Environmental Conservation Faculty Publication Series

Environmental Conservation

2021

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Abstract

Small pelagics, or forage fish, link lower and higher trophic levels in marine food webs. Recently, attention has been given to the management of forage fish, including anadromous river herring (Alewife *Alosa pseudoharengus*, blueback herring *A. aestivalis*) and American shad (*A. sapidissima*) due to their current depleted status and historically important ecological and economic roles. Little is known about the impact of changes in their biomass on marine food webs and what management practices will promote their recovery. Estimated historical riverine productivity was utilized to evaluate potential ecosystem impacts of the increasing river to ocean connectivity to resemble 19th-century conditions. The Ecopath with Ecosim modeling framework was used to simulate management strategies, focused on anadromous forage fish, by creating scenarios of fisheries reduction (mixed fishery effort reduction) and river to ocean habitat connectivity (75% of historical connectivity achieved). Sixty-year simulations covered the entire time series including a 36-year forecast period to evaluate the ecosystem impacts of management strategies. Results suggest nonlinear relationships and large changes in biomass flows from forage fish to upper trophic levels in the Gulf of Maine ecosystem. Increases in biomass were observed for pelagic sharks, demersal piscivores, and species of conservation concern such as pinnipeds and seabirds, although overall results were strongly influenced by indirect trophic effects. Promoting anadromous forage fish recovery through increased connectivity resulted in the redundancy of marine ecosystem niches that would increase resilience to climate, fisheries, and other perturbations. This study highlights the value of employing ecosystem models for testing management scenarios to contrast different approaches to recover anadromous forage fish towards its former ecological prominence.

There are no small parts, only small actors—Konstantin Stanislavski.

Forage fish (e.g., herrings, menhaden, shad, sardines, anchovies, etc.), small-bodied planktivorous species responsible for linking food webs by transferring energy from low (e.g., phytoplankton and zooplankton) to higher trophic

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Additional Supporting Information may be found in the online version of this article.

levels (e.g., piscivorous fishes, marine mammals, sea birds), can play a big role in marine ecosystems (Cury et al. 2003; Alder et al. 2008; Essington et al. 2015). In terms of global fisheries, forage fish currently account for approximately 25%–30% of total landings (FAO, 2015 in Koehn et al., 2017). Most forage fish fishery landings are destined for reduction; in 2011, 75% of small pelagic world catch was turned into fishmeal and fish oil (Béné et al. 2015). Competition among the various uses of small pelagics as resources (e.g., fishmeal, direct human consumption, and fish oil production) can cause a range of conflicts among the industries (Tacon and Metian 2009). This is made more complicated because forage fishes are opportunistic strategists with a small size at maturation, high population intrinsic growth rates and are characterized by large biomass fluctuations (King and McFarlane 2003; Winemiller 2005). Life history characteristics of forage fishes are related to variable population sizes over time, with

relatively frequent sharp collapses and fast recoveries (Lindegren et al. 2013). Fluctuations in the abundance of forage fish have been directly related to marine ecosystem regime shifts (Auber et al. 2015), and resilience (Dias et al. 2019). Given the importance of forage fish to marine ecosystem functioning, fisheries exploitation, and ecosystem-based management approaches (Francis et al. 2007), linking their population dynamics through time to the broader ecosystem is essential for understanding consequences of management decisions.

Increased awareness of the effects of forage fish declines on ecosystem dynamics creates the need for platforms that explore management scenarios in an ecosystem-based modeling context. The Northeast US continental shelf large marine ecosystem, particularly the Gulf of Maine, is among the most productive and biodiverse marine temperate areas in the world (Sherman and Skjoldal 2002; Overholtz and Link 2006). Forage fish, which are composed of anadromous and oceanodromous species with distinct life history traits, are an important component of the Gulf of Maine food webs and fisheries productivity (Dias et al. 2019). The former spends most of their life in the ocean followed by migration into freshwater to reproduce, contrasting a fully marine life history. The anadromous forage fish pool is dominated by alosines, river herring (Alewife *Alosa pseudoharengus*, blueback herring *A. aestivalis*) and American shad (*A. sapidissima*), which have experienced long-term declines primarily associated with high fisheries removals, including incidental catch or bycatch, and loss of spawning habitat (Limburg and Waldman 2009). While anadromous forage fish remain in the contemporary Gulf of Maine ecosystem, their role and abundance has been greatly reduced (Limburg and Waldman 2009; Dias et al. 2019). In addition, oceanodromous species such as Atlantic herring are the focus of large-scale fisheries and have experienced large fluctuations in population size that undercuts system resilience to future change and exploitation which particularly impacts regions like the Gulf of Maine with low forage fish diversity (Dias et al. 2019).

While productivity in the Gulf of Maine historically supported development of economically and culturally important fisheries, a lack of effective management has resulted in stock collapses. The first fishing grounds in the Gulf of Maine were established in the 1600s, with Atlantic cod (*Gadus morhua*) as a flagship fishery. By the 1650s, the stock already showed the first signs of a declining population size (Alexander et al. 2009). As European colonialization expanded throughout New England, local riverine and nearshore resources supplied important export markets in roughly equal numbers until 1815 (Alexander et al. 2009). By 1820 the anadromous fish contribution to exports had decreased, likely as a result of poor recruitment caused by environmental factors and the continuous fragmentation of the riverine habitat, which prompted expansion of marine pelagic fisheries primarily focused on Atlantic mackerel, but also Atlantic herring (Alexander et al. 2017). Through 1850, larger mainstem dams proliferated across the rivers of New England, increasing habitat fragmentation, and systematically decreasing human reliance on anadromous fish as their population declined (Hall et al. 2012).

The loss of anadromous fish affected lake nutrient dynamics (Twining et al. 2013) and were concomitant with multiple species losses and population extirpations due to exploitation and habitat modifications that altered coastal marine ecosystems (Lotze and Milewski 2004). Since then, landings have fluctuated as fisheries build up capacity, collapse populations and cycle through different species (Jordaan et al. 2010). The once important fisheries for Atlantic cod and the suite of anadromous species are now only remnants of their historical pasts.

The continued low abundance of key species provides significant management challenges (Bolster 2018). As a result, stocks managed by the New England Fisheries Management Council show a long-term decline in revenue (Wiedenmann and Jensen 2017). Besides, landings of New England Fisheries Management Council-managed piscivorous, planktivorous, and benthivorous species continue to decline (NOAA 2019). Currently, the low abundance of key populations, including river herring and Atlantic cod, are driving lower catches of other species due to bycatch and quota limits, leading to their designation as "choke species." Thus, some species' low stock sizes have cascading impacts on non-directed fisheries, and recovery of these populations would accomplish multiple objectives, particularly from an ecosystem-based perspective.

Both directed fisheries and the degradation of freshwater spawning habitat impact anadromous alosines. The historical spawning habitat for anadromous alosines was in most cases reduced by 90%–95% and as a result greatly reduced the freshwater input of anadromous biomass to marine and riverine food webs alike (Hall et al. 2011; Mattocks et al. 2017). Rivers such as the Penobscot, Kennebec and Androscoggin all saw decreases in both spawning habitat and fisheries landings during the 1750–1850 period (Hall et al. 2012). This implies that two management levers are available to recover coast-wide populations: (1) fishing mortality can be reduced through fisheries restrictions, (2) the carrying capacity of populations can be improved by restoring spawning habitat. However, decisions regarding the best course of action involve weighting different strategies that often produce nonlinear or unanticipated results due to the nature of aquatic ecosystem dynamics. These two management levers' outcomes can be evaluated utilizing the Ecopath with Ecosim (EwE) modeling framework to explore how the approaches would affect marine ecosystems (Mackinson et al. 2018). Here we aim to: (1) develop a habitat reconstruction forcing function using landscape-based historical river biomass time series, (2) test two fishing effort scenarios to evaluate the degree of biomass change in the system when we consider effort reduction of gears directly affecting alosines, and all the gears, and (3) test how the worse performing fishing effort reduction scenario, from the perspective of alosine recovery, is altered with the addition of the habitat reconstruction forcing function.

Materials

We evaluated how different management strategies altering fisheries effort and habitat connectivity (dam removal) affect

marine ecosystem nonlinear dynamics and other species' biomass trajectory. The analysis took the following steps: (1) an Ecopath model was created that represents the geographic area of the Gulf of Maine representing 1996–2000; (2) times series of biomass, fishing effort, and landings were fitted in Ecosim; (3) scenarios were conducted in Ecosim to forecast the effects of fishing effort reduction on fleets that interact with alosines, fishing effort reduction in all fleets, and the combined effects of increased connectivity and effort reduction in fishing fleets; and (4) Monte Carlo simulations were run to access uncertainty in biomass estimation. Following model simulations, we identified the best management approach considering the various outcomes within the broader ecosystem and management context.

