Original Article

Examining the ecological role of jellyfish in the Eastern Bering Sea

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Within the Eastern Bering Sea, the jellyfish *Chrysaora melanaster* has fluctuated widely over recent decades. We examined the role of *C. melanaster* as an ecosystem-structuring agent via application of ecosystem models representing inner-, mid-, and outer-shelf regions of comparable areal coverage. *Chrysaora melanaster* utilize 1% of total mid-shelf consumer production, or 1/4th the energy required by forage fish (capelin *Mallotus villosus*, Pacific herring *Clupea pallasii*, age-0 Pacific cod *Gadus macrocephalus*, age-0 walleye pollock *Gadus chalcogrammus*). Model simulations show the impacts of *C. melanaster* are broadly distributed across consumer groups with increasingly negative impacts with higher jellyfish biomass. Age-0 pollock represent the greater part of the forage fish biomass, and observed pollock biomass during low jellyfish years (2004–2007) was significantly greater than during high jellyfish years (2009–2014). However, sensitivity among consumer groups to observed jellyfish variability is small, within 5% of baseline (2004–2015) conditions. Estimates using similar models for the Coastal Gulf of Alaska (CGoA) and Northern California Current (NCC) suggest large differences in the role of scyphozoans among northern Pacific shelf ecosystems. Only 0.1% of total summer consumer production is required to support CGoA *Chrysaora*, while the coastal NCC population uses 19%.

Keywords: *Chrysaora melanaster*, competition, Eastern Bering Sea, ecosystem modelling, forage fish, jellyfish, scyphomedusae, zooplankton

Introduction

The Eastern Bering Sea (EBS) is a biologically productive and economically valuable ecosystem, supporting rich populations of zooplankton, forage fish, groundfish, crabs, seabirds, and marine mammals. The EBS ecosystem also supports large populations of jellyfish (scyphomedusae, primarily *Chrysaora melanaster*, and hydromedusae), which have fluctuated greatly over the past four decades (Decker *et al.*, 2014). A steep increase in jellyfish biomass was documented over the EBS shelf by NOAA's RACE groundfish survey through the 1990s, peaking in 2000 (Brodeur *et al.*, 2002; Brodeur *et al.*, 2008a; Decker *et al.*, 2014). The onset of *Chrysaora* expansion during the 1990s, decline after 2000, and expansion after 2007 coincided with transitions from cool (expansion) to warm (decline) climatic regimes (Brodeur *et al.*, 2008a; Decker *et al.*, 2014).

Scyphozoan jellyfish have characteristics that place them in an influential position for structuring energy flow through pelagic food webs, such as high growth and reproduction rates, broad planktivorous diets, and relatively few apparent predators (Richardson *et al.*, 2009). Though jellyfish may benefit some fish species by providing juveniles a safe habitat from predators among their tentacles (Brodeur, 1998), jellyfish are important consumers of zooplankton and can significantly redirect energy flow through food webs when their abundance is high (Deason and Smayda, 1982; Suchman *et al.*, 2008; Condon *et al.*, 2012). Field and modelling studies in other ecosystems indicate that jellyfish can negatively impact fisheries because they compete with zooplanktivorous fish, prey upon fish eggs and larvae, and indirectly compete with higher trophic levels by reducing plankton available to planktivores (Brodeur *et al.*, 2008b; Shoji *et al.*, 2009; Brodeur *et al.*, 2011; Ruzicka *et al.*, 2012; Schnedler-Meyer *et al.*, 2016; D'Ambra *et al.*, 2018; Tilves *et al.*, 2018).

Despite their high abundance levels, there is limited understanding of how gelatinous predators affect energy flow through
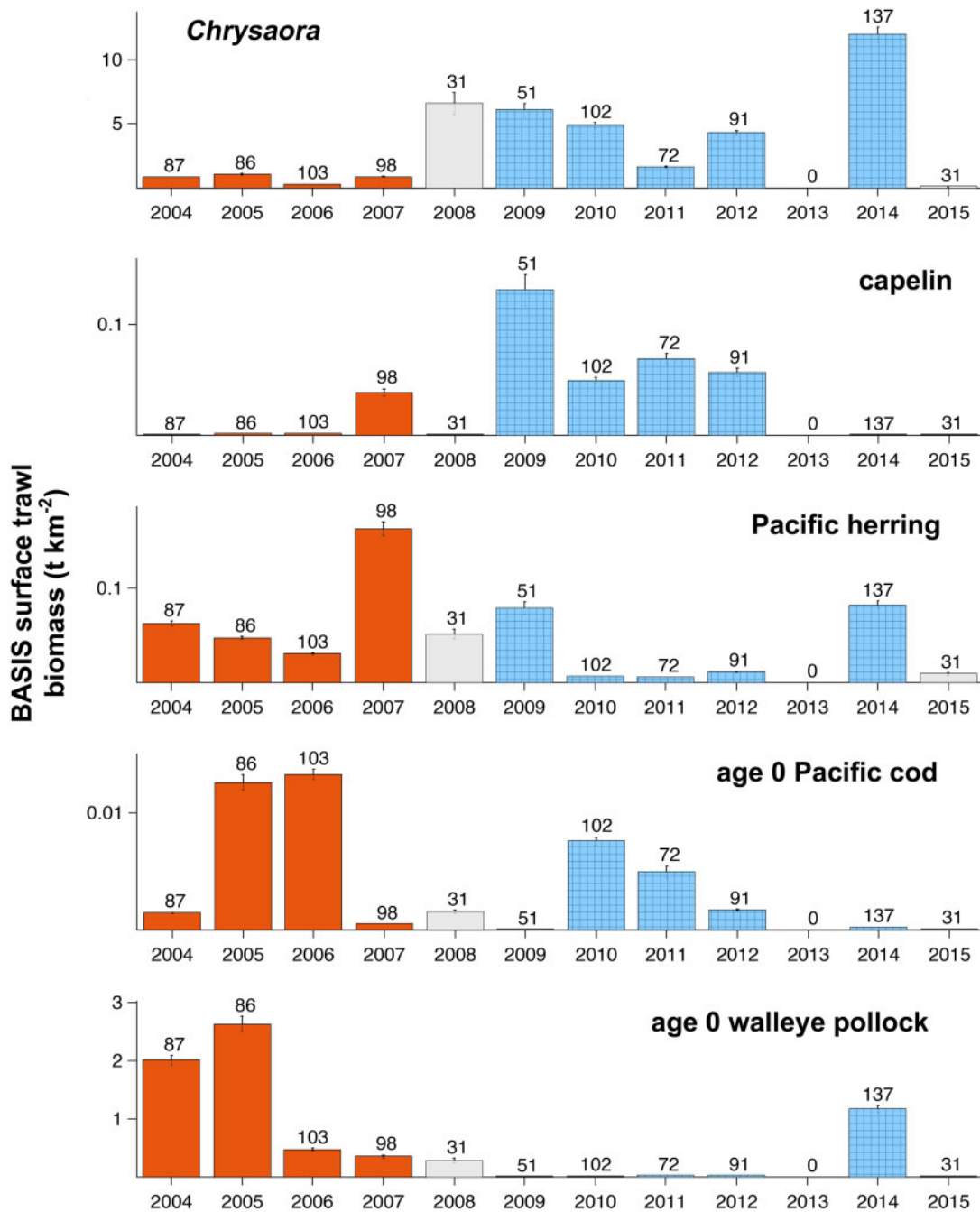
Figure 1. Biomass of *C. melanaster*, capelin, Pacific herring, age-0 Pacific cod, and age-0 walleye pollock in the EBS south of 60°N, derived from the late summer/early fall BASIS surface trawl survey. Blue, cross-hatched bars represent high *Chrysaora* years as used in model analyses. Red bars represent low *Chrysaora* years. Error bars represent ±1 CV (coefficient of variation) of all trawls. Numbers above error bars represent the number of trawls. No corrections were made in this figure to account for differences in water content of *Chrysaora* and fish.

