

Simulations to evaluate management trade-offs among marine mammal consumption needs, commercial fishing fleets and finfish biomass

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ABSTRACT: In setting fisheries management quotas, fish interactions with marine mammals are seldom considered. Even less often considered are indirect effects from fishing and species interactions or potential changes to ecosystem structure as marine mammal populations rebuild. To explore these interactions, we used a multi-species production model to evaluate the interactions between mixed fleet fisheries, their target species, and marine mammals, in an ecosystem representative of the Northeast USA continental shelf. We simulated changes to biomass and catch trajectories and compared these to the associated biological reference points for commercially important finfish and the current biomass levels of marine mammals. Marine mammal populations increased over time in our simulations (even with varying degrees of dependence on commercial species as prey) except when direct human-induced mortality was set much higher than observed. Greatly increased fishing mortality can reduce the rate of population increase for marine mammals, slowing recovery for some populations. This is due to the combination of reduced prey and increased interactions with fishing vessels (bycatch or vessel strikes) as fishing effort increases. Our model suggests that managing human-induced direct mortality of marine mammals is the most important factor for the recovery of their populations, but fishery management plays an important role in avoiding the additional stress of reduced prey populations. Marine mammal predation can also affect trajectories and reference points for commercially fished species. These types of evaluations of direct human-induced mortalities as well as trade-offs between mixed fishery fleets and protected species requirements are essential for the transition to ecosystem-based fisheries management.

KEY WORDS: Multi-species modelling · Trade-off evaluation · Reference points · Competing fishing fleets · Protected species requirements · Ecosystem-based fisheries management

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INTRODUCTION

Issues concerning marine mammals generate a great deal of attention and arise from different perspectives. Some of these issues have caused heated debates in the international community, e.g. the whaling carried out by countries that either oppose the 1982 International Whaling Commission moratorium on commercial whaling, or conduct lethal scientific sampling to determine whether predation by marine mammals impacts finfish populations (Nor-

mile 2000, Kasuya 2007, Corkeron 2009). Another heavily debated issue is whether the increases seen in seal populations in the Northwest Atlantic over the past several decades (Bowen et al. 2003, Gilbert et al. 2005, Bowen 2011) have prevented the recovery of groundfish stocks (Mohn & Bowen 1996, Savenkoff et al. 2008, O'Boyle & Sinclair 2012), and thus whether the annual Canadian seal hunts should be expanded to reduce the seal populations (DFO 2008, 2009b). Such issues highlight the need for fisheries management to address the trade-offs in energy flow

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among upper trophic level species within an ecosystem.

Trade-offs include some direct human–marine mammal interactions, such as entanglement in gear and ship strikes of marine mammals (e.g. Crowder & Murawski 1998, Merrick & Cole 2007, Waring et al. 2013) and gear damage and bait depredation by marine mammals (e.g. Northridge 1984, Payne & Selzer 1989, Nichols et al. 2014). However, broader ecosystem interactions could affect the entire energy flow and possibly have larger ecosystem-level consequences such as competition between marine mammals and fishing fleets (Trites et al. 1997, Trzcinski et al. 2006, Savenkoff et al. 2007, Swain & Chouinard 2008); competition between marine mammal and fish populations for common prey (Merrick 1997, Yodzis 2000); and secondary effects of predation by marine mammals (Punt & Butterworth 1995, Yodzis 2000, Bundy 2001, Morissette et al. 2006). Most of these energy flows are poorly understood and all of them add complexity when attempting to rebuild depleted fish stocks concurrently with rebuilding endangered marine mammal populations. Although a great deal of effort is given to assessing and rebuilding individual fish stocks, relatively little attention is given to how fishing removals affect marine mammal populations. Marine mammals are particularly important within an ecosystem for several reasons: their large body size and relative abundance can have a major influence on the structure and function of an ecosystem (Bowen & Siniff 1999, Springer et al. 2003); they can affect all trophic levels of the ecosystem (Kenney et al. 1997, Harvey et al. 2012); they are widely distributed throughout the ecosystem; they shape the behavior and life history of prey; they provide nutrient cycling; and they modify benthic habitats (Katona & Whitehead 1988, Bowen & Siniff 1999, McQuinn 2009).

Energy flows through an ecosystem can have economic as well as ecological ramifications. Predation by marine mammals may alter the population and community dynamics of fish and other prey species, particularly if the prey is already depressed into a 'predator pit' due to other factors such as overfishing (Savenkoff et al. 2007, Swain & Chouinard 2008, O'Boyle & Sinclair 2012). This could result in reduced yields, or even collapses of commercially important fish stocks (Chouinard et al. 2005, Morissette et al. 2006, Bundy et al. 2009). Conversely, the population and community dynamics of marine mammals can be impacted if their prey is insufficient or of inadequate quality (Haug et al. 2002, DeLorenzo Costa et al. 2006, Hlista et al. 2009). This could not only be detri-

mental to endangered marine mammals, but could also impact eco-tourism industries such as whale-watching. Indirect competition between fisheries and marine mammals is also hypothesized, where marine mammals may compete with commercially important fish for the same prey (Stefánsson et al. 1997, Trites et al. 1997), amounting to forgone fishery yield. Alternatively, marine mammals may prey on predators of commercially important fish (Punt & Butterworth 1995, Yodzis 1998), potentially enabling higher commercial fish populations by keeping predators in check. Finally, alterations to the flows of energy and biomass to marine mammals can be symptomatic of overall ecosystem overfishing (Murawski 2000, Link 2005).

Theories behind these impacts of energy flows have led to polarized positions that advocate for various management and conservation measures. Realized or perceived pinniped impacts have led to pressure on the Canadian government to reduce pinniped populations (DFO 2009a,b, Varjopuro 2011), and the question has been raised as to whether cetaceans should also be culled (Yodzis 2001, Gerber et al. 2009). Conversely, animal rights groups have campaigned against the seal harvest and pelt sales. Environmental groups and scientists have advocated for the complete cessation of whaling, arguing that lethal sampling is not necessary to study foraging ecology, that the scientific methods used are flawed, and that whaling for scientific study is simply a facade to perpetuate whaling (Normile 2000, 2008, Corkeron 2009). In practice, it is difficult to validate or refute the environmental importance of any of these management or conservation claims when energy flows are contextualized in the myriad of possible interactions. This is especially difficult when taking into consideration the indirect as well as direct effects of marine mammal predation, since marine mammals can feed at most trophic levels (Punt & Butterworth 1995, Yodzis 2000, O'Boyle & Sinclair 2012).

Ecosystem model simulations are an appropriate tool to explore a range of different hypothetical trade-offs when it comes to marine mammal and fisheries interactions. Although there are always direct and indirect interactions within an ecosystem that cannot be fully incorporated into an ecosystem model, simulations can usefully elucidate how the system behaves within specified ranges of scenarios and parameters. Often, indirect interactions can emerge from such models that were either not initially considered or are more important than originally thought (Punt & Butterworth 1995, Yodzis 2000). Simulations allow the quantitative evaluation of a range of management options and environmental

conditions, enabling researchers to determine which outcomes are most and least desirable, and which are robust. Several such simulations have already been used in a marine mammal-fisheries context (e.g. Bundy 2001, Trzcinski et al. 2006, Link & Bundy 2012, Morissette et al. 2012, Nye et al. 2013).