Spatial extent

To compare the management scenarios, we built an ecosystem model focusing on the Gulf of Maine ecoregion, which has a total of 79,128 km^2 (Fig. 1). Our model considered the efforts of the Energy Modeling and Analysis eXercise (EMAX) project (Link et al. 2006, 2008). The EMAX model's goal was to establish an ecological network model for Northeast U.S. marine food webs in four ecoregions: Gulf of Maine, Georges Bank, Southern New England, and Middle Atlantic Bight (Link et al. 2008). We based our model on the EMAX Gulf of Maine and expanded the 31 nodes (or functional groups) to 45, including multistanza groups. To calculate alewife lost biomass based on the river to ocean connectivity and productivity potential, we incorporated in our analysis three Northern New England Watersheds: Androscoggin, Kennebec, and Penobscot.

Species of interest

The model had eight forage fish functional groups: alosine (*Alosa pseudoharengus*, *A. aestivalis*, and *A. sapidisima*); Atlantic herring (*Clupea harengus*); Atlantic mackerel (*Scomber scombrus*); butterfish (*Prepilus triacanthus*); shrimp; squids; mesopelagics; and other small pelagics (Supporting Information). Among the forage fish functional groups, we were especially interested in the alosine node, composed of river herring (alewife, *Alosa pseudoharengus* and blueback herring, *A. aestivalis*) and American shad (*A. sapidissima*). Our focus was on testing management scenarios that promote recovery of the alosine group, specifically alewife, by reducing fisheries impacts on the species and simulating increased river to ocean habitat connectivity using productivity of historically available connected habitat.

The ecosystem modeling approach

Ecosystem models can be developed using different approaches (Heymans et al. 2011), and for this study, we chose the Ecopath with Ecosim model framework (EwE 6.5, Christensen and Walters, 2004). Ecopath is known worldwide, and a full description can be found in several publications (Christensen and Walters 2004; Christensen et al. 2008; Araújo and Bundy 2011). The mass-balance

ecotrophic model represents the ecosystem as functional groups or nodes (different species, ontogenetic phases, or groups with the same ecological importance) connected by trophic relationships. Ecopath with Ecosim was originally developed to address questions regarding the ecosystem structure, and how external drivers affect the food web (Christensen and Pauly 1992; Walters et al. 1997). Our study was developed within the Ecopath core routine, which provides a static snapshot of an ecosystem (Polovina 1984; Libralato et al. 2006). Ecopath's presents two main equations, the first takes the following form:

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + P_i \cdot (1 - EE_i)$$

where P_i is the total production rate of group i, Y_i is the total fishery catch rate of group i, $M2_i$ is the total predation rate for the group i, B_i the biomass of the group, E_i is the net migration rate (emigration–immigration), BA_i is the biomass accumulation rate for the group i, EE_i is ecotrophic efficiency or the proportion of the production used in the system, and $P_i (1 - EE_i)$ represents the rate of other sources of mortality ($M0_i$) for the group i (Christensen et al. 2005, 2008; Dias et al. 2019). The second main Ecopath equation is:

$$Q = P + R + U$$

where Q is consumption, P is production, R is respiration, and U is unassimilated food. The first step was to generate an Ecopath model for the Gulf of Maine region, which will provide a snapshot of the ecosystem and the trophic relationships at a given period. We then proceeded with the model parametrization of biomass (B), production (P/B), consumption (Q/B), ecotrophic efficiency (EE), and diet (DC) information (Buchheister et al. 2017) for the 1996–2000 year block.

Ecopath is a mass-balance model approach, where at least three of the parameters need to be provided, in addition to diet data, and the model will estimate the missing parameters using the balanced sets of equations (Heymans et al. 2016). To diagnose the input data, we used the pre-balance routine (PREBAL), which checks for all parameters' slope, identifying issues of model structure and data quality before the balancing process (PREBAL, Link, 2010). This routine checks the slope of the biomass ratio, production, and consumption concerning trophic positions to check if the model passes the PREBAL diagnostics' assumptions. To achieve a balanced model, ecotrophic efficiency estimates should be used to tune the model by maintaining values between 0 and 1, with values approaching 1 for groups with high predation and exploitation pressures. For groups where the EE value is higher than 1, the remainder of the parameters should be tuned or "balanced" during model parametrization (Christensen et al. 2008).

Once model parametrization was achieved in Ecopath, the next step was to add the dynamic simulation component. Ecosim uses Ecopath as a reference model combined with a series of parameters and follows the provided diet matrices to
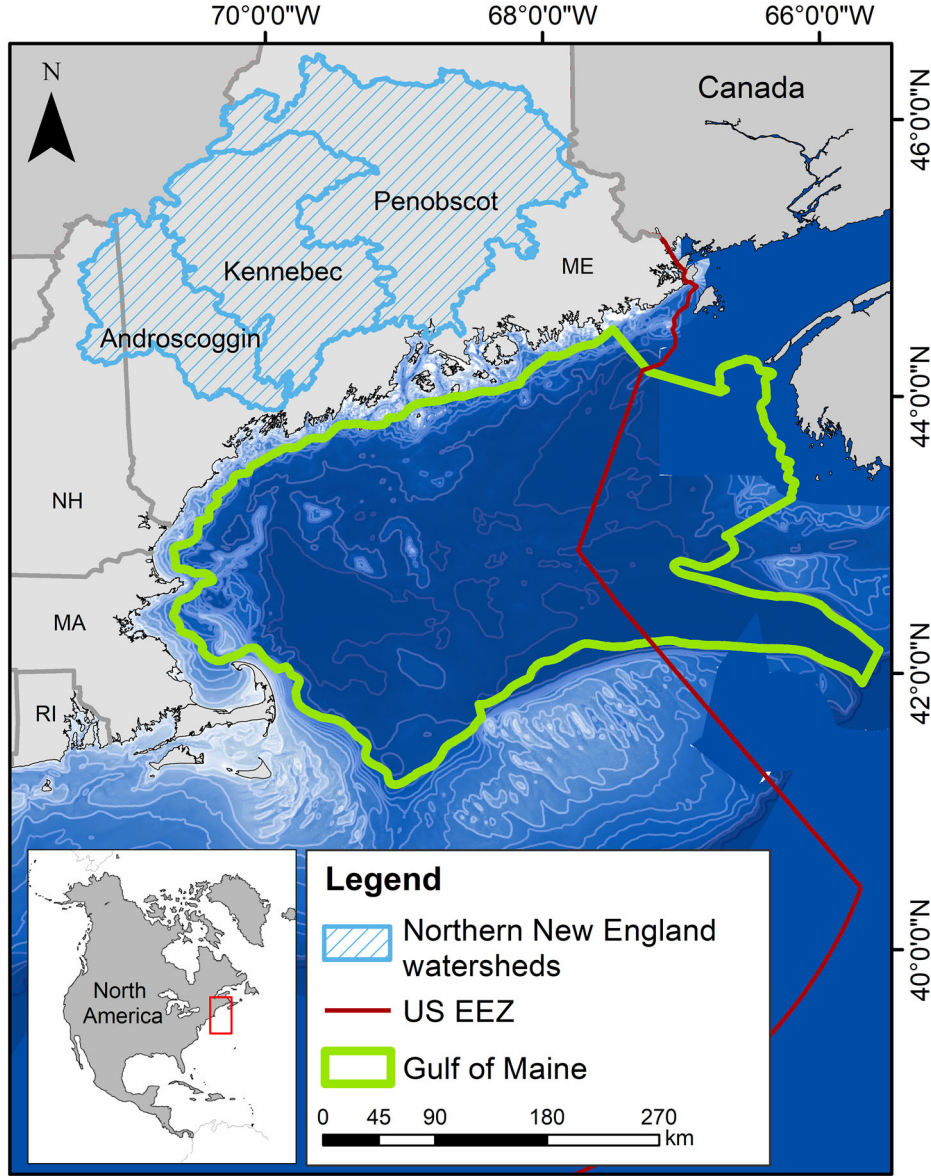
Fig 1. Map of the spatial limits of the Gulf of Maine model. The map shows the bathymetric profile of the coastal region. US Exclusive Economic Zone (EEZ) is delimited by the red line. The three Maine watersheds used in the analysis are signaled by the dashed blue polygons.

make inferences regarding the feeding behavior. Ecosim uses differential equations, and passes through parameterization routines by fitting both biomass and catch time series (Christensen et al. 2005).

The basic Ecosim equation expresses the rate in variation in biomass B over time t for each group i as:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M0_i + F_i + e_i)B_i$$

where g_i is the net growth efficiency, Q_{ji} is the consumption rate of group i on group j, Q_{ij} is the consumption rate of group j on group

i. I_i is the immigration rate, $M0_i$ is the natural mortality rate (not including predation), F_i is fishing mortality rate, and e_i is emigration rate (Christensen et al. 2008). In Ecosim, consumption Q_{ij} is calculated using foraging arena theory, which assumes that all trophic relations are limited to spatially restricted foraging areas, and a functional groups consumption is a function of their prey vulnerability to predation (Walters et al. 1997; Ahrens et al. 2012), and is represented by

$$Q_{ij} = \frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot P_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot M_{ij}/D_j}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot P_j \cdot S_{ij} \cdot T_j/D_j}$$

or the following equation if the vulnerability is set to 1, which uses bottom-up control conditions

$$Q_{ij} = a_{ij} \cdot B_i \cdot T_j \cdot S_{ij}$$

where a_{ij} is the effective search rate by predator i feeding on a prey j, v_{ij} is the base vulnerability, wherein biomass pools, regulated by the vulnerability parameter, are divided into those that are available and those that are unavailable for predation. A low vulnerability (~ 1) indicates that the predator biomass will not cause any noticeable increase in the predation mortality in the given prey, while high vulnerability values (> 100) indicates that an increase in the predator biomass will cause a proportional increase of the predation mortality for the given prey (Christensen et al. 2008). Bi is the prey biomass, P_j the predator abundance, T_i the prey relative feeding time, T_j the predator relative feeding time, S_{ij} the user-defined seasonal or long-term forcing effects, M_{ij} the mediation forcing effects, and D_j represents the handling time as a limit to consumption rate (Christensen et al. 2005, 2008).

