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Modeling 25 years of food web changes in Narragansett Bay (USA) as a tool for ecosystem-based management

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ABSTRACT: Narragansett Bay (Rhode Island, USA) is an estuary undergoing changes from a combination of rising water temperatures, nutrient fluxes, and human uses. In this study, we created an ecosystem food web model and evaluated its ability to predict functional group biomasses. Specifically, we used Ecopath to construct 2 mass-balanced models covering different time periods in Narragansett Bay: a historical model using data from 1994–1998 and a present-day model that represents 2014–2018. With the historical model as a starting point, we used Ecosim fit to time series data and projected forward to present-day values, forcing the model with both phytoplankton biomass and fishing mortality. The biomass of most mid- and upper trophic level groups increased by 2018, with the exception of carnivorous benthos, which experienced a large decline. There were changes in the composition of fisheries, with a large increase in recreational benthivorous fish landings and a decrease in commercial landings of planktivorous fish and suspension feeding benthos. The inclusion of fishing mortality and phytoplankton biomass as forcing functions, as well as adjusting the vulnerability levels of prey, greatly improved our model fits for all functional groups with the exception of gelatinous zooplankton. Our ecosystem model was able to correctly predict the direction of change for all fish and fished invertebrate groups with a relatively high degree of precision, particularly for the upper trophic levels. Thus, this ecosystem model is broadly applicable and suitable to project trends in the Narragansett Bay food web associated with localized and adaptive ecosystem-based management.

KEY WORDS: Ecopath · Ecosim · Climate change · Fisheries management · Estuarine ecology

1. INTRODUCTION

Altered environmental conditions in marine ecosystems have resulted in widespread changes to community structure, species interactions, and dispersal patterns (Hoegh-Guldberg & Bruno 2010, Doney et al. 2012, McCauley et al. 2015). These shifts have been caused by human pressures such as climate change, habitat degradation, and exploitation (Johnson & Welch 2009, Brander 2010). For example, approximately one third of global fisheries are harvested at biologically unsustainable levels (FAO 2020) and nearly one quarter of them have collapsed (Mullon et al. 2005, Pinsky et al. 2011). Climate change has shifted species distributions considerably, altering predator–prey dynamics and triggering trophic cascades (Hazen et al. 2013, Pinsky et al. 2013). Therefore, properly managing marine ecosystems and fish-

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eries in a rapidly changing environment remains critical (Duarte et al. 2020). As such, policy-makers recognize the importance of ecosystem-based management (EBM) to account for the interdependence among physical, biological, and socioeconomic components within and among ecosystems (McLeod et al. 2005).

Ecosystem modeling is becoming an increasingly powerful tool in support of EBM (Christensen & Walters 2011). Ecopath with Ecosim (EwE) is a type of ecosystem food web model that accounts for biomasses of species or species groups and energy flows between them (Polovina 1984, Christensen & Pauly 1992, Walters et al. 1997). EwE is based on principles of mass-balance, such that for each group in a model, the energy removed (i.e. predation or fishing) must be balanced by the energy consumed (Coll et al. 2009). Users can employ a time-dynamic component (Ecosim) to run simulations and use EwE to investigate how the food web responds to changing species interactions (Moreau 1995, Haputhantri et al. 2008) as well as the ecosystem impacts of rising temperatures (Serpetti et al. 2017), invasive species (Lercari & Bergamino 2011, Langseth et al. 2012), nutrient loading (Kao et al. 2014), fishing pressure (Martell et al. 2002, Shin et al. 2004, Geers et al. 2016), or a combination of the above (Kao et al. 2014, Tecchio et al. 2015, Corrales et al. 2017). This wide array of uses makes EwE a valuable modeling tool for EBM (Plagányi & Butterworth 2004).

Narragansett Bay, Rhode Island (USA), is an estuarine ecosystem that is experiencing rapid bottom-up changes in the environment as well as top-down human uses. Anthropogenic factors like variations in commercial and recreational fishing pressure, as well as ecological changes such as increasing water temperature, are important drivers in Narragansett Bay (Nixon et al. 2009). For example, rising water temperatures have led to shifts in the species community composition, with the bay seeing an increasing abundance of Mid-Atlantic species and a decreasing abundance of northern, cold-water species (Oviatt et al. 2003, Collie et al. 2008). In particular, there has been an increase in striped searobin *Prionotus evolans*, scup *Stenotomus chrysops*, alewife *Alosa pseudoharengus*, bluefish *Pomatomus saltatrix*, butterfish *Peprilus triacanthus*, little skate *Leucoraja erinacea*, crabs (*Cancer* spp.), and lobsters *Homarus americanus* leading up to the 1990s (Collie et al. 2008). Concurrently, there has been an overall decline of northern species like the northern sea robin *Prionotus carolinus* and winter flounder *Pseudopleuronectes americanus* (Oviatt et al. 2003). In addition to these changes in abundance, the residence periods of warm-water species, including scup, butterfish, summer flounder *Paralichthys dentatus*, striped searobin, and longfin squid *Doryteuthis pealeii* have expanded, while those of many cold-water species have contracted (J. Langan unpubl. data). These studies indicate that due to rising water temperatures and fishing pressure, Narragansett Bay is experiencing dramatic shifts in species assemblage and phenology. Thus, the bay may begin to resemble a more warm-water, Mid-Atlantic estuary with weakened benthic–pelagic coupling in the future. Understanding if ecosystem food web models can represent and predict these dynamics will be important for policymakers and managers to know as they plan for these changes.

A previous Ecopath model of Narragansett Bay was developed by Byron et al. (2011) for the purpose of calculating the carrying capacity of shellfish aquaculture. They used the data from an ecosystem food web model of the bay created by Monaco & Ulanowicz (1997). The model of Byron et al. (2011) was focused solely on aquaculture and is not applicable to many EBM questions, particularly those surrounding fisheries. For example, Byron et al. (2011) grouped piscivorous and benthivorous fish together as ‘carnivorous fish,’ and grouped squid and ctenophores together as ‘invertebrate carnivores.’ Unlike squid, ctenophores often occur as blooms. Additionally, squid, unlike ctenophores, are a commercial fishing target, which was not included in this previous Narragansett Bay food web model. In the original model of Monaco & Ulanowicz (1997), production and consumption were calculated by Ecopath. These values were unchanged in the model of Byron et al. (2011) and may not be representative of Narragansett Bay. This model was also not made temporally dynamic; therefore, it could not be used to run simulations of how this ecosystem changes over time and is of limited use for management strategy evaluation.

The objective of this study was to use EwE to describe recent changes in Narragansett Bay, including shifts in animal biomasses and external drivers, and evaluate the precision of our model and its utility for ecosystem management. To do so, we constructed 2 new Ecopath models representing different periods in time: a 1994–1998 model (hereafter the ‘1994 model’), and a 2014–2018 model (hereafter the ‘2018 model’). We did not use input values from previous Narragansett Bay models to parameterize these new models, with the exception of benthic algae biomass. We compared input values for the 2 models to describe notable changes in biomass and fisheries landings. Using the 1994 Ecopath model as a starting point, we used Ecosim to create a temporally dynamic model, and quantified the respective importance of each external driver (fishing mortality, primary production [PP], cultured shellfish) on model fit. We then compared the model-projected 2018 fish and invertebrate biomasses to the empirically-derived 2018 Ecopath model. We expanded on this technique by evaluating our Ecosim projection not only against a biomass time series but also against a distinct Ecopath model representing the current (2018) food web of the system.

