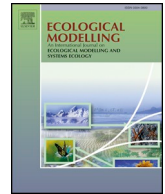




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Assessing the sensitivity of three Alaska marine food webs to perturbations: an example of Ecosim simulations using Rpath

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ABSTRACT

Ecosystem modelling is a useful tool for exploring the potential outcomes of policy options and conducting experiments that would otherwise be impractical in the real world. However, ecosystem models have been limited in their ability to engage in the management of living marine resources due in part to high levels of uncertainty in model parameters and model outputs. Additionally, for multispecies or food web models, there is uncertainty about the predator-prey functional response, which can have implications for population dynamics. In this study, we evaluate the sensitivity of large marine food webs in Alaska to parameter uncertainty, including parameters that govern the predator-prey functional response. We use Rpath, an R implementation of the food web modeling program Ecopath with Ecosim (EwE), to conduct a series of mortality-based perturbations to examine the sensitivity and recovery time of higher trophic level groups in the eastern Chukchi Sea, eastern Bering Sea, and Gulf of Alaska. We use a Monte Carlo approach to generate thousands of plausible ecosystems by drawing parameter sets from the range of uncertainty around the base model parameters. We subjected the ecosystem ensembles to a series of mortality-based perturbations to identify which functional groups the higher trophic level groups are most sensitive to when their mortality was increased, whether the food webs returned to their unperturbed configurations following a perturbation, and how long it took to return to that state. In all three ecosystems, we found that the number of disrupted ensemble food webs was positively related to the biomass and the number of trophic links of the perturbed functional group, and negatively related to trophic level. The eastern Chukchi Sea was most sensitive to perturbations to benthic invertebrate groups, the eastern Bering Sea was most sensitive to shrimp and walleye pollock, and the Gulf of Alaska was most sensitive to shrimps, pelagic forage fish, and zooplankton. Recovery time to perturbations were generally less than 5 years in all three ecosystems. The recovery times when fish groups were perturbed were generally longer than when benthic invertebrates were perturbed, and recovery times were shortest when it was pelagic invertebrates. The single model ensemble approach produced simulation results that described a range of possible outcomes to the prescribed perturbations and provided a sense for how robust the results are to parameter uncertainty.

1. Introduction

In recent decades the incorporation of ecosystem considerations into the management of living marine resources has been undertaken to varying degrees in several jurisdictions and large marine ecosystems (FAO 2003, Pitcher et al. 2009, National Ocean Council 2013). To consider the broader ecosystem effects of marine resource management actions, it is necessary to make decisions between policy options based on predicted or expected outcomes and to consider tradeoffs among competing interests (Walters and Martell 2004, Link 2010). Thus, ecosystem modelling of possible outcomes to policy actions or inaction are required to explore potential future ecosystem states that may result

from management decisions (Walters and Martell 2004, Hollowed et al. 2011, Lehuta et al. 2016). Modelling in its many forms is integral to the management of living marine resources and to the implementation of an ecosystem-based approach to management (Plagányi 2007, Coll and Libralato 2012, Fogarty 2014, Busch et al. 2016, National Marine Fisheries Service 2016). Models can be qualitative or quantitative and can be used to enhance general ecosystem understanding or to inform strategic guidance and tactical management decisions (Hollowed et al. 2000, Plagányi 2007, Harvey et al. 2016). Additionally, experiments can be conducted with models that would otherwise be impractical in the real world, permitting the exploration of policy options, climate effects, or other

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anticipated stressors, and help to discern important ecological thresholds and tradeoffs.

A major impediment to the adoption and use of ecosystem models in ecosystem-based management (EBM) is addressing uncertainty in models and their outputs in a satisfactory manner (Murawski 2007, Link et al. 2012, Patrick and Link 2015). There are a wide range of ecosystem models with differing levels of complexity, from multispecies and models of intermediate complexity (MICE, Plaganyi et al. 2014), to models of whole food webs, bio-economic models and end-to-end biophysical models. There is a tradeoff between increasing the realism and complexity of a model and a commensurate increase in the overall uncertainty associated with the model (Collie et al. 2016). This has led to a concern among some scientists and stakeholders that some ecosystem models are too complex and too ambitious in the scope and scale of the processes they are attempting to represent, that these models require more data and information than we possess or could ever attain, and therefore their outputs are of little value (Beckage et al. 2011, Ruiz and Kuikka 2012, Planque 2016). Thus, it is critically important for models intended to support EBM to be candid about uncertainty and to provide accurate accounts of the sources and degree of uncertainty in a model and its parameters, and to characterize that uncertainty in model results (Link et al. 2012).

Several modeling studies and workshops have attempted to address concerns about uncertainty and have assembled lists of best practices for modelling in support of marine EBM (e.g., FAO 2008, Townsend et al. 2008, Link et al. 2010, Kaplan and Marshall 2016). These comprehensive lists of best practices are often applicable to a broad range of ecosystem models and do not necessarily target one model type or specific model framework. A common entry to these best practices is a call for explicit characterization of uncertainty in model inputs and parameters, and to carry this uncertainty through the modelling or simulation process to indicate the uncertainty in model outputs. Including the uncertainty in simulation results helps to avoid a false sense of certainty in model outcomes and can help to communicate the strength of results to managers and stakeholders. Another recommended best practice for multispecies ecological models is to consider the importance of the predator-prey functional response to biomass dynamics, and to evaluate the robustness of model results to alternative forms of this response (FAO 2008). The specific form of the predator-prey functional response is generally not well known for any particular trophic relationship, however it can have a profound impact on biomass dynamics (Mackinson et al. 2003, Gaichas et al. 2011, Gaichas et al. 2012).

In this study, we focus our attention on the treatment of parameter uncertainty in the widely used marine food web modelling framework Ecopath with Ecosim (EwE, ecopath.org, Christensen and Walters 2004). We employ a simplified Bayesian synthesis routine (Givens et al. 1993) for EwE that addresses the aforementioned best practices by including uncertainty in the predator-prey functional response for each trophic interaction, incorporating uncertainty into model simulations for all of the base model parameters, and capturing the effect of that parameter uncertainty in model outputs. We use a single-model ensemble approach (Gal et al. 2014) to generate multiple versions of the same EwE model by allowing the base model parameters and the predator-prey functional response to vary within a prescribed range based on a data pedigree. We then perform simulations on the ensemble of generated models to produce a range of outcomes to the simulated scenarios and examine the robustness of model outcomes to parameter uncertainty.

The static mass-balance model Ecopath was originally developed by Polovina (1984) to produce estimates of biomass and production for species and functional groups in a coral reef ecosystem in the French Frigate Shoals. The program has since had the time dynamic modeling framework Ecosim (Walters et al. 1997) added, which allows for simulations, hypothesis testing, and policy exploration. Since its introduction, more than 400 unique EwE models have been developed

describing freshwater and marine ecosystems from the tropics to polar regions (Coll  ter et al. 2015).

There have been several efforts to address input parameter sensitivity and uncertainty in EwE models. Previous versions of EwE contained a Monte Carlo routine called ‘EcoRanger’, which used a data pedigree and corresponding confidence intervals to generate an ensemble of static Ecopath models to explore model sensitivity to uncertain parameter estimates. Recently, Steenbeek et al. (2018) has developed the Ecosampler module for the EwE program, which also uses a Monte Carlo routine and data pedigree to generate ensembles of balanced Ecopath models which can be passed to Ecosim, Ecospace, or other EwE plug-ins for further analysis. Other routines for generating Ecopath model ensembles have been developed independent of EwE and implemented in Matlab (Kearney 2017) and R (Koehn et al. 2016). Aydin et al. (2005) developed a similar routine called Ecosense, for generating ensembles of Ecosim parameters from a single Ecopath model in the C++ environment, enabling dynamic simulations with all ensemble members (Aydin et al. 2003, Gaichas et al. 2015). With Ecosense, the user can vary the base model parameters, diet compositions, non-predation natural mortality, and the parameters governing the predator-prey functional response (Gaichas et al. 2012). For this study we use the Ecosense routine to generate EwE model ensembles but have adapted the routine to work with a prototype of an independent version of EwE called ‘Rpath’ (Lucey et al., 2020), which was developed to work with the open source statistical program R (R Core Team 2015). Rpath uses the same equations and algorithms of EwE but has the advantages of improved access to the model code and the flexibility to modify the code for user-defined analyses and simulations.

In this study, we execute a series of time-dynamic simulations with EwE model ensembles of three distinct marine ecosystems in Alaska, the eastern Chukchi Sea, the eastern Bering Sea, and the Gulf of Alaska, to investigate the sensitivity of higher trophic level groups to mortality-based perturbations. A perturbation analysis is a useful way to gain insight into population dynamics and how species interact with each other in a food web, mediated by their trophic interactions (Bender et al. 1984, Schmitz 1997). Using a comparative approach can help highlight results that distinguish one ecosystem from the others, features that might otherwise go unnoticed (Megrey et al. 2009). We attempt to identify which functional groups the higher trophic levels are most sensitive to when their mortality is increased, whether the food webs returned to their unperturbed configurations following a perturbation, and how long it took to return to that state. By incorporating the uncertainty in the base Ecopath model parameters, the predator-prey functional response, and using an ensemble approach, we are able to characterize uncertainty in Ecosim results by describing the range of possible outcomes among ensemble members. Additionally, we look for correlations between the number of disrupted ensemble food webs and the trophic level, biomass, and number of trophic links of the perturbed group.

