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ARTICLE

Modeling Predator–Prey Linkages of Diadromous Fishes in an Estuarine Food Web

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Abstract

Historically, multiple species of diadromous fishes served as a coastal food source for commercially valuable nearshore predators. However, severe declines in diadromous fish populations in the nearshore Gulf of Maine (GOM) have impacted trophic dynamics and increased pressure on other estuarine-dependent forage resources. The objective of this study was to compare the trophic positions and interspecific interactions of diadromous fishes as predators and prey in relation to current GOM forage fishes. Empirical biomass data along with diet compositions and vital rates were used to construct a static model of a representative GOM coastal food web: the Saco River estuary (SRE) in Maine. A series of sensitivity analyses based on model outputs was performed to determine the trophic role of diadromous fishes in this estuarine food web. Model results suggested that juvenile marine transients played a greater role as forage species for SRE predators than did the anadromous Blueback Herring *Alosa aestivalis* and Alewife *Alosa pseudoharengus*. Due to the abundant forage fish base, Atlantic Sturgeon *Acipenser oxyrinchus* and Shortnose Sturgeon *Acipenser brevirostrum* were estimated to have a greater trophic position than reported in past literature. Lower-trophic-level fishes functioned as keystone prey species for sturgeon. The use of holistic approaches to update the ecological data on predator–prey interactions among diadromous fishes and forage resources within coastal ecosystems is necessary for the future management of these ecologically significant and threatened species.

In freshwater, estuarine, and marine environments, diadromous fishes provide key ecosystem services as predators, prey, and competitors (Limburg and Waldman 2009). As part of their life cycles, diadromous fish species import nutrients to upstream areas (Saunders et al. 2006) and export energy to marine food chains (Walters et al. 2009). In the Gulf of Maine (GOM) and associated New England river systems, diadromous fishes like river herring (Alewife *Alosa pseudoharengus* and Blueback Herring *Alosa aestivalis*) traditionally serve as food sources for commercially important coastal predators, such as Atlantic Cod *Gadus morhua* and harbor seals *Phoca vitulina* (Ames 2004; Fogarty 2007; McDermott et al. 2015). Diadromous fishes support important trophic interactions in riverine food webs as prey for higher-trophic-

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level species, such as the osprey *Pandion haliaetus*, double-crested cormorant *Phalacrocorax auritus*, and North American river otter *Lontra canadensis* (Mather 1998; Saunders et al. 2006). Within an estuary, young-of-the-year (age 0) emigration and adult spawning immigration can impact the population dynamics of predator and prey communities (Schindler et al. 2003; Walters et al. 2009; Trinko Lake et al. 2012). Migratory diadromous predators, such as the Striped Bass *Morone saxatilis*, transfer biomass across a series of estuarine systems, thereby helping to maintain connectivity and trophic structure across systems (Mather et al. 2013).

In addition to their ecological value, diadromous fishes serve as economically valuable and culturally important resources for historic and present-day coastal communities in the GOM (Link 2002; Hall et al. 2012). Despite their significance, most diadromous fish stocks have been depleted to a mere fraction of their historical abundance (Trinko Lake et al. 2012; Willis et al. 2013). Observed declines have been attributed to coastal development and pollution (Hall et al. 2012), overharvest, bycatch, and marine predation (Davis and Schultz 2009). The greatest factor impacting diadromous populations remains the fragmented access to spawning habitat, which is attributable to the damming of rivers (Saunders et al. 2006). In response to these declines, multiple diadromous species in the GOM are federally listed as endangered (Atlantic Salmon *Salmo salar* and Shortnose Sturgeon *Acipenser brevirostrum*) or threatened (Atlantic Sturgeon *Acipenser oxyrinchus*), are designated as National Oceanic and Atmospheric Administration (NOAA) species of concern (Alewife, Blueback Herring, and Rainbow Smelt *Osmerus mordax*), or are ecologically absent from many river systems (Saunders et al. 2006; ASSRT 2007).

For current management considerations of diadromous fishes such as river herring, it is necessary to quantify nearshore food web dynamics (Wilson et al. 2009; McDermott et al. 2015). The recent Endangered Species Act status review of river herring highlighted a need for increased research on predator–prey relationships due to the river herrings' historic importance as forage resources for commercially important predator species (NMFS 2013). Altered metapopulation structure of Atlantic Cod and other gadids in the nearshore GOM has been attributed to the substantial decline in abundance of age-0 Alewives. Although alternative forage (e.g., juvenile lobsters, echinoderms, mollusks, annelids, and Atlantic Herring *Clupea harengus*) has persisted during this collapse, river herring are hypothesized to be preferred as prey items (Ames and Lichter 2013).

Given the depressed population status of multiple diadromous fish species in the nearshore GOM, the main objective of this study was to investigate current trophic relationships of diadromous fishes in estuarine food webs. Traditional methods that have been used to describe the foraging ecology and predation rates of highly migratory pelagic fishes (e.g., diadromous species) remain challenging (Hunsicker et al. 2011). To describe trophic structure, trophic positions are conventionally estimated from gut contents. However, fish are highly omnivorous and can occupy multiple trophic levels (Odum and Heald 1975; Pimm 1982; Marsh et al. 2012). Trophic position can vary naturally due to ontogenetic shifts and can vary over spatial scales due to annual and seasonal changes in food supply (Marsh et al. 2012). Thus, to account for this variability, it is important to examine the mean trophic level and the variation from the mean throughout a species' geographic range (Branch et al. 2010).

We utilized an ecological modeling framework to explore these interactions in a representative coastal river system: the Saco River estuary (SRE) in Maine. Although multiple ecosystem models have been created for the GOM (Link et al. 2006, J. Link et al. 2008, J. S. Link et al. 2008; Overholtz and Link 2009; Zhang et al. 2012), none has particularly focused on estuaries within the GOM or on diadromous fishes. A static ecosystem model was used to estimate the trophic levels and determine the interspecific linkages of diadromous fishes in an estuarine network where they interact with marine and freshwater species. Our specific focus was to investigate interactions between diadromous fishes that occupy lower trophic levels as forage (i.e., river herring) and nondiadromous fish species (e.g., juvenile marine transients) that use estuaries as nursery grounds. In addition, by using a series of sensitivity analyses (e.g., Byron et al. 2011), we (1) evaluated the direct and indirect impacts of modeled species groups on each other, and (2) estimated the ranks of individual compartments as keystone species.

STUDY AREA

A static food web model was created for the SRE (43° 27.5′N, 70°22′W), a coastal river system located in Biddeford and Saco, Maine (Figure 1). The SRE is a partially mixed, temperate estuary that extends approximately 10 river kilometers. Tidal flats, fringing marshes, and bedrock bluffs border the main stem of the river. The estuary floor is characterized by wide, shallow regions, deepening where the channel narrows, with fine- to coarse-grain sand and mud sediments (Kelley et al. 2005). Local communities utilize the SRE as an important outlet for recreation and tourism. Baseline environmental monitoring has revealed that this ecosystem is used for nursery and feeding purposes by a diverse bird and fish community, including many federally protected species, such as the anadromous Atlantic Sturgeon and Shortnose Sturgeon (Furey and Sulikowski 2010; Little et al. 2013; Feurt and Morgan 2015).