the EBS ecosystem and how commercially important fish may be impacted. Due to their high abundance and spatial overlap, there is a potential for jellyfish, especially *C. melanaster*, to negatively impact commercially important fish through direct predation or through competition for plankton prey (Decker *et al.*, 2018). The biomass time series of the most abundant EBS forage fish (age-0 walleye pollock and Pacific herring) appear to be the inverse of *Chrysaora* (Figure 1; Brodeur *et al.*, 2002; Decker *et al.*, 2018). In other ecosystems where the spatial overlap between jellyfish and

fish eggs and larvae is high, predation by jellyfish on early life stages and competition for plankton may be important factors regulating the dynamics of commercially or ecologically important fish species (Brodeur *et al.*, 2008b; Eriksen *et al.*, 2012; Robinson *et al.*, 2015; Chiaverano *et al.*, 2018). Lynam *et al.* (2005a) found negative relationships between jellyfish abundance and herring recruitment in the North Sea, suggesting a negative impact of jellyfish. Ruzicka *et al.* (2016a) noted negative relationships between *Chrysaora fuscescens* biomass along the
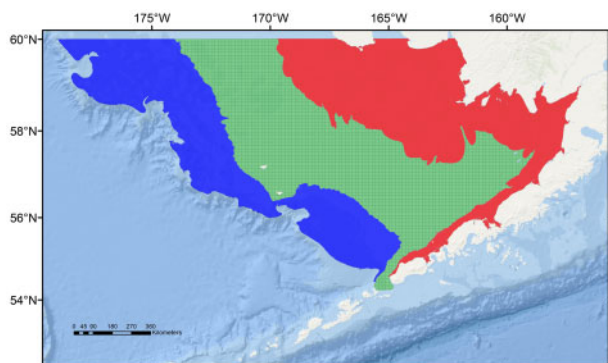
Washington coast, feeding incidence of juvenile salmon, and subsequent adult salmon returns to the Columbia River system.

Because jellyfish populations fluctuate widely in the Bering Sea (Decker *et al.*, 2014) and jellyfish have a documented potential to affect the dynamics of fish stocks in other ecosystems (e.g. Lynam *et al.*, 2005a, b; Ruzicka *et al.*, 2016a), an understanding of the trophic roles of gelatinous predators is required for the successful management of not only the EBS ecosystem but of marine ecosystems in general. The overarching goals of this research were to examine the role of jellyfish in the EBS as an ecosystem-structuring agent by estimating the scale and impact of competition with forage fish for plankton prey and by estimating the importance of jellyfish predation upon fish eggs and larvae. We integrate observed diet and community biomass data within an end-to-end trophic model framework (Steele and Ruzicka, 2011), *EBS-ECOTRAN*, to estimate grazing pressure of *C. melanaster* upon zooplankton production and the effect this grazing pressure has on the rest of the ecosystem. We apply the model to identify important energy transfer nodes within the food web, evaluate the importance of jellyfish as consumers, and compare ecosystem states during periods of low and high jellyfish biomass. We use the model to conduct simulation analyses to estimate the impact of jellyfish blooms upon other components of the ecosystem. Using similarly structured ecosystem models, we compare the role of the dominant large scyphozoan jellyfish in other northeast Pacific shelf ecosystems.

Methods
Ecosystem model
The EBS end-to-end model suite (*EBS-ECOTRAN*) describes food webs for three shelf zones south of 60°N (Figure 2): the inner shelf (between the 0 and 50 m isobaths, 120 034 km^2), the mid-shelf (51–100 m, 212 359 km^2), and the outer shelf (101–200 m, 134 209 km^2). Details about model construction and the parameters for each sub-region are provided as Supplementary data. Each model describes >6000 trophic connections between planktonic (2 phytoplankton size classes) and benthic primary producers (1 macroalga group), zooplankton (10 groups), gelatinous zooplankton (4 groups), micronekton (3 groups), pelagic fishes and squids (26 groups), benthic invertebrates (22 groups), groundfish (38 groups), seabirds (10 groups), marine mammals (20 groups), fishing fleets (20 fleets), planktonic eggs (2 pools), detritus (3 pools), and nutrients (3 nitrogen pools). The cross-shelf model suite represents the 2004–2015 period. Two additional mid-shelf models were developed from community composition and diet observations made during contrasting low (2004–2007) and high (2009–2014) *Chrysaora* biomass periods. Scyphozoan jellyfish biomass used in each model was scaled so that a unit of jellyfish biomass had approximately the same water content as that of fish (Shenker, 1985; Ruzicka *et al.*, 2012).
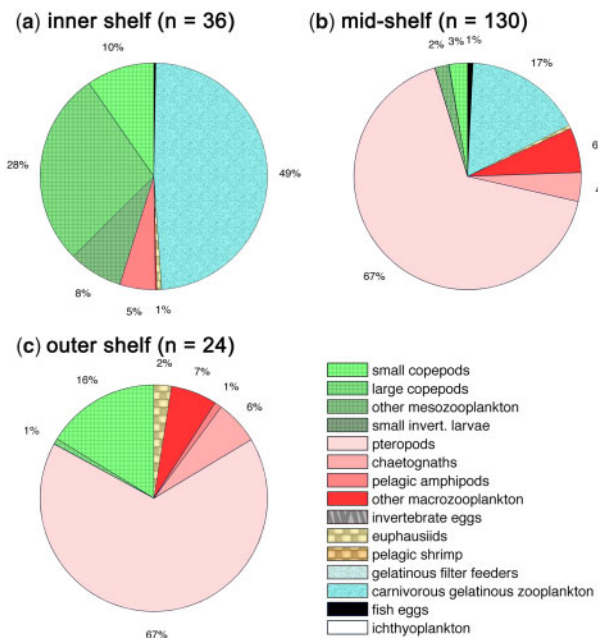
EBS-ECOTRAN builds upon an earlier ECOPATH model representing the EBS food web during the 1990s (Aydin *et al.*, 2007). Zooplankton biomass time series for each shelf sub-region were estimated from bongo and juday net sampling during the NOAA AFSC Bering Arctic Subarctic Integrated Survey (BASIS) and provided by L. Eisner (NOAA AFSC; Eisner *et al.*, 2014). Forage fish, jellyfish, and juvenile salmon biomasses were also estimated from the BASIS pelagic survey. BASIS surveys are conducted annually in late summer/early fall (August to October; Parker-Stetter *et al.*, 2013) and show that *Chrysaora* biomass was low through 2007, high through 2014, but declined again in 2015 (Figure 1).

Groundfish and benthic invertebrate biomass densities were estimated from the annual AFSC Resource Assessment and Conservation Engineering (RACE) Division bottom trawl survey (Conner and Lauth, 2016; http://www.afsc.noaa.gov/RACE/groundfish/survey_data/). For both surveys, species were aggregated into functional groups, and the mean trawl biomass of each group was calculated for each shelf sub-region using the method of Pennington (1996) for log-normally distributed data that include zero-catch stations. Adult salmon run size and salmon harvest data were obtained from Alaska Department of Fish and Game Finfish Management Reports (www.adfg.alaska.gov) for management areas overlapping the *EBS-ECOTRAN* model domain. Adult and juvenile groundfish diet information was obtained from the AFSC Resource Ecology and Ecosystem Modeling (REEM) Groundfish Trophic Interactions Database (https://www.fisheries.noaa.gov/resource/data/alaska-groundfish-diet-data). Diet information for pelagic fishes (forage fishes and juvenile salmon) was obtained from the BASIS survey database. Jellyfish diet information was obtained from BASIS cruises in 2014–2016 (Figure 3; see Supplementary data). Seabird and marine mammal abundances and diets were taken from the 1990s ECOPATH model (Aydin *et al.*, 2007) as were most harvest and discard rates for non-salmon fisheries. Zooplankton physiological rates were defined based upon size and temperature relationships established for different trophic groups in Hirst *et al.* (2003). Physiological rates for fish, seabirds, and mammals were taken from Aydin *et al.* (2007).