2. Methods

2.1. Modeling Framework

We use existing trophic mass-balance food web models of the eastern Chukchi Sea (Whitehouse and Aydin 2016), eastern Bering Sea, and Gulf of Alaska (Aydin et al. 2007) that were developed using the EwE framework. Ecopath is a biomass compartment model where each compartment represents a species or functional group of multiple species and describes the network of energy flows between groups in a food web. Ecopath is a static, mass-balanced model and it provides a spatially homogeneous ‘snapshot’ of the trophic structure and function of an ecosystem. The mass-balance requirement ensures there is sufficient production in any compartment to meet the modeled demand from predators or any fishery removals. The interactions between species in a

food web are described by Ecopath with a set of linear equations for each group i with predator j as

$$B_i \left(\frac{P}{B} \right)_i * EE_i = C_i + BA_i + \sum_j B_j \left(\frac{Q}{B} \right)_j * DC_{ij} \quad (1)$$

where B is biomass (t km^{-2}), P/B (yr^{-1}) is the production to biomass ratio, Q/B (yr^{-1}) is the consumption to biomass ratio, DC_{ij} is the proportion of prey i in the diet of predator j , BA is a biomass accumulation term, C is subsistence harvest or fisheries catch (t km^{-2}), and EE is ecotrophic efficiency which is the proportion of production ($B_i^*(P/B)_i$) that is consumed by predators and removed by harvests/fisheries included in the model. Mass-balance is achieved when the system of linear equations is solved for one missing parameter for each functional group. A diet matrix (DC_i) and BA_i term (if $BA_i > 0$) must be entered by the user and typically, estimates for B , P/B , Q/B , are C are also provided by the user and the equation(s) solved for EE . Values of EE range from 0 to 1, and are close to one for groups subject to heavy predation and/or fishing pressure, and it is close to zero for groups that experience little predation and/or fishing pressure (Christensen et al. 2005). Often, initial attempts to balance a model are unsuccessful and several functional groups may be out of balance ($EE > 1$) indicating they are being consumed and/or removed at a rate greater than their production. This is often the result of an incompatible set of model inputs (e.g., predator consumption in excess of prey production) or due to an error in the model (e.g., misplaced decimal). When parameters are determined to be incompatible, they will need to be reconciled to bring the model into balance. This can involve recalculating or manually adjusting a parameter based on new information, selecting an alternative parameter from the literature, or using Ecopath to solve for the parameter in question by fixing EE and solving for the suspect parameter. A data pedigree (see section 2.3 Incorporating Parameter Uncertainty) can be used to determine which parameters have the greatest uncertainty and should be considered first for adjustment. The models used in the current study are already balanced and no additional modifications were required.

Ecosim is the time dynamic counterpart of Ecopath and provides the user with the ability to conduct simulations and to test hypotheses on the entire food web (Walters et al. 1997). In Ecosim the system of Ecopath mass balance equations are converted to a set of differential equations describing the biomass dynamics of functional groups, linked together through their trophic interactions and predator-prey functional responses. The biomass dynamics of each functional group is modeled as

$$\frac{dB_i}{dt} = GE_i \sum_{prey} Q(B_i, B_{prey}) - F_i B_i - M_{O_i} B_i - \sum_{pred} Q(B_{pred}, B_i) \quad (2)$$

where GE is the growth efficiency and is equal to the production rate (P/B) divided by the consumption rate (Q/B), Q is consumption ($\text{t km}^{-1} \text{yr}^{-1}$), F is the fishing exploitation rate (yr^{-1}), and M_O is "other" mortality (yr^{-1}) not explicitly represented in the model. M_{O_i} is equal to $1 - EE_i$ and includes mortality sources such as disease, senescence, starvation, or outmigration. The terms $Q(B_i, B_j)$ represent the functional response equations.

The strength of predator-prey interactions can have a strong impact on biomass dynamics and the shape of the functional response can be different for each trophic link in the food web. Ecosim employs a "foraging arena" model to represent the functional response of groups to changing biomass and consumption (Walters et al. 1997, Ahrens et al. 2012). The foraging arena model assumes that at any given time only a proportion of the prey population is vulnerable to a predator. Following Aydin (2004), the predator-prey functional response is expressed as

$$\left(\frac{Q}{B_{pred}} \right)_{pred, prey, t} = \frac{\left(\left[\frac{Q}{B_{pred}} \right]^* X_{predprey}^* \right) DC_{predprey}^* \frac{(B_{prey})_t}{B_{prey}^*}}{(X_{predprey}^* - 1) + \frac{(B_{pred})_t}{B_{pred}^*}} \quad (3)$$

where Q/B^* is the predator Q/B from the base Ecopath starting point, DC^* is the proportion of the prey in the predator's diet at the starting point, $B_{pred, t}$ and $B_{prey, t}$ are the biomasses of the predator and prey at time t , B_{pred}^* and B_{prey}^* are the predator and prey biomasses at the starting point, and $X_{predprey}^*$ is the vulnerability parameter which describes the rate of prey movement between vulnerable and invulnerable states. Low prey vulnerabilities are associated with bottom-up effects where increasing the predator population does not necessarily have measurable impact on the prey population. High vulnerabilities are consistent with top-down effects, where vulnerable prey populations are more severely impacted by fluctuations in predator abundance. In theory, the vulnerability parameter ranges from one to $+\infty$ and is centered on two. The effective range of $X_{predprey}^*$ is from 1.01 to 91 (Gaichas et al. 2012), and the default value in EwE is two.

2.2. The Food Web Models and System Descriptions

2.2.1. Eastern Chukchi Sea

The eastern Chukchi Sea is a broad and shallow continental shelf ecosystem off the coast of northwest Alaska (Figure 1), with most depths less than 60 m (Jakobsson 2002). The Chukchi Sea is connected to the Pacific Ocean through the Bering Strait at its southern edge. There is a net northward flow of water through Bering Strait and across the continental shelf, although seasonal and episodic variation can affect the direction and magnitude of flow (Coachman and Aagaard 1981, Woodgate et al. 2012, Danielson et al. 2014). The Chukchi Sea is subject to polar night and is seasonally covered by sea-ice. Primary production in the spring begins with production from ice algae within and along the underside of sea-ice (Cota and Smith 1991, Horner et al. 1992), and large pelagic blooms have recently been observed in the water column beneath the ice (Arrigo et al. 2014). Waters flowing into the Chukchi Sea through Bering Strait during the ice-free season can be rich with nutrients and fuels areas of intense productivity in the southern Chukchi Sea (Sambrotto et al. 1984, Springer and McRoy 1993). Only a limited portion of the annual primary production is consumed by zooplankton (Cooney and Coyle 1982, Coyle and Cooney 1988, Campbell et al. 2009) and much of it sinks to the seafloor and supports an abundant benthic community (Grebmeier et al. 2015). Currently, there are no industrial scale commercial fisheries in the US territorial waters of the eastern Chukchi Sea (NPFMC 2009). However, there are subsistence fisheries and harvests of marine mammals (Craig 1987, Hovelsrud et al. 2008, Fall et al. 2011). The eastern Chukchi Sea food web model covers an area of $\sim 192,000 \text{ km}^2$ in the eastern portion of the Chukchi Sea within US territorial waters. There was no ecosystem basis for modeling only the eastern half of the Chukchi Sea, this decision was based on the availability of data (Whitehouse et al. 2014).

2.2.2. Eastern Bering Sea

The eastern Bering Sea is a broad continental shelf ecosystem encompassing an area of $\sim 495,000 \text{ km}^2$. The modelled area extends from Unimak Pass and Bristol Bay northwestward to about 61°N (Aydin et al. 2007) (Figure 1). The major inputs of water to the continental shelf are through Unimak Pass in the south, advection through canyons along the continental slope to the west, and seasonal fresh-water input from river drainage (Stabeno et al. 2016b). Portions of the southeastern Bering Sea continental shelf are seasonally covered by sea-ice which moves in from the northern Bering Sea in late winter. A "cold pool" of water ($< 2^\circ \text{C}$) remains over the shelf following the retreat of sea-ice in the spring; the extent of which varies from year to year with the extent of sea-ice coverage (Sullivan et al. 2014). The size and



Figure 1. Alaska marine ecosystems used in this study.

location of the cold pool has important implications for species distribution and community composition at multiple trophic levels (Mueter and Litzow 2008, Stevenson and Lauth 2012, Eisner et al. 2018), and for recruitment of commercially important fishes (Hunt et al. 2011, Duffy-Anderson et al. 2016). The eastern Bering Sea has several productive commercial fisheries, including fisheries for species of gadids, flatfishes, and crabs (NPFMC 2011, 2017a). Fisheries are executed with multiple gear types including trawls, longlines, and pots. The walleye pollock (*Gadus chalcogrammus*, hereafter referred to as pollock) fishery is one of the largest single-species fisheries in the world with average catches of 1.2 million t per year since the 1970s (Ianneli et al. 2017).

