and Walters 2009; West et al. 2010; Twining et al. 2017). Individual Alewife residence times in a river can be more than 25 d; however, a study in the Ipswich River in Massachusetts reported an average residence time of 10 d (Frank et al. 2010).

Juvenile export.— The final portion of the nutrient balance calculations was total juvenile export from the watershed in year t and was calculated as follows:

$$Export_t = J_t \times W_{juvenile} \times n_{juvenile}.$$

Juvenile abundance in year t (J_t) was calculated as described above and then multiplied by the average

juvenile mass ($W_{juvenile}$; Havey 1973) and the nitrogen or phosphorus content of emigrating juveniles ($n_{juvenile}$; Table 2). Total phosphorus export was based on a concentration of 0.0058 g P/g wet mass as measured in West et al. (2010). In the absence of a juvenile-specific nitrogen concentration, we estimated a value based on the measured adult content (0.02735 g N/g wet mass; Durbin et al. 1979).

Sensitivity analysis.— Once values for the parameters of the model were selected, simulations were run and the local sensitivity of model outputs to model parameters was evaluated. We assessed sensitivity of (1) total ocean population, (2) spawning population, (3) age-3 recruitment, (4) spawning stock biomass, (5) import of nutrients, and (6) export of nutrients (both nitrogen and phosphorus) to a suite of parameters (Table 3). We varied mortality rates, maturity

rates, stock–recruitment constants, fecundity coefficients, and demographic parameters such as mass and fork length (Table 3). Analyses were performed by shifting each parameter input 1, 10, 15, and 25% and evaluating model output (Bailey and Zydlewski 2013; Childress et al. 2014). When inputs were age-specific, all of the values were changed in parallel for simplicity (Table 1). For example, M_{ocean} was increased for ages 1–7 as opposed to increasing this parameter for each age-class separately. Because the probability of maturity after age 5 was 1.0, sensitivities in changes of m only influenced ages 2–4.

The sensitivities of all major outputs to base model inputs were estimated (Table 3). A sensitivity index was calculated for each input change by output combination. Sensitivities were calculated as follows:

$$S = \frac{(O_i - O_n)/O_n}{(I_i - I_n)/I_n},$$

where O_i is the output value after the input was increased, O_n is the base output value, I_i is the altered input value, and I_n is the original input value. Inputs were considered "highly sensitive" to change if $|S| > 1.00$.

Population variability and nutrient exchange.— Scenarios were run to explore among-population variability using Stella 10.0.6 (High Performance Systems, Hanover, New Hampshire). To explore changes in spawner abundance and nutrient dynamics due to variability in life history traits and habitat carrying capacity, the model was run using the 10th, 50th, and 90th percentiles of the log lifetime reproductive rate (α) and the asymptotic recruitment level (R_{asy}) measured in Gibson (2004; Table 1). These scenarios represented the range of realistic "low," "medium," and "high" levels of freshwater productivity for Alewife populations sampled in New Brunswick, Maine, and New Hampshire (Gibson 2004). Thus each percentile represents the fraction of Alewife populations that are assumed to be lower than that value (i.e., for the 10th percentile value, 10% of Alewife populations are expected to have lower values while 90% would have higher values; Figure 2; Gibson and Myers 2003a).

The combined effect of freshwater productivity and an in-river intercept fishery on nutrient dynamics was explored by comparing spawner abundance as well as net annual exchange (adult import − juvenile export, hereafter referred to as Δ) for nitrogen and phosphorus. Fishing mortality was assumed to remove a percentage of the spawning population each year after individuals matured but before they contributed reproductively to the juvenile abundance. The model was run using low (10% of the spawning run removed annually), medium (40%), and high (70%) fishing mortality ($M_{Fishery}$). Total spawner abundance after fishing mortality (SF_t) was calculated by multiplying the spawner abundance

for fish of age a in year t that spawned p times previously by the survival rate as follows:

$$SF_t = \sum_{a,p} S_{a,t,p} \times (1 - M_{Fishery}) \times \varphi.$$

Each of the models with these differing levels of imposed fishing mortality was assessed at the low, medium, and high productivity scenarios described above. Results for each scenario were compared graphically.

Model initialization and output evaluation.— The model was initialized with the starting spawning run size set at 1,000 adults that were distributed among age-classes using the proportions at age from a stable population determined by simulation. The model was run for 250 years to ensure the SR relationship reached its plateau. However, the spawning population stabilized around 55 years into the model run, so only the first 100 years of data are presented in the results. Adult nutrient import, juvenile export, and Δ values were calculated annually for both nitrogen and phosphorus. Import was estimated separately for carcass inputs, excretion, and gamete inputs. The dynamics between import, export, and net nutrient balance were evaluated in the context of spawning run size, as well as temporally for the first 30 years of the model. The shifts between these nutrient components were also evaluated between scenarios and relative to the population's location on the SR curve.

RESULTS

Sensitivity Analyses

Several trends were seen in output sensitivities in response to 1, 10, 15, and 25% shifts in input parameters. An increase in escapement did not affect any outputs at any level of increase (Table 3). All model outputs, regardless of the percentage of increase, were sensitive to R_{asy} (asymptotic recruitment) and habitat size, both of which are related to the estimate of carrying capacity of the spawning habitat. The calculated sensitivity value (S) for these two inputs was virtually proportional to the percent increase in input, was the same value for all outputs, and was the widest range of sensitivities observed (1–25; Table 3). For α, all outputs were sensitive to an increase of 10% or more, though S only ranged between 1.7 and 3.5. All outputs were highly sensitive to a 25% increase of input values except escapement and juvenile mass. These outputs were also sensitive to a 15% increase in all inputs except probability of maturity, which did not result in |S| > 1 for ocean and juvenile abundance, as well as nutrient export. However, other adult metrics were sensitive to probability of maturity.

