DR. JAMES J. RUZICKA (Orcid ID : 0000-0003-2722-8905)

Article type : Original Article

Comparing the roles of Pacific halibut and arrowtooth flounder within the Gulf of Alaska ecosystem and fishing economy

James J. Ruzicka[a], Stephen Kasperski[b], Stephani Zador[b], Amber Himes-Cornell[c]

[a] Cooperative Institute for Marine Resources Studies, Oregon State University, Newport, Oregon, USA (Jim.ruzicka@oregonstate.edu)

[b] NOAA Alaska Fisheries Science Center, Seattle, Washington, USA

[c] Fisheries Policy, Economics and Institutions Branch, Fisheries and Aquaculture Department, Food and Agriculture Organization of the United Nations

ABSTRACT

The fishing industry of the western and central regions of the coastal Gulf of Alaska (CGoA) directly employs over 17,000 people and processes fish with a wholesale value of US$618 million annually. Pacific halibut (*Hippoglossus stenolepis*) are a valued groundfish species because of the high quality of their flesh. In contrast, arrowtooth flounder (*Atheresthes stomias*) are much more abundant but of low value because their flesh degrades upon heating. Both are high trophic level predators but play different roles in the ecosystem because of differences in abundance and diet. Using an end-to-end ecosystem model, we evaluate the impact of alternate levels of fishing effort and large-scale changes in oceanographic conditions upon both species, the ecosystem, and the fishing economy. Reduction of longline efforts to reduce Pacific halibut mortality led to reduction in total value of all CGoA landings but increase in value landed by sport fisheries, trawl fleets, and fish pot vessels as they exploit a greater share of available halibut, sablefish, and Pacific cod. Increased trawl effort to raise arrowtooth flounder mortality led to increase in total value of all landings but large reductions in value landed by longline, jig, fish pot, and sport fleets with greater competition for available Pacific cod, halibut, and sablefish. Oceanographic conditions that enhance pelagic food chains at the expense of benthic food chains negatively impact groundfish in general, though Pacific halibut and arrowtooth flounder are resilient to these effects because of the high importance of pelagic fish in their diets.

KEYWORDS: Pacific halibut; arrowtooth flounder; management; end-to-end ecosystem model; ECOTRAN; food web; economics

1 INTRODUCTION

This study considers the ecological and economic roles of two important large flatfish species, Pacific halibut (*Hippoglossus stenolepsis*, hereafter halibut) and arrowtooth flounder (*Atherestes stomias*, hereafter arrowtooth) within the western and central portions of the coastal Gulf of Alaska (CGoA). Halibut and arrowtooth are both high trophic level predators, but because of differences in their relative abundance, diet preference, and economic value they play different roles in the CGoA ecosystem and fishing economy. Both stocks have also undergone large changes in abundance over the last 50 years along with changes in oceanographic conditions and shifts in food web structure (IPHC, 2018; Spies et al., 2017).

The commercial fishing industry within the western and central regions of the CGoA directly employed over 17,000 Alaskan residents and non-residents and produced processed fish with a wholesale value of US$618 million (nominal) on average in 2015-2016 (ASMI, 2017). Groundfish (fish living on or near the bottom, such as Pacific cod, *Gadus macrocephalus*, and various flounders) represent approximately one half of ex-vessel and one-third of the total wholesale value of processed CGoA seafood, including salmon and crab (ASMI, 2017; Fissel et al., 2017).

Halibut are the most highly priced groundfish caught in the CGoA, while arrowtooth are the most abundant (Fissel et al., 2017; Spies et al., 2017). Halibut receive a high price because of the quality of their flesh and their large size. They support a large directed commercial fishery, are sought after by recreational fishers, and have long been an important part of the subsistence harvest for Alaska Natives and other residents. The commercial, recreational, and subsistence fisheries together landed 9,100 tons (t) caught in the Gulf of Alaska in 2015 (IPHC, 2015). The halibut fishery is particularly valuable to the region's economy. The real wholesale value of commercially caught and processed Gulf of Alaska halibut has averaged over $115 million per year (2016 US$), and nearly 2,000 people have been directly employed for at least part of the year in the commercial harvesting of halibut on average from 2012-2016 (Fissel et al., 2017).

In contrast, arrowtooth have been a low-value fish because their flesh degrades upon heating (Kang & Lanier, 2005; Kasperski, 2016). Only 10,000 t per year were caught through the 1980s and 1990s with less than 10% retained. However, improved processing techniques have been developed to neutralize the enzymatic reactions and provide a marketable product (e.g., Kang & Lanier, 2005). This has led to the development of a small, directed fishery within the central region of the CGoA, the region of peak abundance (Spies et al., 2017). On average from 2000-2017, 24,000 t have been caught per year with over 65% retained (over 90% retention from 2014-2016) (Spies et al., 2017). The wholesale value of commercially caught and processed CGoA arrowtooth has averaged almost US$12.9 million (2016 US$) per year from 2012-2016 (values from Fissel et al., 2017, adjusted for inflation using the GDP deflator). Note that halibut are jointly managed with Canada via the International Pacific Halibut Commission (IPHC) and are not managed under the Fishery Management Plan (FMP) for groundfish of the Gulf of Alaska but are considered groundfish for the purposes of this study.

The CGoA is a highly productive, subarctic downwelling system (Stabeno et al., 2004). Oceanic surface waters advected onto the shelf during downwelling events originate from the high nutrient, low-chlorophyll, iron-limited region of the North Pacific gyre. Seasonally high primary and secondary production supports many fish, shellfish, seabird and marine mammal populations, which in turn provide subsistence foods for and economic input to numerous small and remote coastal human communities (Zador et al., 2017). Over the past 50 years, the CGoA has experienced several major changes in oceanographic conditions, including prolonged shifts between warm and cold phases of the Pacific Decadal Oscillation (PDO), shifts in downwelling intensity and input from ocean surface currents (Bakun upwelling index and PAPA trajectory index, Hare & Mantua, 2000), and the marine heatwave of 2014-2016 (Bond et al., 2015).

Changes in oceanographic conditions have been followed by large rearrangements in the structure of the CGoA pelagic and benthic communities. Following a climate shift of the PDO to warmer conditions in 1976/77, there were declines among shrimp and crab populations and increases among groundfish stocks throughout the CGoA (Mantua et al. 1997, Anderson and Piatt 1999). Halibut and arrowtooth stocks also grew following the 1976/77 PDO shift (IPHC, 2018; Spies et al., 2017). Commercial landings of halibut throughout the Gulf of Alaska peaked between 2000 and 2005 (IPHC, 2014). IPHC and National Oceanic and Atmospheric Association (NOAA) bottom trawl surveys show the arrowtooth population growing from 400,000 t in the 1960s (age 1+ biomass) to over 2,000,000 t in 2015 (Spies et al., 2015). Following the 2014-2016 marine heatwave, groundfish such as Pacific cod suffered a very significant crash (Barbeaux et al., 2017), while the impact upon halibut and arrowtooth does not appear to have been as great or may have not yet been realized. Halibut and arrowtooth stock sizes are still large, but both have been declining over the last decade (IPHC, 2018, Spies et al., 2017).

Adult halibut are generally demersal piscivores. Walleye pollock (*Gadus chalcogrammus*), Pacific sand lance (*Ammodytes* sp.), arrowtooth, Pacific cod, sablefish (*Anoplopoma fimbria*), rockfish (*Sebastes* sp.), sculpins (Cottoidea), and other flatfish make up the major portion of their diet, though benthic invertebrates (shrimp, crabs, and clams) and pelagic fish (coho salmon (*Oncorhynchus kisutch*), eulachon (*Thaleichthys pacificus*), capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*), may often be found in their diet (Yang et al., 2006; IPHC, 2014). Fishing mortality is estimated to exceed predation mortality among halibut (Aydin et al., 2007).

Adult arrowtooth feed upon fish and invertebrates throughout the water-column. Arrowtooth are major predators of walleye pollock, herring, eulachon, capelin, Pacific sand lance, cephalopods, euphausids, and Pandalid shrimp (Yang et al., 2006; Aydin et al., 2007; Knoth & Foy, 2008). By virtue of their abundance and the predatory pressure they exert upon important forage species (e.g., walleye pollock, capelin, and euphausiids), arrowtooth have the potential to play an important role in both lower trophic dynamics and in the population dynamics of top trophic level predators (Yang et al., 2006; Hollowed et al., 2000). In turn, arrowtooth are preyed upon by killer whales, seals and sea lions, walleye pollock, sharks, and skates; however, taken together, predation and fishing pressure accounts for little of the total known arrowtooth mortality (Aydin et al., 2007). They are still known to be important prey sources for some predators. The observed frequency of occurrence of arrowtooth within the diets of CGoA Steller sea lions (*Eumatopias jubatus*) ranged from 20%-35% in the 1990s and 2000s (Sinclair et al., 2013).

We present an end-to-end (nutrients-to-fisheries) ecosystem model of the western and central regions of the CGoA (*CGoA-ECOTRAN*). *CGoA-ECOTRAN* builds directly upon the CGoA mass-balanced food web models of Aydin et al. (2007) and Gaichas et al. (2011). *CGoA-ECOTRAN* adds separate descriptions for the food webs of five sub-regions within the western and central CGoA. The model is run within a platform allowing for rapid estimation of the consequences of changes to community structure and fishing pressure and is intended to be coupled with ocean current and plankton production models for time-dynamic simulations under alternate physical regimes in future studies (e.g., Ruzicka et al., 2016; Ruzicka et al., 2018). We apply the model to (1) quantify the importance of halibut and arrowtooth to the ecosystem in terms of energy demand upon lower trophic levels and energy contribution to higher trophic levels. Through model simulations, (2) we investigate the impacts of fishery management changes aimed at fleets targeting halibut (longline fleets) and arrowtooth (trawl fleets). We ask whether increased fishing pressure upon the ecologically important, but economically undesirable arrowtooth can lead to positive changes in more valued stocks and be a net benefit to the main CGoA fishing sectors. Finally, (3) we simulate changing energy flow patterns through pelagic and benthic food chains arising from the changes in lower trophic community structure observed during the 2014-2016 marine heatwave. We ask what effect prolonged or more frequent heatwave conditions would have upon halibut and arrowtooth stocks and the fisheries that exploit them.

2 METHODS

2.1 Ecosystem model structure

To investigate impacts of changes in the abundances of halibut and arrowtooth and changes in fishing effort upon the ecosystem and fleet economies of the shelf and upper slope of the central and western Gulf of Alaska (CGoA, Fig. 1), we ran simulations within an ECOTRAN end-to-end ecosystem model (Steele & Ruzicka, 2011). The *CGoA-ECOTRAN* model describes the trophic connections between phytoplankton (2 size classes) and benthic primary producers (8 functional groups), zooplankton (12 groups), gelatinous zooplankton (4 groups), pelagic fishes and squids (28 groups), benthic invertebrates (37 groups), demersal fishes (32 groups), seabirds (15 groups), marine mammals (16 groups), fisheries (15 vessel groups), pelagic and benthic microbes (3 groups), eggs (2 pools), detritus (3 pools), and nutrients (3 pools). There are more than 2,700 defined trophic linkages and more than 1,700 defined fishery linkages. Our model is based upon an earlier *Ecopath* food web model of the CGoA developed by S. Gaichas at NOAA's Alaska Fisheries Science Center (AFSC) (Aydin et al., 2007). The earlier *Ecopath* model was based primarily upon field survey data from a variety of sources representing the period from 1979 to 2002: fish and epifauna (AFSC Resource Assessment and Conservation Engineering (RACE) groundfish surveys), shellfish (Alaska Department of Fish and Game), seabirds (U.S. Fish and Wildlife Service), mammals (National Marine Mammal Laboratory), and fisheries (Alaska Department of Fish and Game, NOAA, and the Alaska Fisheries Information Network). Plankton community composition and production in the earlier model was estimated as that required to support higher trophic levels.

The *CGoA-ECOTRAN* model describes separate food webs for five cross-shelf sub-regions between 147°-159°W (Fig. 1) corresponding to NOAA Statistical Areas 620 and 630: the inner shelf (shoreline-15 km, 44,479 km^2), the mid-east shelf (15-90 km, 41,367 km^2), the mid-west shelf (15-90 km, 46,376 km^2), the outer-east shelf and upper slope (90 km-1000 m depth, 26,477 km^2), and the outer-west shelf and upper slope (90 km-1000 m depth, 20,503 km^2). Eastern and western sub-regions are divided at the northern-most point of Kodiak Island (152.32°W) to keep the Shelikof Strait fully contained within the western region. Biomasses of fish and epifauna are distributed into sub-regions based upon observations from RACE surveys conducted between 2003 and 2013. Zooplankton community composition and biomasses are based upon 1997-2012 data from the University of Alaska Fairbanks' Seward Line transect across Alaska's central Pacific shelf (Coyle et al., 2013; www.sfos.uaf.edu/sewardline). Zooplankton growth rate parameters are based upon size and temperature relationships established for different trophic groups (Hirst et al., 2003). Inter-tidal groups are defined using biomass density observations and intertidal habitat type coverage (i.e., rocky or soft-bottom intertidal). Inter-tidal habitat areas, soft vs. hard substrate and intertidal vs. subtidal, are based on estimates of shoreline lengths of various habitat types given in Ford et al. (1996). Further details about model construction and the parameters for each sub-region are provided as Supplementary Materials.

