



Potential role of spiny dogfish in gray and harbor seal diets in the Gulf of Maine

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ABSTRACT: Harbor seal *Phoca vitulina* and gray seal *Halichoerus grypus* populations have increased by 28.7% (1997–2001) and 8.6% (1999–present), respectively, in the Gulf of Maine. Here, we investigated what seals are eating and how their diet influences the food web in the Gulf of Maine. There is suggestion, but little evidence, that seals are eating spiny dogfish *Squalus acanthias*, currently an abundant species (standing stock biomass = 235 000 t) in the Gulf of Maine and surrounding areas. We used an Ecopath food web model to explore the potential of dogfish being a primary food source for seals and how this may be impacting the ecosystem. We explored various plausible diets for seals and the implications for other non-prey species in the ecosystem. In addition, white sharks *Carcharodon carcharias* have increased in abundance regionally, and shark predation on seals is documented in the southern Gulf of Maine. We therefore also explored top-down impacts of white shark predation on seals and lower trophic level fish species. Our results suggest that (1) dogfish could be contributing to the recovery of seal populations by providing an alternative prey base, (2) there is a tipping point between 10 and 20% of dogfish in seal diet that elicits a linearly increasing trend in seal biomass over time, and (3) seals as prey will have a continued impact on the projected increase in white shark biomass. This work advances our understanding of top-down control and may help to inform fisheries and resource management.

KEY WORDS: Food web · Ecopath with Ecosim · *Phoca vitulina* · *Halichoerus grypus* · *Squalus acanthias* · Cod · White shark · *Carcharodon carcharias*

INTRODUCTION

Although seals have been observed eating spiny dogfish *Squalus acanthias* in the Gulf of Maine, little to no evidence of this predator–prey interaction has been documented or quantified in the scientific literature. There is reason to suspect that this predator–prey interaction could have major implications for the Gulf of Maine food web. To date, much work has been done on the role of gray seals *Halichoerus grypus* and harbor seals *Phoca vitulina* in food webs (Morissette 2006, Bundy et al. 2009, Benoit et al. 2011). The discussion around this body of literature is primarily focused on the interactions between seals and Atlantic cod *Gadus morhua* and is restricted to the geographical range around the Eastern Scotian Shelf and the Gulf of St. Lawrence. Gray and harbor

seals do migrate into the Gulf of Maine, where their interactions with cod and other species are less well studied and where public perception of their interactions is highly polarized. Local newspapers capture this debate in dramatic headlines ranging from ‘As numbers of gray seals rise, so do conflicts’ (Whittle, Associated Press, July 2014; www.washingtontimes.com/news/2014/jul/20/as-numbers-of-gray-seals-rise-so-do-conflicts/?page=all), and ‘The Seal Problem - The population of seals on the Cape has expanded in recent years. Is it time to cull the herd?’ (Starobin, Boston Magazine, July 2013; www.bostonmagazine.com/news/article/2013/06/25/gray-seal-population-problem-cape-cod/) to the opposite extreme of ‘Marine animal lovers lament the loss of UNE [seal rehabilitation] program’ (Waugh, WCSH, May 2014; <http://legacy.wcsh6.com/story/news/local/biddeford-saco/>

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2014/05/25/loss-une-marc-program/9575047/). From these articles, it is clear that some individuals believe seals are a source of conflict for fishery resources. Fueling this argument are those who blame seals for the decline in cod, as captured by the headline 'Fishermen: Protected seals threatening cod population' (Morris, WGBH, 11 July 2013). Others believe that seal populations are still in danger and should continue to be rehabilitated. It is surprising that more is not known about seal–fish interactions in a food web where social contention is so high. In this study, we examined the food web dynamics of seal–dogfish–cod interactions in the Gulf of Maine.

The Gulf of Maine has experienced extreme declines in species such as Atlantic cod over the past several decades. For example, the spawning stock biomass of Atlantic cod has generally declined since 1982, and the current biomass is well below threshold levels (NEFSC 2013a). In contrast, seal populations have been on the rise (Waring et al. 2014). Atlantic cod has several predators in the Gulf of Maine, including fishermen, seals, and sharks (Smith & Link 2010). However, while seals are natural predators of Atlantic cod, it is not certain that they are a contributing cause to Atlantic cod declines in the region. Waring (2012) investigated this and found that seal-induced mortality rates on cod are low. Atlantic cod compete for resources with species such as spiny dogfish, which currently have a very large biomass in the Gulf of Maine (Rago & Sosebee 2013, Morgan & Sulikowski 2015). Populations of spiny dogfish have been variable throughout history, with a strong rebound since 2008 (Rago & Sosebee 2013). The interactions between these key predator and prey species (i.e. seals, cod, and spiny dogfish) are not well documented in the primary literature. It has been observed that spiny dogfish and harbor seals share some of the same food sources (Askin et al. 2012, Rafferty et al. 2012). It has also been observed in photographs that gray seals eat dogfish. To our knowledge, no research has been published scientifically documenting dogfish in seal diet due to the lack of hard parts in stomach and scat analyses. Furthermore, white shark *Carcharodon carcharias* predation on seals could indirectly impact dogfish and/or cod populations. Recent increases in the number of white sharks in Massachusetts (USA) have been partially attributed to increased seal populations (Skomal et al. 2012). Previous works have suggested that increases in pinniped abundance in the region could lead to increased predation by white sharks (Skomal et al. 2012). More work is needed on these key predator and prey species to fully understand the role of seals in the Gulf of Maine food web.

The Gulf of Maine food web is large and complex, and the above mentioned species comprise only a small portion of the species and interactions in the entire food web. Although this paper is focused on predator–prey interactions involving seals, white sharks, and dogfish and, to a lesser extent, Atlantic cod, we need to consider implications of these interactions across the entire ecosystem food web if we are to advise fisheries management or influence public perception. We therefore began our investigation by asking: (1) What is the capacity of the food web for perturbations in biomass of each species? We focused our investigation on our key species by asking (2) How does increased seal predation on spiny dogfish affect the food web? (3) What is the impact of combined seal and spiny dogfish predation on Atlantic cod? Finally, we asked: (4) How might white shark predation on seals impact the food web? To examine these questions, we built and manipulated an Ecopath with Ecosim food web model which allowed us to simulate these different scenarios.

METHODS

Gulf of Maine ecosystem

The Gulf of Maine region extends from Cape Cod, Massachusetts, USA, to Nova Scotia, Canada, and is often studied as a sub-ecosystem within the Northwest Atlantic Ocean. This body of water contains several basins and banks with the deepest water approximately 3000 m and a mean water depth of 139 m. Large tides result in intense tidal mixing (Loder & Greenberg 1986) and influence biological productivity (Townsend 1991, 1992). The Gulf of Maine's cyclonic circulation driven by density contrasts between surface and bottom waters and strong coastal currents also influences biological oceanography and nutrient budget, yielding high rates of primary production (O'Reilly & Busch 1984, Schlitz & Cohen 1984, Townsend et al. 1987). High primary production supports a biologically diverse ecosystem and several fisheries that have experienced many changes over the centuries (Auster 2002, Nye et al. 2010). Historically, groundfish have been the primary fishery in the Gulf of Maine (Acheson & Gardner 2014).

Modeling approach

The following section outlines the techniques that were used to answer our 4 overarching questions. To

answer question (1) we built a mass-balanced Ecopath model and increased the biomass of the included species until the model was no longer balanced. The remaining questions, viz. (2), (3), and (4), were addressed through scenarios using the time-dynamic simulation model (Ecosim). The Ecosim simulations are projected forward in time from the static mass-balanced Ecopath model. Before simulation scenarios were run, we fit a baseline simulation model to relevant time series data for species groups that are represented in the ecosystem. Details for each of these techniques are given below.

Ecopath model

The Ecopath with Ecosim (EwE) software package, based on Polovina (1984), has been widely used since the 1980s to analyze aquatic ecosystems through the use of food-web models (Kitchell et al. 2002, Libralato et al. 2006, Zhang & Chen 2007, Coll & Libralato 2012). The Ecopath modeling approach uses the Ecopath model to analyze the ecosystem's trophic mass balance. The model produces a static mass-balance 'snapshot' of the resources within an ecosystem and their interactions. These resources are commonly referred to as biomass 'pools' and they are trophically linked within the model (Christensen et al. 2008). There are 2 master equations within the Ecopath model: one that describes system production (Eq. 1) and another that describes energy balance for each group/species (see Eq. 6 below) (Christensen et al. 2008).

The first master equation used to describe this mass balance is:

$$\begin{aligned} \text{Production} = \\ \text{catch} + \text{predation mortality} + \text{biomass accumulation} \\ + \text{net migration} + \text{other mortality} \end{aligned} \quad (1)$$

Also written as:

$$P_i = Y_i + B_i M2_i + E_i + BA_i + P_i(1 - EE_i) \quad (2)$$

where P_i is the total production of species group i , Y_i is the total fishery catch rate of i , $M2_i$ is the total predation rate for group i , B_i is the biomass of group i , E_i is the net migration rate (emigration–immigration) of group i , BA_i is the biomass accumulation rate for group i , and EE_i is the ecotrophic efficiency of group i . Other mortality not caused by predation, MO_i , is internally computed by:

$$MO_i = P_i(1 - EE_i) \quad (3)$$

The total predation ($M2$) links predator and prey through:

$$B_i M2_i = \sum_{j=1}^n \left(B_j \frac{Q_j}{B_j} DC_{ji} \right) \quad (4)$$

where Q_j is the total consumption rate for the group and DC_{ji} is the fraction of predator j 's diet contributed by prey i . The mass-balance equation can also be rewritten as:

$$B_i \frac{P_i}{B_i} EE_i - \sum_{j=1}^n \left(B_j \frac{Q_j}{B_j} DC_{ji} \right) - Y_i - E_i - BA_i = 0 \quad (5)$$

The second master equation is the energy balance equation, which assumes energy input and output of all living groups is balanced in an ecosystem:

$$\begin{aligned} \text{Consumption } (Q_i) = \\ \text{production } (P_i) + \text{respiration } (R_i) \\ + \text{unassimilated food } (U_i) \end{aligned} \quad (6)$$

Input parameters and model balancing

The 103 000 km² Gulf of Maine was modeled and included a total of 11 individual species and 18 species groups (including detritus) known to inhabit this area under current conditions. Information on at least 3 of the following 4 parameters, i.e. biomass (B), production/biomass (P/B), consumption/biomass (Q/B), and ecotrophic efficiency (EE , the proportion of the production used in the system), are required for each species group in order for the model to balance. If one of the parameters is missing, the Ecopath model sets up a series of linear equations to solve the unknown values. When all parameters are available, the model estimates biomass accumulation or net migration (Christensen et al. 2008). Parameters B , P/B , and Q/B were collected from published literature and stock assessment reports (Tables 1 & 2).