Juvenile mass only affected nutrient export but at all levels of input increase, as would be expected. Juvenile

TABLE 3. Sensitivity index calculated after each input was individually increased by 1, 10, 15, and 25%. When inputs had different values for different age-classes, all of the values were increased simultaneously. Outputs were recorded for each increase and sensitivity was calculated using $S = \frac{(Oi - On)/On}{(Ii - In)/In}$, where O and I are output and input, respectively, and i and n are altered and original values, respectively. Absolute values >1.00 (shown in bold italics) are considered sensitive. Abbreviations are as follows: SSB is the spawning stock biomass, F:M is the female to male ratio, a is the slope of the origin of the spawner–recruit curve, and R_{asy} is the asymptotic recruitment level.

		Output							
Input	Change (%)	Ocean population	Spawner population	Juvenile population	SSB	N adult	N age-0	P adult	P age-0
Escapement	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ocean mortality	1	*−1.19*	*−2.46*	−0.38	*−2.52*	*−2.52*	−0.38	*−2.52*	−0.38
	10	*−7.56*	*−19.90*	*−3.71*	*−20.47*	*−20.48*	*−3.71*	*−20.48*	*−3.71*
	15	*−10.20*	*−26.02*	*−5.18*	*−26.73*	*−26.73*	*−5.18*	*−26.73*	*−5.18*
	25	*−16.99*	*−39.91*	*−9.39*	*−40.86*	*−40.86*	*−9.39*	*−40.86*	*−9.39*
Probability of maturity (only ages 2–4)	1	−0.04	0.63	0.07	0.53	0.53	0.07	0.53	0.07
	10	−0.44	*6.30*	0.66	*5.17*	*5.15*	0.66	*5.15*	0.66
	15	−0.61	*8.33*	0.85	*6.80*	*6.77*	0.85	*6.78*	0.85
	25	*−1.05*	*13.44*	*1.31*	*10.88*	*10.83*	*1.31*	*10.84*	*1.31*
Spawning mortality	1	−0.10	−0.10	−0.10	−0.10	0.26	−0.10	0.37	−0.10
	10	*−1.18*	*−1.18*	*−1.18*	*−1.18*	*2.63*	*−1.18*	*3.84*	*−1.18*
	15	*−1.62*	*−1.62*	*−1.62*	*−1.62*	*3.46*	*−1.62*	*5.07*	*−1.62*
	25	*−2.78*	*−2.78*	*−2.78*	*−2.78*	*5.33*	*−2.78*	*7.91*	*−2.78*
Probability of spawning	1	0.23	0.83	0.27	0.86	0.89	0.27	0.88	0.27
	10	*1.12*	*4.39*	*1.37*	*4.52*	*4.68*	*1.37*	*4.65*	*1.37*
	15	*1.12*	*4.39*	*1.37*	*4.52*	*4.68*	*1.37*	*4.65*	*1.37*
	25	*1.12*	*4.39*	*1.37*	*4.52*	*4.68*	*1.37*	*4.65*	*1.37*
α	1	0.17	0.17	0.17	0.17	0.17	0.17	0.17	0.17
	10	*1.72*	*1.72*	*1.72*	*1.72*	*1.72*	*1.72*	*1.72*	*1.72*
	15	*2.25*	*2.25*	*2.25*	*2.25*	*2.25*	*2.25*	*2.25*	*2.25*
	25	*3.45*	*3.45*	*3.45*	*3.45*	*3.45*	*3.45*	*3.45*	*3.45*
R_{asy}	1	*1.01*	*1.01*	*1.01*	*1.01*	*1.01*	*1.01*	*1.01*	*1.01*
	10	*11.09*	*11.09*	*11.09*	*11.09*	*11.09*	*11.09*	*11.09*	*11.09*
	15	*14.99*	*14.99*	*14.99*	*14.98*	*14.99*	*14.99*	*14.99*	*14.99*
	25	*25.01*	*25.01*	*25.01*	*25.01*	*25.01*	*25.01*	*25.01*	*25.01*
Habitat size	1	*1.00*	*1.00*	*1.00*	*1.00*	*1.00*	*1.00*	*1.00*	*1.00*
	10	*11.10*	*11.10*	*11.10*	*11.10*	*11.10*	*11.10*	*11.10*	*11.10*
	15	*15.00*	*15.00*	*15.00*	*15.00*	*15.00*	*15.00*	*15.00*	*15.00*
	25	*25.00*	*25.00*	*25.00*	*25.00*	*25.00*	*25.00*	*25.00*	*25.00*
Fecundity slope	1	0.25	0.25	0.25	0.25	0.30	0.25	0.29	0.25
	10	*2.43*	*2.43*	*2.43*	*2.43*	*2.95*	*2.43*	*2.82*	*2.43*
	15	*3.13*	*3.13*	*3.13*	*3.13*	*3.83*	*3.13*	*3.66*	*3.13*
	25	*4.65*	*4.65*	*4.65*	*4.65*	*5.84*	*4.65*	*5.54*	*4.65*
Fecundity intercept	1	−0.08	−0.08	−0.08	−0.08	−0.10	−0.08	−0.09	−0.08
	10	−0.96	−0.96	−0.96	−0.96	−1.12	−0.96	−1.08	−0.96
	15	*−1.32*	*−1.32*	*−1.32*	*−1.32*	*−1.54*	*−1.32*	*−1.48*	*−1.32*
	25	*−2.32*	*−2.32*	*−2.32*	*−2.32*	*−2.67*	*−2.32*	*−2.59*	*−2.32*

TABLE 3. Continued.