We inferred the food web structure for each sub-region from the available data using *Ecopath* algorithms, and then converted the food webs to an ECOTRAN end-to-end model following the technique of Steele and Ruzicka (2011). *Ecopath* (Christensen & Walters, 2004) is a software package that infers mean annual biomass transfer rates between all living and detritus components of a food web based upon linear estimates of the bioenergetic demands of each consumer group upon all of its prey types. The solution of an *Ecopath* food web is constrained by two thermodynamic limitations: the predation (or fishing) demands on any producer cannot exceed the production rate of that group, and all biomass consumed by any group must be partitioned between growth (production), metabolism, and non-assimilated excreta as defined by the physiology of that group. Thus, an *Ecopath* model may also be called a "mass-balanced" food web.

ECOTRAN models are based on the transformation of the solution for a system of linear equations describing predation pressure upon all members of a food web, such as solved by *Ecopath*, into a donor-driven trophic matrix $\boldsymbol{A_{cp}}$ that maps the fate of all production by groups *p* through the food web to consumers *c* (Steele, 2009; Steele & Ruzicka, 2011):

$$\boldsymbol{A_{cp}} = \frac{\boldsymbol{D_{pc} q_c}}{\sum_c \boldsymbol{D_{pc} q_c}} \qquad (1)$$

where matrix $\boldsymbol{D_{pc}}$ is the fraction of each producer *p* within the diet of each consumer *c*, $\boldsymbol{q_c}$ is the total consumption rate of consumer *c*, and term $\sum_c \boldsymbol{D_{pc} q_c}$ is the total grazing or predation rate upon each producer *p* by all consumers *c*. Trophic matrix $\boldsymbol{A_{cp}}$ is expanded to include nutrient and detritus pools and account for the distribution of all consumption by group *p* between its consumers, between nutrient and detritus pools via feces and ammonium excretion, or to detritus as senescence. A model expressed in this format can readily be used to quantify the consequences of changes to community composition (Ruzicka et al., 2012; Robinson et al., 2015), changes to external subsidies of nutrients and plankton (Treasure et al., 2015; Treasure et al., 2018), changes in oceanographic regime through coupled physical models (Ruzicka et al., 2016; Ruzicka et al., 2018), changes in fishery management policy, or changes to the physiology or diet of any functional group.

2.2 Ecosystem model analyses

The *CGoA-ECOTRAN* ecosystem model describes the flow of energy, as living biomass, through all trophic pathways in the food web. For every group, the model defines the fate of all consumed biomass divided between mortality by each of the group's predators, excretion of metabolic wastes and feces, population growth, and senescence (e.g., Ruzicka et al., 2016). The demands of halibut and arrowtooth upon ecosystem production and their contribution to higher trophic levels are expressed with the model-derived "footprint" and "reach" metrics (as detailed in Ruzicka et al., 2012). The footprint of a consumer group upon the ecosystem is the fraction of total ecosystem production (excluding detritus) that supports the group's production. The reach of that same group expresses its importance as a producer or energy transfer node. The reach is the fraction of total consumer production within the ecosystem that originates with (or passes through) halibut or arrowtooth and flows throughout the food web via all direct and indirect pathways. Fishery and predation pressure exerted upon halibut and arrowtooth by each fleet and predator group are estimated directly from the trophic network matrix (A_{cp}).

We run four sets of model scenarios to investigate the ecosystem's response to changes in the abundance of halibut and arrowtooth, to simulate changes in fishing mortality and in fishing effort, and to simulate changes in lower trophic structure observed during the 2014-2016 marine heatwave (Table 1). In the first scenario set, we investigate ecosystem sensitivity to identical relative changes in halibut and arrowtooth abundance. Halibut abundance is increased and arrowtooth abundance decreased by the same relative amounts (20%), separately, with no other forced changes to the food web (scenarios A and B).

In the second scenario set (scenarios C and D), we alter the catch rates of halibut and arrowtooth within the fleets responsible for catching most of each species so that each species is subject to the fishing mortality rate experienced by the other. The production rates (p = biomass · p/b, the production to biomass ratio) of halibut and arrowtooth within the full model domain are 48,000 t

y^{-1} and 553,000 t y^{-1}, and the mean total catch rates (landings + discards) over the 2006 - 2015 period are 22,000 t y^{-1} and 34,000 t y^{-1}, respectively (Supplemental Material Tables A3 and A6). Thus, the fishery mortality experienced by halibut (45% of production) is approximately 8 times greater than that experienced by arrowtooth (6%). Most halibut are caught by the targeted halibut longline and non-halibut longline fleets (Table 2), and in scenario C we scale the landings and discards of halibut in these fleets down by a factor of 0.1 to simulate the fishery mortality rate currently experienced by arrowtooth. Most arrowtooth are caught by the catcher processor (C/P) bottom trawl, catcher vessel (CV) bottom trawl, and CV pollock trawl fleets, and in scenario D we scale the landings and discards of arrowtooth in these fleets up by a factor of 10 to simulate the fishery mortality rate currently experienced by halibut. Catch rates of other species caught are not altered in scenarios C and D. In the third scenario set (scenarios E and F), we alter fishing effort by scaling the landings and discards of all species, whether targeted or bycatch. Effort by the targeted halibut longline and non-halibut longline fleets are reduced by 90% (scenario E), and the effort of the C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets is increased 10-fold (scenario F).

In the fourth scenario (scenario G), we simulate observed changes in the plankton community during the 2014-2016 marine heatwave. Continuous Plankton Recorder observations across the CGoA shelf show a 50% decline in the relative abundance of large diatoms in the phytoplankton community and a 150% increase in total mesozooplankton biomass during heatwave years 2015 and 2016 relative to the 2004-2017 mean (Batten 2017, 2018). Euphausiid biomass along the Seward line in 2015 and 2016 was 48% below the 2004-2017 mean (Hopcroft & Coyle, 2018). Stratification and nutrient depletion led to low phytoplankton biomasses and an increase in the relative abundance of smaller taxa in oceanic surface waters (Peña et al., 2018), but there are as of yet no comprehensive estimates of primary production in shelf waters during the heatwave years. We therefore maintain the overall level of primary production in scenario G, reducing diatom production by 50% but increasing productivity of small cells by 20%.

We consider the ecosystem at steady state where each scenario represents a linear, asymptotic solution of a time-dynamic simulation (Collie et al., 2009; Steele, 2009). The importance of a consumer fish or fishery fleet *c* was modified by changing the fraction of the production of each prey group *p* that is consumed by *c*. This was offset by an opposite change in the predation pressure by all other consumers competing for each prey group. Thus, we assumed that the total predation pressure upon prey group *p* was unchanged by the scenario. We also assumed that changes in energy flow to competing consumers for each prey group *p* were proportional to their original relative importance as consumers. The effects of a scenario were evaluated by comparing changes in the biomass of individual groups under scenario conditions to the biomass under base model conditions (or landings in the case of fishery fleets):

$$\Delta B = (B_{scenario} - B_{base}) / B_{base}. \quad (2)$$

An accounting of the propagation of uncertainty across trophic linkages was necessary to provide a confidence index about model-derived indices and simulations. Alternate potential food webs were randomly generated by drawing from a defined normal distribution about each trophic linkage defined in matrix A_{cp}. As each element of trophic network matrix A_{cp} is a function of defined physiological, diet, predation, senescence, population growth, and emigration terms, the uncertainty of each element of A_{cp} is also a function of the defined uncertainty levels about each of these parameters. We adopted a general assumption that the uncertainty about each physiological parameter (assimilation efficiency, metabolism, gamete production) was ± 25% and the uncertainty about each trophic interaction was greater, ± 75%, given that diets are more flexible than physiologies. Each randomly generated matrix A_{cp} was re-normalized so that, for every functional group, the fate of all production was accounted for and predation pressure did not exceed production for any producer. During re-normalization, physiological terms took precedence over predation and senescence; i.e., physiological terms were not readjusted, contingent upon thermodynamic constraints (feces production, metabolism, and gamete production cannot exceed consumption). Each scenario was simultaneously run on 1,000 randomly generated models, and scenario results are reported with an error range of ± 1 coefficient of variation.

2.3 Economic impacts

In order to estimate the economic impacts of changes to ecosystem composition resulting from each scenario, we scaled each biomass change by the ex-vessel price per unit landed weight. Values are mean ex-vessel prices over the 2005-2015 period for the Gulf of Alaska region and were obtained from the Alaska Fisheries Information Network (www.akfin.org). Prices were adjusted to 2015 values using the GDP deflator (Supplementary Material Table A9). Halibut landings and ex-vessel values are reported for their headed and gutted condition which represents approximately 75% of the live weight across the adult size range (Clark, 1992). All other species' prices are given per live weight landings (round weight).

3 RESULTS

3.1. Footprint, reach, and predation

Comparisons of estimated halibut and arrowtooth production, predation, and fishing mortality rates are shown in Table 3. Within the western and central CGoA region as a whole, arrowtooth have eight times the biomass and are an order of magnitude more productive than are halibut.

The footprint and reach metrics show how important each group is ecologically (Fig. 2). The footprint expresses the demand of halibut and arrowtooth on the total production by all consumers in the ecosystem, and the reach expresses their contribution to total consumer production. Arrowtooth have a much larger footprint and larger reach than halibut in all sub-regions. Arrowtooth are especially important in the inner and mid-shelf regions and have their largest reach on the mid-west shelf. However, halibut have a larger reach:footprint ratio than arrowtooth (0.09 vs. 0.01 on the inner shelf and 0.07 vs. 0.01 on the mid and outer shelf), showing that in all sub-regions halibut pass along, to higher trophic levels and fisheries, a higher proportion (7-9%) of the ecosystem production that they consume than do arrowtooth (1%).

During the 2005-2015 period, halibut suffered a substantially higher fishery mortality rate than do arrowtooth (Table 3). In all regions, 43-49% of halibut production is taken by humans compared to 6% of arrowtooth production. Our model also suggests that halibut suffer higher predation than do arrowtooth, exceeding 45% of halibut production in all sub-regions and reaching nearly 60% in both of mid-shelf and the eastern outer-shelf regions. In contrast, only 20%-34% of arrowtooth production is consumed in any region (Table 3).

The relative importance of each predator class that prey upon halibut and arrowtooth is shown in Figs. 3 and 4. For halibut, arrowtooth and sharks (salmon sharks, *Lamna ditropis,* and sleeper sharks, *Somniosus pacificus*) are the major predators, accounting for 40-50% of the total predation and fishery mortality. Arrowtooth alone account for 32% of the total non-senescence mortality on the inner shelf. Sharks (salmon sharks) account for 40%-50% of all non-senescence mortality on the mid- and outer-shelf. Fisheries catch accounts for 42-47% of total non-senescence mortality, of which the targeted halibut longline fleet accounts for 68% of all commercial, recreational, and subsistence halibut catch (landings + discards; Table 2).

The arrowtooth predator field is more diverse than that of halibut. Demersal elasmobranchs (sleeper sharks, skates and rays), "other fish" (rougheye rockfish, *Sebastes aleutianus*, over the outer-shelf), marine mammals (pinnipeds and resident killer whales, *Orcinus orca*, over the mid- and outer-shelf) are all important predators of arrowtooth (Fig. 4). Fisheries represent 13-23% of the total predation and fishery pressure upon arrowtooth. The C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets account for 99% of total arrowtooth landings and discards (Table 2).

3.2 Model simulations

3.2.1 System sensitivity to changes in halibut and arrowtooth biomass: Scenarios A and B examined the effects of increasing halibut and decreasing arrowtooth abundance by the same relative amounts (20%), separately with no other forced changes to the food web (Table 4 and Supplemental Material Tables B1 and B2). Increased halibut biomass (scenario A) leads to only small increases among groups that prey heavily upon halibut, e.g., salmon sharks (Fig. 5). However, other groups in the food web declined as greater halibut production requires the support of more ecosystem resources. Demersal fish (greenling/lingcod, sculpins, and skates) were most strongly affected. Steller sea lions and resident seals were also negatively impacted, but declined by less than 1%. The fishing fleets and sectors that target halibut directly increased (halibut longline, non-halibut longline, recreational fishing, subsistence fishing, and halibut sport charters), but other commercial fleets declined.