Information on the diet and fishery removals for each species group is included in the model. For this study, individual species were used when there was sufficient information to parameterize the model. Species groups were used to represent other important organisms in this ecosystem (Christensen et al. 2008). Landings data, also needed in the model, were extracted from the National Marine Fisheries Service landings database and were combined with information on discards from available stock assessment reports to represent the total catch. Diet composition data were collected from the literature for all species and species groups (Tables 1 & 3). We used the Pedigree option within Ecopath to assign confidence intervals to the data (B , P/B , Q/B , diet, and catch) based on their origin (Pauly et al. 2000).

Table 1. Ecopath food web model species group names and their assigned group number used in subsequent tables. References are provided for diet and basic parameter data used in both the 2014 and 1950 models

Group no.	Group name (species included in group)	Diet data source	Basic parameters data source
1	Toothed whale (<i>Eubalaena glacialis</i> , <i>Physeter macrocephalus</i> , <i>Globicephala melas</i> , <i>G. macrorhynchus</i> , <i>Lagenorhynchus acutus</i> , <i>Delphinus delphis delphis</i> , <i>Tursiops truncatus truncatus</i> , <i>Phocoena phocoena phocoena</i>)	Link et al. (2006)	Link et al. (2006), Waring et al. (2014)
2	Baleen whale (<i>Balaenoptera physalus</i> , <i>B. cutostrata</i> , <i>Megaptera novaeangliae</i> , <i>Eubalaena glacialis</i> , <i>B. musculus</i> , <i>B. borealis</i>)	Link et al. (2006)	Link et al. (2006), Waring et al. (2014)
3	White shark (<i>Carcharodon carcharias</i>)	LeBoeuf et al. (1982), Cliff et al. (1989, 1996), Skomal et al. (2012)	Link et al. (2006)
4	Shark (<i>Lamna nasus</i> , <i>Prionace glauca</i> , <i>Isurus oxyrinchus</i>)	Joyce et al. (2002), McCord & Campana (2003)	Kitchell et al. (2002), ICCAT (2012b)
5	Harbor seal (<i>Phoca vitulina</i>)	Wood (2001), Smith et al. (2015)	Waring et al. (2000, 2009), Link et al. (2006)
6	Gray seal (<i>Halichoerus grypus</i>)	Ampela & Ferland (2006), Beck et al. (2007)	Waring et al. (1997, 2009)
7	Tuna (<i>Thunnus obesus</i> , <i>T. albacares</i> , <i>T. thynnus</i>)	Logan (2009), Froese & Pauly (2012)	ICCAT (2010, 2011, 2012a)
8	Spiny dogfish (<i>Squalus acanthias</i>)	Smith & Link (2010)	Clark (1998), TRAC (2010b), Rago & Sosebee (2013)
9	Skates (<i>Raja eglanteria</i> , <i>Leucoraja erinacea</i> , <i>L. garmani</i> , <i>L. ocellata</i> , <i>Malacoraja senta</i> , <i>Amblyraja radiata</i>)	Ebert & Bizzarro (2007)	Savenkoff et al. (2001), Zhang & Chen (2007), NEFSC (2009b)
10	Atlantic cod (<i>Gadus morhua</i>)	Smith & Link (2010)	NEFSC (2013a)
11	Other groundfish (<i>Anarhichas lupus</i> , <i>Pollachius virens</i> , <i>Zoarces americanus</i> , <i>Melanogrammus aeglefinus</i> , <i>Sebastes</i> spp.)	Smith & Link (2010)	NEFSC (1997, 2001, 2012b), Froese & Pauly (2012), TRAC (2012a,b)
12	Mackerel (<i>Scomber scombrus</i>)	Smith & Link (2010)	TRAC (2010a), Byron et al. (2011), Froese & Pauly (2012)
13	Flatfish (<i>Pleuronectes ferruginea</i> , <i>Hippoglossoides platessoides</i> , <i>H. hippoglossus</i> , <i>Glyptocephalus cynoglossus</i> , <i>Scophthalmus aquosus</i> , <i>Pleuronectes ferruginea</i> , <i>Pseudopleuronectes americanus</i> , <i>Paralichthys denatus</i>)	Smith & Link (2010)	NEFSC (2011, 2012b, 2013c), Froese & Pauly (2012)
14	Hake spp. (<i>Urophycis chuss</i> , <i>U. tenuis</i> , <i>Merluccius albidus</i> , <i>M. bilinearis</i>)	Smith & Link (2010)	NEFSC (2011), Froese & Pauly (2012)
15	Atlantic butterfish (<i>Peprilus triacanthus</i>)	Smith & Link (2010)	NEFSC (2014)
16	Atlantic herring (<i>Clupea harengus</i>)	Smith & Link (2010)	Shepherd et al. (2009), Froese & Pauly (2012)
17	Sand lance (Ammodytidae)	Smith & Link (2010)	Link et al. (2006)
18	Squid (<i>Loligo pealei</i>)	Smith & Link (2010)	Kitchell et al. (2002), NEFSC (2011)
19	Crustaceans (<i>Homarus americanus</i> , <i>Callinectes sapidus</i>)	Laughlin (1982), Elner & Campbell (1987)	Link et al. (2006), Walters et al. (2008), ASMFC (2009), DEM (2011)
20	Shrimp (<i>Pandalus borealis</i>)	Savenkoff et al. (2006)	Walters et al. (2008), NEFSC (2007, 2014), Overholtz & Link (2009)

Table 1 (continued)

Group no.	Group name (species included in group)	Diet data source	Basic parameters data source
21	Other fish	Smith & Link (2010)	Sissenwine (1987), Zhang & Chen (2007)
22	Bivalves (<i>Arctica islandica</i> , <i>Spisula solidissima</i> , <i>Placopecten magellanicus</i>)	NEFSC (2009a, 2010), Tam & Scrosati (2011)	NEFSC (2009a, 2010, 2011), Tam & Scrosati (2011)
23	Benthic invertebrates	Link et al. (2006)	Link et al. (2006)
24	Polychaetes	Feder & Jewett (1988)	Savenkoff et al. (2001), Link et al. (2006)
25	Gelatinous zooplankton	Link et al. (2006)	Link et al. (2006)
26	Macrozooplankton	Link et al. (2006)	Overholtz & Link (2009)
27	Microzooplankton	Link et al. (2006)	Zhang & Chen (2007)
28	Phytoplankton	Cahoon & Cooke (1992)	Zhang & Chen (2007)
29	Detritus	–	Heymans (2001), Link et al. (2006)

Table 2. Basic estimates of the balanced 2014 static Ecopath food web model. See Table 1 for species group descriptions. Habitat area is the fraction of the study area considered for each species group. Production/biomass (P/B), consumption/biomass (Q/B), and production/consumption (P/Q) are rates per year. Ecotrophic efficiency (EE) is the proportion of production used

Group	Trophic level	Habitat area (fraction)	Biomass in habitat area ($t\ km^{-2}$)	Biomass ($t\ km^{-2}$)	P/B (yr^{-1})	Q/B (yr^{-1})	EE	P/Q (yr^{-1})
1	4.13	1	0.12	0.12	0.10	1.00	0.26	0.10
2	3.25	1	0.19	0.19	0.10	1.00	0.19	0.10
3	4.58	1	0.004	0.004	0.16	1.27	0.00	0.13
4	4.25	0.01	2.10	0.02	0.32	3.05	0.09	0.10
5	4.28	1	0.05	0.05	0.12	1.00	0.08	0.12
6	4.31	1	0.04	0.04	0.12	1.00	0.24	0.12
7	4.08	0.01	4.33	0.04	0.80	5.41	0.85	0.15
8	4.02	1	2.30	2.30	0.90	4.79	0.06	0.19
9	3.65	1	0.95	0.95	0.65	3.59	0.11	0.18
10	3.96	1	0.31	0.31	0.65	3.09	0.21	0.21
11	3.40	1	4.50	4.50	1.20	4.40	0.86	0.27
12	2.89	1	1.09	1.09	0.85	4.45	0.85	0.19
13	3.68	1	0.90	0.90	0.65	4.01	0.60	0.16
14	3.83	1	0.92	0.92	0.95	4.27	0.93	0.22
15	2.85	1	0.80	0.80	1.10	6.00	0.48	0.18
16	3.02	1	6.50	6.50	1.00	3.83	0.83	0.26
17	3.05	1	1.20	1.20	1.00	5.26	0.85	0.19
18	3.30	1	0.92	0.92	1.60	6.93	0.50	0.23
19	2.76	1	7.00	7.00	3.00	11.59	0.14	0.26
20	2.85	1	0.50	0.50	2.60	13.50	0.86	0.19
21	2.88	1	10.50	10.50	1.20	4.38	0.96	0.27
22	2.34	1	15.46	15.46	1.50	7.00	0.33	0.21
23	2.66	1	15.00	15.00	2.00	13.50	0.97	0.15
24	2.28	1	16.00	16.00	2.70	24.68	0.63	0.11
25	2.32	1	11.00	11.00	40.00	141.56	0.18	0.28
26	2.20	1	42.00	42.00	30.00	103.42	0.14	0.29
27	2.00	1	50.00	50.00	50.00	227.65	0.57	0.22
28	1.00	1	90.00	90.00	160.00	0.00	0.60	
29	1.00	1	100.00	100.00			0.48	

Model validation

In order to validate biological parameter estimates, we applied several pre-balance diagnostics identified by Link (2010). We assessed the biomass levels across taxa and trophic levels, the production to consumption (P/Q) ratio, and compared the biomass (B) ratios of predator and prey and the ratios of production to biomass (P/B), consumption to biomass (Q/B), and respiration to biomass (R/B) (i.e. vital rates) by taxon. In a biologically realistic model, the biomass levels will show a generally increasing trend as the trophic levels decrease, the P/Q ratios will be <1 and confined between 0.1 and 0.3, the predator to prey B ratios will be <1 , and the vital rates will also show a general decrease with increasing trophic levels (Link 2010). In addition, we compared our values with values used in other Ecopath models from the region (Morgan & Sulikowski 2015). The input parameter values, after they underwent diagnostics, were used in mass balancing the model according to Eqs. (1–6). This final static mass-balanced model is hereafter referred to as the 'baseline' model.