Input	Change (%)	Ocean population	Spawner population	Juvenile population	SSB	N adult	N age-0	P adult	P age-0
				Output					
F:M	1	0.17	0.17	0.17	0.17	0.20	0.17	0.19	0.17
	10	*1.73*	*1.73*	*1.73*	*1.73*	*2.07*	*1.73*	*1.99*	*1.73*
	15	*2.25*	*2.25*	*2.25*	*2.25*	*2.73*	*2.25*	*2.61*	*2.25*
	25	*3.45*	*3.45*	*3.45*	*3.45*	*4.25*	*3.45*	*4.05*	*3.45*
Adult mass	1	0.25	0.25	0.25	*1.25*	0.73	0.25	0.55	0.25
	10	*2.43*	*2.43*	*2.43*	*13.80*	*7.81*	*2.43*	*5.79*	*2.43*
	15	*3.13*	*3.13*	*3.13*	*18.60*	*10.45*	*3.13*	*7.71*	*3.13*
	25	*4.65*	*4.65*	*4.65*	*30.81*	*17.04*	*4.65*	*12.40*	*4.65*
Juvenile mass	1	0.00	0.00	0.00	0.00	0.00	*1.00*	0.00	*1.00*
	10	0.00	0.00	0.00	0.00	0.00	*11.10*	0.00	*11.10*
	15	0.00	0.00	0.00	0.00	0.00	*15.00*	0.00	*15.00*
	25	0.00	0.00	0.00	0.00	0.00	*25.00*	0.00	*25.00*
Juvenile mortality	1	−0.08	−0.08	0.35	−0.08	−0.08	0.35	−0.08	0.35
	10	*−5.49*	*−5.49*	*−0.85*	*−5.49*	*−5.49*	*−0.85*	*−5.49*	*−0.85*
	15	*−7.36*	*−7.36*	*−1.16*	*−7.36*	*−7.36*	*−1.16*	*−7.36*	*−1.16*
	25	*−12.01*	*−12.01*	*−1.97*	*−12.01*	*−12.01*	*−1.97*	*−12.01*	*−1.97*
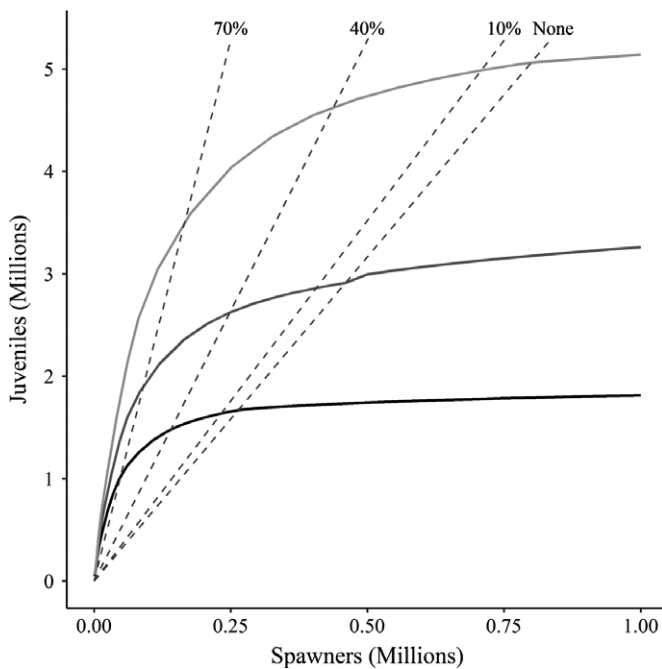
FIGURE 2. Spawner–juvenile relationship for three productivity scenarios that varied α and R_{asy} (black = 10th percentile, dark gray = 50th percentile, light gray = 90th percentile). Dashed lines indicate replacement lines associated with four fishery mortality scenarios (no mortality, 10% spawner mortality, 40% spawner mortality, and 70% spawner mortality).

metrics, including abundance and nitrogen and phosphorus export, were highly sensitive to a 10–25% change in ocean mortality but not a 1% change. Interestingly, juvenile metrics were not sensitive to juvenile mortality until it was increased by at least 15%, but adult metrics were all sensitive at a 10% increase and above. All adult metrics, including the ocean population, spawning run, spawning stock biomass, and nitrogen and phosphorus import rates, were sensitive to ocean mortality with an expected decrease in output value as mortality increased. Increasing the mass of each age-class by 1% led to a higher spawning stock biomass and at 10% and above demonstrated sensitivity for all outputs. Inputs related to egg estimation did not result in sensitivity values greater than 1 when increased by 1%. All outputs were sensitive to a 10–25% increase in both the fecundity slope and female to male ratio and a 15–25% increase in the fecundity intercept.