When arrowtooth biomass was reduced by 20% (scenario B), upper trophic level groups (pinnipeds, halibut, seabirds, and odontocetes) responded most positively because of increased production among many pelagic fish and groundfish species (Fig. 6, Table 4). Among these, greenling/lingcod (4.3% ± 0.8 CV), chum salmon (3.4% ± 0.7), Chinook salmon (3.4% ± 0.8), Pacific cod (3.1% ± 0.5), and juvenile arrowtooth (2.4% ± 0.4) showed the largest increases (Supplemental Material Table B2). Few groups declined when arrowtooth were removed from the ecosystem; these are the species that prey directly upon arrowtooth (sleeper sharks and skates). All fishing fleets and sectors, except for the C/P bottom trawl fleet, showed increased landings. The longline fleets and the halibut sport charter fleet that target halibut showed large improvements. However, the fleets that land Pacific cod (jig, fish pot, and CV pollock trawl fleets) showed the largest improvements.

3.2.2 Reduction of halibut mortality: When the fishing mortality of halibut within the longline fleets was reduced by 90% with no change to bycatch (scenario C, Table 5, Supplemental Material Table B3), there were only small increases (< 2%) in the biomasses of higher trophic level consumer groups. Groups responding most strongly were those that prey directly upon halibut (elasmobranchs and marine mammals) and were able to take advantage of "surplus" halibut production that was no longer being caught by the fishery. Food web changes were not much different when fishing effort, which includes changes to bycatch, was reduced (scenario E, Fig. 7, Table 6, Supplemental Material Table B5). Small increases in the biomasses of other fish species that do not prey upon halibut (e.g., the greenling/lingcod group) may be attributed to an increase in prey availability through the reduction of bycatch mortality.

Landings by other fishery fleets increased when the longline fleets' efforts were reduced (scenario E, Fig. 7, Table 6, Supplemental Material Table B12). Landings by the halibut sport charter fleet, recreational fishing, and subsistence fishing increased as fewer halibut were removed by the competing longline fleets. Landings made by the jig, fish pot, and trawl fleets, which are prohibited from retaining and selling halibut, increased because the longline fleets also removed fewer of the non-halibut species (Pacific cod, pollock, and sablefish) that are landed by these fleets.

3.2.3 Increase in arrowtooth mortality: When the fishing mortality of arrowtooth caught in the C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets was increased by 10-fold, with no change to non-halibut species (scenario D, Table 5, Supplemental Material Table B4), there was a decrease in the biomasses of groups that prey directly upon arrowtooth (i.e., sleeper sharks, skates, resident killer whales, and Steller sea lions). The responses to the C/P bottom trawl, CV bottom trawl, and CV pollock trawl effort scenario (scenario F, which includes changes to bycatch) again show the greatest decreases among groups that prey directly upon arrowtooth (sleeper sharks, skates, Steller sea lions, resident killer whales, and resident seals; Fig. 8, Table 6, Supplemental Material Table B6). The biomass of the greenling/lingcod group decreased despite being neither a targeted nor a bycatch species in the trawl fleets because they prey upon bycatch species (e.g., sculpins) that are removed at greater rates in this scenario. In both fishing mortality scenario D and fishing effort scenario F, dogfish biomass increased (2.9% ± CV 1.5 and 5.4% ± CV 2.1, respectively) because of the increased input of discarded fish offal to the system (Supplemental Material Tables B4 and B6).

Following increased effort by the C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets, many fleets were negatively and strongly impacted as the bycatch of multiple species within the trawl fleets also increased. Landings by the jig, fish pot, and longline fleets were all reduced by over 50% (scenario F, Table 6, Fig. 8, Supplemental Material Table B13). Increased bycatch of halibut in the trawl fleets is responsible for reduced landings by recreational fishing (-42% ± CV 0.4), subsistence fishing (-16% ± 1.0), and halibut sport charter fishing (-40% ± 0.4).

3.3 Economic impacts of fishing effort simulations

Assuming prices are exogenously determined by international markets for seafood and the quantities produced does not impact the price received by harvesters such that prices per pound landed are the same across scenarios, the ex-vessel value of landings by each fleet in the base model and the ex-vessel values following each fishing effort scenario are given in Table 7 (see also Supplemental Material Tables B12 and B13). A 90% reduction in effort by the targeted halibut longline and non-halibut longline fleets (scenario E; bycatch also reduced) led to comparable reductions (90%) in the total landed value of both fleets. Increased availability of halibut benefited halibut sport charter (34% increase) and recreational fishers (26% increase). Reduced bycatch of non-halibut species by both longline fleets led to greater landed value by the trawl fleets and fish pot vessels as they exploited a greater share of available sablefish and

Pacific cod, but there was still an overall 27% net loss in the total landed value across all modeled fleets.

A 10-fold increase in effort by the C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets (scenario F, bycatch increased) led to 400-500% increases in the gross value landed by each of these three fleets. However, increased effort by the trawl fleets led to large reductions in the value landed by all other fleets that target groundfish (i.e., halibut longline, non-halibut longline, jig, fish pot vessels, and sport fisheries). Increased halibut bycatch caused reductions in the landed value of the halibut sport charter fleet (-45%) and by recreational fishers (-37%). The landed value by non-groundfish fleets (salmon commercial, herring sac roe, crab pot, shrimp trawl & pot, and sea urchin dive fleet) were little affected by changes to effort by either the longline fleets (scenario E) or the trawl fleets (scenario F).

3.4 Impacts of marine heatwave conditions

Scenario G simulated the effects of prolonged marine heatwave conditions, as they impact the plankton community composition, by forcing changes to the phytoplankton and mesozooplankton community as observed during the summers of 2015 and 2016 (Fig. 9; Table 8, Supplemental Material Table B7). In this simulation, we allowed senescence mortalities of phytoplankton and pelagic microbes to be reduced in order to meet increased mesozooplankton grazing demands. However, the ecosystem could only sustain a 72% increase in mesozooplankton production under the assumption that total primary productivity did not change during the heatwave. Euphausiid biomass along the Seward Line was observed to decrease by 48% in 2015 and 2016 relative to the 2004-2017 mean (Hopcroft & Coyle, 2018). We did not force a change in euphausiid biomass in the simulation as the changes to phytoplankton and mesozooplankton production resulted in a similar reduction in euphausiid biomass (-44% ± 0.3). In general, increased mesozooplankton production resulted in improved foraging conditions for pelagic planktivores (gelatinous zooplankton, forage fishes) which, in turn, most benefitted the groups that prey upon forage fish (salmon, seabirds, fur seals, sei and right whales). Groups most harmed include macrozooplankton, euphausiids, shrimps, benthic invertebrates, juvenile groundfishes, benthivorous rockfishes and thornyhead, and most flatfishes. Adult halibut and arrowtooth were negatively impacted, though only weakly (-4% ± 4.3 and -2% ± 12.8, respectively). However, juvenile halibut were strongly impacted (-22% ± 0.4) while juvenile arrowtooth were not (-2% ± 12.8).

The effect of these heatwave conditions on the fishing economy (Table 7, Supplemental Material Table B14) was an overall reduction in the total landed value by all fleets of only -8%. The herring sac roe fleet expanded by 40%, but all other fleets declined. Most negatively affected were the crab pot (-35%), CV pollock trawl (-15%), CV bottom trawl (-11%), and the non-halibut longline fleets (-10%).

4 DISCUSSION

Halibut are the most highly valued groundfish caught in the coastal Gulf of Alaska (CGoA) (Fissel et al., 2017), but their abundance has declined since the late 1990s (IPHC, 2014). In contrast, arrowtooth are the most abundant groundfish in the CGoA (Spies et al., 2017), but they have limited marketability and receive low prices because of the poor quality of their flesh upon heating (Kang & Lanier, 2005). Each species plays a different role within the CGoA ecosystem because of the differences in their abundance and diet. While halibut are demersal predators, arrowtooth prey upon pelagic and semi-pelagic fish and invertebrates. We employed an end-to-end ecosystem model to evaluate ecosystem sensitivity to changes in the abundance of each species and to investigate the ecological and economic impacts of fishery management changes aimed at different fleets targeting each species. We explored whether increased fishing pressure upon the ecologically important, but economically less desirable arrowtooth can lead to positive changes in more valued stocks and be a net benefit to the main CGoA fishing sectors.

This study considered the implications of changing resource demands by halibut, arrowtooth, and specific fishing fleets as they affect the competition for living resources and alter rates of energy flow through defined trophic pathways across multiple trophic steps. This study did not consider changes in migration or physical transport between model sub-regions. The scenarios applied here provide steady state solutions to forced changes in food web structure within each model sub-region. They represent linear, asymptotic solutions of time-dynamic simulations (Collie et al., 2009; Steele, 2009).

4.1 How are the ecosystem and different fishing sectors affected by changes in halibut and arrowtooth abundance?

The halibut stock, from northern California to the Bering Sea, declined steadily between the late 1990s and 2010, but has since stabilized (IPHC, 2018). The stock assessment estimates of the age 1+ CGoA arrowtooth have grown by 5% since 2003 (Spies et al., 2015). The NOAA groundfish surveys in the western CGoA suggest that arrowtooth and halibut biomasses have both declined by more than 40% over the past decade from record high abundances in 2003-2005 (Spies et al., 2015; Zador & Yasumiishi, 2017; Ruzicka et al., unpub.). To estimate the sensitivity of the ecosystem to variability in each species, we imposed a conservative change of 20% to the modeled biomasses (scenarios A and B).

The central and western CGoA ecosystem is much more sensitive to changes in arrowtooth abundance than to changes in halibut abundance. The biomass of arrowtooth is roughly eight times that of halibut, and therefore arrowtooth have a much larger footprint on ecosystem production (Fig. 2). A 20% relative change in arrowtooth abundance is larger in absolute terms than the same relative change in halibut abundance and has a greater impact upon the ecosystem (Table 4, Figs. 5 and 6). However, different sets of species responded most strongly to the forced changes to either group. Halibut and arrowtooth are both high trophic level flatfish, and changes to the biomass of each directly affected few predators. Salmon sharks benefitted from a greater availability of halibut as prey (scenario A). Sleeper sharks and skates suffered from reduced availability of arrowtooth as prey (scenario B). The greatest effects were upon species that compete with halibut and arrowtooth for common prey. Arrowtooth are water-column foragers (preying upon pollock, euphausiids, and shrimp) and had the greatest effect upon pinnipeds and seabirds that are also water-column foragers. Indeed, while seals and sea lions prey directly upon arrowtooth, they actually benefitted from a reduction in arrowtooth abundance. Halibut are generally demersal feeders. Increased halibut abundance negatively affected other demersal foragers (skates, sculpins, greenling/lingcod, and Pacific cod).

Changes in halibut and arrowtooth abundance also impacted different sets of fishery fleets. Increased halibut abundance most strongly and positively impacted the halibut sport charter fishery and the halibut longline fleet as both fleets directly target halibut (scenario A, Table 4, Supplemental Material Table B8). The crab pot fleet was most negatively impacted as crabs are a substantial part of the halibut diet. Reduced arrowtooth abundance had a positive but indirect effect upon most fleets (scenario B, Table 4, Supplemental Material Table B9). Fleets that do not target arrowtooth benefitted the most (i.e., jig, fish pot, halibut sport charter, targeted halibut longline, and non-halibut longline fleets). These fleets catch a large proportion of fish species that became more productive with reduced competition with arrowtooth (i.e., halibut, greenling/lingcod, Pacific cod, pollock, and sablefish). Only the C/P bottom trawl fleet, where arrowtooth constitute a substantial one-third of landings, was negatively impacted. The commercial salmon fleet was little affected by changes in either halibut or arrowtooth abundance. The pelagic herring fleet benefitted slightly from reduced arrowtooth abundance because herring and arrowtooth both prey on euphausiids.

4.2 What influence can we exert upon the CGoA ecosystem through harvest management of halibut and arrowtooth?

In fishing simulations where bycatch was not changed (scenarios C and D), only high trophic level predators (sharks, skates, pinnipeds, and odontocetes) and fishing fleets that land halibut and arrowtooth were directly affected (Table 5; Supplemental Material Tables B3, B4, B10, and B11). The collateral effects upon living groups and fishing fleets that do not prey upon or catch halibut or arrowtooth were small. Because arrowtooth are much more abundant than halibut, changes to their fishing mortality involve a larger reapportionment of available prey between the predators and fleets that compete for arrowtooth. Thus, increased fishing mortality of arrowtooth had a larger effect upon the predators that consume arrowtooth than a change of similar relative magnitude to halibut fishing mortality.