2.2.3. Gulf of Alaska

The Gulf of Alaska is located in the northeast Pacific and has a continental shelf of varying width that stretches along the Alaska coast from the US-Canada border, then north and west around the margin of the Gulf to the Aleutian Islands at its western end (Figure 1). The Gulf of Alaska model encompasses the continental shelf waters of the Gulf of Alaska from 140°W to 170°W, a total area of 291,840 km² (Aydin et al. 2007, Gaichas et al. 2010). The continental shelf is detailed with islands and bays and the continental slope has many gullies carved into its margins. The net circulation in the gulf is in the counterclockwise direction. Productivity in the gulf is influenced by the development of eddies, gap winds between mountains along the coast, upwelling, and freshwater runoff from the coast (Ladd and Cheng 2016, Ladd et al. 2016, Stabeno et al. 2016a). The community composition and relative species abundance on a multi-year timescale is influenced by large-scale climate drivers such as the El Niño Southern Oscillation and the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997,

Hollowed et al. 2001). A regime shift in community organization was observed in the mid-1970s and coincided with a shift in the PDO from a negative phase (cooler SST) to a positive phase (warmer SST) (Mantua et al. 1997). Prior to the regime shift the community composition was dominated by shrimp and capelin; afterwards groundfish (including gadids and flatfish) became increasingly abundant while the relative abundance of shrimp and capelin decreased (Anderson and Piatt 1999). Historically, the Gulf of Alaska hosted several commercially valuable crab fisheries that peaked in ex-vessel value in the early 1980s, then catch for crabs declined rapidly to less than 20% of their maximum, with most crab fisheries closed by the mid-1980s (Orensanz et al. 1998). Currently, the Gulf of Alaska has several productive finfish fisheries including pollock, Pacific cod (*Gadus macrocephalus*), sablefish (*Anoplopoma fimbria*), flatfish (Pleuronectidae), and rockfish (Sebastidae) (NPFMC 2017b).

2.2.4. Functional Groups

The three EwE models used in this analysis originally had different numbers of functional groups, with 149 in the eastern Bering Sea, 138 in the Gulf of Alaska, and 67 in the eastern Chukchi Sea. Differences in the level of trophic aggregation can make comparisons between models difficult to interpret (Pinnegar et al. 2005). To make the models more comparable a minimum amount of aggregation prior to conducting simulations was necessary. However, we also need to balance this with maintaining some of the functional groups or species of heightened interest in each food web (e.g., commercially important species, protected species, keystone species). The eastern Bering Sea and Gulf of Alaska models had finer levels of taxonomic resolution among several categories including fishes, zooplankton, and marine mammals. To make these groups more comparable across all three models, species-specific groups were consolidated to a common functional group. For

Table 1

Functional groups aggregated from each of the three food web models. The aggregated groups used in this study are listed in the left column. For the species composition of a functional group please consult the original model source documentation; [Aydin et al. \(2007\)](#) for the eastern Bering Sea (EBS) and Gulf of Alaska (GOA) models, and [Whitehouse and Aydin \(2016\)](#) for the eastern Chukchi Sea (ECS).

Aggregated Group	EBS	GOA	ECS
Polar bears			Polar Bear Chukchi Polar Bear S Beaufort
Toothed whales	Beluga Transient killer whales Sperm and beaked whales Resident killer whales Porpoises	Transient killer whales Sperm and beaked whales Resident killer whales Porpoises	Beluga
Gray whale	Gray whale	Gray whale	Gray whale
Bowhead whale	Bowhead whale		Bowhead whale
Other baleen whales	Humpbacks Fin whales Sei whales Right whales Minke whales	Humpbacks Fin whales Sei whales Right whales Minke whales	
Walrus/bearded seal	Pac. walrus/bearded seal		Pacific walrus Bearded seal
Wintering seals	Wintering seals		Ringed seal Spotted seal
Other pinnipeds	Northern fur seal (juv) Northern fur seal Steller sea lion (juv) Steller sea lion Resident seals Sea otters	Northern fur seal (juv) Northern fur seal Steller sea lion (juv) Steller sea lion Resident seals Sea otters	
Procellarids	Shearwaters Fulmars	Shearwaters Fulmars	Procellarids
Alcids piscivorous	Murres Puffins	Murres Puffins	Alcids piscivorous
Alcids planktivorous	Auklets	Auklets	Alcids planktivorous
Larids	Gulls Kittiwakes	Gulls Kittiwakes	Larids
Cormorants	Cormorants	Cormorants	Cormorants
Other seabirds	Storm petrels Albatross/Jaeger	Storm petrels Albatross/Jaeger	Scolopacids
Sharks	Sleeper shark	Sleeper shark Salmon shark Dogfish	
Skates	Alaska skate Other skates	Other skates Longnosed skate Big skate	Alaska skate
Walleye pollock	Walleye pollock (juv) Walleye pollock	Walleye pollock (juv) Walleye pollock	Walleye pollock
Pacific cod	Pacific cod (juv) Pacific cod	Pacific cod (juv) Pacific cod	Pacific cod
Arctic cod			Arctic cod
Large-mouth flatfish	Arrowtooth flounder (juv) Arrowtooth flounder Kamchatka flounder (juv) Kamchatka flounder Greenland turbot (juv) Greenland turbot Pacific halibut (juv) Pacific halibut	Arrowtooth flounder (juv) Arrowtooth flounder Pacific halibut (juv) Pacific halibut	Large-mouth flatfish
Small-mouth flatfish	Yellowfin sole (juv) Yellowfin sole Flathead sole (juv) Flathead sole Northern rock sole (juv) Northern rock sole Alaska plaice Dover sole Dover sole Rex sole Miscellaneous flatfish	Yellowfin sole Flathead sole (juv) Flathead sole Southern rock sole Northern rock sole Alaska plaice Dover sole Rex sole Miscellaneous flatfish	Small -mouth flatfish
Eelpouts	Eelpouts	Eelpouts	Eelpout
Large-mouth sculpins	Large sculpins	Large sculpins	Large-mouth sculpin
Other sculpins	Other sculpins	Other sculpins	Other sculpin
Miscellaneous shallow fish	Misc. fish shallow	Misc. fish shallow	Misc. shallow fish Saffron cod
Salmon returning	Salmon returning	Salmon returning	Salmon returning
Salmon outgoing	Salmon outgoing	Salmon outgoing	Salmon outgoing
Pelagic forage fish	Bathylagidae Myctophidae	Bathylagidae Myctophidae	Pelagic forage fish

(continued on next page)

Table 1 (continued)

Aggregated Group	EBS	GOA	ECS
Other demersals	Capelin	Capelin	
	Sandlance	Sandlance	
	Eulachon	Eulachon	
	Other managed forage	Other managed forage	
	Other pelagic smelt	Other pelagic smelt	
	Pacific herring (juv)	Pacific herring (juv)	
	Pacific herring	Pacific herring	
	Sablefish (juv)	Sablefish (juv)	Other snailfish
	Sablefish	Sablefish	Variegated snailfish
	Atka mackerel (juv)	Atka mackerel (juv)	
	Atka mackerel	Atka mackerel	
	Greenlings	Greenlings	
	Pacific ocean perch	Pacific ocean perch (juv)	
	Sharpchin rockfish	Pacific ocean perch	
	Northern rockfish	Sharpchin rockfish	
	Dusky rockfish	Northern rockfish	
	Shortraker rockfish	Dusky rockfish	
	Rougheye rockfish	Shortraker rockfish	
	Shortspine thornyhead	Rougheye rockfish	
	Other Sebastes	Shortspine thornyhead (juv)	
Grenadiers	Shortspine thornyhead		
Miscellaneous fish deep	Other Sebastes		
	Grenadiers		
	Miscellaneous fish deep		
Octopods	Octopi	Octopi	Cephalopods
Snow crab	Opilio		Snow crab
Other crabs	Bairdi	Bairdi	Other crabs
	King Crab	King Crab	
	Hermit crabs	Hermit crabs	
	Miscellaneous crabs	Miscellaneous crabs	
Shrimps	Pandalidae	Pandalidae	Shrimps
	NP shrimp	NP shrimp	
Sea stars	Sea stars	Sea stars	Sea stars
Brittle stars	Brittle stars	Brittle stars	Brittle stars
Basket stars			Basket stars
Urchins, dollars, cucumbers	Urchins dollars cucumbers	Urchins dollars cucumbers	Urchins, dollars, cucumbers
Snails	Snails	Snails	Snails
Miscellaneous crustaceans	Miscellaneous crustaceans	Miscellaneous crustaceans	Miscellaneous crustaceans
Benthic amphipods	Benthic amphipods	Benthic amphipods	Benthic amphipods
Anemones	Anemones	Anemones	Anemones
Corals and sea pens	Corals	Corals	Corals
	Sea Pens	Sea Pens	
Benthic urochordate	Urochordata	Urochordata	Benthic urochordate
Sponge	Sponges	Sponges	Sponge
Bivalves	Bivalves	Bivalves	Bivalves
Polychaetes	Polychaetes	Polychaetes	Polychaetes
Worms etc.	Miscellaneous worms	Miscellaneous worms	Worms etc.
	Hydroids	Hydroids	
Squid	Squids	Squids	
Scyphozoid Jellies	Scyphozoid Jellies	Scyphozoid Jellies	Jellyfish
Copepods	Copepods	Copepods	Copepods
Other zooplankton	Fish Larvae	Fish Larvae	Other zooplankton
	Chaetognaths	Chaetognaths	
	Euphausiids	Euphausiids	
	Mysids	Mysids	
	Pelagic amphipods	Pelagic amphipods	
	Gelatinous filter feeders	Gelatinous filter feeders	
	Pteropods	Pteropods	
Pelagic microbes	Pelagic microbes	Pelagic microbes	Pelagic microbes
Benthic microbes	Benthic microbes	Benthic microbes	Benthic microbes
Primary Production	Macroalgae	Macroalgae	Phytoplankton
	Large phytoplankton	Large phytoplankton	
	Small phytoplankton	Small phytoplankton	
	Outside production	Outside production	
Pelagic detritus	Pelagic detritus	Pelagic detritus	Pelagic detritus
	Discards	Discards	
	Outside detritus	Outside detritus	
Benthic detritus	Benthic detritus	Benthic detritus	Benthic detritus
	Offal	Offal	
Fishery/Subsistence	Pollock trawl	Halibut longline	Polar bear Chukchi Russ. harvest
	Cod trawl	Crab pots	Polar bear Chukchi US harvest
	Cod pots	Herring fishery	Polar bear S Beaufort US harvest
	Cod longline	Salmon fishery	Beluga subsistence
	Atka trawl	Indigenous and subsistence	Bowhead subsistence
	Rslflats trawl	Flatfish trawl	Walrus subsistence

