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

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HIGHLIGHTS

• A system dynamics model was developed to simulate different dam management options.
• The basin-scale hydropower and alewife population tradeoffs were investigated.
• Size of reopened habitats and fish pass rate largely influence fishway effectiveness.
• Turbine shutdowns during peak migration periods effectively increase fish abundance.
• Combining multiple dam management strategies can best balance energy-fish tradeoffs.

ABSTRACT

Management activities to restore endangered fish species, such as dam removals, fishway installations, and periodic turbine shutdowns, usually decrease hydropower generation capacities at dams. Quantitative analysis of the tradeoffs between energy production and fish population recovery related to dam decision-making is still lacking. In this study, an integrated hydropower generation and age-structured fish population model was developed using a system dynamics modeling method to assess basin-scale energy-fish tradeoffs under eight dam management scenarios. This model ran across 150 years on a daily time step, applied to five hydroelectric dams located in the main stem of the Penobscot River, Maine. We used alewife (Alosa pseudoharengus) to represent the local diadromous fish populations to link projected hydropower production with theoretical influences on migratory fish populations on the model river system. Our results show that while the five dams can produce around 427 GWh/year of energy, without fishway installations they would contribute to a 90% reduction in the alewife spawner abundance. The effectiveness of fishway installations is largely influenced by the size of reopened habitat areas and the actual passage rate of the fishways. Homing to natal habitat has an insignificant effect on the growth of the simulated spawner abundance. Operating turbine shutdowns during alewives’ peak downstream migration periods, in addition to other dam management strategies, can effectively increase the spawner abundance by 480–550% while also preserving 65% of the hydropower generation capacity. These data demonstrate that in a river system where active hydropower dams operate, a combination of dam removals, fishway installations, and periodic turbine shutdowns can effectively balance energy production and fish population recovery.

Keywords:
System dynamics modeling
Energy-fish tradeoffs
Hydropower generation
Turbine shutdown
Fishway installation
Dam removal

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management strategies at the basin scale can best balance the tradeoff between energy production and the potential for migratory fish population recovery.

1. Introduction

Hydropower is currently the largest source of renewable energy in the United States of America (USA), 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 U.S. east coast have declined ~90% following the construction of a series of dams in the early 20th century (McClanahan 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 USA 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).

Though 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 farther 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 avoid 90% loss of European eels (Anguilla anguilla) during seaward migration 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 is a computational method using a set of linked differential equations to simulate the behavior of complex systems over a certain time period. SDM is grounded in system thinking and has been widely recognized as a powerful tool to study interactions among system components through capturing system feedback loops and delays (Forrester, 1997; Sterman, 2001). SDM has been previously applied to simulate hydropower production (Bosona and Gebresenbet, 2010; Shariff 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 USA, with a drainage area of approximately 22,000 km² (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 (McClanachan et al., 2015). Alewives are small anadromous fish that have high rates of iteroparity (reproduce multiple times over their lifetime) in Maine. Alewives are also the base of marine, freshwater, and terrestrial food webs (ASMFC, 2009). Changes in alewife 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 period (McClanachan et al., 2015). Alewife habitat areas (HAs) are unevenly distributed among the river segments created by the dams (Fig. 1). A much larger HA is located upstream of the Milford Dam than downstream of it. Restoration efforts began in the 1940s to combat diadromous fish declines (Rousefell and Stringer, 1945). One of the largest efforts was the Penobscot River Restoration Project (PRRP), which from 2012 to 2013 removed the two dams farthest downstream and improved fish passages at the remaining dams (Fig. 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 Fig. 1). Dams located on the tributaries were ignored for simplification.

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 Vensim® DSS, one of the most widely used platform for SDM (Ford, 2000). Fig. 2 presents an abstracted version of the stock-and-flow diagram of SDM model developed in this study. The energy model and the age-structured fish population model are integrated through three dam management practices: fishway installations, turbine shutdowns, and dam removals. A complete version of the model is provided as a Vensim file in the supporting information. The model runs 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 (Adeva Bustos et al., 2017; Hadjerioua et al., 2012; Power, 2015; Singh and Singal, 2017) is:

\[ E = P \times t = Q \times H \times \eta \times \rho \times g \times 10^{-6} \times t \]  

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, m³/s; \( H \) is the design net head, meters; \( \eta \) is the overall efficiency, assumed to be 0.85 (Hadjerioua et al., 2012; Power, 2015); \( \rho \) is the density of water, 1000 kg/m³; and, \( g \) is the acceleration due to gravity, 9.8 m/s².