Capacity of the food web

To examine the capacity of the food web model for perturbations, sensitivity analyses were performed on the balanced static baseline model. First, the biomass of each species was independently increased by factors of 2 \times , 10 \times , and 100 \times until the model became unbalanced. The biomass of each species was reset to its original balanced value before examining the subsequent species. Second, a mixed trophic impact (MTI) analysis was performed (Christensen et al. 2008). An MTI analysis allows for graphical representation of the magnitude of positive or negative impacts each species has on all other species. From this analysis, the most impactful species interactions in the food web can be identified.

Ecosim

Ecosim was used to run model simulations over several decades. Ecosim uses the mass-balance results from Ecopath for parameter estimation and can use time series of fishing mortality rates, abundance, catch, or total mortality to calibrate the model (Christensen et al. 2008). Ecosim allows the user to utilize a search routine for fitting. This routine estimates the sum of squares between log observed and log esti-

mated values, can be used to fit primary production anomalies, and fit vulnerabilities, which control bottom-up and top-down occurrences.

Ecosim uses the balanced Ecopath parameters to produce estimates of biomass and catch rates over time. Ecosim uses the following equations to do this:

$$dB_i / dt = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i) B_i \quad (7)$$

where dB_i/dt is the growth rate in terms of biomass (B_i) over time for group i , and g_i is the production to consumption ratio. Q_{ji} is the total consumption by group i , Q_{ij} is the predation by all predators on group i . The immigration rate is I_i and emigration is e_i , natural mortality is MO_i , and F_i is the fishing mortality rate (Christensen et al. 2008).

Consumption rates, based on the foraging arena concept that assumes there are different states during which prey are vulnerable and invulnerable to predation (Walters et al. 1997, Ahrens et al. 2012), are calculated using the following equation:

$$Q_{ij}(B_i, B_j) = \frac{a_{ij} v_{ij} B_i B_j}{2v_{ij} + a_{ij} B_j} \quad (8)$$

where a_{ij} is the search rate for prey i by predator j , v_{ij} is the vulnerability parameter (low vulnerabilities close to 1 indicate bottom-up control and high vulnerabilities lead to top-down control), and B_i and B_j are the prey and predator biomass, respectively (Christensen et al. 2008).

Model fitting and performance testing

To project change over time, we developed an Ecosim model that ran forward in time, using time series data (Table 4), from a static baseline model describing conditions in 1950 (Table 5). Time series of abundance, catch rates, fishing mortality, and catch were used to verify the predictions of the model. The Ecosim model was run from 1950 to 2074. This time frame was chosen to maximize the use of historical data for parametrizing Ecosim (fishing data has been collected since 1950, approximately 6 decades) and to mirror a similar duration into the future. Time series, abundance, and fishing mortality data were collected from the most recent stock assessment reports (Table 4). We calibrated the model using a non-linear optimization routine to (1) estimate vulnerability parameters, (2) indicate how well the model fit the data, and (3) investigate the impact of primary production forcing functions on the model fit (Mackinson et al. 2009). To start, the model

Table 4. Time series data used for each species group (defined in Table 1) in the Ecosim model

Species group	Time series used in Ecosim model	References
3	White shark observer (1998–2008) White shark tournament (1964–1989)	Curtis et al. (2014)
4	Irish fishery blue shark (1980–2005) Japanese longline blue shark (1971–2005) Spanish longline blue shark (1997–2005) US logbook blue shark (1986–2005) Spanish longline shortfin mako shark (1990–2010) Japanese longline shortfin mako shark (1994–2010) Marine Recreational Fisheries Statistics Survey (MRFSS) shortfin mako shark (1981–2010) Portuguese longline shortfin mako shark (2000–2010) US logbook shortfin mako shark (1986–2010)	ICCAT (2008, 2012b)
7	Yellowfin tuna Japan (1965–2009) Yellowfin tuna Taiwan (1968–2008) Bigeye tuna (1961–2008) Albacore Taiwan (1967–2011) Albacore Japan (1977–2011)	ICCAT (2010, 2011, 2013)
8	Spiny dogfish fishing (F) (1990–2012) Spiny dogfish standing stock biomass (SSB) (1991–2013) Spiny dogfish Northeast Fisheries Science Center (NEFSC) spring trawl (1968–2013) Spiny dogfish NEFSC winter trawl (1992–2006)	Rago & Sosebee (2013)
9	Little skate NEFSC fall survey (1995–2005) Little skate NEFSC spring survey (1976–2006) Little skate NEFSC winter survey (1992–2006) Winter skate NEFSC spring survey (1968–2006) Winter skate NEFSC autumn survey (1967–2005) Thorny skate NEFSC spring survey (1968–2006) Thorny skate NEFSC autumn survey (1963–2005)	NEFSC (2009b)
10	Atlantic cod F (1987–2011) Atlantic cod Massachusetts Department of Marine Fisheries (MADMF) spring (1978–2010) Atlantic cod National Marine Fisheries Service (NMFS) fall (1963–2010) Atlantic cod NMFS spring (1963–2010)	NEFSC (2013a)
12	Atlantic mackerel SSB (2000–2008)	NEFSC (2006)
13	Winter flounder New Jersey Department of Environmental Protection (NJDEP) spring (1984–2010) Winter flounder MADM spring F (1978–2010) Winter flounder F (1981–2010) Winter flounder NEFSC fall trawl (1976–2010) Winter flounder NEFSC trawl spring (1976–2010) Winter flounder NEFSC winter (1992–2007) Winter flounder Rhode Island Department of Fish and Wildlife (RIDFW) spring (1979–2010) Summer flounder F (1987–2012) Summer flounder SSB (1987–2012) Summer flounder NEFSC spring trawl (1968–2008) Summer flounder NEFSC winter trawl (1992–2007) Yellow flounder F (1994–2011) American plaice F (1980–2010) American plaice SSB (1980–2010) American plaice NEFSC spring (1968–2011) American plaice NEFSC autumn (1963–2009) Witch flounder F (2002–2010) Witch flounder NEFSC spring trawl (1968–2011) Witch flounder NEFSC autumn trawl (1963–2010)	NEFSC (2011, 2013c)
14	White hake F (1991–2011) White hake otter trawl (1975–2011) White hake sink gillnet (1994–2011) Red hake F (2000–2009) Red hake NEFSC fall survey (1963–2009) Red hake NEFSC spring survey (1963–2009) Offshore hake NEFSC fall survey (1969–2008)	NEFSC (2011, 2013b)

Table 4 (continued)

Species group	Time series used in Ecosim model	References
15	Atlantic butterfish F (1994–2012) Atlantic butterfish Connecticut (CT) spring bottom trawl (1992–2008) Atlantic butterfish Massachusetts (MA) fall bottom trawl (1982–2008) Atlantic butterfish NEFSC fall bottom trawl (1975–2008) Atlantic butterfish NEFSC spring bottom trawl (1968–2008) Atlantic butterfish NEFSC winter bottom trawl (1992–2007)	NEFSC (2010)
16	Atlantic herring F (1998–2011) Atlantic herring SSB (1998–2011) Atlantic herring NEFSC spring survey (1968–2008) Atlantic herring NEFSC winter survey (1992–2007)	NEFSC (2012a)
18	Loligo F (1992–2009) Loligo SSB (1987–2009) Loligo NEFSC fall survey (1975–2008) Loligo NEFSC spring survey (1976–2008)	NEFSC (2011)
19	American lobster F (1982–2006) American lobster Southern New England (SNE) spring trawl, male (1982–2007) American lobster SNE spring trawl, female (1982–2007) American lobster SNE fall trawl, male (1982–2007) American lobster SNE fall trawl, female (1982–2007) American lobster Gulf of Maine (GOM) spring, male (1982–2007) American lobster GOM fall, male (1982–2007) American lobster GOM spring, female (1982–2007) American lobster GOM fall, female (1982–2007) American lobster MA fall trawl, male (1982–2007) American lobster MA fall trawl, female (1982–2007)	ASMFC (2009)
20	Shrimp Northern Shrimp Technical Committee (NSTC) (1984–2006)	NEFSC (2007)
22	Atlantic surfclam F (1991–1999) Atlantic surfclam SSB (1991–1999) Atlantic surfclam Southern Virginia (SVA) (1982–2011) Atlantic surfclam Delmarva (DMV) (1998–2011) Atlantic surfclam New Jersey (NJ) (1982–2011) Atlantic surfclam SNE (1982–2011) Atlantic surfclam Georges Bank (GBK) (1986–2008) Quahog NEFSC GBK (1987–2007)	NEFSC (2013b)

was rescaled from the current 2014 baseline to the historic 1950 baseline level (Table 5). We used information in stock assessments and other published literature to inform our decisions to increase biomass and decrease catch and fishing mortality levels. To provide confidence in these rescaled parameters, we compared the 1950 model's final predicted biomass estimates to our original parameter estimates (Fig. 1). We used the following 3 methods to tune the model by reducing the sum of squares. The final model was used in all scenarios.

1. Simulate the base case model with a default vulnerability level of 2 and all time series.

2. Search for sensitive vulnerabilities. Vulnerability parameters were searched for (1) all predator–prey interactions and (2) groups with time series. We used the Ecosim built-in Vulnerability Search for this procedure. Any gross deviations that resulted in clearly unrealistic results were manually corrected.