(continued on next page)

Table 1 (continued)

Aggregated Group	EBS	GOA	ECS
	YFSflats trawl	Other groundfish trawl	Bearded seal subsistence
	ATFflats trawl	Cod longline	Ringed seal subsistence
	FHSflats trawl	Cod pots	Spotted seal subsistence
	Other flatfish trawl	Cod trawl	
	Turbot trawl	Pollock trawl	
	Turbot longline	Rockfish trawl	
	Sablefish longline	Sablefish longline	
	Rockfish trawl	Shrimp trawl	
	Halibut longline		
	Crab pots		
	Salmon fishery		
	Herring fishery		
	Indigenous		
	Subsistence		

example, capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*) and other functional groups of primarily pelagic forage fish were combined into a single pelagic forage fish group in each model. The biomasses and fisheries catch of functional groups aggregated into a single group were summed together. The P/B, Q/B, and DC for the aggregated groups were weighted by the biomass of the constituent groups.

The total number of functional groups in the aggregated models are 54 in the eastern Bering Sea, 50 in the Gulf of Alaska, and 53 in the eastern Chukchi Sea (Table 1). Forty-six of the groups are common to all three models. The polar bear (*Ursus maritimus*), Arctic cod, and basket star (*Gorgonocephalus* sp.) groups are unique to the eastern Chukchi Sea model. The bowhead whale, Pacific walrus/bearded seal, wintering seals, and snow crab groups are only present in the eastern Bering Sea and eastern Chukchi Sea models. Other baleen whales, other pinnipeds, sharks, and the squids group are only present in the eastern Bering Sea and Gulf of Alaska models. Because the use of functional group names in the text can be confusing, from here on when referring to a functional group from one of the models the name will be italicized. The eastern Bering Sea and Gulf of Alaska models included more fishing groups, detrital compartments, and sources of primary production than the eastern Chukchi Sea model. The primary production and detritus groups in the eastern Bering Sea and Gulf of Alaska models were aggregated to match the number of respective groups in the eastern Chukchi Sea model: one primary production and two detrital compartments. Because we are not exploring fishery policy options in this study, we have aggregated all fisheries/subsistence harvests to a single compartment in each model.

2.3. Incorporating Parameter Uncertainty

The precision of parameter estimates across functional groups is usually uneven, and in many cases, the uncertainty is high. We incorporate parameter uncertainty into our simulations with a Monte Carlo routine used to generate entire sets of food web model (EwE) parameters based on the Ecosense routine of Aydin et al. (2005). The Ecosense routine generates entire sets of Ecosim food web parameters randomly drawn from prior distributions based on a data pedigree.

All model parameters and/or data were graded for quality using a data pedigree described by Christensen et al. (2005), with specific definitions from Aydin et al. (2007). Model parameters and data were assigned a data pedigree based upon the data source, collection methodology, temporal and spatial coverage of the dataset, and taxonomic relevance (Table 2). Complete explanations of data pedigree values for the base Ecopath models used in this study can be found in the model's source documentation (Aydin et al. 2007, Whitehouse and Aydin 2016). Each data pedigree corresponds to a prescribed range as a proportion of the point estimate (coefficient of variation, CV), intended to characterize parameter uncertainty, ranging from 0.1 to 0.8 (Table 3). Parameters for B, P/B, and Q/B were drawn from uniform distributions

Table 2

The criteria for the data pedigrees (or data quality grade). B = biomass, P/B = production/biomass ratio, Q/B = consumption/biomass ratio, DC = diet composition, and C = fishery catch or subsistence harvest. This table recreated from Aydin et al. (2007).

Data pedigree and corresponding data characteristics B, P/B, Q/B, DC, and C			
1	Assessment data is established and substantial, from more than one independent method (from which the best method is selected) with resolution on multiple spatial scales.		
2	Data is a direct estimate but with limited coverage/corroboration, or established regional estimate is available while subregional resolution is poor.		
3	Data is proxy, proxy may have known but consistent bias.		
4	Direct estimate or proxy with high variation/limited confidence or incomplete coverage.		
B and C	P/B, Q/B, and DC		
5	Estimate requires inclusion of highly uncertain scaling factors or extrapolation	5	Estimation based on same species but in "historical" time period, or a general model specific to the area.
6	Historical and/or single study only, not overlapping in area or time.	6	For P/B and Q/B, general life history proxies or other Ecopath model. For DC, same species in adjacent region or similar species in the same region.
7	Requires selection between multiple incomplete sources with wide range.	7	General literature review from a wide range of species, or outside the region. For DC, from other Ecopath model.
8	Estimated by Ecopath	8	Functional group represents multiple species with diverse life history traits. For P/B and Q/B, estimated by Ecopath.

Table 3

The range, as a proportion of the input parameter, associated with the assigned data pedigree for the basic model input parameters (Aydin et al. 2003). B = biomass, P/B = production/biomass ratio, Q/B = consumption/biomass ratio, and DC = diet composition.

Pedigree	B	P/B	Q/B	DC
	Coefficient of variation (+/-)			
1	0.1	0.1	0.1	0.1
2	0.1	0.2	0.2	0.3
3	0.5	0.3	0.3	0.5
4	0.5	0.4	0.4	0.6
5	0.5	0.5	0.8	0.7
6	0.8	0.6	0.6	0.8
7	0.8	0.7	0.7	0.8
8	0.8	0.8	0.8	0.8

centered on the base Ecopath model parameter estimates with the specified CVs. M_0 is selected from a uniform distribution centered on the base Ecopath value using the respective species P/B CV. M_0 is normally set by Ecopath during initial model balancing as 1 minus EE.

By selecting M_O independently, the ecosystem begins away from equilibrium. The DC of a predator consists of proportions for each prey type and must sum to one, therefore the drawing of random diet proportions was treated differently than the other base parameters. Diet composition in terms of the presence or absence of a trophic link does not vary in the Ecosense routine. Diet proportions for each prey item in a predator's diet were drawn from a Dirichlet distribution and not allowed to be equal to zero.

While fishery catch (C) is not directly drawn in the Ecosense routine, the observed catch will vary between drawn ecosystems due to differences in the drawn starting biomass values and the subsequent effect on catch. In Rpath, the catch of a group can be regulated by effort (E), fishing mortality (F), or by manually entering catch (C^{input}). The catch of a functional group i is calculated as

$$C_{it} = \sum_g q_{ig} E_{ig} + F_{it} B_i + C_{it}^{input} \quad (4)$$

where C_{it} is the catch of group i at time t , g is gear type, q_i is a catchability coefficient of group i with gear g and is equal to the ratio of the Ecopath base catch for group i with gear g to the starting biomass of group i , E_{ig} is the effort at time t for gear g and is either zero or one, $F_{it} B_i$ is the F at time t multiplied by biomass (B) for group i , and C^{input} is catch that is manually entered. By default, Rpath calculates the catch of functional groups by effort ($E=1$) with q equal to the quotient of the Ecopath catch and the starting biomass. The F and C^{input} terms are set to zero by default. To instead fish by F rate, E can be set equal to zero and a value entered for F that can vary by time step if desired. Similarly, specific catch values can be entered for C^{input} if desired and E and F set to zero. Below in section 2.4 we utilize the F term in this equation to increase mortality during simulations.

The results of Ecosim simulations have been shown to be sensitive to predator-prey functional responses, and use of the Ecosim default vulnerability ($X_{predprey}^* = 2$) for all trophic links is not recommended (Plagányi and Butterworth 2004, Gaichas et al. 2011, Gaichas et al. 2012). Following the methods of Gaichas et al. (2012), we vary vulnerability for each trophic link with random draws over the effective range of vulnerability (1.01 to 91), centered on the default value of two:

$$X_{predprey}^* = 1 + \exp(9 * [Uniform(0, 1) - 0.5]) \quad (4)$$

There are additional functional response parameters in Ecosim including, prey handling time, foraging time, and prey-switching rate. We held these additional functional response parameters at their default values.