2. MATERIALS AND METHODS

2.1. Model structure

The ecosystem model for Narragansett Bay was constructed using the EwE program (Polovina 1984, Christensen & Pauly 1992, www.ecopath.org). Our model-building process began with specifying the ecosystem compartments and sorting species into functional groups, i.e. single species, size/age groups, or ecologically/taxonomically related groups of species. To trace energy transfer between these functional groups, EwE uses a diet matrix and 4 main inputs: biomass (B), production/biomass (P/B), consumption/biomass (Q/B), and ecotrophic efficiency (EE) (Text S1A, Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m654p017_supp1.pdf). In this application, we entered B, P/B, Q/B, and let the model solve for EE using its 2 main equations (Text S1A; Table S2 in Supplement 1), as recommended by Heymans et al. (2016) because EE is a parameter that cannot be reliably measured in the field.

To describe changes in Narragansett Bay and test the ability of Ecosim to predict these changes, we created 2 separate Ecopath models. The 1994 model is based on biomass and catch data from 1994–1998, while the 2018 model is based on biomass and catch data from 2014–2018. The input values were collected from the same sources and scaled the same way for both models.

An overview of our methods is given below, and additional information can be found in the Supplements: Supplement 1 details the Ecopath methods and results, including EwE equations and equation inputs (Text S1A), establishment of the functional groups (Text S1B), and pre-balance (PREBAL) diagnostics (Text S1C). Supplement 2 (www.int-res.com/articles/suppl/m654p017_supp2.xlsx) contains all of the species and functional group input values and data sources. Supplement 3 at www.int-res.com/articles/suppl/m654p017_supp3.pdf contains the supplementary Ecosim methods and results referenced in Section 2.8 (Ecosim methods) and Sections 3.2 and 3.4 (Ecosim results).

2.2. Functional groups

We grouped species into functional groups to create the Ecopath models. We chose broad functional groups as we were not interested in any single species, but rather had a broad focus in fisheries, community dynamics, and EBM. These groupings also allowed us to smooth over individual species variation and allow for more reliability in the diet, as predators can switch prey species without switching prey functional groups (McPhee et al. 2015). The mid- and upper trophic level (UTL) functional groups (carnivorous benthos, squid, suspension feeding benthos, cultured shellfish, seabirds, piscivorous fish, planktivorous fish, benthivorous fish) comprised 38 species (Table S3 in Supplement 1). Species were assigned to their functional groups via hierarchical clustering, using a Bray Curtis similarity index with a fourth-root transformation based on detailed diet data (Fig. S1 in Supplement 1). In the 1994 model, squid were split into 2 size categories because cannibalism made up over 10% of the squid diet. The use of a multi-stanza group for squid was necessary to prevent numerical instabilities in the time dynamics of Ecosim (Christensen et al. 2005). The cutoff size of 12 cm mantle length was chosen, as this is the length where cannibalism becomes common in the diet (Vovk & Khvichiya 1980, Vovk 1985). The stock recruitment dynamics of squid in our model were linear (Fig. S2 in Supplement 1) as discussed in Text S1B. In the 2018 model, small and large squid were represented as 2 distinct functional groups, as these numerical instabilities do not occur in a static Ecopath model, and a multi-stanza group does not account for the migration of squid in and out of the bay. Given that many of these species in this model only occupy the bay for part of the year, multi-stanza dynamics were not ideal for this system. and thus were only included in Ecosim when necessitated by high levels of cannibalism. Seabirds were included in the model as a separate functional group because of their importance as predators (of planktivorous and benthivorous fish) in the food web. The lower trophic level functional groups included in the model were deposit feeding benthos, gelatinous zooplankton, zooplankton, phytoplankton, benthic algae, and detritus.

2.3. Biomass

Biomass values were input into Ecopath in wet weight (g m^{-2}) for the 2 models (Table 1). Fish and invertebrate biomass values came from either the University of Rhode Island Graduate School of Oceanography (URI GSO) or Rhode Island Department of Environmental Management (RI DEM) bottom trawls, both of which sample at stations throughout the bay (Fig. 1). The RI DEM biomass time series ran from 1990 to present, while the URI GSO biomass time series ran from 1994 to present. Biomass (g), averaged across stations and time points (including tows where a species was not present), for each species per trawl was divided by the swept area (m^2) of the trawl to get a g m^{-2} value, which was assumed to represent the biomass throughout the bay, as our model did not address spatial dynamics. If data existed in both trawls for the same species, the larger of the biomass values was chosen to assist in model balancing and to account for the underestimation of fish biomass by (some) trawling surveys (Engås & Godø 1989, Stockwell et al. 2006, Kaartvedt et al. 2012). Initially, our Ecopath model would not balance using these low biomass values, prompting us to account for species-specific catchability in the trawling data. Therefore, each value was divided by a species-specific bottom trawl catchability coefficient, estimated from regional stock assessment documents, resulting in an upwards adjustment in the biomass levels of small, pelagic, and/or fast-swimming species which trawls have difficulty in catching. Atlantic menhaden *Brevoortia tyrannus* biomass was obtained from the RI DEM aerial menhaden survey.

Functional group biomasses were obtained by summing the biomasses of all relevant species. When biomasses were entered into Ecopath, several were too low to achieve a balanced model (all EEs <1). Therefore, biomasses for benthivorous fish, planktivorous fish, piscivorous fish, carnivorous benthos, and squid were scaled to account for young of the year not captured in the trawls and species not explicitly included in the model but that appear in the diets of other species, and to achieve realistic production/consumption (P/Q) values (Text S1C), as recommended by Lucey (2019). These scaling factors can be

Table 1. Four main Ecopath inputs and fisheries landings for the 2 models. P: production; B: biomass; Q: consumption; EE: ecotrophic efficiency (calculated by Ecopath). Some values are rounded

Functional group	1994 Model						2018 Model					
	Biomass (g m^{-2})	P/B (yr^{-1})	Q/B (yr^{-1})	Commercial landings (g m^{-2})	Recreational landings (g m^{-2})	EE	Biomass (g m^{-2})	P/B (yr^{-1})	Q/B (yr^{-1})	Commercial landings (g m^{-2})	Recreational landings (g m^{-2})	EE
Phytoplankton	22.982	225.7				0.355	18.881	274.7				0.409
Benthic algae	30.795	17.01				0.270	30.795	17.01				0.242
Zooplankton	7.125	78.32	215.0			0.498	8.389	78.32	215.0			0.339
Gelatinous zooplankton	42.357	2.000	5.600			0.072	8.737	2.000	5.600			0.499
Deposit feeding benthos	70.125	4.580	24.36			0.978	70.125	4.580	24.36			0.751
Susp. feeding benthos	26.760	4.650	12.81	6.142		0.352	26.760	3.715	12.81	3.003		0.161
Cultured shellfish	0.014	0.145	23.15			0.000	0.153	1.145	23.15	0.153		0.873
Carnivorous benthos	15.906	0.839	8.386	0.962		0.941	3.368	1.510	8.428	1.197		0.999
Small squid	0.461	3.950	23.65			0.999	1.201	3.265	13.63			0.845
Large squid	0.643	5.364	12.50	0.196		0.993	1.022	3.425	12.86	0.164		0.967
Planktivorous fish	12.304	2.376	10.88	13.261		0.997	18.423	1.305	10.57	4.455		0.984
Benthivorous fish	9.225	0.878	4.527	0.246	0.990	0.800	13.277	1.000	4.659	0.682	3.201	0.958
Piscivorous fish	2.081	1.494	4.635	0.290	2.144	0.988	3.805	0.962	4.561	0.259	1.976	0.990
Seabirds	0.043	0.141	7.750			0.824	0.040	0.141	7.750			0.824
Detritus	3.866					0.262	4.522					0.258