Nutrient Dynamics Over Range of Productivity and Mortality Scenarios

In all scenarios, the spawning population and juvenile abundances produced by each year of spawners increased until recruitment reached its equilibrium. The value at which equilibrium was attained was dependent on the scenario, within a range of approximately 500,000 spawners and 3.4 million juveniles between populations with low

and high freshwater productivity (Figure 2). The median scenario demonstrated a stabilized population of 459,000 spawners and 2.9 million juveniles. Replacement lines shifted toward lower juvenile production for a given spawner abundance as adult mortality rates increased.

Results were qualitatively similar for all three productivity scenarios in that at a low spawning population net export of both nitrogen and phosphorus occurred, but as spawner abundance increased dynamics switched to net import (Figure 3). The spawner abundance at which this switch occurred was lower for nitrogen than for phosphorus in all three productivity scenarios. Adult import dominated ΔN except for the first 2–6 years after recruits produced by the model (year 4) entered the spawning population (Figures 3 and 4). This net nitrogen export may not occur in a scenario with the same habitat size if the initial spawning population is already near the equilibrium and is unimpacted by additional adult mortality. The magnitude of net nitrogen export for all three productivity scenarios was low relative to the stabilized maximum adult import. The maximum net export of nitrogen for low and medium freshwater productivity scenarios was less than 1 kg and 5.5 kg, respectively. In the high productivity scenario, a maximum difference of 16 kg was seen with 23,000 spawners present and 1 million juveniles produced. Adult nitrogen import increased linearly with the spawning population, so ΔN quickly became larger than the amount of nitrogen that juveniles were removing from the system. Nutrient import dominated as the number of juveniles approached their carrying capacity, but export plateaued at low spawner abundance (Figure 3). The magnitude of adult import and juvenile export, as well as the number of years net export occurred, increased with freshwater productivity (Figure 4). Despite large differences in spawner and juvenile abundance between productivity scenarios, the shift from net export to net import for all three scenarios occurred within a similar time frame (6 to 10 years).

Net phosphorus dynamics were similar to the trend seen in nitrogen except that export occurred for a longer time period and at higher spawner abundance. Initially, juvenile phosphorus export dominated when spawner density was low (Figure 3) and the per-capita production of juveniles was the highest. However, ΔP increased over the course of 11–13 years. This corresponded to a maximum export for the low, medium, and high scenarios of 2.8, 6.5, and 14.7 kg, respectively. The spawner abundances associated with these maximums also increased with increasing freshwater productivity (low = 15,600 spawners; medium = 32,000 spawners; high = 60,900 spawners). After this, per-capita export declined, though it still outweighed import for two more years in all three scenarios. Phosphorus dynamics then switched from net export to net import at 35,000, 61,000, and 116,000 spawners for

the low, medium, and high scenarios, respectively (and 859,000, 1.6 million, and 3 million juveniles, respectively). At this point, age-0 recruitment was starting to plateau as density-dependent effects began to dominate the SR relationship. Thus, fewer juveniles were being produced per capita as a result of larger numbers of spawners entering the system (Figures 2 and 3). Juvenile export mirrored this pattern, plateauing at 34, 59, and 103 kg for the low, medium, and high scenarios, respectively, even as adult import continued to increase from 1 year to the next, reaching a maximum value of 133, 232, and 404 kg, respectively (net differences of 99, 173, and 302 kg, respectively).

Within each productivity scenario, the same pattern was seen in the nitrogen and phosphorus dynamics but the magnitude of import and export differed. As freshwater productivity increased, the number of juveniles produced per spawner also increased and led to net export at low spawner abundance. This was less pronounced for nitrogen than in phosphorus because of the relative nutrient content of adults and juveniles. At a stabilized population, phosphorus values were smaller by an order of magnitude than the values for nitrogen because the N:P ratio in Alewives is high. The amount of nitrogen in adult tissue was 6 times higher than phosphorus for a carcass, 10 times higher for ovaries, 4 times higher for testes, and 13 times higher for excretion. This dynamic was highlighted in the sharp increase in N:P value coincident with increasingly high population growth (Figure 5). At a low spawner number, net export was seen for both nitrogen and phosphorus, and the ratio was both small and positive. Nitrogen switched to net import before phosphorus for all three scenarios, resulting in a negative N:P. This phosphorus export was only seen for a small range of spawner abundances within all three scenarios, and nutrient dynamics quickly switched to net import as juvenile production began to plateau. The highest N:P value for net import was seen in the medium productivity scenario and the lowest in the high productivity scenario. As the population stabilized, a consistent ratio of 8.75:1 was seen for N:P in all three scenarios.

