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Managing dams for energy and fish tradeoffs: What does a win-win solution take?

1. Introduction

Hydropower is currently the largest source of renewable energy in the United States (US), accounting for 44% of the total renewable energy generation in 2017 (EIA, 2018a; Song et al., 2018; Uría-Martínez et al., 2015). This energy is generated by around 2300 hydroelectric dams, with an installed capacity ranging from 50 W to 6495 MW (Samu et al., 2018). An additional 50% increase in generation capacity is expected by 2050 through the conversion of non-powered dams, capacity expansion of existing hydroelectric dams, and construction of pumped storage facilities (DOE, 2016). However, these dams are often cited as a major causal factor in the dramatic decline of fish populations, especially the diadromous fish species that migrate between marine and freshwater habitats to spawn (Brown et al., 2013; Limburg and Waldman, 2009; Trancart et al., 2013; Ziv et al., 2012). For example, alewife landings on the east coast of the US have declined more than 90% following the construction of a series of dams in the early 20th century (McClenachan et al., 2015; Opperman et al., 2011). Hydroelectric dams affect fish populations both directly and indirectly through turbine injuries (Schaller et al., 2013; Stich et al., 2015), loss of accessible spawning habitat (Hall et al., 2011), and degradation of habitat quality (e.g., changes in temperature, morphology, and discharge) (Johnson et al., 2007).

Various management actions such as dam removals (Magilligan et al., 2016; O'Connor et al., 2015), the installation of fish passage structures (hereafter referred to as fishways) (Nyqvist et al., 2017b; Schilt, 2007), and periodic turbine shutdowns (Eyler et al., 2016), have been implemented to restore river connectivity and mitigate impacts on diadromous fish species. According to data collected by American Rivers, more than a thousand dams have been removed in the US in the last two decades (American Rivers, 2017). In cases where hydroelectric dams remain intact, fishways are often installed to assist with upstream and downstream fish migrations (Silva et al., 2018), and have been mandated by the Federal Energy Regulatory Commission (FERC) as part of dam relicensing process since the 1960s (Gephard and McMenemy, 2004). Turbine shutdowns are also employed to reduce mortalities during peak fish downstream migration periods and have been widely applied to lessen injuries and mortality due to blade strikes, pressure changes, and cavitation (Jacobson et al., 2012).

While these approaches have been useful in lessening the impacts of hydropower operation on diadromous fish species, a loss of hydropower generation is inevitable in all three practices (Gatke et al., 2013; Null et al., 2014; Trancart et al., 2013). For example, a loss of $57 million annual hydropower revenue resulted from the removal of the Shasta Dam in California’s Central Valley, though this removal reopened around 1700 km of upstream salmonid habitat (Null et al., 2014). Fishway installations reduce hydropower production by diverting water discharge to fish passage structures (Gatke et al., 2013). Power cannot be generated during turbine shutdowns. From the perspective of the dam operator, carefully planning of shutdown periods to maximize downstream migrant survival is important to minimize hydropower generation losses (Trancart et al., 2013).

Though researchers and decision-makers have widely recognized energy-fish tradeoffs, quantification of such tradeoffs to inform the decision-making process remains limited (Lange et al., 2018). Simplified proxies, such as habitat gains (Null et al., 2014) and reconnected areas (Kuby et al., 2005), are widely used to estimate the potential increase of fish populations. However, these methods largely neglect factors such as the effectiveness of dam management strategies on both upstream and downstream passage, environmental capacities of reopened habitats, and other dynamics within the entire fish life cycle (Godinho and Kynard, 2009; Sweka et al., 2014; Ziv et al., 2012). Structured fish population models are another means to quantitatively simulate fish populations by considering and incorporating different mortality sources at each of the individual fish life cycle stages. Previous studies have developed and applied structured population models to assess the effect of dam passage rates on diadromous fish populations (Burnhill, 2009; Nieland et al., 2015; Stich et al., 2018). However, this method has not been used to explore the energy-fish tradeoffs of dam management. Furthermore, these studies run on annual or monthly time steps and could not capture the effect of turbine shutdowns that only operate for several days or weeks during peak migration (Trancart et al., 2013).

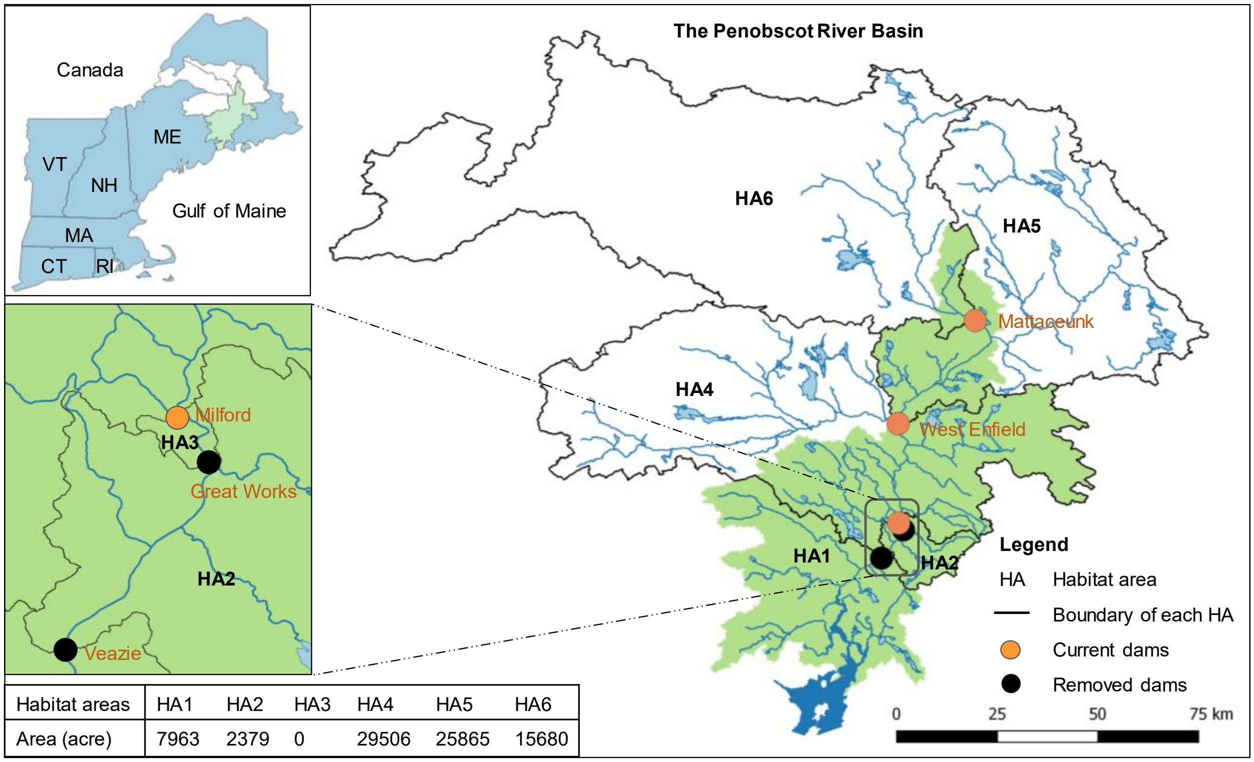
In river systems with multiple dams, regional or basin-scale approaches are preferred over site-specific approaches because of the cumulative effect of dam passage on migrants moving further upstream (Neeson et al., 2015; Opperman et al., 2011; Winemiller et al., 2016). Basin-scale outcomes under various dam management practices could differ dramatically as hydropower potential and fish habitats are unevenly distributed (Roy et al., 2018). However, many previous studies exploring energy-fish tradeoffs on a regional scale have focused on only a single type of management practice (e.g., dam removal or construction) rather than comparing multiple different strategies. For instance, a new dam construction project in the Mekong River Basin was investigated by Ziv et al (2012) to understand the tradeoffs between hydropower production, migratory fish biomass, and fish diversity using the production possibility frontier method (Ziv et al., 2012). Null et al. (2014) analyzed tradeoffs between habitat gains and hydropower generation under dam removal scenarios in California's Central Valley using an economic-technical optimization model (Null et al., 2014). Trancart et al (2013) optimized the timing and duration of turbine shutdowns that would save 90% of the silver eels on the Oir River, France, by forecasting eels' migration peaks based on an auto-regressive integrated moving average model (Trancart et al., 2013). Only one study, conducted in the Willamette basin, Oregon, simulated both dam removal and fishway installation to co-optimize their effects on salmon and hydropower generation (Kuby et al., 2005). This study concluded that fishway installations could be as effective as dam removals at connecting upstream and downstream habitat. However, this study did not measure the actual effectiveness of the fishways, which were treated as either entirely passable or not passable for salmon. The effect of turbine fish kills during downstream migration was also neglected.

