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3
4 **A temporal perspective to dam management: Influence of dam life and threshold fishery**
5 **conditions on the energy-fish tradeoff**

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13
14 **Abstract**

15 While hydroelectric dams play a significant role in meeting the increasing energy demand
16 worldwide, they pose a significant risk to riverine biodiversity and food security for millions of
17 people that mainly depend upon floodplain fisheries. Dam structures could affect fish populations
18 both directly and indirectly through loss of accessible spawning and rearing habitat, degradation
19 of habitat quality (e.g., changes in temperature and discharge), and/or turbine injuries. However,
20 our understandings of the impacts of dam life span and the initial fishery conditions on restoration
21 time and hence the dynamic hydropower (energy)-fish (food) nexus remain limited. In this study,
22 we explored the temporal energy-food tradeoffs associated with a hydroelectric dam located in the
23 Penobscot River basin of the United States. We investigated the influence of dam life span,
24 upstream passage rate, and downstream habitat area on the energy-food tradeoffs using a system
25 dynamics model. Our results show that around 90% of fish biomass loss happen within five years
26 of dam construction. Thereafter, fish decline slowly stabilizes and approaches the lowest value at
27 around 20th year after dam construction. Fish restoration period is highly sensitive even to a short
28 period of blockage. The biomass of alewife spawners need 18 years to recover with only one-year
29 of blockage to the upstream critical habitats. Hydropower generation and loss of fish biomass
30 present a two-segment linear relationship under changes in dam life span. When the dam life span
31 is less than five years, generating 1 GWh energy cause around 0.04 million kg loss of fish biomass;
32 otherwise, the loss of fish biomass is 0.02 million kg. The loss of fish biomass could be
33 significantly decreased with minimal energy loss through increasing upstream passage rate and/or
34 the size of downstream habitat area.

35
36
37 **Keywords:**

38 System dynamics modeling, energy-fish nexus, hydroelectric dam construction and removal,
39 diadromous fish restoration.

41 **1. Introduction**

42 Balancing hydropower generation and fish population to meet both human and ecosystem needs
43 has become a pressing issue of dam decision-making (Grumbine and Xu 2011; Poff and Olden
44 2017; Ziv et al. 2012; Winemiller et al. 2016; Wild et al. 2018). There are more than 45,000 large
45 dams (>15 meters in height) around the world, which are mainly used for hydropower generation
46 and irrigation (WCD 2000; Vörösmarty et al. 2010; Bartle 2002). In addition, over 3,700 large
47 hydroelectric dams with a total capacity of more than 1,000 GW are to be constructed in the next
48 few decades, which will increase current hydropower generation by more than 70% (Zarfl et al.
49 2015). Though these dams play a key role in meeting the increasing energy demand, they pose a
50 great risk to sustainable fisheries (Limburg and Waldman 2009; Song et al. 2019) as well as the
51 wellbeing of fish-dependent communities (Zarfl et al. 2015; Winemiller et al. 2016; Limburg and
52 Waldman 2009; Song et al. 2018; Chen et al. 2016). Dams can substantially decrease fish
53 populations by fragmenting migration corridors (Hall et al. 2011; Beasley and Hightower 2000),
54 degrading habitat quality (e.g., changes in temperature and discharge) (Johnson et al. 2007; Piffady
55 et al. 2013; Zhao et al. 2012), and causing severe turbine injuries (Schaller et al. 2013; Stich et al.
56 2015). In the North Atlantic basin across US, Canada, and Europe, the abundance of 23 out of 24
57 diadromous fish species has dropped to less than 10% of their historical levels as a result of heavy
58 dam construction (Limburg and Waldman 2009). Some of these species (e.g., Atlantic salmon) are
59 currently listed as endangered species under the federal Endangered Species Act (Lichter et al.
60 2006).

61
62 Such energy-fish nexus has manifested in many previous, current, and future dam decisions. For
63 example, Mekong River is currently under an ambitious agenda of hydropower development.
64 Eleven hydroelectric dams have been proposed to be constructed on the lower main stem across
65 Laos, Thailand, and Cambodia (ICEM 2009; Grumbine and Xu 2011). Once completed, these
66 dams will generate roughly 15,000 MW of hydropower, projected to account for 8% of the regional
67 demand by 2025 with \$3.7 billion/year of gross income (Grumbine and Xu 2011). However, it has
68 been estimated that these projects would reduce up to 30% of annual protein intake by the national
69 populations of Laos and Cambodia (Grumbine and Xu 2011). Similar energy-fish tradeoff studies
70 under various new dam construction or dam removal scenarios have been performed in other
71 regions, including the entire Mekong River basin (Ziv et al. 2012), the Willamette basin (US)
72 (Kuby et al. 2005), the Penobscot River basin, (US) (Song et al. 2019), New England watersheds
73 (Roy et al. 2018), and the Oir River basin (France) (Trancart et al. 2013). Researchers found that
74 desired energy-fish outcomes may be achieved by strategically removing or avoiding building
75 dams at locations that significantly affect fish migration (Kuby et al. 2005; Song et al. 2019; Roy
76 et al. 2018; Ziv et al. 2012). Other studies have also found that installing effective fish upstream
77 passage structures (hereafter referred to as fishways) (Null et al. 2014; Thorncraft and Harris 2000;
78 Katopodis and Williams 2012; Larinier 2000) and properly shutting down turbines during fish
79 peak downstream migration period (Trancart et al. 2013; Watene and Boubée 2005; Eyler et al.
80 2016) can be effective ways in balancing the energy-fish tradeoffs.