Multi-species production models are an especially useful class of ecosystem simulation models because of their relative simplicity and relatively low number of parameters. More importantly for management, they can be used to generate fishery reference point estimates that are comparable to those that are output from standard single-species fishery stock assessments (Mueter & Megrey 2006, Gaichas et al. 2012, Lucey et al. 2012). Production models are also useful for data-poor species such as marine mammals, since production models in their simplest form only require biomass and catch or other removals (Gamble & Link 2009, 2012, Link et al. 2012).

Interactions between marine mammals, fisheries and finfish are particularly pronounced in the Northeast USA continental shelf Large Marine Ecosystem (NE USA LME) (Fig. 1), where production is very high in the Gulf of Maine and Georges Bank regions (Clarke et al. 1946, Cohen et al. 1982, Link et al. 2011, Ecosystem Assessment Program 2012). The high zooplankton and small pelagic fish populations in the area make these regions important feeding grounds for marine mammal species, including 5 endangered cetaceans and the critically endangered northern right whale *Eubalaena glacialis* (Mayo &

Marx 1990, Wishner et al. 1995, Beardsley et al. 1996). For the same reasons, the area is an important fish foraging area and thus an important area for commercial harvest (Brown et al. 1976, Cohen et al. 1982, Link et al. 2011, Link & Bundy 2012). Therefore, there is a high possibility of copious trade-offs in this region.

Smith et al. (2015) estimated predation by marine mammals on the NE USA LME to be roughly equal to or higher than commercial catch for several commercially important fish groups, including clupeids, gadids and flatfish. In a recent Atlantic herring *Clupea harengus* assessment (NEFSC 2012a), both fish and marine mammal predation were used to inform natural mortality rates in the herring assessment model, and fish predation on herring was found to be ~2-fold the biomass of commercial herring catch, while marine mammal predation on herring was similar to the biomass of commercial herring catch. These are large amounts of removals in this region, which can greatly impact the outcomes of stock assessments and should be considered for other species as well. These general patterns are thought to hold globally (Bax 1991, Bax 1998, Hollowed et al. 2000). However, in addition to incorporating consumption by marine mammals, the direct and indirect effects of this consumption throughout the system need to be further understood. Better understanding is also needed on how commercial fishery removals indirectly affect fish and marine mammal populations, and how changes in fish or marine mammal biomass can affect the system. One tool that has been effectively used in the NE USA LME to examine these types of interactions is the multi-species production model, MS-PROD (Gamble & Link 2009).

In this context and with that particular tool, we aimed to do 4 things: (1) explore through simulations how changes to groundfish and pelagic fishing levels may affect other components of the system; (2) see how these changes relate to the biomass reference points for the fish groups and the current biomass levels for the marine mammal groups; (3) given these fishing level changes, see how the components of harvest, predation and competition change over the long term; and (4) evaluate the model's sensitivity to the parameter inputs. To do this, we incorporated the interactions of 6 aggregate functional groups (comprising 12 species of marine mammals and 15 species of commercially important finfish) into a production model. We evaluated the trade-offs through commercial fishing harvest scenarios and included parameter sensitivity tests.

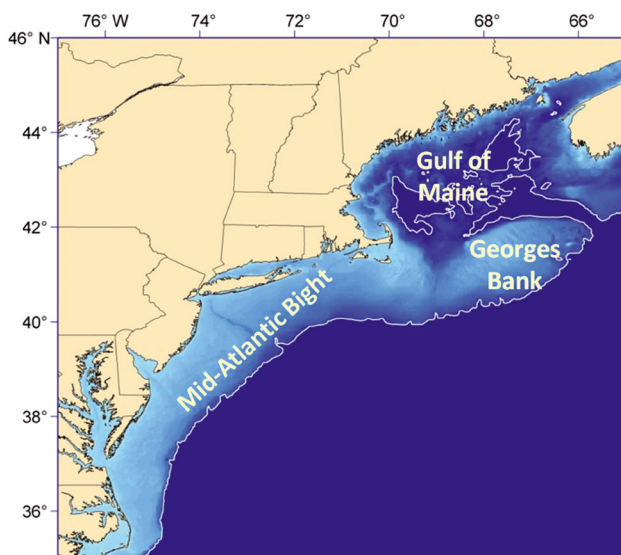


Fig. 1. Northeast US continental shelf Large Marine Ecosystem study area. White line represents the 200 m isobath

METHODS

Study area, species groups and background

The NE USA LME region has been heavily fished for more than a century by a mixed-gear demersal groundfish fishery, targeting primarily gadids and flatfish, and for about half a century by a pelagic-gear fishery, targeting small pelagic fish (Table 1) (Link et al. 2011). These fisheries are concentrated in the Gulf of Maine and Georges Bank region, and extend south to the Mid-Atlantic region (Fig. 1). The fisheries are not highly selective, resulting in some bycatch of pelagic fish in the groundfish fishery and vice versa. Fishing regulations are in place to help rebuild many of these commercially important fish species, and some species have responded better than others to regulation. Atlantic herring were at low biomass levels in the 1980s but have rebounded to current levels of almost twice the biomass needed to deliver maximum sustainable yield (B_{MSY}) (NEFSC 2012a). Flatfish such as witch flounder *Glyptocephalus cynoglossus*, yellowtail flounder *Limanda ferruginea* and Atlantic halibut *Hippoglossus hippoglossus* have remained, or are currently in, an overfished state (NEFSC 2012a,b). Meanwhile, gadids have had mixed results, including a strong rebuilding of Georges Bank haddock (*Melanogrammus aeglefinus*) and continued low biomass of Gulf of Maine Atlantic cod (*Gadus morhua*) (NEFSC 2012b, 2013).

Similarly, marine mammal species were historically depleted or even eradicated (e.g. grey seals *Hali-*

choerus grypus) from this region due to harvest, and species have rebounded to different levels under current protections (Waring et al. 2013). Some mysticetes have been slow to rebound, such as North Atlantic right whales *Eubalaena glacialis*, whereas pinnipeds such as grey (*H. grypus*) and harbor (*Phoca vitulina concolor*) seals have shown greater gains in abundance (Waring et al. 2013). In addition to fish bycatch, the groundfish and pelagic fisheries have some bycatch of marine mammals, particularly young pinnipeds and odontocetes, and entanglements of marine mammals in active and inactive groundfish and pelagic fishing gear.

For simplicity in this initial iteration of our model, we selected a few functional groups of marine mammals with differing target prey and fisheries interactions, and a few finfish groups that were commercially important but fulfill different niches. The six functional groups in our model therefore included three marine mammal groups (mysticetes, odontocetes, and pinnipeds) and three fish groups (small pelagic fish, flatfish, and gadids, Table 1), where fish species were aggregated across stock areas.