The limited consideration of multiple dam management options and important fish mortality factors could potentially lead to sub-optimized decision-making (Sweka et al., 2014). Accordingly, this study developed a system dynamics modeling (SDM) framework to investigate the tradeoffs between hydropower generation and potential diadromous fish abundance. SDM uses a set of linked differential equations to simulate the feedbacks and interactions among different elements. SDM has been previously applied to simulate hydropower production (Bosona and Gebresenbet, 2010; Sharifi et al., 2013) and fish abundance (Barber et al., 2018; Ford, 2000; Stich et al., 2018), but it has not been used to explore the tradeoffs between these two sectors. In this study, the developed framework was used to investigate the potential of three different dam management practices, including dam removals, fishway installations, and periodic turbine shutdowns. Four critical questions regarding dam management were asked, including (1) how and to what extent does each dam management practice influence the energy-fish tradeoffs? (2) what might be the best dam management solution in minimizing energy loss and maximizing fish population on a basin scale? (3) how do upstream and downstream passage rates influence population abundance? and (4) what are the key determinants in managing the dam related energy-fish tradeoffs?

2. Materials and methods

2.1 Model river description

The model framework assessed for decision-making was based on an abstraction of the Penobscot River, Maine, which is the second largest river system in the northeast US, with a drainage area of approximately 22,000 km^2 (Izzo et al., 2016; Trinko Lake et al., 2012). This large river system historically provided important spawning and rearing habitat for 11 native diadromous fish species that have high commercial, recreational, and ecological value to local communities (Kiraly et al., 2015). Among these species, alewives (*Alosa pseudoharengus*) have been a major source of traditional river fisheries since the beginning of human settlement in the region (McClenachan et al., 2015). Alewives are small anadromous fish that have high rates of iteroparity in Maine. Alewives are also the base of marine, freshwater, and terrestrial food webs. Changes in their abundance may also influence the population dynamics of their predators, including the endangered Atlantic salmon (*Salmo salar*) (Lichter et al., 2006). From 1634 to 1900, industrial dams were heavily developed on the Penobscot River, and little or no access to spawning habitat was later identified as the main cause for the alewife population crash during that time (McClenachan et al., 2015). Alewife habitat areas (HAs) are unevenly distributed among the river segments created by the dams (Figure 1). A much larger amount of HA is located upstream of the Milford Dam than downstream of it. Restoration efforts began in the 1940s to combat diadromous fish declines (Rounsefell and Stringer, 1945). One of the largest efforts was the Penobscot River Restoration Project (PRRP), which from 2012-2013 removed the two dams furthest downstream and improved fish passages at the remaining dams (Figure 1) (Opperman et al., 2011). To test the effectiveness of the PRRP and alternative basin-scale dam management strategies, the five run-of-river hydroelectric dams historically on the main-stem of the river was chosen to study, which from downstream to upstream included Veazie, Great Works, Milford, West Enfield, and Mattaceunk dams (Table 1 and Figure 1). Dams located on the tributaries were ignored for simplification.



Habitat areas	HA1	HA2	HA3	HA4	HA5	HA6
Area (acre)	7963	2379	0	29506	25865	15680

Figure 1. Map of the study area showing the locations of the five hydroelectric dams as well as current and historic alewife spawning lakes/ponds in the Penobscot River Basin. The inserts show the Penobscot River basin within the northeastern US (upper map) and the partial Penobscot River main-stem from Veazie to Milford Dam (lower map).

Table 1. Project information for the five studied dams in the main-stem of the Penobscot River, Maine.

Dams (distance to ocean)	Year completed	Primary function	Installed capacity (Amaral et al., 2012) (MW)	Turbine's maximum flow (Amaral et al., 2012) ($\times 10^6$ m^3/d)	Rated head (Amaral et al., 2012)	Dam length (USACE, 2016) (m)	Dam height (USACE, 2016) (m)	Upstream passage facilities (Amaral et al., 2012)	Potential downstream passage routes (Amaral et al., 2012)
Veazie (Dam 1) (rkm 55, removed summer 2013)	1912	Hydro	9.3	13.6	7.3	257	10	One vertical slot fishway	Sluice gate, turbine units (15 Francis units, 2 Propeller units), and spillway
Great Works (Dam 2) (rkm 69, removed summer 2012)	1900	Hydro	7.6	21.1	5.3	331	6.1	Two Denil fishways	Bypass pipe (2000), 3 gated outlet[a], turbine units (8 Francis units, 3 Kaplan units), and spillway
Milford (Dam 3) (rkm 73)	1906	Hydro	8.0	17.2	5.8	426	10	One Denil fishway, one fish elevator (installed in 2014)	Log sluice gate[b], turbine units (1 Propeller, 5 Kaplan units), and spillway
West Enfield (Dam 4) (rkm 114)	1894	Hydro	25.4	22.0	7.9	296	14	One vertical slot fishway, one Denil	Gated section, turbine units (2 Kaplan units), and spillway

		(started from 1988)						fishway (backup fishway)	
Mattaceunk (Dam 5) (rkm 175)	1939	Hydro	21.6	18.2	11.9	357	14	One pool and weir fishway, one fishlift	Bypass system, roller gate, debris sluice gate, turbine units (2 Kaplan, 2 Propeller), and spillway

Note:

[a] - The 3 gated outlets are currently used to increase discharge capacity under flood conditions rather than downstream fish passage;

[b] - The 3-meter wide gate is used as downstream bypass at the Milford dam. The gate flow is set at 3 m^3/s during the established migration periods.