81
82 However, previous studies on dam related energy-fish tradeoffs have widely used simplified
83 proxies, such as habitat gains (Null et al. 2014; Roy et al. 2018) and reconnected areas (Kuby et
84 al. 2005; Ziv et al. 2012), to estimate the potential changes in fish populations. These indicators
85 are fixed values which do not reflect the temporal changes of fish populations in response to
86 different dam management activities. The temporal perspective provides important information

87 regarding whether the effects take place relatively rapidly or slowly, potential time delays in
88 response to certain management actions (Limburg and Waldman 2009), as well as the key temporal
89 thresholds for a certain phenomenon to occur (e.g., depletion of a fish stock) (Rodríguez et al.
90 2006). Such information is fundamental to inform the type of dam management efforts needed and
91 the best timing of conducting these efforts. However, only a few previous studies have examined
92 the temporal changes of fish populations in response to dam management actions. Burroughs et al
93 (2010) measured the response of fish communities to the removal of Stronach Dam, a 2-MW
94 hydroelectric dam on the Pine River, Michigan. They found that the abundance of Brown trout and
95 rainbow trout increased by more than twofold 4 years after the dam removal (Burroughs et al.
96 2010). Lundqvist et al (2008) predicted temporal changes of salmon populations passing a fish
97 ladder during a 20-year period using a matrix population model. They found that a fivefold
98 population increase in 10 years can be achieved by improving fishway upstream passage rate from
99 the current 30% to around 75% (Lundqvist et al. 2008). Nevertheless, none of the previous studies
100 investigated the influence of a dam's life span on the rate of fish population decline and the time
101 needed for fish recovery once the dam is removed. Furthermore, none of the studies have further
102 linked the dynamic fish population changes to the losses/increases of hydropower generation to
103 explore the temporal energy-fish tradeoffs.

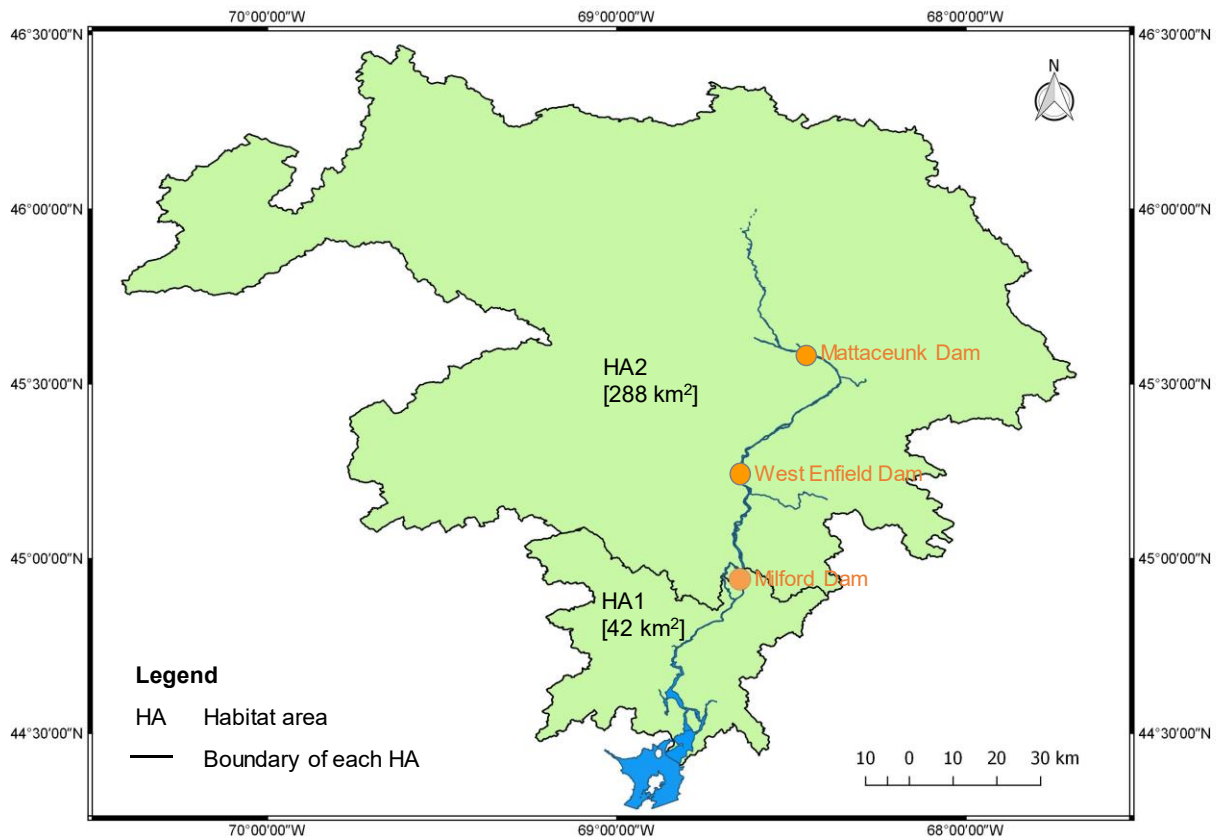
104
105 To address these knowledge gaps, this study aims to answer the following question: How do dam
106 life span, upstream passage rate, and downstream habitat area influence the temporal changes of
107 fish population, fish restoration period, and the energy-fish tradeoff? In order to achieve this goal,
108 we chose system dynamics model (SDM) to simulate the temporal energy-fish tradeoffs under
109 different dam life span and management scenarios. SDM is a computational method that simulates
110 the behavior of different components of a complex system over a certain time period. Particularly,
111 SDM can capture the embedded feedback and interactions among different system elements using
112 a set of linked differential equations (Forrester 1997). It is an appropriate approach to simulate the
113 dynamic energy-fish changes which has been previously applied in modeling temporal
114 hydropower production (Bosona and Gebresenbet 2010; Sharifi et al. 2013) and fish abundance
115 (Barber et al. 2018; Ford 2000; Stich et al. 2018) separately. However, the impacts of dam
116 management on the energy-fish tradeoffs, especially those from a temporal perspective, have not
117 been studied yet. This study adapted an energy-fish model presented in (Song et al. 2019) to
118 explore temporal dam management strategies. Case selection, methodologies, and data sources are
119 described in section 2. Section 3 conducts results analysis and discussion. Section 4 is the
120 conclusions, significance, and policy implications of this study.

