ECOGRAPHY

Research

Shifting fish distributions impact predation intensity in a sub-Arctic ecosystem

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An abundance of studies in marine systems have documented species range shifts in response to climate change, and many more have used species distribution models to project species ranges under future conditions. However, there is increasing interest in moving beyond a single-species focus to understand how species redistribution alters ecosystem dynamics via changes in trophic interactions. We employed spatiotemporal models to characterize decadal-scale changes in spatial overlap between the distribution of juvenile walleye pollock *Gadus chalcogrammus* and the distributions of four of its groundfish predators: arrowtooth flounder *Atheresthes stomias*, Pacific cod *Gadus macrocephalus*, Pacific halibut *Hippoglossus stenolepis* and adult walleye pollock. These fishes represent ecologically and commercially important species in a rapidly changing sub-Arctic ecosystem, the eastern Bering Sea, Alaska, USA. We then examined whether changes in spatial overlap corresponded to changes in predation, using spatiotemporal models of predator stomach contents. We found marked shifts in spatial overlap between juvenile pollock and two predators (arrowtooth flounder and Pacific halibut) over 34 years, with changes in overlap corresponding to increases in population-scale predation pressure. By contrast, we did not find clear relationships between spatial overlap and predation for Pacific cod and adult pollock, the two predators for which juvenile pollock constitute a much smaller diet proportion. Our findings highlight the complexity of predicting predation dynamics for generalist marine species and suggest a need for better process-based methods for understanding the potential future ecological impacts of coupled species range shifts. However, simple metrics of spatial overlap between relatively specialized predators and their prey offer promise as a means to integrate predictions from species distribution models into ecosystem-based fisheries management.

Keywords: biogeography, climate change, eastern Bering Sea, predator–prey, range shifts, spatial overlap

Introduction

The geographic ranges of many marine and terrestrial organisms are shifting as a result of anthropogenic climate change, tracking changes in environmental gradients across horizontal and vertical space (Parmesan and Yohe 2003, Pinsky et al. 2013, Fredston et al. 2020). As species redistribute in a warming world, it is inevitable that their ecological relationships with habitat, prey, predators and competitors will change in fundamental ways (Albouy et al. 2014, Alexander et al. 2015, Pecl et al. 2017). Yet, most studies on recent and projected distributional shifts in marine and terrestrial systems consider species in isolation, and consequently, the implications of species range shifts for ecological communities remain poorly understood. There is an immediate need for integrated assessments of climate change impacts on community assembly and species interactions (Gilman et al. 2010, Gravel et al. 2019, Holsman et al. 2020a, Pinsky et al. 2020, Schleuning et al. 2020, Thorson et al. 2021).

Species-specific responses to climate driven change are altering the spatial overlap and phenological synchrony between populations of predators and prey (Kordas et al. 2011, Kharouba et al. 2018, Carroll et al. 2019). This is likely to affect encounter rates between them, ultimately influencing the strength of predation interactions (Durant et al. 2007, Yang and Rudolf 2010). Basic physiological principles and a substantial breadth of laboratory studies indicate that the strength of predator–prey interactions is also mediated by temperature and other abiotic factors both directly via kinetic effects on consumption rates (Englund et al. 2011, Deslauriers et al. 2017, Pepi et al. 2018) and indirectly via effects on predator foraging (Lemoine et al. 2013, Edwards et al. 2015, Evans and Moustakas 2018, Holsman et al. 2019) and prey escape behaviors (Domenici et al. 2019). Consequently, climate change can alter both spatial overlap between predators and prey and the strength of trophic interactions where predators and prey co-occur, and may therefore impact predator–prey dynamics in complex, nonlinear ways (Rall et al. 2010, Boukal et al. 2019).

Despite the breadth of research demonstrating that climate change alters both 1) species distributions, and 2) trophic interactions, relatively few studies have jointly examined changes in spatial predator–prey overlap and predation rates (sensu Barnes et al. 2020, Grüss et al. 2020, Thorson et al. 2021). Various metrics have been applied to characterize spatial overlap between species distributions (Saraux et al. 2014, Greer and Woodson 2016, Carroll et al. 2019), and changes in these overlap metrics have been presumed to be proportional to changes in prey consumption (Hunsicker et al. 2013, Grüss et al. 2018, Selden et al. 2018). However, overlap metrics remain largely untested in their ability to predict the strength of trophic interactions using empirically derived estimates of predator diet. Consequently, there is a need to examine the ecological relevance of spatial overlap metrics, and to assess their ability to approximate predator–prey interactions in multi-species and ecosystem models (Greer and Woodson 2016, Carroll et al. 2019). Characterizing the effects of species redistributions on trophic interactions will ultimately improve our understanding of how climate change

may affect population processes and food web structure (Harley 2003, Northfield et al. 2017, Boukal et al. 2019).