3. Apply primary production as a driver (forcing function) of bottom-up ecosystem changes. The Ecosim 'anomaly search' button was used in 2 fitting scenarios (see Figs. S1 & S2 in the Supplement, available at www.int-res.com/articles/suppl/m550p249_supp.pdf; Table 6). This allows the model to search for a primary production anomaly and set of vulnerabilities that minimize the sum of squares. One primary producing forcing function was manually drawn within Ecosim (Fig. S3) and one was developed based on phytoplankton abundance estimates in the Gulf of Maine (Fig. S4).

We recorded the results of each model run in Table 6.

Simulation scenarios

In total, 11 different scenarios were investigated (Table 7), using the best fitting model (based on

Table 5. Basic estimates of the balanced 1950 static model used as the starting point for Ecosim simulations. See Table 1 for species groups and Table 2 for column header abbreviations

Group	Trophic level	Habitat area (fraction)	Biomass in habitat area (t km ⁻²)	Biomass (t km ⁻²)	<i>P/B</i> (yr ⁻¹)	<i>Q/B</i> (yr ⁻¹)	<i>EE</i>	<i>P/Q</i> (yr ⁻¹)
1	4.13	1	0.10	0.10	0.10	1.00	0.03	0.10
2	3.25	1	0.18	0.18	0.10	1.00	0.00	0.10
3	4.34	1	0.004	0.004	0.20	1.27	0.71	0.16
4	4.23	0.01	2.90	0.03	0.32	3.05	0.11	0.10
5	4.28	1	0.01	0.01	0.12	1.00	0.72	0.12
6	4.31	1	0.01	0.01	0.12	1.00	0.80	0.12
7	4.08	0.01	6.00	0.06	0.80	5.41	0.12	0.15
8	4.01	1	2.20	2.20	0.90	4.79	0.00	0.19
9	3.64	1	1.00	1.00	0.65	3.59	0.01	0.18
10	3.96	1	0.65	0.65	0.65	3.09	0.59	0.21
11	3.40	1	4.50	4.50	1.30	4.40	0.91	0.30
12	2.89	1	1.30	1.30	0.85	4.45	0.82	0.19
13	3.68	1	1.00	1.00	0.65	4.01	0.69	0.16
14	3.83	1	1.10	1.10	1.00	4.27	0.91	0.23
15	2.85	1	1.00	1.00	1.10	6.00	0.38	0.18
16	3.02	1	6.50	6.50	1.10	3.83	0.73	0.29
17	3.05	1	1.35	1.35	1.35	5.26	0.97	0.26
18	3.30	1	1.00	1.00	1.60	6.93	0.48	0.23
19	2.76	1	7.00	7.00	3.00	10.00	0.13	0.30
20	2.85	1	0.80	0.80	3.00	13.50	0.47	0.22
21	2.88	1	12.00	12.00	1.30	4.38	0.99	0.30
22	2.34	1	15.00	15.00	1.50	7.00	0.36	0.21
23	2.66	1	17.00	17.00	2.60	13.50	0.73	0.19
24	2.28	1	16.00	16.00	2.70	24.68	0.67	0.11
25	2.32	1	11.00	11.00	40.00	141.56	0.19	0.28
26	2.20	1	40.00	40.00	30.00	103.42	0.15	0.29
27	2.00	1	50.00	50.00	50.00	227.65	0.55	0.22
28	1.00	1	90.00	90.00	160.00	0.00	0.59	
29	1.00	1	100.00	100.00			0.47	

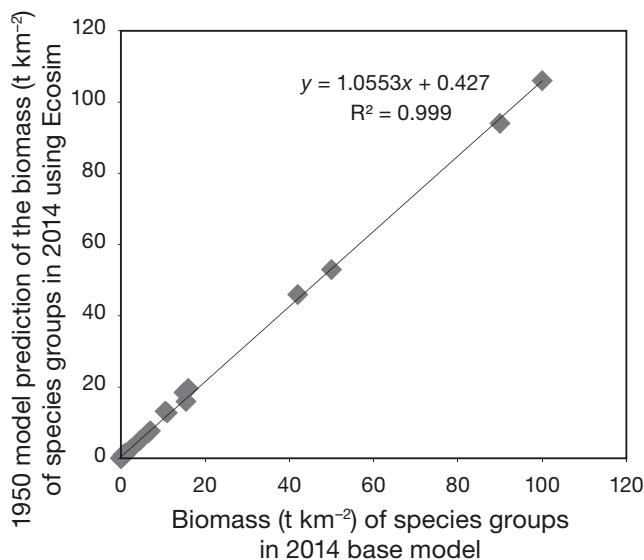


Fig. 1. Linear relationship between the predicted and observed biomass conditions of species groups in the 2014 baseline model

Akaike's Information Criterion, AIC) from Table 6. In each scenario, the diet of a predator was manipulated in the baseline model and allowed to project over time using Ecosim.

Scenarios 1–6: Increased seal predation on dogfish

Six simulation scenarios were run to address the question: How does increased seal predation on spiny dogfish affect the food web? Ecosim scenarios 1–3 (gray seal) and 4–6 (harbor seal) investigated the impact of increased seal predation on dogfish (Table 7). Although only gray seals, and not necessarily harbor seals, have been observed eating spiny dogfish, it is still possible that harbor seals could eat them given their relative sizes, and therefore both seal species were examined as potential predators of dogfish in these scenarios. The baseline diet matrix was manipulated to increase seal predation on dogfish in 3 different scenarios for each species. In scenarios 1–3, the

Table 6. Ecosim fitting statistics. The number of Akaike's Information Criterion (AIC) data points was 240 for all species groups (see Table 1 for groups). The model was allowed to project forward 124 yr from 1950. 'Setup' describes factors included in each model. The primary production forcing function (PP FF) shape number describes FFs that were investigated to determine the impact on the model (see Figs. S1–S4 in the Supplement at www.int-res.com/articles/suppl/mm550p249_supp.pdf for shapes). Anomaly search/splines refers to the number of splines tested. Minimum sum of squares (SS) was calculated in Ecosim. Ecosim vulnerabilities (Christensen et al. 2008) were searched in 2 ways: (1) to find the relative sensitivities of the vulnerability parameter for predator–prey interactions and (2) for groups with time series. K: number of parameters estimated. The model finally selected (run 9) is highlighted in **bold**; na: not applicable

Model run	Setup	Model structure			Model fit statistics		
		PP FF shape no.	Anomaly search no. years/splines	No. of time series fitted to model	Min SS	K	AIC
1	Baseline – vulnerability = 2 with time series	na	0	92	7692.9	0	361.4
2	Vulnerability search sensitivity of SS to V	na	0	92	6004.9	30	389.6
3	Vulnerability search groups with time series	na	0	92	5993.5	15	371.4
4	Fishing + FF + vulnerability search sensitivity of SS to V	10	0	92	5931	30	388.3
5	Fishing + FF + search groups with time series	10	0	92	6188	15	374.7
6	Fishing + FF + vulnerability search sensitivity of SS to V	17	0	92	7220	27	408.8
7	Fishing + FF + search groups with time series	2	1	92	5982	20	375.2
8	Fishing + FF + search groups with time series	5	4	92	5255	35	391.7
9	Fishing + FF + with time series	10	0	92	4099.5		295.8

percentage of dogfish in gray seal diet was set at 5, 10, and 20%, respectively. In scenarios 4–6, the percentage of dogfish in harbor seal diet was also set at 5, 10, and 20%. The percentage of other species in each of the seal diets was adjusted proportionally so the total diet still added up to 100%. The gray seal scenarios were run independently of the harbor seal scenarios. Twenty percent represents the upper bound of dogfish in harbor seal diet and is likely higher than what is observed. However, it is considered as a model scenario to capture an extreme situation and to put some bounds on what might be possible.

Scenarios 7–9: Combined predation of seals and spiny dogfish on Atlantic cod

Three simulation scenarios were run to address the question: What is the impact of combined seal and spiny dogfish predation on Atlantic cod? We attempted to increase the amount of Atlantic cod in the diet of both seals and spiny dogfish at the same time to investigate the combined predation effect. However, the Ecosim model would not allow an increase of Atlantic cod in the diet of both seals and spiny dogfish. Instead, we investigated additional predation of spiny dogfish on Atlantic cod. For scenarios 7–9, the diet matrix was manipulated so that spiny dogfish diet included 5, 10, and 20% Atlantic cod, respectively (Table 7). The percent diet for other species consumed by spiny dogfish was also manipulated proportionally so that the total diet summed to 100%.

Scenarios 10 & 11: Increased white shark predation on seals

Two simulation scenarios were run to address the question: How might white shark predation on seals impact the food web? We attempted to manipulate the baseline diet matrix so that white shark predation on seals was increased to 5, 10, and 20% of total diet. This was done by adjusting the diet matrix, so that in seals made up 5, 10, and 20% of white shark diet. However, the model became unbalanced and would not allow increases to 10 and 20%. Therefore, only scenarios with a diet increase to 5% were considered. The gray seal scenarios were done independently of the harbor seal scenarios, so we could detect trends for individual species. Scenario 10 examined 5% of gray seal in the diet of white shark and scenario 11 examined 5% of harbor seal in white shark diet (Table 7).