METHODS

Modeling approach.—The food web model for the SRE was created with Ecopath, the most extensively used ecosystem modeling software for fisheries management (Polovina 1984;

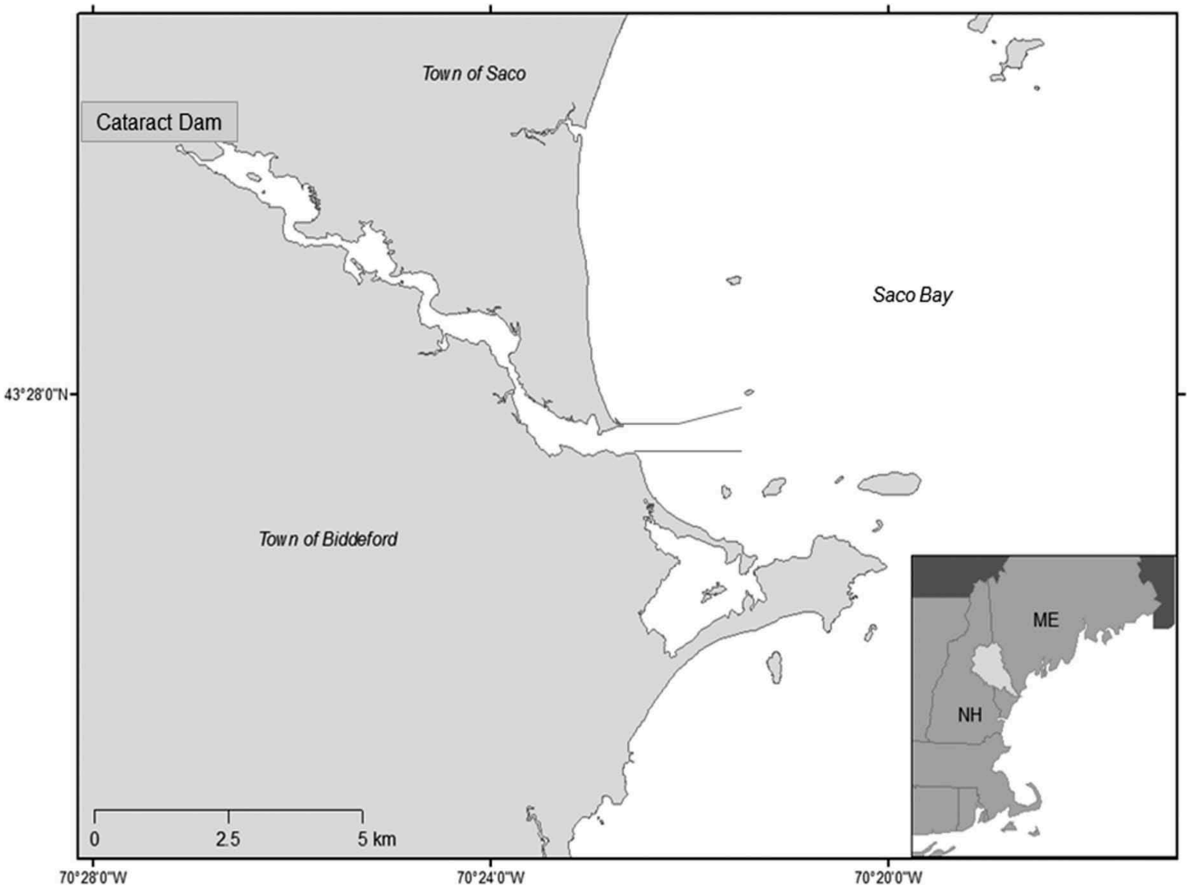

FIGURE 1. Map of the modeled Saco River estuary, Maine. The inset map displays the Saco River watershed in the northeastern USA.

Essington 2007; www.ecopath.org). Ecopath uses a static mass-balance modeling approach to capture flows of energy between species groups within a food web (Christensen and Walters 2004). Two fundamental master equations are used to create an Ecopath model: the first (equation 1) defines a production term for each species group, and the second (equation 2) establishes mass balance based on the principle of conservation of matter (Christensen and Walters 2004; Christensen et al. 2008). The production equation is

$$P_i = \sum_i B_j \cdot M2_{ij} + Y_i + E_i + \mathrm{BA}_i + P_i \cdot (1 - \mathrm{EE}_i), \qquad (1)$$

where P_i is the production of group i; B_j is the biomass of group j, $M2_{ij}$ is the predation rate for group i, Y_i is the total fishery catch of group i, E_i is the net migration rate (emigration – immigration) for group i, BA_i is total accumulated biomass for group i, and EE_i is the ecotrophic efficiency (a model-specific term representing the amount of production used within or exported to detritus) for group i:

$$B_i \cdot (P/B)_i = \sum_i B_j \cdot (Q/B)_j \cdot \mathrm{DC}_{ji} + Y_i + E_i + \mathrm{BA}_i + B_i \cdot (P/B)_i \cdot (1 - \mathrm{EE}_i), \qquad (2)$$

where B_i and B_j are the biomass values for groups i and j; $(P/B)_i$ is the production-to-biomass ratio, equal to an estimate of total mortality (Z; Allen 1971); $(Q/B)_j$ is the consumption by predator j per unit biomass; and DC_{ji} is the proportion of prey i in the diet of predator j.

Required input parameters for modeling the total production and consumption of each functional group included an estimate of B, P/B, and Q/B. A diet matrix was constructed to characterize the diet of each predator group by estimating the percentage contribution of each prey source to the overall diet (Christensen et al. 2008). The three required parameters (B, P/B, and Q/B) and the diet matrix are simultaneously solved by Ecopath through linear equations to calculate an estimate of EE representing the total exported production (1 – EE) or the total used production (EE) within the system. The EE parameter is constrained to a set of values between 0 and 1 and is used by Ecopath in order to establish mass-balance and static conditions (Christensen and Walters 2004).

*Model parameterization.—*The SRE food web model was constructed by using 20 functional groups at various trophic levels in this ecosystem (Table 1). To simplify model construction, focal functional groups included predators, prey, and competitors of diadromous fish species but still encompassed all trophic levels in the estuarine food web. The spatial scale of the model was limited to interactions occurring in the immediate river channel. Functional groups were selected based on our understanding of the system and available data. Ongoing ecological studies of the species assemblage in the SRE system provided primary data sources that were used during model creation. Empirical data were collected during May–September in 2010–2013; those months represent the growing season in this system. Biomass data ($g \cdot m^{-2} \cdot year^{-1}$) were averaged over locations, seasons, and years (e.g., Byron et al. 2011; Deehr et al. 2014). Conversions from wet weight to dry weight were made by assuming a coefficient of 0.20 for most species (Baird and Ulanowicz 1989). Energetic information (P/B and Q/B) was estimated using published models from geographically similar areas (Rybarczyk et al. 2003; Link et al. 2006; Lobry et al. 2008; Byron et al. 2011). Additional information for B, P/B, and Q/B values used in this model can be found in Supplementary

TABLE 1. Functional species groups used in the food web model of the Saco River estuary, Maine.

Group number	Functional group	Species included
1	Seals	Harbor seal *Phoca vitulina*
2	Eagles	Bald eagle *Haliaeetus leucocephalus* and osprey *Pandion haliaetus*
3	Colonial waterbirds	Belted kingfisher *Megaceryle alcyon*, black-crowned night-heron *Nycticorax nycticorax*, glossy ibis *Plegadis falcinellus*, great blue heron *Ardea herodias*, great egret *Ardea alba*, green heron *Butorides virescens*, little blue heron *Egretta caerulea*, and snowy egret *Egretta thula*
4	Gulls and terns	Bonaparte's gull *Chroicocephalus philadelphia*, common tern *Sterna hirundo*, great black-backed gull *Larus marinus*, American herring gull *Larus smithsonianus*, and ring-billed gull *Larus delawarensis*
5	Piscivorous ducks	Common eider *Somateria mollissima*, common loon *Gavia immer*, common merganser *Mergus merganser*, double-crested cormorant *Phalacrocorax auritus*, and white-winged scoter *Melanitta deglandi*
6	Adult and subadult sturgeon	Atlantic Sturgeon *Acipenser oxyrinchus* and Shortnose Sturgeon *Acipenser brevirostrum*
7	Adult Striped Bass	Striped Bass *Morone saxatilis*
8	American Eel	American Eel *Anguilla rostrata*
9	Other diadromous fishes	American Shad *Alosa sapidissima*, Atlantic Tomcod *Microgadus tomcod*, and Rainbow Smelt *Osmerus mordax*
10	Benthic-feeding fishes	Mummichog *Fundulus heteroclitus*, Banded Killifish *Fundulus diaphanus*, White Perch *Morone americana*, Winter Flounder *Pseudopleuronectes americanus*, and Windowpane *Scophthalmus aquosus*
11	Atlantic Menhaden	Atlantic Menhaden *Brevoortia tyrannus*
12	Juvenile river herring	Alewife *Alosa pseudoharengus* and Blueback Herring *Alosa aestivalis*
13	Planktivorous fishes	Atlantic Herring *Clupea harengus*, Atlantic Silverside *Menidia menidia*, Fourspine Stickleback *Apeltes quadracus*, Spottail Shiner *Notropis hudsonius*, Ninespine Stickleback *Pungitius pungitius*, Bluefish *Pomatomus saltatrix*, and American Sand Lance *Ammodytes americanus*
14	Green crab	Green crab *Carcinus maenas*
15	Sand shrimp	Sand shrimp *Crangon septemspinosa* and *Crangon* spp.
16	Macroinvertebrates	Gammarid amphipods
17	Zooplankton	Calanoid copepods and *Evadne* cladocerans
18	Bacteria	
19	Phytoplankton	
20	Detritus	Dissolved organic matter and carcasses

Table S.1 available separately online. When species-specific parameters were unavailable, ratios were averaged for the functional group. The model was built as an average “snapshot” of interactions that occur during the growing season for the SRE river channel, as data were insufficient for creating seasonal models. In the defined growing season, the biomass of migratory functional groups, including diadromous fishes and birds, was assumed to be static. Therefore, the net migration rate (including immigration and emigration) for model groups was set to zero. Additionally, the catch rate was set to zero. Although limited recreational harvest for Striped Bass occurs at the immediate mouth of the Saco River, the SRE does not support an important fishery for Striped Bass (Feurt and Morgan 2015) and therefore harvest is not considered in this model.