Changes to fishing effort affect not only the targeted species but also the fate of bycatch species, whether landed or discarded, with unintended consequences. In the longline and trawl fishing effort scenarios (scenarios E and F; Tables 6 and 7; Supplemental Material Tables B5, B6, B12, and B13), change in fishing effort rescales bycatch and halibut and arrowtooth catch rates by the same relative amount. In both scenarios, high trophic level predators that prey directly upon halibut and arrowtooth (sharks, skates, pinnipeds, and odontocetes) remain the most sensitive groups while the effects upon other living groups were modest. The greatest collateral affect that the fishing effort scenarios appear to have is through changes in the availability of discard offal upon the actual productivity of a small number of groups, and this is discussed below. Forced changes to bycatch rates have larger consequences for the other fishing fleets than to the production of the bycatch species themselves, and this can be attributed to redistribution of bycatch species between fleets. For example, reduced longline fleet effort allowed the jig and fish pot fleets to land more Pacific cod that were otherwise landed by the longline fleets (scenario E). Increased effort by the trawl fleets caused a large reduction in the landings of all other fleets targeting groundfish (scenario F). The other groundfish fleets lost most of their catch and revenue from Pacific cod, halibut, and pollock that were instead landed by the C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets.

Few groups that are not predators of halibut or arrowtooth responded strongly to changes in fishing effort. The productivity of halibut and the greenling/lingcod group changed as their prey (e.g., sculpins) were taken from the system at different rates as bycatch. The productivity of other species changed as the availability of discarded bycatch ("offal" in the model) changed under the two fishing effort scenarios. Discard offal is most important for dogfish, seagulls, shortspine thornyhead, and the crab groups but never exceeds 2% of the model diet for any of these groups. The change in these groups to the large increase in offal production under increased trawl effort (scenario F) was relatively small. Other than crab, groups that consume offal contribute little to the landings of any fleet that does not also catch halibut or arrowtooth, and crab pot landings were little changed by either of the fleet effort scenarios.

Changes in discarded bycatch from the longline or the trawl fleets had only small impact on the landings of other fleets. The major discard bycatch of the longline fleets, those exceeding catches of 50 t y^{-1} and 50% discard rates, are the skate, dogfish, arrowtooth, and sculpin groups. These groups together contribute substantially only to landings by the trawl fleets, mostly as discarded arrowtooth. However, landings by the trawl fleets increased only slightly (< 5%) when longline fleet efforts were drastically reduced (scenario E), and little of this increase could be attributed to trawl landings of fish otherwise discarded by the longline fleets. The arrowtooth discard by the longline fleets is trivial (< 200 t y^{-1}, together) compared to arrowtooth landings within the three trawl fleets (each fleet landing > 2,000 t of arrowtooth per year). Halibut are a major discard bycatch group of the C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets and increasing the halibut catch and discard rate in the trawl fleets (scenario F) did have a large negative impact on the landings and landed value of the longline fleets as well as the other fleets targeting halibut. The other major bycatch groups of the trawl fleets (other sculpins, Dover sole, other skates, dogfish, sleeper shark, and sharpchin rockfish) together contribute very little (< 1%) to the landings of any other fleet. Increased discard rate of these groups with increased trawl effort had little effect on landings by other fleets.

4.3 What are the economic consequences of harvest management of halibut and arrowtooth?

The value of fish and crab landings within the CGoA was sensitive to both changes in food web dynamics and changes in the repartitioning of fish production between fishing fleets caused by forced changes in longline and trawl fleet efforts. A 90% reduction in effort by the longline fleets targeting halibut (scenario E) led to an overall 27% reduction of the total value of landings within the central and western CGoA. But this reduction allowed a > 15% increase in the value of jig and fish pot fleet landings and a > 25% increase in the value of recreational and halibut sport charter landings (Table 7), driven by landings of Pacific cod and halibut. Changes in longline fleet effort had little impact on food web dynamics, and neither halibut nor Pacific cod substantially increased their production following effort reduction (Table 6, Supplemental Material Table B5). The jig and fish pot fleets, and to a lesser extent the C/P and CV bottom trawl and CV pollock trawl fleets, increased their share of landed cod and halibut due to reduced competition with the longline fleets. The large increased effort by the trawl fleets (scenario F) led to an overall 102% increase of the total landed value by all fleets in the CGoA but had large negative impacts upon the other groundfish fleets (Table 7, Supplemental Material Table B13), as well as large impacts upon the ecosystem (Table 6, Supplemental Material Table B6). Reduced landed value of the other groundfish fleets was mostly driven by increased competition with the three trawl fleets for Pacific cod, pollock, sablefish, and halibut, the latter due to increased bycatch in the trawl fleets. Landings of halibut in the longline fleets were also reduced in part by food web effects; halibut production was 18% lower following increased effort by the trawl fleets (Supplemental Material Table B6).

Our fishing effort scenarios consider the effects of re-apportioning fish and crab production among predators and fishing fleets. They do not consider changes in recruitment dynamics that may or may not occur with changes in fishing mortality, nor do they consider changes in ex-vessel prices as a result of changes in quantity harvested. To consider the economic sensitivity of the CGoA to long-term changes in halibut or arrowtooth abundance, we ran the model with forced abundance changes (scenarios A and B). Increased halibut abundance and decreased arrowtooth abundance of 20% would each allow the total value landed by CGoA fleets to increase by roughly 13% (Table 7, Supplemental Material Tables B8 and B9). The benefits of increased halibut abundance fall mostly upon the longline and fish pot fleets that land halibut. Effects of increased halibut abundance upon other fleets are small except for the crab pot fleet which would lose a large share of crab production to predation by halibut. Note that fleets are defined at the vessel level using a majority of their revenues from a particular gear/species grouping, so the halibut landings referenced here are a result of the fish pot fleet's use of longlines to catch halibut, even though they are primarily fish pot vessels.

Changes in arrowtooth abundance cause greater changes throughout the food web and to fishing fleets than do changes to halibut abundance. Other fish species and higher trophic level predators become more productive in response to reduced competition with arrowtooth. The fleets that benefit (the jig, fish pot, CV pollock trawl, halibut sport charter, recreational, and halibut longline fleets) do so because of higher production of Pacific cod, halibut, walleye pollock, and sablefish. A 20% reduction of arrowtooth abundance had minimal direct impact, reducing the value of C/P bottom trawl landings by < 1%.

The opportunity for non-commercial subsistence harvest of halibut is available to rural Alaskan residents and Native Alaskans to supplement their food supply (https://alaskafisheries.noaa.gov/fisheries/subsistence-halibut). Halibut is an important part of the subsistence harvest, but as halibut abundance has declined since the mid-2000s, so too has halibut as part of the subsistence harvest. Halibut as part of the subsistence harvest has declined by roughly 30% since 2005, and this may increase the vulnerability of Alaskan communities to other economic shocks (Wise & Sparks, 2017). Our model simulations show how the subsistence harvest is sensitive to changes in food web dynamics and to changes in the partitioning of resources between fishing fleets under different effort scenarios (Table 6, and Supplemental Material Tables B12 and B13). Reduced longline fleet efforts (scenario E) allowed subsistence harvest to grow (4%) by taking a portion of the halibut and Pacific cod no longer caught by the longline fleets. However, increased effort by bottom trawl fleets (scenario F) resulted in a large reduction in subsistence landings (-16%) as fewer halibut and Pacific cod are available to local communities.

4.4 What are the consequences of prolonged or more frequent marine heatwave conditions?

Several mechanisms have been proposed by which changes in oceanographic conditions drive large-scale changes in community structure. Shifts in phytoplankton and zooplankton productivity lead to changes in the overall productivity of the ecosystem. Temperature-driven changes in metabolic rates lead to changes in foraging demands, tipping the balance between survival and growth of adult populations (e.g., Pacific cod; Barbeaux et al., 2017). Shifts in the seasonal timing of development and production among important zooplankton forage species (e.g., *Neocalanus* spp.) lead to changes in the recruitment dynamics of different taxa via match/mis-match between the timing of larval first-feeding and presence of appropriately-sized prey (Cushing, 1995; Anderson & Piatt, 1999). Changes in the proportion of primary production flowing to pelagic zooplankton vs. benthic invertebrate communities may lead to changes in the dominance of pelagic crustacean/forage fish communities and demersal groundfish communities (Hunt et al., 2002; Litzow, 2006).

Our heatwave simulation considers the impacts of large-scale changes in lower trophic food web structure, particularly changes in the relative scale of pelagic vs. benthic food chains. We did not consider the effects that changes in temperature would have on the metabolic demands of different species. This may explain why our heatwave simulation did not predict the observed crash of Pacific cod (Barbeaux et al., 2017). Our simulation was based upon three observed changes in the plankton community in 2015 and 2016: a reduction in the abundance of large diatoms relative to other phytoplankton (Batten 2017, 2018), an increase in mesozooplankton biomass (Batten 2017, 2018), and a decrease in euphausiid biomass (Hopcroft & Coyle, 2018). These changes had the general effect of enhancing pelagic food chains and reducing benthic food chains. Thus, pelagic fish benefited, but benthic invertebrates, groundfish, and the fishing fleets that exploit them suffered declines. The effect on adult halibut and arrowtooth were small compared to other groundfish stocks (-4% and -2%, respectively). Forage fish (walleye pollock, Pacific sand lance, capelin) are major components of arrowtooth and halibut diets, affording them insulation against reductions in euphausiid, shrimp, and benthic invertebrate production that other flatfish species lack. However, juvenile halibut are less piscivorous (Aydin et al., 2007) and more reliant upon shrimps and benthic invertebrates. Juvenile halibut were shown to suffer during the heatwave conditions as we defined them (-22%), and the adult stock would seem likely to also decline from reduced recruitment under prolonged heatwaves.

Physical exchange between the shelf and ocean may also affect the relative scale of pelagic and benthic food chains. Coupled ocean-ecosystem model simulations (Ruzicka et al., 2018) suggest that high productivity among upper trophic levels of the CGoA is a consequence of physical setting. Downwelling systems are more retentive with respect to particle export to the ocean than other systems (e.g., upwelling), allowing a greater fraction of plankton production to be consumed upon the shelf and increasing the overall efficiency of the food web. These simulations also show that in downwelling settings, a greater amount of detritus can be recycled back into the food web, enhancing benthic productivity. Following the 1976/77 shift in the PDO to a warm phase, the Bakun upwelling index anomalies indicated a strengthening of downwelling conditions (Hare & Mantua, 2000). Changes in particle residence time on the shelf with resultant changes in food web efficiency and the relative scales of benthic and pelagic food chains may be a contributing factor to the large changes in CGoA community structure after 1977. During this period groundfish populations, including halibut and arrowtooth, expanded greatly (Anderson & Piatt, 1999).

4.5 Comments on the capabilities of the ECOTRAN end-to-end model platform

ECOTRAN was originally developed to extend the capabilities of *Ecopath with Ecosim* models by providing for (1) direct coupling of mass-balanced food webs with physical models to account for the import and export of nutrients, detritus, and plankton to and from the model domain and (2) assessment of the consequences to all consumer groups of changes to the internal structure of the food web (Steele & Ruzicka, 2011). The central feature of an *ECOTRAN* model is the expression of the whole food web as a donor-driven trophic matrix (A_{cp}, eq. 1) describing the fate of all unassimilated consumption, excreta, and production of each group among all defined nutrient pools, detritus pools, and consumer groups. Trophic matrix A_{cp} can be derived directly from an *Ecopath* solution for the consumption rate of each consumer upon each producer; thus, the name *ECOTRAN* stands for "*Ecopath* transform" (Steele & Ruzicka, 2011). Expression of the food web as a matrix describing the fate of all production between consecutively higher trophic levels allows for inherently stable simulations of perturbation under linear and non-linear assumptions (Steele, 2009), direct coupling with physical models, and rapid assessment of the propagation of parameter uncertainty.

ECOTRAN shares the same basic capabilities and assumptions for modeling ecosystem processes and the impact of fishing pressure upon ecosystem dynamics as the *ATLANTIS* end-to-end modeling platform (Fulton et al., 2004) used in many NOAA ecosystem-based fisheries management studies (e.g., Horne et al., 2010; Link et al., 2010; Masi et al., 2017). Both platforms model the transfer of biomass as nitrogen through food webs of varying complexity, and both allow for the use of alternate predator-prey relationships. However, *ATLANTIS* accounts for the condition and age-structure of vertebrate groups (Audzijonyte et al., 2018) while *ECOTRAN* considers functional groups as biomass pools. As with *ATLANTIS*, *ECOTRAN* applications may be spatially resolved in 1, 2, or 3 dimensions and may be coupled with physical oceanographic models (e.g., ROMS) and lower trophic models (e.g., NPZD) of varying complexity (Ruzicka et al., 2016). As with *ATLANTIS*, *ECOTRAN* allows for seasonal and environmentally-driven changes in functional group physiologies. However, *ATLANTIS* is supplied with well-established protocols for modeling changes in physiological parameters based on temperature, salinity, hypoxia, ocean acidification, and biomass density.