2.2 Integrated energy and fish population model

An integrated energy-fish model that couples hydropower generation and age-structured fish population models was used to analyze the tradeoffs between energy and fish abundance under various dam management scenarios at a basin scale. The energy-fish model was built in the platform of Vensim® DSS and run across 150 years on a daily time step to ensure stabilization.

2.2.1 Hydropower generation

Hydroelectric dams convert the natural flow of water into electricity when falling water turns the blades of a turbine connected to a generator. The general equation for hydropower generation is provided by Equation 1 (Adeva Bustos et al., 2017; Hadjerioua et al., 2012; Power, 2015; Singh and Singal, 2017):

$$E = P \times t = Q \times H \times \eta \times \rho \times g \times 10^{-6} \times t \qquad \text{(Equation 1)}$$

Where E is the generated energy, MWh; P is the power produced at the transformer, MW; t is turbine operation period, hours; Q is the volume flow rate passing through the turbine, m^3/s; H is the design net head, m; η is the overall efficiency, assumed to be 0.85 (Hadjerioua et al., 2012; Power, 2015); ρ is the density of water, 1,000 kg/m^3; and, g is the acceleration due to gravity, 9.8 m/s^2.

Given that run-of-river dams do not have large reservoirs and generally have limited impacts on river flows, the total water inflow was assumed to always be equal to the total outflow for each dam. Evaporation and system leakages were assumed to be zero. At hydropower dams, river flow is diverted to different paths following a minimum flow discharge rule (Basso and Botter, 2012; Lazzaro et al., 2013). First, a portion of the water is diverted to meet the operation needs of the fish passage structures, including ensuring that fish will be attracted to the fishways. Previous studies have reported fishway attraction flow in a range of 1-5% of the streamflow (Bolonina et al., 2016). In this study, we assume the fishway attraction flow to be 5% of the streamflow for a conservative energy generation estimate. The remaining water was then assumed to be available for hydropower generation. The actual amount of water releasing from turbine facilities is determined by the remaining water flow in the river, the turbine's minimum admissible flow rate, and its maximum flow rate. If the remaining water flow is less than the turbine's minimum admissible flow rate, it will be released from the spillway. If the remaining water flow is greater than the turbine's maximum flow rate, water volume in excess of the maximum flow rate will also be released from the spillway. Otherwise, all remaining water will be released from the turbines.

We used the drainage-area ratio method to extrapolate the river inflow of all five hydroelectric dams from the daily streamflow data obtained from two U.S. Geological Survey gages (01034500 Penobscot River at West Enfield and 01034000 Piscataquis River at Medford (USGS, WaterWatch)) for the period of January 2001 to December 2015 (Archfield and Vogel, 2010; Gianfagna et al., 2015) (Section S1 of the SI). This calculated river inflow was then repeated and expanded to 150 years. The maximum turbine flow rate at each studied dam was collected from the related reports (Table 1) (Amaral et al., 2012; Great Lakes Hydro America LLC, 2016). The minimum admissible flow rate was assumed to be 40% of the maximum flow (Power, 2015). The design net head at each dam was assumed to be equal to the rated head of installed turbines obtained from Amaral et al (2012) (Table 1). Turbine units only operate when river discharge satisfies turbines' hydraulic capacities (Power, 2015). The influence of market demand on hydropower generation was ignored.

2.2.2 Age-structured fish population model

The daily age-structured alewife population model used in this study was adapted from a yearly age-structured model presented in Barber et al (2018). Alewife abundance was simulated by keeping track of the activities and survivals of different age groups on a daily stepwise progression (Figure 2). Alewives mature between the ages of three and eight, and spawners generally enter rivers when water temperature is between 5 and 10 °C and swim upstream into slack waters (such as lakes and ponds) to spawn (Eakin, 2017; Hasselman et al., 2014). After spawning, surviving adults return to the ocean. Low dam passage rates for fish migrating upstream can affect accessibility to spawning habitat (Cooke and Hinch, 2013; Hall et al., 2011; Pess et al., 2014a). Dams can also cause migratory delays and increased mortality rates for spawners moving both upstream and downstream, which can potentially result in a population decline. In freshwater spawning habitat, eggs hatch into larvae and grow to juveniles. Juveniles move downstream between mid-July and early December, and can also experience dam-related delay and mortality during their migration. The surviving juveniles enter the ocean and continue to grow until reaching sexual maturity, thus completing the cycle. Alewives generally survive up to 9 years in the wild. In our model, alewives older than 6 years were not included in simulations because these age groups only account for around 5% of the total spawner population (Messieh, 1977). It has to be noted that alewife activities such as spawner upstream migration, egg production, and post-spawner and juvenile downstream migration were assumed to happen once every year on designated days.