121 122 **2. Materials and Methods**

123 2.1 Study site

124 The Penobscot River is the second largest river system in the New England region of the US with
125 a drainage area of 22,300 km² (NRCM 2019). The river system historically provided important
126 freshwater habitats for 12 native sea-run fish species (Schmitt 2017). However, these fish
127 populations have declined significantly after a heavy damming period between late 1800s and
128 early 1900s. The Milford Dam is currently the lowermost dam on the main stem of the Penobscot
129 River, around 61 kilometers away from the river mouth (Figure 1) (Maynard et al. 2017). It is a
130 run-of-river hydroelectric dam with an installed capacity of 8 MW (Amaral et al. 2012). This
131 modeling exercise will be focused on the Milford Dam, given that it is the first anthropogenic
132 barrier to a vast amount of upstream habitat areas. The fishway performance in facilitating fish

133 upstream migration at this site is critical in determining the distribution and abundance of native
 134 diadromous fish species (Gardner et al. 2013; Gardner et al. 2012; Gehrke et al. 2002; Tonra et al.
 135 2015). Decision-making of this dam also presents interesting energy-fish tradeoffs. We modelled
 136 alewife (*Alosa pseudoharengus*) as a representative sea-run fish species because it is ecologically
 137 important in freshwater, estuarine, and marine environments, providing food source for other
 138 species such as brown trout, Atlantic cod, and other aquatic furbearing mammals (Dalton et al.
 139 2009; McClenachan et al. 2015; ASMFC 2009). In addition, alewife is at the focal point of
 140 restoration as their commercial harvest has dropped from around 3.5 million pounds in the 1950s
 141 to less than one million pounds as of 2000 (MaineDMR 2018; Goode 2006). This dramatic decline
 142 was considered to be attributed to existing dams.
 143



144
 145 **Figure 1.** Map of the study area showing the locations of Milford Dam as well as the size of alewife spawning
 146 lakes/ponds in the Penobscot River Basin.

147
 148 **2.2 System dynamics modeling of the energy-fish nexus**
 149 A quantitative SDM usually consists of four elements: stocks, flows, auxiliary variables, and
 150 connectors (Ford 2000). Stocks are variables that accumulate or deplete over time (e.g.,
 151 populations of different alewife age groups). Flows represent the inflows and outflows of a stock
 152 (e.g., maturation or death in an alewife age group), which determine the stock's rate of change.
 153 Auxiliary variables are other important endogenous and exogenous variables that influence system
 154 behavior. Connectors show the flow of information in the system and links the stocks, flows, and
 155 auxiliary variables. The connections among the four elements are usually visualized as stock-and-

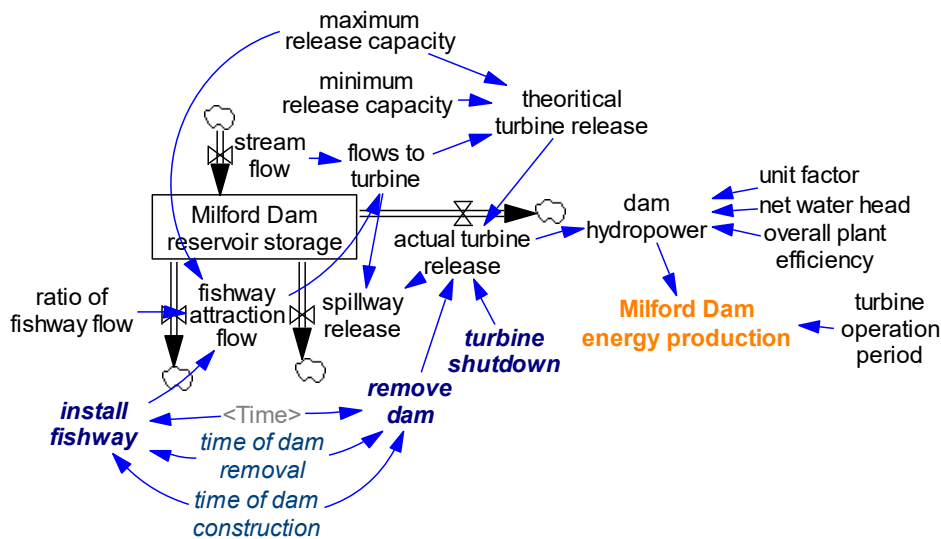
156 flow diagrams. In this study, we used Vensim[®] DSS to develop the stock-and-flow diagrams and
157 the energy-fish model.

158
159 The energy-fish model was built upon an existing model of the Penobscot River basin developed
160 in (Song et al. 2019). The Song et al. (2019) model has been validated using the historical alewife
161 landing and hydropower production data obtained from the Department of Marine Resources
162 (MaineDMR 2018) and the U.S. Energy Information Administration (EIA 2018), respectively.
163 This validated model was adjusted in this study to include the three existing dams on the Penobscot
164 main stem: Milford dam, West Enfield dam, and Mattaceunk dam (Figure 1). For simplicity, we
165 assumed the upstream pass rates of the West Enfield dam and the Mattaceunk dam to be 100%,
166 given that they each have installed at least two types of fishways with relatively high passage rates
167 (Amaral et al. 2012; Bunt et al. 2012; Noonan et al. 2012). Hence, this study is only focused on
168 the potential outcomes resulted from changes in the Milford dam. It has to be noted that this study
169 does not intend to develop a predictive tool of the real alewife populations and hydropower
170 generation in the Penobscot River, but rather to provide an understanding of the potential energy-
171 fish trends and tradeoffs under hypothetical scenarios. This model runs on a daily time step over
172 200 years.