Functional groups.—Twenty bird species that are known to consume or compete with the SRE fish community have been observed. These species were classified into four functional groups based on diet: (1) gulls and terns, (2) birds of prey (eagles), (3) piscivorous ducks, and (4) colonial waterbirds. Nonpiscivorous bird species were excluded from the model, as this functional group was assumed to have no direct impact on diadromous fishes within the river channel. Biomasses for bird groups were estimated from sightings within a 300-m-diameter area at multiple shoreline locations (Feurt and Morgan 2015). The number of individuals that were observed in one sampling event was multiplied by the average weight per species (obtained from Poole 2005) and divided by the area surveyed in the SRE. Bird P/B and Q/B ratios and diets were estimated from a seabird consumption study conducted in the Wadden Sea (Europe) and from other peer-reviewed literature (Zwarts and Wanink 1993; Scheiffarth and Nehls 1997; Poole 2005; Table 2). Diet compositions were simplified so that the eagle group consumed only fish species, as this model was created to represent interactions around the river channel (Table 2). Harbor seal biomass was estimated from opportunistic visual sampling. The mean number of sightings was multiplied by an estimate of harbor seal biomass from the peer-reviewed literature (Hammill and Stenson 2000; Morissette and Brodie 2014). Harbor seal diet composition and vital rates (P/B and Q/B) were also obtained from peer-reviewed literature (Morissette and Brodie 2014; Table 2).

Twenty-two fish species were included in the model; 9 of the species were considered diadromous, and 13 were considered estuarine. Nine diadromous fish species have been observed in the SRE system and were included in the model to be equally analyzed; however, there are additional diadromous species in the GOM that were not considered in our model. Fishes were grouped based on life history, foraging habits, and ecologic function through FishBase (Froese and Pauly 2013; Table 1). The diets of adult and juvenile estuarine resident or marine transient fish species were

TABLE 2. Parameters of the balanced food web model for the Saco River estuary (B = biomass; P = production; Q = consumption; EE = ecotrophic efficiency). All biomass estimates are expressed in dry weight. Values in bold italics were estimated by Ecopath (see Table 1 for definitions of the taxa included in each group).

Group number	Group	Trophic level	B (g/m^2)	P/B (per year)	Q/B (per year)	EE	P/Q
1	Seals	***4.1***	0.005	0.071	6.963	***0.000***	***0.010***
2	Eagles	***3.9***	0.016	0.772	77.162	***0.000***	***0.010***
3	Colonial waterbirds	***3.9***	0.005	1.084	108.361	***0.000***	***0.010***
4	Gulls and terns	***3.7***	0.007	0.963	96.310	***0.000***	***0.010***
5	Piscivorous ducks	***3.6***	0.025	0.685	68.496	***0.000***	***0.010***
6	Sturgeon	***3.8***	2.872	0.1	2.45	***0.004***	***0.041***
7	Striped Bass	***3.8***	0.401	0.3	4.41	***0.080***	***0.068***
8	American Eel	***3.5***	0.604	1	6.3	***0.611***	***0.159***
9	Other diadromous fishes	***2.9***	0.499	3	8	***0.635***	***0.375***
10	Benthic-feeding fishes	***2.9***	0.523	3	6.358	***0.787***	***0.472***
11	Atlantic Menhaden	***2.2***	0.137	0.8	31.4	***0.713***	***0.025***
12	Juvenile river herring	***3.0***	0.356	3	8.23	***0.906***	***0.365***
13	Planktivorous fishes	***2.9***	3.725	3	13.700	***0.779***	***0.219***
14	Green crab	***2.7***	1.036	2.4	8.5	***0.721***	***0.282***
15	Shrimp	***2.2***	1.900	3.82	54.15	***0.461***	***0.071***
16	Macroinvertebrates	***2.1***	4.05	6.5	32.6	***0.667***	***0.199***
17	Zooplankton	***2.1***	6.432	6.761	25.926	***0.845***	***0.261***
18	Bacteria	***2.0***	3.3	150	300	***0.102***	***0.500***
19	Phytoplankton	***1.0***	10.9	80	0	***0.193***	
20	Detritus	***1.0***	200			***0.807***	

characterized into planktivorous (filter feeding) or benthic feeding guilds (Dionne et al. 2006; Froese and Pauly 2013). Biomasses were calculated from routine fish sampling with gill nets and beach seines. To capture actively swimming adult fish, bottom-set monofilament gill nets were used; the nets were 91 or 30 m long × 2 m deep and had stretched-mesh sizes ranging from 1.9 to 15.2 cm (Smith 2015). The total area fished by each gill net was assumed to equal the square of the net length (e.g., Deehr et al. 2014). A beach seine (14 m long × 2 m deep; 2-mm square mesh) was used to sample juvenile fish (e.g., Furey and Sulikowski 2010). Mean weight per species was calculated from fish counts by using length–weight relationships (Froese and Pauly 2013). The total biomass of each species caught per sampling event was averaged over the swept sampling area. Corrections for gear efficiency were made by using a catchability coefficient (q) that was applied to all fish and invertebrate groups for typical nekton gear types (q = 0.5; e.g., Pauly 1980). The biomass of schooling forage fishes, such as Atlantic Herring and American Sand Lances, was increased by a factor of 4 to account for common underestimation (Guy and Brown 2007). The P/B ratios were estimated by considering estimates of Z (e.g., Hoenig 1983) or from allometric relationships with body mass (Randall and Minns 2000). We increased P/B values for fish groups that primarily consisted of juvenile fishes, as the SRE is an established fish nursery ground (P/B = 3.0; e.g., Liew and Chan 1987). An online estimator was used to calculate Q/B for fish groups while adjusting for the mean temperature of the study area (Froese and Pauly 2013). Diet matrices (Table S.2) were created by using empirical data from opportunistic stomach content analyses for some fish species, as well as by using literature estimates (Froese and Pauly 2013).

The benthic crustacean community was predominately represented by green crabs and sand shrimp that were observed in the beach seine catch (Furey and Sulikowski 2010). Crustacean biomass was estimated for these two functional groups by using species-specific length–weight relationships and accounting for sampling effort and area (McKinney et al. 2004; Taylor and Peck 2004). Other observed macrobenthos consisted of gammarid amphipods and polychaete worms with the complete absence of bivalves and gastropods (Little 2013). A benthic macroinvertebrate functional group was included to represent these species; benthic macroinvertebrate biomass was estimated from a qualitative benthic sediment grab survey and from the peer-reviewed literature (Hughes et al. 2000; Little 2013). Benthic invertebrate P/B, Q/B, and diet data (Table 2) were obtained from the published literature (Robertson 1979; Deehr et al. 2014).

Zooplankton biomass was estimated from surface densities observed in Saco Bay by using a 1-m plankton net with 333-µm mesh. Calanoid copepods made up the majority of the zooplankton, followed by cladocerans *Evadne* spp. and crab zoeae (Bauer 2015). A single functional group for zooplankton was included in the model; the biomass of that group was calculated by multiplying the total number of individuals per square meter by an average weight (Cohen and Lough 1981). Zooplankton P/B and Q/B (Table 2) were obtained from the peer-reviewed literature (Robertson 1979). Zooplankton feed on phytoplankton and particulate detritus, and their assimilation efficiency was assumed to be 0.40 (Wetzel 2001).