Spawner abundance decreased as mortality rate increased, but the most striking differences seen between scenarios were in the magnitudes of ΔN and ΔP (Figure 6). Freshwater productivity determined the level of juvenile export that occurred, and this was especially pronounced in ΔP. For all three mortality rates, increasing juvenile productivity resulted in a higher occurrence of net export (Figure 6). The shift from net export to net import occurred at approximately the same number of spawners regardless of mortality rate, but was much higher when the productivity level was at the 90th percentile than the 10th percentile. Both mortality rate and productivity level determined the magnitude of adult import, and so the maximum ΔN and ΔP decreased drastically as mortality increased and productivity decreased.
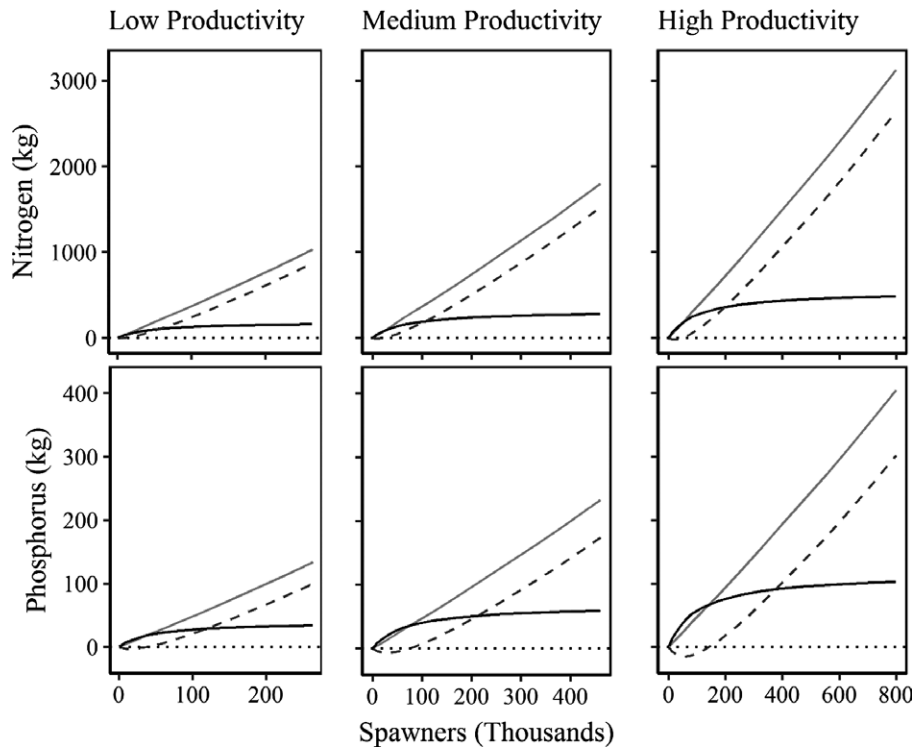
FIGURE 3. Nitrogen and phosphorus dynamics in relation to spawner abundance for three freshwater productivity scenarios assuming unconstrained access to spawning habitat. The gray solid line = import, the black solid line = export, and the gray dashed line = the net nutrient flow (import − export). The dotted line delineates the transition between net export (below) and net import (above). Productivity scenarios included the 10th (low), 50th (medium), and 90th (high) percentiles of the parameters α (lifetime reproductive rate) and R_{asy} (asymptotic recruitment level).

DISCUSSION

Spawner Abundance and Nutrient Import and Export

Within a specific lake or watershed, the ecological role that Alewives play in net nutrient balance will depend on many factors. These include, but are not limited to, the status of the population relative to its potential within the watershed and the spawner mortality rate. We found that at a low spawning density, where the effect of density-dependence on recruitment was negligible, ΔP was negative as high juvenile production and subsequent nutrient export outweighed adult delivery. The magnitude of export was dependent on productivity level, as this determined the number of juveniles produced per spawner. For ΔN, this initial export phase was smaller than for ΔP (in relation to maximum import) because each adult contained greater nitrogen than phosphorus. The model demonstrated that density-dependent production of juveniles related to the SR curve became more pronounced as the spawning population grew. Therefore, an established Alewife population with no fishery or other impediments to habitat access would persist with high adult returns and relatively low per-capita juvenile production.

When comparing productivity scenarios, the measured range of values for the SR relationship resulted in a change in the magnitude of spawner abundance, adult nutrient import, and juvenile export. However, the same pattern in nutrient dynamics was seen regardless of the scenario. Net export occurred at low spawner abundance, but the dynamics switched to net import as the number of adults increased. The spawner abundance at this transition point was determined by the values being used in the SR curve. For α, standard deviation of the distribution for this parameter was relatively small (Gibson and Myers 2003a) so the difference between the 10th and 90th percentiles was also small. However, variability in the asymptotic recruitment level (R_{asy}) per unit area among Alewife populations was much greater and resulted in large differences in nutrient dynamics as this determined maximum juvenile production.