Table 7. Simulation scenarios used to investigate trophic responses of different diets

Scenario	Investigation	Diet matrix manipulation
1	Increased seal predation on dogfish	5% of gray seal diet was dogfish
2		10% of gray seal diet was dogfish
3		20% of gray seal diet was dogfish
4	Increased harbor seal predation on dogfish	5% of harbor seal diet was dogfish
5		10% of harbor seal diet was dogfish
6		20% of harbor seal diet was dogfish
7	Combined predation of seals and dogfish on Atlantic cod	5% of spiny dogfish diet was cod
8		10% of spiny dogfish diet was cod
9		20% of spiny dogfish diet was cod
10	Increased white shark predation on seals	5% of white shark diet was gray seals
11		5% of white shark diet was harbor seals

Table 8. Ecopath summary statistics of balanced 2014 baseline food web model

Parameter	Value	Units
Sum of all consumption	18213.63	t km ⁻² yr ⁻¹
Sum of all exports	8388.206	t km ⁻² yr ⁻¹
Sum of all respiratory flows	5851.242	t km ⁻² yr ⁻¹
Sum of all flows into detritus	16211.6	t km ⁻² yr ⁻¹
Total system throughput	48664.68	t km ⁻² yr ⁻¹
Sum of all production	18752.11	t km ⁻² yr ⁻¹
Mean trophic level of the catch	2.993231	
Gross efficiency (catch/net primary production)	0.000252	
Calculated total net primary production	14400	t km ⁻² yr ⁻¹
Total primary production/total respiration	2.461016	
Net system production	8548.758	t km ⁻² yr ⁻¹
Total primary production/total biomass	51.73879	
Total biomass/total throughput	0.005719	yr ⁻¹
Total biomass (excluding detritus)	278.3211	t km ⁻²
Total catch	3.631613	t km ⁻² yr ⁻¹
Connectance index	0.248725	
System omnivory index	0.252891	

RESULTS

The Gulf of Maine food web

Ecopath produced a number of summary statistics of the ecosystem (Table 8). Included in these statistics are that the trophic levels ranged from 1 (detritus and phytoplankton) to 4.58 (white shark). The highest trophic level species included sharks, seals, toothed whales, and tuna (Fig. 2). Harbor seals had the highest prey overlap with gray seals (0.93), tuna (0.74), and spiny dogfish (0.73). Gray seals had the highest prey overlap with tuna (0.68) and spiny dogfish (0.62). Spiny dogfish had the highest prey overlap with Atlantic cod (0.88) and hake spp. (0.82). White sharks had the highest prey overlap with other sharks (0.80). Harbor seals had the highest predator overlap

with gray seals and tuna (1.0). For gray seals, the highest predator overlap was with tuna (1.0). Spiny dogfish had the highest predator overlap with skates (0.93). White sharks are top predators.

Capacity of the food web

Within the Gulf of Maine marine ecosystem, our food web model suggests that the ecosystem may support more seal and white shark biomass. The model allowed for an order of magnitude increase in seal and white shark biomass but had no capacity for increased dogfish biomass (Fig. 3). Sand lance, a prey item of seals and dogfish, had the greatest capacity for increase in the food web at 2 orders of magnitude. Interestingly, the model would only allow for a doubling of cod biomass, despite historic biomass levels being much higher.

The MTI analysis showed a strong negative impact of white sharks on seals and toothed whales (Fig. 4). Spiny dogfish negatively impact other groundfish, flatfish, and hake spp. The fisheries also impact most of the top predators, elasmobranchs, and groundfish in the food web (Fig. 4). Little impact is observed between other species.

Time series data

Information on the time series for individual species/groups included in the final model are presented in Table 4. These included time series for sharks, Atlantic butterfish *Peprilus triacanthus*, spiny dogfish, Atlantic cod, Atlantic herring *Clupea harengus*, skates, American lobster *Homarus americanus*, squid (*Loligo*), groundfish, hake spp., flatfish, crustaceans, and tuna, among others. Model fits were generally good for most species groups, including spiny dogfish (Fig. S5), Atlantic cod (Fig. S6), and white shark (Fig. S7). Model fits to time series data were good for sharks and tuna. Trend lines for skates, hake spp., and lobsters showed no real trends for individual time series.

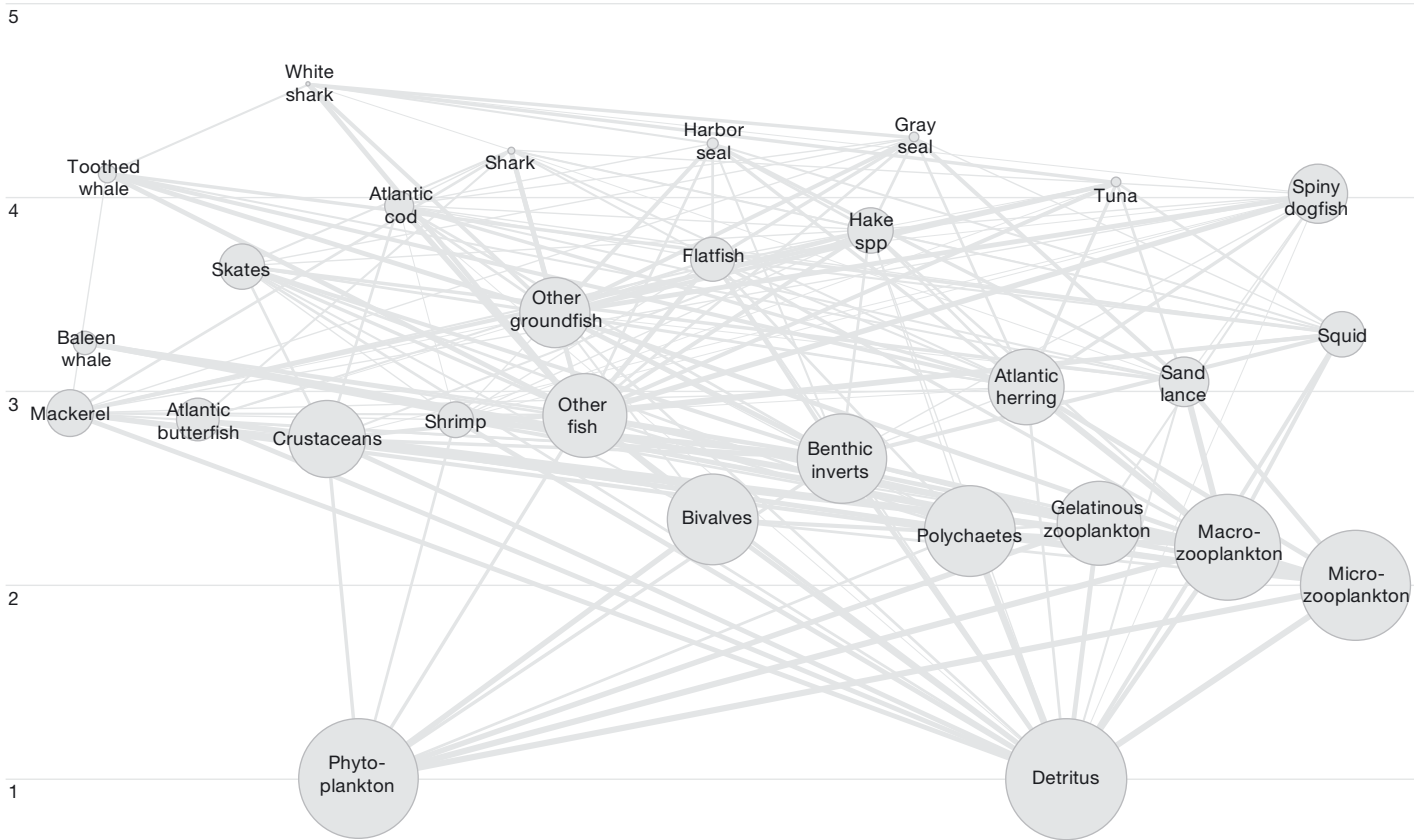


Fig. 2. Gulf of Maine balanced 2014 baseline food web model. The size of nodes represents relative biomass of each species group. The thickness of lines represents relative flow of energy between species groups. All groups are arranged according to trophic level. Inverts: invertebrates

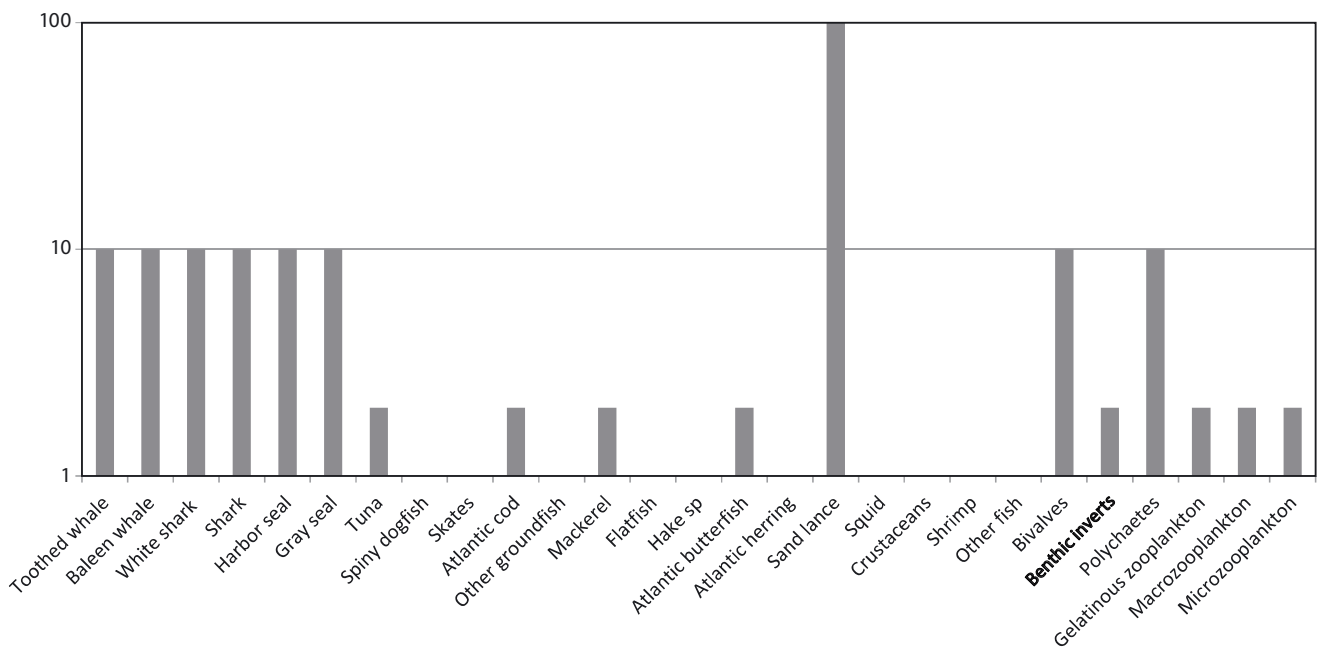


Fig. 3. Sensitivity analysis of balanced 2014 baseline model. Bar graph depicting the total allowable increase in biomass of each consumer species at intervals of 2x, 10x, and 100x the initial biomass. Only 1 species was manipulated at a time and then reset to the original biomass for subsequent species manipulations. Inverts: invertebrates