The generated Ecosim parameter sets are not necessarily starting from a stable or equilibrium-like state. We ran the generated ecosystems forward for a 50-year "burn-in" period, during which any numerically unstable configurations were eliminated according to pre-specified criteria. If during this initial 50-year run a functional group dies out (B_i decreases to $< 1/1000$ of starting B_i) or grows without limit (B_i increases to > 1000 times starting B_i), that entire ecosystem is considered to have failed and that Ecosim parameter set is not retained for further analysis (Aydin et al. 2005, Gaichas et al. 2015). This typically happens because of thermodynamically inconsistent parameter draws. For example, parameter draws with exceptionally high predator biomass and high consumption rates in an ecosystem with low prey biomass and low prey production, incapable of supporting the randomly drawn predator parameters. Such failed ecosystems tend to "crash" during the first few years of the burn in period, and 50 years is generally sufficient to eliminate all such thermodynamically inconsistent systems. Ecosystem parameter sets that do not crash during burn-in are retained for further analyses.

The uncertainty in the model parameters combined with the thermodynamic constraints of the mass-balance framework and the burn-in period of the Ecosense routine is sufficiently restrictive to eliminate more than 90% of the generated food web parameter sets.

Gaichas et al. (2015) used Ecosense and the same rejection criteria and rejected ~98% of generated ecosystems. Using the same criteria, rejection rates will vary across studies due to inherent differences in the ecosystems modeled, the data pedigree, and other study-specific differences in model design. For this study, we retained a minimum of 500 plausible ecosystem parameter sets for each of the three modeled ecosystems. In the eastern Chukchi Sea, we generated 5,000 ecosystem parameter sets and retained 511 ecosystems. For the eastern Bering Sea, 9,500 parameter sets were generated and 505 survived the burn-in period with no crashes. In the Gulf of Alaska, we generated 12,000 food web parameter sets in order to find 553 that were numerically stable enough to survive burn-in.

The csv files required to operate Rpath with all three aggregated ecosystem models used in this study are available in the supplementary material. Additionally, an R file with the Ecosense parameter generation function is included in the supplementary material. The Rpath package can be downloaded from <https://github.com/NOAA-EDAB/Rpath>. This version of Ecosense presented here was developed to work with a prototype version of the Rpath package (Lucey et al., 2020). Ecosense will be included in a future release of Rpath and we anticipate refinements to the Ecosense code will be necessary in order for it to be formally included within the Rpath package.

2.4. Mortality-based perturbations

To examine the sensitivity of upper trophic level groups to mortality-based perturbations, we first ran each retained model forward for a 50-year run in Ecosim without any perturbation. This created a 50-year simulated baseline from which we would be able to compare the perturbation results against for each unique ecosystem configuration. We conducted mortality-based perturbations by increasing the total mortality 50% for each living functional group in the food web (excluding primary production and microbes), one at a time, and holding that increased mortality rate in place for the first 10 years of a 50-year simulation. Under equilibrium conditions, P/B is assumed to be equal to the instantaneous mortality rate, Z (Allen 1971). Total mortality was increased in our simulations by setting the F rate in equation four equal to half of the respective group's P/B . When the adjusted F is multiplied by the respective group's biomass, the product is added to the existing catch by effort (E) already included in equation four and the functional group's biomass is reduced accordingly. Following year 10, the perturbed mortality rate was returned to the baseline level and the simulation allowed to run without any other perturbations for the remaining 40 years. This meant that for the three ecosystems included in this analysis, the number of simulations was equal to the number of living groups times the number of retained food web parameter sets. This was equal to more than 24,000 simulations for each of the three ecosystems included in this analysis.

To identify and follow any disturbance to the food web that resulted from a perturbation we tracked the aggregated biomass of upper trophic level groups. This is the sum of biomass for all groups with a trophic level (TL) of 2.6 or higher, excluding fisheries. The eastern Chukchi Sea, eastern Bering Sea, and Gulf of Alaska had 36, 35, and 31 functional groups with TL of 2.6 or higher, respectively. This division at trophic level 2.6 effectively separated predators from those that primarily preyed directly on basal resources. The diet compositions of groups with TL < 2.6 all consist of at least 50% from detritus and/or primary production. These lower trophic level consumers were mostly benthic invertebrate groups, also zooplankton and microbes. If the upper TL biomass deviated more than $\pm 10\%$ from the baseline trajectory during a simulation, that ecosystem was considered to have been disrupted by the perturbation. For each perturbation, we kept track of the number of ecosystems that were disrupted by that perturbation. When an ecosystem was disrupted, we measured the recovery time of the food web as the time it took for upper TL biomass to return to within $\pm 10\%$ of its baseline trajectory. We additionally kept track of

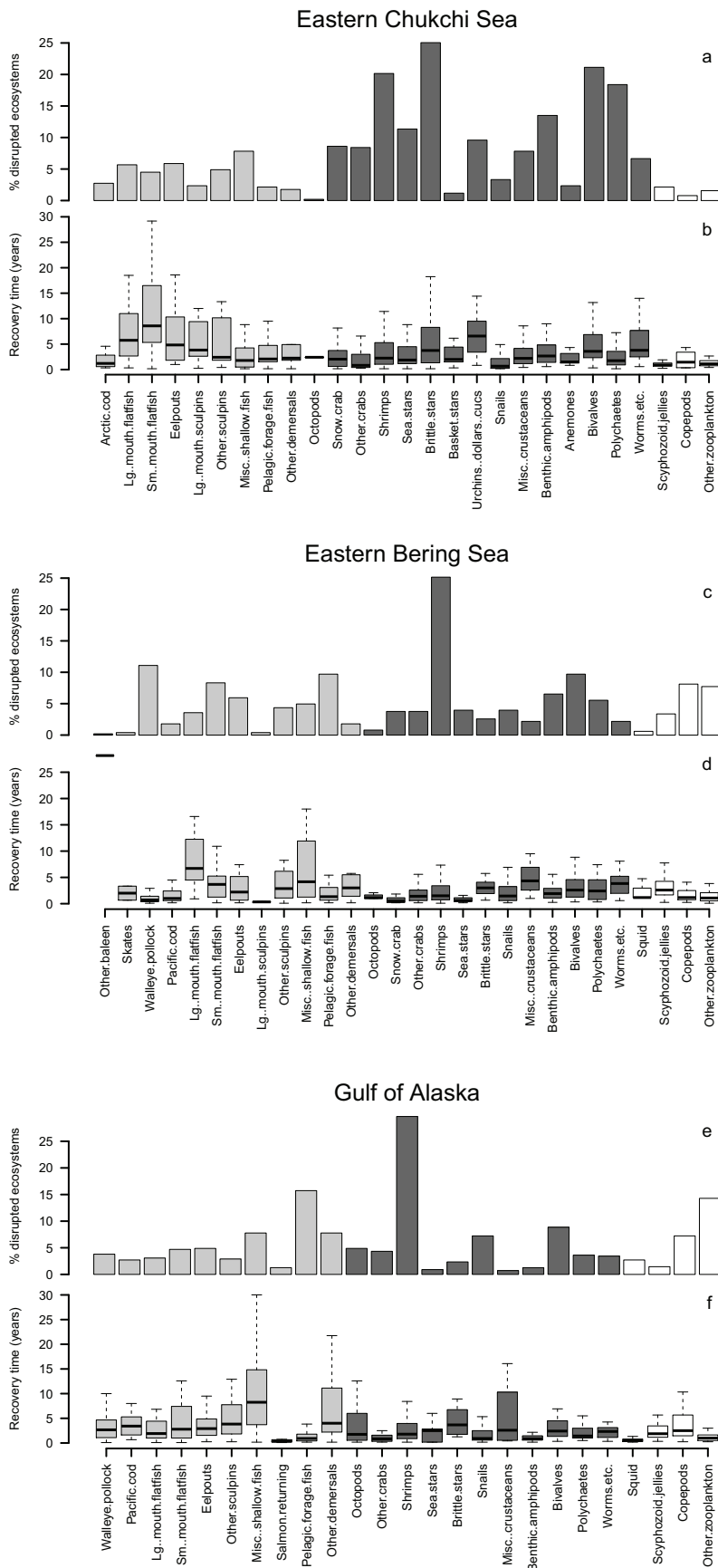


Figure 2. (a, c, e) The percentage of generated ecosystems where upper trophic level biomass deviated more than $\pm 10\%$ from the baseline trajectory in response to perturbing of a functional group. (b, d, f) The recovery time (years) of generated ecosystems to a perturbation. The horizontal black bars in the box plots represents the median recovery times, boxes are the interquartile range, whiskers extend to furthest point within 1.5 x the interquartile range, and outliers are not shown. 2a – b are eastern Chukchi Sea (n = 511), 2c – d are eastern Bering Sea (n = 505), 2e – f are Gulf of Alaska (n = 553). White boxes are pelagic invertebrates, dark gray boxes are benthic-oriented invertebrates, light gray boxes are fish groups, and black is marine mammals (c and d).

and enumerated instances where ecosystems did not return to their baseline trajectory for upper TL biomass. We also looked for underlying patterns in the simulation results and checked for correlations (Pearson product-moment correlation, ρ , $\alpha = 0.05$) between the number of ecosystems disrupted by a perturbation and the trophic level, log biomass, and the number of trophic links of the perturbed group.