For the simulation, we employed time series of biomass, landings, and fishing effort in days at sea or days absent. More details are provided in the section below and in the Supporting Information. The vulnerability parameters are an important component of fitting the models to time series data (Christensen et al. 2008). For each scenario, we estimated the vulnerability parameter via time series fitting and then selected the trial with the lowest ranking sum of squared deviation (SS) from the vulnerability searches to run the final scenarios (Christensen et al. 2008).

In addition to the EwE software, we also used ecopath_matlab (Kearney 2017) and Rpath (R Core Team 2013; Lucey et al. 2020) to generate graphs and record full model documentation.

Timeframe of analysis

The model was established using the year block 2000 as the reference point (Biomass, Consumption, Production, Diets, Mortality, and Fishing Mortality). The year block, chosen based on data availability, included the years 1996 to 2000, and was the same block used in the EMAX Gulf of Maine model (Link et al. 2006, 2008). In addition to our baseline model, we incorporated biomass time series from 1992 to 2014. We ran the simulations for the entire 60-year period, including the 36 years of forecast, we also included a 2-year spin-off period to allow for model calibration. As we focused on fisheries-based management scenarios, we defined seven fleets based on different gear types, as described below.

Data sources

The EMAX Gulf of Maine model presented 31 functional groups with low taxonomic resolution. To create our baseline model, we used EMAX inputs and expanded the functional groups to include higher taxonomic resolution resulting in 45 functional groups. A full description of the model parametrization procedures is available in the Supporting Information.

We used stock assessment data for all managed species and calculated landings and discards from all Gulf of Maine ecoregion coastal states (Maine, New Hampshire, and Massachusetts). Based on the resolution of the effort data we aggregated gear types into seven distinct categories: dredge, gillnet, purse seine, trap, trawl, recreational and other fisheries, which aggregated pound and dip nets, weirs, and haul seines under the same category, due to low data resolution. For non-commercial species, we relied on data from literature and NOAA surveys (Supporting Information).

Some species had higher data resolution, which allowed for different size classes, or multistanza categories, representing ontogenetic shifts in diet and vulnerability to fishing mortality and predation (Walters and Martell 2004). To account for ontogenetic differences, we divided three functional groups into distinct age classes using catch-at-age data from stock assessments to determine landings and discards. The multistanza categories were Atlantic cod (small, medium, large), hake (small and large), and dogfish (small and large; Table 1). In this case, we provided the von Bertalanffy K parameter, the weight (W) at maturity, infinity ratio (W_{mat}/W_{inf}) for the group, estimates of age, total mortality for each stanza, and the biomass and consumption for the leading groups (Supporting Information). In the multistanza approach, one leading stanza or group is defined. The consumption biomass ratio is provided to compute the remaining stanzas' consumption biomass ratio, based on a stable age distribution (Christensen et al. 2008).

Table 1. Fish species and size classes for the multistanza groups.

EwE result	Species	Age (yr)	Size (cm)
Small cod	Atlantic cod	0–1	≤20
Medium cod	Atlantic cod	2–3	21–50
Large cod	Atlantic cod	4+	>50
Small dogfish	Spiny dogfish	0–5	≤60
Large dogfish	Spiny dogfish	6+	>60
Small hake	Includes white, silver, offshore, red, spotted hakes	0–5	≤40
Large hake	Includes white, silver, offshore, red, spotted hakes	6+	>40

Time series

Time series are essential for the Ecosim model calibration procedure. We fitted the time series for the years 1996 (the beginning of NOAA's Vessel Trip Report [VTR] program) to 2014. The VTR contains days absent or days at sea data. We used this information as a measure to create an effort time series (Fig. 2). We also obtained time series of landings, biomass, fishing mortality from the NEFSC trawl survey and stock assessment reports, and NOAA's NMFS landing data.

Biomass time series used data from the NEFSC trawl survey. They encompassed the following functional groups: Atlantic herring, alosine, Atlantic mackerel, butterfish, other small pelagics, striped bass, Atlantic cod (S, M, and L), haddock, skate, demersal benthivores, and demersal piscivores. Landings time series included the three macrobenthos functional groups, megabenthos filterers and others, shrimp and similar species, Atlantic herring, alosines, Atlantic mackerel, butterfish, other small pelagics, bluefish, striped bass, large dogfish, haddock, small hake, and the demersal groups from NMFSC landings data. Time series of fishing mortality were obtained for medium and large Atlantic cod functional groups and for the Atlantic herring functional group (NEFSC 2012, 2013).

Model scenarios

The simulations compared the effects of river to ocean habitat connectivity and fisheries moratoria on population recovery trajectories for alosines and other key species. The key objective was to promote the recovery of alosine biomass, and considered other species' responses within an ecosystem perspective. Three different scenarios employing distinct fishing effort levels and added habitat connectivity through improving river connectivity and specifically altering alewife productivity were simulated. Due to data availability, only alewife riverine productivity estimates were considered in connectivity scenarios, and we acknowledge that this estimate is conservative because blueback herring and shad would also benefit from restored connectivity. For fishing effort scenarios, we scaled the days absent in relation to the mean.
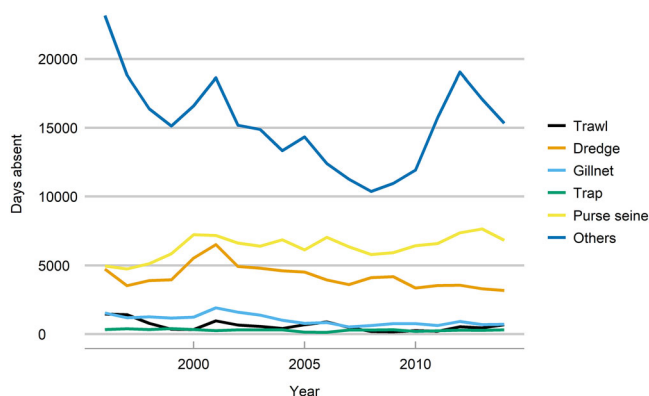

Fig 2. NOAA's vessel trip report program days absent time series. Fishing gears are presented in distinct colors.

The first scenario reduced fishing effort on all gear types that affect alosines by direct or incidental catch (bycatch). These gear types were gillnets, purse seines, trawls, and others (pound and dip nets, weirs, and haul seines). The fishing effort was reduced in three-time steps in 2020, 2028, and 2039 (Supporting Information Table S2).

The second scenario tested alosine and the ecosystem response to total fishing effort reduction except for recreational fisheries (due to the uncertainty of the data). In this case, all gear types were affected; however, the maximum fishing reduction was maintained at 0.5 compared to the baseline and occurred in two-time steps, 2020 and 2028 (Supporting Information Table S11).

The third scenario focused on alosine biomass restoration via fishing reduction (for all fleets) and increased connectivity based on the potential biomass of anadromous alosines (Hall et al. 2011; Mattocks et al. 2017). Our aim was to test how the worse performing fishing effort reduction scenario from the perspective of alosine recovery is altered with the addition of the habitat reconstruction forcing function. Restoration of biomass from alosine production was related to lake/pond habitat availability generated for three New England watersheds: the Penobscot, Kennebec, and Androscoggin rivers systems (Hall et al. 2011; Mattocks et al. 2017) due to dam removal policies in the region and to the availability of alewife productivity data (Supporting Information Table S12, Fig. 1). We generated a time-series of alewife biomass productivity as a function of the habitat connectivity and employed the time series as a forcing function for our model. In other words, added biomass is based on production capacity due to increased habitat connectivity.

The built-in Monte Carlo approach was used to test for sensitivity of Ecosim's outputs to Ecopath input parameters (Christensen et al. 2008). The Monte Carlo routine varies Ecopath input parameters using the coefficient of variance provided by the data pedigree to generate confidence intervals (Steenbeek et al. 2018).

Results

Ecopath model results

The fully parametrized Ecopath model was achieved by modifying some of the initial input parameters based on the data pedigree, reflecting the confidence given to the data based on data source certainty. The documentation of the balancing process can be found in the model documentation section of the Supporting Information. The output result shows the biomass flowing from lower to upper trophic levels and the respective flow magnitude between nodes, including fisheries (Fig. 3). PREBAL diagnostic results indicated a model with realistic parameter outputs (Supporting Information Fig. S1). We also calculated the variance of estimates based on the data pedigree using the ensemble routine at ecopath_matlab (Supporting Information Figs. S2–S5). Multistanza plots show

total population biomass in relation to each age group and calculated total mortality throughout the life history (Table 2, Supporting Information Fig. S6).