A key objective shared by both platforms is flexibility, expandability, and provision of options for exploring ecological and management questions at different levels of complexity. The large community of *ATLANTIS* developers has produced a set of sub-models allowing for detailed evaluation of management actions and their impacts on costs and benefits to individual fleets, home ports, and communities (Fulton et al., 2011). However, while the benefits of highly complex and multi-faceted models like *ATLANTIS* are obvious, their complexity makes them challenging tools for performing "what if?" scenarios on short analysis time-scales, for performing comparative analyses across multiple ecosystems or climate conditions, or for use by small research teams. In this particular *ECOTRAN* application, we were interested in the rapid evaluation of large-scale changes to the CGoA ecosystem and fishing economy arising from prolonged, forced changes to food web structure and to fleet effort and bycatch rates. This did not require the use of *ECOTRAN* in its time-dynamic mode nor adaptive modification of fleet behavior in response to changes in the food web. We took advantage of one of the core strengths of *ECOTRAN*, the ability to run time-independent scenarios with consideration of parameter uncertainty, sparing us much effort in the development and running of an adaptive fleet model within physically coupled time-dynamic scenarios.

4.6 Conclusion

- Changes in arrowtooth abundance have larger effects upon the CGoA ecosystem than do changes in halibut abundance due to the much greater abundance of arrowtooth and the larger demand (footprint) they place upon ecosystem production. Both species are high trophic level consumers, and changes to the abundance of each directly affect few predators. Halibut are demersal feeders, and increased halibut abundance negatively impacted other demersal fish. Arrowtooth are water-column foragers and have the greatest impact upon pinnipeds and seabirds that are competitors for pelagic prey.

- Changes in effort among fleets harvesting halibut (the longline fleets) or arrowtooth (the C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets) had collateral effects upon both the ecosystem and upon other fishing fleets. Most of this impact was due to changes in bycatch rather than the removal of halibut or arrowtooth. To see this, compare scenarios C and D to scenarios E and F. High trophic level predators that compete with, or prey directly upon, halibut and arrowtooth (sharks, skates, pinnipeds, and odontocetes) were among the most sensitive groups. However, groups such as greenling/lingcod responded strongly as their prey (e.g., sculpins) were taken from the system at different rates as bycatch.

- Changes in fishing effort have relatively larger effects upon fishing economies than upon the CGoA ecosystem and are mostly caused by redistribution of available fish and crab production between different fleets. Reduction of longline fleet efforts to reduce halibut catch led to a reduction in the total value landed within the western and central CGoA but with increase to the value landed by sport fisheries, trawl fleets, jig, fish pot, and trawl fleets as they were able to exploit a greater share of the available halibut, sablefish, and Pacific cod. Increase in C/P and CV bottom trawl and CV pollock trawl fleet efforts to increase arrowtooth catch led to an increase in the total value landed within the CGoA but caused large reductions in the value landed by longline, jig, fish pot, subsistence, and sport fleets with greater competition for available Pacific cod, halibut, and sablefish. Fleets targeting pelagic fish, shrimp, and crab were insensitive to forced changes in longline and trawl fleet efforts.

- Subsistence harvest is sensitive to changes in both food web dynamics and changes in the partitioning of resources between fishing fleets. Decreased arrowtooth abundance leads to increased subsistence landings, driven by higher production among the halibut, Pacific cod, and sockeye salmon populations. Reduction of longline fleet efforts also allows subsistence harvest to grow by taking a greater portion of the available halibut and Pacific cod production. Increased trawl fleet effort, however, leads to a reduction in subsistence landings as more halibut and Pacific cod are removed from the system by commercial fleets.

- Large changes in plankton community composition associated changes in oceanographic conditions, such as the 2014-2016 marine heatwave, have broad impacts throughout the food web. Increased mesozooplankton production appear to enhance pelagic food chains at the expense of benthic food chains and groundfish stocks. Unlike other flatfish species, adult halibut and arrowtooth are insulated from this change because of the relatively high importance of pelagic fish in their diets. Juvenile halibut, however, were negatively impacted when euphausiid production was reduced.

Our approach has been to force defined changes in food web structure via manipulating fishery catch and plankton community composition to quantify the propagation and accumulation of effects to higher trophic levels and fishing fleets. A similar approach was taken by Gaichas et al. (2011) using *Ecopath-with-Ecosim* analyses to evaluate climate-driven changes to plankton production, fishing pressure, and predator-prey interactions as drivers of CGoA ecosystem change. A key goal of our work has been to develop a model framework that may be applied in future applications to consider in more detail physical processes as drivers of CGoA ecosystem dynamics. Thus, *CGoA-ECOTRAN* was constructed as a set of spatially-resolved food webs in a format readily allowing the food web to be coupled with ocean current and plankton production models (e.g., Ruzicka et al., 2018). Future applications of the model will consider physical exchange of nutrients, plankton, and detritus, and migration of larger organisms between sub-regions. We hope that this model, or models building upon *CGoA-ECOTRAN*, will prove useful in future applications to study both ecological and resource management questions.

ACKNOWLEDGMENTS

We would like to thank Tom Dean (Gulf Watch) and Tim Wootton (Univ. Chicago) for their large contributions to the intertidal food web components of the CGoA model. Jean Lee (Pacific States Marine Fisheries Commission) ran our queries of the AKFIN database for ex-vessel prices. The map was prepared by Susan Ruzicka (USFS). This work resulted from the Coastal Gulf of Alaska's Working Group conducted at the National Center for Ecological Analysis and Synthesis, a Center funded by the University of California, Santa Barbara, and the State of California. J. Ruzicka and the development of ECOTRAN was supported by NSF project 1259057.

CONFLICTS OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

J.J.R.: model construction and analyses. S.K.: economic data and scenario design. S.Z.: project concept and scenario design. A.H.-C.: interpretation of social impacts and subsistence fishing effects. J.J.R., S.K., S.Z., A.H.-C.: interpretation of results and manuscript writing and editing.

REFERENCES

Anderson, P.J. & Piatt, J.F. (1999). Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series*, 189, 117-123.

ASMI (2017). The economic value of Alaska's seafood industry. Alaska Seafood Marketing Institute. Prepared by McDowell Group. 38 p. Retrieved from http://www.mcdowellgroup.net/publications/

Audzijonyte, A., Gorton, R., Kaplan, I., & Fulton, E. A. (2018). Atlantis User's Guide Part I: General Overview, Physics & Ecology. *CSIRO*, 223 p. Retrieved from https://research.csiro.au/atlantis/home/links/.

Aydin, K., Gaichas, S., Ortiz, I., Kinzey, D., & Friday, N. (2007). A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. *NOAA Technical Memorandum NMFS-AFSC-178*, 298 p.

Barbeaux, S. Aydin, K., Fissel, B. Palsson, W., Shotwell, K., Yang, Q., Zador, S. (2017). Assessment of the Pacific cod stock in the Gulf of Alaska. In: *Stock Assessment and Fishery Evaluation Report for Groundfish Resources of the Gulf of Alaska*. Prepared by the Gulf of Alaska Groundfish Plan Team, North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK. 144pp.

Batten, S. (2017). Zooplankton. Continuous plankton recorder data from the Northeast Pacific: Lower Trophic Levels in 2016. In S. Zador, & E, Yasumiishi (Eds.), *Ecosystem considerations 2017: status of the Gulf of Alaska marine ecosystem* (pp. 80-83). North Pacific Fishery Management Council, Anchorage, AK, Retrieved from https://www.afsc.noaa.gov/refm/stocks/plan_team/2017/ecosysGOA.pdf

Batten, S. (2018). Zooplankton. Continuous plankton recorder data from the Northeast Pacific through 2017. In S. Zador, & E, Yasumiishi (Eds.), *Ecosystem Status Report 2018: Gulf of Alaska* (pp.65-66). North Pacific Fishery Management Council, Anchorage, AK, Retrieved from https://www.afsc.noaa.gov/refm/stocks/plan_team/2018/ecosysGOA.pdf

Bond, N.A., Cronin, M.F., Freeland, H., & Mantua, N. (2015). Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophysical Research Letters*, 42, 3414–3420.

Christensen, V., & Walters, C. J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling,* 172, 109-139.

Clark. W. G. (1992). Validation of the IPHC length-weight relationship for halibut. In International Pacific Halibut Commission, *Report of Research and Assessment Activities 1991* (pp. 113-116).

Collie, J. S., Gifford, D. J., & Steele, J. H. (2009). End-to-end foodweb control of fish production on Georges Bank. *ICES Journal of Marine Science*, 66, 2223-2232.

Coyle, K. O., Gibson, G. A., Hedstrom, K., Hermann, A. J., & Hopcroft, R. R. (2013). Zooplankton biomass, advection and production on the northern Gulf of Alaska shelf from simulations and field observations. *Journal of Marine Systems*, 128, 185-207.

Cushing D (1995). Population production and regulation in the sea: a fisheries perspective. Cambridge University Press, Cambridge.

Fissel, B., Dalton, M., Garber-Yonts, B., Haynie, A., Kasperski, S., Lee, J., Lew, D., Lavoie, A., Seung, C., Sparks, K., & Wise, S. (2017). Stock assessment and fishery evaluation report for the groundfish fisheries of the Gulf of Alaska and Bering Sea/Aleutian Islands area: economic status of the groundfish fisheries off Alaska, 2016. *NPFMC Economic SAFE*, 412 p. Retrieved from https://www.afsc.noaa.gov/REFM/Docs/2017/economic.pdf

Ford, G. R., Bonnell, M. L., Varoujean, D. H., Page, G. W., Carter, H. R., Sharp, B. E., Heinemann, D., & Casey, J. L. (1996). Total direct mortality of seabirds from the Exxon Valdez oil spill. In S. D. Rice, R. B. Spies, D. A. Wolfe, & B. A. Wright (Eds.) *Proceedings of the Exxon Valdez oil spill symposium. American Fisheries Society Symposium*, 18, 684-711.

Fulton, E. A., Link, J. S., Kaplan, I. C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R. J., Smith, A. D. M., & Smith, D. C. (2011). Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and Fisheries*, 12, 171–188.

Fulton, E., Smith, A., & Johnson, C. (2004). Biogeochemical systems models I: IGBEM – a model of marine bay ecosystems. *Ecological Modelling*, 174, 267–307.

Gaichas, S. K., Aydin, K., & Francis, R. (2011). What drives dynamics in the Gulf of Alaska? Integrating hypotheses of species, fishing, and climate relationships using ecosystem modeling. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 1553-1578.

Hare, S. R., & Mantua, N. J. (2000). Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, 47, 103e145.

Hirst, A. G., Roff, J. C., & Lampitt, R. S. (2003). A synthesis of growth rates in marine epipelagic invertebrate zooplankton. *Advances in Marine Biology*, 44, 1-142.

Hollowed, A. B., Ianelli, J. N., & Livingston, P. A. (2000). Including predation mortality in stock assessments: A case study involving Gulf of Alaska walleye pollock. *ICES Journal of Marine Science*, 57, 279-293

Hopcroft, R.R. & Coyle, K.O. (2018). May large copepod and euphausiid biomass along the Seward Line. In S. Zador, & E, Yasumiishi (Eds.), *Ecosystem considerations 2017: status of the Gulf of Alaska marine ecosystem* (pp. 66-67). North Pacific Fishery Management Council, Anchorage, AK, Retrieved from https://www.afsc.noaa.gov/refm/stocks/plan_team/2017/ecosysGOA.pdf

Horne, P. J., Kaplan, I. C., Marshall, K. N., Levin, P. S., Harvey, C. J., Hermann, A. J., & Fulton, E.A. (2010). Design and parameterization of a spatially explicit ecosystem model of the central California Current. *NOAA Technical Memorandum NMFS-NWFSC-104*, 155 p.

Hunt, G. L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R. D., Napp, J. M., & Bond, N. A. (2002). Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 49, 5821-5853.

IPHC (2014). The Pacific halibut: biology, fishery, and management. International Pacific Halibut Commission. *Technical Report No. 59*, 60 p.

IPHC (2015). Annual Report 2015. International Pacific Halibut Commission. 98 p.

IPHC (2018). Assessment of the Pacific halibut (*Hippoglossus stenolepis*) stock at the end of 2017. International Pacific Halibut Commission. *IPHC-2018-AM094-10*, 25 p.

Kang, I., & Lanier, T. C. (2005). Inhibition of protease in intact fish fillets by soaking in or injection of recombinant soy cystatin or bovine plasma. *Journal of Agricultural and Food Chemistry*, 53, 9795-9799.

Kasperski, S. (2016). Optimal multispecies harvesting in the presence of a nuisance species. *Marine Policy*, 64, 55-63.

Knoth, B. A., & Foy, R. J. (2008). Temporal variability in the food habits of arrowtooth flounder (*Atheresthes stomias*) in the Western Gulf of Alaska. *NOAA Technical Memorandum NMFS-AFSC-184*, 30 p.