173
174 Figure 2 shows an abstracted version of the stock-and-flow diagram of the alewife population
175 model used in this study. The complete version of the SDM is provided in the supporting
176 information. The alewife model is an age-structured model that mimics the actual life cycle of
177 alewives represented by different age groups. Alewives spend most of their life in the ocean, but
178 spawn in freshwater bodies. Once eggs are hatched, juveniles only live in the freshwater grounds
179 for several months before migrating seaward. In this model, we assume alewives could live up to
180 six years old in the ocean (Messieh 1977). The adult fish have to reach sexual maturity to
181 participate in the annual spawning runs. We assume the earliest time for an alewife to reach sexual
182 maturity is at age three; however, it is also possible to take longer. The distribution of probabilities
183 in reaching sexual maturity at different ages was obtained from (Gibson and Myers 2003) and
184 (Barber et al. 2018). Once sexual maturity is reached, the mature fish can participate in multiple
185 spawning runs in the following years until its physical death. Alewife populations at each age
186 group are modelled as stocks. There are primarily two types of stocks beyond the juvenile stock:
187 1) stocks that keep track of the different age groups in the ocean, and 2) stocks that keep track of
188 number of alewives that enter the spawning runs every year. For the first type of stocks, inflows
189 are surviving alewives returning from the spawning run and surviving alewives from the previous
190 age stock that remain in the ocean. The outflows include alewife loss due to natural mortality in
191 the ocean and advancement to the next age stock. For the second type of stocks, the inflow is the
192 amount of mature alewives from each age group, and the outflows are alewife losses due to natural
193 (i.e., predation) and anthropogenic (i.e., fishing, turbine kill) reasons and advancement to the next
194 age group in ocean. For each spawning run, the number of reproduced eggs is an auxiliary variable
195 which is calculated as a product of three main variables: the number of female spawner, spawner
196 fecundity of each age group, and spawning probability. The population of juveniles is
197 characterized using the Beverton-Holt spawner-recruit curve (Barber et al. 2018; Gibson 2004).
198 The detailed equations for the model were obtained from (Barber et al. 2018) and (Song et al. 2019)
199 and can be found in the supporting information.

200

208 Figure 3 shows an abstracted version of the stock-and-flow diagram of the hydropower generation
 209 model (see supporting information for the complete model). Reservoir storage behind the Milford
 210 dam is a stock variable. Streamflow from upstream that goes into the reservoir is an inflow.
 211 Fishway attraction flow, spillway release, and actual turbine release are the three outflows of the
 212 reservoir storage. As the dam is a run-of-river dam, we assume the reservoir storage does not
 213 change over time. Hence, the inflow always equals to the summed value of the three outflows. The
 214 allocation of inflow to the three outflows are based upon rules developed in Song et al. (2019).
 215 Hydropower generation at the Milford dam is an auxiliary variable, which is calculated as a product
 216 of actual turbine release, net water head, plant overall efficiency, turbine operation period, and two
 217 constant variables including water density, 1000 kg/m^3 and gravitational acceleration, 9.8 m/s^2
 218 (Singh and Singal 2017; Hadjerioua et al. 2012; Power 2015; Adeva Bustos et al. 2017).



219
 220 **Figure 3.** Schematic stock-and-flow diagram of energy generation model.
 221

222 The energy and fish models are connected through changes in the dam’s life span. The amount of
 223 hydropower generation/loss is roughly linearly related to a dam’s life span. The longer the dam is
 224 in operation; the more hydropower will be generated. Dam removal will result in a termination in
 225 hydropower generation. On the other hand, fish population changes after dam construction or
 226 removal are expected to be non-linear. We will investigate the temporal energy-fish tradeoffs
 227 under different dam life span scenarios.
 228

229 **2.3 Assessed indicators and studied scenarios**

230 The dynamic changes of alewife spawner abundance, loss of fish biomass, and alewife restoration
 231 period were analyzed. Alewife spawner abundance in the freshwater habitats is of interest because
 232 they are the main source of fishery (Havey 1961). In addition, spawner abundance and biomass
 233 are commonly used indicators to assess the effects of fish-related conservation projects (e.g.,
 234 stocking program, dam removal) (Pelletier et al. 2008) and the adverse impacts of dam
 235 construction (Ziv et al. 2012). In this study, spawner abundance was calculated as the sum of
 236 alewife spawners of different age groups that successfully reach freshwater spawning habitats and
 237 ready to spawn. Loss of fish biomass was the time summed spawner biomass loss compared to the
 238 pre-damming level during dam’s life span and the alewife restoration period. Spawner biomass
 239 loss was quantified in terms of weight, which is estimated as a product of the loss of spawner
 240 populations and their body weights. The average weights of age- 3, 4, 5, and 6 alewife spawners

241 are 144, 186, 209, and 244 g, respectively, according to previously reported alewife trap data in
 242 Brunswick, Canada (Barber et al. 2018; Fisheries and Oceans Canada et al. 1981-2016). Alewife
 243 restoration period is defined as the period between a specific dam management action (e.g., dam
 244 removal) and the full restoration of fish population to the pre-damming level. In this study, the
 245 time of full restoration was assumed to be the time point when alewife spawner population reaches
 246 99.5% of the pre-damming level.

247
 248 Changes of the aforementioned three indicators were investigated under scenarios with different
 249 dam life span, upstream passage rate, and size of the downstream accessible habitat area. Dam life
 250 span is defined as the total time period that a dam exists in the river channel. We investigated 9
 251 scenarios in dam life span, ranging from 1 to 30 years. The maximum 30-year dam life span is
 252 selected considering that the licenses issued by the Federal Energy Regulatory Commission
 253 (FERC) for operating non-federal owned hydroelectric dams are usually valid for 30 years (Madani
 254 2011). During this period, big changes in dam management (e.g., removal, fishway installation)
 255 are uncommon. Upstream passage rate is the percentage of fish individuals that are attracted to,
 256 enter, and successfully ascend a fishway (Silva et al. 2018). Seven scenarios in upstream passage
 257 rate ranging from 0 to 100% were investigated. The range was selected based upon the previously
 258 reported effectiveness of fishways (Bunt et al. 2012; Noonan et al. 2012). Size of the downstream
 259 habitat area is the accessible spawning habitat areas (in km²) located downstream of the Milford
 260 dam. The current size of the downstream habitat area and the total habitat area in the Penobscot
 261 River Basin are 42 and 330 km², respectively, according to data collected by Maine Stream Habitat
 262 Viewer (MaineDMR 2017). Ten different sizes of the downstream habitat areas ranging from 0 to
 263 330 km² were examined in this study.