3. Results

3.1. Eastern Chukchi Sea

Upper trophic levels in the eastern Chukchi Sea were most sensitive to mortality-based perturbations of benthic invertebrate groups. In general, upper trophic level biomass was disrupted in more of the generated ecosystems by perturbations to benthic invertebrate groups than perturbations to other functional groups (Figure 2a). In particular, the food webs were most sensitive to perturbations of the *brittle stars*, *bivalves*, *shrimps*, and *polychaete worm* functional groups. Each of these four groups disrupted approximately 20% of the generated ecosystems. Perturbations to fish groups generally disrupted upper trophic level biomass in less systems than the benthic invertebrate groups. The *miscellaneous shallow fish*, *eelpouts*, *large-mouth flatfish*, and *other sculpins* were the most disruptive fish groups, each disrupting between 5 and 7% of the generated ecosystems. Pelagic invertebrate groups when perturbed were less disruptive, each affecting less than 2.3% of ecosystems. Perturbations to marine mammal and seabird groups did not disrupt any of the ecosystems.

The median recovery times of the generated eastern Chukchi Sea food webs to all of the perturbations were less than 10 years, and most less than five (Figure 2b). The highest median recovery times were for perturbations to *small-mouth flatfish* (9.9), the *urchins*, *dollars*, and *cucumbers* group (8.9), and *large-mouth flatfish* (5.7). The range of recovery times for benthic invertebrate perturbations were generally narrow, exceptions were for the *urchins*, *dollars*, *cucumbers* group and *brittle stars*. The range of recovery times for the fish groups were generally wider than the benthic invertebrate groups. The median recovery times for perturbations of pelagic invertebrate groups were all less than 1.5 years.

In all of the simulations ($n=24,017$) with the eastern Chukchi Sea food web there were two instances where upper trophic level biomass was disrupted by a perturbation and it did not return to within $\pm 10\%$ of its baseline trajectory. There was no indication from the relative biomass trajectories of functional groups that either ecosystem had shifted to an alternative stable state following the perturbation. In one instance, the perturbed group itself accounted for a disproportionate share of upper trophic level biomass, and in combination with a P/B that was much lower than the base Ecopath P/B for that group, led to a slow recovery following the perturbation (Figures S1 and S2). In the second instance, some strong predator-prey functional responses (i.e., high vulnerabilities) produced an unrealistic high amplitude rapid oscillation of upper trophic level biomass that rendered this system impossible. Further details on these outliers are available in the supplementary material.

3.2. Eastern Bering Sea

The perturbation that was most disruptive to upper trophic level biomass in the eastern Bering Sea was *shrimps*. When *shrimps* were perturbed 23.4% of the generated ecosystems were disrupted (Figure 2c). The next most disruptive group was *pollock*, which disrupted 11.3% of the systems. Other disruptive groups included *pelagic forage fish* (9.9%), *small-mouth flatfish* (9.3%), and *bivalves* (8.7%). Perturbations to *copepods* and *other zooplankton* were also disruptive to upper trophic level biomass in 8.1% and 7.7% of systems, respectively. With the exception of *other baleen whales*, the generated ecosystems were insensitive to perturbations of marine mammal and seabird

groups. One generated ecosystem was disrupted by the perturbation to *other baleen whales*.

The median recovery time of the generated ecosystems to perturbations were all less than seven years and most less than four, with the exception of the perturbation to *other baleen whales* (Figure 2d). The single ecosystem where upper trophic level biomass was disrupted by the perturbation to *other baleen whales* took 34.3 years to recover from the perturbation. The next highest median recovery time was for *miscellaneous shallow fish* (6.6 years), *large-mouth flatfish* (5.3 years), and *miscellaneous crustaceans* (4.3 years). In general, the range of recovery times for all the perturbations were relatively narrow.

In all the simulations ($n=24,240$) with the eastern Bering Sea food web there were four occasions where upper trophic level biomass did not return to within $\pm 10\%$ of the baseline trajectory following a perturbation. In the first instance, the perturbed group represented the majority of upper trophic level biomass, and in combination with a P/B that is much lower than the base Ecopath P/B for this group, prevented a recovery by the simulation's end. In the second food web, most groups were already experiencing a gradual monotonic decline in biomass. The perturbed group expedited this decline in biomass, reducing upper trophic level biomass well below the -10% threshold, and preventing a return to within the $\pm 10\%$ threshold by the end of the simulation (Figure S5). In a third case, high vulnerabilities led to high amplitude, low frequency oscillations that prevented upper trophic level biomass from stabilizing within the $\pm 10\%$ threshold by the end of the simulation (Figures S6 and S7). In the fourth instance, high vulnerabilities led to high amplitude, high frequency oscillations that were completely unrealistic. Further details on these outliers are available in the supplementary material.

3.3. Gulf of Alaska

Similar to the eastern Bering Sea, perturbations to *shrimps* were the most disruptive to upper trophic level biomass in the Gulf of Alaska food webs, affecting 30.6% of the generated ecosystems (Figure 2e). The Gulf of Alaska food webs were also sensitive to perturbations of pelagic oriented groups including *pelagic forage fish* (14.8%), *other zooplankton* (14.3%), and *copepods* (7.2%). Perturbations to most of the remaining fish groups produced some level of disruption in upper trophic level biomass, ranging from 0.2 to 8% of the generated ecosystems. Among benthic invertebrates, perturbations to *bivalves* (8.7%) and *snails* (7.1%) were most disruptive to upper trophic level biomass. Perturbations to marine mammals and seabirds did not disrupt upper trophic level biomass in any of the generated ecosystems.

Among the functional groups whose perturbations disrupted upper trophic level biomass, the median recovery time of the food web once the perturbation ended was less than 5 years for all groups except *miscellaneous shallow fish*, which had a median return time of 9.5 years (Figure 2f). Perturbations to *shrimps*, *pelagic forage fish*, and *other zooplankton* disrupted the most generated ecosystems but all three have median return times of less than 2 years. Eight of the 10 longest median return times belong to fish groups.

Of the simulations with the Gulf of Alaska food web ($n=24,332$) there were two instances where upper trophic level biomass did not return to within $\pm 10\%$ of the baseline trajectory and in both cases the perturbed group was *miscellaneous shallow fish*. In both of these generated ecosystems *miscellaneous shallow fish* accounted for sizeable portions of upper trophic level biomass at 64% and 16%. It is their loss in biomass that explains the overall loss in upper trophic level biomass in both systems. Upper trophic level biomass slowly increases in both systems following the end of the perturbation but does not increase fast enough to return to the baseline trajectory by the end of the simulation. Upper trophic level biomass was 17% and 16% below the baseline value at the conclusion of the two simulations.

Table 4

Pearson product-moment correlation (ρ) between the percentage of generated food webs where upper trophic level biomass was disrupted by perturbing a particular functional group and properties of that functional group. Bolded p-values are significant correlations ($\alpha = 0.05$).

Variable	ECS		EBS		GOA	
	ρ	P	ρ	P	ρ	P
trophic level	-0.48	<0.001	-0.31	0.034	-0.25	0.102
ln(biomass)	0.64	<0.001	0.64	<0.001	0.58	<0.001
trophic links	0.36	0.012	0.41	0.003	0.22	0.155

3.4. Correlation with disrupted ecosystems

We tested for correlations between the percentage of ecosystems where upper trophic level biomass was disrupted and properties of the functional groups being perturbed including, log biomass, trophic level, and the number of trophic links. Log biomass was positively correlated with the percentage of disrupted food webs and was the most strongly correlated of the three variables in all three ecosystems ($p < 0.05$, Table 4). Trophic level of the perturbed group was negatively correlated with the percentage of disrupted food webs in all three study systems, but not significant in the Gulf of Alaska ($p = 0.101$). The total number of trophic links for a perturbed group had a significant ($p < 0.05$) positive correlation with the percentage of disrupted ecosystems for the eastern Chukchi Sea and eastern Bering Sea simulations, but was not significant for the Gulf of Alaska simulations.

4. Discussion

Our analysis identified a number of key sensitivities of upper trophic level groups from a selection of marine ecosystems in Alaska. We found upper trophic levels in the eastern Chukchi Sea food web to be most sensitive to perturbations to benthic invertebrates, in the eastern Bering Sea upper trophic level groups were sensitive to perturbations of shrimp and pollock, and in the Gulf of Alaska they were sensitive to perturbations of shrimp, pelagic forage fish, and zooplankton. Across ecosystems, the median recovery times of upper trophic level biomass to most perturbations were less than 5 years and there were no indications of ecosystems flipping to alternate stable states in response to perturbations. This indicates these modeled food webs were robust to the parameter uncertainty present and the simple first-order perturbations conducted here. The Ecosense routine permitted a wide exploration of the parameter space around the vulnerability parameter of the functional response and the base model parameters. This provided us with a range of outcomes to the specific perturbations and indicated the median recovery time and how robust the outcomes were to different parameter combinations. These analyses also shed light on instances where combinations of parameter draws led to unsustainable biomass dynamics or systems that were unable to recover from perturbations. However, given the total number of simulations across all three ecosystems (>72,000), such circumstances were extremely rare.