In terms of primary production, although the GOM is considered to be a highly productive ecosystem (1–2 $g \cdot m^{-2} \cdot year^{-1}$; J. Link et al 2008), the in-estuary surface estimate of phytoplankton during late-spring and summer months is relatively low (2.0 µg/L; Bauer 2015). Phytoplankton biomass was calculated from averaged depth-integrated chlorophyll-*a* (µg/L) measurements (A. Brewer, Maine Department of Environmental Protection, personal communication). Mean chlorophyll-*a* values were multiplied by 0.47 to convert to grams carbon and algal weight under an assumed ratio of 10:1 (e.g., de Jonge 1980; Link et al. 2006). The biomass of bacteria was not directly measured and was assumed to be equal to 0.30 of the phytoplankton biomass (Cole et al. 1988). Detrital biomass, vital rates, and ratios of vital rates were obtained from peer-reviewed literature descriptions of ecologically similar systems (Mann 2000; Rybarczyk et al. 2003).

Model balancing.—A series of pre-balancing diagnostics (PREBAL) developed by Link (2010) was obtained prior to mass-balancing of the model (Figure 2). The PREBAL routine reduces uncertainty in input parameters by utilizing fundamental ecological theory. Estimated B, P, and vital rate ratios are visually compared using a simple graphical approach whereby an increase in trophic level is characterized by a decrease in B (e.g., Link 2010). Parameters for each functional group were considered biologically reasonable if an increasing log-linear trend line was observed for B, P/B, and Q/B plotted in relation to decreasing trophic level (Figure 2). Additionally, production-to-consumption (P/C) and production-to-respiration (P/R) ratio values were all required to be less than 1.0 and to fit the same general increasing trend (e.g., Link 2010). Model parameters were then adjusted accordingly before model balancing. Zooplankton biomass and invertebrate biomass were increased by the greatest amount (i.e., by a factor of 10) due to gross underestimation and use of literature sources.

Input parameters for functional groups with EE values greater than 1.0 were manually adjusted to obtain a balanced model, as the model estimated EEs for all functional groups. Biomass values were primarily adjusted in groups for which we were least confident in the accuracy of estimates. This was done by using a systematic approach for each similarly measured species group. The biomasses of individual groups were adjusted one at a time before the auto-balance routine was performed again.

Outputs and sensitivity analyses.—We present a summary statistics table and flow diagram to provide information on trophic flows and energy pathways between species. In addition, for each functional group, we calculated a fractional

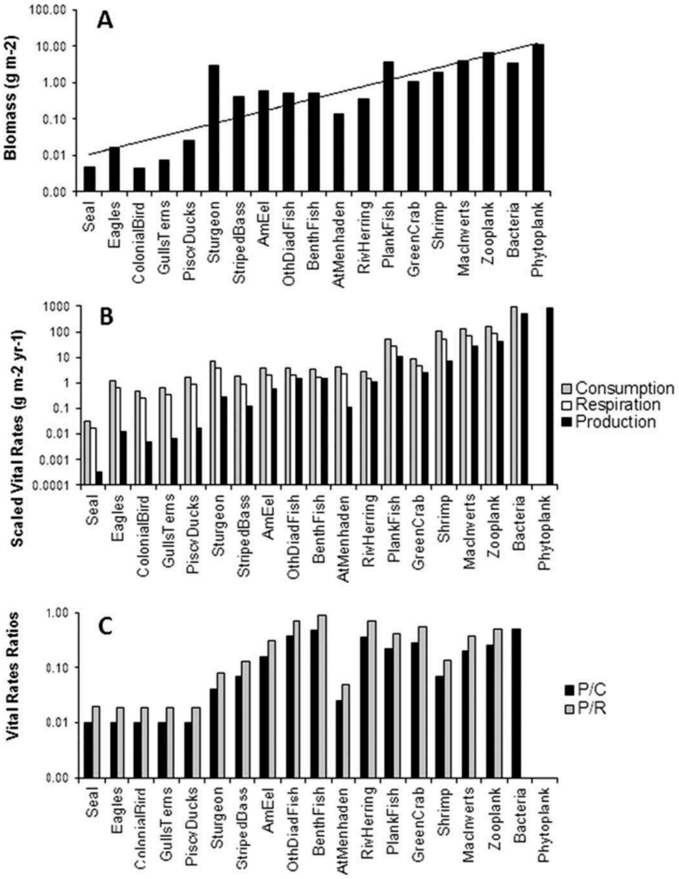

FIGURE 2. Post-balancing diagnostics for the food web model of the Saco River estuary: **(A)** decreasing biomass (*B*; log-scale) with trophic level among modeled functional groups; **(B)** vital rates (g·m^{-2}·year^{-1}; *C* = consumption; *R* = respiration; *P* = production), showing higher *C* relative to *R* and *P* with trophic level among modeled functional groups; and **(C)** ratios of vital rates, showing lower *P*/*C* relative to *P*/*R* among modeled functional groups (Seal = harbor seals; Eagles = bald eagles and ospreys; ColonialBird = colonial waterbirds; PiscvDucks = piscivorous ducks; AmEel = American Eel; OthDiadFish = other diadromous fishes; BenthFish = benthic-feeding fishes; AtMenhaden = Atlantic Menhaden; RivHerring = river herring; MacInverts = macroinvertebrates; Zooplank = zooplankton; Phytoplank = Phytoplankton).

trophic level (TL), which can be used as an estimate of trophic position (Odum and Heald 1975; Christensen and Pauly 1992),

$$\mathrm{TL}_j = 1 + \sum_{j=1}^{n} \mathrm{DC}_{ji}\mathrm{TL}_i, \tag{3}$$

where DC_{ji} is the proportion of prey *i* in the diet of predator *j*, and TL_i is the fractional trophic level of prey *i*.

We constructed a niche overlap plot, which assigned a value to the degree of diet overlap between each pair of species in the food web (Christensen and Pauly 1992). Species that share similar food resources can be categorized into the same trophic guild. We calculated (1) the predator overlap index, which implies whether two groups tend to be preyed upon by the same predators; and (2) the prey overlap index, which highlights whether two groups consume similar prey resources.

Two types of sensitivity analysis were performed to evaluate the trophic interactions of diadromous fishes in this estuarine food web. The first set of sensitivity analyses was conducted by altering the biomass of a single species group in the model by at least one order of magnitude. Biomass was incrementally increased for one species group at a time until an EE value of greater than 1.0 was reached for any group—meaning the model was no longer mass-balanced (e.g., Byron et al. 2011). This factor was used to calculate the capacity by which biomass can be perturbed for each species group in the modeled food web. Groups of interest included Striped Bass and harbor seals, which have demonstrated increasing biomass due to their expanding distribution and abundance in similar ecosystems within the GOM (Friedland et al. 2012).

The second type of sensitivity analysis performed was a mixed trophic impact analysis. This analysis identifies the net impact (q_{ij}) that a species will have on other groups (directly or indirectly) if its biomass increases (Christensen and Pauly 1992),

$$q_{ij} = \mathrm{DC}_{ji} - \mathrm{FC}_{ij}, \tag{4}$$

where q_{ij} is the net impact of group *i* on group *j*, DC_{ji} is the proportion of group *i* in the diet of group *j*, and FC_{ij} is the proportion of group *j* that is consumed by group *i*.

Predator–prey interactions between modeled groups were examined via the mixed trophic impact analysis to evaluate the direct (predation) and indirect (competition) impacts of one group on other groups in the ecosystem (Christensen et al. 2008; e.g., Byron et al. 2011). The analysis was represented as a matrix of assigned impact values (negative or positive) for each pair of functional groups.

A keystone index identifies a species of low biomass that has a large role in the structure of a food web. “Keystoneness” plots based on keystone index 1 (KS_1) and keystone index 2 (KS_2) rank functional groups according to their roles as keystone species influencing the abundances of other groups (Libralato et al. 2006):

$$\mathrm{KS}_{1i} = \log[\varepsilon_i \cdot (1 - p_i)] \tag{5}$$

and

$$\mathrm{KS}_{2i} = \log[\varepsilon_i \cdot (1/p_i)], \tag{6}$$

where ε_i is a measure of the total impact of group *i* on all other groups from the mixed trophic impact analysis and p_i is a measure of the contribution of group *i* to the total biomass.