In this study we aim to quantify whether changes in spatial overlap between predators and a key prey species can predict changes in population-level predation pressure. We use 34 years (1982–2015) of species biomass and stomach content data from trawl surveys in the eastern Bering Sea (EBS) to explore overlap and predation among four predators – arrowtooth flounder *Atheresthes stomias*, Pacific cod *Gadus macrocephalus*, Pacific halibut *Hippoglossus stenolepis* and adult walleye pollock *G. chalcogrammus* – and a primary prey species, juvenile walleye pollock. The EBS is a highly productive and dynamic marine ecosystem, where species distributions and interactions among species vary annually in relation to climate variability, most notably the spatial extent of the 'cold pool,' a mass of water < 2°C on the bottom of the continental shelf that is determined by the distribution and quality of sea ice in the previous winter (Fig. 1; Kotwicki and Lauth 2013, Hermann et al. 2016, Ortiz et al. 2016, Grüss et al. 2021). For example, some species including juvenile walleye pollock use the cold pool as a thermal refuge, while others such as arrowtooth flounder experience the position of the cold pool as a thermal barrier to their movements onto the shelf (Mueter and Litzow 2008, Rooper et al. 2021). Interannual variation in cold pool extent can therefore interact with species thermal preferences to shape annual patterns of overlap between juvenile pollock and their predators (Fig. 1). We directly relate spatial overlap between the distributions of juvenile pollock and their predators to changes in predation over time, allowing us to empirically evaluate the relationship between spatial predator–prey overlap and basin-scale predation pressure (Fig. 2). Jointly assessing changes in spatial overlap and predation will improve our understanding of the potential ecological consequences of changes in species distributions within ecological communities.

Methods

Species of interest

In this study, we consider four species of groundfish – walleye pollock, arrowtooth flounder, Pacific cod and Pacific halibut – as predators on juvenile walleye pollock in the EBS. Walleye pollock is a species of central importance to the EBS marine ecosystem, serving as forage fish for a variety of demersal and pelagic predators, including marine mammals and birds (Mueter et al. 2011), and comprising the largest single-species commercial fishery by landings for the USA (Holsman et al. 2020a). In the EBS, juvenile walleye pollock are the main prey for adult arrowtooth flounder and Pacific halibut by both frequency of occurrence and biomass (Livingston et al. 2017). They are less commonly encountered in Pacific cod stomachs, but still constitute an important food source by biomass (Livingston et al. 2017; Table 1 and Supporting information) and a key source of mortality for juvenile pollock. Juvenile pollock are typically a minor
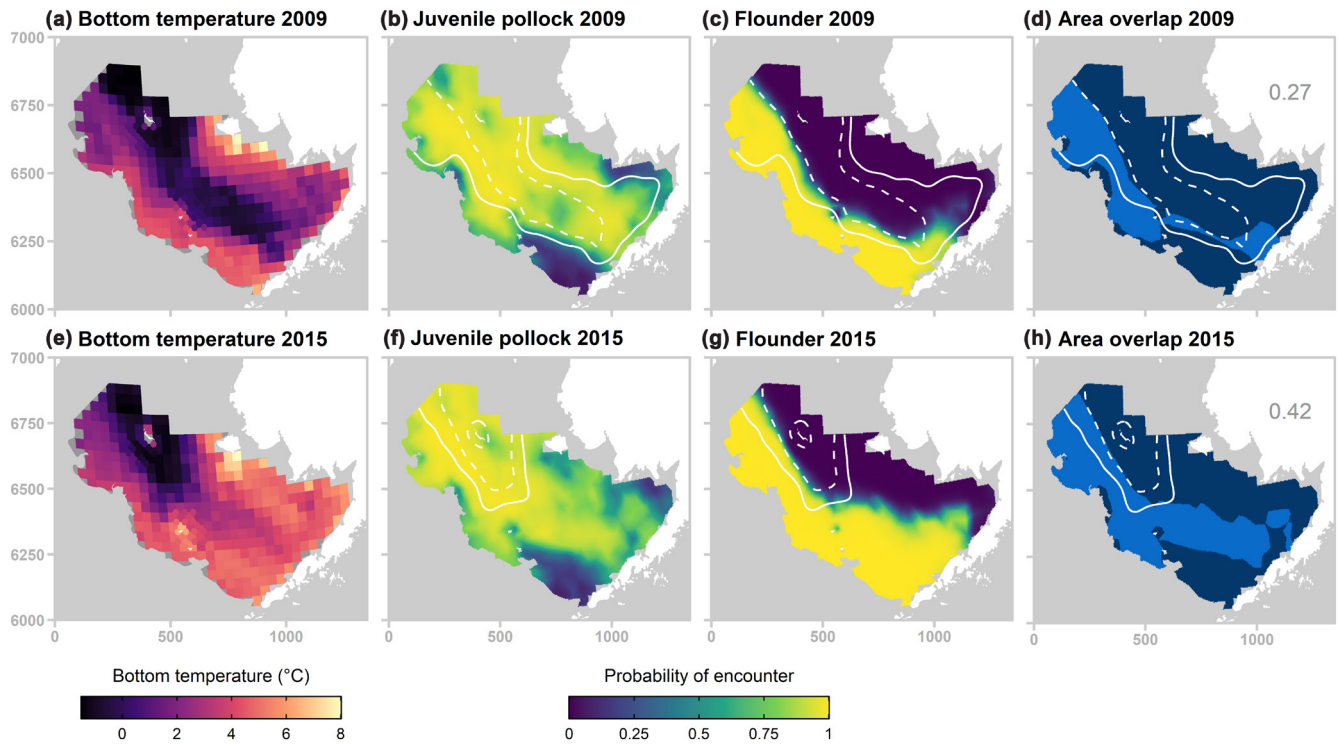
Figure 1. During years with extensive sea ice, melting sea ice results in the formation of a deep 'cold pool' of water below 2°C in the eastern Bering Sea (EBS). The cold pool can restrict the movement of some predators into the northeast EBS shelf, such that years with less extensive cold pools may result in greater spatial overlap between juvenile pollock and their predators. For example, area overlap between juvenile pollock and flounder was about 15% higher during 2015, when the cold pool was receded (~124 500 km²), than in 2009, when it was more extensive (~333 000 km²). For ease of interpretation, smoothed 2 and 0°C isotherms are shown as solid and dashed lines, respectively.