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.,...
Table 1

<table>
<thead>
<tr>
<th>Dams* (distance to ocean)</th>
<th>Year completed</th>
<th>Installed capacityb (MW)</th>
<th>Turbine’s maximum flow (Amaral et al., 2012)</th>
<th>Rated headc (Amaral et al., 2012) (m)</th>
<th>Dam length (USACE, 2016) (m)</th>
<th>Dam height (USACE, 2016) (m)</th>
<th>Upstream passage facilities (Amaral et al., 2012)</th>
<th>Potential downstream passage routes (Amaral et al., 2012)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vezzie (Dam 1) (rkm 55, removed summer 2013)</td>
<td>1912</td>
<td>9.3</td>
<td>13.6</td>
<td>7.3</td>
<td>257</td>
<td>10</td>
<td>One vertical slot fishway</td>
<td>Sluice gate, turbine units (15 Francis units, 2 Propeller units), and spillway</td>
</tr>
<tr>
<td>Great Works (Dam 2) (rkm 69, removed summer 2012)</td>
<td>1900</td>
<td>7.6</td>
<td>21.1</td>
<td>5.3</td>
<td>331</td>
<td>6.1</td>
<td>Two Denil fishways</td>
<td>Bypass pipe (2000), 3 gated outletc, turbine units (8 Francis units, 3 Kaplan units), and spillway</td>
</tr>
<tr>
<td>Milford (Dam 3) (rkm 73)</td>
<td>1906</td>
<td>8.0</td>
<td>17.2</td>
<td>5.8</td>
<td>426</td>
<td>10</td>
<td>One Denil fishway, one fish elevator (installed in 2014)</td>
<td>Log sluice gate, turbine units (1 Propeller, 5 Kaplan units), and spillway</td>
</tr>
<tr>
<td>West Enfield (Dam 4) (rkm 114)</td>
<td>1894</td>
<td>25.4</td>
<td>22.0</td>
<td>7.9</td>
<td>296</td>
<td>14</td>
<td>One vertical slot fishway, one Denil fishway (backup fishway)</td>
<td>Gated section, turbine units (2 Kaplan units), and spillway</td>
</tr>
<tr>
<td>Mattanunk (Dam 5) (rkm 175)</td>
<td>1939</td>
<td>21.6</td>
<td>18.2</td>
<td>11.9</td>
<td>357</td>
<td>14</td>
<td>One pool and weir fishway, one fishlift</td>
<td>Bypass system, roller gate, debris sluice gate, turbine units (2 Kaplan, 2 Propeller), and spillway</td>
</tr>
</tbody>
</table>

Notes:
- * All five dams are run-of-river dams. The primary function of these dams is hydropower generation.
- † Installed capacity refers the maximum output of electricity that a generator can produce under ideal conditions (EIA, 2019).
- ‡ The 3 gated outlets are currently used to increase discharge capacity under flood conditions rather than downstream fish passage.
- § The 3-meter wide gate is used as downstream bypass at the Milford Dam. The gate flow is set at 3 m³/s during the established migration periods.

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. Two approaches have been reported for determining fishway attraction flow: 1–5% of the mean annual streamflow (Bololina et al., 2016) and at least 5% of powerhouse hydraulic capacity as fishway attraction flow. The remaining water was then assumed to be available for hydropower generation. The actual amount of water re-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, all of the remaining water flow 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 (USGS) streamgages (01034500 Penobscot River at West Enfield, Maine, and 01034000 Piscataquis River at Medford, Maine (USGS, WaterWatch, 2001–2015)) for the period of January 2001 to December 2015. The detailed calculation process at each dam site is provided in Section S1 of the SI. This calculated daily river inflow in a 15-year time period 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 (Fig. 3). Alewifes mature between the ages of three and eight. The probabilities in reaching sexual maturity at different ages were obtained from (Gibson and Myers, 2003) and (Barber et al., 2018). The matured alewifes migrate upstream to

Fig. 2. An abstracted stock-and-flow diagram showing the key components of the age-structured fish population model (A) and the hydropower generation model (B).
freshwater habitats to spawn between March and June (Eakin, 2017; Hasselman et al., 2014; Rosset et al., 2017). After spawning, surviving adults return to the ocean. Low dam passage rates for fish migrating upstream can affect accessibility to spawning habitat. 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. Dam passage rates were explicitly modeled in this study. 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). Alewife activities such as spawning upstream migration, egg production, and post-spawner and juvenile downstream migration were assumed to happen on each year ever on designated days. The detailed equations are provided below.