The mortality-based perturbations of the eastern Chukchi Sea food web revealed that upper trophic levels in this ecosystem were generally more sensitive to perturbations of benthic invertebrate functional groups than to fishes, pelagic invertebrates, seabirds, or marine mammals. We found that the percentage of generated ecosystems disrupted by a perturbation was positively correlated with the perturbed group's biomass, the number of trophic links, and negatively correlated with their TL. In general, benthic invertebrate functional groups in the eastern Chukchi Sea model closely align with this profile, as they are high biomass, lower trophic level, and have many trophic links. In contrast, the percentage of ecosystems disrupted by a perturbation in the Gulf of Alaska had a significant positive correlation with the perturbed group's biomass, but did not have a significant correlation with the perturbed groups trophic level or the number of trophic links

($\alpha = 0.05$). Smith et al. (2011) simulated fishing on lower trophic level groups with an ensemble of ecosystem models, including EwE models, and found that the relative abundance of the perturbed group and their level of connectance to the rest of the food web helped explain the response of other groups in the food web. This is consistent with the positive correlations we observed between the number of food webs with disrupted upper trophic levels and the biomass and number of trophic links of the perturbed group.

System recovery times to perturbations were interpreted in this study as a measure of the stability of the model ecosystems; that is, their ability to endure a perturbation and to return to their baseline configuration following a perturbation (Holling 1973, Pimm 1984). Previous studies with EwE have also considered system recovery time in response to a perturbation as a measure of food web stability. Vasconcellos et al. (1997) examined the stability of EwE models for 18 different ecosystems when key mid-trophic level groups were perturbed. They found that system recovery time was negatively correlated with Finn's Cycling Index, which provides a measure of energy flow that is recycled within the ecosystem (Finn 1976). They concluded that ecosystems with higher recycling had a greater capacity to return to starting conditions. A study using EwE models to examine the trophic role of snappers (Lutjanidae) in the Gulf of Mexico found that system recovery time was positively correlated with the maximum observed proportional change in biomass from a group during a simulation (Arreguin-Sanchez and Manickchand-Heileman 1998). When the impact of a perturbation was the greatest, in terms of biomass, they observed longer system recovery times. This is consistent with our observation that the number of disrupted food webs was positively related to the perturbed group's biomass.

Other studies with EwE models have examined system recovery time under different global vulnerability settings, where all vulnerabilities were set to low, intermediate (default), or high values. Across multiple ecosystems and a range of perturbations, system recovery time was lowest with low vulnerability settings, higher at the intermediate default value, and highest at high vulnerabilities (Ortiz and Wolff 2002, Ortiz 2010, Rodriguez-Zaragoza et al. 2016, Hermosillo-Nunez et al. 2018). Although system recovery time could often not be evaluated at high vulnerabilities due to the emergence of chaotic oscillations (Ortiz et al. 2009, Ortiz et al. 2013, Caceres et al. 2016). Similarly, we observed a few instances where high vulnerabilities resulted in oscillations preventing an estimation of recovery time. The oscillations we observed may in part be due to the choice of using Adams-Bashforth numerical integration for our simulations. Rpath also offers fourth order Runge-Kutta numerical integration that integrates over finer time steps and may have better resolved rapid biomass dynamics, reducing the appearance of oscillations.

Recovery times to perturbations in all disrupted food webs in all three ecosystems were generally less than 5 years; however, the eastern Chukchi Sea had the slowest mean recovery time across all disrupted food webs at 4.7 years. The mean recovery times in the eastern Bering Sea and Gulf of Alaska were 3.1 and 3.4 years, respectively. This indicates that the eastern Chukchi Sea may be more vulnerable to mortality events or extractive activities than the other two ecosystems included in this study. The eastern Bering Sea and Gulf of Alaska are currently subject to multiple anthropogenic stressors including commercial fisheries, shipping, and tourism. The eastern Chukchi Sea is not presently subject to commercial fisheries (NPFMC 2009) but improved access due to sea-ice reduction has led to increasing ship traffic (Smith and Stephenson 2013, Huntington et al. 2015). Additionally, recent observations of commercial species from the southeastern Bering Sea in the northern Bering Sea has prompted questions about what the potential ecosystem impacts could be for the northern Bering Sea and Chukchi Sea if sub-Arctic species from the southeastern Bering Sea expand their range northward, and what the implications of such stock movement would be for fisheries and fisheries management (Stevenson and Lauth 2019). Modeling tools that incorporate

uncertainty, such as Ecosense, could be useful in the exploration of potential ecosystem impacts due to immigration of new species, changing community composition, and the exploration of fishery management strategies.

As an alternative to recovery time, Smith et al. (2011) examined the impact of simulated fishing on lower trophic level groups by tracking the number of functional groups whose biomass deviated beyond a threshold in response to the intensity of fishing on the target species. In contrast to recovery time, this allowed them to quantify the level of disruption the fishing strategy caused in terms of how many groups in the food web experienced an adverse effect. We did not take this approach in our current analysis, but the approach of Smith et al. (2011) could be utilized with Ecosense to examine which functional groups show consistent responses to perturbations or experimental fishing strategies. This could be a particularly useful strategy if there are particular commercial or protected species that are believed to be especially vulnerable.

Ecosense in its original C++ format has previously been used in a comparative framework to contrast the response of multiple ecosystems to the same set of pressures. Aydin et al. (2003) examined the response of the eastern and western basins of the subarctic Pacific to increasing primary production and the removal of selected prey and predator groups. The removal of mid-trophic level groups had direct effects on prey, who often increased in abundance under the predatory release, and select predators decreased who were particularly dependent on the removed group. Other groups who shared prey resources with the removed group often benefited from the removal of competitors and increased in abundance. The direct effects observed by Aydin et al. (2003) are consistent with our observation that the number of ecosystems disrupted by a perturbation was positively correlated with the number of trophic links of the perturbed group and negatively correlated with trophic level.

Aydin et al. (2007) used Ecosense to examine variation in predation mortality for important prey groups and the consequences of changing predator production across the eastern Bering Sea, Gulf of Alaska, and Aleutian Islands ecosystems. Although many taxa are shared across these ecosystems, the uncertainty captured by the Ecosense routine helped to identify key forage species that each food web was uniquely sensitive to. These sensitivities were often the result of little data or structural differences in the food webs. Similarly, in our study, key sensitivities in our perturbation analysis generally reflected structural differences between the food webs examined and poor data pedigree scores. The sensitivity of upper trophic levels in the eastern Chukchi Sea to benthic invertebrates reflects their structural dominance in this food web and, in part, uncertainties about their productivity and trophic relationships (Hunt et al. 2013, Whitehouse et al. 2014). The sensitivity of the eastern Bering Sea to pollock reflects their structural dominance in the food web and their importance as both a predator and prey (Aydin and Mueter 2007). The sensitivity of the Gulf of Alaska model to the pelagic forage fish and zooplankton groups reflects the greater balance between the pelagic and benthic energy pathways in this ecosystem and the prevalence of high trophic level predators such as arrowtooth flounder (*Atheresthes stomias*) and Pacific halibut (*Hippoglossus stenolepis*) (Gaichas et al. 2015).

Ruzicka et al. (2013b) used Ecosense to investigate the food web impacts of doubling forage fish abundance in four large coastal marine ecosystems, including the northern California Current, central Gulf of Alaska, Georges Bank, and the southwestern Antarctic Peninsula. An important finding of their study was that the immediate short-term response of selected seabird, whales, and pinnipeds to the perturbations was often dramatically different from their long-term response. In our study, we did not directly contrast short-term and long-term response of individual groups, but indirectly we looked at this in terms of the recovery time of disrupted food webs. A key distinction between our study and that of Ruzicka et al. (2013b) is that our perturbations ended after 10 years and theirs were maintained over their entire simulations.

We were concerned with the sensitivity of upper trophic levels and their recovery time while they examined short-term and long-term impacts from sustained pressures. Using the same four study ecosystems, Ruzicka et al. (2013a) examined the ecosystems response to increasing the abundance of selected marine mammal groups to their pre-exploitation levels. They found these perturbations to be of minimal impact, which is consistent with our findings. While our perturbations decreased marine mammal abundance rather than an increase, the results were similar; perturbing marine mammals produced only minor responses in the rest of the food web. This is largely due to the relatively low biomass and low total consumption of these groups.

In the three models used in our study, there is a greater level of disaggregation at higher trophic levels as opposed to lower trophic levels. A consequence of this for upper trophic levels is that the individual groups have lower biomass and thus lower total consumption. If higher trophic level groups were more aggregated, they may have stronger top-down effects on the food web. Additionally, a study examining the sensitivity EwE food webs to varying levels of aggregation found that models that were highly aggregated at lower trophic levels were inherently more resistant to perturbations (Pinnegar et al. 2005).