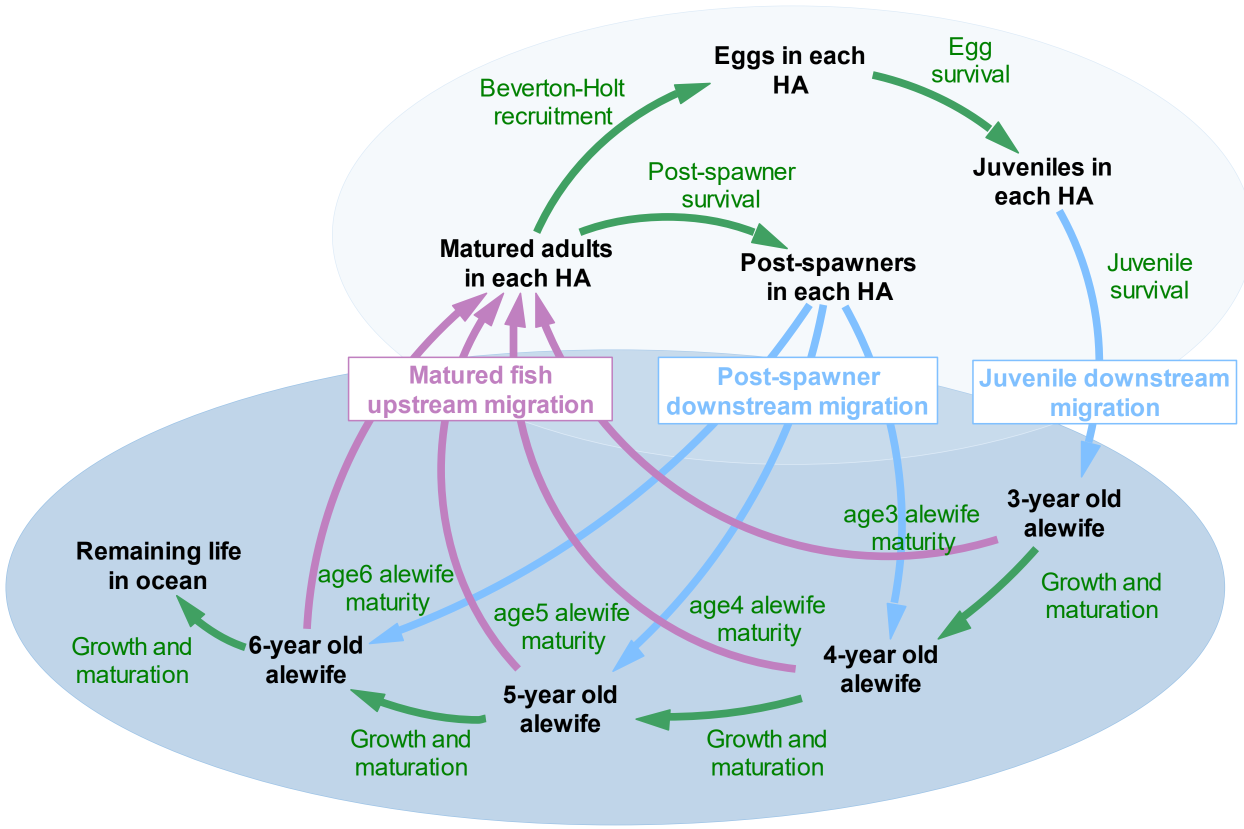


Figure 2. Life stages of alewife included in the age-structured fish population model. The light and dark blue ellipses refer to the freshwater and ocean habitats of alewife, respectively.

For a given spawning period, the number of eggs produced in each HA is a function of females that survived to spawn in that area and their fecundity (Equation 2).

$$E_{HA_j,t,a} = \sum_{i=3}^{6} (S_{HA_j,i,t,a} \times r_{F:M} \times \varphi \times F_i) \qquad \text{(Equation 2)}$$

Where, $E_{HAj,t,a}$ is egg production of alewife in HA_j (j =1-6) for a given year t on the a^{th} day (a was assumed to be the 140th day of each year), millions; $S_{HAj,i,t,a}$ is the total number of surviving age-i alewife to spawn at HA_j in year t on the a^{th} day, millions; $r_{F:M}$ is female to male ratio that was assumed to be 0.5 (Barber et al., 2018); φ is the probability of spawning, 0.95 (Barber et al., 2018);

and, F_i is the fecundity of age-i alewife which was assumed to be linearly related to the mass of age-i alewife (Table S1).

Juvenile production was modeled as a density-dependent process, which was characterized using the Beverton-Holt spawner-recruit (B-H) curve (Equation 3). The B-H curve was chosen for this model because a study of eight alewife populations in the northeast region of the US indicated it was a better fit than the Ricker curve (Barber et al., 2018; Gibson, 2004).

$$J_{HA_j,t,b} = \frac{\alpha \times E_{HA_j,t,a}}{1 + \frac{\alpha \times E_{HA_j,t,a}}{A_j \times R_{asy}}} \qquad \text{(Equation 3)}$$

Where $J_{HAj,t,b}$ is the number of juveniles at HA_j at the beginning of the downstream migration for a given year t on the b^{th} day (juveniles spend around 90 days in freshwater before migrating to the ocean (Iafrate and Oliveira, 2008), and b was assumed to be the 230th day of each year), millions; R_{asy} is the asymptotic recruitment level, 3283 age-0 fish/acre (Barber et al., 2018); α is the lifetime reproduction rate of alewife, 0.0015 (Gibson, 2004); A_j is the size of HA_j (j =1-6), acres.

During downstream migration, juveniles pass each dam through one of three routes: the spillway (or sluiceway), the fish bypass system, or a turbine (Schilt, 2007). The partitioning of alewives to each route was based upon the relative amount of water being released through each route at a given time step (Nyqvist et al., 2017a). Other factors that could potentially affect fish distributions, including installation of screening system and sensory stimuli (e.g., light, sound, turbulence, and electric fields) (Schilt, 2007), were not considered. Turbine mortality rates were assumed to be 30% when in operation and 0% during shutdowns (Pracheil et al., 2016). The other two migration routes are generally considered benign (Muir et al., 2001; Stich et al., 2014) and the simplifying assumption was made that their mortality rates were zero. The number of juveniles entering the ocean was determined by the cumulative turbine mortality (Equation 4).

$$J_{ocean,t,c} = \sum_{j=1}^{6}(J_{HA_j,t,b} \times \prod_{k=1}^{j-1}\frac{Q_{turbine_k,t,c}}{Q_{dam_k,t,c}} \times (1 - M_{turbine_k})) \qquad \text{(Equation 4)}$$

Where $J_{ocean,t,c}$ is the number of surviving juveniles entering ocean in year t on the last day of the downstream migration period c (c was assumed to be the 240th day of each year), millions; $Q_{turbine_k,t,c}$ and $Q_{dam_k,t,c}$ are the turbine and the total water flow rate of Dam k (k =1-5) in year t on the c^{th} day, respectively, m^3/d; $M_{turbine_k}$ is the turbine mortality rate of Dam k, 0.3 (Pracheil et al., 2016) during operation and 0 during turbine shutdowns.

In the ocean, immature alewives between ages 2 and 6 have a probability of reaching sexual maturity and entering the spawning run the next year. Alewife maturity at each age is provided in Table S1. The population of age-i fish in the ocean in year t, $O_{i,t,d}$, was calculated based on the populations of both immature fish, $NS_{i,t,d}$, and mature fish, $S_{i,t,d}$ (Equation 5) where d denotes the beginning of each fish upstream migration period, which was assumed to be the 120th day of each year (Chadwick and Claytor, 1989; Ellis and Vokoun, 2009).

$$O_{i,t,d} = NS_{i,t,d} + S_{i,t,d} \qquad \text{(Equation 5)}$$

Immature fish remain in the ocean, and their abundance was calculated by applying an annual ocean mortality rate (including all natural causes of death in the ocean), M_{ocean} (assumed to be 0.648 (Barber et al., 2018)), on the d^{th} day every year, and the probability of maturation at each age, m_i (Equation 6 and Table S1). The abundance of age-0 immature fish, $NS_{0,t,d}$, was assumed to be equal to juveniles entering the ocean, $J_{ocean,t,c}$.

$$NS_{i,t,d} = NS_{i-1,t-1,d} \times e^{-M_{ocean}} \times (1 - m_i) \qquad \text{(Equation 6)}$$

The mature fish stock in the ocean (Equation 7) included first-time spawners, $S_{i,t,0,d}$ (calculated in Equation 8) and repeat spawners, $S_{i,t,p,d}$.