Model description

We used an aggregate group production model based on MS-PROD (Gamble & Link 2009) and AGG-PROD (Gamble & Link 2012). The specific form of the model used in this study is a discrete difference equation based on a Schaefer production model with

Table 1. Functional groups included in the model

Group	Common names	Species included in Group	Taxa
Mysticetes	Fin whale, humpback whale, North Atlantic right whale, sei whale, minke whale	<i>Balaenoptera physalus</i> , <i>Megaptera novaeangliae</i> , <i>Eubalaena glacialis</i> , <i>B. borealis</i> , <i>B. acutorostrata</i>	
Odontocetes	Pilot whale, bottlenose dolphin, Atlantic white-sided dolphin, common dolphin, harbor porpoise	<i>Globicephala</i> sp., <i>Tursiops truncatus</i> , <i>Lagenorhynchus acutus</i> , <i>Delphinus delphis</i> , <i>Phocoena phocoena</i>	
Pinnipeds	Gray seal, harbor seal	<i>Halichoerus grypus</i> , <i>Phoca vitulina concolor</i>	
Small pelagic fish	Atlantic herring, river herring, saury, anchovies, Atlantic mackerel, jacks, scads	<i>Clupea harengus</i> , <i>Alosa</i> spp., <i>Scomberesox saurus</i> , <i>Anchoa</i> spp., <i>Engraulis eurystole</i> , <i>Scomber scombrus</i> , Carangidae	
Flatfish	Yellowtail flounder, winter flounder, summer flounder, witch flounder, American plaice, Atlantic halibut, windowpane flounder	<i>Limanda ferruginea</i> , <i>Pseudopleuronectes americanus</i> , <i>Paralichthys dentatus</i> , <i>Glyptocephalus cynoglossus</i> , <i>Hippoglossoides platessoides</i> , <i>Hippoglossus hippoglossus</i> , <i>Scophthalmus aquosus</i>	
Gadids	Red hake, white hake, spotted hake, silver hake, rocklings, Atlantic cod, haddock, pollock	<i>Urophycis chuss</i> , <i>U. tenuis</i> , <i>U. regia</i> , <i>Merluccius bilinearis</i> , <i>Enchelyopus cimbrius</i> , <i>Gadus morhua</i> , <i>Melanogrammus aeglefinus</i> , <i>Pollachius virens</i>	

added competitive and predator–prey interactions (Eq. 1):

$$B_{i,t+1} = B_{i,t} + r_i B_{i,t} \left(1 - \frac{B_{i,t}}{K_i} - \frac{\sum_j \beta_{ij} B_{j,t}}{(K_\sigma - K_i)}\right) - B_{i,t} \sum_p \alpha_{ip} B_{p,t} - H_i B_{i,t} \quad (1)$$

Where $B_{i,t}$ and $B_{j,t}$ are the biomasses of groups i and j at time t respectively, r_i is the intrinsic growth rate of group i , K_i is the carrying capacity of group i , K_σ is the system carrying capacity, β_{ij} is the competition coefficient between groups i and j , α_{ip} is the predator–prey interaction coefficient between prey group i and predator group p (if positive, it is the proportion of prey removed by the predator; if negative, it is the positive feedback by the prey on the predator), $B_{p,t}$ is the biomass of predator p at time t , and H_i is the harvest rate on group i .

Our model thus distinguishes between sources of mortality such as catch and predation, and limitations on growth due to competition. It also separates population growth into two components: intrinsic rate of growth and growth due to prey consumption. Finally, the model can track changes to these mortality sources over a projected time period and how the biomass trajectories of each group in the model relate to biological reference points.

Model parameterization

We parameterized the model to run in simulation mode using the steps outlined in detail below. Our approach was to consider all sources of data available to inform and refine model parameters. The preliminary model outputs were compared to the data and parameters were adjusted iteratively to achieve reasonable correspondence with the available information for all groups (e.g. interaction parameters were adjusted to achieve observed diet composition). Statistical parameter estimation from fitting the model to time series data was not attempted because we currently lack consistent time series of marine mammal abundance, mortality, and diet estimates. Instead, our goal was to create a starting point similar to the 2013 observations in the NE USA LME, and to explore the outcomes and tradeoffs under (1) different harvest levels on the fish groups and (2) assumptions of human-induced mortality for marine mammals.

Finfish

Biological parameters. The most recent year of population biomass (in metric tonnes, t) from individual species stock assessments (Table 2; NEFSC 2006,

Table 2. Parameterization of the MS-PROD model base scenario, assuming the lower limits of marine mammal bycatch (H_i , i = Group). System carrying capacity (K_σ) = 5 000 000 t. This is lower than the sum of the group carrying capacities (K_i), since all groups are not at carrying capacity simultaneously. A positive predator–prey interaction coefficient is the proportional removal of prey biomass from the system by that predator. A negative predator–prey interaction coefficient is the prey-feedback on predators, allowing for the examination of the effects of lower prey biomass in the system. All parameters were informed by, but not tuned to, empirical data, as described in ‘Materials and methods: Model parameterization’

Parameter	Group					
	Gadids	Flatfish	Small pelagics	Mysticetes	Odontocetes	Pinnipeds
Growth rate (r_i)	0.55	0.9	1.0	0.037	0.031	0.07
Initial biomass ($B_{\text{Current},i}$)	558 398	66 728	3.37×10^6	1.2×10^5	1.6×10^4	1.1×10^4
Carrying capacity (K_i)	1×10^6	5×10^5	4×10^6	3×10^5	2.8×10^4	1.4×10^4
Harvest rate (H_i)	0.09	0.22	0.06	7.3×10^{-4}	1.03×10^{-3}	6.33×10^{-4}
Between-species competition coefficient (β_{ij}) (Group i on Group j)						
On Gadids	0	0.5	0	0	0	0
On Flatfish	1	0	0	0	0	0
On Small pelagics	0	0	0	0	0	0
On Mysticetes	0	0	0	0	0	0
On Odontocetes	0	0	0	0	0	0
On Pinnipeds	0	0	0	0	0	0
Predator–Prey interaction coefficient (α_{ip}) (Group i on Prey p)						
On Gadids	0	0	-2.75×10^{-8}	3.2×10^{-7}	2.5×10^{-6}	7.2×10^{-6}
On Flatfish	0	0	0	0	0	2.8×10^{-5}
On Small pelagics	6.48×10^{-8}	0	0	2.3×10^{-7}	9.9×10^{-7}	1.67×10^{-6}
On Mysticetes	-8.00×10^{-10}	0	-9.00×10^{-10}	0	0	0
On Odontocetes	-6×10^{-9}	0	-2.60×10^{-9}	0	0	0
On Pinnipeds	-9×10^{-9}	-3.3×10^{-8}	-2.40×10^{-9}	0	0	0

2007a, 2008a,b, 2009, 2010a,b, 2011, 2012a) were summed across species to give the starting biomass of each group ($B_{\text{Current},i}$ in Table 2). Growth rates and carrying capacity (t), derived as the sum of twice the single-species B_{MSY} estimates for each group, were taken from the same stock assessments. The growth rates for each species within the aggregate groups were averaged with a weighting proportional to the biomass of each species within the group, in the same manner as in Gamble & Link (2012). These were further adjusted as necessary to achieve stable biomasses comparative to observed recent biomass levels for the individual groups under the base fishing levels.

The inclusion of the carrying capacity terms in the model simulates the density dependence caused by the limits on productivity in the system and within each aggregate group. The sum of each group's carrying capacity is greater than the system carrying capacity. This is to allow for resilience in the system, such that as one group is depleted, another will be able to take its place. Additionally, it has been shown that aggregate groups may have an aggregated B_{MSY} (and therefore carrying capacity) that is lower than the sum of the single-species B_{MSY} (Brown et al. 1976, May et al. 1979, Overholtz et al. 2008, Mackinson et al. 2009). It is therefore likely that a system-level B_{MSY} may also be lower than the sum of B_{MSY} for functional groups. We remained conservative in the increase of the system B_{MSY} over the sum of the functional-group B_{MSY} , as the expected ratio between these two levels of aggregation in the NE USA LME is unknown.

Interaction parameters. Although we acknowledge that prey switching occurs in marine mammals and in many fish species, our model implies a Type I functional feeding response, since we do not currently have the data to parameterize prey switching, especially for the marine mammals. Predation, prey-feedback and competition coefficients were therefore linear scalar (Table 2). To inform these coefficients for the finfish groups, we used observed food habits data sets from Northeast Fisheries Science Center (NEFSC) bottom trawl surveys spanning 1973–2013. This data was aggregated by weight across the study region and by each functional group in our model to provide the amount of removals by each group on each other group (which in many cases was 0). Diet overlap was compared between groups to determine if the groups were likely competitors when also considering mobility and habitat usage.