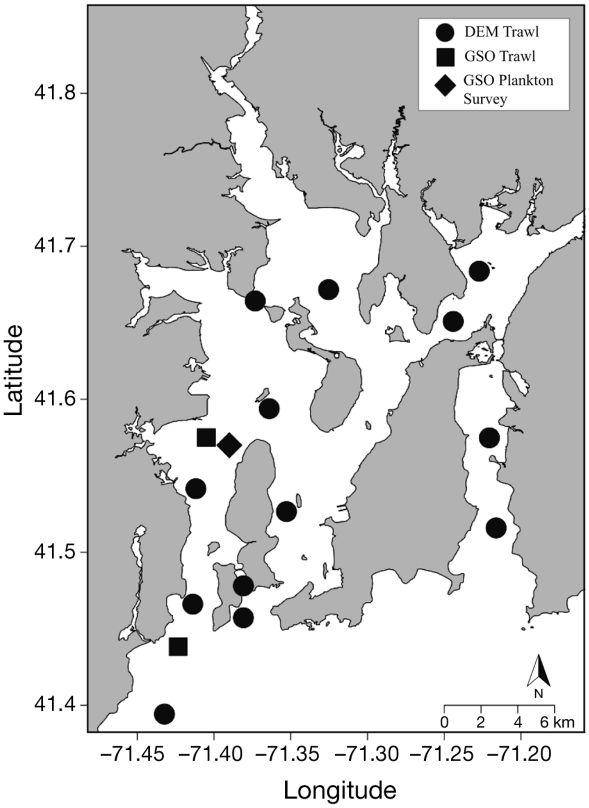

Fig. 1. Sampling stations in Narragansett Bay, Rhode Island, USA. DEM: Rhode Island Department of Environmental Management; GSO: University of Rhode Island Graduate School of Oceanography

found in the 'Functional group input' section of Supplement 2. Plankton data came from the URI GSO plankton survey (Fig. 1). Biomass for gelatinous zooplankton was calculated after square root transforming count data to account for extreme blooms during the time period of interest and using conversions between length and wet weight (Kremer & Nixon 1976). Biomasses for cultured shellfish, suspension feeding benthos, deposit feeding benthos, benthic algae, birds, and detritus were sourced from the literature (Supplement 2).

2.4. Other Ecopath parameters

For the majority of species, P/B was calculated as total mortality (Z), which is equal to the sum of natural (M) and fishing (F) mortality. This method of calculation was recommended by Christensen et al. (2005). Natural mortality (M) was obtained from FishBase (Froese & Pauly 2019), SeaLifeBase (Palomares & Pauly 2019), stock assessments, invertebrate M equations of Brey (2001), and other literature (Supplement 2). Fishing mortality (F) was calculated as catch divided by biomass (see Sections 2.5 and 2.3 for details on the origins of these values). P/B values for benthivorous fish, planktivorous fish, and carnivorous benthos were scaled up during model balancing ('Functional group input' section in Supplement 2). Species' Q/B values were obtained from FishBase (Froese & Pauly 2019), invertebrate consumption equations of Brey (2001), and other literature (Supplement 2). To calculate P/B and Q/B values for the functional group level, P/B or Q/B values at the species level were weighted by their biomass and then averaged. EE was calculated by Ecopath for all groups.

2.5. Fisheries landings

Recreational fisheries landings came from the National Oceanographic and Atmospheric Administration (NOAA) National Marine Fisheries Service query tool (www.st.nmfs.noaa.gov), selecting 'Inland Rhode Island' as the area of interest. Species landings were summed to get landings for each functional group, and were scaled down slightly to account for some release (Supplement 2). In the 1994 model, there was no commercial harvest of cultured shellfish. In the 2018 model, all commercial shellfish was assumed to be harvested. Commercial landings of other species were calculated in 1 of 2 ways. For several species, we used NOAA Vessel Trip Report (VTR) data for species caught within the latitude/longitude boundaries of Narragansett Bay (NOAA GARFO APSD Division unpubl. data). For other species, we used Rhode Island (RI) landings obtained through a custom data request from the Atlantic Coastal Cooperative Statistics Program (https://www.accsp.org/). RI landings data included all catch landed in RI regardless of area caught. Therefore, this catch was scaled to include only Narragansett Bay using data from the Northeast Fisheries Observer Program (National Marine Fisheries Service Northeast Fisheries Observer Program unpubl. data), since many species landed in RI are not caught locally (Hasbrouck et al. 2011). When using the landings-based method, the first scaling factor, determined through fisheries observer data of federal vessels, was the percentage of catch landed in RI that was caught in Northeast Fisheries Science Center Statistical Area 539 (averaged across years, https://www.fisheries.noaa.gov/resource/map/greater-atlantic-region-statistical-areas). The second scaling factor was the ratio of catch from Statistical Area 539 that was caught within Narragansett Bay (averaged across years, see Supplement 2 for more details). While these scaling factors were based on federally permitted vessel data only, and therefore assume the same proportions for landings from state-permitted vessels, they represent the best data available to estimate RI landings that were actually caught in the bay. Carnivorous benthos catch was scaled down additionally to account for other species, not included in our model, that were grouped into the reported catch (Supplement 2). Catch data source for each species (landings vs. VTRs) was determined based on personal communication and anecdotal evidence about the contribution of state-permitted only vessels to the landings. Higher state boat involvement favored the landings-based data, as only federally permitted vessels require observers and VTRs. While our methods for calculating catch require the previously stated assumptions, we believe these adjustments are appropriate to ensure that we are able to account for the activity of state-permitted vessels while not including local landings that were caught in other regions.

2.6. Diet

Diet information was sourced from a variety of literature, data collection, and data requests for more localized values (Supplement 2). The data reflect adult diets from studies conducted primarily in Narragansett Bay or other nearby estuaries in New England. We prioritized the data based on a number of factors, including date of publication, sample size, and level of prey identification detail. One consideration was standardizing reporting units across multiple studies. In general, diet studies in the literature were reported in 1 of 2 ways: percentage weight (preferred) or counts. We converted the latter to percentage weight through volumetric conversion, assuming spherical planktonic prey. Another important consideration that became apparent in our survey of the diet literature was how to standardize differences in life stages or taxonomic classification. Several types of adjustments were required. For studies that reported different categorizations of the predator (i.e. size, sex, sampling year), median prey percent weight was used. Grouped prey categories such as ‘unknown fish’ were assumed to have a consistent proportion of the identified species in a particular diet. For some species with a large amount of ‘unknown remains’ in their prey (e.g. menhaden, butterfish, squid), diet was adjusted based on the group most likely to make up those remains (based on qualitative or anecdotal evidence in literature). Non-organic material such as sand or rock was also removed from the diet. After these different adjustments, categories were reapportioned to sum to one and aggregated at the functional group level. Finally, we had to consider the origin of each prey species. To properly account for biomass brought into Narragansett Bay from outside the study system, prey species that occur in freshwater, are exclusively found in southern estuaries, or are found offshore, were assigned to the ‘import’ diet category, meaning the model will consider this biomass as coming from outside the system. Diet was researched for each individual species, and a biomass-weighted average was used for the diet of each functional group (Table 2). Minor adjustments were made to the diet matrices during model balancing, following the principle of parameter adjustment based on our confidence in the source data. The diet matrices varied slightly between the 2 models due to differences in biomass weighting between the time periods and adjustments to balance the model (Table 2).