Link, J. S., Fulton, E. A., & Gamble, R. J. (2010). The north-east US application of ATLANTIS: a full system model exploring marine ecosystem dynamics in a living marine resource context. *Progress in Oceanography*, 87, 214-234.

Litzow, M.A. (2006). Climate regime shifts and community reorganization in the Gulf of Alaska: how do recent shifts compare with 1976/1977. *ICES Journal of Marine Science,* 63, 1386–1396.

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, 78, 1069–1079.

Masi, M. D., Ainsworth, C. H, & Jones, D. L. (2017). Using a Gulf of Mexico Atlantis model to evaluate ecological indicators for sensitivity to fishing mortality and robustness to observation error. *Ecological Indicators*, 74, 516–525.

Peña, M. A., Nemcek, N. and Robert, M. (2018). Phytoplankton responses to the 2014–2016 warming anomaly in the northeast subarctic Pacific Ocean. *Limnology and Oceanography*, doi:10.1002/lno.11056.

Robinson, K. L., Ruzicka, J. J., Hernandez, F. J., Graham, W. M., Decker, M. B., Brodeur, R. D., & Sutor, M. (2015). Evaluating energy flows through jellyfish and gulf menhaden (*Brevoortia patronus*) and the effects of fishing on the northern Gulf of Mexico ecosystem. *ICES Journal of Marine Science*, 72, 2301-2312. doi:10.1093/icesjms/fsv088.

Ruzicka, J. J., Brodeur, R. D., Emmett, R. L., Steele, J. H., Zamon, J. H., Morgan, C. A., Thomas, A. C., & Wainwright, T. C. (2012). Interannual variability in the Northern California Current food web structure: changes in energy flow pathways and an End-to-End model to investigate system response to alternate forcing scenarios. *Progress in Oceanography*, 102, 19-41.

Ruzicka, J. J., Brink, K. H., Gifford, D. J., & Bahr, F. (2016). An intermediate complexity, physically coupled end-to-end model platform for coastal ecosystems: simulating the effects of changing upwelling conditions on the Northern California Current ecosystem. *Ecological Modelling*, 331, 86-99.

Ruzicka, J.J., Steele, J.S., Brink, K.H., Gifford, D.J., & Bahr, F. (2018). Understanding large-scale energy flows through end-to-end shelf ecosystems - the importance of physical context. *Journal of Marine Systems*, 187, 235-249

Sinclair, E. H., Johnson, D. S., Zeppelin, T. K., & Gelatt, T. S. (2013). Decadal variation in the diet of Western Stock Steller sea lions (*Eumetopias jubatus*). *NOAA Technical Memorandum NMFS-AFSC-248*, 67 p.

Spies, I., Ianelli, J. N., Kingham, A., Narita, R., & Palsson, W. (2015). Assessment of the arrowtooth flounder stock in the Gulf of Alaska. *NPFMC Gulf of Alaska SAFE*, Retrieved from http://www.afsc.noaa.gov/REFM/Stocks/assessments.htm

Spies, I., Aydin, K., Ianelli, J. N., & Palsson, W. (2017). Assessment of the arrowtooth flounder stock in the Gulf of Alaska. *NPFMC Gulf of Alaska SAFE*, Retrieved from https://www.afsc.noaa.gov/REFM/Docs/2017/GOAatf.pdf

Stabeno, P. J., Bond, N. A., Hermann, A. J., Kachel, N. B., Mordy, C. W., & Overland, J. E. (2004). Meteorology and oceanography of the northern Gulf of Alaska. *Continental Shelf Research*, 24, 859–897.

Steele, J. H. (2009). Assessment of some linear food web methods. *Journal of Marine Systems*, 76, 186–194.

Steele, J. H., & Ruzicka, J. J. (2011). Constructing end-to-end models using ECOPATH data. *Journal of Marine Systems*, 87, 227-238.

Treasure, A., Ruzicka, J., Moloney, C., Gurney, L., & Ansorge, I. (2015). Land-sea interactions and consequences for sub-Antarctic marine food webs. *Ecosystems*, 18, 752-768

Treasure, A. Ruzicka, J.J., Pakhomov, E.A., & Ansorge, I.J. (2018). Physical transport mechanisms driving sub-Antarctic island marine ecosystems. *Ecosystems* https://doi.org/10.1007/s10021-018-0326-

Wise, S. P., & Sparks, K. (2017). Halibut and salmon subsistence trends in the Gulf of Alaska. In S. Zador, & E, Yasumiishi (Eds.), *Ecosystem considerations 2017: status of the Gulf of Alaska marine ecosystem* (pp. 183-186). North Pacific Fishery Management Council, Anchorage, AK, Retrieved from https://www.afsc.noaa.gov/refm/stocks/plan_team/2017/ecosysGOA.pdf

Yang, M-S., Dodd, K., Hibpshman, R., & Whitehouse, A. (2006). Food habits of groundfishes in the Gulf of Alaska in 1999 and 2001. *NOAA Technical Memorandom NMFS-AFSC-164*, 199 p.

Zador, S., & Yasumiishi, E. (2017). Ecosystem considerations 2017: status of the Gulf of Alaska marine ecosystem. 213 p. North Pacific Fishery Management Council, Anchorage, AK, Retrieved from https://www.afsc.noaa.gov/refm/stocks/plan_team/2017/ecosysGOA.pdf.

Zador, S. G., Gaichas, S. K., Kasperski, S., Ward, C. L., Blake, R. E., Ban, N. C., Himes-Cornell, A., & Koehn, J.Z. (2017). Linking ecosystem processes to communities of practice through commercially fished species in the Gulf of Alaska. *ICES Journal of Marine Science*, 74, 2024–2033.

SUPPLEMENTARY MATERIALS

Model parameters and citations to data sources used in model construction may be found online in the Supplementary Materials section at the end of the article. The ECOTRAN model code is available online at the NSF Biological and Chemical Oceanography Data Management Office (https://www.bco-dmo.org/dataset/546765). Please contact corresponding author J.J.R. for possible code updates.

TABLES

Table 1. Summary of model scenario design.

Scenario Set 1: What effects do adult halibut and arrowtooth have upon the CGoA food web structure? - Simulate changes to halibut and arrowtooth abundance.		
A	halibut abundance	Halibut abundance increased by 20%
B	arrowtooth abundance	Arrowtooth abundance decreased by 20%
Scenario Set 2: What effects do changes in fishing mortality of halibut and arrowtooth have upon the CGoA ecosystem and fishing economy? - Changes made to fishing ***mortality*** (landings + discards) of arrowtooth and halibut in the most important commercial fleets for each species. No other targeted or bycatch groups were altered. Fishing mortality of arrowtooth was *increased* within the C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets. Fishing mortality of halibut was *decreased* within the targeted halibut longline and non-halibut targeted longline fleets.		
C	halibut fishing mortality	Halibut landings and discards within the targeted halibut longline and non-halibut targeted longline fleets decreased by 90% so that halibut fishing mortality matches arrowtooth mortality in the base model.
D	arrowtooth fishing mortality	Arrowtooth landings and discards within the C/P bottom trawl, CV

		bottom trawl, and CV pollock trawl fleets increased 10-fold so that arrowtooth fishing mortality matches halibut mortality in the base model.
Scenario Set 3: What effects do changes in fishing effort and bycatch by the fleets targeting halibut and arrowtooth have upon the CGoA ecosystem and fishing economy? - Changes made to fishing ***effort*** by the C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets (major arrowtooth harvesters) and by the targeted halibut longline and non-halibut targeted longline fleets (major halibut harvesters). Landings and discards of all targeted and bycatch groups within these fleets were also altered.		
E	halibut fishing effort	Effort by the targeted halibut longline and non-halibut targeted longline fleets decreased by 90% so that halibut fishing mortality matches arrowtooth fishing mortality in the base model.
F	arrowtooth fishing effort	Effort by the C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets increased by 10-fold so that arrowtooth fishing mortality matches halibut fishing mortality in the base model.
Scenario Set 4: What effects would prolonged or more frequent heatwave conditions have upon halibut and arrowtooth stocks, the CGoA ecosystem, and the fishing economy? - Changes made to simulate the phytoplankton size class distribution, mesozooplankton biomass, and euphausiid biomass observed during the 2014-2016 marine heatwave.		
G	heatwave simulation	Large diatom biomass was reduced by 50%, but small phytoplankton biomass was increased by 20% to maintain constant primary production. Mesozooplankton biomass was increased by 250%. Euphausiid biomass fell spontaneously as a result of forced changes to phytoplankton and mesozooplankton, so a reduction was not forced.

Table 2. Mean annual landings and discards (t y^{-1}) of Pacific halibut and arrowtooth flounder by groundfish fleets, sport fisheries, and subsistence take. Values represent mean annual rates from 2006 - 2015 within the full CGoA model domain.

	Pacific halibut		arrowtooth flounder	
	landings (t y^{-1})	discards (t y^{-1})	landings (t y^{-1})	discards (t y^{-1})
C/P bottom trawl	0	395	6,640	3,935
CV bottom trawl	75	717	8,392	2,214
CV pollock trawl	47	370	2,189	431
halibut longline	7,443	7,348	43	89
non-halibut longline	993	129	11	92

recreation	969	557	0	0
halibut sport charter	1,436	825	0	0
subsistence	129	0	0	0
all others	250	33	9	6

Table 3. A comparison of the size of the CGoA Pacific halibut and arrowtooth flounder populations and importance of predation and fishery mortality rates (as percentages of production rates). Values are the means (and coefficient of variation) of 1000 random food webs.

	inner shelf	mid shelf		outer shelf	
		east	west	east	west
Pacific halibut					
biomass (t)	59,318 (0.92)	93,641 (0.75)	57,011 (0.95)	23,265 (0.97)	18,846 (0.89)
production (t y^{-1})	11,270 (0.92)	17,792 (0.75)	10,832 (0.95)	4,420 (0.97)	3,581 (0.89)
predation (%)	48% (0.84)	59% (0.77)	57% (0.83)	58% (0.80)	50% (0.87)
fisheries (%)	44% (0.88)	44% (0.83)	46% (0.86)	49% (0.96)	43% (0.89)
arrowtooth flounder					
biomass (t)	750,369 (0.72)	552,600 (0.79)	583,977 (0.73)	182,471 (0.72)	59,054 (0.75)
production (t y^{-1})	195,096 (0.72)	143,676 (0.79)	151,834 (0.73)	47,442 (0.72)	15,354 (0.75)
predation (%)	28% (1.02)	20% (1.19)	23% (1.13)	23% (1.06)	33% (0.98)
fisheries (%)	6% (1.50)	6% (1.29)	6% (1.34)	6% (1.26)	5% (1.17)

Table 4. Food web and fishery fleet responses to a 20% increase in Pacific halibut biomass and responses to a 20% decrease in arrowtooth flounder biomass (scenarios A and B). Food web responses show the ten largest changes for each scenario. Responses shown are for the entire model domain, pooling inner, mid, and outer sub-regions. Relative change in biomass B, or landings L, is calculated as $\Delta B = (B_{scenario} - B_{base}) / B_{base}$. Values are the means (and coefficient of variation) of 1000 random food webs, and negative changes are highlighted in gray.