prey for adult walleye pollock, but cannibalism during some years can be a substantial contributor to adult pollock diets, and typically represents the largest estimated source of predation mortality for juvenile pollock (Boldt et al. 2012, Holsman et al. 2016, 2020a, b, Spencer et al. 2016, Livingston et al. 2017).

Data description

In this study, we employ annual bottom trawl survey data collected in the EBS by the Alaska Fisheries Science Center (AFSC) during spring and early summer since 1982 (Lauth et al. 2019). Surveys are conducted at (typically) 376
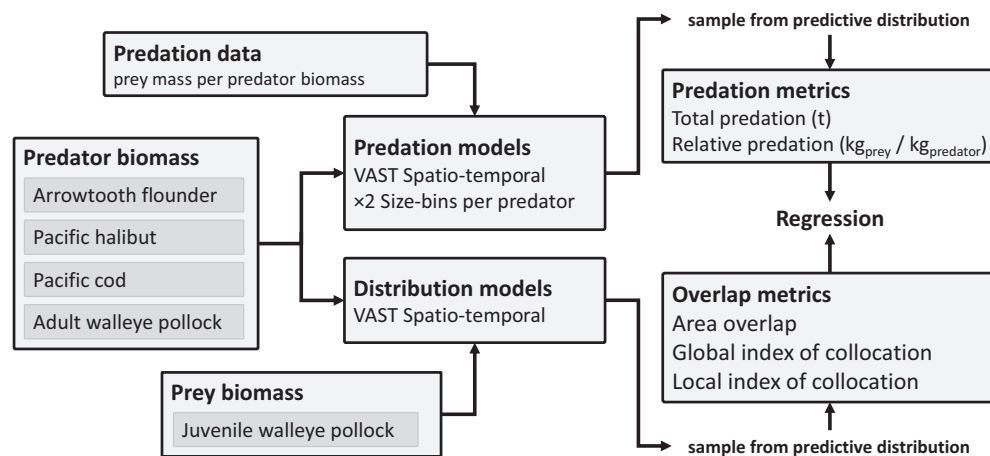

Figure 2. Diagram of data and statistical analyses used in this study. For each species of predator, VAST (vector autoregressive spatio-temporal) models are employed to generate annual estimates of spatial overlap with, and predation on, juvenile pollock. Predation is measured annually as both the total biomass of juvenile pollock consumed (in tonnes) by each species of predator across the EBS annually ('total predation'), and as the average biomass of juvenile pollock consumed per biomass of predator ('relative biomass').