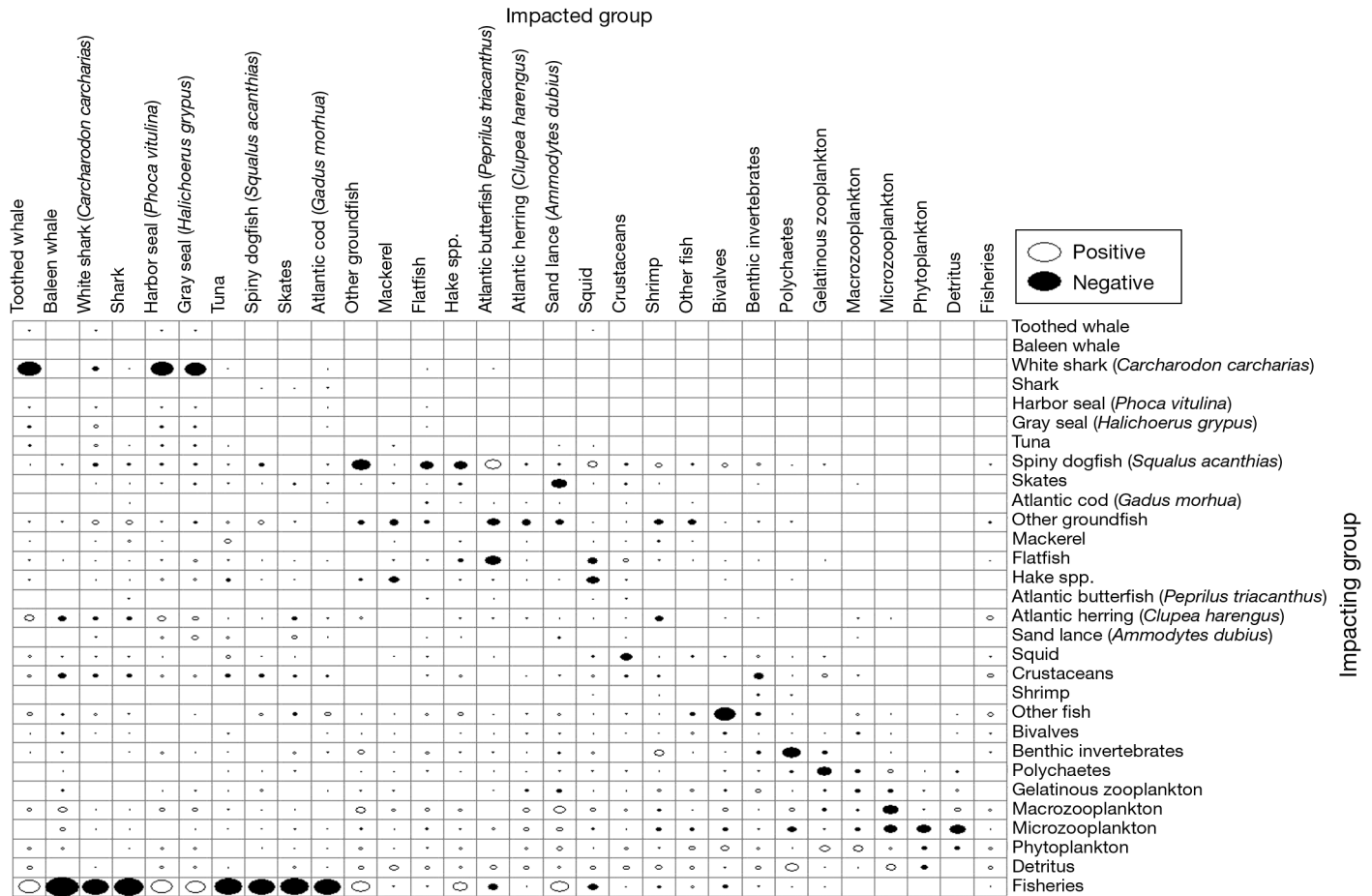


Fig. 4. Mixed trophic impact analysis of 2014 balanced baseline model. Bubble size indicates relative impact

Ecosim model fitting and biomass parameters

The final model, which had the lowest AIC score of all model runs (Model 9 in Table 6) included time series, estimated vulnerabilities, and a forcing function (shape 10, shown in Fig. S3). Four different forcing functions were tried (Table 6). One was based on phytoplankton abundance estimates over time in the Gulf of Maine (Kane 2011) (shape 17, Fig. S4), 2 were estimated using an anomaly search with splines (each spline indicates a change over time; shapes 2 and 5 in Figs. S1 & S2), and the final one selected was drawn manually (shape 10, Fig. S3). Although the 2 alternative forcing functions 2 and 5 resulted in lower sums of squares, they also resulted in unrealistic biomass estimates (based on comparing them to abundance series) and were therefore not used.

The model fit to biomass estimates for many of the species were very good, showing trends similar to corresponding time series trends, including sharks, skates, tuna, spiny dogfish, Atlantic cod, hake spp., and Atlantic herring (Figs. S8–S14, respectively). The flatfish biomass curve was very flat (Fig. S15).

The model had trouble fitting the Atlantic butterfish biomass for the entire time period (Fig. S16); it also had trouble fitting the squid biomass, but this may be a function of the variability in time series data (Fig. S17). Crustaceans showed a flat trend, and the shrimp biomass fit the modeled data fairly well (Figs. S18 & S19, respectively). Bivalve biomass showed no real trend over time, despite time series data showing a downward trend towards the end of the time series (Fig. S20). Mackerel showed a fairly constant trend over time (Fig. S21). Sand lance and other fish showed an increase in biomass between 1980 and 1990, followed by a variable trend line (Figs. S22 & S23, respectively). Other groundfish showed 2 peaks, during the late 1990s and late 2000s (Fig. S24). The biomass plot for both seal species reflected actual trends in abundance over time well (see Figs. 5 & 6, and Figs. S25 & S26), as did the biomass plots for toothed and baleen whales (Waring et al. 2014) (Figs. S27 & S28). The white shark biomass plot showed recovery of the population occurring slightly earlier in time than that shown by Curtis et al. (2014) (Fig. S29).

Increased seal predation on dogfish

The percentage of spiny dogfish in seal diet was increased at 3 different levels: 5, 10, and 20%. If seals are eating dogfish, which have a large population size, seal biomass is expected to increase. However, the response, in terms of seal biomass increasing, was not uniform for gray seals under these 3 scenarios (Fig. 5). Gray seal biomass peaked in the year 2015, and then in the 5 and 10% scenarios, seal biomass decreased gradually, whereas it continued to increase in the 20% scenario. In contrast, all 3 scenarios elicited a similar response in harbor seal biomass, even as spiny dogfish became the primary prey item (20%; Fig. 6). All 3 scenarios depicted a nearly linear increase in harbor seal biomass over time, with the 20% scenario resulting in the largest increase and the 5% scenario resulting in the smallest increase, as would be expected. Regardless, for both gray and harbor seals, a dramatic separation in the trajectory lines occurred between the 20% scenario and all other scenarios.

This trend is also visible in Figs. 7 & 8, where both gray and harbor seal biomasses continue to increase through time in the 20% scenario but level out and stabilize over time with all other scenarios. Furthermore, even though we are artificially increasing the percent of dogfish in seal diet in the baseline model, dogfish do not emerge as the dominant prey over time in all scenarios except the 20% scenarios (Fig. 7 & 8). Figs. 5–8 demonstrate a tipping point between 15 and 20% of dogfish in gray seal diet, whereby perturbation in the food web becomes more severe over time.

Increased white shark predation on seals

The percent of seals in white shark diet could not be increased greater than 5% without the model becoming unbalanced. Under both simulations of increased harbor

and gray seals in the diet of white sharks, there was a very large increase in white shark biomass through 2010 followed by a plateau. This trend contrasts from the baseline scenario with current diet of only 1% gray and 3% harbor seals, which continues to increase steadily from the 1980s through the next several decades (Fig. 9). The potential total white shark biomass is greatest with an increased diet proportion of harbor seals and still higher than the baseline with increased diet proportion of gray seals (Fig. 10).

We observed similar changes in the percent prey in the white shark diet over time under both simulations (Fig. 10). Seals as prey biomass quickly increase from 5 to 50%, replacing all other prey species as the dominant prey item by the year 2000 (Fig. 10). All other prey items quickly decline, accounting for only a small portion of white shark diet over time.