2.7. PREBAL

We conducted PREBAL diagnostics following recommended best practices in EwE models (Ainsworth & Walters 2015, Heymans et al. 2016). This included studying trends in biomass, production, consumption, respiration (R), and vital rates (P/B, Q/B, R/B), which should all decrease with increasing trophic level (Fig. S3 in Supplement 1) (Link 2010). This analysis also included examining production/consumption (P/Q) values, which generally fell between 0.1 and 0.3, and production/respiration (P/R) values, which should be <1 (Fig. S4 in Supplement 1). The majority of the PREBAL diagnostics for both the 1994 and 2018 models were met, leading us to be confident that we were using biologically realistic input values (Tables S4 & S5 in Supplement 1). There were some values that did not follow the expected patterns in PREBAL (e.g. seabirds, cultured shellfish), but we deemed them acceptable for the model based on differences in data collection methodologies and variance; as stated by Heymans et al. (2016), values that do not follow the expected patterns are acceptable when justified (see Text S1C for these descriptions).

2.8. Ecosim

The 1994 model was made time-dynamic in Ecosim by using top-down and bottom-up forcing time series to fit the model to observed biomass time series. First,

Table 2. Diet matrices used in the 1994 and 2018 Ecopath models. Columns are predators and rows are prey. Values are proportions and are rounded to 4 decimal places

	Functional group	3	4	5	6	7	8	9	10	11	12	13	14
1994													
1	Phytoplankton	1.0000	0.0001	0.0197	0.8100	0.8100							
2	Benthic algae			0.0720			0.1355				0.0042	0.0005	
3	Zooplankton		0.5051	0.0039	0.1900	0.1900	0.0006	0.4763	0.1002	0.5995	0.0019		0.0002
4	Gelatinous zooplankton									0.0445	0.0022	0.0026	
5	Deposit feeding benthos		0.4374	0.0514			0.3186	0.2276	0.1386	0.3268	0.7777	0.0090	0.0151
6	Suspension feeding benthos		0.0428	0.0010			0.1533	0.0201	0.0002	0.0108	0.0875	0.0002	0.0029
7	Cultured shellfish												
8	Carnivorous benthos		0.0024	0.0001			0.0530			0.0022	0.0757	0.0324	0.0608
9	Small squid						0.0020		0.0900		0.0060	0.0600	
10	Large squid						0.0030	0.0010	0.0350		0.0085	0.2263	
11	Planktivorous fish		0.0122					0.2700	0.4682	0.0150	0.0282	0.3081	0.3742
12	Benthivorous fish						0.0170		0.0245		0.0045	0.2582	0.2837
13	Piscivorous fish								0.0245		0.0031	0.0322	0.0012
14	Seabirds												0.0150
15	Detritus			0.8419			0.2512					0.0705	
	Import		0	0.0100			0.0658	0.0050	0.1188	0.0012	0.0005		0.2469
2018													
1	Phytoplankton	1.000	0.0001	0.0197	0.8100	0.8100							
2	Benthic algae			0.0720			0.1355				0.0023	0.0005	
3	Zooplankton		0.5051	0.0039	0.1900	0.1900	0.0006	0.4713	0.0760	0.5995	0.0008		0.0002
4	Gelatinous zooplankton									0.0445	0.0005	0.0016	
5	Deposit feeding benthos		0.4374	0.0514			0.3188	0.2276	0.1386	0.3268	0.8649	0.0109	0.0151
6	Suspension feeding benthos		0.0428	0.0010			0.1533	0.0201	0.0002	0.0108	0.0384	0.0002	0.0029
7	Cultured shellfish												
8	Carnivorous benthos		0.0020				0.0003			0.0012	0.0500	0.0254	0.0408
9	Small squid						0.0020	0.0001	0.0900		0.0050	0.1014	
10	Large squid							0.0010	0.0138		0.0011	0.1703	
11	Planktivorous fish		0.0122					0.2710	0.4982	0.0150	0.0151	0.2092	0.3842
12	Benthivorous fish						0.0352		0.0345		0.0042	0.4053	0.2832
13	Piscivorous fish								0.0345		0.0026	0.0446	0.0017
14	Seabirds												0.0150
15	Detritus			0.8419			0.2497					0.0235	
	Import		0.0004	0.0101			0.1046	0.0089	0.1142	0.0022	0.0151	0.0071	0.2569

each 1994 Ecopath model input and diet value was assigned an uncertainty ranking (from 1–6, least to most certain) through the use of the pedigree function, based on our evaluation of each data source (Table S6 in Supplement 3). The forcing function time series used in our Ecosim model were empirically derived phytoplankton biomass (g m^{-2}), fishing mortality (F) for functional groups targeted by the fisheries, and cultured shellfish biomass (g m^{-2}). Fishing mortality was calculated as catch divided by biomass. In order to adjust the Ecosim model to resemble actual observed biomass data, we imported biomass time series for all available functional groups (piscivorous fish, planktivorous fish, benthivorous fish, carnivorous benthos, squid, gelatinous zooplankton). These observed biomass time series data, as well as the catch and biomass forcing function values, were collected and scaled in the same way as the numbers in the initial Ecopath model. Vulnerabilities, which refer to the extent to which a change in the predator's biomass will cause changes in predation mortality for a given prey group, often play a large role in model fitting (Text S1A, Eq. S4) (Christensen et al. 2005). To adjust vulnerabilities (from their default of 2.0), we used the 'Fit to Time Series' tool, which optimizes each vulnerability parameter by attempting to minimize the overall sum of squares (SS) (Christensen et al. 2005). We then made manual adjustments to reach the lowest SS in combination with the best trend matching for the functional groups of interest (Table S7 in Supplement 3). In addition, we modified 3 of the 'Group Info' parameters to improve model fit (Table S8 in Supplement 3). When tuning this model, we prioritized the piscivorous fish, benthivorous fish, planktivorous fish, and carnivorous benthos groups because of our confidence in these observed biomass time series data and interest in fisheries management. We then ran Monte Carlo simulations to quantify the uncertainty in biomass predictions, with confidence values imported from the pedigree matrix.

2.9. Analysis

We examined system-level indicators calculated from the output of the 2 Ecopath models, including total biomass, catch, production, consumption, respiration, throughput, mean trophic level of catch, and the primary:secondary production (PP:SP) ratio. Total biomass, catch, production, consumption, and respiration are sums of the respective values for each functional group. Total throughput is the sum of all flows in a system, estimated by summing total consumption, total export, total respiration, and total flows to detritus (Christensen et al. 2005). We calculated the PP:SP ratio by dividing the net PP output by the difference in the total system production and net PP (SP).

We ran the temporally dynamic Ecosim model both with and without forcing functions and adjusted vulnerabilities to quantify the variance in SS caused by each of these parameters (Shannon et al. 2004, Araújo et al. 2006). Using the fitted Ecosim model, we compared its projected 2018 biomass values to the empirical biomass input values of the 2018 static Ecopath model. We reported a scaled difference between these 2 values, calculated as the difference between the 2018 projection and the 2018 input, divided by the 2018 input. We also determined whether the realized direction of change was correctly predicted by the model.

3. RESULTS

3.1. System-level indicators

At both time periods, our models depicted functional groups with trophic levels ranging from 1 (phytoplankton, benthic algae) to >4 (seabirds, piscivorous fish) (Fig. 2). Of the 12 predatory functional groups, 9 preyed on 6 or more functional groups. The benthivorous and piscivorous fish groups had the most diverse diets, each consuming prey from more than 11 functional groups. Total consumption, respiration, throughput, biomass, catch, and mean trophic level of catch differed slightly between the 2 models (Table 3). Total production and PP:SP ratio were virtually the same in both models. Throughput from PP was higher than throughput from detritus in both models, albeit not by a large amount (Table 3).