264
 265 **2.4 Sensitivity analysis**
 266 A Monte Carlo simulation (also known as multivariate sensitivity simulation) was performed to
 267 understand the influence of parameter uncertainties on alewife spawner abundance (Sterman 1984;
 268 Ventana 2002; Cheng et al. 2018). All constant variables within the base model were varied by -
 269 20% to 20% of their original values as provided in Table 1. The Monte Carlo simulation was
 270 repeated for 200 times.

271
 272 **Table 1.** Tested variables in the Monte Carlo simulation

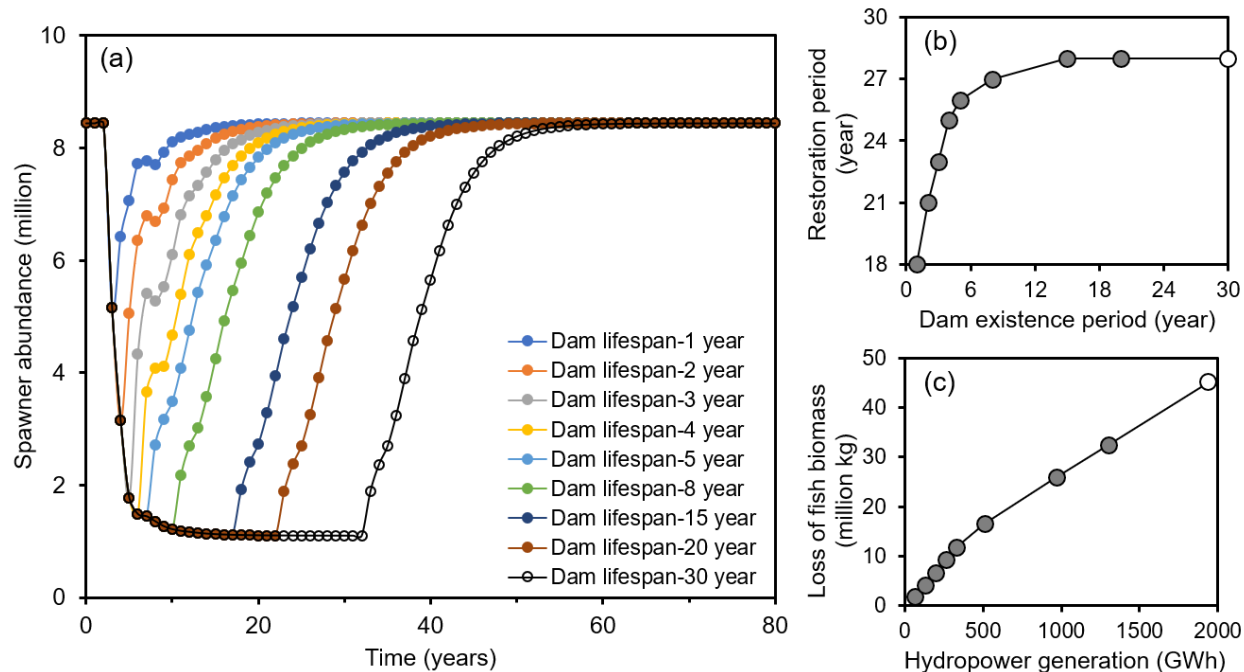
Tested variable	Original value	Test range
Spawning mortality	0.45	[0.36, 0.54]
Fishing mortality	0.4	[0.32, 0.48]
Ocean mortality	0.648	[0.518, 0.778]
Turbine mortality	0.15	[0.12, 0.18]
Fecundity slope	872	[697, 1046]
Fecundity intercept	50916	[40732, 61099]
Alpha	0.0015	[0.0012, 0.0018]
Recruits per HA (age-0 fish/km ²)	811246	[648997, 973495]
Age-3 mature probability	0.35	[0.28, 0.42]
Sex ratio	0.5	[0.4, 0.6]
Total habitat area (km ²)	330	[264, 396]

273
 274 **3. Results and Discussions**
 275 **3.1 Energy-fish nexus under different dam life spans**
 276 Figure 4 (a) depicts the temporal changes of alewife spawner abundance with different dam life
 277 spans. For this investigation, we keep the size of downstream habitat area to be 42 km² and assume

278 the upstream passage rate at the Milford dam is zero given that there is no fishway installed at this
279 site for at least 60 years (Song et al. 2019; Maynard et al. 2017). According to the results, the
280 undammed Penobscot River could support around 8.45 million of alewife spawners. Construction
281 of the Milford Dam in Year 0 could cause a dramatic decrease in spawner population. This sharp
282 population decline happens mainly within eight years after dam construction. Thereafter, fish
283 population decline slows down and reaches the lowest point at around the 20th year. The spawner
284 population then stabilizes at around 1.10 million, which is 87% below the pre-damming value. It
285 should be noted that spawner population decline does not happen until three years after dam
286 construction. This delayed effect is attributed to the amount of time needed (i.e., 3 years) for the
287 reproduced offspring after dam construction to mature and replace the older generations in the
288 spawning runs. Dam construction blocks alewife spawners' passage to the upstream areas and
289 hence, limits spawning activities to the downstream habitat areas. This limits the amount of
290 offspring being produced due to a higher competition for food and other resources within a smaller
291 size of spawning area. This delayed effect on fish population has been reported and discussed in
292 previous field and modeling studies (Beckerman et al. 2002; Ford 2000; Einum and Fleming 2000;
293 Mousseau and Fox 1998).