$$S_{i,t,d} = S_{i,t,0,d} + \sum_{p} S_{i,t,p,d} \qquad \text{(Equation 7)}$$

$$S_{i,t,0,d} = NS_{i-1,t-1,d} \times e^{-M_{ocean}} \times m_i \qquad \text{(Equation 8)}$$

Repeat spawners have spawned at least one time and are subject to natural (i.e., predation, delayed migration, or senescence), fishing (both commercial and recreational), and other anthropogenic (i.e., turbine) mortalities. Natural mortality included both ocean mortality and spawning mortality, with the latter incorporating all natural causes of death in freshwater. For a given spawning run, the total number of spawners reaching the suitable habitat areas was calculated using Equation 9.

$$\sum_{j=1}^{6} S_{HA_j,t,a} = S_{t,d} \times (1 - M_{fishing}) \times (1 - M_{spawn}) \qquad \text{(Equation 9)}$$

Where, $S_{HAj,t,a}$ is the number of spawners at HA_j that are ready to spawn in year t, millions; $S_{t,d}$ is the abundance of mature fish in the ocean before the spawning run in year t, millions; $M_{fishing}$ is the interval fishing mortality, 0.4 (Barber et al., 2018; MaineDMR, 2016); M_{spawn} is the interval spawning mortality associated with each spawning run, 0.45 (Barber et al., 2018; Durbin et al., 1979; Kissil, 1974). The spawning run was assumed to last 30 days with upstream migration, spawning, and downstream migration each taking 10 days (Frank et al., 2011; Franklin et al., 2012).

The value of $S_{HAj,t,a}$ was determined by the cumulative upstream passage rate of dams downstream of HA_j as well as a dispersal rule. In this study, upstream passage rate was defined as the percentage of individuals that are attracted to, enter, and successfully ascend a fishway (Silva et al., 2018). Alewives have a tendency to return to their natal area to spawn (McBride et al., 2014; Pess et al., 2014b). Accordingly, two dispersal rules were investigated in this study to investigate two opposing conditions related to fish dispersal. The first rule assumed that alewife distribution was based on the habitat size of the entire basin despite the influence of dam structures. The second rule took into account the long-term blockage effect of dams. With this rule, alewives had no motivation to seek habitats that were suitable for spawning but no longer accessible due to the dam structures. Equation 10 and 11 describe the calculations of the two dispersal rules.

$$\text{If } \frac{A_j}{A} > D_{HA_j}, S_{HA_j,t,a} = \left(\frac{A_j}{A} + \left(D_{HA_j} - \frac{A_j}{A}\right) \times \left(1 - P_j\right)\right) \times \sum_{j=1}^{j=6} S_{HA_j,t,a} \quad \text{(Equation 10)}$$

$$\text{If } \frac{A_j}{A} \leq D_{HA_j}, S_{HA_j,t,a} = D_{HA_j} \times \sum_{j=1}^{j=6} S_{HA_j,t,a} \quad \text{(Equation 11)}$$

Where, A_j is the size of HA_j (j = 1-6), acres. The size of each HA was estimated as the summed acreage of the documented alewife spawning ponds within each river segment, obtained from the Maine Stream Habitat Viewer provided by the Maine Department of Marine Resources Coastal Program (MaineDMR, 2017). A was the total habitat area, which equaled 81,393 acres when alewives were homing to the entire basin under the first dispersal rule or the sum of HAs used by alewives (based upon results obtained from the first dispersal rule) under the second dispersal rule. D_{HA_j} was a dispersal factor that was calculated using Equation 12.

$$D_{HA_j} = (D_{HA_{j-1}} - \frac{A_{j-1}}{A}) \times P_{j-1} \quad \text{(Equation 12)}$$

$D_{HA_1} = 1$. P_j is the upstream passage rate of the j^{th} dam. P_j was assumed to be 0 when no fishway was present and 0.7 (Bunt et al., 2012; Noonan et al., 2012) when fishways were present.

Shortly after spawning, post-spawners migrate seaward and encounter turbine and ocean mortalities prior to their next spawning run. The abundance of repeat spawners in the ocean at the beginning of upstream migration was calculated using Equation 13 (Table S1).

$$S_{i+1,t+1,p+1,d} = \sum_{j=1}^{6} (S_{HA_j,i,t,p,a} \times \prod_{k=1}^{j-1} \frac{Q_{turbine_k,t,c}}{Q_{dam_k,t,c}} \times (1 - M_{turbine_k})) \times e^{-0.92 M_{ocean}} \quad \text{(Equation 13)}$$

Where, the annual ocean mortality, M_{ocean}, was prorated to 0.92 indicating that 335 out of 365 days, spawners live in the ocean and are subject to ocean mortality.

A few additional assumptions were made for simplification. Alewives at each age were assumed to experience the same delay time as well as ocean and spawning mortality rates during both downstream and upstream migrations. The carrying capacities of each unit of habitat area were assumed to be the same. The influence of temperature on the timing of upstream migration and spawning was ignored.

2.3 Model validation and sensitivity analysis

2.3.1. Behavior test

Once values for the parameters of the integrated model were selected, the accuracy of the model was tested through a behavior test. For the energy model, annual hydropower generation at Milford and West Enfield dams were calculated and compared with the historical data (2001-2015) obtained from the U.S. Energy Information Administration (EIA, 2018b). The correlation coefficient (r^2) was used to test the goodness of fit between simulated and historical yearly hydropower generation. Correlation was relatively high, with a calibrated r^2 of 0.60 for Milford Dam and 0.86 for West Enfield Dam (Section S3 of the SI).

The behavior test of the fish model was conducted by checking that the simulated fish abundance entering the Penobscot River was within the range of total alewife abundance entering rivers in Maine. Total abundance for the state of Maine was calculated based on Alewife landings data (in million pounds, 1950-2016) collected from the Department of Marine Resources (DMR) (MaineDMR, 2018), average alewife spawner weights (in pound, 0.4 (Barber et al., 2018)), and alewife harvest rates which were assumed in the range of 10-70% (Barber et al., 2018; MaineDMR, 2016). Additionally, the DMR also provided alewife trap counts at the Milford Dam, which were compared against the simulated results at the Milford Dam. Our fish model was initialized with 1 million juveniles entering the ocean. The results showed that the simulated number of alewife spawners after model stabilization was within the range of the historical data (Section S4 of the SI). Additionally, the abundance of simulated spawners passing through Milford dam compared with the trap counts at the same location was within 5-84% difference.

2.3.2 Sensitivity analysis

Sensitivity analysis was conducted to determine which input parameters had the biggest influence on system behavior (Sterman, 1984). We assessed the sensitivity of alewife spawner abundance and hydropower generation to a set of input parameters. Selected inputs were tested for changes between ±10% and ±90% to capture their practical low and high values. However, a narrower range (e.g., −90 to 50% changes in ocean mortality) was applied when the extreme values became unrealistic. A sensitivity index was calculated for each input change using Equation 14 (Barber et al., 2018; Zhuang, 2014).

$$S = \frac{\frac{O_i - O_b}{O_b}}{\frac{I_i - I_b}{I_b}} \qquad \text{(Equation 14)}$$

Where O_i is the output value after the input was changed; O_b is the base output value; I_i is the altered input value; and I_b is the original input value. Inputs were considered "highly sensitive" if $|S| > 1.00$.