3.2. Input comparison

Biomass varied between models across nearly all functional groups. The exceptions were benthic algae, deposit feeding benthos, and suspension feeding benthos, where only a single data source was available, not a time series, so the same values were used for the biomass in both models. Gelatinous zooplankton, consisting of a blooming ctenophore species (*Mnemiopsis leidyi*), had the largest change in biomass between the 2 models, from 42.357 to 8.737 g m^{-2} (Fig. 3). The most dramatic difference in the mid-

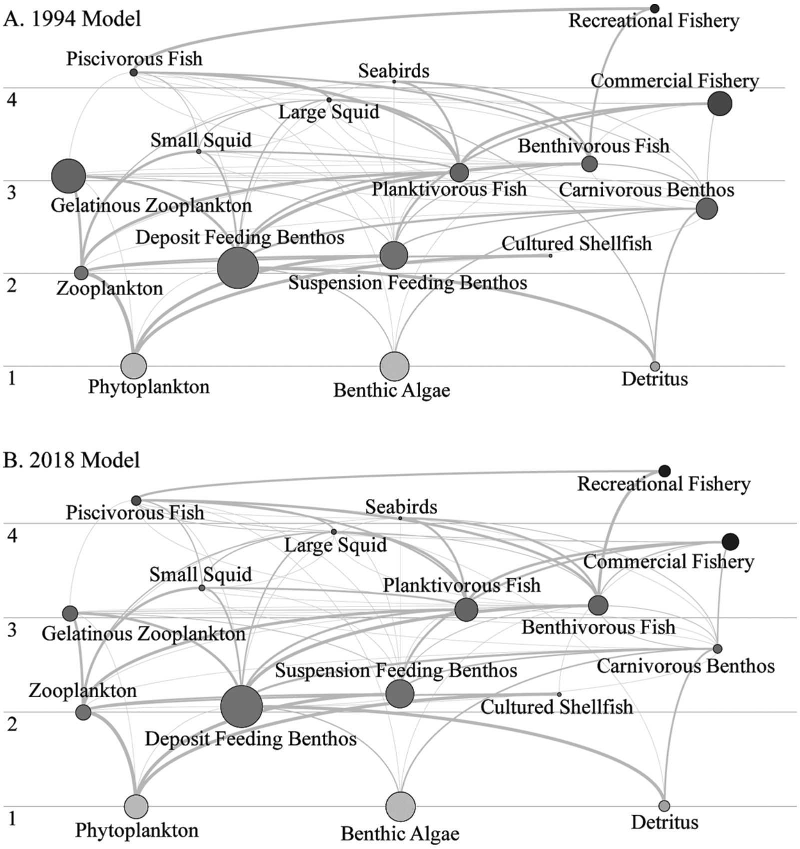

Fig. 2. Ecopath flow diagrams for the (A) 1994 and (B) 2018 models. Nodes are scaled to log(biomass) and the width of the line represents the amount of energy flow. Numbers on the *y*-axis indicate trophic level and are reflected by progressively darker colors (1: light grey to 4: black)

Table 3. Comparison of ecosystem indicators in the 1994 and 2018 Ecopath models. PP: primary production; SP: secondary production

Indicator	1994	2018
Total biomass, excluding detritus (g m^{-2} yr^{-1})	240.819	204.976
Total catch (g m^{-2} yr^{-1})	24.23	15.09
Mean trophic level of catch	2.963	3.061
Sum of all production (g m^{-2} yr^{-1})	6859	6860
Sum of all consumption (g m^{-2} yr^{-1})	4158	4239
Sum of all respiration (g m^{-2} yr^{-1})	1559	1564
Total throughput (g m^{-2} yr^{-1})	15525	15575
Throughput from PP (g m^{-2} yr^{-1})	8060	8239
Throughput from detritus (g m^{-2} yr^{-1})	7388	7221
PP:SP ratio	4.98	4.97

and UTL groups was in carnivorous benthos, for which biomass was almost 5 times larger in the 1994 model than in the 2018 model (Fig. 3). Examining species trends within each functional group, we found that Atlantic rock crab *Cancer irroratus* was the species responsible for much of this biomass decline. Rock crab biomass peaked in the 1990s and has since decreased (Fig. S5 in Supplement 3). All other mid- and UTL groups (with the exception of seabirds) had increased biomass in the 2018 model (Fig. 3). Within planktivorous fishes, there were increasing biomass trends in all species with the exception of blueback herring *Alosa aestivalis* (Fig. S5). The species that made up the majority of the planktivorous fish functional group biomass was Atlantic herring *Clupea harengus*, which has shown several biomass peaks since the mid-2000s (Fig. S5). The positive trends in piscivorous and benthivorous fish were largely due to increasing summer flounder and scup, respectively (Fig. S5).

Production rates (P/B) of squid, planktivorous fish, and piscivorous fish were higher in the 1994 model because both of these groups had lower biomass in the earlier model. The P/B values of carnivorous benthos and benthivorous fish were both higher in the 2018 model because of an increase in fisheries harvest of both species and a decrease in carnivorous benthos biomass. Cultured shellfish P/B also increased in the 2018 model (from 0.145 to 1.145), due to increased harvest. Consumption rates (Q/B) of the majority of functional groups were similar between the 2 models, since the same consumption rates for individual species were used, but weighted differently in the functional group average based on the biomass of that time point (Fig. 3). There was an exception to this in the 1994 model, for which Ecopath was required to calculate the Q/B and biomass for small squid due to the multi-stanza nature of this group.

The amount and composition of fisheries landings differed between the 2 models (Fig. 3). The recreational fishery landings increased in the 2018 model, and the proportions of functional groups in the catch changed. In both models, the recreational fishery targeted piscivorous and benthivorous fish. However, the recreational fishery landed mainly piscivorous fish in the 1994 model compared with landing mainly