The KS_1 index is highly influenced by inputs from the mixed trophic impact analysis and identifies species of high biomass, whereas KS_2 assigns high keystoneness values to groups with low biomass and low overall effect, which can be considered rare (Power and Mills 1995; Valls et al. 2015). Due to limitations in comparison of these functional indices across models, we calculated an additional keystone index (KS_3) that was developed by Valls et al. (2015) from a meta-analysis of 101 Ecopath models. The KS_3 index is calculated by using model outputs and highlights species that have a greater balance between their trophic impacts and biomass contributions (Valls et al. 2015):

$$KS_{3i} = \log[\varepsilon_i \cdot (\text{decreasing rank of } B_i)], \qquad (7)$$

where the relative total impact (ε_i) is multiplied by the biomass contribution (B_i) ranked in descending order for each species group (Valls et al. 2015).

RESULTS

Summary Statistics and Estimated Trophic Level

The SRE ecosystem model yielded an estimated net production of 285.05 $g \cdot m^{-2} \cdot year^{-1}$, with a total system biomass of 36.79 g/m^2. Fish groups comprised 67% of the total system biomass (24.78 g/m^2); diadromous fishes made up 35% of the total ecosystem biomass (12.8 g/m^2; Table 2). At the top of the food web were harbor seals (TL = 4.1), followed by the colonial waterbird group (TL = 3.9) and the eagle group (TL = 3.9; Table 2; Figure 3). Among the modeled fish groups, upper-trophic-level predators included the diadromous sturgeons (Atlantic Sturgeon and Shortnose Sturgeon; TL = 3.8) and Striped Bass (TL = 3.8). The planktivorous fish group (TL = 2.9) contributed 71% of all lower-trophic-level (TL = 2–3) forage fish biomass, which included river herring (TL = 3.0), benthic fishes (TL = 2.9), other diadromous fishes (TL = 2.9), and Atlantic Menhaden (TL = 2.2).

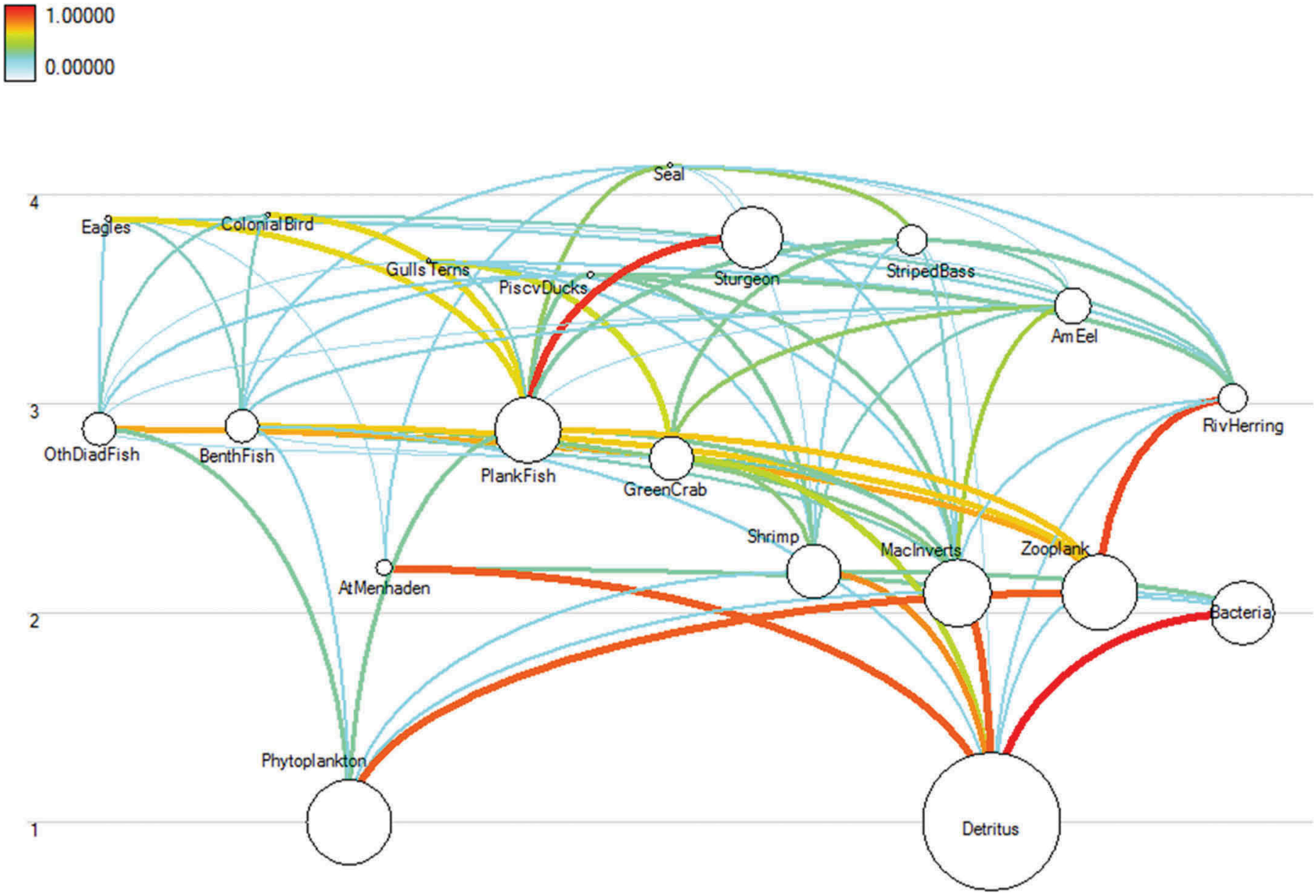

FIGURE 3. Trophic structure diagram (Ecopath output) for the food web model of the Saco River estuary. Each node represents a species or functional group (abbreviations are defined in Figure 2); node position on the y-axis indicates the trophic level. Node size is proportional to the respective biomass of the group. Lines between nodes represent the flow of energy, with line thickness and color contrast indicating the degree of importance.

Among trophic levels, the food web contained 412 total energy pathways, with a mean path length of 4.39 between functional groups. Seals had the greatest number of pathways (203), followed by eagles (90 pathways). Of the diadromous fish groups, Striped Bass (106 pathways) and American Eels (57 pathways) had the greatest number of paths.

Sensitivity Analyses

Sensitivity analyses revealed species groups that had the greatest capacity or the narrowest capacity to increase in biomass without impacting the modeled food web (Byron et al. 2011). Multiple functional groups (including the following diadromous fish groups: sturgeon, Striped Bass, and American Eel) could not exceed twice their current biomass without causing the model to become unbalanced, thus indicating that these groups serve a greater role in the functioning of the food web. Additional groups with a narrow capacity to increase biomass in this system included eagles, piscivorous ducks, planktivorous fishes, and green crabs (Figure 4). In contrast, river herring and the "other diadromous fish" group each had the capacity to increase four times their current biomass estimate. The harbor seal and Atlantic Menhaden had the greatest capacity for increases in biomass, indicating their smaller roles in maintaining the integrity of this food web. The current biomass estimates for Atlantic Menhaden and harbor seals could increase by a factor of 12. Striped Bass and all bird groups were constrained by the biomass of river herring (0.15% of the total system biomass). The sturgeon group was the only group that was constrained by the biomass of the planktivorous fish group (1.57% of the total system biomass).

Using the mixed trophic impact analysis, positive and negative impacts were observed for the effect of increased biomass on modeled groups, including diadromous fishes. Of the positive impacts, the most significant was the impact of harbor seals on planktivorous fish. The planktivorous fish group had a positive impact on several species, including the sturgeon group and all of the bird groups (Figure 5). Additionally, the detritus pool had positive impacts on multiple functional groups, including all invertebrate groups and the Atlantic Menhaden. The most significant negative impact was that of harbor seals on Striped Bass and sturgeon. The next-largest negative impact was the eagle group's impact on Atlantic Menhaden. Among diadromous fish species, Striped Bass had a negative impact on American Eels and river herring (Alewife and Blueback Herring). River herring did not have a large impact on any of the other groups. In addition, the sturgeon group negatively impacted the planktivorous fish group while exerting positive impacts on benthic macroinvertebrates, Atlantic Menhaden, and benthic fishes.