The EBS end-to-end model was constructed and analysed within the *ECOTRAN* platform to investigate the ecosystem-wide effects of changing jellyfish abundances and consumption demands. *ECOTRAN* models are based on a simple mathematical transformation that converts the demand-driven, linear solutions for the consumption rate of each consumer group upon each predator group, as may be calculated by ECOPATH food web modelling software (Christensen and Walters 2004; www.ECOPATH.org), into donor-driven maps of production fate through the food web (Steele, 2009; Steele and Ruzicka, 2011):

$$A_{cp} = \frac{D_{pc}q_c}{\sum_c D_{pc}q_c}, \tag{1}$$

where A_{cp} = the trophic network matrix defining the fraction of the total production of each producer p consumed by each

Figure 2. Three sub-regions of the EBS ecosystem model suite: inner shelf, 0–50 m isobaths (red); mid-shelf, 50–100 m (green, cross-hatched); and outer shelf, 100–200 m (blue).

Figure 3. Diet composition by percent weight of *C. melanaster* on the (a) inner, (b) mid-, and (c) outer EBS shelf south of 60°N as sampled during BASIS pelagic surveys in 2014–2016.

consumer *c*, matrix D_{pc} is the fraction of each producer *p* within the diet of each consumer *c*, q_c is the total consumption rate of consumer *c*, and term $\sum_c D_{pc} q_c$ is the total grazing or predation rate upon each producer *p* by all consumers *c*. The food web model is expanded into an end-to-end model representing all trophic flows from nutrients to fishery harvest by including nutrient pools as explicitly defined producer groups and accounting nutrient recycling via microbial metabolism of detritus and consumer metabolism. A model expressed in this format can readily be used to quantify the consequences of changes to community composition (Robinson *et al.*, 2015), changes in nutrient subsidies (Treasure *et al.*, 2015), changes in oceanographic regime through coupling with physical models (Ruzicka *et al.*, 2016b), changes in fishery management policy (Ruzicka *et al.*, 2019), or physiological or diet changes to any functional group.

Model analyses—metrics and simulations

The demands of *C. melanaster* upon EBS ecosystem production and their contribution to higher trophic levels are expressed with model-derived footprint and reach metrics (detailed in Ruzicka *et al.*, 2012). The footprint represents the fraction of total consumer production within the ecosystem supporting a specific group. The footprint is calculated as the summed fraction of production by each consumer contributing to the group's production, whether across one or several trophic steps, divided by the total production of all consumers (excluding micrograzers). 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 (excluding micrograzers) that originates with, or passes through, a specific group and flows throughout the food web via all direct and indirect pathways. Footprint and reach metrics exclude losses from non-assimilated consumption and metabolism. Footprint and reach

metrics for multiple consumer classes are compared between cross-shelf zones and between mid-shelf food webs representing low (2004–2007) and high (2009–2014) *Chrysaora* biomass periods. We also compare the role of *Chrysaora* to other planktivores as predators of zooplankton and the early life-history stages of fish. The relative predation pressures of different consumers upon a specific producer are estimated directly from trophic network matrix (A_{cp}).

Two model scenarios were run to investigate the EBS ecosystem's response to changes in the abundance of *C. melanaster*. These scenarios simulate the effects of low and high *Chrysaora* biomass as observed during the low jellyfish and high jellyfish periods relative to average conditions over the 2004–2015 period (Figure 1). Scenarios were run within each shelf sub-region. During the low jellyfish period, *Chrysaora* biomasses within the inner-, mid-, and outer-shelf models were scaled down by factors of 0.15, 0.19, and 0.85, respectively. During the high jellyfish period, *Chrysaora* biomasses were scaled up by factors of 1.68, 1.65, and 1.12. In each scenario, the importance of *Chrysaora* was modified by changing the fraction of the production of each prey group that was consumed by *Chrysaora*. This was offset by an opposite change in the predation pressure by all other consumers competing with *Chrysaora* for each prey group. Thus, each scenario represents a redistribution of available resources and we assume that the total predation pressure upon prey group was unchanged. We also assumed that changes in energy flow to competing consumers for each prey group were proportional to their original relative importance as consumers.

The effects of a scenario are evaluated by comparing changes in the production rates of individual groups under scenario conditions to the production under baseline conditions, where the baseline model represents mean 2004–2015 conditions:

$$\Delta P = (P_{scenario} - P_{base})/P_{base}. \tag{2}$$

Scenario results are presented for the full shelf, where the effect upon each sub-region is weighted by its geographic area. Modelled changes in production are compared to observed changes in forage fish and juvenile salmon biomasses. Inter-annual differences in biomasses observed by the BASIS pelagic survey during the low and high *Chrysaora* periods are evaluated by one-sided Wilcoxon rank-sum test (Gibbons and Chakraborti, 2011).

An accounting of the propagation of uncertainty across trophic linkages is necessary to provide a confidence index about predation indices and model scenarios. Alternate potential food webs were generated by randomly drawing from a defined normal distribution about each trophic linkage in matrix A_{cp} and re-normalizing each generated matrix so that, for every group, the fate of all production is accounted for and predation pressure does not exceed production for any producer. As each element of matrix A_{cp} is a function of defined physiological, diet, predation and fishing mortality rate, senescence or natural mortality rate, population growth, and emigration terms, the uncertainty of each element of matrix A_{cp} is a function of the defined uncertainty levels about each of these parameters. For every group, we assumed that the level of uncertainty about each physiological parameter (assimilation efficiency, metabolism, gamete production) is ±25%, uncertainty about each diet element is ±50%, and uncertainty about the relative importance of predation vs. senescence rates is ±50%. Population growth and emigration terms, and

their uncertainties, were defined as zero. Predation indices and scenario results were estimated from 1000 randomly generated models and reported with an error range of ± 1 coefficient of variation.

Comparison of *Chrysaora's* trophic role in different ecosystems

We compared the role of *Chrysaora* spp. in three different shelf ecosystems using similarly constructed *ECOTRAN* models for the EBS (Figure 2), the Coastal Gulf of Alaska (*CGoA-ECOTRAN*, Figure 4a, Ruzicka *et al.*, 2019), and the Northern California Current (*NCC-ECOTRAN*, Figure 4b, Ruzicka *et al.*, 2012). Each model was constructed using survey data from approximately the same period. In each ecosystem, *Chrysaora* is the dominant large jellyfish, though the species differ. *Chrysaora melanaster* is dominant in the EBS, and *C. fuscescens* is dominant in the Coastal Gulf of Alaska and the NCC. The demands of *Chrysaora* upon production within each ecosystem and their contribution to higher trophic levels are expressed with model-derived footprint and reach metrics.
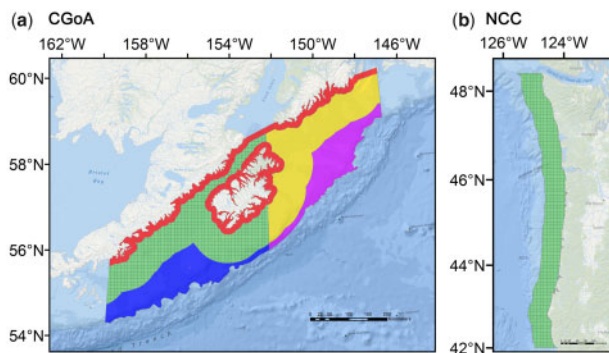
Figure 4. (a) Sub-regions of the Coastal Gulf of Alaska ecosystem model (*CGoA-ECOTRAN*): inner shelf (0–15 km from coastline and Kodiak Island, red), eastern and western mid-shelf (16–90 km from coastline; yellow and green, respectively), eastern and western outer shelf (region encompassing all RACE stations beyond 91 km from the coastline; purple and blue, respectively). East and west sub-regions are divided at 152.32°W. (b) Domain of the NCC ecosystem model (*NCC-ECOTRAN*) represents the full shelf from the coastline to the upper slope approximately 50 km from the coastline. Sub-regions used for ecosystem comparisons of footprint and reach metrics are indicated by green cross-hatching.