Ecosim scenario results

We observed a biomass density increase of 27%, 17%, and 34% for all forage species for scenarios 1, 2, and 3, respectively (Fig. 4). We observed 8, −1%, and 280% biomass changes for the anadromous alosine group for scenarios 1, 2, and 3, respectively (Fig. 4). The third scenario resulted in a final biomass per unit area of 0.58 mt.km^{-2} (Figs. 5 and 6). Atlantic herring presented a final biomass per unit area of 17.5 mt.km^{-2}, 16 mt.km^{-2}, and 18.1 mt.km^{-2} for the 1, 2, and 3 scenarios, respectively (Figs. 4 and 5). Except for the shrimp functional group, the remaining forage species showed reductions for all scenarios (Figs. 4 and 6).

Among forage fish predators, groundfish species (large and medium Atlantic cod, large hake, haddock, and yellowtail flounder and summer flounder) increased 149%, 105%, and 110% in total biomass per unit area, respectively, for the three

scenarios. The groundfish functional groups, however, had different responses for each scenario. Large and medium Atlantic cod size classes and haddock performed better in scenario 1, obtaining final biomass densities of 0.89 and 1.02 mt. km^{-2}. Large hake showed an increase of 91.5% under scenario 2, resulting in a biomass per unit area of 0.1 mt.km^{-2}. Summer flounder had its best response to scenario 3, with a biomass per unit area in the year 2050 of 0.06 mt.km^{-2}, a 36% increase from the baseline scenario (Fig. 7). Yellowtail flounder biomass densities decreased in all three scenarios (15%, 4%, and 3% decrease for scenarios 1, 2, and 3; Fig. 7).

For species of concern (odontocetes, baleen whales, pelagic sharks, pinnipeds, seabirds, and highly migratory large pelagics), the second scenario presented the highest biomass density change, with a total increase of 19% against 15% for the first scenario and 13% for the third. The total percent change for each group is shown in Fig. 4. The marine mammals, odontocetes, and pinnipeds had similar responses, with scenario 2 performing the best, followed by scenario 1, then 3. Baleen whales were negatively impacted by scenarios 2 and
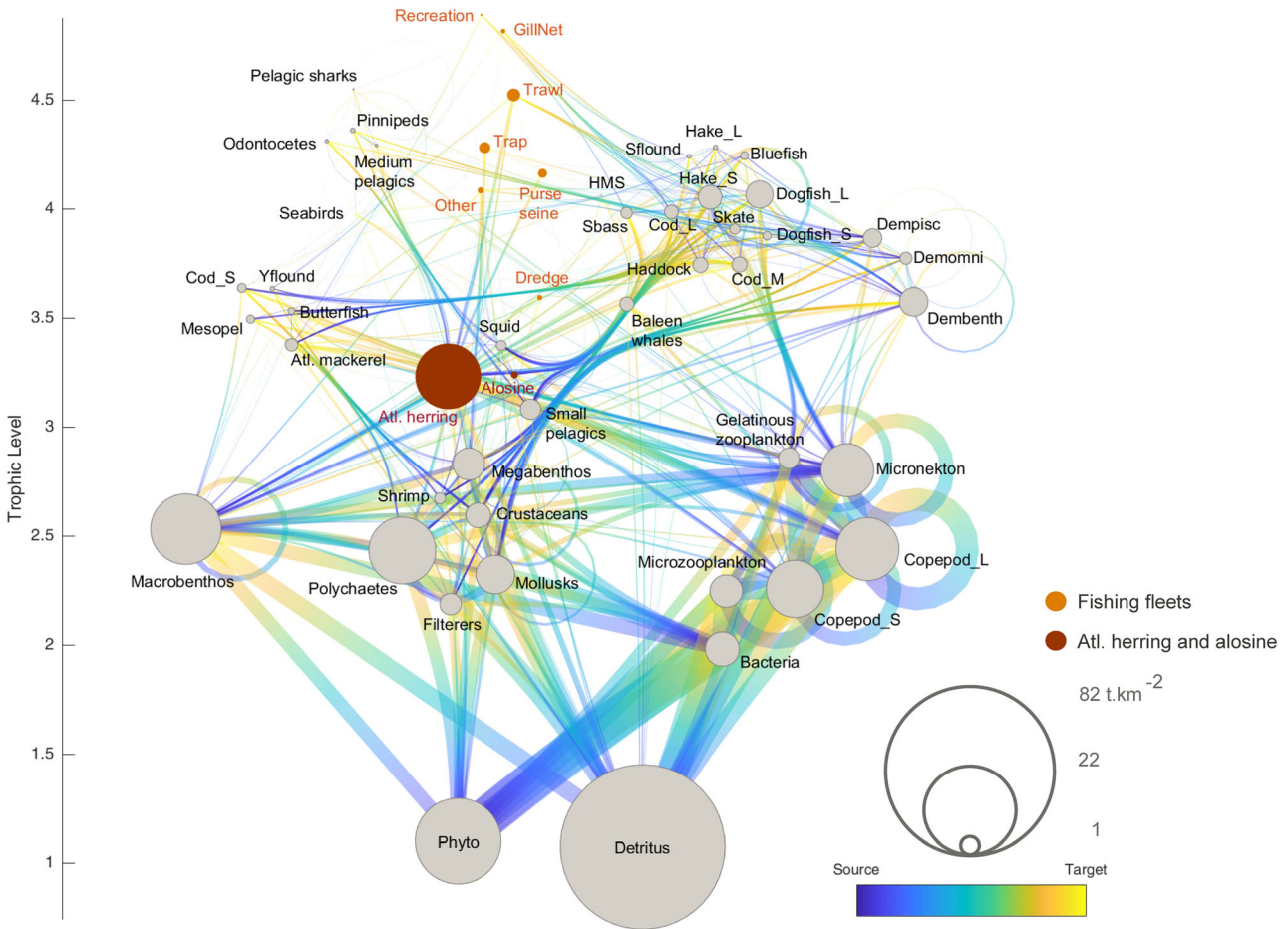

Fig 3. Flow diagram of the Gulf of Maine ecosystem. Fishing gears are shown in orange, Atlantic herring and alosine are represented by maroon. Line thickness represents the magnitude of biomass flow from prey, in blue, to predator in yellow. Bubble sizes represent the tonnage per square kilometer. Nodes are grouped by predator/prey overlap index.

Table 2. Model inputs and outputs for the balanced Ecopath Gulf of Maine model. TL indicates trophic level, *B* is the biomass, *Z* is total mortality for the multistanza categories, *P/B* the production ratio, *Q/B* the consumption ratio, EE the ecotrophic efficiency, and *P/Q* the production to consumption ratio. Output values, in bold, were calculated by Ecopath.