Niche Overlap and Keystone Indices

The greatest niche overlap for predators and prey resources was observed between the benthic fish group (i.e., species in the perch, killifish, and flounder families) and the "other diadromous fish" group (American Shad, Atlantic Tomcod, and Rainbow Smelt; Figure 6). The American Eel and green crab groups consumed dissimilar food items and were preyed upon by different predators and therefore may be components of different trophic pathways. Pelagic fish groups were consumed by a wide variety of predators, whereas benthic prey

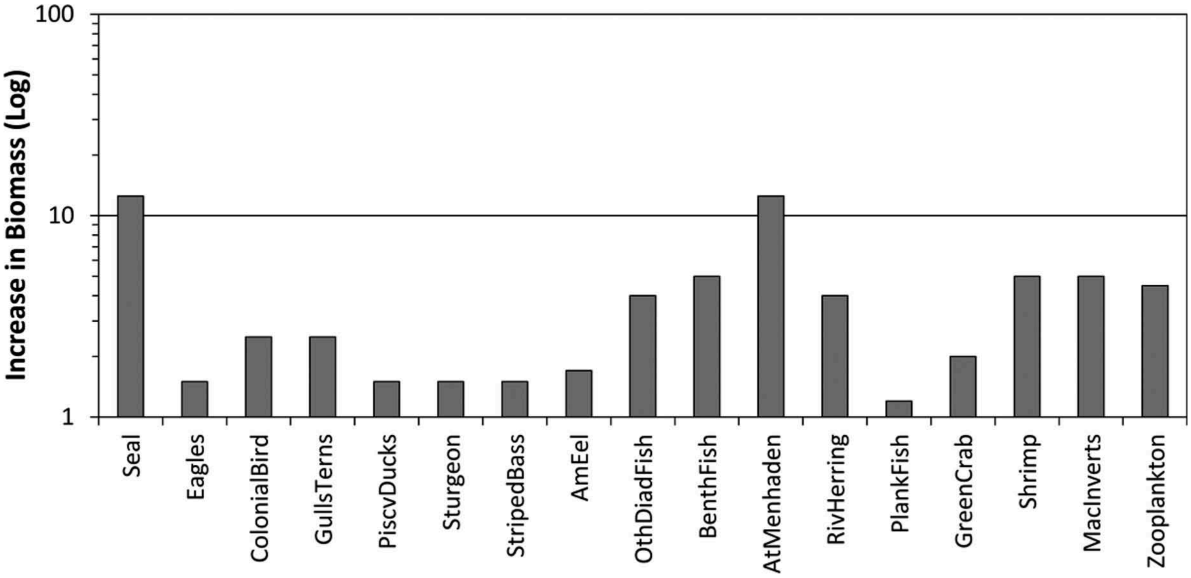

FIGURE 4. Allowable change in biomass of each functional group (abbreviations are defined in Figure 2) during sensitivity analysis. Biomass values of each compartment were increased until the model became unbalanced (i.e., until the ecotrophic efficiency of another group exceeded a value of 1.0).

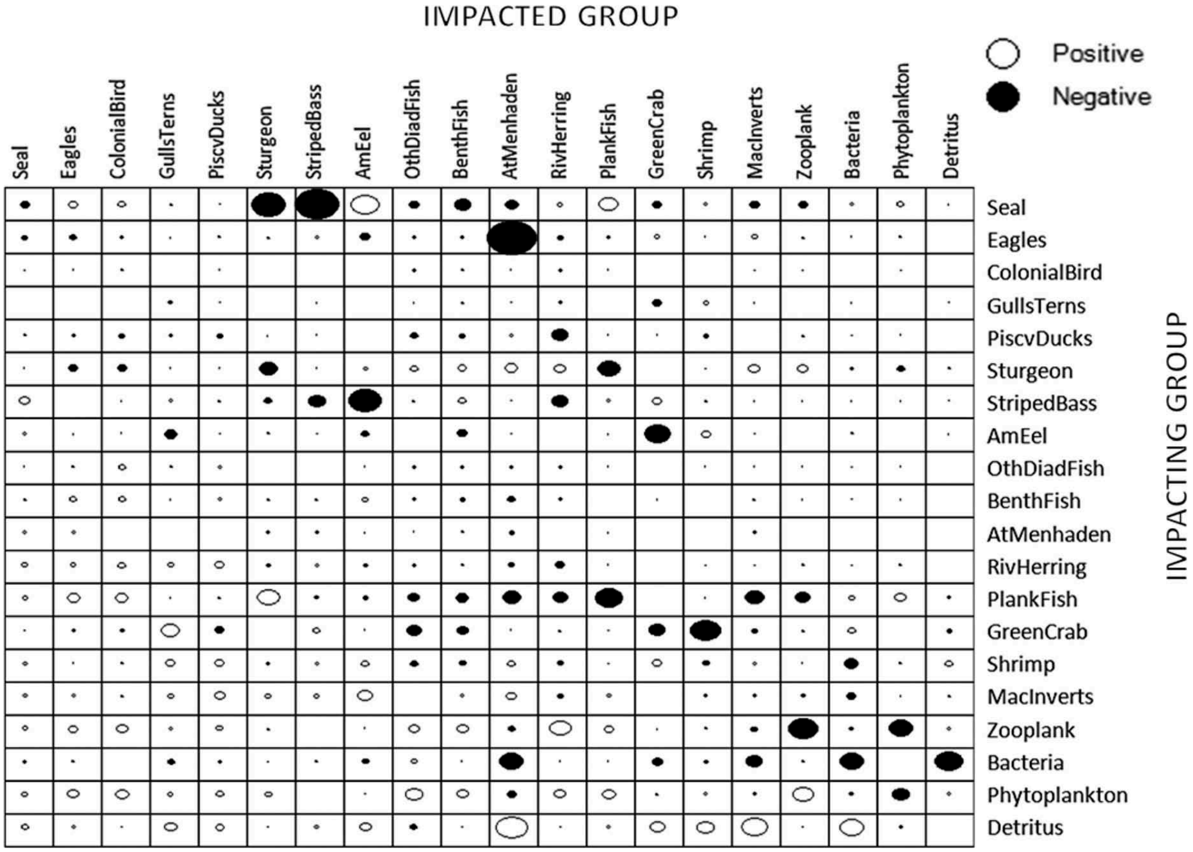

FIGURE 5. Mixed trophic impact analysis of functional groups (abbreviations are defined in Figure 2) at all trophic levels in the food web model of the Saco River estuary. The oval size represents the relative impact; black shading indicates that the impact is negative.

resources (green crabs, sand shrimp, and benthic fishes) had a smaller suite of predators.

The highest-ranking groups from the analysis of KS_2 and KS_3 included phytoplankton (KS_2 = 0.369 [rank = 1]; KS_3 = 0.570 [rank = 1]), macroinvertebrates (KS_2 = 0.611 [rank = 3]; KS_3 = 1.109 [rank = 2]), and zooplankton (KS_2 = 0.601 [rank = 2]; KS_3 = 0.570 [rank = 3]). In contrast, the KS_1 index scored colonial birds (–0.992), Atlantic Menhaden (–0.847), and other diadromous fishes (–0.7446) as the highest-ranking groups. Both KS_2 and KS_3 ranked the planktivorous fish group (KS_2 = 0.909 [rank = 6]; KS_3 = 2.703 [rank = 10]) higher than river herring (KS_2 = 1.505 [rank = 11]; KS_3 = 3.308 [rank = 13]; Figure 7). Alternatively, according to the KS_1 index, the planktivorous fish group ranked 17th (–0.1318), whereas the river herring group ranked sixth (–0.5137; Figure 7). On the plots of keystoneness versus relative total impact (Figure 7), seals, eagles, and planktivorous fishes were displayed as high-ranking functional groups for all three keystone indices. The higher position of the planktivorous fish group relative to that of river herring was highlighted as gray circles in the plots for all three keystone indices (Figure 7).

DISCUSSION

In the current study, an ecosystem approach was utilized to evaluate the trophic role of diadromous fishes in estuarine food webs. To our knowledge, the results presented herein provide the first characterization of a food web in a GOM estuary by using Ecopath. This allowed links between predators and lower-trophic-level prey that drive bottom-up processes in the SRE food web to be elucidated.