Spawner mortality can shift the population from higher to lower recruitment levels due to density-dependent effects. Many Alewife populations are harvested as fish ascend a river to spawn, and most streams have some additional impediment to passage (i.e., dams, sediment buildup, water quality issues, etc.) that affects spawner survival and the ability to reach spawning habitat (Hall
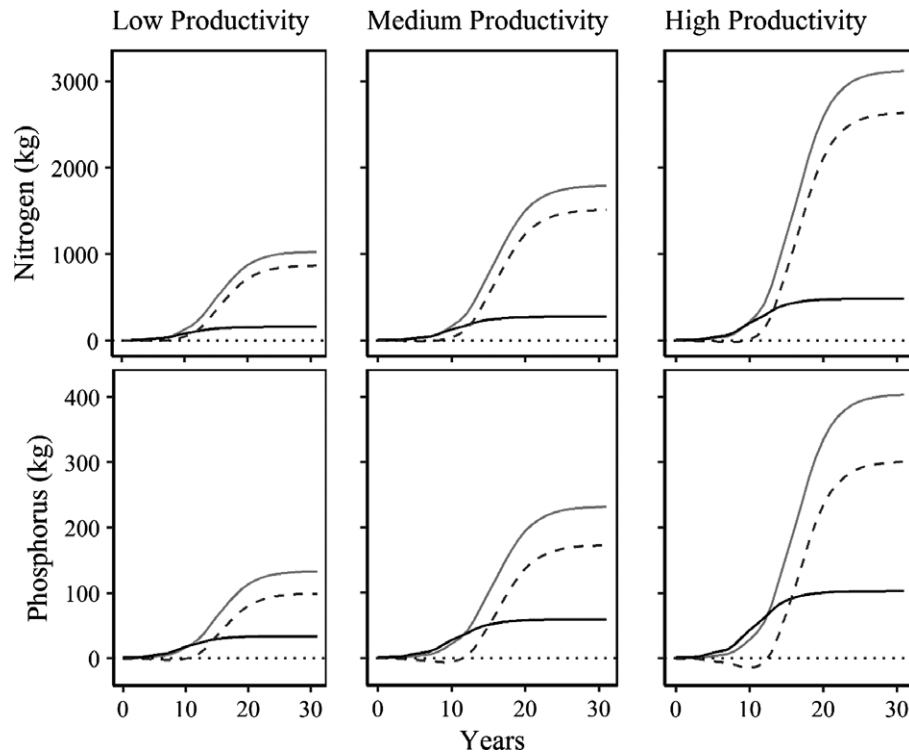
FIGURE 4. Nitrogen and phosphorus nutrient dynamics for the first 30 years of the model run for three freshwater productivity scenarios assuming unconstrained access to spawning habitat. The gray solid line = import, the black solid line = export, and the gray dashed line = the difference (import − export); the dotted line is the shift between the net export and net import. Productivity scenarios included the 10th (low), 50th (medium), and 90th (high) percentiles of the parameters α (maximum lifetime reproductive rate) and R_{asy} (asymptotic recruitment level).

et al. 2011). Passage success or mortality (both upstream and downstream) can also influence population demographics (Maynard et al. 2017). As was demonstrated (and is intuitive), a population with an in-stream fishery will have fewer spawners than an unfished population. If a population persists with sustained increased mortality, age-0 recruitment will be defined by the steeper part of the SR curve. As a result, more recruits will be produced per capita due to reduced density-dependent effects, resulting in persistent net nutrient export.

However, the magnitude of maximum spawner abundance changes when considering the synergistic effects of spawner mortality and freshwater productivity. Spawner mortality limited adult import, but productivity levels determined juvenile export. Within a productivity scenario, maximum net export levels were similar regardless of spawner mortality. More juveniles were produced when spawner survival was high, but this was balanced by higher adult import making maximum net export values similar regardless of mortality scenario. As a result, maximum net import was affected more by changes in spawner mortality than by productivity.

The results from this analysis may help explain some of the variation in nutrient dynamics seen in other Alewife studies. As was shown by this modeling work, it is important to consider the number of spawners in a run relative to the SR curve when estimating ΔP. Previous studies that have estimated net nutrient balance have indicated that juvenile export is negligible in smaller lakes with established Alewife runs (Durbin et al. 1979; West et al. 2010). This result falls in line with the results from the modeling work presented in this paper as recruitment for these populations is defined by the plateau of the SR curve. However, our model suggests that a lake with a spawning population that is maintained at a low level relative to the habitat's capacity could see the magnitude of juvenile phosphorus export increase (West et al. 2010).

Alewife populations and run sizes may change over time and alter recruitment based on the dynamics of the SR curve. For a founding population, an initially small spawning abundance will result in a high recruitment rate and net phosphorus export, though the magnitude of ΔP is also sensitive to juvenile mass and ocean mortality rates. However, as the number of spawners increases steadily with time, the asymptotic recruitment level for that habitat will be approached and the population will plateau with import as the dominant nutrient dynamic (Figure 3). Given the high variability in carrying capacity found by
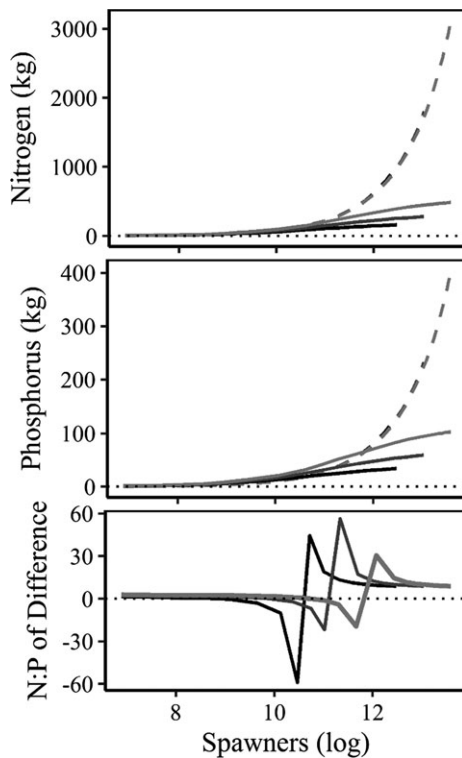
FIGURE 5. Nitrogen, phosphorus, and the N:P ratio for the difference (import − export) related to the log of spawner abundance. Nutrient import is shown as dashed lines and export is shown as solid lines in the top two panels. For all panels, the 10th percentile scenario is shown in black, the 50th is shown in dark gray, and the 90th is in light gray. The N:P ratio is negative when nitrogen import and phosphorus export are occurring but switches to positive as phosphorus import dominates.