| Node	Group name	TL	*B* (t.km^{-2})	*Z* (yr^{-1})	*P/B* (yr^{-1})	*Q/B* (yr^{-1})	EE (yr^{-1})	*P/Q* (yr^{-1})
1	Phytoplankton	1.000	22.126		163.143		**0.665**	
2	Bacteria	2.000	3.452		91.250	**182.500**	**0.929**	0.500
3	Micro-zooplanktons	2.297	3.158		72.000	242.424	**0.919**	**0.297**
4	Copepod-S	2.124	9.879		30.918	127.750	**0.949**	**0.242**
5	Copepod-L	2.405	11.955		35.000	109.500	**0.863**	**0.320**
6	Gelatinous zooplankton	3.063	1.283		35.000	146.000	**0.950**	**0.240**
7	Micronekton	2.922	8.357		14.250	36.500	**0.718**	**0.390**
8	Macrobenthos polychaetes	2.493	13.492		2.550	17.500	**0.864**	**0.146**
9	Macrobenthos crustaceans	2.769	1.835		3.300	21.000	**0.956**	**0.157**
10	Macrobenthos mollusks	2.305	4.491		2.240	13.720	**0.932**	**0.163**
11	Macrobenthos others	2.530	15.000		2.040	11.777	**0.939**	**0.173**
12	Megabenthos filterers	2.119	1.400		0.864	10.000	**0.987**	**0.086**
13	Megabenthos others	3.126	3.037		1.680	11.030	**0.918**	**0.152**
14	Shrimp	2.915	0.369		2.000	5.000	**0.988**	**0.400**
15	Mesopelagics	3.683	0.200		0.950	1.825	**0.921**	**0.521**
16	Atl. herring	3.384	12.987		0.370	1.978	**0.852**	**0.187**
17	Alosine	3.394	0.153		0.437	2.000	**0.945**	**0.219**
18	Atl. mackerel	3.512	0.477		0.520	3.826	**0.854**	**0.136**
19	Squid	3.537	0.300		1.400	2.000	**0.897**	**0.700**
20	Butterfish	3.712	0.140		1.270	1.977	**0.925**	**0.642**
21	Small pelagics	3.177	1.240		0.849	2.000	**0.936**	**0.425**
22	Bluefish	4.485	0.193		0.349	2.106	**0.787**	**0.166**
23	Striped bass	4.172	0.012		0.491	2.300	**0.878**	**0.213**
24	Dogfish-S	3.961	0.210	0.130		3.820	**0.787**	**0.034**
25	Dogfish-L	4.130	2.246	0.150		1.810	**0.157**	**0.083**
26	Cod-S	3.822	0.226	0.870		4.460	**0.957**	**0.195**
27	Cod-M	3.877	0.692	0.720		2.256	**0.396**	**0.319**
28	Cod-L	4.113	0.559	0.980		1.500	**0.155**	**0.653**
29	Haddock	3.795	0.689		0.450	0.905	**0.390**	**0.497**
30	Hake-S	4.040	1.696	0.935		3.850	**0.753**	**0.243**
31	Hake-L	4.487	0.056	1.000		2.361	**0.739**	**0.424**
32	Yellowtail flounder	3.813	0.051		0.670	2.900	**0.906**	**0.231**
33	Summer flounder	4.475	0.045		0.483	2.900	**0.890**	**0.167**
34	Skate	3.951	0.316		0.450	0.905	**0.229**	**0.497**
35	Demersal benthivorous	3.678	2.454		0.450	0.905	**0.696**	**0.497**
36	Demersal piscivorous	3.997	1.047		0.550	1.213	**0.996**	**0.453**
37	Demersal omnivorous	3.858	0.450		0.450	0.814	**0.877**	**0.553**
38	Medium pelagics	4.400	0.023		0.649	1.428	**0.787**	**0.454**
39	Pelagic sharks	4.783	0.004		0.150	0.623	**0.817**	**0.241**
40	Highly migratory large pelagics	4.236	0.018		0.500	2.362	**0.002**	**0.212**
41	Pinniped	4.466	0.063		0.067	4.850	**0.016**	**0.014**
42	Baleen whales	3.584	0.602		0.042	2.300	**0.001**	**0.018**
43	Odontocetes	4.425	0.034		0.040	8.500	**0.438**	**0.005**
44	Seabirds	3.931	0.004		0.275	5.362	**0.069**	**0.051**
45	Detritus	1.000	81.333				**0.494**	
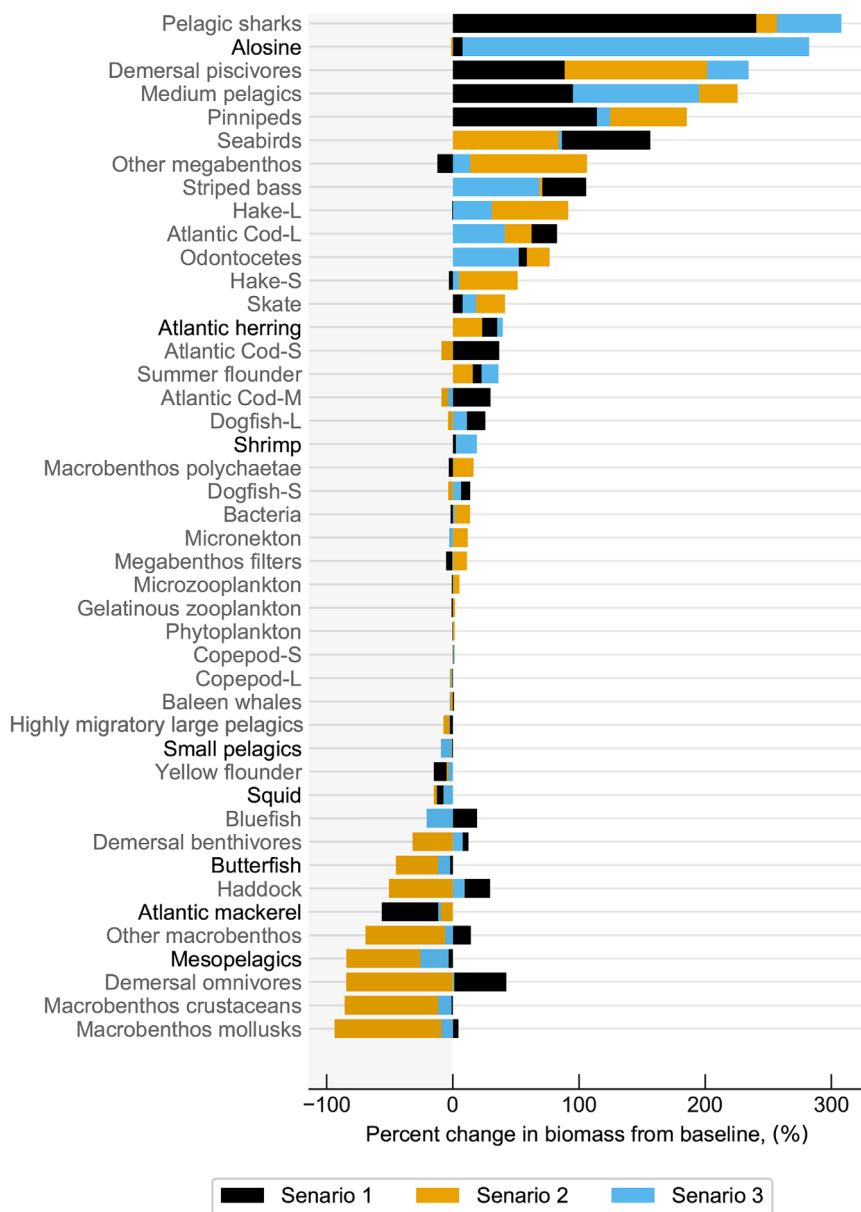
Fig 4. Percentage change among the three different scenarios. Midpoint (0) is the baseline Ecopath model using year block 2000, and the percent change is for the last year of the simulation. Functional groups are ordered from the greatest increase (top) to greatest decrease (bottom) in biomass per unit area, with the shaded area signifying negative density changes. Forage fish species are in black. The bars are overlapping.

3, showing biomass density decreases of around 2%, whereas for scenario 1 they showed a 1% increase from the baseline value (Figs. 4 and 8). Seabirds presented positive change under all three scenarios. Scenario 1 was the leading scenario for this functional group, with a biomass density increase of 156%, followed by scenario 3 with 86% and scenario 2 with 83% (Fig. 4). The biomass density of highly migratory large pelagics decreased by 2% for scenarios 1 and 3% and 7% for scenario 2. For the Monte Carlo routine from 100 trial runs for the first and second scenarios, 57 and 48 were successful trials that generated balanced models, while in 200 trial runs for the third scenario, 12 were successful (Supporting Information Figs. S7–S17).

Discussion and conclusions

Overview and synthesis

The alosine functional group demonstrated little response to fishing effort changes, but when increased habitat connectivity was combined with fishing effort reduction, a multiple order of magnitude biomass density increase was generated. This suggests that river to ocean habitat connectivity, captured in the models as a forcing function, will be more effective in recovering alosine populations. The final alosine biomass was estimated to be equivalent to 1830s levels; when 25% of lakes and ponds in three Maine watersheds remained
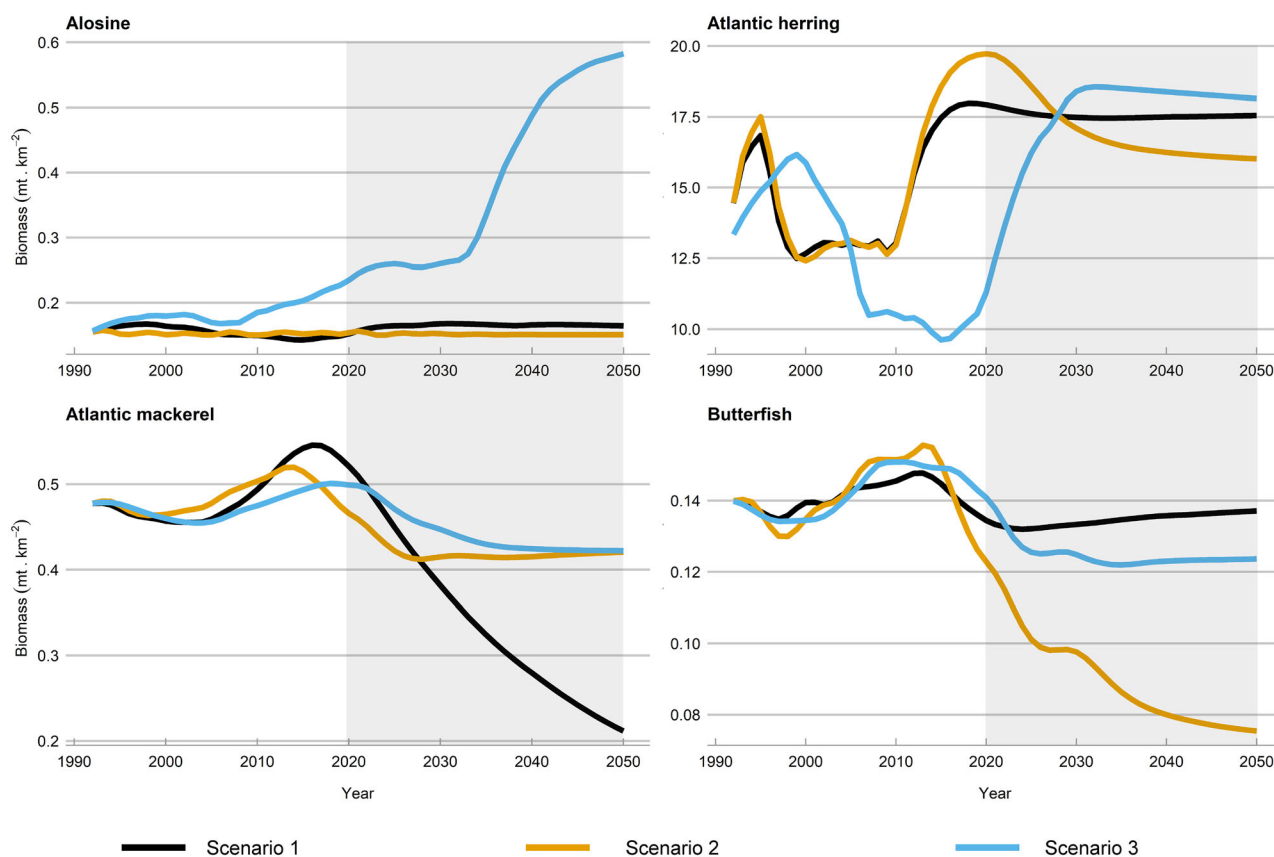
Fig 5. Forage fish functional group responses to the three different scenarios. The scenarios are represented by lines: Fishing scenario 1 in black, fishing effort reduction scenario 2 in yellow, and fishing effort reduction combined with alewife biomass restoration scenario 3 in blue. Shaded areas indicate the years simulated in the scenarios. Y-axis present different scales.