Table 1. Summary of pollock contribution to predator diets for the eastern Bering Sea survey region between 1982 and 2015. Diets are summarized as the frequency of pollock in predator stomachs or the proportion of recorded prey biomass in predator stomachs (with SD between annual frequencies or proportions) and ranked relative to other prey items. Diets are summarized only for predators above the minimum sizes used for analysis, which are arrowtooth flounder ≥ 30 cm, Pacific cod ≥ 30 cm, Pacific halibut ≥ 50 cm and walleye pollock ≥ 40 cm. Empty stomachs were excluded from summary.

| Predator | By frequency of occurrence | | By biomass | |
	Rank	Frequency (SD)	Rank	Proportion (SD)
Arrowtooth flounder	1	0.36 (0.15)	1	0.70 (0.23)
Pacific cod	7	0.17 (0.09)	1	0.37 (0.16)
Pacific halibut	1	0.29 (0.14)	1	0.46 (0.2)
Walleye pollock	8	0.06 (0.12)	3	0.07 (0.11)

stations annually along the continental shelf in waters less than 200 m deep, with most sampling sites spaced about 20 nautical miles (~37 km) apart. Trawl duration at each station is 30 minutes (for an average swept area of ~0.05 km^2), and depth and temperature are recorded in real time. Fish catch rates (biomass per area swept) are obtained using the area-swept method (Alverson and Pereyra 1969), multiplying the distance fished (determined from bottom contact sensor; Somerton and Weinberg 2001) by the average net width measured using acoustic spread sensors (Weinberg and Kotwicki 2008). Additionally, data for juvenile and adult pollock are corrected to account for bias introduced by the density-dependent sampling efficiency of the bottom trawl survey (Kotwicki et al. 2014).

During the annual bottom trawl surveys, stomach contents are analyzed for a subset of the Pacific cod, Pacific halibut, walleye pollock and arrowtooth flounder catch at each survey station (Livingston et al. 2017). Fish showing signs of regurgitation or net feeding are not selected, and excised stomachs are transported to the AFSC Trophic Interactions Laboratory where individual stomach contents are counted, weighed and identified to species when possible (Livingston et al. 2017). As these fish undergo size-dependent ontogenetic shifts in habitat and diet preference, we analyze distribution and predation by predators only at the size classes when they begin to predate extensively on juvenile pollock. We therefore fit species distribution models for juvenile (≤ 25 cm) and adult (≥ 40 cm) walleye pollock, Pacific cod (≥ 30 cm), Pacific halibut (≥ 50 cm) and arrowtooth flounder (≥ 30 cm, Grüss et al. 2020), and assume that these sizes are fully selected by the trawl survey gear. Because individuals are sub-selected for stomach content analysis following species-specific length bins at finer scales (Livingston et al. 2017, Grüss et al. 2020), predation models (section 'Quantifying predation') are further subdivided by surveyed size class: 30–49 and 50+ cm for arrowtooth flounder, 30–59 and 60+ cm for Pacific cod, 50–69 and 70+ cm for Pacific halibut and 40–54 and 55+ cm for adult walleye pollock. Before analysis, we divide total prey (juvenile pollock) mass from each stomach sample by the corresponding predator biomass to obtain

prey-mass-per-predator-biomass (in kg prey per kg predator), averaging across all samples from a given survey to obtain one mean prey-mass-per-predator-biomass value for each survey and predator species/size class (Grüss et al. 2020, 2021). Due to insufficient sample sizes, we exclude some years from analyses of predator stomach contents data for each species; in total, there are 26 years of data for arrowtooth flounder, 31 for Pacific cod, 23 for Pacific halibut and 29 for adult walleye pollock (Supporting information).

Species distribution models

To obtain spatially-explicit estimates of biomass for juvenile walleye pollock and each predator species, we fit delta-generalized linear mixed models using the 'VAST' (vector autoregressive spatio-temporal) package in R (Kristensen et al. 2016, Thorson 2019a, <www.r-project.org>). Delta (also known as 'hurdle') models accommodate zero-inflated data using two separate models for zero biomass observations (an encounter probability model) and positive (non-zero) biomass catch rates (a positive biomass model); overall grid cell biomass estimates are obtained as the product of encounter probability estimates, positive biomass catch rate estimates and grid cell area (Chyan-Huei Lo et al. 1992, Martin et al. 2005).