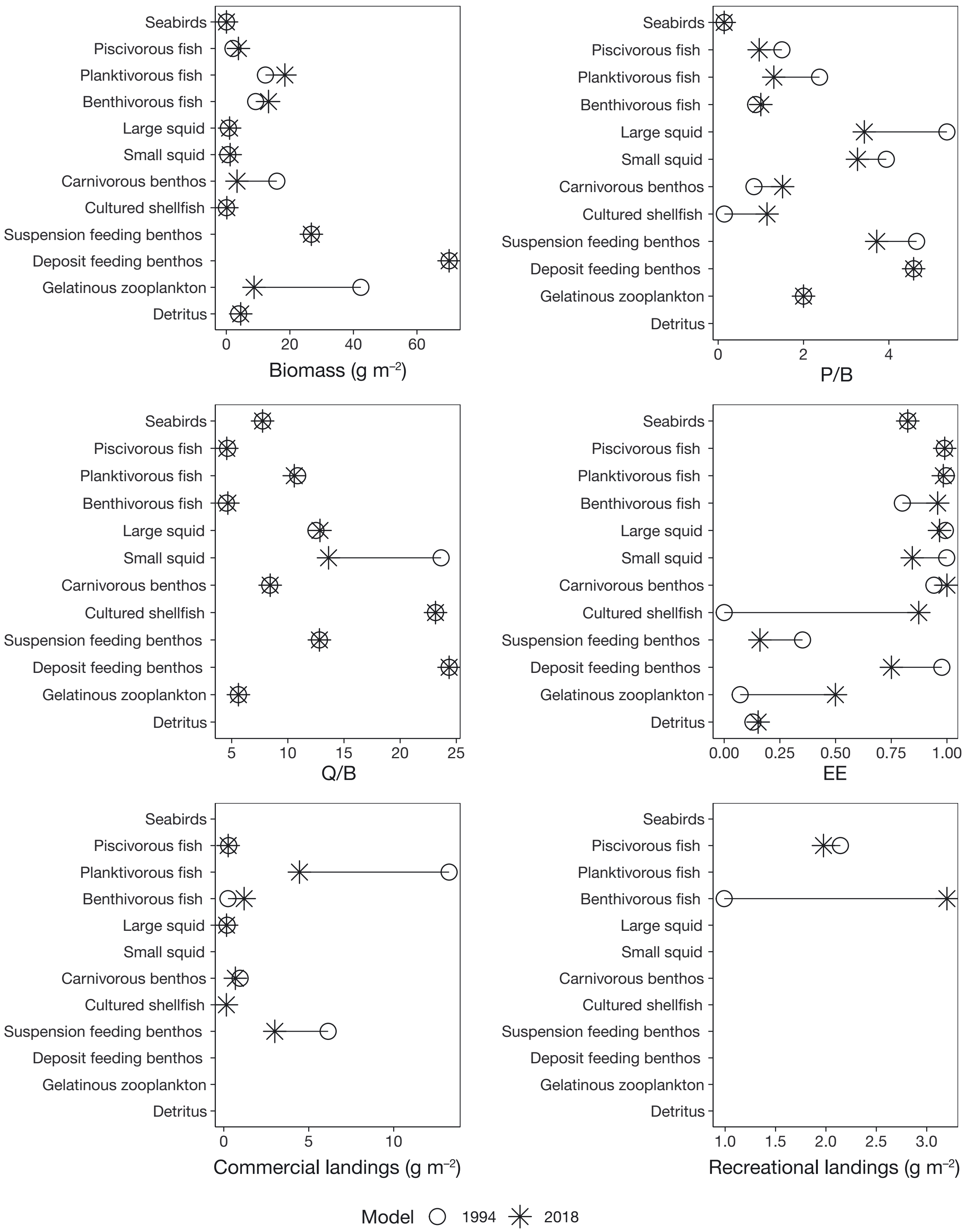

Fig. 3. Comparison of biomass, production/biomass (P/B), consumption/biomass (Q/B), ecotrophic efficiency (EE), and fisheries landings between the 1994 and 2018 Ecopath models. The horizontal line connecting the two points highlights the extent to which the values differ from 1994 to 2018. Phytoplankton, benthic algae, and zooplankton are not included due to their larger scales, but input values can be found in Table 1

benthivorous fish in the 2018 model (Fig. 3). There were no clear trends in piscivorous fish species landings, while landings of all species within the benthivorous fish functional group displayed increasing trends, with the largest increase seen in scup (Fig. S6 in Supplement 3). In the 1994 model, commercial landings were more than double what they were in the 2018 model, with most of this change being attributed to a decrease in planktivorous fish harvest (Fig. 3). Landings of both Atlantic herring and Atlantic menhaden showed declining trends (Fig. S7 in Supplement 3). There was also a noticeable decrease in commercial suspension feeding benthos harvest (Fig. 3).

3.3. Model sensitivity to external drivers

Using the 1994 Ecopath model as a starting point, we used time series data to create a time-dynamic Ecosim model. This model was run both with and without forcing functions and adjusted vulnerabilities, to determine the effect that these parameters have on model fit. We found that forced fishing mortality (F), forced phytoplankton biomass, and adjusted vulnerabilities all had large impacts on model fit, while forced cultured shellfish biomass did not (Table 4). All groups benefitted from the inclusion of these parameters, except gelatinous zooplankton, which had a lower SS when no forcing functions and vulnerability adjustments were used. When gelatinous zooplankton were excluded, the total SS decreased by over 50 % through the use of forcing functions and vulnerability adjustments. The SS for piscivorous fish showed particular improvement (89 % decrease) when forcing functions were used and vulnerabilities were changed, as did SS for benthivorous fish (53 % decrease) and carnivorous benthos (48 % decrease).

3.4. Projections

The fitted Ecosim model had the best fits for piscivorous fish and benthivorous fish, with poorer fits for planktivorous fish, large squid, carnivorous benthos, and small squid (Fig. 4). The model failed to capture the dynamics of gelatinous zooplankton (Fig. 4). The remainder of the functional groups did not have biomass time series data to compare to the model projections (Fig. S8 in Supplement 3). We projected the Ecosim model until 2018. The 2018 values predicted by this Ecosim model were compared to the empirical 2018 Ecopath model inputs to assess the similarity of these 2 sets of values. The Ecosim model predicted the correct direction of change for the biomass for all mid- and UTL groups (with the exception of seabirds) and had the best predictions of planktivorous fish (scaled difference = 0.002) and benthivorous fish biomass (scaled difference = 0.032) (Table 5). The model did not, however, predict the correct direction of change for gelatinous zooplankton biomass (Table 5). The difference between the biomass projections and 2018 input values varied across groups, with the largest difference seen in gelatinous zooplankton (scaled difference = 0.886) and carnivorous benthos (scaled difference = 0.758) (Table 5).

4. DISCUSSION

4.1. Insights into the Narragansett Bay food web and ecosystem

Our models showed strong benthic–pelagic coupling in Narragansett Bay. In the 2018 model, EE was lower for zooplankton, deposit feeding benthos, and suspension feeding benthos, meaning there were higher levels of other mortality in the model. This

Table 4. Sum of squares values produced for each functional group by the inclusion of each forcing function (FF): phytoplankton (phyto.), fishing mortality (F), and cultured shellfish (CS)

	No FF	Phytoplankton	F	CS	Phyto. / F / CS	Phyto. / F / CS + vulnerabilties	% Change from without FF
Benthivorous fish	9.92	5.10	13.33	9.92	5.59	4.66	−53.00
Piscivorous fish	26.56	11.28	6.21	26.56	3.95	2.77	−89.55
Planktivorous fish	8.53	11.16	7.93	8.53	11.75	7.94	−6.97
Carnivorous benthos	18.67	29.75	11.70	18.67	21.10	9.74	−47.83
Small squid	22.05	19.45	16.46	22.06	14.49	12.63	−42.74
Large squid	11.72	11.82	9.57	11.73	9.62	8.05	−31.34
Gelatinous zooplankton	76.39	91.64	74.32	76.39	89.69	100.64	+31.74
Total	173.85	180.21	139.51	173.86	156.21	146.43	−15.77
Total (no gel. zooplankton)	97.46	88.57	65.20	97.47	66.52	45.79	−53.02