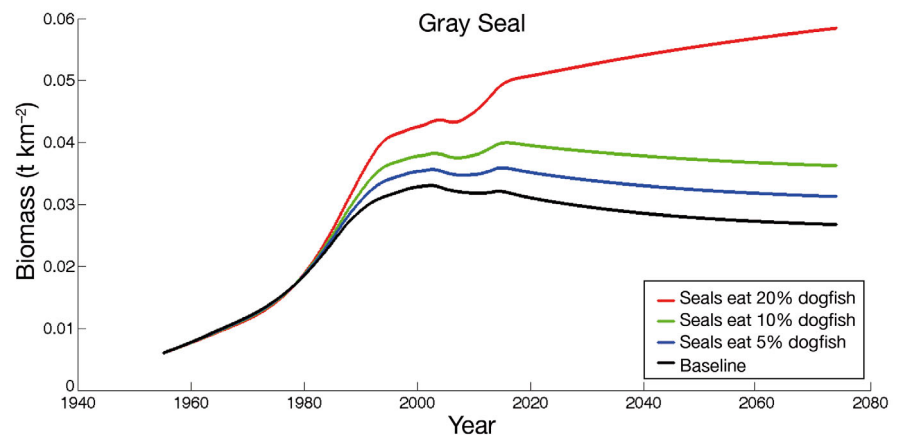


Fig. 5. Expected increase in gray seal *Halichoerus grypus* biomass over time with increased predation on spiny dogfish *Squalus acanthias* from the baseline diet matrix. This figure represents the results of simulation scenarios 1 to 3 (Table 7)

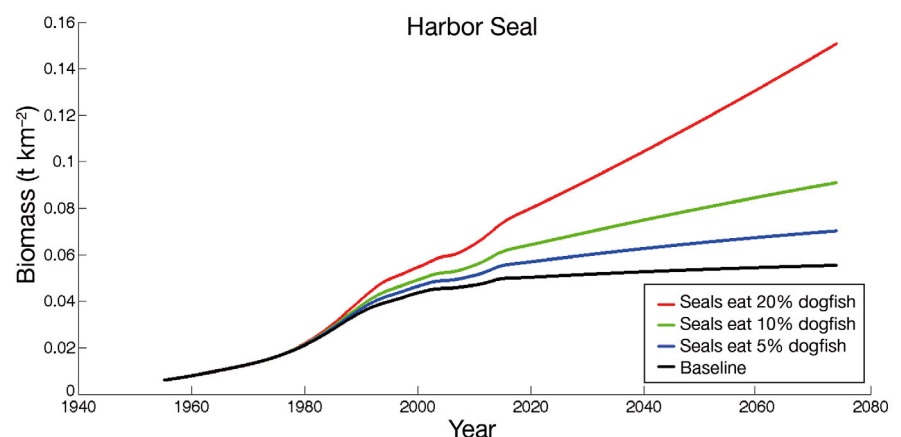


Fig. 6. Expected increase in harbor seal *Phoca vitulina* biomass over time with increased predation on spiny dogfish *Squalus acanthias* from the baseline diet matrix. This figure represents the results of simulation scenarios 4 to 6 (Table 7)

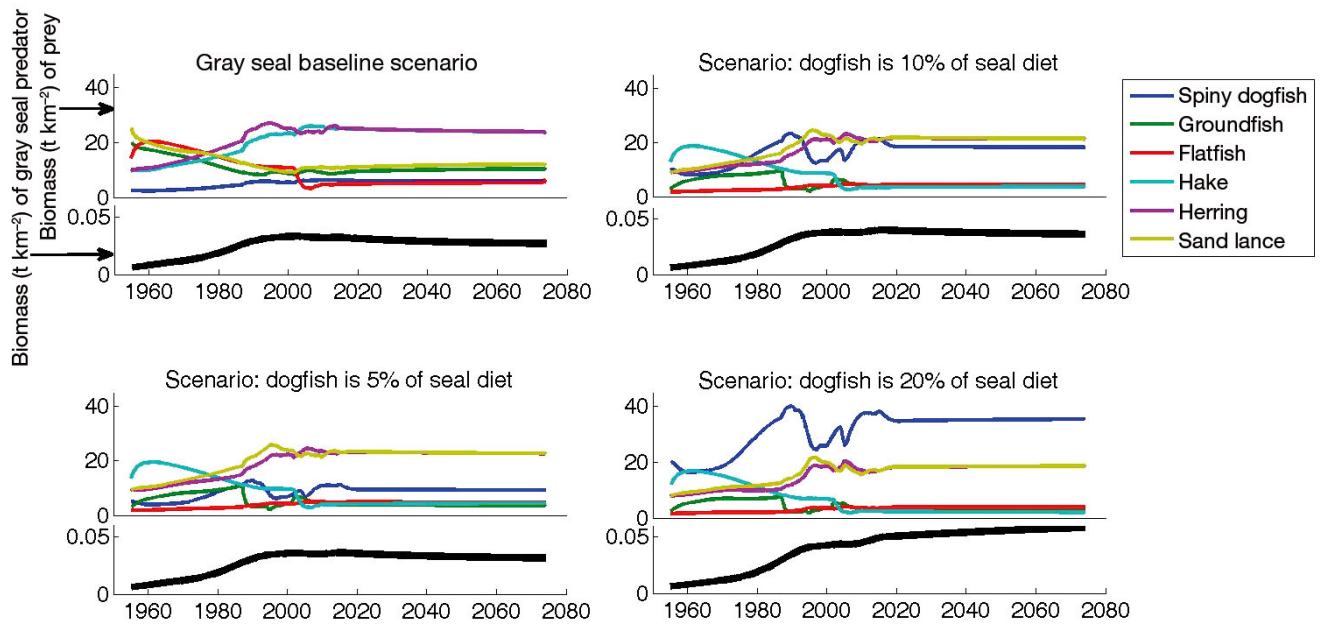


Fig. 7. Gray seal *Halichoerus grypus* biomass (t km⁻²; black line in bottom panels) and percent composition of primary prey biomass (% of diet; colored lines in top panels) under the baseline model and 3 different diet scenarios (1–3, Table 7) projected over time (years). The scenario describes the manipulation to the baseline diet matrix in Ecosim prior to projecting change over time using Ecosim. Seals consumed no spiny dogfish *Squalus acanthias* in the baseline diet matrix

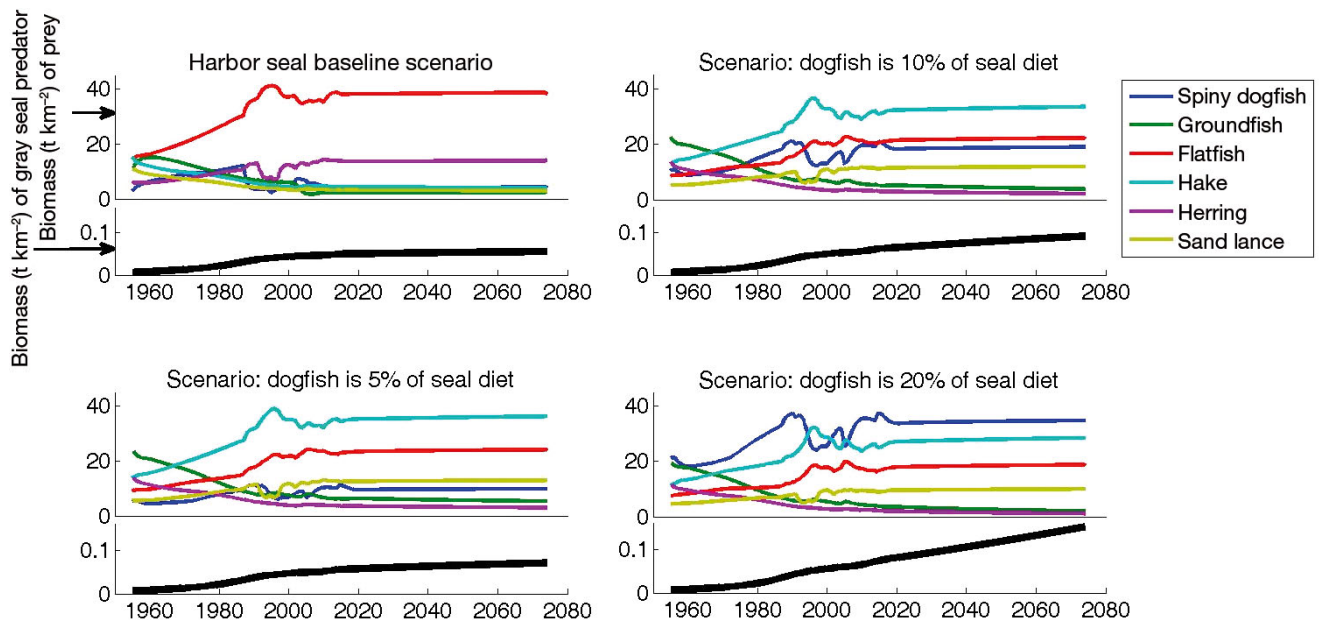


Fig. 8. As in Fig. 7, but for harbor seals *Phoca vitulina* under the baseline model and 3 different diet scenarios (4–6, Table 7)

Combined predation of seals and spiny dogfish on Atlantic cod

There is little capacity in the food web to allow for combined predation mortality on Atlantic cod by both seals and dogfish at the same time. It was not possible to increase the percentage of cod in the diet of both seals and dogfish at the same time.

DISCUSSION

The trophic structure of our model is supported by other research in the Gulf of Maine (Link et al. 2006, Zhang et al. 2012, Morgan & Sulikowski 2015). Not surprisingly, sharks, seals, toothed whales, and tuna are top predators. Seals show high prey overlap with tuna, as both feed on other groundfish, hake spp.,

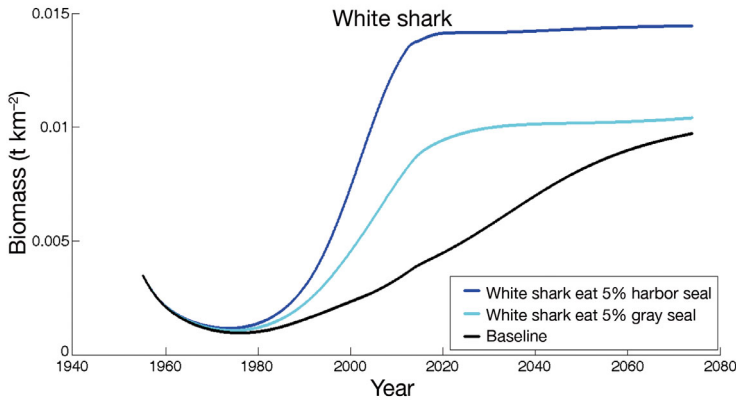


Fig. 9. Expected increase in white shark *Carcharodon carcharias* biomass over time with 5% increase in predation on gray seals *Halichoerus grypus* and harbor seals *Phoca vitulina* compared to original balanced biomass in the baseline diet matrix

Atlantic herring, sand lance, and squid. Similarly, the high prey overlap of seals with spiny dogfish is a reflection of their shared diets of other groundfish, hake spp., Atlantic herring, and sand lance. The high prey overlap of spiny dogfish with Atlantic cod is similar to other published research for the region (Morgan & Sulikowski 2015) and is a reflection of both species consuming other groundfish, Atlantic herring, sand lance, shrimp, and other invertebrates.