Gibson (2004), habitat quality is also a key determinant of the magnitude of adult import. When testing model sensitivities, we found that all output variables were sensitive to R_{asy} and habitat size because these two parameters determined the asymptotic recruitment level; thus, an increase in either resulted in greater fish production. However, nutrient delivery does not guarantee assimilation into the freshwater habitat. Hocking and Reimchen (2009) found lower rates of nutrient incorporation as watershed size increased.

The opposite trend will occur when a declining population has consistently high mortality, especially when the number of spawners that enter the habitat is small relative to its productivity level. In this scenario, phosphorus export will dominate as spawner abundance continues to decrease. In addition to adult mortality rates, changes in density-dependent juvenile survival can influence nutrient export, and vice versa. In a large habitat with reduced resource competition, larger juveniles are produced that will export a higher level of nitrogen and phosphorus (Moore and Schindler 2004). On the other hand, if the

Alewife spawning population is persistently small, a negative feedback loop could develop with net phosphorus export reducing the productivity of a watershed, increasing density-dependence for juveniles (Scheuerell et al. 2005). This pattern has been seen for both Chinook Salmon *Oncorhynchus tshawytscha* and Atlantic Salmon for which, as spawner abundance decreased, smolts exported proportionally higher levels of phosphorus from the watershed (Nislow et al. 2004; Scheuerell et al. 2005).

It is important to note that we did not include environmental stochasticity in our model. Effects of environmental variability would be expected to have relatively modest influences on the relationships between spawner abundance and nutrient import, primarily via its effect on the age structure of the population. In contrast, the effect of environmental variability on nutrient export could be greater through direct influence on recruitment variability. For example, Tommasi et al. (2015) reported that environmental variability explained more of the variance between adult and juvenile Alewife abundance than density dependence for four Alewife populations in the northeastern USA. Additionally, it is important to remember that the model is not intended as a dynamic forecasting model but rather a heuristic simulation that represents the "average" scenario based on the inputs that are used (Ford 1999). If environmental stochasticity were included, it is possible that it would take more or less time for the population to reach its equilibrium abundance. However, as the model is run for several hundred years, instances of poor recruitment would be expected to be balanced by years of excellent recruitment. A large number of simulations, each with random variability drawn from the same distribution, would give the same "average" result. The general trends will therefore remain the same regardless of variation in the endpoints.

The Role of Alewives in Freshwater Productivity

The results of this model indicate that when freshwater productivity is high and spawner mortality is low, Alewives have the potential to deliver substantial nutrient loads to freshwater systems. Whether these nutrients are incorporated into a system will depend on baseline nutrient limitations, the method of delivery, and the existing freshwater community. Whether a system is nitrogen or phosphorus limited, or colimited, can determine the influence of a nutrient subsidy. Previous studies have shown that nutrient input from anadromous species often boosts the productivity of a stream or lake, but these effects seem to be most pronounced when the habitat is oligotrophic (Cederholm et al. 1999; Chaloner et al. 2002; Bellmore et al. 2014; Samways and Cunjak 2015). A high N:P value during the recovery of a population, as was seen in this study, could mean that much of the nitrogen brought into a system is not retained and immediately used by organisms.
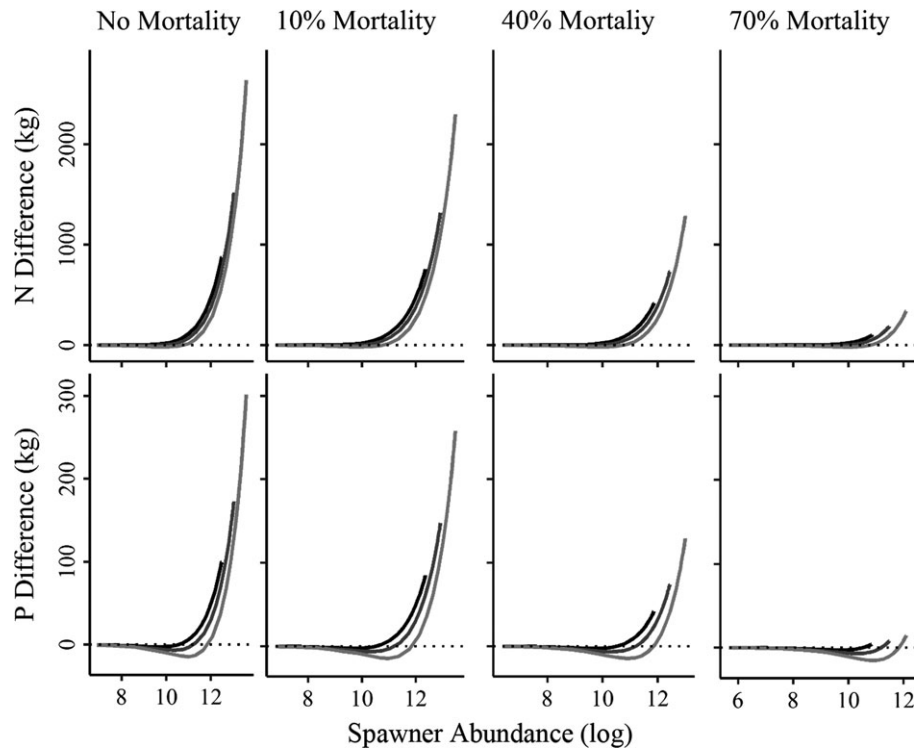
FIGURE 6. Nitrogen and phosphorus difference (import − export) for four levels of spawner mortality as might be experienced through harvest (none, 10, 40, and 70%) and three productivity levels (black = 10th percentile, dark gray = 50th, and light gray = 90th). The dotted line indicates a nutrient balance of zero, meaning import and export are equal. Negative values indicate net export, while positive values indicate net import.