Two proportions were then calculated from the diet data, which were averaged over all years of data available: (1) the proportion of removals for a given prey group in our model by each predator group in

our model, and (2) the diet proportion of a prey group in a given predator's diet. The parameters were then adjusted until the proportions within the model at the starting biomasses for all groups were within 1% of the calculated proportions from the diet data. An additional constraint was that the removals by marine mammals on the small pelagic group were equivalent to removals by the pelagic fishery in the model, in accordance with Smith et al. (2015).

There is no strong agreement on how important competition is in the NE USA LME between the groups in the model, but competition is suspected between some groups (Link & Auster 2013). Indirect competition is included in the model through the use of the predation and prey-feedback coefficients. If a prey item decreases for a given predator group then the growth for the group decreases due to the lost prey consumption. However, since important prey items held in common between the flatfish and gadid groups are not included in this model, we explicitly parameterized the competition coefficients such that competition occurred between the two groups (Table 2). We adjusted these values in tandem with the growth rates and predator–prey coefficients to achieve stable biomasses under the current fishing conditions. We assumed that flatfish, being somewhat less mobile than gadids, would be more strongly affected by competition with gadids than the reverse. Due to the high productivity of the area and relatively opportunistic feeding habits of these species, we do not think the groups are highly resource-limited and therefore kept competition as the least important source of mortality on the gadid and flatfish groups (Link et al. 2008, Link & Auster 2013).

Exploitation parameters. Commercial exploitation rates (averaged over the most recent 5 yr), were taken from the same stock assessments referred to in the biological parameterization section. Although the commercial exploitation rates from the fish groups are intended to estimate total catch instead of being specific to a fishery or gear type, we considered the gadids and flatfish groups to be targeted by the groundfish fishery (predominantly bottom trawls, longlines, gill-nets and handlines), and the small pelagic fish group to be targeted by the pelagic fishery (predominantly mid-water trawls and purse seines).

Marine mammals

Biological parameters. For marine mammals, starting biomass estimates ($B_{\text{Current},i}$ in Table 2) came from dedicated NEFSC marine mammal surveys (Waring

et al. 2013) which were re-estimated to include biomass only from the NE USA LME region (our Fig. 1; Smith et al. 2015). Annual productivity rates reported in marine mammal stock assessments (Waring et al. 2013) were used to inform r_i (Table 2). These productivity rates are fairly uncertain for most species and considered to be roughly maximum rates of population increases. K_i for the marine mammal groups was assigned to maintain the overall rate of population growth for each group between 50 and 100% of these reported productivity rates. Further assumptions were that mysticetes are still well below their historical population levels, odontocetes are also below historical levels, and pinnipeds appear to be closer to their maximum population, in the study region (DFO 2011, Waring et al. 2013).

Interaction parameters. Diet data compilations from published literature (Smith et al. 2015) were used to inform predation and prey-feedback coefficients for the marine mammal groups, and parameterization was done in the same manner as for the fish groups (described above) (Table 2). Since the species groupings in this model exclude important prey for marine mammals, ratios of excluded prey groups to included prey groups, weighted by the biomass of mean prey consumed, were used to parse biomass growth into logistic growth and the effects of prey consumption (in the form of prey-feedback coefficients).

No direct mammal–mammal or mammal–fish competition was included in the model; these parameters were set to 0 (Table 2). This is thought to be a reasonable simplification, since the habitats of marine mammals and the 2 groundfish groups are generally different from each other, and the movements of odontocetes and mysticetes are far greater than those of the fish groups in the model. The small pelagic fish and the mysticete groups hold some prey in common, but in the absence of good diet data for the mysticetes, and with the assumption that food would not be limiting due to competition for these 2 groups (Nye et al. 2013, Ruzicka et al. 2013), we did not include direct competition between them. Indirect competition occurs mainly through the removals of prey groups that overlap between the marine mammal groups.

Exploitation parameters. Estimated mortalities and serious injuries reported in the marine mammal assessment (Waring et al. 2013) were used to inform the fleet 'harvest' on marine mammals (Table 2). The likely mortalities were partitioned into groundfish and pelagic fishing gear, as defined for the fish groups. For large whales, an annual average of likely

mortalities from entanglement incident reports (Cole & Henry 2013) were added to the bycatch mortalities. The incident reports spanned the time period 1989–2013, and although annual mortality events are admittedly highly variable, a time series average was used to approximate a standard annual mortality rate. Incidents without a reported gear type or those that were indistinguishable between groundfish and pelagic fisheries were pro-rated into the two fisheries with the known gear data. Relative harvest rates were estimated by dividing estimated mortalities by abundance estimates (Smith et al. 2015) for each marine mammal group. In the scenarios of changing fish harvest levels, the harvest rate by a fleet on each marine mammal group changed in proportion to the change in harvest rate for the fish groups being targeted, while the removals of each marine mammal group for the other fleet remained the same.

Model scenarios

The parameterization described above is the base scenario against which all other scenarios were compared. We developed harvest scenarios that explore different levels of harvest on the finfish groups (and therefore different levels of mortality on the marine mammal groups). Additionally we developed sensitivity scenarios to explore the effects of lower or higher prey dependence by the marine mammal groups, and higher mortality caused by human activities. All model simulations were run for 50 yr, with an annual time step, starting from a configuration reflective of the present conditions.

Two fleet-based harvest scenarios were created to simulate biomass projections for each species group under varying harvest rates. The first set of harvest scenarios simulated changes in pelagic fishery harvest rates by changing the harvest rate on small pelagic fish by 0, $\frac{1}{4}$, $\frac{1}{2}$, 4, 8 and $15\times$ the level of catch in the base scenario. The second set of harvest scenarios simulated changes in groundfish harvest rates by changing harvest rates simultaneously on flatfish and gadids by 0, $\frac{1}{4}$, $\frac{1}{2}$, 2 and $4\times$ the level of catch in the base scenario.

We performed 2 parameter sensitivity scenarios. The first bracketed 2 extreme assumptions regarding prey dependence of marine mammals around the default parameterization of intermediate prey-feedback while maintaining fishing harvest rates at the same level as in the base scenario. The high prey-dependence parameterization reduced r_i by 80% while increasing prey-feedback to allow similar long

term overall population growth as occurred in the base scenario. The low prey-dependence parameterization increased r_i and set prey-feedback to 0. The value for r_i in this case was analytically calculated.

The second sensitivity analysis explored a higher level of marine mammal mortality caused by interactions with fishing fleets, given current fishing harvest and maintaining the default level of prey-feedback on marine mammals. The reported marine mammal mortalities in the default parameterization are likely at, or close to, the minimum level, and there is the possibility of higher mortality due to unreported incidents. To test the sensitivity of the model to these mortalities, we used a parameterization with 10× the default level of mortality.

Reference points

An important element of this study is how fishing under different harvest strategies might result in changes in the biomass time series for the modeled groups in relation to reference points. Thus, our results from the scenarios are compared to reference points that we define below.

Currently there are no target population biomass reference points for marine mammal species and fin, sei, humpback and North Atlantic right whales included in the mysticete functional group are presently listed as Endangered (Waring et al. 2013). Thus, $B_{\text{Current},i}$ were chosen as the marine mammal reference points under the assumption that marine mammal biomass should not be allowed to fall below current levels.