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:

\[ E_{HA_j,t} = \sum_{t=1}^{6} \left( S_{HA_j,t,a} \times F_{FM} \times \varphi \times F_1 \right) \]  

where \( E_{HA_j,t,a} \) is egg production of alewife in \( HA_j \) for a given year \( t \) on the \( a^{th} \) day (\( a \) was assumed to be May 10th, the 140th day of each year (Rosset et al., 2017)), millions; \( S_{HA_j,t,a} \) is the number of surviving age-\( a \) alewife to spawn in \( HA_j \) in year \( t \) on the \( a^{th} \) day, millions; \( F_{FM} \) is female to male ratio that was assumed to be 0.5 (Barber et al., 2018); \( \varphi \) is the probability of spawning, 0.95 (Barber et al., 2018); and, \( F_1 \) is the fecundity of age-\( a \) alewife which was assumed to be linearly related to the mass of age-\( a \) alewife (Table S1).

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

\[ J_{B-H,t,b} = \frac{\alpha \times E_{HA_j,t,a}}{1 + \alpha \times E_{HA_j,t,b} / A_j \times R_{asy}} \]  

where \( J_{B-H,t,b} \) 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 (\( b \) was assumed to be August 18th, the 230th day of each year (Iafrate and Oliveira, 2008; Yako et al., 2002)), millions; \( R_{asy} \) is the asymptotic recruitment level, which indicates the carrying capacity of freshwater habitats expressed as the amount of survived juveniles per acre, 3283 age-0 fish/acre (Barber et al., 2018); \( \alpha \) 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 on 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 (Johnson et al., 2005; Mueller et al., 2001), sound (Nestler et al., 1992), turbulence (Coutant, 2001), and electric fields (Schilt, 2007)) were not considered. Turbine mortality rates were assumed to be 30% when in operation and 0% during shutdowns (Prachell 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 (Eq. (4)).

\[ J_{ocean,t,c} = \sum_{t=1}^{6} \left( J_{B-H,t,b} \times \prod_{k=1}^{c-1} \frac{Q_{turbine,c,k}}{Q_{dam,c,k}} \times (1 - M_{turbine}) \right) \]  

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; \( Q_{turbine,c,k} \) and \( Q_{dam,c,k} \) are the turbine and the total water flow rate of Dam \( k \) (\( k = 1–5 \)) in year \( t \) on the \( c^{th} \) day, respectively, \( m^3/d \); \( M_{turbine} \) is the turbine
mortality rate of Dam \( k \) 0.3 (Prachiel et al., 2016) during operation and 0 during turbine shutdowns.

In the ocean, immature alewife 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, \( N_{i,t,d} \), and mature fish, \( S_{i,t,d} \) (Eq. (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).

\[
O_{i,t,d} = N_{i,t,d} + S_{i,t,d}
\]

(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), \( M_{\text{ocean}} \) (assumed to be 0.648 (Barber et al., 2018)), on the \( d^{th} \) day every year, and the probability of maturation at each age, \( m_i \) (Eq. (6) and Table S1). The abundance of age-0 immature fish, \( N_{0,t,d} \), was assumed to be equal to juveniles entering the ocean, \( J_{\text{ocean},t,c} \).

\[
N_{i,t,d} = N_{i-1,t-1,d} \times e^{-M_{\text{ocean}}} \times (1-m_i)
\]

(6)

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

\[
S_{i,t,d} = S_{i,0,d} + \sum_p S_{i,p,d}
\]

(7)

\[
S_{i,0,d} = N_{i-1,t-1,d} \times e^{-M_{\text{mature}}} \times m_i
\]

(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 Eq. (9).

\[
\sum_{j=1}^{6} S_{i,j,t,a} = S_{i,t,d} \times (1-M_{\text{fishing}}) \times (1-M_{\text{spawning}})
\]

(9)

where \( S_{i,j,t,a} \) is the number of spawners at \( H_{A_j} \) that are ready to spawn in year \( t \), millions; \( S_{i,t,d} \) is the abundance of mature fish in the ocean before the spawning run in year \( t \), millions; \( M_{\text{fishing}} \) is the interval fishing mortality, 0.4 (Barber et al., 2018; MaineDMR, 2016); \( M_{\text{spawning}} \) 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 \( S_{i,j,t,a} \) was determined by the cumulative upstream passage rate of dams downstream of \( H_{A_j} \) 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; Tess et al., 2014). 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 that restricts alewives’ motivation to seek habitats that were suitable for spawning but no longer accessible. Eqs. (10) and (11) describe the calculations of the two dispersal rules.