Evidence from model outputs supports the use of juvenile marine transients (i.e., the planktivorous fish group) as a more important forage base than river herring in this estuarine ecosystem. Results from mixed trophic impact analysis indicated that river herring did not exert a large impact on any of the other groups in the SRE food web. In contrast, the planktivorous fish group had positive impacts on multiple functional groups; this supports output from the keystone index analysis and sensitivity analysis, suggesting that the planktivorous fish group is important as a source of forage and as a node in this food web. Our findings are comparable with previous modeling efforts for the GOM ecosystem as a whole, suggesting the importance of lower-trophic-level prey resources (Overholtz and Link 2009). A large

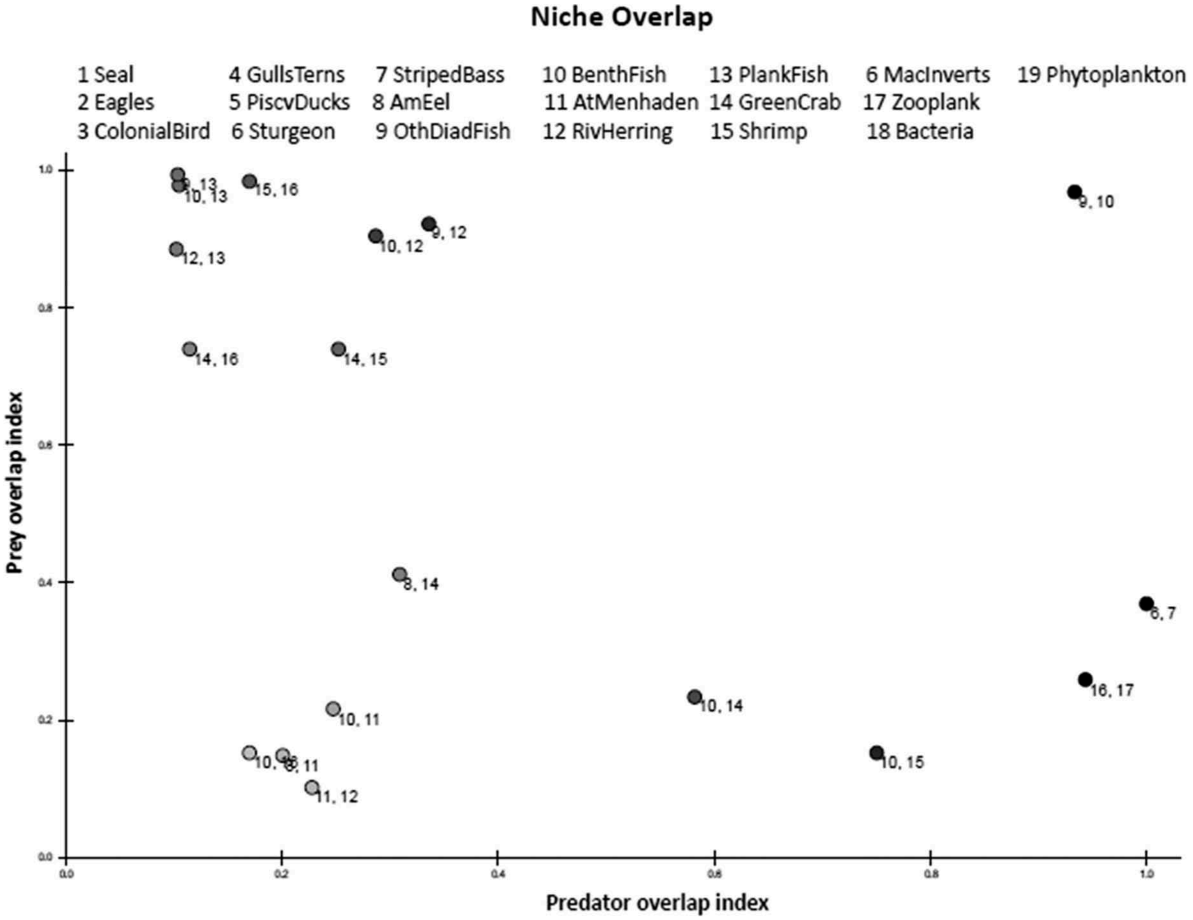

FIGURE 6. Predator–prey niche overlap index plot of functional groups (abbreviations are defined in Figure 2) included in the food web model of the Saco River estuary. Groups with similar prey resources (lighter-shaded dots) are oriented on the left side of the plot; complete overlap of predator and prey resources (darker-shaded dots) is shown on the right side of the plot.

diversity of small pelagic forage fishes serving as ecologically valuable “key prey species” is present within the GOM; these species include the American Sand Lance, Atlantic Herring, Alewife, and Blueback Herring (Pikitch et al. 2012, 2014; I. Altman and coauthors, paper presented at the Regional Association for Research on the Gulf of Maine symposium, 2014). Atlantic Herring and American Sand Lances constitute a vital source of food for many marine predators, including Atlantic Bluefin Tuna *Thunnus thynnus* (Chase 2002; Golet et al. 2015), humpback whales *Megaptera novaeangliae* (Weinrich et al. 1997), seals (Bowen and Harrison 1996), and seabirds (Pikitch et al. 2012, 2014). Although river herring have traditionally served as important forage species in estuarine and nearshore habitats, their ecological role has dwindled (Wilson et al. 2009; Pikitch et al. 2012). In a recent study, McDermott et al. (2015) found that alosines (river herring and American Shad) represented only a small component (<10% by weight) of marine piscivore diets in areas just offshore of the Kennebec and Penobscot River mouths.

Based on the sensitivity analysis, another important forage fish was found to have a large capacity to increase biomass in this estuarine food web: the detritivorous Atlantic Menhaden, which is highly migratory and commercially valuable (McBride 2014). The detritus pool positively impacted the Atlantic Menhaden group and several other groups, corresponding with previous documentation that detritus-derived carbon powers benthic food webs exerting bottom-up control in estuaries (Baird and Ulanowicz 1989; Blomberg and Montagna 2014; Buchheister and Latour 2015). These findings highlight the value of preserving marsh habitat—which contributes significant detrital biomass to the SRE—to maintain total system function. Additional ecosystem services provided by fringing tidal marshes include their use as fish nurseries and as feeding habitat and refuge for trophically important juvenile fish, such as those in the planktivorous fish group (Morgan et al. 2009).

Fluctuations in forage fish stocks can influence both top-down and bottom-up processes (Pikitch et al. 2012, 2014).