2.4 Dam management scenarios

Eight scenarios were designed to compare the effectiveness of different dam management practices (Figure 3). In the NR (no removal) scenario, all five dams remained in place and no fishway or turbine shutdown was used. In contrast, the R scenario referred to a condition in which all five dams were removed. The remaining scenarios were divided into three pairs: PF and PF-S, F and F-S, and PR-PF and PR-PF-S. The only difference between the two scenarios within each pair is whether turbine shutdowns were operated or not. "S" in the scenario name indicated that this scenario operated turbine shutdowns in dams with fishways. Comparing across the pairs, "PF" indicated fishway installations at the two most downstream dams. "F" indicated fishway installations at all five dams. "PR-PF" indicated removal of the two most downstream dams, and fishway installations at the remaining three dams. The PR-PF-S scenario approximates the PRRP's dam management strategy. Turbine shutdown periods were assumed to be 20 days each year which occurred during the 141^{th}-150^{th} day and the 231^{th}-240^{th} day corresponding to the assumed peak downstream migration periods of adults and juveniles, respectively.

The influence of upstream and downstream passage efficiency on spawner abundance was further investigated under the F scenario. We assumed upstream passage efficiency to be uniform for all five studied dams and explored changes from 0, 20, 40, 60, 80, and 100% successful passage for each simulation. The same assumption was made for both juvenile and adult downstream passage efficiency.

3. Results and Discussions

3.1 Energy-fish tradeoffs under various dam management scenarios

We are reporting hydropower dam influences on fish population potential using alewife spawner abundance as a surrogate for diadromous fish in general, as they are the main source of the fishery (Havey, 1961). Figure 3 presents the tradeoffs between annual hydropower generation and the stabilized alewife spawner abundance each year under the eight basin-scale dam management scenarios. A comparison between the NR and R scenarios show that the five dams can reduce the alewife abundance by 90%. On the other hand, an average of 427 GWh of annual hydropower generation will be lost when all dams are removed, which is around 14% of the annual hydropower generation in Maine (EIA, 2018b).

The performance of fishway installations is heavily influenced by the amount of accessible upstream habitat, the dam mortalities, and the dispersal rules. For instance, in the PF scenario a 30% increase in the total habitat area can lead to a 35% decrease in spawner abundance when spawners home to the entire basin (the first dispersal rule), or a 16% increase when spawners only home to accessible habitats (the second dispersal rule). The decrease of spawner abundance under the first dispersal rule is related to the extremely small sizes of HA2 and HA3. Under this dispersal rule, most spawners have the motivation to move upstream. As Dam 3 is entirely impassible under the PF scenario, this homing instinct result in large amounts of spawners (63%) cumulating in HA2 and HA3 and competing for limited resources, which eventually leads to a reduced survival rate (Section S7 of the SI). Furthermore, as turbines are still in operation in the PF scenario, significant turbine kills could occur when post-spawners and juveniles migrate downstream. In this case, fishways could work as ecological traps and potentially cause a further collapse of the regional fishery (Pelicice and Agostinho, 2008). Taking the F scenario as another example, the entire watershed becomes accessible to spawners in this scenario, and spawners will mainly be distributed across the four most downstream HAs because HA4 is large enough to support the limited amount of spawners that could successfully pass Dams 1-3. Although the combined size of HAs 1-4 in the F scenario is four times larger than the NR scenario, only a roughly 45% increase in the stabilized spawner abundance is observed. This is due to the high downstream mortality resulting from turbine kills. When turbine shutdown is in operation, an additional 114-134% increase in spawner abundance could be observed (compared to the F-S scenario). When the two most downstream dams are removed (Scenario PR-PF-S), the downstream mortality is further reduced. Hence, an increase of 300-338% of spawner abundance is observed when comparing the PR-PF-S and F scenarios.

The effect of the two dispersal rules is the most prominent in the PF and the PF-S scenarios with a 40-56% difference in spawner abundance. The alewife spawner abundance is lower under the first dispersal rule, as compared to the second one. This is a combined effect of spawner behavior under the two dispersal rules and the availability of the HAs. Unlike the first dispersal rule where spawners moving upstream are mainly driven by homing instincts, under the second dispersal rule, spawners moving upstream are mainly driven by competition for resources, and hence the general motivation of moving upstream is comparatively weaker. In this case, the resources in HAs 1-2 could be maximally utilized, resulting in higher spawner abundance. Conversely, under the F, F-S, PR-PF, and PR-PF-S scenarios, alewife spawner abundance is slightly higher under the first dispersal rule than the second one. This is because under these scenarios, a much larger habitat area becomes open and a stronger motivation of moving upstream facilitates spawners reaching the reopened critical habitat. Note, however, that the impacts of dispersal rules on spawner population are marginal (within 2-10% difference) in these scenarios.

If turbine shutdowns reduce mortality as assumed, this approach would be an effective way of lessening fish kills during downstream migration. A comparison of the three scenario pairs (PF vs. PF-S, F vs. F-S, PR-PF vs. PR-PF-S) shows that turbine shutdowns during fish peak downstream migration periods could increase spawner abundance by around 8-30%, 114-134%, and 78-92%, respectively, with small losses of hydropower capacity (~5%). Based upon our results, turbine shutdown is the most effective when applied to the F scenario, where the cumulative turbine mortalities associated with three dams (Dams 1-3) are significantly reduced. When turbine shutdowns are applied to the PF or PR-PF scenarios, turbine mortalities associated with two dams (Dams 1 and 2 in the PF scenario and Dams 3 and 4 in the PR-PF scenario) are significantly reduced. As the PR-PF scenario has a much larger size of accessible upstream habitat than the PF scenario, a larger spawner population could benefit from turbine shutdowns and lead to a higher effectiveness of fish restoration. In general, the effectiveness of turbine shutdowns is highly dependent upon spawner dispersal among the habitats, size and location of the accessible HAs, and the number of dam structures that alewives need to traverse in the freshwater environments.

In terms of the energy-fish tradeoffs, the R scenario is the most effective in restoring fish abundance, but would result in the total loss of hydropower capacity. The PF, PF-S, and F scenarios resulted in negligible energy losses, but effects on the spawner abundance are marginal or even negative. The F-S and PR-PF scenarios are able to preserve around 60-92% of the overall hydropower capacity, but only restore spawner abundance to around 35% of the undammed condition. The PR-PF-S scenario, on the other hand, is effective in restoring the spawner population to around 60% of the abundance in the R scenario, with only around a 37% loss of energy. The PR-PF-S scenario also closely reflects the actual management decisions enacted through the PRRP. This project also upgraded hydropower capacity at two tributary dams, which further compensated for energy losses through the removal of the two lowermost dams. Our results suggest that energy-fish tradeoffs could be balanced through utilizing multiple dam management activities at a basin scale. Although dam removal alone is the best option for fish restoration, the resulting hydropower losses could be undesirable in places where hydropower is an important source of energy.