294
295 Dam life span determines the number of initial fishery populations at the time of dam removal
296 (Figure 4 (a)), as well as the time needed to restore alewife population to its pre-damming level
297 (Figure 4 (b)). According to the results, dam life span has a significant influence on alewife
298 restoration period within the first 5 years of dam construction. Alewives need 18 years to recover
299 even if they only experience a one-year blockage to the upstream critical habitats. Within 5 years
300 of dam blockage, alewife restoration period has a linear relationship with the duration of blockage,
301 with a 1-year increase in blockage resulting in a 2-year increase in alewife restoration time. If the
302 blockage duration is longer than five years, alewife restoration period will gradually approach and
303 stabilize at 28 years, which is the maximum alewife restoration period needed under the assumed
304 condition. Our results show that the number of initial fish population at the time of dam removal
305 has a vital influence on the alewife restoration time; however, it is only true when the duration of
306 blockage is 5 years or less. This is an extremely short period of time given that most of the dams
307 in the US have a nominal 50 years of designed life span (Ho et al. 2017). Once the threshold (e.g.,
308 5 years for alewife) is passed, the restoration time is no longer sensitive to dam life span. On the
309 other hand, the extensive harm that can be caused by even short periods of passage blockages
310 needs to be recognized and addressed in future river restoration projects.

311
312 The energy-fish nexus was analyzed under different dam life span scenarios as shown in Figure 4
313 (c). In our model, the amount of hydropower generation is linearly related to dam life span.
314 However, hydropower generation and loss of fish biomass present a two-segment linear
315 relationship. If dam life span is less than 5 years, generating 1 GWh energy could cause around
316 0.04 million kg loss of fish biomass, otherwise, the loss of fish biomass is reduced to 0.02 million
317 kg. For a 30-year life span, the Milford dam could provide around 1900 GWh energy with a loss
318 of 45 million kg of fish biomass. The fish biomass loss rate of 0.02 million kg/GWh also applies
319 if the dam life span is longer than 30 years. This is because alewife population stabilizes 20 years
320 after the dam construction, and the annual loss of fish biomass thereafter keeps constant no matter
321 how long the dam life span is. Hence, there are always tradeoffs between hydropower generation
322 and fish biomass losses regardless of dam life span, while the tradeoff is more prominent within
323 the immediate years following dam construction.



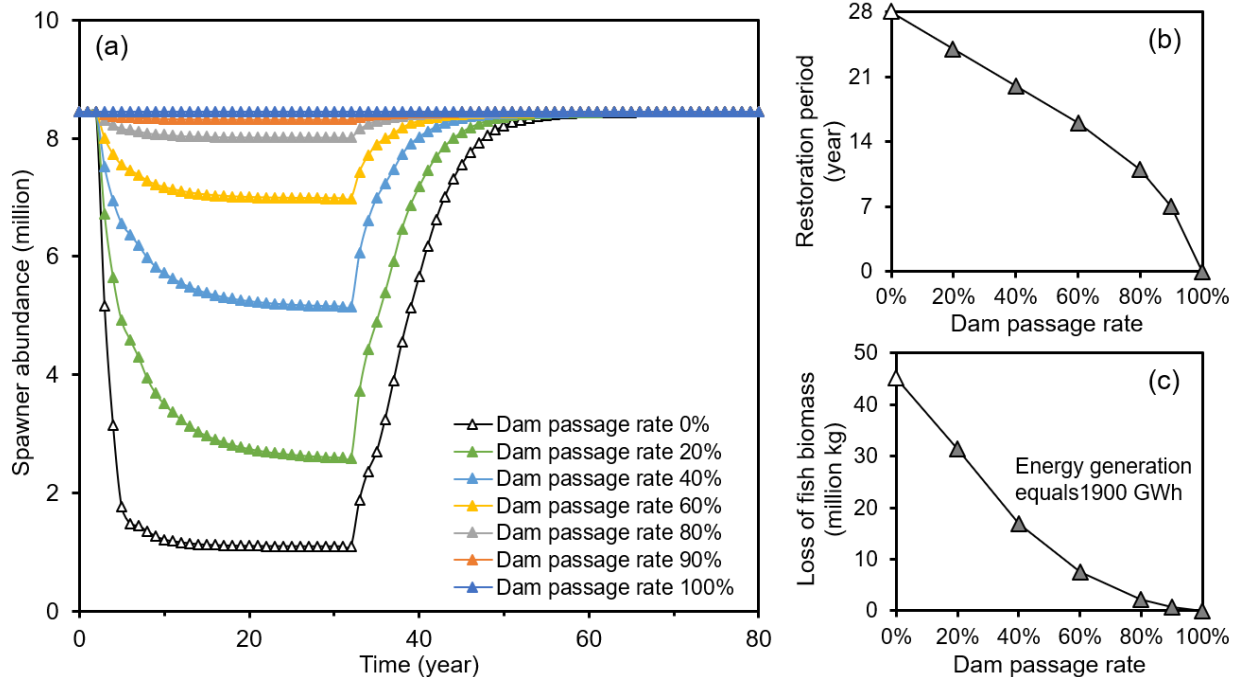
324
325 **Figure 4.** Temporal changes of alewife spawner abundance with dam life span (a), relationship between
326 dam life span and fish restoration period (b), and the energy-fish nexus (c).
327

328 3.2 Energy-fish nexus under different dam upstream passage rates

329 Dam upstream passage rate determines the number of alewife spawners that can reach the upstream
330 critical habitats. In this section, we keep dam life span and size of downstream habitat area to be
331 30 years and 42 km², respectively, and explore the impacts of different upstream passage rates on
332 temporal changes of alewife spawner abundance (Figure 5 (a)). With the improvement of dam
333 upstream passage rate from 0 to 100%, alewife spawner population increases correspondingly from
334 around 1.1 million to around 8.45 million. Conversely, fish restoration period decreases from 28
335 years to zero year (Figure 5 (b)). This is consistent with our previous finding that the more initial
336 fishery population at the time of conducting dam removal, the shorter the restoration period. The
337 relationship between upstream passage rate and alewife restoration period is in a convex shape,
338 which turns at the point with an 80% upstream passage rate. When the dam upstream passage rate
339 is less than 80%, alewife restoration period decreases by around 2.1 years with a 10% increase in
340 the upstream passage rate. When the upstream passage rate is larger than 80%, alewife restoration
341 period decreases by around 5.5 years with a 10% increase in upstream passage rate. Thus, the
342 negative impacts of damming on diadromous fish species could be significantly reduced through
343 installing effective fishways (i.e., >80% upstream passage rate). In practice, however, such a high
344 passage rate is rare. The five commonly used fishways, including pool-and-weir, vertical slot,
345 natural, Denil, and fish lock/elevator, have reported an average upstream passage rate of 61.7%
346 for salmonids, and only 21.1% for non-salmonids (Noonan et al. 2012).
347