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

If \( A_j \leq D_{HA_j} \), \( S_{i,j,t,a} = D_{HA_j} \times \sum_{j=1}^{6} S_{i,j,t,a} \) (11)

where \( A_j \) is the size of \( H_{A_j} \) (\( j = 1-6 \)), 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 on results obtained from the first dispersal rule) under the second dispersal rule. \( D_{HA} \) was a dispersal factor that was calculated using Eq. (12).

\[
D_{HA} = \left( \frac{A_j}{A} \right) \times P_{j-1}
\]

(12)

\( D_{HA} = 1 \), \( P_i \) is the upstream passage rate of the \( i^{th} \) dam. \( P_i \) 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 Eq. (13) (Table S1).

\[
S_{i,t-1,1-p,1+1,d} = \sum_{j=1}^{6} \left( S_{i,j,t,a} \times \prod_{k=1}^{j-1} \frac{Q_{\text{turbine},k,t,c}}{Q_{\text{dams},k,t,c}} \times (1-M_{\text{turbine}}) \right) \times e^{-0.92M_{\text{ocean}}}
\]

(13)

where the annual ocean mortality, \( M_{\text{ocean}} \), 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.,...
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 have the biggest influence on system behavior (Sternen, 1984). We assessed the sensitivity of alewife spawner abundance and hydropower generation to all constant variables within the model. The tested variables related to alewife spawner abundance were spawning mortality, fecundity (slope and intercept), B−H curve related variables (alpha (lifetime reproductivity rate) and asymptotic recruitment level), probability of maturity, sex ratio, total habitat area in the basin, turbine mortality, fishing mortality, ocean mortality, and fishway passage rate. The tested variables related to hydropower generation were net head, over-all efficiency, and turbine operation period. 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 Eq. (14) (Barber et al., 2018; Zhuang, 2014).

\[
S = \frac{O_i - O_0}{I_i - I_0} \frac{I_0}{I_0 - I_b}
\]

where \(O_i\) is the output value after the input was changed; \(O_0\) is the base output value; \(I_i\) is the altered input value; and \(I_0\) is the original input value. Inputs were considered “highly sensitive” if \(SI > 1.00\).

### 2.4. Dam management scenarios

Eight scenarios were designed to compare the effectiveness of different dam management practices (Table 2). The PR-PF-S scenario approximates the PRRP’s dam management strategy. Turbine shutdown periods were assumed to be 20 days each year, which occur during the 141th–150th day and the 231th–240th 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 chose alewife spawner abundance as an indicator to show the potential changes of the total alewife populations, because spawners are the main source of fishery (Havey, 1961). The tradeoffs between annual hydropower generation and the stabilized alewife spawner abundance each year under the eight basin-scale dam management scenarios (Table 2) are presented in Fig. 4. 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 results 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 (Pelice 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 (PR-PF-S scenario), 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 PR 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, 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 on 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. Besides, the timing, frequency, magnitude, and duration of seaward migrants each year are also important to the effectiveness of turbine shutdowns (Trancart et al., 2013).

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. The PRRP also upgraded hydropower capacity at two tributary dams, which further compensated for energy losses through the removal of the two lowermost dams. Our results indicate 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.

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. Fig. 5 illustrates the resulting population changes of alewife spawners homing to the accessible areas. Under a relatively low downstream passage rate of <60%, spawner abundance is lower than or similar to the NR scenario (the dashed line in Fig. 5) and inversely related to the upstream passage rate at each dam.
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 60% or less at each dam. Unless the downstream survival rate exceeds 60%, efforts or investments to improve upstream passage rates could be entirely ineffective. When downstream passage rates are relatively high (e.g., >70%), spawner abundance is larger than the NR scenario and positively related to both upstream and downstream passage rates. In this condition, the upstream passage rate becomes the primary limiting factor. When the upstream passage rate is lower than 60%, a 10% increase in downstream passage rate leads to ~0.3 million increase in spawner abundance. However, when upstream passage rate surpasses 60%, spawner abundance is highly sensitive to changes in both upstream and downstream passage rates. A 10% increase in downstream passage rate can result in up to 2.7 million increase in spawner abundance. This shows a threshold exists related to the upstream passage rate, which needs to be accounted for 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).

### 3.3. Sensitivity analysis

Energy generation is sensitive to net head, turbine operation period, and overall efficiency regardless of the percentage of increase as these parameters have a linear relation with energy (Eq. (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 Fig. 6. Spawner abundance was the most sensitive to ocean mortality, spawning mortality, fishing mortality, the size of the habitat area, and the asymptotic recruitment level for all investigated ranges. The high sensitivity of alewife spawner abundance to asymptotic recruitment level indicates the importance of increasing or maintaining a high habitat quality. In addition, spawner abundance was sensitive to any decrease, or <10% increase, in the alpha value and sex ratio. It was also sensitive to any decrease, or <70% increase in the fecundity slope. Accurate quantification of these sensitive variables is important in improving the confidence of model outputs.

### 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). Although 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 could warrant inclusion of all fish species for a comprehensive assessment of the energy-fish tradeoff.

Although 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 involve multiple owners time and cost prohibitive. From a policy perspective, hydroelectric dams in the USA 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 U.S. 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 U.S. Department of Energy’s Integrated Basin-Scale Opportunity Assessment Initiative reports...
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