In each model, we estimate encounter probability and positive biomass catch rate assuming Bernoulli and Gamma distributions, respectively. We account for temporal variation by fitting year (1982–2015) as a fixed effect and estimating a separate intercept for each year. We estimate spatial variation using a Gaussian Markov random field (GMRF) defined at 300 pre-defined 'knots,' which are evenly distributed across the eastern Bering Sea survey region (Thorson 2019a, Grüss et al. 2020). We include spatio-temporal variation using separate GMRFs for each year (Thorson 2019b). We estimate probability of encounter and biomass catch rate across the EBS by predicting across an extrapolation grid, where estimates for each ~14 km grid cell are obtained using bilinear interpolation between knot means (Lindgren et al. 2011). To allow for propagation of model uncertainty into predator–prey overlap metrics, we draw 1000 samples (for each year and grid cell) from the predictive distributions for probability of occurrence and biomass catch rate by sampling from the joint distribution of the fixed and random effects.

Quantifying predation

In order to relate changes in spatial overlap between juvenile pollock and their predators to changes in predation on juvenile pollock, we derive annual, spatially-explicit estimates of predation across the EBS survey region. For each predator and size class (eight models in total), we use the VAST modeling framework developed in Grüss et al. (2020) to jointly estimate 1) predator biomass catch rate (kg km^{-2}) and 2) prey-mass-per-predator-biomass (kg kg^{-1}). Multiplying these estimates together results in spatially-explicit estimates of predation on juvenile pollock at the grid-scale level (in kg

km^{-2}), which can be aggregated across the EBS survey region and summed across predator size classes to produce annual snapshot estimates of the total biomass of juvenile pollock consumed by each species of predator (hereafter referred to as 'total predation,' in kg; Grüss et al. 2020).

To estimate prey-mass-per-predator-biomass and predator biomass catch rate, we specify a Poisson-link delta model. Most delta models (e.g. the Bernoulli–Gamma model, section 'Species distribution models') estimate encounter probability and positive biomass independently. In reality, however, the percent frequency of occurrence of a prey in a predator stomach is likely correlated with the prey biomass in predator stomachs where encountered. The Poisson-link delta model developed in Grüss et al. (2020) accounts for this by deriving both biomass catch rate and prey-mass-per-predator-biomass assuming that 1) the spatial distribution of individual fish in the vicinity of sampling is random so that the probability of non-zero values is expressed as a function of the expected numbers-density, and 2) biomass catch rates are derived from the expected numbers density multiplied by the expected biomass-per-individual (Thorson 2018). As the probability of non-zero values is a function of the expected numbers-density, biomass catch rate (and prey-mass-per-predator-biomass) is also given by the product of estimated encounter probability and positive biomass catch rate. We fit the predation models with the same suite of temporal fixed effects, spatial and spatiotemporal random effects and spatial knots used for the species distribution models. We also obtain grid scale estimates of predation using bilinear interpolation, as in the species distribution models.

After calculating total predation for each species of predator in each year, we compute an additional metric which we refer to as 'relative predation' by normalizing the annual estimates of total predation by the annual estimates of predator biomass (integrated across the EBS survey region, Supporting information). Estimates of relative predation therefore reflect biomass-specific trends in predation, in units of kg prey per kg predator. The inclusion of both metrics allows us to characterize changes in basin-scale predation as resulting from changes in predator distribution and biomass (total predation), or, alternatively, changes in 'per-capita' consumption rates that may more closely track juvenile pollock density if predators consume pollock in proportion to its availability (relative predation). One caveat to this approach is that, because relative predation estimates are not integrated across time, they represent an instantaneous 'snapshot' of average pollock biomass in predator stomachs, differing from specific consumption rates measured in kg kg^{-1} day^{-1}. Species-level gastric evacuation rates, which may depend on temperature (and may also covary with overlap), can decouple instantaneous summaries of stomach contents from realized specific predation over time (Holsman and Aydin 2015). As in the species distribution models, we draw 1000 samples from the predictive distribution of each model, aggregating each of them to arrive at 1000 annual samples of total and relative predation for each species of predator.

Predator–prey overlap metrics

To assess the impacts of coupled shifts in the distribution of juvenile pollock and their predators on predation, we compute metrics of overlap for juvenile pollock with each predator in each year of the study period from modeled distributions (from subsection 'Species distribution models'). Various metrics are available to characterize spatial overlap between two species, using both observed and modeled patterns of species encounter and abundance (for a review of several metrics and their application to understanding spatial predator–prey interactions, see Carroll et al. 2019). These metrics function at different spatial scales and can be employed to make different ecological inferences using the observed or modeled distributions of predators and prey (Supporting information). We use three metrics to characterize overlap: 1) area overlap, an estimate of basin-scale range overlap which can be used with encounter/non-encounter data alone, 2) the global index of collocation, which employs estimated abundances to compare the center of gravity and dispersions of predator and prey distributions at a regional scale and 3) the local index of collocation, which estimates correlations between predator and prey densities at the grid-scale (Hurlbert 1978, Woillez et al. 2007, Saraux et al. 2014, Carroll et al. 2019). All three metrics are bounded between 0 and 1, with higher values indicating greater spatial overlap between predators and prey. To propagate uncertainty in the species distribution models into our calculations of range overlap, we apply these metrics to probability of encounter or biomass at both the maximum likelihood estimate and to 1000 draws from the predictive distribution (Thorson et al. 2016).