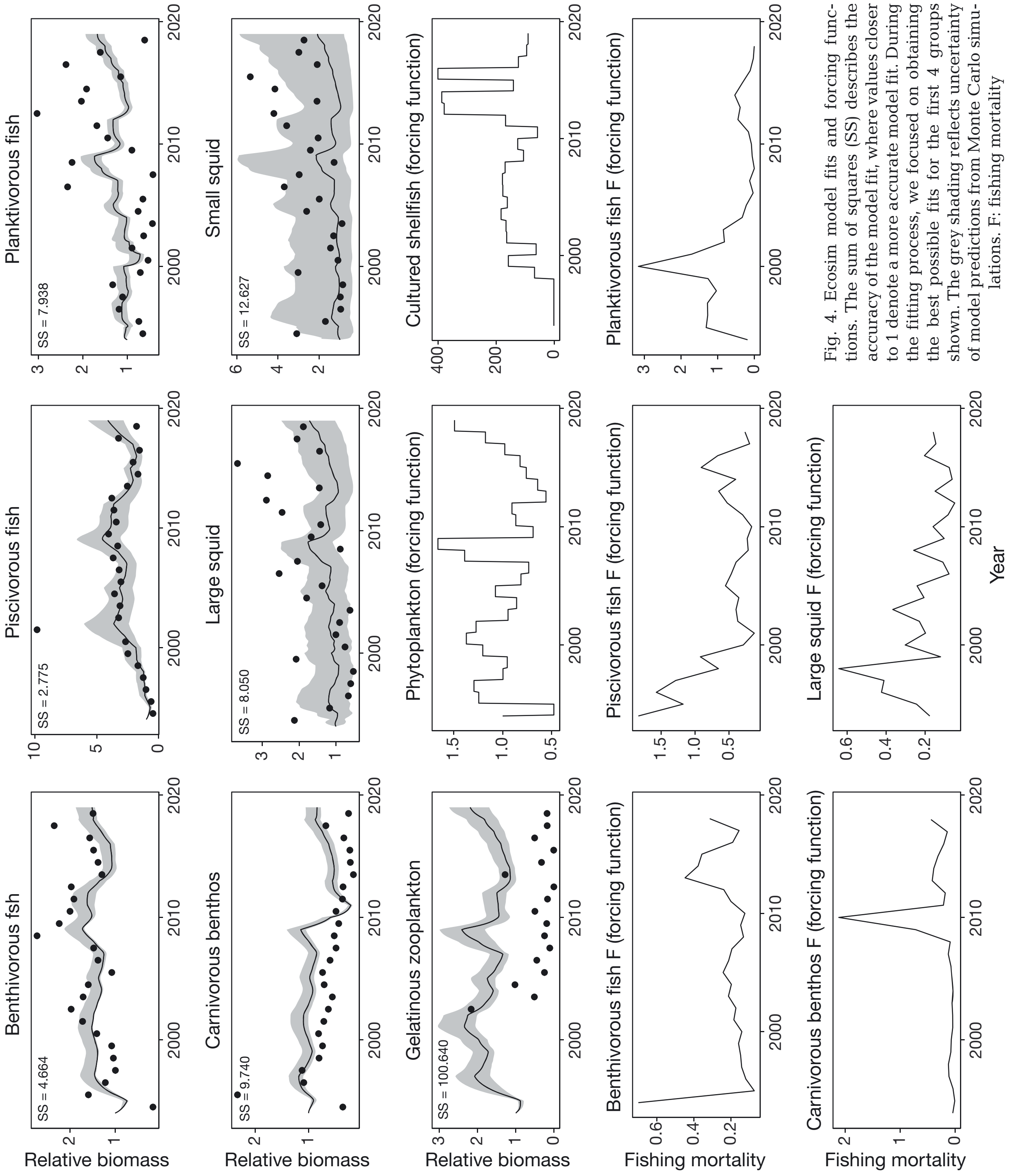

Fig. 4. Ecosim model fits and forcing functions. The sum of squares (SS) describes the accuracy of the model fit, where values closer to 1 denote a more accurate model fit. During the fitting process, we focused on obtaining the best possible fits for the first 4 groups shown. The grey shading reflects uncertainty of model predictions from Monte Carlo simulations. F: fishing mortality

could indicate that more energy is being recycled or exported in the current Narragansett Bay food web than in 1994. Slightly more energy in the system came from PP than detritus in both models; however, these values were similar and both close to 50%. The sizable proportion of energy that came from detritus could denote heightened system resilience in the face of climate change (Moore et al. 2004). Rising temper-

Table 5. Comparison of the Ecosim 2018 biomass (g m^{-2}) projections with the biomass inputs to the 2018 model. 2018 Projection denotes the value predicted by the Ecosim model for the year 2018. Scaled difference was calculated as (Projection — 2018 input) / 2018 input. NA: Not applicable

Functional group	1994 input	2018 projection	2018 input	Scaled difference	Correct direction of change?
Detritus	3.866	8.183	4.522	0.447	Yes
Phytoplankton	22.982	Forcing	18.811	NA	NA (forcing function)
Benthic algae	30.795	31.871	30.795	0.034	NA (no new data)
Zooplankton	7.125	7.131	8.3891	−0.176	Yes
Gelatinous zooplankton	42.357	76.822	8.737	0.886	No
Deposit feeding benthos	70.125	96.435	70.125	0.273	NA (no new data)
Suspension feeding benthos	26.76	32.847	26.76	0.185	NA (no new data)
Cultured shellfish	0.014	Forcing	0.153	NA	NA (forcing function)
Carnivorous benthos	15.906	13.940	3.368	0.758	Yes
Small squid	0.461	0.803	1.201	−0.496	Yes
Large squid	0.643	0.944	1.022	−0.083	Yes
Planktivorous fish	12.304	18.458	18.423	0.002	Yes
Benthivorous fish	9.225	13.716	13.277	0.032	Yes
Piscivorous fish	2.081	6.784	3.805	0.439	Yes
Seabirds	0.043	0.050	0.040	0.200	No

atures and acidification can increase primary producer biomass, but this biomass is converted to detritus rather than UTLs (Ullah et al. 2018). This pathway reduces the energy flow to UTLs and constrains production to the base of the food web, contributing to a reliance on recycling via the microbial loop (Monaco & Ulanowicz 1997). Thus, Narragansett Bay may be a more stable food web under changing environmental conditions than other estuaries with weaker benthic–pelagic coupling (e.g. Great South Bay, NY) (Nuttall et al. 2011).

By comparing our results to other estuarine models, we see that the system-level indicators of our model fall within the range of other estuaries. In our model, total biomass, production, consumption, respiration, and throughput are lower than those found in models of Delaware Bay (Frisk et al. 2011) and the Vellar Estuary, India (Murugan et al. 2012), which are larger and warmer systems than Narragansett Bay. These same measures are higher than those in models of Seine Bay (Tecchio et al. 2015) and the Bay of Mont Saint Michel, France (Arbach Leloup et al. 2008). While these 2 estuaries are also larger than Narragansett Bay, they experience less fishing pressure, which may result in lower estimated production. The comparability of our system-level indicators to other estuaries indicates that our model is a reasonable snapshot of Narragansett Bay.

In order to achieve balanced models, the diet matrices were slightly adjusted. For example, predation pressure from several groups (e.g. benthivorous fish, piscivorous fish, carnivorous benthos, and squid) was shifted in small amounts away from carnivorous benthos, planktivorous fish, and squid in the 2018 model and applied to other groups that had become more abundant in this time period. These adjustments were made due to uncertainty surrounding the diets, as well as potential diet flexibility in predators. Demersal fishes and crustaceans in the Chesapeake Bay have been shown to adapt their diets in the face of environmental change (Pihl et al. 1992). Larger piscivorous fishes, like striped bass and bluefish, have also been shown to exhibit plasticity in their diet (Nobriga & Feyrer 2008). Additionally, Szczepanski (2013) suggested that benthivorous fishes in Narragansett Bay are opportunistic or generalist feeders. It seems plausible that predators in Narragansett Bay have shifted their diets based on changing prey availability, but we would require diet studies from different time points to confirm this hypothesis.