fully accessible to river herring, the response could be much greater if restoration of an entire watershed or across more watersheds occurred. These numbers are modest, realizing only a partial restoration of riverine connectivity equivalent to the 19th century and only a subset of available watersheds. A bolder restoration goal would restore access to all watersheds. Assuming productivity is equal in small and large systems, it would increase biomass gains over those observed in the current simulations.

Atlantic herring was the only forage fish that increased in all scenarios. This highlights the importance of fishing effort controls as a tool to increase stock biomass. Also, Atlantic herring is the main contributor to small pelagic fisheries' landings and predators in the region. Atlantic herring is the only planktivorous species managed by the New England Fishery Management Council and the focus of high levels of predation in an ecosystem that relies on them as a key forage fish (Dias et al. 2019). According to our scenarios, Atlantic herring would benefit from a fishing effort reduction and increased overall forage base biomass through increased habitat connectivity for anadromous forage fish. Decisions regarding the two management levers, habitat connectivity and fishing effort

reduction, hinge on the costs and benefits of actions, including impacts to the socioeconomic system that utilizes the Gulf of Maine resources.

The remaining forage species groups, except for Atlantic herring, had the worst performance in scenario 2, where effort was reduced for all commercial fisheries. The Gulf of Maine ecosystem contains intricate trophic relationships and interactive effects, and indirect effects of fisheries and restoration decisions will propagate across trophic levels manifesting in potentially adverse outcomes. Effort reduction resulted in increased piscivore biomass density, and a decrease in forage species biomass density followed. Restoration of river herring habitat, on the other hand, provides additional biomass that alleviated predation on the limited forage fish pool (Dias et al. 2019). These indirect effects, and whether they run counter to management actions, differentiated the effort-based and restoration scenarios and supported the latter in providing the result of increasing alosine biomass. To ensure species' sustainability might require more than effort-based fisheries management actions, particularly in mixed-species fisheries, with consideration of habitat productivity and ecosystem linkages as critical underpinnings.
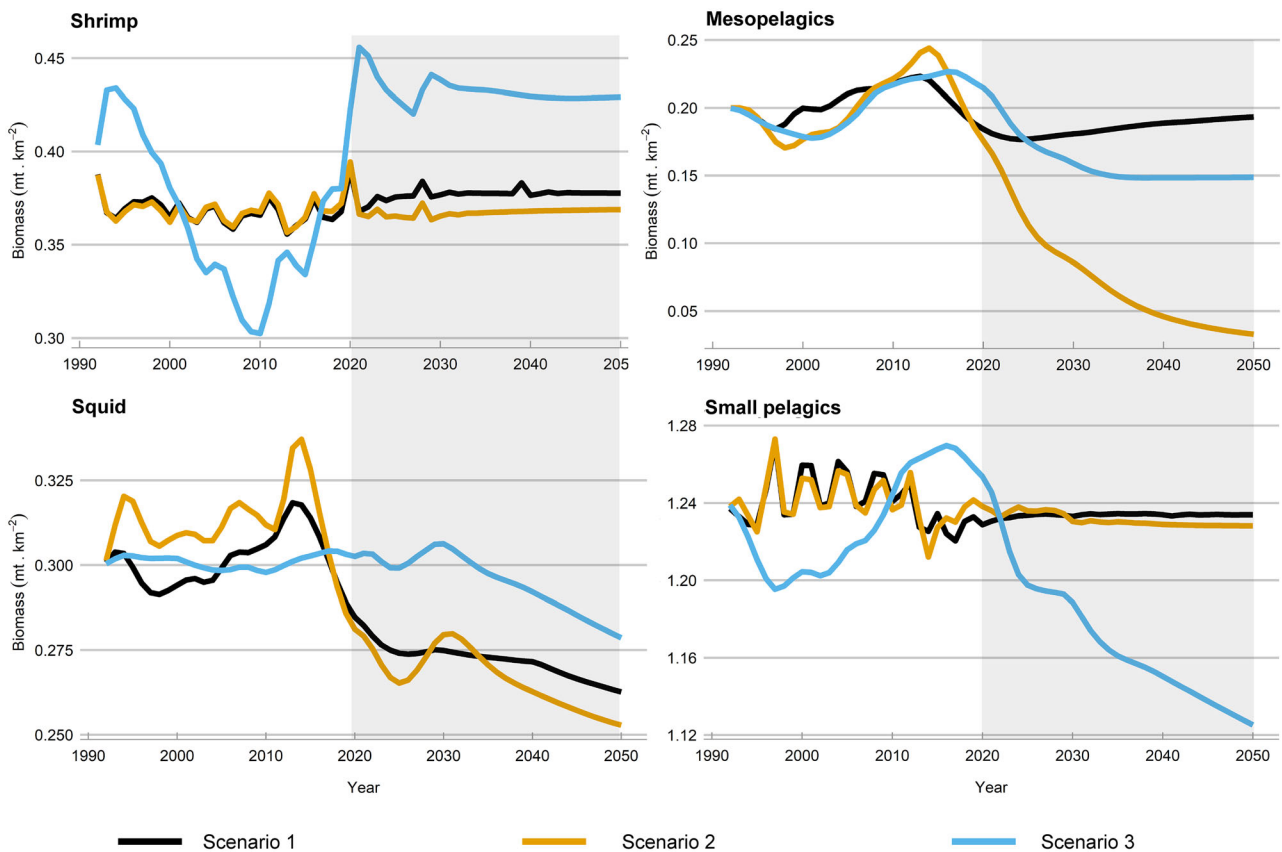
Fig 6. Continuation of the forage fish functional groups and their responses to the three different scenarios. The scenarios are represented by lines: Fishing scenario 1 in black, fishing effort reduction scenario 2 in yellow, and fishing effort reduction combined with alewife biomass restoration scenario 3 in blue. Shaded areas indicate the years simulated in the scenarios. Y-axis present different scales.

Similar trophic-related shifts were observed in Scenario 1, which reduced effort in alosines fisheries, had the most pronounced positive impact on the groundfish complex and medium and large Atlantic cod and haddock. Groundfish stock status recommendations for the 19 stocks show that 10 stocks are overfished, and four are experiencing overfishing (NEFSC, 2017) while haddock among several species are at historical high biomasses. These imbalances are resulting in forgone fisheries production. For the Gulf of Maine region, Atlantic cod and yellowtail flounder are well below target biomass levels (NEFSC, 2017). Yellowtail flounder experienced biomass fluctuations during the simulation period; however, the scenarios' final year showed a minor decrease. The demersal piscivore group increased substantially, likely due to a broad diet and the additional flow of energy across the mid-trophic levels. Shifts in diet and spatial variability of predation on alosines would also impact their recovery (Ames and Lichter 2013). Therefore, future studies need to consider predators' dietary flexibility and spatial dynamics.

For species of conservation concern, each of the scenarios presented over 500% biomass density increases, with pelagic sharks providing the largest contribution. Except for baleen whales and highly migratory large pelagics, all the other species of concern functional groups exhibited major biomass changes by the end of the simulation. Odontocetes, pinnipeds, and sea birds rely on forage fish as primary dietary items, therefore increasing the forage base during the simulation period might be responsible for the increase in these functional groups. This also suggests that most predators are unlikely to demonstrate strong interactions with a single forage species, consistent with recent research (Hilborn et al. 2017). Decreasing pelagic fisheries had only muted effects on many other taxa, thus it may not be possible to assume a specific predator response while multiple management objectives are in play, and system-wide responses will be hard to measure or anticipate. Further, trade-offs exist in management decisions involving each of fisheries and restoration actions to promoting alosine recovery that need to be considered during decision making.