Capacity of the food web

The capacity of the food web model to absorb perturbations of fluxes in species abundances is an indicator of resilience. The food web is able to accommodate dramatic increases in species biomass of particular species, and no increase of other species. When the food web model is not able to accommodate increases in species biomass, it is an indicator of a bottleneck of energy flow in the food web. It is these species groups that should be of greatest concern to ecological managers.

The results from our analysis on the capacity of the food web suggest that spiny dogfish population levels are so high that the ecosystem has no capacity for large increases in dogfish biomass. Although seal populations have been increasing exponentially in recent years, it appears that the ecosystem, in its current state, can allow for a continued increase in seal biomass. This exact trend has been observed on Sable Island, Nova Scotia, where the annual rate of increase in pup production has been nearly constant for more than 25 yr, with an exponential increase observed over 4 decades (Bowen et al. 2003). More recent counts show a leveling of the population increase (Bowen et al. 2003). The energetic demands of a growing seal population may be attributed to concurrent changes in the fish

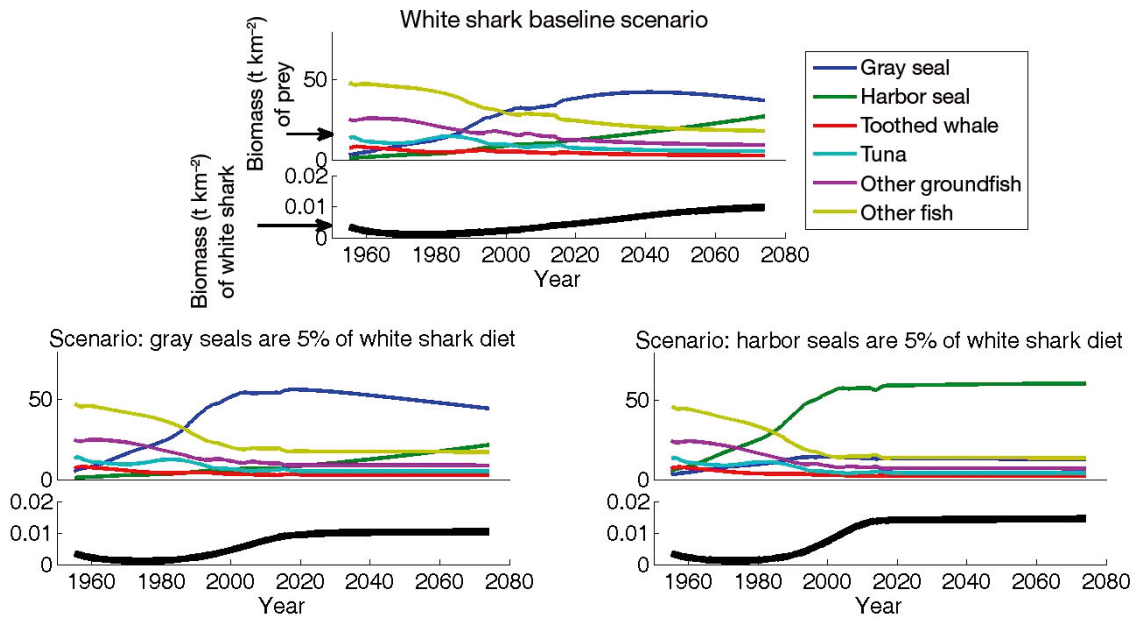


Fig. 10. White shark *Carcharodon carcharias* biomass ($t\ km^{-2}$; black line in bottom panels) and percent composition of primary prey biomass (% of diet; colored lines in top panels) under the baseline model and 2 different diet scenarios (7 and 8, Table 7) projected over time (years). The scenario describes the manipulation to the baseline diet matrix in Ecopath prior to projecting change over time in Ecosim. The baseline scenario includes 1% harbor seal *Phoca vitulina* and 3% gray seal *Halichoerus grypus* in the diet of white sharks (Table 3)

community. An alternative prey base for seals may support the changing energetic demands of a growing population (Link & Garrison 2002a).

It is not surprising that the model allows for an order of magnitude increase in white shark biomass, as their biomass, although increasing, is generally fairly low (Curtis et al. 2014). White sharks prey upon pinnipeds and a variety of fish species and are known scavengers of cetacean carcasses (Skomal et al. 2012). The food web model does not show any indication that current or projected population abundances of white sharks would be food limited.

The fact that the model only allows for a doubling of cod suggests that a shift in cod predators and/or cod prey may have occurred over time. Cod exhibit an opportunistic and omnivorous diet, and there has been a documented diet shift of Atlantic cod on the northeast US continental shelf over the last 3 decades (Link & Garrison 2002b, Smith & Link 2010). Total fish consumption by major predators has remained generally consistent, despite changes in predator size, structure, and abundance (Link & Garrison 2002a). The dominant piscivore in this ecosystem has shifted from cod to spiny dogfish. Based on our food web model, it appears that cod populations cannot return to historic levels given current food web structure and function.

Increased seal predation on dogfish

As dogfish become the dominant piscivore in the Gulf of Maine (Link & Garrison 2002a, Morgan & Sulikowski 2015), it is expected that seal diet would also shift to incorporate the increasing percentage of dogfish. When running this scenario in the food web model, there appears to be some threshold or tipping point between a 10% increase and a 20% increase in dogfish in both gray and harbor seal diets that allows for exponential increase in seal biomass as spiny dogfish become the primary prey item (Figs. 5 & 6). The slope of the line changes in a uniform way from the baseline to 5% and to 10% and then jumps at a larger interval between 10 and 20% (Fig. 6).

These model results suggest that dogfish may be contributing to the recovery of seal populations by providing an alternative prey base. A slight increase in the percent of dogfish in seal diet increased seal biomass in such a way that it plateaued over time, as if a carrying capacity had been reached. However, if seal diet comprises a large percentage of dogfish (>20%), there are major impacts to the trajectory of seal populations over time, eliciting a linearly increasing trend. Field studies will need to be con-

ducted that quantify the specific portion of dogfish in seal diet to know whether seal consumption of dogfish is approaching this tipping point that exists somewhere between 10 and 20% of dogfish biomass in seal diet. It might not be realistic to think that dogfish will become a dominant prey item comprising 20% of seal diet, but all scenarios (baseline, 5, 10, and 20% increase) suggest that this direction of change in the biomass of seals over time is possible.

Increased white shark predation on seals

White sharks are known to scavenge carcasses of cetaceans but also opportunistically prey on live seals. There has been a documented increase in attacks on live animals as seal populations increase on both the east and west coasts (Pyle et al. 1996, Skomal et al. 2012). This observation is supported by historical trends where white sharks would attack live seal prey when abundances were high, prior to the extirpation of seals at the end of the 17th century (Wood LaFond 2009, Skomal et al. 2012). It is possible that even though white sharks are responding to an increase in gray seals, they also may impact the harbor seal population (Lucas & Stobo 2000, Bowen et al. 2003, Skomal et al. 2012).

Previous studies suggest that increased seal populations in the Gulf of Maine have elicited an increase in white shark attacks on live seal prey, which may be aiding in increasing white shark populations (Pyle et al. 1996, Skomal et al. 2012, Curtis et al. 2014). Our model results support this theory, with the population of white sharks continuing to increase with increased predation on seals. The fact that white shark predation on seals could not be increased beyond 5% is likely a factor of the low seal biomass in the 1950 baseline model. As is evident in the simulations, both seals become predominant prey species in white shark diets after the late 1990s to early 2000s. Even in the base case scenario, the importance of gray and harbor seals as prey items increases over time. Current literature on what percentage marine mammals make up of white shark diet is generally lacking. According to our results, it appears that even a small percentage of seals in white shark diets can have a large impact on their population size. It is therefore not surprising that white shark populations have begun to increase in recent years as seal populations have also increased. On an ecosystem level, it is of interest and importance that these 3 top predators have such a large impact on each other and signifies the importance of ecosystem-based management into the future.

Combined predation of seals and spiny dogfish on Atlantic cod

It is unlikely that seals and dogfish are natural competitors for cod or are contributing directly to increased total predation mortality on cod in the Gulf of Maine (Smith & Link 2010, Waring 2012). The limited information suggests that cod make up a small proportion of harbor seal diet in areas such as the Gulf of Maine (Wood 2001), and overall cod mortality caused by seals is thought to be low (Waring 2012). Although it has been suggested that dogfish may opportunistically eat smaller cod (Bowman et al. 2000, Morgan & Sulikowski 2015), it is unlikely that they are a major predator of cod contributing to their total mortality in the Gulf of Maine (Link et al. 2002). Only 5% of fish in dogfish diet was unidentified gadoids, including cod (Bowman et al. 2000). Although dogfish and cod are capable of sharing common prey, as they are both opportunistic predators (Askin et al. 2012) and have been shown to have a high prey overlap according to this and previous studies (Morgan & Sulikowski 2015), it is unlikely that this type of interaction is strong enough to elicit major responses in the food web structure or function.

Gulf of Maine outlook

With the change in dominant piscivorous fish and other large predators in the Gulf of Maine over the last few decades, several questions arise regarding trophic dynamics of commercial species and protected species. Our focus on predator-prey interactions between seals and dogfish stems out of concern regarding the collapse of groundfish stocks and the rise in the numbers of seals and some shark predators. Although it is acknowledged that dogfish populations are also increasing, it can be difficult to accurately measure their contribution as prey in seal diets due to the lack of hard bony structures. Therefore, modeling realistic and extreme scenarios helps us to understand what may be plausible for trophic dynamics in the ecosystem.

Our model results suggest the following major findings:

- Dogfish could be contributing to the recovery of seal populations by providing an alternative prey base.
- There is a tipping point between 10 and 20% of dogfish in seal diet that elicits a linearly increasing trend in seal biomass over time.
- Seals will have a continued impact on the pro-

jected white shark population, with harbor seals having a greater effect compared to gray seals.

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