Fish reference points in the USA have traditionally been based on B_{MSY} , but this is complicated in a multispecies or aggregate group context. In a system where there are interactions between species and groups, B_{MSY} for any one species is a surface conditioned on the biomasses of the other species or groups and not a single point; a unique biomass distribution must be selected for all other species groups in the ecosystem to determine a unique B_{MSY} for an individual species. Given this, we defined a simpler proxy B_{MSY} for each group as half of its average biomass in an unfished system. After setting all harvest in each scenario to 0, we calculated the average unfished biomass for each group over the model run, excluding the first 5 yr to reduce the effects of the model burn-in time. If there were no species interactions, setting harvest rates to 0 would result in each species achieving its carrying capacity. Thus, our calculation can be considered a proxy for calculating the

carrying capacity (K) for a group, given the species interactions that occur in the model. We then calculated B_{MSY} as half of this unfished biomass.

Since the base scenario and the sensitivity scenario had the same competitive and predation interactions, the calculated B_{MSY} is the same for both under a no-fishing harvest parameterization. Because the predation interactions are different in the 2 prey dependence scenarios, B_{MSY} was different for each of those scenarios. We then report the final values relative to these reference points for each scenario.

RESULTS

Groundfish harvest scenarios

We found that when considering interactions, even the base scenarios of current harvest levels resulted in flatfish biomass declines below the aggregate proxy B_{MSY} level after 50 yr (Fig. 2). For the scenarios of harvest reductions on the flatfish and gadid groups, assuming reported marine mammal mortalities, the greatest gains in biomass were seen for flatfish, which increased up to $\sim 2\times B_{\text{MSY}}$ over a 50 yr projection, and for odontocetes and mysticetes, which increased slightly $>2\times$ the current biomass (Fig. 2A). However, small pelagic fish decreased in biomass with harvest reductions to the groundfish fishery, due to increased predation pressure (Fig. 2A). In the sensitivity scenario which explored a 10-fold higher marine mammal mortality from harvest, all marine mammal groups required zero flatfish and groundfish harvest to achieve similar population increases as occurred in the base scenario (Fig. 2B). As expected, gadid and flatfish populations were reduced with increases in harvest over the 50 yr projection, but only the highest harvest rates resulted in gadid biomass dropping below the B_{MSY} proxy (Fig. 2A). Marine mammal population growth was most inhibited when gadid and flatfish harvest was quadrupled from base harvest, and when marine mammal mortalities were assumed to be 10× the current reported rate. Odontocete biomass was predicted to drop by 50% from current levels (Fig. 2B).

Pelagic harvest scenarios

For the scenarios of decreasing harvest on small pelagic fish, assuming reported marine mammal mortalities, biomass of small pelagic fish increased slightly from 1.8 at base fishing to $2\times$ the B_{MSY} over a

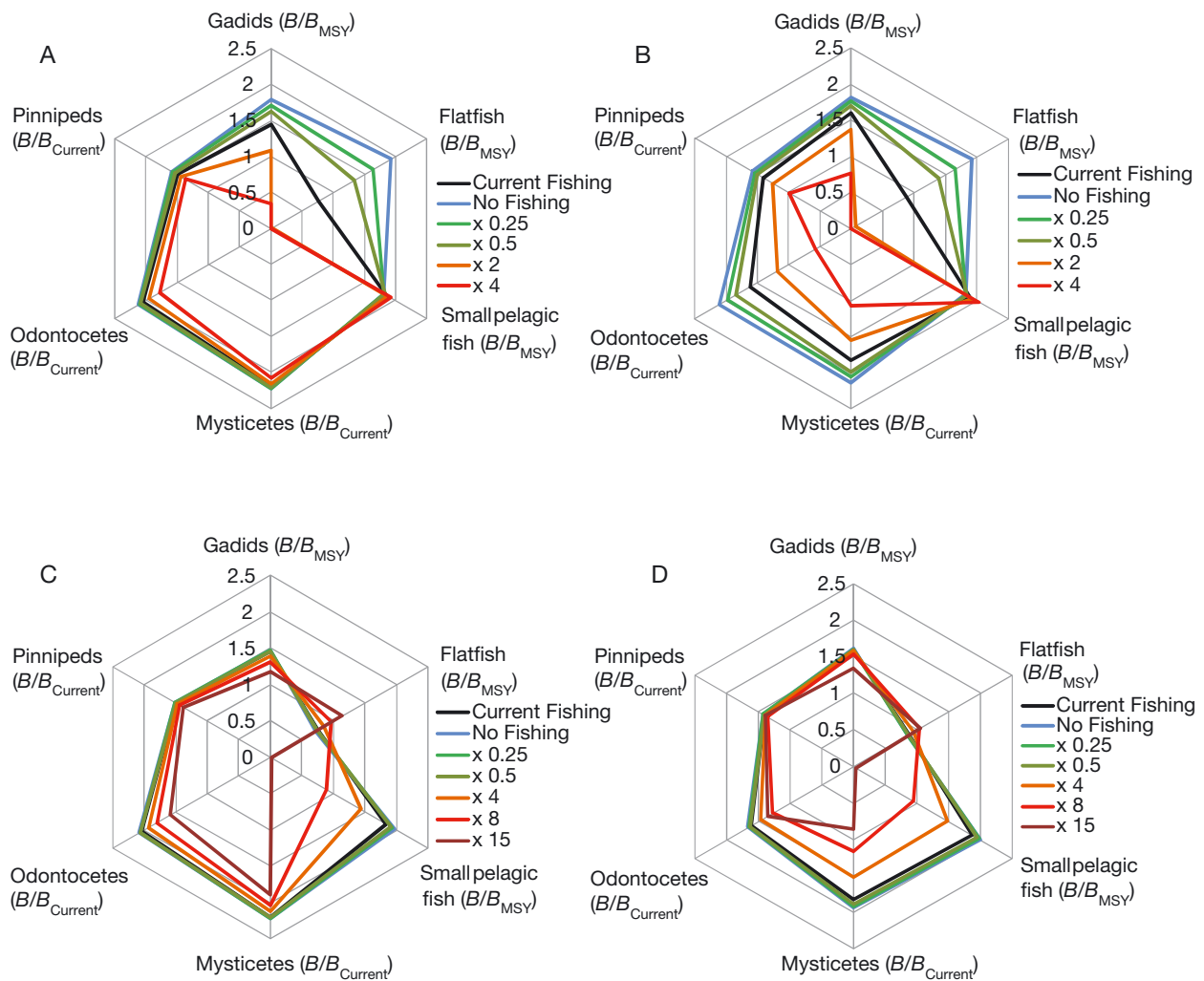


Fig. 2. Changes in biomass (B) over 50 yr relative to biomass targets, due to (A) changes in groundfish harvest (gadids and flatfish removals) under the base scenario, (B) changes in groundfish harvest under 10 \times the reported human-induced marine mammal mortalities sensitivity scenario, (C) changes in pelagic fish harvest under the base scenario, and (D) changes in pelagic fish harvest under 10 \times the reported human-induced marine mammal mortalities. B_{MSY} (biomass needed to deliver maximum sustainable yield) for the fish groups was a proxy defined as half of each group's average biomass in an unfished system, and $B_{Current}$ for the marine mammal groups is the starting biomass in the model

50 yr projection (Fig. 2C). This increase in small pelagic biomass remained similar when assuming 10 \times the reported marine mammal mortalities (Fig. 2D). Small pelagic fish biomass only fell below aggregate B_{MSY} proxy levels when fished at 8 \times the current harvest rate, but collapsed completely when fished at 15 \times the current harvest (Fig. 2C). When assuming 10 \times the reported marine mammal mortalities, increases in pelagic fishing reduced the potential marine mammal population growth for all marine mammals, and mysticete biomass declined \sim 10% from current levels at the highest small pelagic fish harvest rate of 15 \times the current rate (Fig. 2D). Pelagic har-

vest, assuming reported marine mammal mortalities, had to increase 15 \times the current level (Fig. 2C) to see the same reductions of biomass growth in marine mammals as the current pelagic harvest with 10 \times the marine mammal mortalities (Fig. 2D).