Scenario A: Pacific halibut biomass increased by 20%		Scenario B: arrowtooth biomass decreased by 20%	
food web response	change (ΔB)	food web response	change (ΔB)
greenling/lingcod	-2.7% (1.0)	mammal - resident seals	7.4% (0.7)
large sculpins	-2.2% (1.0)	sleeper shark	-5.4% (1.0)
big skate	-1.4% (1.2)	big skate	-5.4% (1.0)
mammal - Steller sea lion	-0.9% (1.2)	Pacific halibut	5.2% (0.6)

Pacific cod	-0.9% (0.6)	mammal - northern fur seal	4.8% (0.5)
mammal - resident seals	-0.7% (1.2)	mammal - northern fur seal (juvenile)	4.6% (0.5)
mammal - Steller sea lion (juvenile)	-0.7% (1.3)	greenling/lingcod	4.3% (0.9)
other skates	-0.7% (0.9)	mammal - steller sea lion	4.2% (1.2)
salmon - Chinook	-0.6% (1.7)	nearshore seabird - marbled murrelet	4.1% (0.8)
salmon shark	0.6% (1.4)	seabird - cormorants	3.9% (0.8)
fleet response	change (ΔL)	fleet response	change (ΔL)
C/P bottom trawl	-1.9% (1.3)	C/P bottom trawl	-2.9% (1.3)
CV bottom trawl	-1.4% (0.9)	CV bottom trawl	2.9% (2.0)
CV pollock trawl	-1.5% (0.9)	CV pollock trawl	7.4% (1.0)
halibut longline	6.9% (0.5)	halibut longline	7.3% (0.5)
non-halibut longline	1.3% (1.4)	non-halibut longline	6.3% (0.7)
jig	-1.2% (0.8)	jig	11.2% (0.6)
fish pot	-0.7% (1.6)	fish pot	10.8% (0.6)
salmon commercial	0.0% (1.2)	salmon commercial	1.0% (0.8)
herring sac roe	-1.1% (2.1)	herring sac roe	4.3% (1.0)
crab pot	-4.9% (1.0)	crab pot	0.2% (1.2)
shrimp trawl & pot	0.0% (0.8)	shrimp trawl & pot	2.8% (0.8)
urchin & cucumber dive fleet	-0.1% (1.5)	urchin & cucumber dive fleet	0.7% (1.5)
subsistence	1.8% (1.5)	subsistence	4.2% (0.8)
recreation	7.7% (0.5)	recreation	4.2% (0.7)
halibut sport charter	19.9% (0.0)	halibut sport charter	7.5% (0.7)

Table 5. Food web responses to targeted fishing mortality scenarios (bycatch not changed) showing five groups with the largest change before and after changes to landings + discards. Scenario C: Pacific halibut mortality reduced in targeted halibut longline and non-halibut targeted longline fleets. Scenario D: arrowtooth flounder mortality reduced in the C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets. Responses shown are for the entire model domain, pooling sub-regions, and are listed in order of decreasing magnitude. Relative change in biomass is calculated as $\Delta B = (B_{scenario} - B_{base}) / B_{base}$. Values are the means (and coefficient of variation) of 1000 random food webs, and negative changes are highlighted in gray.

Scenario C: A 90% reduction in halibut fishing mortality via decreased landings + discards by targeted halibut longline and non-halibut longline fleets

food web response	base biomass (t)	scenario biomass (t)	relative change (Δ*B*)
sleeper shark	37,535 (0.6)	37,960 (0.6)	1.3% (1.2)
salmon shark	42,326 (0.4)	42,812 (0.4)	1.2% (0.9)
longnose skate	36,406 (0.5)	36,749 (0.5)	1.0% (1.1)
mammal - resident killer whales	316 (0.5)	318 (0.5)	0.6% (1.1)
mammal - steller sea lion	2,501 (0.7)	2,509 (0.7)	0.4% (1.1)

Scenario D: A 10-fold increase in arrowtooth fishing mortality via increased landings + discards by C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets

food web response	base biomass (t)	scenario biomass (t)	relative change (Δ*B*)
sleeper shark	37,004 (0.6)	25,543 (0.5)	-26.3% (0.7)
big skate	23,352 (0.7)	17,193 (0.7)	-22.6% (0.9)
longnose skate	36,729 (0.5)	27,450 (0.4)	-22.0% (0.7)
mammal - resident killer whales	322 (0.5)	272 (0.5)	-14.6% (0.8)
mammal - Steller sea lion	2,561 (0.6)	2,340 (0.6)	-9.0% (0.9)

Table 6. Food web and fishery fleet responses to fishing effort scenarios (bycatch is changed) showing five living groups and five fleets with the largest change before and after changes to fishing effort. Scenario E: reduced effort by the targeted halibut longline and non-halibut longline fleets. Scenario F: increased effort by the C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleets. Responses shown are for the entire model domain, pooling sub-regions, and are listed in order of decreasing magnitude. Relative change in biomass, or landings, are calculated as $\Delta B = (B_{scenario} - B_{base}) / B_{base}$. Values are the means (and coefficient of variation) of 1000 random food webs, and negative changes are highlighted in gray. Forced changes are not shown.

Effort scenario E: A 90% reduction in halibut fishing mortality via decreased targeted halibut longline and non-halibut longline fleet ***effort***

food web response	base biomass (t)	scenario biomass (t)	relative change (Δ*B*)
salmon shark	43,075 (0.4)	44,084 (0.4)	2.4% (0.6)
mammal - sperm & beaked whales	8,838 (0.8)	8,976 (0.8)	2.0% (1.7)
mammal - Steller sea lion	2,568 (0.5)	2,611 (0.5)	1.8% (1.3)
greenling/lingcod	16,157 (0.7)	16,410 (0.7)	1.5% (1.8)
longnose skate	37,381 (0.5)	37,885 (0.5)	1.4% (0.9)

fleet response	base landings (t)	scenario landings (t)	relative change (ΔL)
halibut sport charter	1,514 (1.0)	2,000 (1.0)	31.7% (0.6)
recreation	2,619 (1.0)	2,968 (0.9)	14.1% (0.8)
jig	1,403 (0.8)	1,618 (0.8)	13.3% (0.6)
fish pot	11,327 (0.7)	12,862 (0.7)	13.1% (0.5)
subsistence	1,367 (0.9)	1,413 (0.9)	3.7% (1.7)

Effort scenario F: A 10-fold increase in arrowtooth fishing mortality via increased C/P bottom trawl, CV bottom trawl, and CV pollock trawl fleet ***effort***

food web response	base biomass (t)	scenario biomass (t)	relative change (ΔB)
sleeper shark	37,316 (0.6)	20,459 (0.5)	-40.7% (0.4)
longnose skate	36,982 (0.5)	22,722 (0.4)	-35.0% (0.4)
greenling/lingcod	16,035 (0.6)	10,794 (0.6)	-29.4% (0.6)
mammal - Steller sea lion	2,525 (0.5)	1,752 (0.5)	-28.3% (0.5)
mammal - resident killer whales	317 (0.4)	224 (0.4)	-27.4% (0.5)

fleet response	base landings (t)	scenario landings (t)	relative change (ΔL)
jig	1,440 (0.8)	220 (1.3)	-81.8% (0.2)
fish pot	11,397 (0.7)	2,245 (1.1)	-77.0% (0.2)
non-halibut longline	11,699 (0.7)	4,477 (0.8)	-59.4% (0.3)
halibut longline	17,941 (0.6)	7,527 (0.6)	-56.6% (0.2)
recreation	2,533 (0.7)	1,516 (1.0)	-41.5% (0.4)

1036
1037

Table 7. Total gross ex-vessel landed value following each scenario for the full CGoA model domain. Heavy shading highlights changes > 10% relative to the base, unaltered model. Light shading highlights changes > 5%. Green indicates positive changes, red indicates negative changes. Forced changes are not highlighted.

		fish abundance scenarios		fishing ***mortality*** scenarios		fishing ***effort*** scenarios		heatwave
	base model‡	A	B	C	D	E	F	G
C/P bottom trawl	$15,908,537	$15,641,370	$15,802,023	$16,607,903	§ $27,951,961	$19,262,052	§ $83,681,169	$15,178,441
CV bottom trawl	$33,656,850	$33,355,983	$35,260,845	$34,288,118	§ $49,798,504	$40,034,901	§ $213,103,629	$29,743,528
CV pollock trawl	$30,165,451	$29,847,583	$30,900,347	$28,178,360	§ $33,360,922	$32,139,917	§ $185,225,430	$23,235,245
halibut longline	$95,484,540	$106,731,485	$93,685,284	§ $41,139,225	$92,345,428	§ $10,179,096	$53,271,591	$85,512,516
non-halibut longline	$54,351,122	$55,848,911	$53,808,234	§ $46,676,148	$58,471,389	§ $5,688,255	$30,355,521	$46,975,854
jig	$1,178,817	$1,173,845	$1,318,996	$1,225,891	$1,180,248	$1,508,765	$202,907	$1,102,504
fish pot	$13,021,325	$13,323,410	$13,696,468	$13,383,901	$13,081,941	$16,619,709	$3,801,432	$12,499,903
salmon commercial	$82,877,226	$82,844,526	$90,277,908	$87,107,629	$83,713,000	$94,450,072	$90,801,837	$78,245,578
herring sac roe	$4,324,935	$4,314,494	$4,543,386	$4,412,525	$3,939,855	$4,034,772	$4,449,750	$5,740,371
crab pot	$2,664,356	$2,500,225	$2,729,473	$2,713,038	$2,435,666	$2,732,662	$3,074,077	$1,763,319
shrimp trawl & pot	$6,687	$6,685	$7,070	$6,595	$6,689	$7,132	$6,517	$4,801
urchin divers	$54,718	$54,698	$51,327	$52,822	$51,898	$41,776	$59,015	$50,667
subsistence†	NA	NA	NA	NA	NA	NA	NA	NA
recreation	$11,583,253	$13,355,814	$11,643,208	$13,279,806	$11,339,727	$14,461,256	$7,121,915	$11,024,200
halibut sport charter	$12,838,835	$15,397,397	$13,298,769	$15,585,334	$12,432,789	$17,587,869	$7,054,820	$12,000,474
TOTAL	$358,116,651	$374,396,426	$367,023,337	$304,657,295	$390,110,019	$258,748,234	$682,209,609	$323,077,401

† Assumed for personal use. No monetary value assigned.

‡ Mean value of 1000 models randomly generated for each scenario. Mean baseline values shown are for scenario A and will change slightly for each scenario.

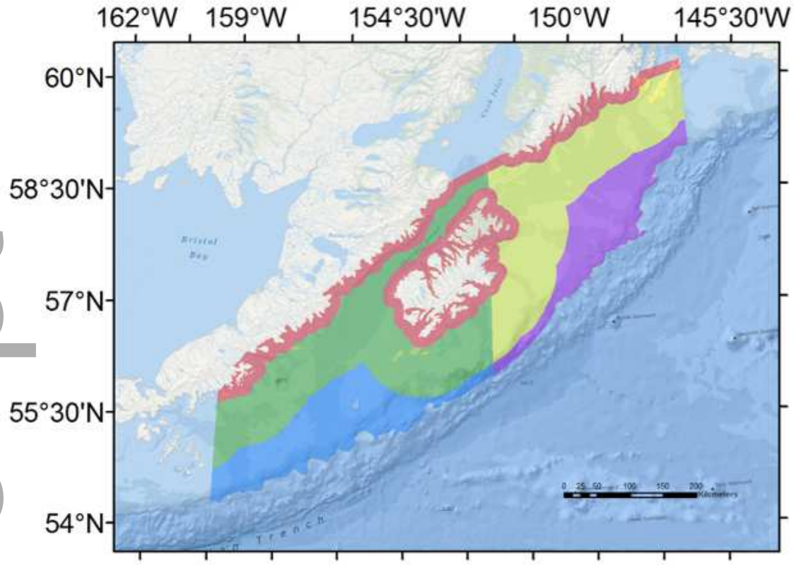
§ Forced change in scenario

1045

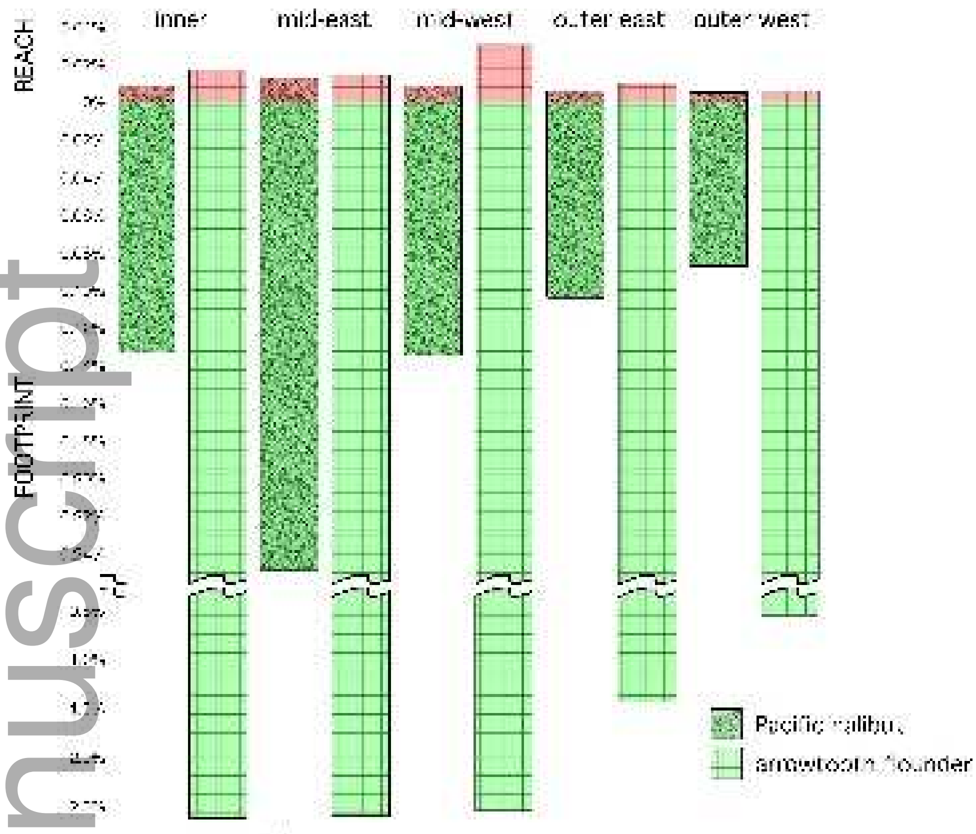
Table 8. Food web and fishery fleet responses to a simulated plankton community during the 2014-2016 heatwave conditions (scenario G). Food web responses show the ten groups with the largest changes. Responses shown are for the entire model domain, pooling inner, mid, and outer sub-regions. Relative change in biomass B, or landings L, is calculated as $\Delta B = (B_{scenario} - B_{base}) / B_{base}$. Values are the means (and coefficient of variation) of 1000 random food webs, and negative changes are highlighted in gray. Forced changes are not shown.