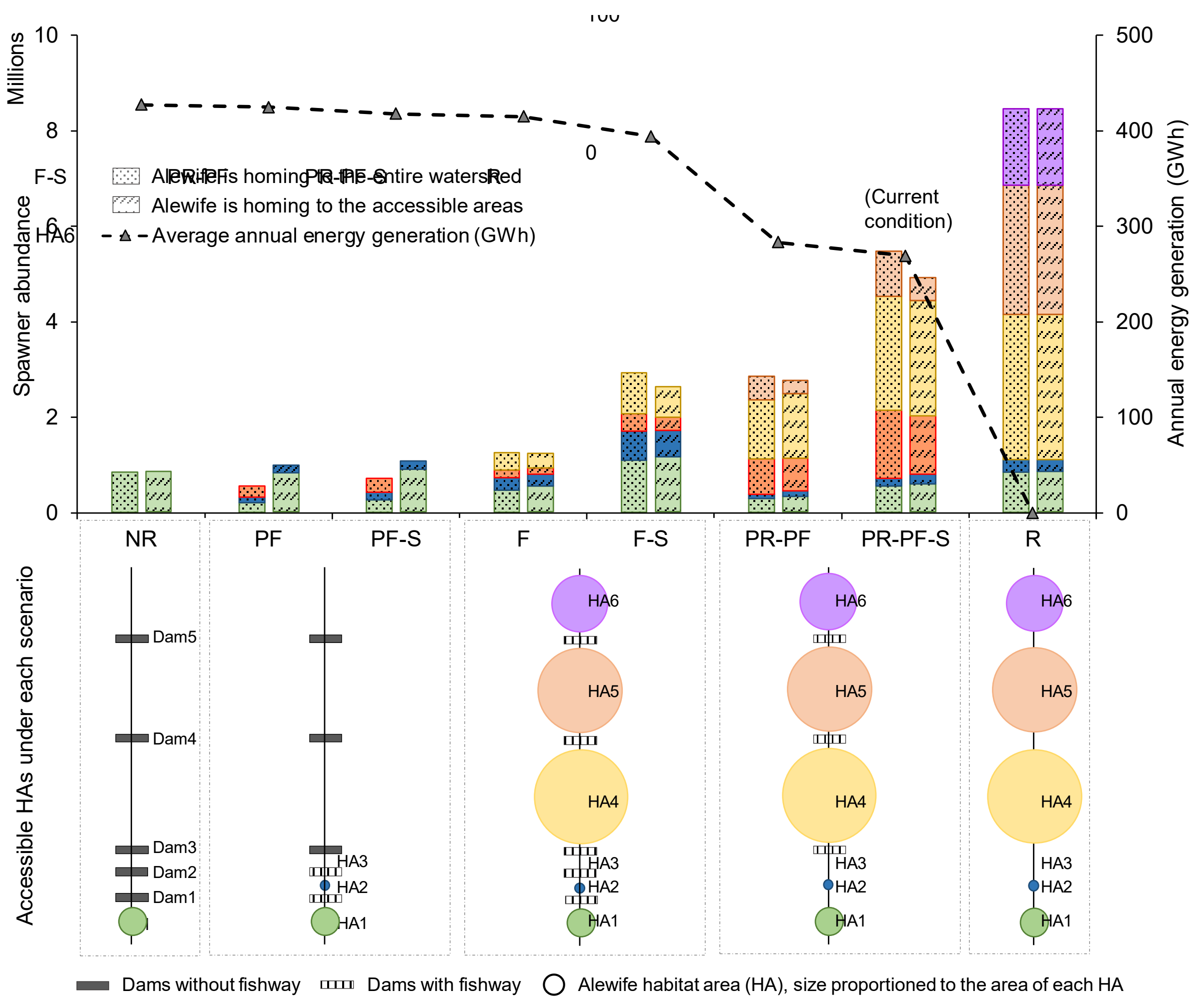


Figure 3. Tradeoffs between energy and Alewife spawner abundance under different dam management scenarios. Bars filled with different colors are spawner abundance in different HAs. Stabilized spawner abundance of the two dispersal rules are shown as bars filled with dots (homing to the entire basin) and slashes (homing to the accessible areas).

3.2 Aggregated influence of upstream and downstream migration on fish population

Alewife spawner abundance was simulated for the two homing patterns, and results were very similar between the two. This further supports our previous conclusion that the different dispersal rules have limited effects on spawner abundance under the F scenario. Figure 4 illustrates the resulting population changes of alewife spawners homing to the accessible areas. Under a relatively low downstream passage rate of less than 70%, spawner abundance is lower than the NR scenario and inversely related to the upstream passage rate. With this low downstream passage rate, reopening upstream habitat areas may have an adverse effect on the spawner abundance. This is because downstream mortality increases as improved upstream passage rates encourage more spawners to reach habitats upstream of one or more dams. Downstream passage is therefore a limiting factor for spawner abundance when it is 70% or less at each dam. Unless the downstream survival rate exceeds 70%, efforts or investments to improve upstream passage rates could be entirely ineffective. When downstream passage rates are relatively high (>70%), spawner abundance is positively related to both upstream and downstream passage rates. In this condition, the upstream passage rate becomes the primary limiting factor. When upstream passage rates surpass 60%, spawner abundance is highly sensitive to changes in both upstream and downstream passage rates. However, if upstream passage rates are lower than 60%, spawner abundance is less sensitive to changes to both upstream and downstream passage rates. This shows a threshold also exists related to the upstream passage rate, which needs to be taken account of when designing dam management strategies. The upstream passage rate through a fishway has traditionally been used as a metric for assessing the success of restoration projects (Cooke and Hinch, 2013). However, our findings show that this is potentially misleading. Both upstream and downstream pass rates influence the objectives being considered when evaluating decisions related to dams (Pompeu et al., 2012).

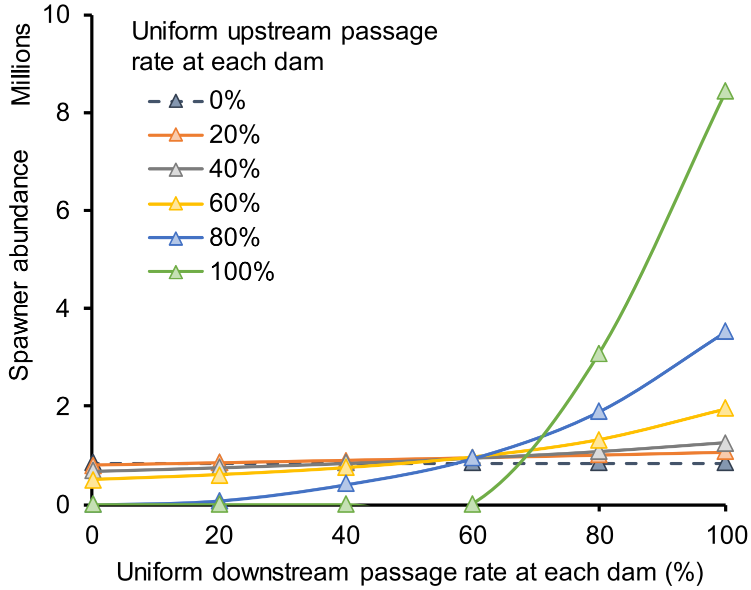


Figure 4. Alewife spawner abundance in the Penobscot River under various scenarios of upstream fishway passage rates and downstream passage rates. The colored lines correspond to various levels of upstream passage rates at all five dams.