Results

Chrysaora as a predator

Model-derived estimates of biomasses, consumption rates, and production rates for *Chrysaora* and the four major EBS forage fish groups (capelin, Pacific herring, age-0 Pacific cod, age-0 walleye pollock) are compared in Table 1 (estimates for other groups are provided as extended results in Supplementary Tables S1 and S2). *Chrysaora* have a much higher consumption to biomass ratio than forage fishes ($48\,y^{-1}$ vs. $8.4\,y^{-1}$ for age-0 pollock; parameter q/b in Supplementary Table A3; Aydin *et al.*, 2007), yet within every sub-region, forage fish were the more important consumer because of their greater biomass and consumption demand. Over the 2004–2015 period, the mid-shelf forage fish population consumed nearly five times as much as do the jellyfish. During the high *Chrysaora* period (2009–2014), the forage fish consumption rate was still more than twice that of the jellyfish.

From our diet observations made during late summer BASIS cruises (2014–2016), the major prey of *Chrysaora* is copepods and other small crustacean zooplankton, pteropods, chaetognaths, and other gelatinous zooplankton (Figure 3). To estimate the importance of *Chrysaora* as a predator upon specific groups, we applied the observed inner-, mid-, and outer-shelf diets across all time periods. The relative importance of different predators upon major plankton groups is shown in Figure 5 (see also extended results in Supplementary Table S3). *Chrysaora* are not among the most important predators of copepods and other crustacean zooplankton, even during the high jellyfish period (Figure 5a), but they can become important predators of other specific groups when abundant. Notably, they are among the most important predators of pteropods (Figure 5b) during both low and high jellyfish biomass periods. During the high jellyfish period (2009–2014), *Chrysaora* are of comparable importance to fish as predators of copepods, other crustacean zooplankton, and gelatinous zooplankton.

Fish eggs were not a large part of the *Chrysaora* diet in our observations, accounting for a maximum of only 0.8% of the diet by weight on the mid-shelf. As predators of the early life-history stages of fish, *Chrysaora* were less important predators than zooplankton, gelatinous zooplankton, or micronekton (euphausiids and pelagic shrimps). But in the high jellyfish period, *Chrysaora* became moderately important predators of fish eggs and were more important than fish themselves (Figure 5c). Ichthyoplankton were very rarely observed in the BASIS *Chrysaora* diets, and *Chrysaora*

Table 1. A comparison of the size of EBS *Chrysaora* and forage fish (capelin, Pacific herring, age-0 Pacific cod, age-0 walleye pollock) biomasses, consumption rates, and production rates.

	Inner shelf	Mid-shelf			Outer shelf
	Base (2004–2015)	Base (2004–2015)	Low *Chrysaora* (2004–2007)	High *Chrysaora* (2009–2014)	Base (2004–2015)
Chrysaora					
Biomass (t)	0.35 (0.89)	0.63 (0.84)	0.12 (0.84)	1.06 (0.64)	0.02 (1.01)
Consumption (t km^{-2}y^{-1})	16.7 (0.89)	30.0 (0.84)	5.89 (0.84)	50.9 (0.64)	0.78 (1.01)
Production (t km^{-2} y^{-1})	4.17 (0.89)	7.50 (0.84)	1.47 (0.84)	12.7 (0.64)	0.20 (1.01)
Forage fish					
Biomass (t)	24.6 (0.50)	21.4 (0.51)	24.4 (0.50)	17.7 (0.50)	10.9 (0.50)
Consumption (t km^{-2} y^{-1})	159 (0.51)	142 (0.52)	159 (0.51)	119 (0.52)	90.1 (0.50)
Production (t km^{-2} y^{-1})	28.6 (0.51)	25.6 (0.52)	28.5 (0.51)	21.5 (0.52)	115.6 (0.50)

Values are the means [and coefficient of variation (CV)] of 1 000 randomly generated models using defined levels of uncertainty for all model parameters.

were not an important predator of ichthyoplankton during any model period.

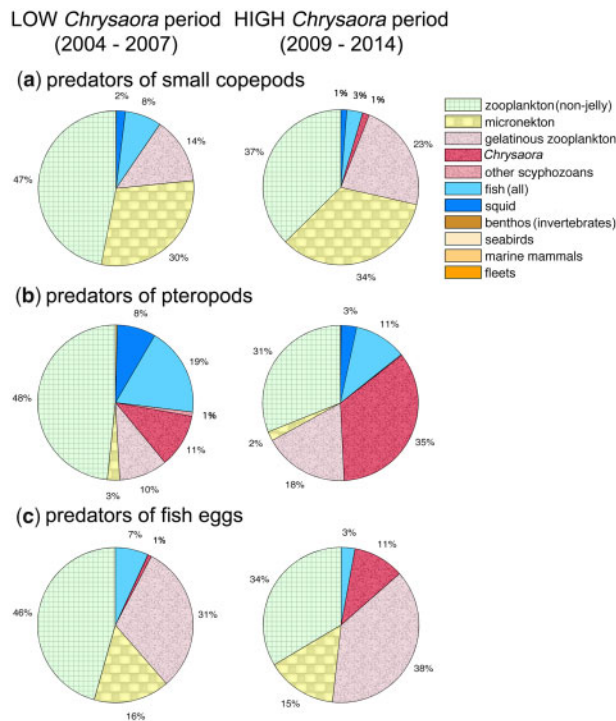## *Chrysaora* as energy transfer nodes—footprint and reach metrics

The footprint and reach metrics for several groups in the different sub-regions across the EBS shelf are provided in Table 2 and shown graphically in Figure 6. The footprint represents the fraction of total consumer production within the ecosystem supporting a specific group's production, via direct predation and indirect trophic transfer. *Chrysaora* exert their largest footprint upon the mid-shelf ecosystem where they are estimated to utilize

Figure 5. The relative importance of each predator class that prey directly upon (a) small copepods, (b) pteropods, and (c) fish eggs during the low and the high *Chrysaora* biomass periods.

a little over 1% of the total consumer production. The four main forage fish groups together use four times as much of the total consumer production on the mid-shelf (5.1%) as *Chrysaora*. However, the *Chrysaora* footprint on the mid-shelf ecosystem is still substantial. It is much greater than that of seabirds (0.04%), marine mammals (0.2%), and salt-water fisheries (0.1%), and it is more than half that of adult groundfish (1.8%).

The reach represents the contribution of a specific group to total consumer production within the ecosystem. Reach metrics are much smaller than footprint metrics. Only a small proportion of any group's production actually supports higher trophic levels. For all fish, the reach is just under 3% of their footprint across the whole shelf. For *Chrysaora*, the reach is only 0.1% of their footprint within the inner- and mid-shelf sub-regions (compare reach/footprint ratios in Table 2). Over the outer shelf, a greater proportion of *Chrysaora* production is consumed, giving them a reach/footprint metric similar to forage fish (1.3% and 1.1%, respectively). However, the *Chrysaora* footprint on the outer shelf is only 1/40th that on the mid-shelf, and in absolute terms *Chrysaora* contribute very little to the productivity of the outer-shelf ecosystem (reach = 0.0004%).