Overall, our results demonstrate the nonlinear nature of the Gulf of Maine marine ecosystem in response to different management actions. Nonlinearity is an intrinsic component of historical and contemporary aquatic ecosystems due to the complex nature of trophic interactions and responses to
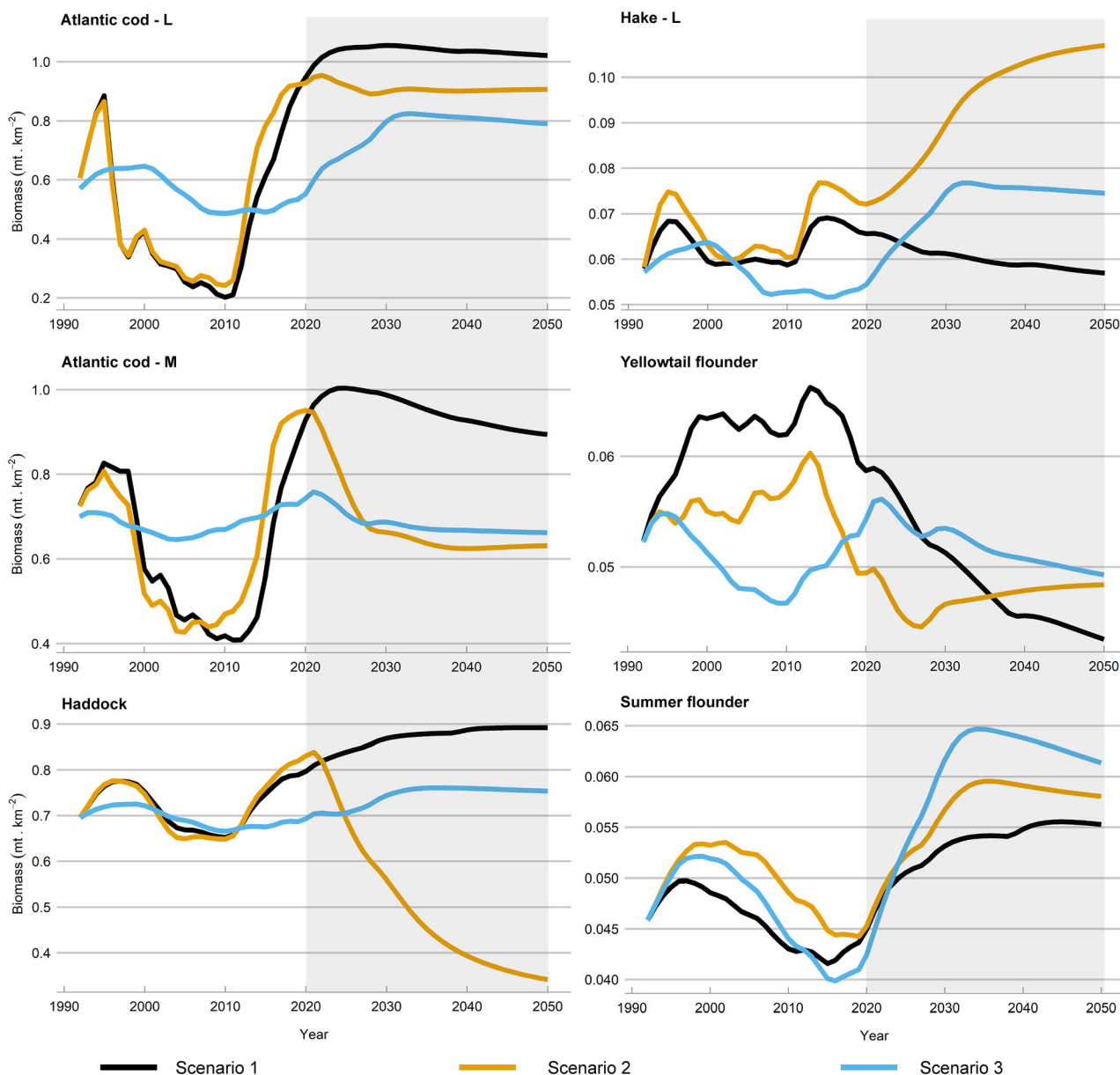
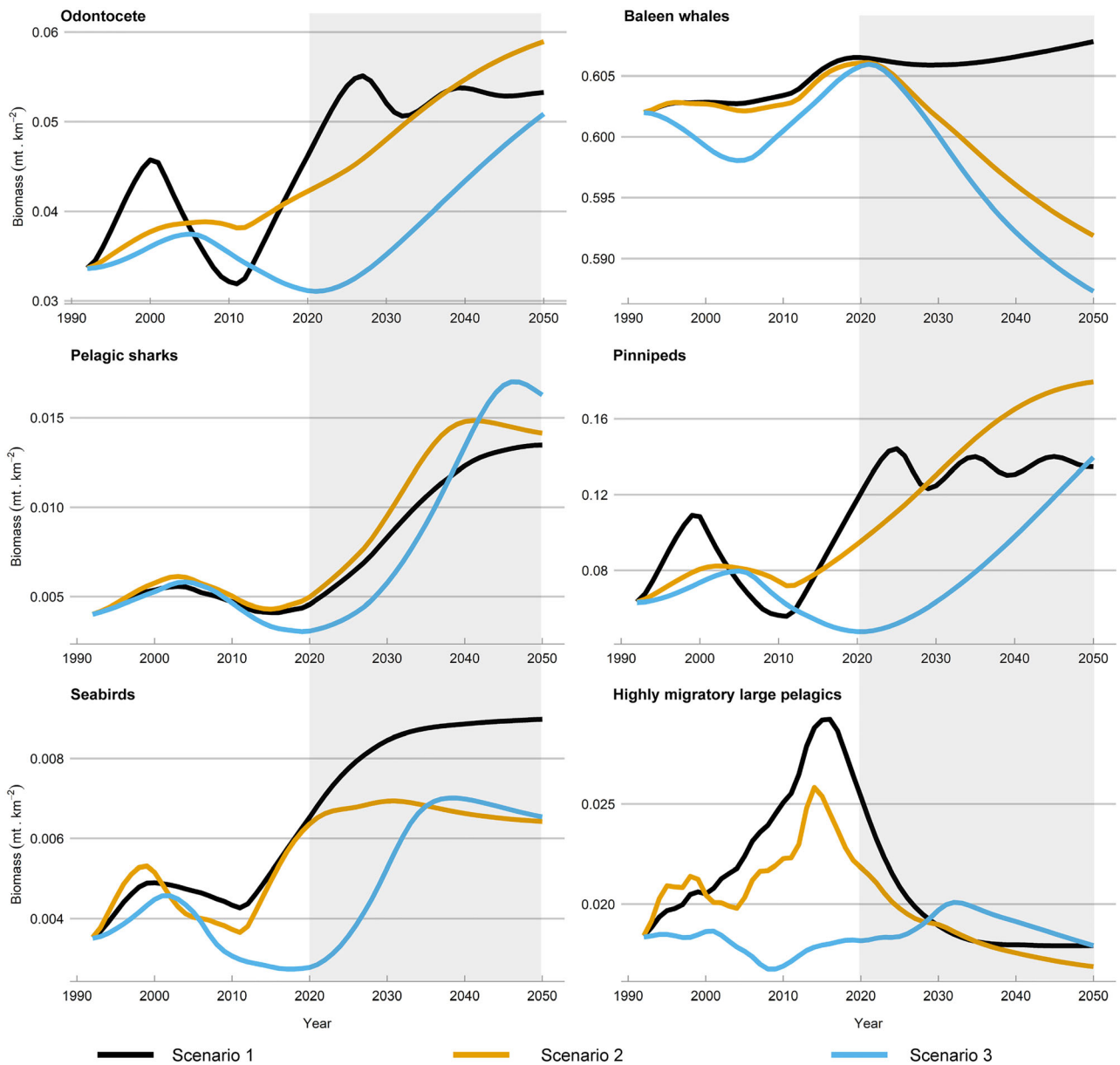**Fig 7.** The groundfish complex responses to the three different scenarios. The scenarios are represented by lines: Fishing scenario 1 in black, fishing effort reduction scenario 2 in yellow, and fishing effort reduction combined with alewife biomass restoration scenario 3 in blue. Shaded areas indicate the years simulated in the scenarios. Y-axis presents different scales.

physical forcing (Klein et al. 2016). Our simulations demonstrated significant variability in species level responses even within scenarios, except for habitat forcing impacts on alosines. Once the response of restoration in the form of alosine biomass enters the food web, other stressors such as fishing and climate (Staudinger et al. 2019) will modify the response driving less predictable outcomes at the species level. A better understanding of diets and seasonal movements would help remove some of the uncertainty. Still, the consequences of a large habitat restoration effort are likely to be positive across the system, particularly for associated species.

For example, in the present simulations, herring benefitted from the diversification of the prey base and a suite of predators associated with alosines. These positive outcomes achieved multiple conservation and restoration goals, but they will likely be harder to measure on a species-by-species basis over the shorter timescale employed in management decision-making.