3.3 Sensitivity analysis

Energy generation is sensitive to flow rate, net head, turbine operation period, and overall efficiency regardless of the percentage of increase as these parameters have a linear relationship with energy (Equation 1). For spawner abundance, the absolute value of the sensitivity index in response to a −90% to −10% decrease and a 10% to 90% increase of model inputs are shown in Figure 5. Spawner abundance was the most sensitive to ocean mortality, spawning mortality, fishing mortality, the size of the habitat area, and the asymptotic recruitment level (R_{asy}) for all investigated ranges. In addition, spawner abundance was sensitive to any decrease, or less than 10% increase, in the alpha value and sex ratio. It was also sensitive to any decrease, or less than 70% increase in the fecundity slope. Accurate quantification of these sensitive variables is important in improving the confidence of model outputs.

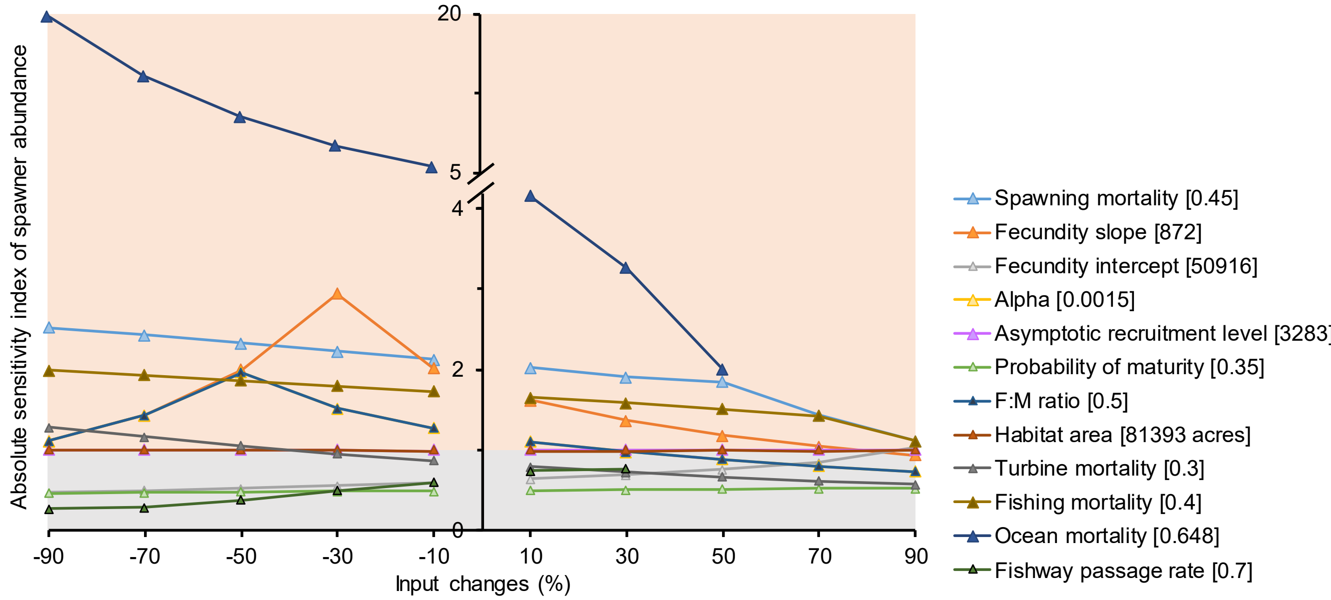


Figure 5. Sensitivity analysis index of alewife spawner abundance. Outputs of parameters distributed in the light orange shadow are considered highly sensitive, while those distributed in the light grey shadow are not. Numbers in the bracket represent the default value of each input parameter.

4. Policy Implications

As dam management decisions become increasingly contentious due to conflicting stakeholder interests, coordinated decisions that balance both energy production and fish abundance could be appealing (Roy et al., 2018). While dam removal is often heavily discussed and/or advocated when comes to dam decision-making, our results suggest that combining multiple dam management strategies including dam removals, fishway installations, and turbine shutdowns during the peak downstream migration periods could achieve a desirable fish restoration outcome, while preserving most of the hydropower capacity. Furthermore, the effectiveness of opening habitat through fishway installations is heavily influenced by the size of accessible upstream habitat and the downstream passage rates. For the Penobscot River, our analysis indicated that installing fishways in two lowermost dams could have minimal or even negative effect on alewife spawner abundance. This was mainly due to the unevenly distributed habitat areas in the watershed and potentially high cumulative downstream mortalities. This shows the importance of understanding the habitat distribution as well as upstream and downstream fish passage rates to inform proper decision-making associated with dam management. Our results also show that the commonly used "reopened/reconnected habitat area" could be an ineffective indicator of fish population recovery without an understanding of the potential upstream and downstream passage rates. Future studies also need to include all fish species for a comprehensive assessment of the energy-fish tradeoff.

While our study underscores the advantages of the systematic management actions made under the PRRP, such coordinated decisions are generally rare in the field (Opperman et al., 2011). One major barrier is the prevalence of private dam ownership, which can make basin-scale dam negotiations that involves multiple owners time and cost prohibiting. From a policy perspective, hydroelectric dams in the US are licensed on an individual basis without a coherent basin-scale management plan, which reduces opportunities for co-optimization. Despite these significant challenges, there are a growing number of funding mechanisms and resources that encourage efficient basin-scale decisions (Owen and Apse, 2014). Compensatory mitigation is one funding model used to offset ecological damage caused by development in wetlands, and the US Army Corps of Engineers has established a method for including pro-environmental dam decisions in the compensatory mitigation scheme (USACE, 2008). Institutional initiatives and frameworks such as National Oceanic and Atmospheric Administration's Habitat Blueprint (Chabot et al., 2016) and US Department of Energy's Integrated Basin-Scale Opportunity Assessment Initiative reports (Kosnik, 2010; Lowry, 2003) encourage basin-scale planning and there is growing federal support for this approach. Further research on the advantages of basin-scale dam decisions will support the use of these funding opportunities, improve co-optimization of fish and energy resources, and ultimately better reflect the preferences of stakeholders.

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