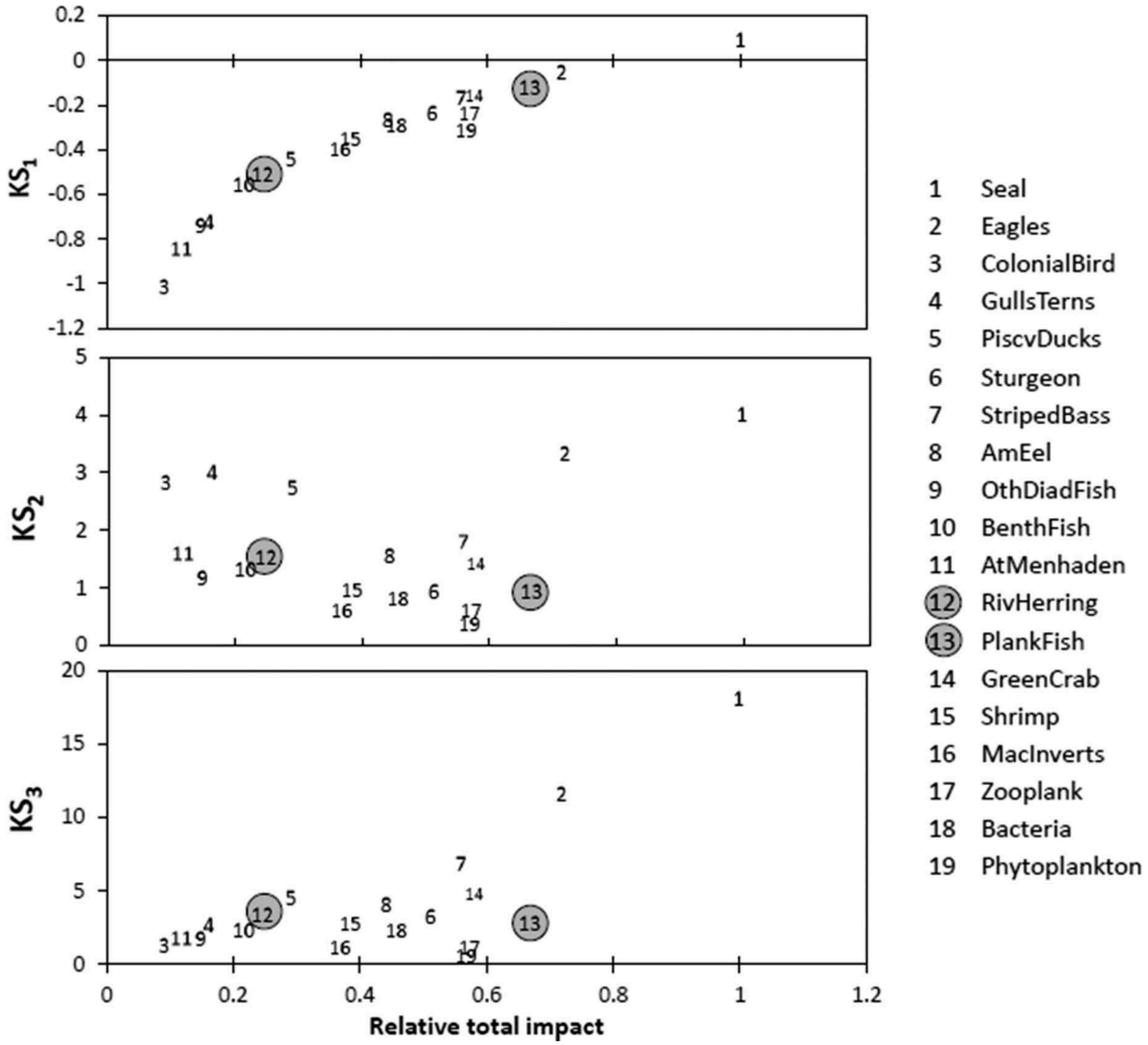

FIGURE 7. Plots of keystone index 1 (KS_1), keystone index 2 (KS_2; e.g., Libralato et al. 2006), and keystone index 3 (KS_3; e.g., Valls et al. 2015) versus the relative total impact of each functional group (abbreviations are defined in Figure 2). Groups that are oriented toward the top right of a plot play a greater role as keystone species. The positions of groups 12 (river herring) and 13 (planktivorous fishes) are shown as gray circles to highlight the different positions of these two forage fish groups.

Small pelagic fishes are responsible for transferring energy to higher trophic levels, contributing to increases in the biomass of top predators (Cury et al. 2000; Smith et al. 2011). Our present modeling efforts showed that the Striped Bass group and sturgeon group were the top predators of the fish groups in the SRE food web. The Atlantic Sturgeon and Shortnose Sturgeon were found to occupy a higher TL (3.8) in the SRE than in other ecosystems for which estimation methods were based on food items (TL = 3.4; Froese and Pauly 2013). The TL we estimated may have been greater due to the consumption of higher-trophic-level prey in the SRE. Diet studies in the SRE have reported that American Sand Lances are a primary food item (>90% of the diet) for both of these sturgeon species (Little 2013). In contrast, other studies throughout the range of Atlantic Sturgeon and Shortnose Sturgeon have indicated a greater dietary role of benthic macroinvertebrates (including amphipods, isopods, polychaete worms, and mollusks) in the overall diet composition (Moser and Ross 1995; Johnson et al. 1997; Savoy 2007; McLean et al. 2013). These findings support research suggesting the previously unknown use of the SRE as a foraging ground by Shortnose Sturgeon and Atlantic Sturgeon (Little et al. 2013). In the SRE, sturgeon consumed temporally variable juvenile prey with a higher caloric value (American Sand Lance) more frequently than stable food resources (sand shrimp *Crangon* spp. and benthic macroinvertebrates). The unique prey-switching behaviors of sturgeon in the SRE affects the growth of individuals that use the system, drawing attention to alternative foraging activity among the GOM metapopulation as a whole (Burke and Rive 2002; Ferry and Mather 2012). A greater understanding of Atlantic Sturgeon and Shortnose Sturgeon feeding ecology in estuarine habitats within the GOM is important considering their current conservation status. The Atlantic Sturgeon Status Review Team (ASSRT 2007) emphasized the lack of life history information necessary to identify critical habitats for the GOM distinct population segment of Atlantic Sturgeon (listed as threatened under the Endangered Species Act) and the Shortnose Sturgeon (listed as endangered throughout its range).

In contrast, the estimated TL (3.8) for Striped Bass in our SRE food web model fell within reported ranges: it was lower than values calculated for Chesapeake Bay (TL = 4.5; Walter and Austin 2003) and inshore Cape Hatteras (TL = 4.5; Bowman et al. 2000) but was greater than that calculated for the Hudson River estuary (TL = 3.4; Hurst and Conover 2001). All three of the previous values were calculated by using analysis of food items. Migratory Striped Bass have been observed to enter non-natal coastal rivers, including the Saco River, presumably for feeding purposes (Grothues et al. 2009; Mather et al. 2009). Due to the abundance of juvenile fish and forage fish resources in this estuary, these results suggest that Striped Bass use the SRE as feeding habitat. Although fidelity to non-natal systems is not common for anadromous species (Buzby and Deegan 2000), findings from our modeling effort are consistent with studies of northern GOM estuaries, where Striped Bass consumed a greater amount of American Sand Lances and estuarine-resident fish species than in other areas of their range (Ferry and Mather 2012). For Striped Bass, this alternative feeding strategy is particularly valuable in an ecosystem that has been depleted of historical key prey species, such as the alosines (Mather et al. 2013).

The trophic positions estimated for sturgeon and Striped Bass by the current model support their use of a generalist foraging strategy wherein both groups are opportunistically consuming the most abundant local prey (Chassot et al. 2008). These results suggest the potential occurrence of competition for prey resources, as the two groups occupy the same trophic position. Sturgeon and Striped Bass traditionally rely on benthic trophic pathways in coastal New England (Nelson et al. 2003; Ferry and Mather 2012). Additionally, both groups display high spatial and temporal overlap in their use of estuarine systems along the East Coast. However, the low overlap in the diets of predators as observed from the niche overlap plot implies that similar food sources are not being shared. This finding suggests that prey resources in the SRE system are not limiting and is supported by evidence for a robust biomass of low-trophic-level fishes and the documented function of the SRE as a nursery ground (Krebs 1998). However, at the start of the model-balancing process, the initial biomass of benthic crustaceans and macroinvertebrates was too low to support nonpiscivorous fishes. The high biomass of benthivores, particularly sturgeon, in the SRE may be overutilizing the benthic prey resources (e.g., amphipods, decapod crustaceans, and sand shrimp) that are typically most common in estuarine ecosystems (Hughes et al. 2000; Able and Fahay 2010; Buchheister and Latour 2015).

Another highly opportunistic estuarine predator is the harbor seal, which the sensitivity analysis indicated was one of the groups with a large capacity to increase in biomass without generating a large impact on the food web (Able and Fahay 2010). Harbor seals have exhibited increasing biomass in the GOM within the last few decades, with the potential to occupy estuaries at a greater frequency (Baraff and Loughlin 2000; Friedland et al. 2012). According to the results from the mixed trophic impact analysis, sturgeon species and Striped Bass could be negatively affected in the GOM if the biomass of harbor seals continues to increase (Yodzis 1998).

Findings from this modeling effort provide a greater understanding of the variable trophic roles maintained by diadromous fishes in estuarine food webs. Although similar measures of trophic position were estimated for dominant anadromous piscivores, differentiation among the utilized trophic pathways was observed. Juveniles of marine transient fishes were found to serve as key forage resources, whereas river herring do not currently serve as a significant food source for generalist estuarine predators. Direct comparisons of predation and competition sources among diadromous fish groups would not have been possible without the use of this comprehensive modeling framework. Ecological modeling approaches can provide information that is necessary for the creation of management plans for fish populations with the potential for increased restoration efforts (i.e., river herring; Link 2010). However, there remain limitations to using an Ecopath approach, as this food web model was created using the best available data. Model assumptions were made to represent interactions occurring between these highly dynamic migratory fish populations and aggregate trophic guilds during the spring and summer seasons.

Additional ecosystem models may better capture interactions within estuaries by creating multiple seasonal “domains” that are indicative of the predator response to pulses (i.e., emigrating river herring; Link et al. 2011; McDermott et al. 2015). Future studies should focus on addressing major data gaps for benthic macroinvertebrates, primary productivity, secondary productivity, and marsh-derived detritus. As estuarine fishes themselves display plasticity in diet composition, further research is also needed on feeding habits over temporal scales to elucidate further interactions in these crucial nursery and foraging areas (Able and Fahay 2010).

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