Scenario G: heatwave plankton community simulation. Large diatoms decreased by 50%, small phytoplankton increased by 20%, mesozooplankton increased by 150%

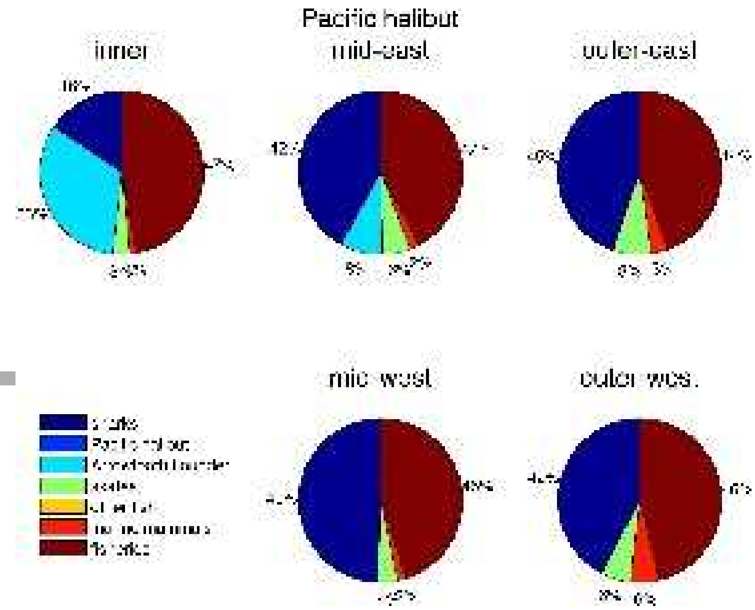
food web response	change (ΔB)	fleet response	change (ΔL)
mammal - right whales	65.6% (0.3)	C/P bottom trawl	-4.9% (3.9)
mammal - sei whales	54.7% (0.4)	CV bottom trawl	-9.6% (1.9)
euphausiids	-44.3% (0.3)	CV pollock trawl	-12.4% (1.6)
other pelagic smelt	44.1% (0.5)	halibut longline	-7.3% (2.1)
eulachon	43.1% (0.5)	non-halibut longline	-8.3% (1.9)
capelin	42.1% (0.5)	jig	-6.9% (2.7)
mysids	-41.4% (0.5)	fish pot	-6.7% (2.8)
shelf benthos - bivalves	-41.0% (0.4)	salmon commercial	-13.2% (1.9)
other macrozooplankton	-40.6% (0.5)	herring sac roe	38.0% (0.9)
Alaska plaice	-40.3% (0.6)	crab pot	-32.7% (0.5)
		shrimp trawl & pot	-26.4% (0.6)
		urchin & cucumber dive fleet	-7.0% (1.0)
		subsistence	0.4% (65)
		recreation	-1.4% (15)



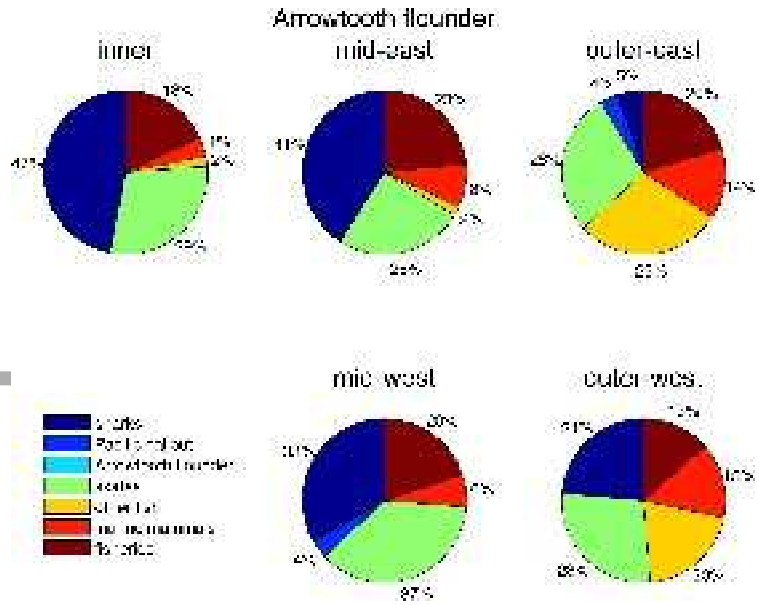
fog_12431_f1.tif



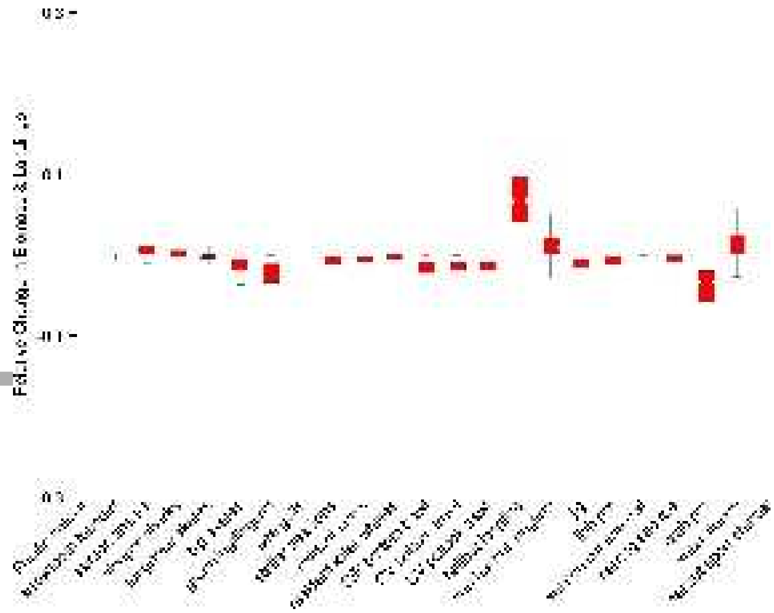
fog_12431_f2.tif



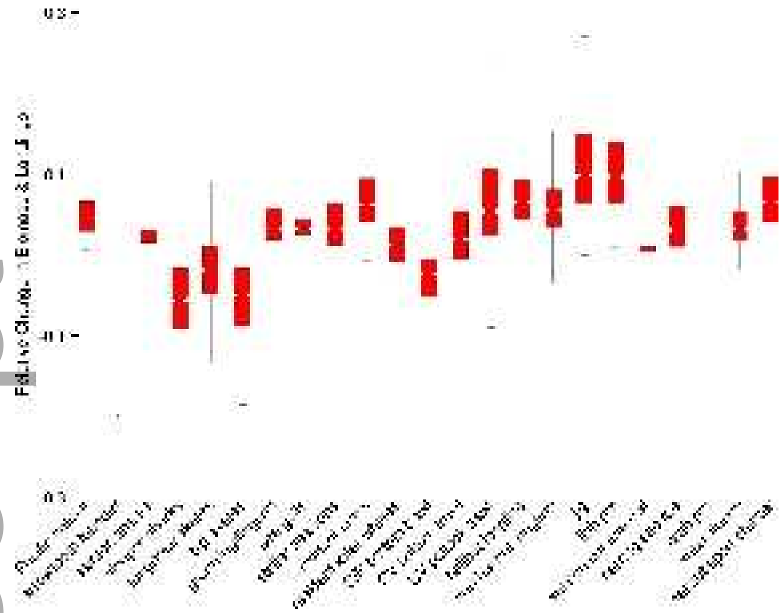
fog_12431_f3.tif



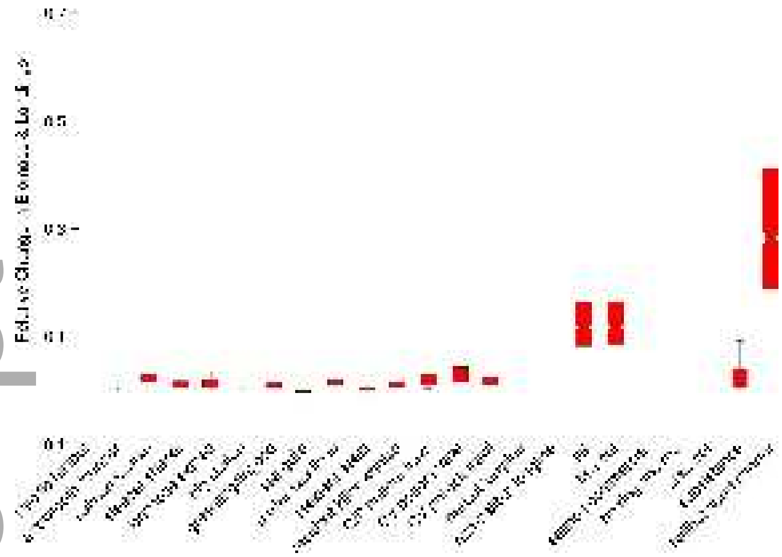
fog_12431_f4.tif



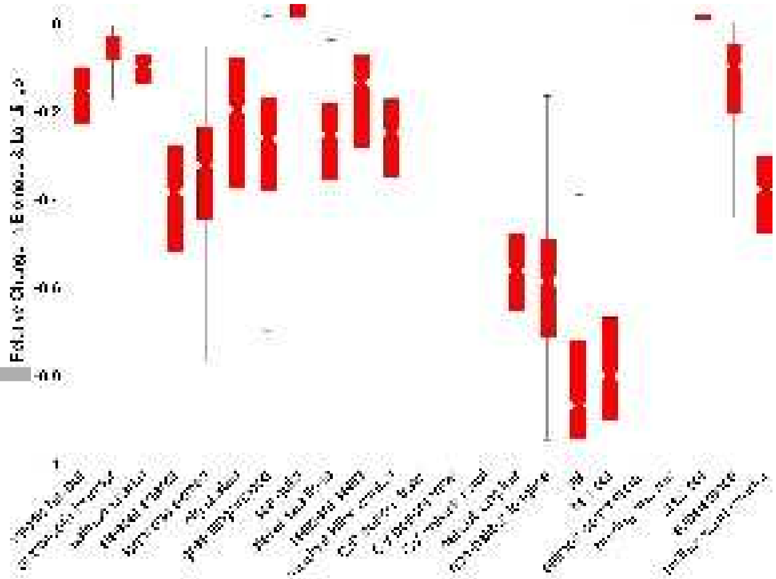
fog_12431_f5.tif



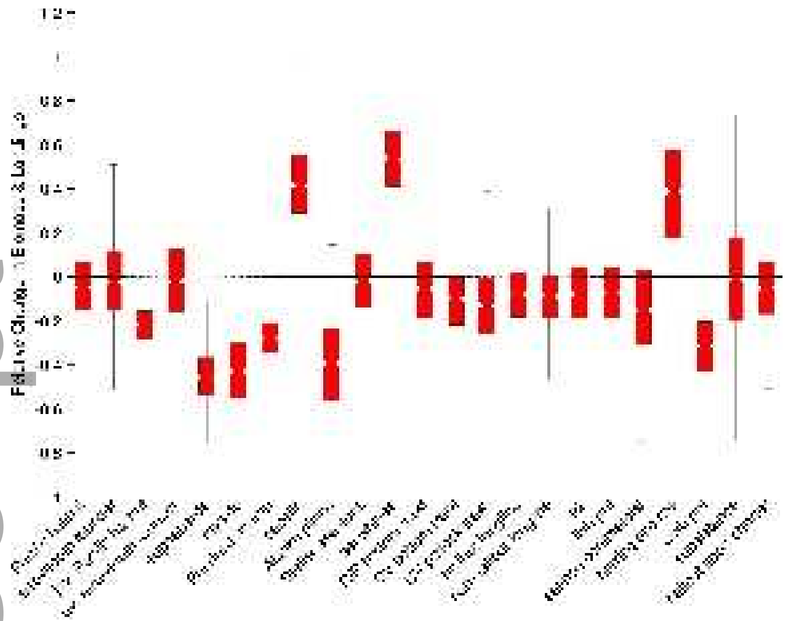
fog_12431_f6.tif



fog_12431_f7.tif



fog_12431_f8.tif



fog_12431_f9.tif