Mortality sources

Mortality sources for gadid and flatfish groups were dominated by predation, under the base model parameterization (Fig. 3A,B). This is due to 2 main reasons: (1) each group included species that are not

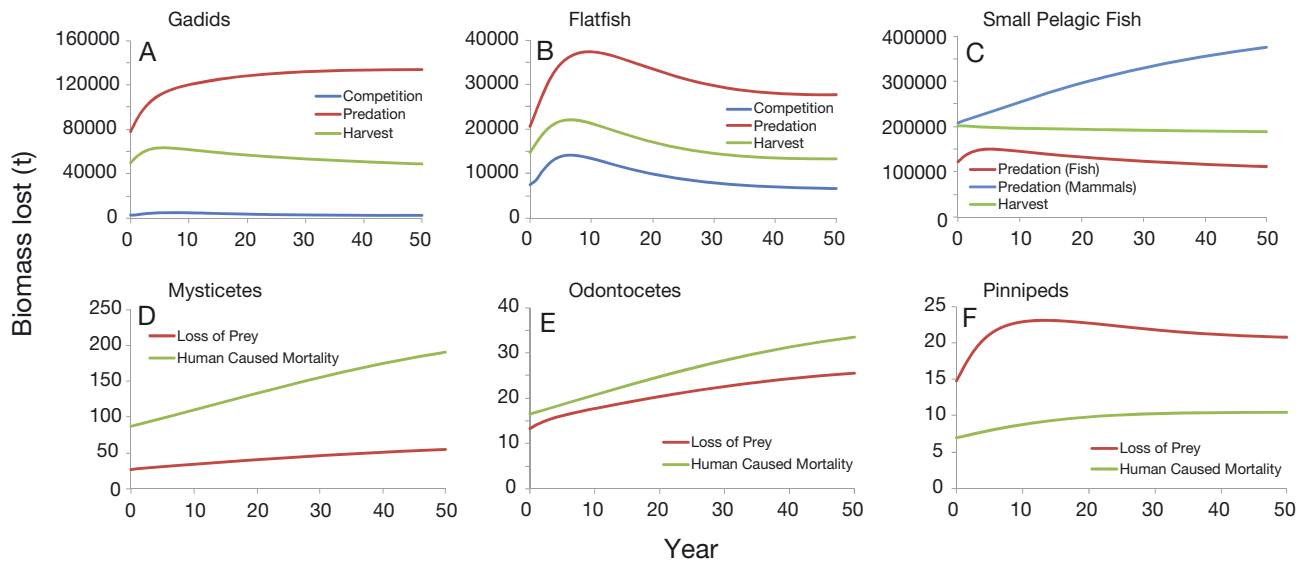


Fig. 3. Changes in mortality over the projected time period for species group under current levels of fisheries catch and reported human-induced marine mammal mortalities (bycatch, entanglements, and collisions with ships)

targeted heavily by the fisheries (e.g. red and spotted hakes in the gadids), and (2) many of the commercially important species in the groups are overfished and harvest rates have thus been restricted by management regulations to achieve rebuilding targets (e.g. yellowtail flounder and Atlantic cod stocks). These two factors combined mean that the overall harvest pressure that each group faced in the model is lower than that of predation. Predation by marine mammals dominated small pelagic fish mortality (Fig. 3C), increasing over the model run as the marine mammals increased in biomass. This explains the declines in biomass of small pelagic fish when biomass increased for gadids and marine mammals (Fig. 2A,B). The high predation mortality for flatfish also explains their decline in biomass when harvest was reduced for small pelagic fish, while the biomass of all the other groups increased (Fig. 2C,D). Human-induced mortality was higher than mortality due to the loss of prey for mysticetes and odontocetes, but the opposite was true for pinnipeds (Fig. 3D–F).

Sensitivity analyses of marine mammal mortalities and prey dependence

For sensitivity analyses assuming current fishing, all aggregate biomass estimates of gadids remained above the B_{MSY} proxy reference points regardless of assumptions of marine mammal mortalities (Fig. 4). Flatfish biomass started below aggregate B_{MSY} and in the short-term increased above B_{MSY} , but ended

slightly below or well below the B_{MSY} proxy after 50 yr, for all sensitivity runs. High prey dependence of marine mammals on flatfish as well as lower marine mammal mortality assumptions resulted in the lowest biomass outcomes for flatfish (Fig. 4). B_{MSY} proxy reference points were different for gadids and flatfish between the high and low marine mammal prey dependence scenarios. Biomass of small pelagic fish was relatively constant over time and all sensitivity runs, and remained well above the B_{MSY} proxy (which was indistinguishable between high and low marine mammal prey dependence scenarios). All of the marine mammal groups increased in biomass relative to current biomass levels over the 50 yr time-frame, although assumptions of no prey dependence and 10× the reported human-induced marine mammal mortalities resulted in the least biomass growth (Fig. 4).

DISCUSSION

Our simulations provide valuable insights into the interactions between commercially fished groups, marine mammals, and humans over the NE USA LME. We found that harvest rates of commercially important fish groups may impact biomass trends of marine mammals due to direct fisheries interactions via bycatch and ship strikes, and indirectly via altered prey availability. Our model suggests that managing human-induced direct mortality is the most important factor for recovery of marine mammal populations, but fishery management also plays an