Regression of overlap and predation metrics

To assess whether there is a linear relationship between predation and each overlap metric, we regress (using ordinary least squares) the maximum likelihood estimates (MLEs) of total and relative predation for each predator in each year against the MLEs of each overlap metric. We do the same for each sample from the predictive distributions of total/relative predation and each overlap metric, and compute 95% confidence intervals for the slope coefficients using a normal approximation, where the standard deviation is derived from regressions on the predictive distribution samples. We consider coefficients with 95% confidence intervals that do not contain 0 to be statistically significant. Because increases in prey availability can impact predation rates without altering spatial predator–prey overlap, we additionally assess whether these estimates are robust to the inclusion of juvenile pollock biomass by fitting (standardized) juvenile pollock biomass (both the MLE and samples from the predictive distribution of juvenile pollock biomass) as covariates. In all models, we standardize the predictors and response, subtracting their means and dividing by their standard deviations, so that coefficients are comparable across species and overlap metrics.

Results

Trends in predator–prey overlap

Species displayed differing trends in distribution and abundance across the 34-year time series, but models generally indicated that overlap between juvenile pollock and its predators has increased over time (Fig. 3). Increasing trends in overlap were most pronounced for arrowtooth flounder and Pacific halibut, which exhibited low spatial overlap with juvenile walleye pollock at the start of the survey period but increased substantially in subsequent years, with shifts in both species' center of gravities towards that of juvenile pollock (Fig. 3 and Supporting information). While juvenile pollock were typically distributed near the cold pool , halibut distributions showed a distinct pattern of cold pool avoidance and flounder have become increasingly more common along the middle EBS shelf (Supporting information). Increases in spatial overlap with halibut and flounder therefore appear to result at least partly from fluctuations in the extent of the EBS cold pool (Supporting information).

Juvenile pollock had generally high overlap with adult pollock and Pacific cod, and overlap between adult and juvenile pollock increased slightly through time (Fig. 3 and Supporting information). Specifically, we found that each year between 2005 and 2015, the global index of collocation between juvenile and adult pollock was near 1, indicating

that the centers of gravity for juvenile and adult pollock were nearly identical across the EBS survey region. For Pacific cod, overlap with juvenile pollock does not appear to have changed directionally over time.