Impacts of river to ocean connectivity

Habitat connectivity can act as a forcing function in ecosystems, impacting different species through trophic interactions

Fig 8. Species of concern responses to the three different scenarios. The scenarios are represented by lines: Fishing scenario 1 in black, fishing effort reduction scenario 2 in yellow, and fishing effort reduction combined with alewife biomass restoration scenario 3 in blue. Shaded areas indicate the years simulated in the scenarios.

as the abundance and vulnerability of prey to predators changes. Yet, alosine biomass restoration comes with a cost, as increasing river to ocean connectivity requires a modification of current infrastructure, impacting energy production, water supply, and flood management (Roy et al. 2018). These costs can be significant, particularly when contrasting river passage for anadromous fish with associated uncertainty and difficulty quantifying biomass changes and ecosystem-wide effects. Infrastructure needs and ecological restoration can be achieved with a balanced approach, examined case by case, as the outcomes are often nonlinear (Roy et al. 2018). The

Penobscot River has been under restoration and, as a result, alosine fishes have experienced pronounced population changes after dam removal (Watson et al. 2018), with blueback herring experiencing the greatest benefit. Without alterations to fish passage in the Penobscot River, alewife spawners would have faced a decrease of 90% in abundance (Song et al. 2019). Thus, under the right circumstances dam removal and fish passage improvements can help achieve similar and synergistic outcomes. The benefits of anadromous species recovery, in turn, impact many key freshwater, estuarine and marine species that currently require restricting human

activities and active management to conserve their populations. Thus, while river infrastructure modifications can be costly, substantial ecological benefits to freshwater and marine food webs exist by providing connectivity to the upper parts of watersheds (Mattocks et al. 2017). Increased resilience of species to natural and anthropic disturbances (Waldman et al. 2016) can translate into revenue for recreational and commercial fisheries, and reduced regulations on restricted activities.

Anadromous fishes rely on multiple habitats throughout their life histories, therefore increased habitat connectivity provides watershed-level habitat complexity that is fundamental to a resilience-based approach (Waldman et al. 2016). Dams impact anadromous fish both through lost connectivity and by altering freshwater systems' physical characteristics (Schmidt and Wilcock 2008). For example, sediment and contaminant transport, and the creation of riverine and estuarine marsh habitat are important additional habitat concerns of dams and their removal (Kondolf et al. 2014). Thus, the full impact of dam removal on the improvement of a variety of habitats is not accounted for, and neither is any of the anticipated changes from climate change. It is important to note that we analyzed the potential of restoration of just three watersheds and one of the three species in the alosine group. Our model underestimates the true potential of restoring the entire alosine group through opening ocean–river–lake connectivity. Unfortunately, habitat data is not available to accurately estimate the improvements for American shad and blueback herring. Still, the example of the Penobscot River, where dam removal benefitted blueback herring even as lake habitat remained inaccessible demonstrates that improved connectivity along any of the marine freshwater continuum increases alosine species abundance due to different life history and habitat requires of the three species.

Impacts of fisheries

Management decisions involving forage species fisheries can lead to trade-offs among different fishing sectors. For example, in the California Current, increased fishing effort targeting forage species led to higher revenue for the sector, but it also impacted the catch of apex predators (Koehn et al. 2017). Although riverine habitat connectivity is the main driver of anadromous fish population losses, marine mortality was found to be a highly sensitive parameter in alewife population estimations (Barber et al. 2018). Part of marine mortality results from bycatch in the Atlantic herring and mackerel fisheries, thus a reduction of fishing effort benefits the target species and anadromous alosine stocks. Directed harvest in Maine rivers continues under river specific plans that consider the productivity of each system and are primarily used as bait in the lobster fishery. In the case of trade-offs among fisheries in the Gulf of Maine related to river herring, only reductions of in-river harvest would reduce catch while not impacting fisheries for other species. Moreover, fisheries

reductions as part of this modeling exercise did not affect alosine biomass at the same scale as increased connectivity.

Decreased fishing effort produces variable responses by different functional groups, as shown in the current study. Obtaining fishing effort information at a finer resolution and further separating fleets would allow the exploration of species-specific management strategies in more detail, including the efficacy of area-based management approaches such as spawning closures and marine protected areas. The coarse fishing effort data we had available produced a moderate positive impact on Atlantic herring and groundfish biomass driven by fishing effort reduction. The loss of access to Atlantic herring and alosines fisheries through moratoria would have consequences for bait-dependent fisheries, including American lobster, which would see increased costs and precipitate the need for sourcing of alternatives. The impacts would be wide-ranging and particularly challenging for several fisheries in the Gulf of Maine and the processors and communities that depend on them.

Management moving forward

Marine food webs support ecosystem goods and services, including those that anadromous fish provide (Limburg and Waldman 2009). Forage fish species should be managed with the goal to maintain a target system biomass, as they fill similar niches and are vulnerable to similar anthropogenic stressors in the marine ecosystem. Future stressors can influence the diversity within functional groups, and the temporal stability of ecosystem functioning leading to decreases in flow of energy that support important ecosystem services, including species' intrinsic productivity and population parameters (Hooper et al. 2005; Burgess et al. 2019; Dias et al. 2019). A portfolio-based approach to forage fish management can help provide resilience to these stressors, including climate change. Anadromous fishes in the alosine node have strong phenological responses to physical processes, as they enter riverine habitat during the spring and exit in the summer and fall (Staudinger et al. 2019). These different responses provide for opportune predation that can produce migratory coupling (Furey et al. 2018).

Anadromy provides a distinct life history trait to the forage complex that complements fully marine species, since recruitment is driven by different physical processes and over different scales. Atlantic herring reproduction is generally limited to the eastern Gulf of Maine and is likely a function of oceanographic processes, while alosine are ubiquitous in coastal streams and rivers along the Atlantic seaboard and recruitment is likely influenced by precipitation and other landscape factors. Restoring lost biomass of some of the forage fish complex (such as the anadromous parcel) will promote the Gulf of Maine marine ecosystem forage base redundancy and niche-based portfolio effect, which links productivity with complementary stocks (Clausen et al. 2018; Dias et al. 2019). Thus, while a forage fish complex in terms of management is

conceptually intuitive, it is still important to account for inter-annual differences in the productivity, recruitment and natural mortality of specific stocks and species (Dickey-Collas et al. 2014; Clausen et al. 2018), but with an eye to maintenance of sufficient flow through mid-trophic level to support the ecosystem's broader fisheries management and restoration goals. At the same time, one must recognize regime shifts that occurred in marine food webs that arose from the era of damming and estuarine habitat loss, which will likely be hard to reverse.

Management decisions should take into consideration the complementarity of forage fish species, and set goals towards a sustained overall biomass, while considering each species dynamics. Reinstating trophic networks for the delivery of ecosystem services is a means to provide resilience to anticipated climate changes (Perring et al. 2015). Species of concern such as sea birds showed nonlinear responses to changes in prey, highlighting the importance of keeping management goals to ensure sufficient forage fish biomass for these species and for less studied predators in marine systems (Cury et al. 2011). There is a lack of forage base redundancy in the Gulf of Maine ecosystem (Dias et al. 2019), and loss of additional functional redundancy could lead to decreased resilience to additional stressors such as climate change, stock collapses and the natural variability present in forage fish populations (Burgess et al. 2019; Dias et al. 2019). Atlantic herring is the main forage species for a broad suite of predators in the Gulf of Maine. Thus, recent low recruitment and likely return to an overfished status raises concerns regarding the consequences of losing biomass of a key forage fish group.

In considering possible outcomes, it is important to consider a few assumptions made when interpreting results. First, we allowed the vulnerability parameters to be estimated during model fitting. Forage fishes' ability to avoid predation is species and context specific with predator avoidance contributing to variability in vulnerability (Scharf et al. 2003). At the same time, predators in the Gulf of Maine exhibit flexibility in their feeding behavior and may respond to the increase of alosines by increasing the consumption of these prey (McDermott et al. 2015). Therefore, we believe our assumptions were compatible to the complexity of prey–predator interactions in the system. As changing abundances and the role as oddity (Almany et al. 2007) appear to play important roles in some systems, these factors should be explored in future work and are beyond the scope of this research. Further ecosystem modeling using different approaches that adapt field testing of changing vulnerability would be a valuable addition. Further, adapting the results into a framework such as marine strategy evaluation would allow scenario evolution to provide more specific recommendations and allow stakeholders to better appreciate potential outcomes of regulations and restoration.

To achieve anadromous fish recovery, management strategies must identify the major threats and design strategies that consider all the different habitats that these versatile fish use throughout their lives. Improved riverine habitat connectivity and reduction in fisheries effort provided the best management results for alosines. We are still filling the gaps regarding impacts on other species within the anadromous forage fish functional group. Moreover, the consequences of management actions will impact different parts of the society and economic groups. Fisheries closures will adversely affect coastal communities with loss of revenue and support services, due to reduced catches. Increased river to ocean habitat connectivity will alter recreational uses and energy production in freshwater. However, considering river restoration within the framework of infrastructure needs, and adopting changes that promote connectivity will lead to widespread improvement of freshwater and marine ecosystems. Finally, it is important to recognize that the increased connectivity presented here is an analogue for improved or restored habitat that provides for increased productivity of forage species. Thus, similar positive impacts are likely to follow from other forms of habitat restoration that increase the diversity of species, including coral and seagrass habitats that support many juvenile stages and smaller bodied fish species. The improvement of habitat and increased connectivity of systems will in turn provide for a system with greater resilience to changes for future generations.

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Conflict of Interest

None declared.