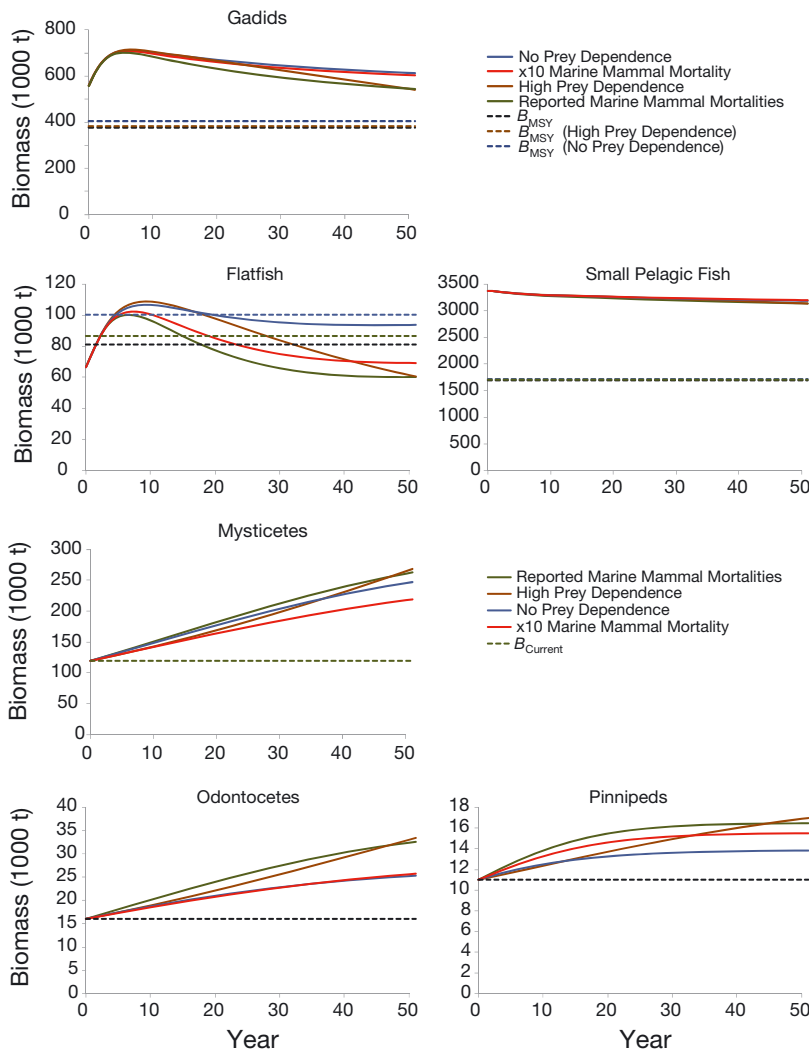


Fig. 4. Sensitivity runs of varying human-induced marine mammal mortalities and dependence of the marine mammal biomass on prey. All runs assume current fishing harvest and reported marine mammal mortalities unless otherwise noted. B_{MSY} for the fish groups was a proxy defined as half of each group's average biomass in an unfished system and $B_{Current}$ for the marine mammal groups is the starting biomass in the model

important role in avoiding the additional stress of reduced prey populations. Marine mammal predation can also affect trajectories and reference points for commercially fished species. We elaborate on these points and the implications for ecosystem-based management that integrates marine mammal and fisheries objectives in the sections below.

Fisheries interactions with marine mammals

Our simulations suggest that current levels of fishing may allow marine mammal recovery in the NE USA LME. Marine mammal biomass increased under

all scenarios except when an order of magnitude increase above observed human-induced marine mammal mortality was assumed. Gadid and small pelagic fish groups could even be reduced below the B_{MSY} proxy in this model and still maintain population increases or stability for marine mammals if presently observed levels of human-induced mammal mortality are accurate. Of course, the most extreme overfishing scenarios did have impacts on marine mammal population trajectories, slowing recovery. Therefore, our results suggest that fisheries management that maintains commercial fish groups at productive levels and prevents overfishing should allow for recovery of marine mammals in this system.

There are 4 important caveats to this finding. (1) We used maximum net productivity rates reported in marine mammal assessments (Waring et al. 2013) to inform the marine mammal population growth; however these are often based on little empirical information and could be unrealistically high for some species. (2) The biomass reference points defined for commercial fish groups in this study are estimated within a multispecies context, so they already take species interactions into account. Fisheries reference points derived from single species analyses which are currently used in management may result in fishing levels less compatible with predation and marine mammal recovery (Hollowed

et al. 2000, Moustahfid et al. 2009a,b, Tyrrell et al. 2011). (3) The marine mammals modeled here get varying portions of their diet from fish and especially invertebrates (zooplankton) that are not included in our analysis (Link et al. 2008); hence we conducted analyses in which mammals were more reliant and less reliant on the aggregate fish groups in our model than assumed under the base scenario. Even assuming higher than expected dependence on these groups as prey, trajectories for marine mammals were very similar to baseline assumptions. However, our model did not include human impacts on the unmodeled non-target species that may also be prey of marine mammals. In a full food web study, total

fisheries catch per unit area was greater than the combined total consumption by marine mammals in the Gulf of Maine, and more than half of the combined marine mammal consumption estimated for Georges Bank (Gaichas et al. 2009); therefore, further investigation of fishery impacts on all marine mammal prey in the NE USA LME is warranted. (4) Our model did not explicitly include competition between marine mammals and commercial fish species for common prey (zooplankton and other invertebrates); however, other simulations with full food webs suggest that increasing or recovered marine mammal populations may not compete strongly with finfish on Georges Bank (Nye et al. 2013, Ruzicka et al. 2013). Ruzicka et al. (2013) found that even the strongest possible assumptions of competition in a static model reduced fish production by only 20–25% when odontocete populations were increased 3-fold or baleen whale populations 20-fold. Allowing for compensatory population responses in scenarios run within a dynamic version of the Georges Bank food web model, increased marine mammal populations had no detectable impact on the biomass of fish groups or fisheries over the long term (Ruzicka et al. 2013). Nevertheless, continued monitoring for competition between commercial fish and marine mammals for unfished resources would be wise as both fish and mammals recover from previous exploitation, especially as climate conditions alter species distributions (Nye et al. 2009) and zooplankton communities (Friedland et al. 2013).

Forage fish harvest in particular has received attention recently for its potential impacts on apex predators, including marine mammals (Smith et al. 2011, Pikitch et al. 2014). Recommendations for fishery management tend towards harvest below single species MSY reference points, but the most appropriate management strategy also depends on characteristics of the ecosystem (Smith et al. 2011). Small pelagic fish, including those modeled here, are recognized as an important forage fish group in the Gulf of Maine and throughout the NE USA LME, with changes in this group affecting marine mammal, fish, and other predators in previous model studies (Link et al. 2009). Extremely high fishing rates for small pelagics in the present study resulted in greatly reduced recovery rates for marine mammals and reductions in gadoid biomass, or even declines in marine mammal populations if human-induced mortality rates are substantially higher than observed. However, within the range of more reasonable fisheries management, which requires maintenance of populations above half B_{MSY} in the USA (and would

therefore not allow the 15-fold pelagic fishery harvest rate simulated here), harvest of small pelagic fish was compatible with recovering marine mammal populations.

We found that maintaining harvest of pelagics at current levels or up to almost 2× the current level of harvest allowed all modeled groups to remain at or above their target biomass. This suggests that an aggregate pelagics harvest rate could be established below the threshold where other species in the ecosystem fall below target levels (or fail to achieve target recovery rates). Large et al. (2013) also found a threshold for a wider range of ecosystem status metrics relative to pelagic biomass, using an empirical approach. Simulations to establish how any given threshold pelagics exploitation rate compares to other suggested pelagic fishing rates (e.g. half of fishing mortality consistent with achieving maximum sustainable yield [F_{MSY}] from Smith et al. 2011) are beyond the scope of the present study, but could be conducted with the following refinements. It is important to consider a full range of predators and their dependence on forage (or other) fish as prey. Dickey-Collas et al. (2014) found North Sea seabirds to be much more dependent on forage fish concentrations in space and time and therefore more sensitive to harvest levels than mobile marine mammals. They still recommend consideration of prey needs for marine mammals in fishery harvest reference points, but suggest that using fishing rate reference points may be easier to use than biomass- (or catch) based reference points (Dickey-Collas et al. 2014). Some modified potential biological removal (PBR) reference points for marine mammal populations have also been suggested to account for fished prey (Moore 2013). Further work would be necessary in the NE USA LME to determine appropriate rate-based reference points since we evaluated primarily biomass, which assumes more stability than may be realistic in this ecosystem with its evident changing conditions (Nye et al. 2009, 2013, Lucey & Nye 2010). Yet clearly the tools to inform and, if need be, modify these reference points are extant and such an evaluation is strongly warranted.

Marine mammal interactions with fisheries

One notable result from this study is that the reference points and biomass trajectories for commercially exploited fish differ when marine mammal predation is included. This has been shown in other studies as well (NEFSC 2008b, Bundy et al. 2009,

Moustahfid et al. 2009a, Tyrrell et al. 2011), however, the direction of the changes to reference points when considering consumption differs depending on model structure and reference point calculations (Moustahfid et al. 2009b). The direction of these reference point changes therefore needs more focused attention, and our understanding of this issue may benefit from further multimodel inference. These changes to biomass and reference points can have significant impacts on stock assessments (Overholtz et al. 2008, NEFSC 2012a), and omitting these important ecosystem interactions could mislead management advice.