Trends in predation on juvenile pollock

Trends in total predation displayed substantial inter-annual and inter-species variation, typically coinciding with trends in both predator biomass and relative rates of predation (Fig. 4). Changes in total predation by arrowtooth flounder appeared to be driven largely by increases in flounder biomass along the EBS shelf, as both flounder biomass and the total predation on juvenile pollock by flounder increased dramatically between 1982 and 2015. The trend in relative predation by flounder showed interannual variability, but was largely flat over time (Fig. 4). In contrast, changes in total predation by Pacific cod, adult pollock and Pacific halibut corresponded more closely to changes in relative predation rates. For Pacific cod, relative predation varied considerably among years, peaking in 1988 at ~50% and declining to ~5% by 2010, mirroring fluctuations in total predation. The biomass of adult walleye pollock across the EBS shelf fluctuated through time, with intermittent declines between peaks in 1988–1990, 2003 and 2014–2015, but increases in both total and relative cannibalism coincided only with the first peak. In most other years, relative rates of cannibalism were
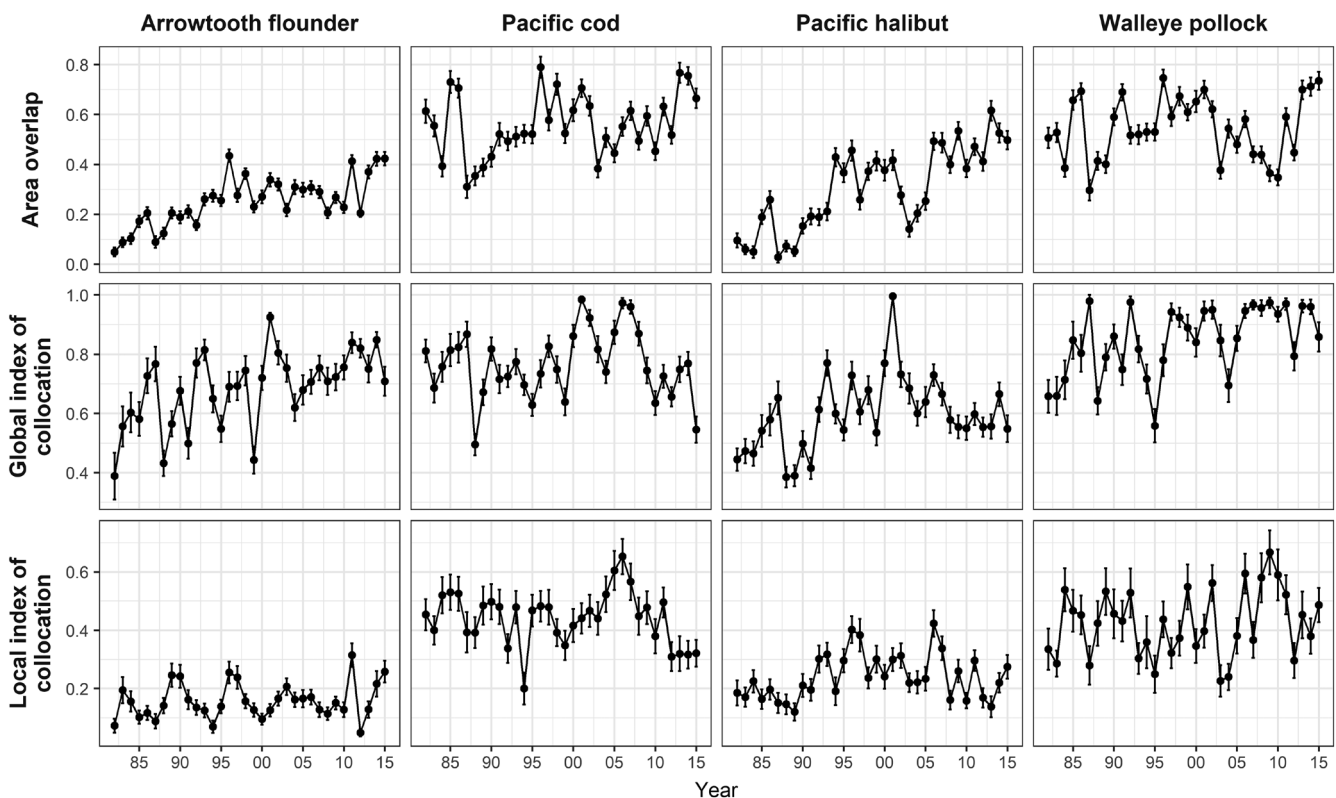