Gaichas et al. (2015) used Ecosense to compare the eastern Bering Sea and Gulf of Alaska food webs and to examine how climate and fisheries interact with food web structure to produce different outcomes for the food webs. In particular, they examined the role of pollock and the combined effects of climate and pollock fisheries in these ecosystems. A key feature of their Ecosense simulation results is the higher level of variability in the Gulf of Alaska response to the same perturbations applied to the eastern Bering Sea. This result has important implications to fisheries management as it suggests we may be less able to predict likely outcomes to anticipated stressors in the Gulf of Alaska as compared to the eastern Bering Sea (Gaichas et al. 2015). In our study, while we found both of these ecosystems to be sensitive to perturbations to pollock, we found the range of recovery times to be much narrower and shorter in the eastern Bering Sea (Figure 2d) than in the Gulf of Alaska (Figure 2f). And consistent with the findings of Gaichas et al. (2015), we found the range of recovery times to perturbations in the Gulf of Alaska ensemble to be more than twice as wide as in the eastern Bering Sea, ranging up to 10 years (Figure 2f). However, it should also be noted that while recovery times to pollock perturbations in the eastern Bering Sea were consistently shorter than in the Gulf of Alaska, the percentage of ensemble ecosystems disrupted was nearly three times as high in the eastern Bering Sea (11.1%) than in the Gulf of Alaska (3.8%). This result highlights the structural importance of pollock to both ecosystems but emphasizes a greater level of stability in the eastern Bering Sea food web regarding the perturbations we applied to pollock.

Other studies utilizing Ecosense have focused on a single species or food web. In a study investigating the production and growth of salmon in the northeast Pacific, Aydin et al. (2005) conducted a perturbation analysis with Ecosense similar to what we did in the present study. However, instead of increasing mortality of each species in turn and examining the effect on upper trophic levels, they increased the biomass of each species one at a time and looked at the effect this had on pink salmon (*Oncorhynchus gorbuscha*). Similar to our results they found bottom-up effects from perturbing mid- and lower trophic level species to be strongest, while top-down effects from perturbing higher trophic levels were difficult to detect. Aydin and Mueter (2007) also conducted a perturbation analysis using Ecosense during their examination of the dynamics of the eastern Bering Sea food web. They decreased production of selected prey groups one at a time and examined their effect on the food web, and in particular the effect on pollock. They found pollock to be sensitive to reduced prey production. They also observed that when pollock recruitment was reduced, competitors of juvenile pollock benefitted from the competitive release and increased in their abundance. This finding suggests that as long as there are other species filling a similar ecological role, a significant loss in one species might

not have much effect on the broader food web.

Previous studies that used Ecosense have taken different approaches to addressing uncertainty in the predator-prey functional response. Aydin et al. (2003) ran their simulations with global vulnerability settings where all links were set to the same high, low, or intermediate values. In general, they found the direction of biological response to perturbations to be consistent but the magnitude of response was higher under the high vulnerability settings (i.e., top-down control). Although we did not use a global vulnerability setting for all groups, we did observe instances where relatively high vulnerabilities led to rapid, high amplitude oscillations for some linked groups. This indicates that links characterized by top-down control may be more sensitive to perturbations or additional stressors, and their response to stressors may be more pronounced.

Gaichas et al. (2012) used Ecosense to evaluate the robustness of their EwE model of the Gulf of Alaska to uncertainty in the functional response under scenarios of varying fishing pressure. They found the outcomes of their simulations to be robust to functional response uncertainty at low to moderate levels of fishing pressure. However, scenarios with high levels of fishing pressure resulted in more frequent species extinctions and there were less successful parameter sets. Their results highlight the need to explore a wide range of functional response parameter space as there is not likely to be a single best combination, and those combinations that are successful may vary subject to the additional pressures experienced by the ecosystem. Ruzicka et al. (2013a) and Ruzicka et al. (2013b) also drew vulnerability parameters for each individual trophic link from the full range of parameter space. Drawing the functional response from the full effective range acknowledges the high level of uncertainty in these interactions and the importance of these interactions to population dynamics. This is comparable to the approach we used in this study where we varied vulnerability over the full effective range for each trophic link individually, in each generated ecosystem. Such wide explorations of parameter space for the functional response, in combination with the draws of base model parameters, addresses a key source of uncertainty in multispecies modelling as identified in the literature (Plagányi and Butterworth 2004, FAO 2008, Gaichas et al. 2012, Link et al. 2012). Including that uncertainty in model results by providing a distribution of simulation outcomes, provides an indication of how robust the results are to uncertainty in the functional response.

A key limitation of our study is the simplicity of the perturbations we employed. Increasing the mortality on one group at a time is a useful approach as a first step toward identifying key sensitivities in the food web but it is not representative of any realistic scenario likely to occur in nature or induced by anthropogenic activity. Additionally, all our perturbations involved increasing mortality and we did not explore the potential impacts of increasing production or changes in primary production. The metric of aggregated upper trophic level biomass, which we used to track any ecosystem disruption, is an admittedly simple and coarse metric, which alone does not carry a clear ecological interpretation. We used this metric here only as a means to detect a relatively large-scale food web response to the prescribed perturbations, and it is not used to provide a theoretical interpretation of any unique food web response to perturbations. We sought only to identify functional groups to which the food web models demonstrated sensitivity.

It is not likely that any disturbance to an ecosystem will only affect a single species in isolation. There will likely be synergistic effects from multiple stressors acting on an ecosystem at any given point in time. For example, in the Pacific Arctic, sea-ice coverage and the duration of the ice-covered season is expected to continue to be reduced in the future (Wang and Overland 2015). Changes to sea-ice phenology can have bottom-up effects on the food web by affecting the timing, magnitude, and nature of primary production (Ji et al. 2013). Changes to primary production will also effect the synchronized life history events of pelagic secondary producers (Edwards and Richardson 2004, Søreide et al. 2010, Leu et al. 2011, Daase et al. 2013) and the delivery

of organic matter to support the benthic food web (North et al. 2014, Grebmeier et al. 2015, Lovvorn et al. 2015). Climate change and increasing water temperatures can effect species growth, bioenergetics, and impact the spatial distribution of predators and prey, changing species composition and altering trophic dynamics. Convening subject matter experts in a workshop setting to outline detailed scenarios for predicted or potential disturbances could produce the detailed framework necessary for simulations with Ecosense that would provide valuable guidance for resource managers in the face of simultaneous stressors to ecosystem structure and function, and competing societal goals.

We used a data pedigree with corresponding confidence intervals to describe uncertainty in model parameters by drawing parameters from uniform distributions (except diet composition, Dirichlet distribution) centered on initial parameter estimates. This simplified approach standardized the generation of parameters across all functional groups for simulations and analyses. However, this approach can potentially increase uncertainty in parameter estimates and even model outputs by not utilizing all available information on a parameters statistical properties such as distribution shape and standard deviation (Regan et al. 2002). If a particular probability distribution is desired for one of the EwE parameters generated in the Ecosense routine, it can be specified by the user in the Ecosense code. Additionally, some life history parameters are thought to be correlated (Charnov et al. 1991) and specific knowledge of some life history parameters may be used to predict other less known parameters (Thorson et al. 2017). A next step for parameter generation will be to investigate how “known” life history parameters can be used to inform parameter draws for unknown parameters and how this may influence uncertainty and simulation results.

The three EwE models compared in this study exist across a near continuous latitudinal gradient in the Northeast Pacific Ocean, and as adjacent systems, they share many taxa and are connected via oceanographic linkages. While it is preferable for all parameters in a food web model to be system specific, it is not practical as the data and rates required to support those parameters do not often exist, particularly for non-commercial and other less studied species. When direct parameter estimates are unavailable they can be obtained from the literature, including other food web models, and preference is often given to parameter estimates for species with a close taxonomic relationship and/or parameter estimates derived from studies in nearby ecosystems. Such is the case with the three food web models used in this study. While parameters estimated specifically for each ecosystem would be ideal, as a practical matter, this is not possible, and there are a number of functional groups who share parameters that are common to all three of the ecosystems in this study or are shared between two of the systems. There are nine functional groups that have the same base P/B and Q/B across all three food web models, including gray whales, shrimps, and copepods. Additionally, there are another 18 functional groups that have the same base P/B and Q/B between the eastern Bering Sea and Gulf of Alaska. These common parameters could contribute to similar dynamics between the compared systems or potentially obscure differences that may be apparent with ecosystem-specific parameters, should those “true” parameters ultimately have different values. Despite the common parameters, there are a large number of structural and functional differences between these food webs and we have observed a number of distinctions between the simulation results across the three systems.

We have demonstrated here how uncertainty in Ecopath model parameters and the predator-prey functional response can be incorporated into scenario-based simulations with Ecosim, using the Rpath package. The inclusion of parameter uncertainty in the simulation framework helps to convey the range of possible outcomes from the modeled perturbations and can help prevent overconfidence in simulation results with a single model. The Ecosense routine allows for the inclusion of uncertainty and can help to identify key sensitivities in food

webs and highlight direct and indirect effects of disturbances mediated by trophic interactions. Adequate characterization of uncertainty in model results improves communication of the strength and direction of modelled results and will help models to support marine EBM. Although the simulations presented here are simple examples, Rpath with Ecosense could be used by fisheries scientists and resource managers to explore a range of possible outcomes to simulations of detailed policy options or for investigating potential outcomes to anticipated climate impacts (Gaichas et al. 2015).

CRedit authorship contribution statement

George A. Whitehouse: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization.
Kerim Y. Aydin: Conceptualization, Methodology, Software, Investigation, Data curation, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2020.109074.

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