The importance of *Chrysaora* as a consumer changes greatly across years (Figure 7, see also extended results in Supplementary Table S4). During the low biomass period (2004–2007), *Chrysaroa* used only 0.3% of the total consumer production within the mid-shelf ecosystem. During the high biomass period (2009–2014), *Chrysaroa* used five times more of the available ecosystem production (footprint = 1.5%). All other fish, seabird, mammal, and fishery groups showed the opposite pattern. Forage fish used more than twice the available ecosystem resources during the low jellyfish period as they did during the high jellyfish period (footprint = 8.0% vs. 3.2%, respectively). While the relative contribution of forage fish to the total consumer production within the mid-shelf ecosystem was higher during the low *Chrysaroa* period (reach = 0.08% vs. 0.04% during low vs. high *Chrysaora* periods, respectively), their reach/footprint ratios were similar between the two periods (1.0% and 1.1%). A sevenfold greater proportion of *Chrysaora* production was passed along to higher trophic-level consumers during the low than the high *Chrysaora* periods (0.64% vs. 0.09%, respectively). However, the relative contribution of *Chrysaora* to total ecosystem productivity was low in both periods.

Table 2. Summer footprint and reach metrics for different consumer classes across the EBS shelf.

Group	EBS inner shelf (%)			EBS mid-shelf (%)			EBS outer shelf (%)		
	footprint	reach	reach/footprint	footprint	reach	reach/footprint	footprint	reach	reach/footprint
Chrysaora	0.503	0.001	0.146	1.184	0.002	0.136	0.029	0.000	1.316
Forage fish[a]	4.386	0.030	0.686	5.133	0.054	1.061	3.674	0.041	1.106
Squid	0.225	0.002	0.734	2.427	0.028	1.166	4.185	0.047	1.124
Pelagic fish[b]	2.600	0.045	1.750	4.149	0.109	2.635	7.410	0.216	2.917
Groundfish[b]	1.268	0.059	4.618	1.843	0.059	3.204	2.183	0.048	2.197
Seabirds	0.036	0.000	0.003	0.040	0.000	0.012	0.046	0.000	0.004
Mammals	0.143	0.000	0.005	0.192	0.000	0.004	0.551	0.000	0.001
Fisheries	0.045	0.000	0.000	0.141	0.000	0.000	0.288	0.000	0.000

Footprint = fraction of total consumer production within the ecosystem supporting the group's production (via direct and indirect trophic pathways). Reach = fraction of total consumer production within the ecosystem that originates with (or passes through) the group.
[a]Capelin, Pacific herring, age-0 Pacific cod, and age-0 walleye pollock.
[b]Excludes juvenile fish, Myctophidae, and Bathylagidae.
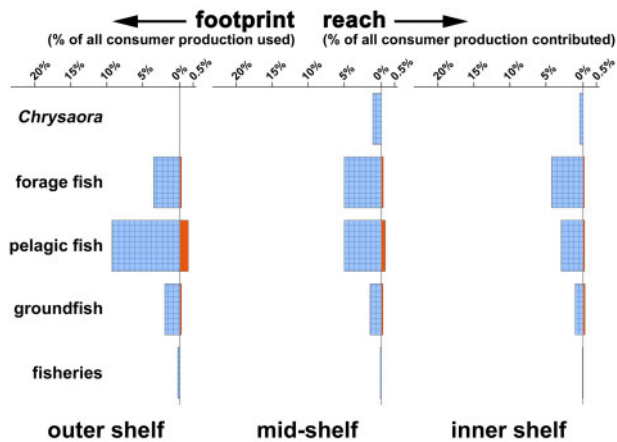
Figure 6. Footprint (blue, cross-hatched) and reach (red) metrics for several functional groups within the inner-, mid-, and outer-shelf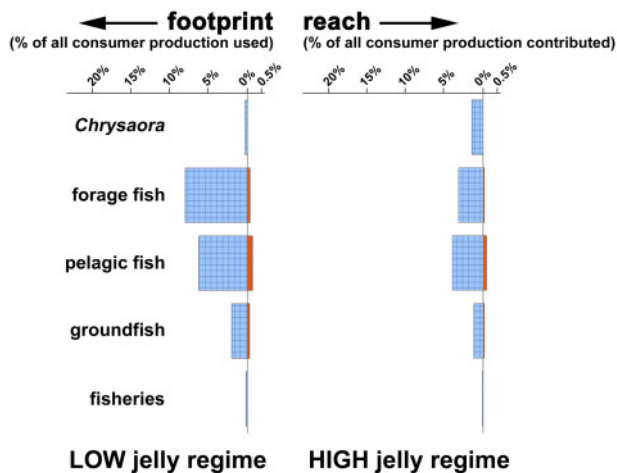 EBS sub-regions during the 2004–2015 period. Footprint = fraction of total consumer production within the ecosystem supporting the group's production (via direct and indirect trophic pathways). Reach = fraction of total consumer production within the ecosystem that originates with (or passes through) the group. Reach values are much smaller than footprint values and are plotted on a smaller scale.

Figure 7. Footprint (blue, cross-hatched) and reach (red) metrics for several functional groups within the mid-shelf EBS during low (2004–2007) and high (2009–2014) *Chrysaora* biomass regimes. Footprint = fraction of total consumer production within the ecosystem supporting the group's production (via direct and indirect trophic pathways). Reach = fraction of total consumer production within the ecosystem that originates with (or passes through) the group. Reach values are much smaller than footprint values and are plotted on a smaller scale.

Sensitivity of the EBS ecosystem to changes in *Chrysaora* abundance

Following an 80% reduction in the *Chrysaora* biomass in the baseline (2004–2015) model to simulate the low jellyfish regime, there was a redistribution of available plankton resources allowing a general expansion of other consumer groups (Figure 8a). A simulation of the high jellyfish regime had the opposite effect (Figure 8b). Most changes throughout the ecosystem were within
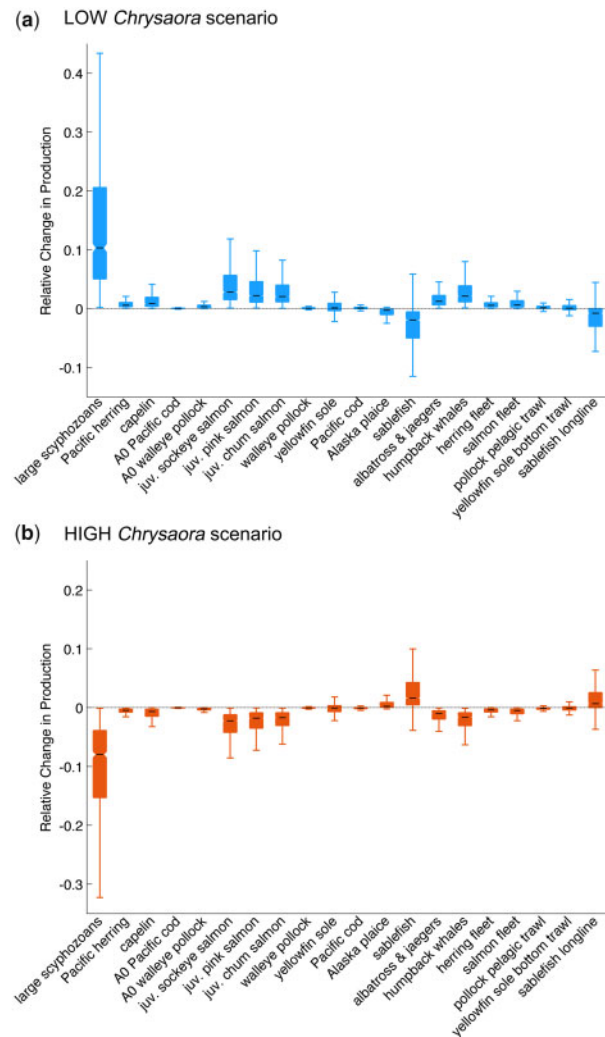
Figure 8. (a) *EBS-ECOTRAN scenario showing the effects of a reduction in* Chrysaora *biomass similar to that of the low* Chrysaora *period (2004–2007). (b) EBS-ECOTRAN scenario showing the effects of an increase in* Chrysaora *biomass similar to that of the high* Chrysaora *period (2009–2014). Scenario effects are evaluated by comparing changes in production rates under scenario conditions to production under baseline (2004–2015) model conditions:* $\Delta P = (P_{scenario} - P_{base})/P_{base}$. *The plot shows the effect across the full shelf. Error bars represent the range of 1000 randomly generated models using defined levels of uncertainty for all model parameters.*