348 The loss of fish biomass decreases with the increase of dam upstream passage rate in a concave
349 shape which turns at the point of around 60% of upstream passage rate (Figure 5 (c)). When
350 upstream passage rate is less than 60%, fish biomass loss is more sensitive to changes in the
351 upstream passage rate. A 10% increase in upstream passage rate at the Milford dam could result
352 in around 6.3 million kg decrease in the loss of fish biomass. This is because a small increase in

353 upstream passage rate under this condition can significantly increase initial fish population at the
 354 time of dam removal as shown in Figure 5 (a). When upstream passage rate is larger than 60%, a
 355 10% increase in upstream passage rate could only lead to around 1.9 million kg decrease in the
 356 loss of fish biomass. From an energy-fish perspective, increasing upstream passage rate is an
 357 effective means of balancing the energy-fish tradeoff as it significantly increases fish biomass with
 358 minimal loss of energy.
 359



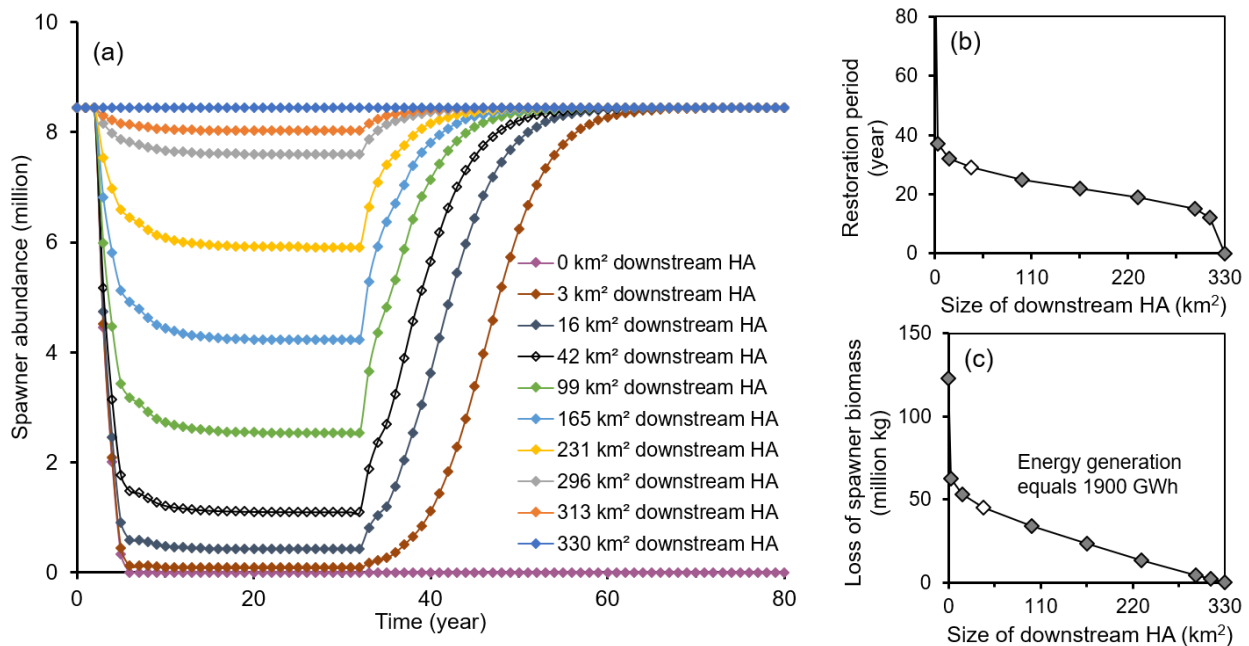
360
 361 **Figure 5.** Temporal changes of alewife spawner abundance with upstream passage rate (a), relationship
 362 between dam passage rate and fish restoration period (b), relationship between dam passage rate and
 363 loss of fish biomass (c).
 364

365 3.3 Energy-fish nexus under different sizes of downstream habitat areas

366 We further examined the response of alewife spawner populations to the sizes of downstream
 367 habitat area. Here, dam life span and upstream passage rate are kept constant at 30 years and 0%,
 368 respectively. Since the Milford dam is assumed to be totally impassable for alewife, the size of
 369 downstream habitat area represents the only accessible habitat areas to alewife spawners. The
 370 temporal changes of spawner abundance under different sizes of downstream habitat area are
 371 presented in Figure 6 (a). When increasing the size of downstream habitat area from 0 to 330 km²,
 372 the stabilized spawner population increases from 0 to 8.45 million. A smaller size of downstream
 373 habitat area leads to a lower spawner abundance (Figure 6 (a)), and a longer fish restoration period
 374 (Figure 6 (b)). There is a “S” shaped relationship between the size of downstream habitat area and
 375 the restoration period which turns at the sizes of around 16 and 295 km² as shown in Figure 6 (b).
 376 For instance, when the downstream habitat area is 16 km² or less, the impaired alewife population
 377 needs more than 32 years to restore to its pre-damming population level after 30 years of dam
 378 existence. Under the extreme condition where downstream habitat area equals to zero, alewife is
 379 likely to extinct in this area after eight years of dam construction. This shows that recovering the
 380 threatened or endangered fish species is usually a slow process which would consequently require
 381 more efforts and money. Meanwhile, a small increase in the habitat area under this condition can
 382 dramatically decrease the length of restoration period. When the downstream habitat area changes

383 between 16 and 295 km², a 40.5-km² increase in habitat area could steadily decrease fish
 384 restoration period at a rate of 2.4 years. When the downstream habitat area further increases to
 385 larger than 295 km², the restoration period once again becomes sensitive to changes in downstream
 386 habitat area. A 40.5-km² increase in habitat area can result in an 18.4-year decrease in restoration
 387 period.
 388