As noted above, marine mammal consumption of commercial species can rival tonnage taken by fisheries in the NE USA LME (NEFSC 2012a, Smith et al. 2015) and most likely other ecosystems (Bax 1991, Trites et al. 1997, Bundy 2001, Kaschner et al. 2004). As marine mammal populations continue to recover, incorporating the effects of this consumption into assessments and reference points may be increasingly important to achieve sustainable fisheries. Our model projects increasing marine mammal biomass over time with commercial fish populations stable and above B_{MSY} , with the exception of flatfish. This is largely due to the relatively high seal predation rate on flounders, as parameterized in the model, but this rate may change as more diet data becomes available or as flatfish rebuild. While flatfish were below B_{MSY} at the end of all scenarios, and further below B_{MSY} in scenarios where marine mammals depended on them as prey, at the end of our model runs, at current fishing rates, flatfish would be considered healthy under current US law, which considers populations to be depleted when they are less than half of B_{MSY} or a proxy value (NOAA 2009). Thus, the tradeoff for fully recovered marine mammal populations may be altered reference points and lower biomass for some commercial fish species.

The resolution of the analysis may also lead to an overly optimistic view of potential tradeoffs in this system. On the aggregate group level, the gadids and small pelagic fish groups are currently above their biomass targets, although this is largely due to one or two species that have rebuilt for each group. Individual species within these groups as well as the flatfish that are currently below their biomass targets could be more susceptible to fishing, competition and predation pressures. Although the marine mammal target in these scenarios is simply the current level of biomass, it appears that all groups can be at or above their biomass targets simultaneously given low enough fishing harvest and human-induced mortality rates. This has been seen in other

studies (Gamble & Link 2009, 2012, Gaichas et al. 2012), although when single species were considered, a number of species were below their target biomass even without harvest due to species interactions. Endangered mysticete species and the critically endangered North Atlantic right whale in particular need individual attention, especially with regard to human-induced mortalities. Therefore, we need to further examine the effects of these interactions on single species when including these interactions in an ecosystem-based fisheries management context.

Implications for ecosystem-based integrated management

Our analyses demonstrate the potential complexity of appropriate management interventions to achieve multiple objectives in even a simplified model system. Here we demonstrate that marine mammal recovery and fisheries yield objectives can be met simultaneously, but that multiple response metrics must be evaluated, and thresholds in these metrics must be established to determine when management responses need to change to meet objectives. Further, our work demonstrates the value of model simulations to outline the range of potential responses, even with considerable uncertainty in key model inputs.

Multiple response metrics included multispecies biomass group responses and also components of mortality. The relative importance of different mortality components did not change over time in our relatively simple model under these scenarios, but each group had differently ranked mortality sources. Importantly, fishing was not the major loss to biomass for commercially fished species under current fishing levels—predation was. As fishing pressure increases, the tradeoffs between species interactions and yield or recovery objectives become more apparent. Therefore, a broad suite of metrics is needed to fully capture this tradeoff (Link 2005, Shin et al. 2010, 2012). One such example that could be included is the exploitation index (e.g. Shackell et al. 2012), which contrasts total removals to total standing biomass. Other examples are the pelagic to demersal biomass ratio (Link 2005, Shackell et al. 2012, Large et al. 2013), and the ratio of marine mammal biomass (or production) to small pelagic biomass (Link et al. 2008). All of these elucidate the amount of realized small pelagic fishing that is possible while maintaining all other populations. However, no one indicator

will be able to singly inform the range of features that give rise to these tradeoffs.

In addition to multiple metrics, the development of thresholds for them is needed to provide a transparent framework for management decision-making (Samhuri et al. 2010, Fay et al. 2013, Large et al. 2013). It is one thing to note the levels of biomass, mortality, or relative ratios of these within a system, and another to note which levels are robust or unacceptable such that management responses are necessary to meet conservation, economic, and social objectives. These thresholds for marine mammals may include a range of critical elements from human-induced mortality (Merrick & Cole 2007, Glass et al. 2010) to food availability (Kenney et al. 1997, Hlista et al. 2009). Capturing these thresholds has been done for over three-quarters of a century in a single species context (NEFSC 2007b, 2008b), but fully capturing the set of indirect and distributed impacts remains an important challenge.

Other system response metrics and thresholds have been considered for this system and others worldwide. Potential system yield has been examined from the fish perspective for the total system, and for different types of fish groups as well as single species (NEFSC 2008b, Fogarty et al. 2012, Gaichas et al. 2012). The total amount of primary production in a system can also be used to estimate limits on fisheries yield (Piroddi et al. 2010, Shackell et al. 2012). Empirical work has shown that fisheries landings thresholds exist in this system (Large et al. 2013) and some of these thresholds have been simulation tested (Fay et al. 2013). Because of this finite nature of productivity in ecosystems, as well as the limits on fish extraction that a system can handle, we need to account for all sources of mortality in the system, including predation and competition, when setting catch limits. Otherwise we could be overfishing commercial stocks due to unaccounted mortality, or inhibiting marine mammal recovery due to reductions of prey biomass.

In other regions, simulation modeling has been used to evaluate marine mammal consumption estimates, recovery strategies for marine mammals, and even the simultaneous objectives of fisheries yield and marine mammal recovery (e.g. Punt & Butterworth 1995, Mohn & Bowen 1996, DeMaster et al. 2001, Constable 2002, O'Boyle & Sinclair 2012). These simulations should continue to afford an opportunity to produce a wide set of metrics, test their threshold levels, and evaluate various management strategies. We recommend that any future simulations of the NE USA LME continental shelf region

also emphasize the need to evaluate both fisheries yield and marine mammal recovery objectives simultaneously, and move towards operational models and management similar to the work that has been done in the Southern Ocean (Constable 2002).

Simulations allow for the consideration of information with a variety of data quality and uncertainty. We were able to address uncertainty in marine mammal diet and mortality parameters in this simulation and found valuable information on the relative importance of these parameters to the recovery of marine mammals and effective management of finfish groups. The fact that human-induced mortality was found to be one of the most important factors affecting the recovery of marine mammals may be an advantage, since regulations to reduce direct marine mammal mortalities (Merrick et al. 2001, Merrick & Cole 2007) can be easier to implement than regulating indirect relationships of marine mammals to prey.

CONCLUSIONS

Historically, management objectives for marine mammal populations and commercially harvested finfish populations have been considered and implemented separately in the NE USA LME and more generally throughout the world, as though these components of marine ecosystems do not interact. This study and others have demonstrated that fisheries interact with marine mammals, and that marine mammals interact with fisheries, both directly and indirectly. The dual objectives for management (recovery of mammals, sustainable yield of fisheries) are not incompatible, and may be combined to optimize fisheries yield subject to the constraints imposed by recovering or maintaining marine mammal populations. Simulation modeling studies focused on the interactions of marine mammals and fisheries can identify where tradeoffs in management and objectives require consideration.

In the NE USA LME region, we find that fishery sustainability and marine mammal recovery are compatible, but that excessive fishing slows mammal recovery and that considering marine mammal consumption changes fishing reference points. Ultimately, a broader discussion among everyone involved in ocean use and sustainability must determine the acceptable tradeoffs in recovery and yield objectives, and considering these objectives together is the first step towards more integrated and effective ecosystem-based management.

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