5% of the baseline production rates. In contrast to other groups, sablefish (*Anoplopoma fimbria*), which include scyphozoan jellyfish as part of their diet, showed a decline in production when *Chrysaora* was reduced and growth when *Chrysaora* was increased. Juvenile salmon were more sensitive to changes in *Chrysaora* than were the forage fishes. Note that this scenario only considers the effects of competition with *Chrysaora* for zooplankton production and does not include effects upon recruitment arising from predation by *Chrysaora* upon fish eggs and larvae.

The expected effects of simulated changes in *Chrysaora* biomass upon other groups were much smaller than the observed inter-annual variability (Table 3). Pelagic survey data (BASIS) generally agree with model predictions in terms of the direction of change. Model simulations and BASIS surveys show higher

Table 3. Changes in group production rates on the EBS shelf following forced changes to *Chrysaora* biomass to simulate low (2004–2007) and high (2009–2014) *Chrysaora* periods.

	LOW *Chrysaora* (2004–2007)					HIGH *Chrysaora* (2009–2014)				
Group	ΔP model (%)	CV	ΔB survey (%)	Biomass (t km^{-2})	CV	ΔP model (%)	CV	ΔB survey (%)	Biomass (t km^{-2})	CV
Chrysaora[a]	−81.1 − **81.1**	0.0	−80.7 − **80.7**	0.742	0.4	64.6	0.0	50.2	5.772	0.7
Scyphozoid jellyfish[a,d]	15.9	1.1	25.6	0.064	0.7	−11.8 − **11.8**	1.0	−12.2 − **12.2**	0.045	1.1
Pacific herring[a]	0.9	1.2	40.8	0.076	0.8	−0.7 − **0.7**	1.0	−31.7 − **31.7**	0.037	1.1
Pacific herring[b]			42.1	0.172	0.8			−19.7 − **19.7**	0.097	1.3
Capelin[a]	1.7	1.5	−70.2 − **70.2**	0.010	1.8	−1.3 − **1.3**	1.5	75.8	0.061	0.8
Capelin[b]			−33.7 − **33.7**	0.005	1.1			31.0	0.010	0.6
Age-0 Pacific cod[a]	0.0	2.0	59.1	0.007	1.0	0.0	2.2	−34.2 − **34.2**	0.003	1.1
Age-0 walleye pollock[a]	0.4	0.9	96.3	1.362	0.8	−0.3 − **0.3**	1.0	−65.0 − **65.0**	0.243	2.1
Juv sockeye salmon[a]	4.4	1.1	66.3	0.081	0.7	−3.3 − **3.3**	1.0	−38.5 − **38.5**	0.030	1.4
Juv pink salmon[a]	3.6	1.2	37.4	0.007	0.7	−3.1 − **3.1**	1.3	−18.8 − **18.8**	0.004	1.4
Juv chum salmon[a]	3.2	1.2	48.4	0.008	0.6	−2.7 − **2.7**	1.3	−24.9 − **24.9**	0.004	1.5
Walleye pollock[b]	0.0	>10	−14.5 − **14.5**	34.099	0.7	0.0	>10	12.6	44.918	0.3
Yellowfin sole[b]	0.1	>10	−12.6 − **12.6**	10.568	0.1	−0.2 − **0.2**	>10	13.7	13.740	0.3
Northern rock sole[b]	0.1	5.4	−8.1 − **8.1**	10.278	0.2	−0.1 − **0.1**	4.5	8.5	12.133	0.2
Pacific cod[b]	0.0	>10	−26.7 − **26.7**	1.590	0.1	0.0	>10	22.3	2.651	0.3
Alaska plaice[b]	−1.4 − **1.4**	3.0	−7.2 − **7.2**	1.426	0.1	1.1	2.7	5.2	1.617	0.2
Flathead sole[b]	0.2	1.4	23.7	2.418	0.1	−0.1 − **0.1**	1.7	−11.8 − **11.8**	1.724	0.4
Arrowtooth flounder[b]	−0.2 − **0.2**	>10	34.4	3.861	0.4	0.0	>10	−21.9 − **21.9**	2.243	0.6
Sablefish[b]	−5.0 − **5.0**	2.0		−[c]		3.9	>10		−[c]	
Albatross and jaegers	1.9	1.3				−1.6 − **1.6**	1.3			
Humpback whales	3.4	1.5				−2.6 − **2.6**	1.2			
Herring fleet	0.9	1.4				−0.6 − **0.6**	1.3			
Salmon fleet	1.2	1.3				−1.0 − **1.0**	1.5			
Pollock pelagic trawl	0.3	4.2				−0.2 − **0.2**	4.1			
Pacific cod longline	0.0	>10				0.0	>10			
Rock sole bottom trawl	0.0	>10				0.0	>10			
Yellowfin bottom trawl	0.1	>10				−0.1 − **0.1**	>10			
Sablefish longline	−3.7 − **3.7**	2.7				2.6	2.6			

Scenario effects are evaluated by comparing changes in production rates under scenario conditions to rates under base model conditions: $\Delta P = (P_{scenario} - P_{base})/P_{base}$. Also shown are observed changes in biomass from BASIS and RACE surveys. Shading highlights declines relative to the 2004–2015 mean. Error terms are ±1 CV (coefficient of variation) of 1 000 randomly generated models and ±1 CV of inter-annual survey estimates. Bold values represent significant differences in median observed biomasses between low and high *Chrysaora* periods (one-sided Wilcoxon rank-sum test).
[a]Observations from the BASIS pelagic survey ($n = 51–103$ trawls for each of nine survey years).
[b]Observations from the RACE groundfish survey ($n = 319–321$ trawls for each of ten survey years).
[c]Poorly sampled, observed in <10% of trawls.
[d]*Aurelia aurita*, *Cyanea capillata*, and *Phacellophora camtschatica*.

forage fish (herring, age-0 Pacific cod, age-0 pollock) and juvenile salmon biomasses during low *Chrysaora* years (2004–2007) and lower biomasses during high *Chrysaora* years (2009–2014). Contrary to other species and model expectations, capelin increased during the high *Chrysaora* period. This was a cold temperature regime period and capelin were encountered further south (Decker *et al.*, 2018) so a greater proportion of the population was likely in the model domain south of 60°N. The biomass of small pelagic fish in the BASIS survey was overwhelmingly dominated by age-0 pollock in both periods. The biomass of age-0 pollock was significantly lower during the high *Chrysaora* period (Wilcoxon rank-sum test, α = 0.05). Changes among the other small pelagic fishes were not statistically significant.

## Comparison of *Chrysaora*'s trophic role in different ecosystems

A comparison of the importance of *Chrysaora* spp. in the EBS to their importance in the CGoA and the NCC is shown in Figure 9 (see also extended results in Supplementary Table S5). The footprint metrics show that *Chrysaora* in the NCC use a much a larger proportion of ecosystem production during the summer than they do in the EBS (18.6% vs. 1.2%, respectively). In the NCC, jellyfish exploit a similar proportion of ecosystem production as do pelagic fish and groundfish combined (18.6% vs. 17.7%, respectively). In the EBS, the *Chrysaora* footprint is only 20% that of pelagic fish and groundfish (1.2% vs. 5.9%, respectively). In contrast, *Chrysaora* are a much less important consumer within the CGoA, with a footprint of only 0.1% compared to that of pelagic fish and groundfish (23.4%). The contribution of *Chrysaora* to total consumer production (reach) is small in each ecosystem. Jellyfish reach is highest in the NCC but still only amounts to 0.01% of total consumer production.