389 The loss of fish biomass decreases with the increase of downstream habitat area. The rate of change
 390 turns at the point of around 16 km² of downstream habitat (Figure 6 (c)). The maximum loss of fish
 391 biomass over a 30-year dam life cycle is 123 million kg when there is no downstream habitat
 392 area available for alewife. This value decreases significantly to around 53 million kg if increasing
 393 downstream habitat area to 16 km². When the size of downstream habitat area is more than 16 km²,
 394 the loss of fish biomass decreases linearly at a rate of 6.9 million kg with the increase of every
 395 40.5-km² downstream habitat area. In order to avoid significant loss of fish biomass, it is important
 396 to not build or to remove dams at sites where extremely small size of downstream habitat area is
 397 available.
 398

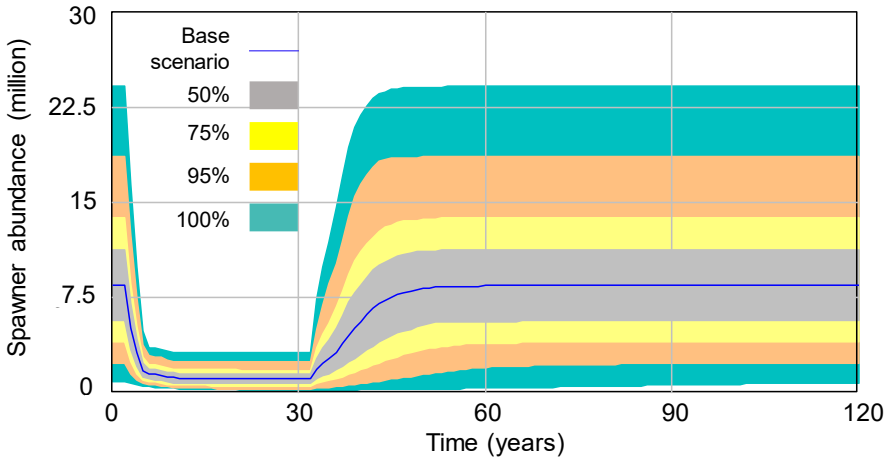


399 **Figure 6.** Time-series changes of alewife spawner abundance with size of downstream habitat area (HA)
 400 (a), relationship between size of downstream habitat area and fish restoration period (b), relationship
 401 between size of downstream habitat areas and loss of fish biomass (c).
 402
 403

404 3.4 Sensitivity analysis

405 The 50%, 75%, 95%, and 100% likelihood of the alewife spawner abundance in response to
 406 changes of the tested variables are shown in Figure 7. The results show that alewife abundance in
 407 the studied river basin stables at a range of 0.9-24.1 million with a 100% confidence, and a range
 408 of 5.9-11.8 million with a 50% confidence. With a 30-year blockage of fish passage, we will have
 409 100% confidence that the restoration period will range from 18 to over 90 years, and 50%
 410 confidence that the restoration period will range from 26 to 40 years with the changes of the tested
 411 model variables. The loss of fish biomass will range from 9.9-118 million kg with a 100%
 412 confidence, and 34-64 million kg with a 50% confidence. Our analysis shows that uncertainties in

413 the values of the model variables are likely to result in alewife populations that are susceptible to
 414 collapse or an extremely long restoration period. This phenomenon could be explained by the low
 415 survival rate at low population levels (Quinn and Collie 2005). In such a case, fish restoration
 416 activities (e.g., lower fishing mortality, fish stocking program) may need to be executed quickly
 417 to shorten the restoration period. The results also show that alewife populations reach equilibrium
 418 under all scenarios. This is an outcome of the necessary biological process of density dependence,
 419 usually in early life history (Quinn and Deriso 1999; Quinn and Collie 2005).
 420



421
 422 **Figure 7.** Monte Carlo simulation of the age-structured fish population model
 423

424 **4. Conclusions**

425 In recent years, a lot of efforts have been made to minimize dams' negative impacts and restore
 426 impaired fish populations through fishway installation (Unami et al. 2012), dam removal
 427 (Burroughs et al. 2010), and stocking programs (Moring et al. 1995). Our study provides a unique
 428 temporal perspective to the hydropower and fish population tradeoffs related to dam life span and
 429 initial fishery conditions. Diadromous fish populations are found to be highly sensitive to even a
 430 short blockage period. In our modeled river basin, alewives need 18 years to recover to pre-
 431 damming level even if they only experience a one-year blockage. Meanwhile, the most dramatic
 432 fish population decline happens within five years of dam construction. These findings suggest that
 433 dam-related improvement/restoration projects need to be carried out simultaneously with or
 434 immediately following dam construction to eliminate dams' impacts on diadromous fish species.
 435 From the perspective of energy-food nexus, we found a two-segment linear relationship between
 436 hydropower generation and loss of fish biomass under changes in dam life span. When the dam
 437 life span is less than five years, generating 1 GWh energy can cause around 0.04 million kg loss
 438 of fish biomass; otherwise, the loss of fish biomass is 0.02 million kg. While building hydroelectric
 439 dams almost always lead to a fish biomass loss, the effect can be minimized through means such
 440 as increasing dams' upstream passage rate, building dams at the sites where large amount of
 441 downstream habitat areas is available, or removing dams that significantly block critical upstream
 442 habitat areas. Our study shows that a 10% increase in upstream passage rate could reduce fish
 443 biomass loss by at least 1.9 million kg in the modelled river basin. Meanwhile, a 40.5-km² increase
 444 in downstream habitat area can reduce fish biomass loss by more than 6.9 million kg. Both
 445 strategies can be achieved with minimal losses of hydropower generation capacities. The
 446 Penobscot River Restoration Project is an example case where the energy-fish outcomes were
 447 optimized through removing two lower most dams (the Veazie dam and the Great Works dam),

448 improving fish passage performance at the Milford dam, and installing turbine facilities at other
449 existing dams (Opperman et al. 2011).

450

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456

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