While the biomasses of most mid- and UTL groups increased over the past 25 yr due to the growing abundance of warm-water species, this was not the case for carnivorous benthos. In Narragansett Bay, the high levels of carnivorous benthos seen in the 1994 model resulted from a documented expansion of the invertebrate populations after the decline of cold-water fish (Collie et al. 2008), which pre-dated our model. The years used for biomass in the 1994 model coincided with the peak of this expansion. The subsequent decline of carnivorous benthos, primarily driven by Atlantic rock crab, could be in part due to the combination of continued commercial harvest and increasing water temperature. In Chesapeake Bay, commercial harvest of the blue crab *Callinectes sapidus*, in combination with environmental degradation, has led to a reduction in its spawning stock, recruitment, larval abundance, and mean size (Abbe 2002, Lipcius & Stockhausen 2002, Zohar et al. 2008). Blue crabs have also been found to mature at smaller sizes, and have decreased fecundity, with increasing water temperature (Fisher 1999, Hines et al. 2010). It is possible that the carnivorous benthos in Narragansett Bay are also susceptible to these same pressures.

The inclusion of both top-down and bottom-up forcing functions in our model improved our model fits, indicating the importance of both processes for model prediction. Incorporating the top-down driver, fishing pressure (as fishing mortality, F) led to more precise model fits, especially for piscivorous fish and carnivorous benthos, suggesting that these fisheries are an important driver of ecosystem dynamics in Narragansett Bay. In addition to the changes in the fisheries, there was also evidence of bottom-up forcing. During the fitting of the model, the trend of forced phytoplankton biomass heavily influenced the model dynamics of some functional groups, with benthivorous and piscivorous fishes being particularly sensitive. This sensitivity indicates that phytoplankton are also an important driver in our modeled system, and by including them as a forcing function, we have adequately represented both top-down and bottom-up drivers of change. Cultured shellfish did not seem to be a main driver of biomass trends in our model. Additionally, adjusting vulnerabilities played an important role in improving model fits. Gelatinous zooplankton was the clear exception to this pattern, as the model was unable to capture its trends under any combination of forcing functions and vulnerabilities. The dynamics of this group are difficult to capture because of the episodic nature of the blooms. Historically, the blooms occurred in late summer and fall, although as temperature has increased in Narragansett Bay, the blooms have shifted earlier into the spring (Sullivan et al. 2001). However, when forced by the 2 main drivers (F and phytoplankton), the model was able to predict the correct direction of changes for all fishes and fished invertebrates. This leads us to believe that our Ecosim model is a good tool to look at biomass trends, particularly for those species groups occupying trophic levels of 3 and above in Narragansett Bay.

4.2. Future research directions

As stated earlier, although other food web models of Narragansett Bay have been created, our model is best suited for future research addressing EBM-related questions for the following reasons. There are some similarities between the Ecopath model of Byron et al. (2011) and ours, such as the use of some of the same data sources for fish and invertebrate species biomass (i.e. the RI DEM and URI GSO bottom trawls). There are also some consistencies in the chosen functional groups, such as planktivorous fish, suspension and deposit feeding benthos, and carnivorous benthos. Our model, however, diverges from that of Byron et al. (2011) in several ways. We have updated production by calculating a unique P/B value for each species, based on natural mortality from the literature and fishing mortality specific to Narragansett Bay. Consumption values were also derived from the best available literature rather than calculated by Ecopath. Unlike the model of Byron et al. (2011), we kept functional groups like squid and ctenophores, as well as piscivorous and benthivorous fish, separate because they consume very different assemblages of organisms and exhibit different population dynamics. By separating piscivorous and benthivorous fish groups, we have isolated how the recreational landings have shifted from one to the other, which is an important dynamic in Narragansett Bay that has not been published before. Lastly, we have made our model time-dynamic through the application of Ecosim, which had not been previously done for Narragansett Bay. Employing Ecosim presents a way to explore a variety of EBM-related questions that are not possible with a static Ecopath model, such as quantifying ecosystem change over time. This has made our model more amenable to a wide array of applications that simulate changes into the future.

Evaluating specific management strategies was not within this scope of this study, which aimed to create and validate a model that could be useful for management-focused questions. In the future, one possible use of this model could be exploring tradeoffs between the commercial and recreational fishing sectors of Narragansett Bay. As shown in our model, these fisheries target species that interact as predator and prey. Using our Ecosim model, one could change the amount harvested by a fishery and study the resulting biomass that remains available for the other fishery. The extent to which the harvest of one fishery influences another could indicate how dependent these fisheries are on each other, and thus whether they should be managed in conjunction. Another possible use of this model would be to study bottom-up impacts, such as how increased or decreased phytoplankton (as a proxy for nutrients) could change the ecosystem over time. This may be of interest to managers given the history of hypoxia in Narragansett Bay (Melrose et al. 2007). Additionally, rising temperatures may alter the physiological rates (i.e. production, consumption, and metabolism) of many species (McKenzie et al. 2016), which could be explored in our model if attempting to predict how the system may evolve under climate change. Simulating these types of scenarios could be useful for successful adaptive management in a changing ecosystem like Narragansett Bay.

A strategic use of ecosystem models is that by synthesizing available data and revealing important gaps, they allow researchers to provide direction and prioritization for future research and ecosystem monitoring activities. For example, a good area of future fieldwork would be to estimate modern day biomass values for deposit and suspension feeding benthos in Narragansett Bay, and to update the 2018 model accordingly. It is likely that suspension feeding benthos biomass would be higher than it was in the 1990s due to increasing restoration work (Griffin 2016) and decreasing commercial fishing pressure. These data would enable us to analyze the direction of change for these groups, for which time series data are currently not available. Incorporating seasonal dynamics, rather than our current annual time-step, could allow the model to capture changing residency times of migratory species and improve projections, particularly of the bloom groups like gelatinous zooplankton. A more recent zooplankton time series would also be beneficial for our 2018 model, given that there are several factors in the bay that may have influenced zooplankton biomass. For example, both menhaden (Durbin & Durbin 1998) and ctenophores (Deason 1982, Deason & Smayda 1982) exert significant control over zooplankton populations. Finally, had species-specific biomass data been available before 1994, it would have been interesting to create a mid-1900s model containing higher biomasses of cold-water species that are no longer prevalent, such as cunner *Tautogolabrus adspersus*, longhorn sculpin *Myoxocephalus octodecemspinosus*, northern searobin, winter flounder, and silver hake *Merluccius bilinearis* (Collie et al. 2008), and explore if Ecosim could predict the declines that occurred. Given that this cold-water regime occurring earlier in the century represented a distinctly different ecosystem state, it would likely have been more difficult for the model to predict these temperature-driven biomass trends.

5. CONCLUSIONS

The precision of Ecosim predictions is likely model- and system-dependent (Christensen & Walters 2004, Forrest et al. 2015). Our model was enhanced by the comparison of an Ecosim projection with present-day values that cover a 25 yr time period in Narragansett Bay. We have confidence in the trend predictions, particularly for the UTL groups in our Narragansett Bay model. However, these values and predictions should not be assumed to be directly applicable for models of other estuaries. Time series data were limited for some lower and mid-trophic levels, which is true of many coastal and estuarine ecosystems, and thus increased the variability of prediction in these groups. Even so, where data were available, such as for gelatinous zooplankton, the projected dynamics did not agree well with the data. Despite this, our model was precise in its prediction of patterns in the UTLs, including trends that have been quite pronounced in this rapidly changing estuarine ecosystem. Thus, our ecosystem food web model of Narragansett Bay is general and thorough enough to address a number of questions in support of EBM, such as studying food web responses to bottom-up drivers including nutrients and temperature as well as top-down impacts such as changing fisheries and top predator abundance levels through time.

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