Discussion

Rapid population growth rates (Condon *et al.*, 2012) and broad planktivorous diets (Pauly *et al.*, 2009) allow jellyfish to rapidly respond to variable environmental conditions. When abundant, jellyfish can negatively affect coastal fish populations and fisheries
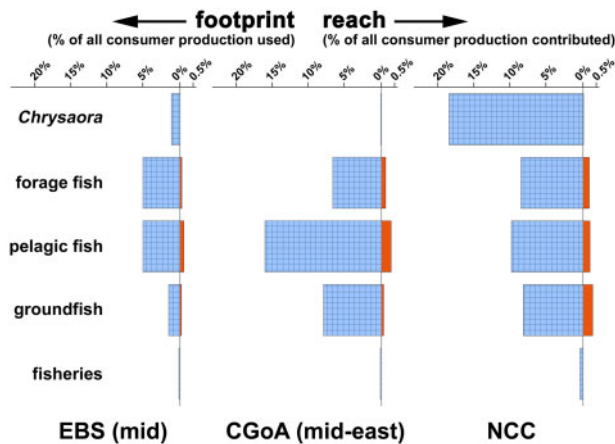
Figure 9. Footprint (blue, cross-hatched) and reach (red) metrics for several functional groups within the mid-eastern CGoA, mid-shelf EBS, and the NCC shelf ecosystems. Footprint = fraction of total consumer production within the ecosystem supporting the group's production (via direct and indirect trophic pathways). Reach = fraction of total consumer production within the ecosystem that originates with (or passes through) the group. Reach values are much smaller than footprint values and are plotted on a smaller scale. Sub-regions used for ecosystem comparisons of footprint and reach metrics are indicated by cross-hatching in Figures 2 and 4.

by limiting fish production via competition for zooplankton resources or by limiting recruitment via direct predation on fish eggs and larvae (reviewed by Purcell and Arai, 2001). Expanding jellyfish populations in diverse coastal ecosystems have been attributed to the ability of jellyfish to take advantage of anthropogenic disturbances to marine food webs and have led to concern that they may suppress fish and higher trophic-level production once large populations become established (Banse, 1990; Kideys et al., 2005; Lynam et al., 2006; Richardson et al., 2009). Brodeur et al. (2002) have drawn attention to an apparent decadal-scale, inverse relation between *C. melanaster* and forage fish within the EBS that appears to persist into recent years (Figure 1). Their estimates of summer feeding rates imply that during years of high biomass *Chrysaora* consume one-third of the zooplankton standing stock over the mid-shelf and may suppress fish production through competitive interactions. We apply spatially resolved end-to-end models of the inner-, mid-, and outer-shelf regions of the EBS (*EBS-ECOTRAN*) to estimate the importance of *Chrysaora* as an ecosystem-structuring agent and the responses of different taxonomic groups to changes in jellyfish biomass.

During the recent high jellyfish biomass period (2009–2014), *Chrysaora* placed a substantial footprint upon ecosystem resources, suggesting the potential for competition with other planktivores. *EBS-ECOTRAN* estimates that *Chrysaora* consumed 1.5% of the total consumer production within the mid-shelf zone. To place this in context, this was roughly one-half that of the four main forage fish groups (capelin, Pacific herring, age-0 Pacific cod, age-0 walleye pollock), and a fivefold greater footprint upon ecosystem resources than seabirds, marine mammals, and marine fisheries combined (Figure 7; Supplementary Table S4). Direct competition for resources between jellyfish and other consumer groups can exist among groups that overlap spatially and share common prey types. Age-0 walleye pollock represent the major portion of the total forage fish biomass and like *Chrysaora* were

most abundant over the mid-shelf sub-region in both low and high jellyfish biomass years (Decker et al., 2018). Isotope and stomach content analyses suggest that *Chrysaora* and age-0 pollock share similar diets (Brodeur et al., 2002). In late summer, age-0 pollock consume a wide size range of crustacean zooplankton (copepods, euphausiids, crab zoaea, and megalopae), pteropods, chaetognaths, fish eggs and larvae, and cannibalize smaller pollock larvae (Moss et al., 2009). Diet analyses of BASIS survey samples collected in late summer 2014–2016 show that *Chrysaora* consumed mostly pteropods, chaetognaths, and gelatinous zooplankton, but crustacean meso- and macrozooplankton made up roughly 10–50% of their diet by weight (Figure 3). Thus, there is a high degree of spatial and diet overlap between forage fish and *Chrysaora* and the potential of direct competition for zooplankton resources.

Indirect "food web competition" (*sensu* Essington, 2006) can also exist among groups that occupy different trophic levels but lie along the same food chain. *EBS-ECOTRAN* simulations of the high *Chrysaora* biomass years show how a redistribution of available plankton resources to jellyfish and away from other planktivores leads to a general reduction in production rates of both forage fishes and piscivores across several trophic levels (Figure 8). Because *Chrysaora* have few documented predators in the Bering Sea, the model shows very little of the ecosystem production they consume is transferred to higher trophic levels (their "reach", Figures 6 and 7). *Chrysaora* may then act as an ecosystem-structuring agent by diverting resources away from higher trophic levels when they are abundant, sablefish being an important counter-example. However, we caution that existing diet data may not fully quantify predation on gelatinous organisms due to poor detection and rapid digestion of these soft-bodied prey (see Hays et al., 2018), leading to underestimates of their importance to higher trophic levels.

In the analysis of BASIS survey data, age-0 pollock, age-0 Pacific cod, and herring biomasses were higher during low *Chrysaora* years (2004–2007) than during high biomass years (2009–2014). Age-0 pollock biomass, representing the greater part of total forage fish biomass, was significantly higher during low jellyfish years ($p = 0.03$, Wilcoxon rank-sum test). This is qualitatively consistent with resource competition, but the observed changes are much larger than estimated by *EBS-ECOTRAN* if competition alone were responsible. Model simulations may underestimate competition by averaging trophic interactions over spatial scales on the order of thousands of square kilometres. *Chrysaora* and forage fish are not homogenously distributed within model sub-regions (Hollowed et al., 2012; Decker et al., 2018). Competition could be more intense than estimated by the model in locations of high spatial overlap. Decker et al. (2018) report evidence of forage fishes avoiding regions of high jellyfish density during years when *Chrysaora* were more abundant, possibly an avoidance of areas with especially high competition. In their global review of ecological interactions between cnidarians and fish, Purcell and Arai (2001) note that available estimates of predation pressure exerted by gelatinous zooplankton upon copepods are generally too low ($<10\%$ d^{-1}) to negatively impact fish stocks. Similarly, *EBS-ECOTRAN* estimates suggest that *Chrysaora* are not a major consumer of late summer copepod production (Figure 5a) despite their relatively large footprint upon ecosystem production. However, *Chrysaora* are important predators upon specific zooplankton groups including pteropods (Figure 5b). Thus, model simulations suggest that the impact of *Chrysaora* upon trophic groups that also prey heavily

upon these plankton classes (e.g. juvenile salmon, Cieciel *et al.*, 2009), may be important and is greater than their impact upon forage fishes (Figure 8).