Geographic variability in life history traits may also affect the N:P ratio. Alewives exhibit a north–south cline in life history traits, with northern populations displaying greater iteroparity (Pardue 1983). For northern populations nutrient delivery is likely dominated by excretion, but for southern populations carcasses are likely the dominant mode of delivery. The latter populations receive a higher biomass of nutrient delivery, and for Alewives the N:P ratio for carcasses is roughly twice that of excretion (Durbin et al. 1979). However, Alewife carcasses can take more than 240 h to decay (Garman 1992), and so this method of nutrient delivery is not immediately bioavailable. Excretion inputs are immediately available for uptake by primary producers, so nitrogen and phosphorus delivered to oligotrophic watersheds in the northern part of the Alewife range can be quickly sequestered and used for the short spring growing period.

Nutrient incorporation can also depend on the method of delivery and how the existing freshwater community is able to access this subsidy. Alewives may have both bottom-up and top-down effects on freshwater communities because they represent both a short-term and long-term subsidy throughout the season. Nutrients immediately available through excretion could boost biofilm and periphyton productivity, though studies have indicated that these effects are short lived, on

the scale of weeks to months (Post and Walters 2009; Collins et al. 2016; García et al. 2017). Decomposition of eggs and carcasses can play the same role and provide a protracted source of nutrients throughout the season for primary production. Marine-derived nutrients can also be incorporated at the top of a food web (Collins et al. 2016). All anadromous fish species represent nutrient-rich subsidies for a variety of predators, including aquatic fish (Willson and Halupka 1995; Jaecks and Quinn 2014) and foraging mammals and birds (Dalton et al. 2009; DeBruyne et al. 2012). Scavenging macroinvertebrates feed on carcasses during their freshwater juveniles phase, then transport marine-derived nutrients into the terrestrial environment after emergence (Polis et al. 1997; Vanni 2002; Hocking and Reimchen 2009). Both bottom-up and top-down pathways likely determine nutrient incorporation, but the relative influence of each will depend on the species that are present and whether freshwater invertebrates are released by predation pressure when subsidies are present (Collins et al. 2016; Sato et al. 2016).

Management Implications

While managers are often concerned about Alewife nutrient import causing water quality issues, the relative magnitude of marine-derived nutrient inputs are likely well

below the extent of anthropogenic influences that already control baseline nutrient levels within New England lakes (Twining et al. 2013). Also, increasing temperatures could lead to elevated metabolic demands at the community level (Woodward et al. 2010), producing a partial outlet for excess nutrients. Several Alewife studies have reported low levels of nutrient delivery because of reduced spawning populations and a trend of shifting to a smaller adult size (Norris 2012; Twining et al. 2017). Currently, watershed contributions to a Connecticut lake, mostly due to lakeshore development, account for 3 times as much phosphorus and 19 times as much nitrogen as are brought in by Alewives (Twining et al. 2013). For an oligotrophic watershed such as the St. Croix River in Maine, from which the demographic information for this model was gathered, Alewife-derived nutrient import may play a more substantial role, especially if the population is large in relation to its carrying capacity. In the St. Croix River, the current Alewife spawning population is only about 0.5% of its estimated capacity (Flagg 2007), so nutrient import could markedly increase if recovery occurred.

As was seen in the results, while Alewives have the potential for rapid population growth, site-specific variability can have a large influence on the net nutrient dynamics. This variability can be determined by sources or spawner mortality, as well as differences in habitat quality within a watershed. In-river fisheries mortality can have the same influence as a dam on net nutrient balance by limiting the number of fish that are allowed to move upstream (Hall et al. 2011), and reduced adult downstream passage could affect the age structure and therefore the fecundity of a population (Jessop 1993). In addition to direct mortality, migratory delays can affect population growth and nutrient dynamics. If dams, waterfalls, or even open stretches of river delay upstream fish passage, then fewer adults successfully enter the spawning habitat (Meixler et al. 2009; Hall et al. 2011; Pess et al. 2014). This causes the population to shift toward a lower equilibrium in which juvenile production and export decreases but to a lesser extent than the decrease in spawner biomass and nutrient import. Many large rivers in New England have multiple dams, and this population reduction can become additive (Brown et al. 2013). This means downstream spawning habitat may demonstrate adult import, but upstream habitat may exhibit relatively greater juvenile export because fewer adults are able to access it.

The output values estimated by a model are only as good as the inputs used, so there are still limitations associated with Alewife population modeling because of data uncertainties related to specific portions of their life history, such as ocean mortality rates. Ocean mortality was one of the more sensitive inputs in the model but is also the most difficult parameter to estimate due to stochasticity in the marine environment (ASMFC Benchmark

Assessment 2012). Mortality is often estimated based on the age structure of spawner returns and the number of repeat spawners within a river because reliable ocean mortality assessments remain elusive. Until more informed estimates are obtained, fisheries managers have to make do with the best available information. Deterministic models such as the one developed here address general trends in a population and can help inform management decisions by testing sensitivities within life histories, but because variation in the spawning run is averaged, these models are not predictive. This model can be tailored to fit any watershed and Alewife population and could be a useful tool where management decisions are made to control either excessive or meager nutrient inputs.

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