EBS-ECOTRAN simulations did not consider the impact that predation by *Chrysaora* upon fish eggs and larvae may have on recruitment. Eggs and small larvae have little or no escape ability and are positively selected as prey by jellyfish across a wide range of densities (Purcell and Arai, 2001; Titelman and Hansson, 2006). In natural settings, jellyfish have been shown to be important predators of eggs and larvae and could reduce recruitment when they are abundant (Möller, 1984; Purcell and Grover, 1990; Tilves *et al.*, 2016). However, after examination of RACE and BASIS survey time series for correlations between *Chrysaora* and total forage fish biomass lagged by 1–3 years, Opdal *et al.* (2019) conclude there is little evidence that *Chrysaora* impact fish recruitment in the EBS. Brodeur *et al.* (2002) observed pollock larvae in late summer *Chrysaora* diets but estimated that even during the high *Chrysaora* biomass year 1999, they ate only 2.8% of the larval stock per day. We also did not see evidence of high predation of larvae as ichthyoplankton were very rare in the gastric cavities and oral arms of *Chrysaora* sampled during the 2014–2016 BASIS surveys (Figure 3). However, fish eggs were positively identified in the diets of *Chrysaora* sampled on the mid- and outer-shelf, and even though eggs constituted <1% of the diet by weight, model estimates show that *Chrysaora* are among the most important predator groups of eggs during periods of high jellyfish biomass (Figure 5c).

Predation by *Chrysaora* upon fish eggs and larvae is limited in the spring by the seasonal emergence and growth of a newly recruited medusa population and limited later in the summer by the growth of fish larvae to a size where they can avoid capture (Purcell and Arai, 2001). Annual BASIS surveys of the pelagic EBS occur in late summer/early fall (August to October) and there is little information about *Chrysaora* abundance and diet in spring to determine if young medusae are important predators of eggs and small larvae (Decker *et al.*, 2018). Large, over-wintering medusae have been encountered in the spring and early summer (Brodeur *et al.*, 2008a; Zavolokin *et al.*, 2008) and could be important predators if large numbers survive and actively feed in the spring. The peak occurrence of pollock eggs is late February to late May (Bacheler *et al.*, 2010). Small pollock larvae (<5 mm SL) are present every month April to September, but the average length grows to >20 mm standard length by July (Bacheler *et al.*, 2010). The average length in the late summer BASIS surveys is >60 mm (Moss *et al.*, 2009). Brodeur *et al.* (2002) have observed pollock larvae as large as 48 mm eaten by *Chrysaora* but only by very large individuals >28 cm bell diameter. Conversely, juvenile pollock may actually benefit from close proximity to a large population of medusae with which they may engage in a commensal relationship as a deterrent to mortality by other predators (Brodeur, 1998), though we did not investigate that idea here.

Analyses with similarly structured *ECOTRAN* models showed large variability in the trophic importance of scyphozoan jellyfish in different northeast Pacific shelf ecosystems. The *Chrysaora* footprint upon available ecosystem production in the NCC is ten times that of their footprint in the EBS, while their footprint upon the CGoA is only one-tenth that of their footprint in the EBS (Figure 9). The large footprint that *C. fuscescens* have within the NCC appears to have an observable effect upon salmon feeding success and recruitment. Juvenile salmon caught in locations

of high *Chrysaora* biomass have significantly lower feeding success than those in locations of low biomass, and there is a significant negative correlation between *Chrysaora* biomass during the summer that smolts enter the ocean and subsequent adult returns to the Columbia River (Ruzicka *et al.*, 2016a). Lynam *et al.* (2005a, b) observed a similar relationship in the North Sea between jellyfish abundance and subsequent Atlantic herring (*Clupea clupea*) and Atlantic salmon (*Salmo salar*) production. Though we did not look at the relationship between salmon returns and *Chrysaora* biomass in the EBS, the *EBS-ECOTRAN* simulations suggest that juvenile salmon there are also sensitive to competition with jellyfish.

Evidence for substantial impacts upon coastal ecosystems by growing jellyfish populations is not readily apparent from available time-series survey data. Failure to find significant negative correlations between jellyfish and zooplankton or between jellyfish and forage fish within four distinct coastal ecosystems lead Opdal *et al.* (2019) to conclude that there was no clear evidence that jellyfish drive down zooplankton stocks so much as to inhibit fish production or that jellyfish predation on eggs and larvae reduces fish recruitment. *EBS-ECOTRAN* simulations based upon survey data of plankton, fish, and diets from specific periods of low (2004–2007) and high (2009—2014) *Chrysaora* biomass support this conclusion. The impact of elevated resource demands by *Chrysaora* during the period of high biomass is small for most consumer groups, with the exception of groups such as juvenile salmon with which they compete for specific zooplankton classes. However, the importance of scyphozoan jellyfish as a competitor or predator may be more complex than revealed by analysis of correlations between zooplankton, jellyfish, and forage fish biomass time series. The *Chrysaora* biomass in the EBS is highly variable over decadal time scales, and the hypothesized drivers of this variability suggest that the ecological importance of *Chrysaora* as a competitor may not be tightly coupled to its biomass. Large expansions in *Chrysaora* biomass appear to be initiated with changes in climate regime that result in increased zooplankton production (Brodeur *et al.*, 1999; Coyle *et al.*, 2008). Bottom-up limitation is indicated by the observation that peaks in zooplankton biomass have preceded expansion of the *Chrysaora* population (Decker *et al.*, 2018). Under such bottom-up limitation, *Chrysaora* and zooplankton stocks would be positively correlated. Only during periods when zooplankton production is falling and *Chrysaora* biomass is high would competition with forage fish be substantial. The jellyfish population declines when it out-grows zooplankton production, when competition with an expanding forage fish population intensifies, or when zooplankton production falls with a change in climate regime (Brodeur *et al.*, 2002).

Conclusions

Even in years of high jellyfish biomass, the four main forage fish groups (capelin, Pacific herring, age-0 Pacific cod, age-0 walleye pollock) together use twice the total EBS consumer production as do the dominant schyphozoan, *C. melanaster*. However, the *Chrysaora* footprint on ecosystem production is still substantial and greatly exceeds that of seabirds, marine mammals, and marine fisheries. The *Chrysaora* footprint is equivalent to that of adult groundfish.

Model simulations show that competition with *C. melanaster* for zooplankton resources during years of high jellyfish biomass

(2009–2014) generally reduces production of fish and higher trophic-level consumers by <10% of the baseline average (2004–2015). Juvenile salmon that rely heavily upon larger zooplankton size classes that are also preyed upon heavily by *C. melanaster* (e.g. pteropods, crab megalopae) are more sensitive than forage fish groups.

Age-0 walleye pollock represent the greater part of the forage fish biomass. The observed age-0 pollock biomass during low *C. melanaster* years (2004–2007) was significantly higher than during high jellyfish years. However, model-estimated sensitivity to changes in *C. melanaster* biomass is small, generally within 5% relative to baseline model conditions, and much less than the inter-annual variability observed by pelagic surveys. For most surveyed fish groups, including juvenile salmon, observed differences between low and high jellyfish years were not significant.

The rarity of fish larvae observed within *C. melanaster* diets does not support the hypothesis that jellyfish are major predators of ichthyoplankton within the EBS, at least not in late summer. However, during years of high *C. melanaster* abundance, jellyfish become important predators of fish eggs in the late summer (although not the major predator) and may influence recruitment dynamics of important fish stocks. Observations of *C. melanaster* biomass, diet, and geographic distributions in the spring and early summer are necessary to accurately evaluate the role of large scyphozoan jellyfish on EBS fish stocks.

The importance of scyphozoan jellyfish in terms of energy demand and transfer to higher trophic levels differs greatly among northeast Pacific shelf ecosystems. The much smaller *Chrysaora* biomass of the western and central Coastal Gulf of Alaska place a relatively small demand upon ecosystem production. In contrast, large summer *Chrysaora* blooms have a much greater impact upon the NCC ecosystem than they do within the EBS.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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