Figure 3. Metrics of spatial overlap between juvenile walleye pollock and four species of predator. Points are at the maximum-likelihood estimate; error bars represent the standard deviation of the predictive distribution. See Methods (section 'Predator–prey overlap metrics') for an overview of the overlap metrics.
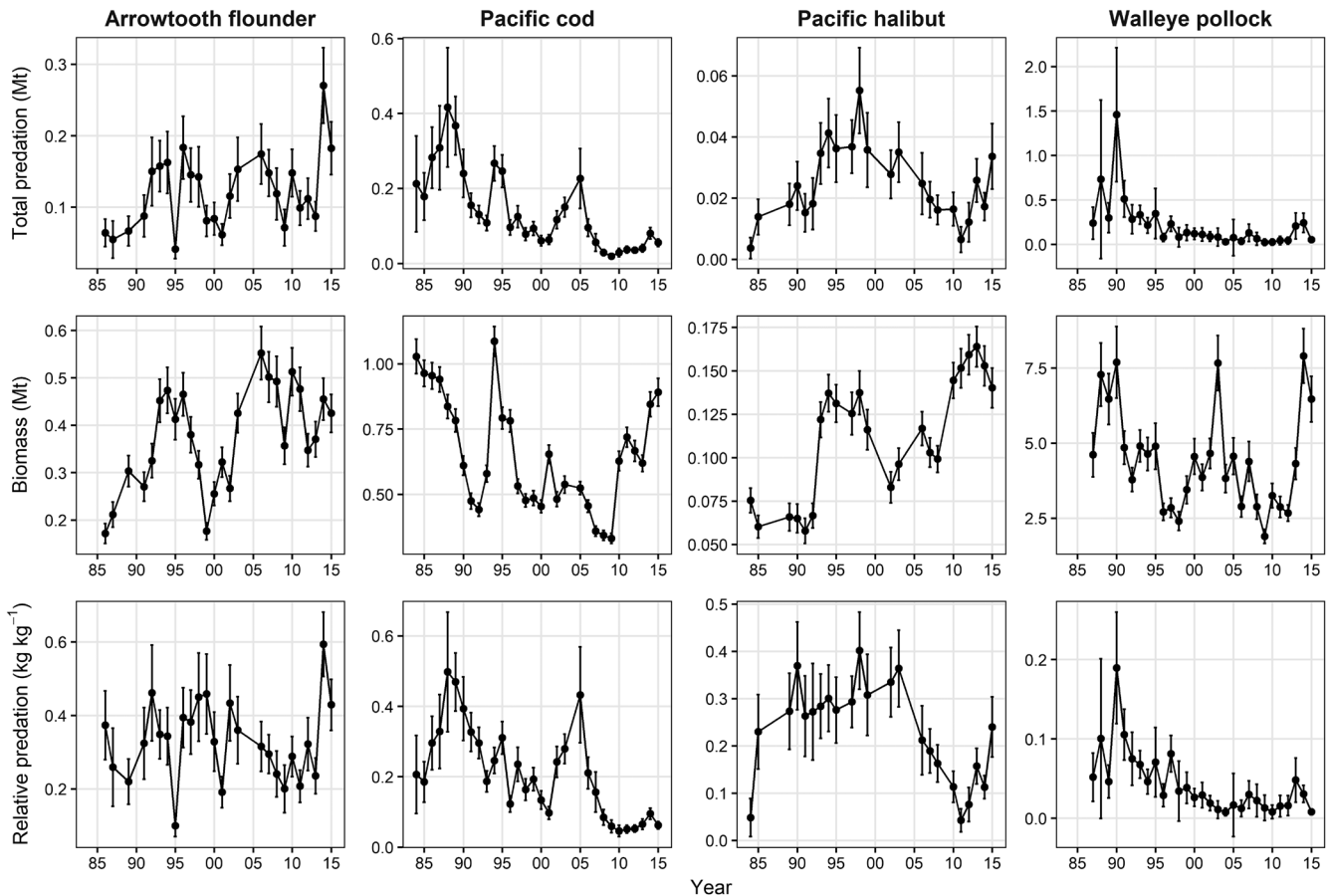
Figure 4. Estimates of annual total biomass predation on juvenile pollock (millions of tonnes), total predator biomass (millions of tonnes) and relative predation (kg prey consumed per kg predator), for each species of predator in each year. Points are at the maximum-likelihood estimate; error bars represent the standard deviation of the predictive distribution. Note that y-axes are scaled by species to highlight temporal trends.

low (less than 5% by biomass), consistent with past studies (Holsman and Aydin 2015). Total predation by halibut on juvenile pollock generally increased between the early 1980s and the early 2000s, coinciding with an increase in relative predation from ~5% in 1984 to ~36% in 2003. After 2003, biomass of halibut continued to increase along the EBS shelf, but both total and relative predation declined abruptly until about 2010 (Fig. 4).

Predation as a function of predator–prey overlap

Total predation was positively associated with spatial predator–prey overlap for two of four predators – arrowtooth flounder and Pacific halibut (Fig. 5) – but relative predation correlated poorly with spatial overlap for all predators (Supporting information). For arrowtooth flounder, there was a significant positive relationship between spatial overlap and total predation on juvenile pollock, regardless of the overlap metric used (Fig. 6), and relationships between relative predation and each overlap metric were positive but nonsignificant (Fig. 6 and Supporting information). Estimates of total predation also scaled positively with each overlap metric

for Pacific halibut (Fig. 5) and were significantly correlated with the global and local indices of collocation (Fig. 6). Relative predation by halibut was not significantly correlated with either the global or local index of collocation, and there was a significant negative relationship between relative predation and area overlap (Fig. 6 and Supporting information). Thus, increases in total predation, but not relative predation, generally coincided with changes in overlap with juvenile pollock for both arrowtooth flounder and Pacific halibut.

For Pacific cod and adult pollock, overlap metrics appear to be poor proxies for both total and relative predation. Results differed markedly across metrics for Pacific cod – there was a significant negative relationship between area overlap and both total and relative predation, yet there was a significant positive relationship between relative predation and the local index of collocation (Fig. 6). For adult walleye pollock, we found no apparent relationship between overlap and either total (Fig. 5) or relative predation (Supporting information).

The lack of significant correlations between relative predation and overlap indicates that changes in per-capita rates of consumption of juvenile pollock by predators may be driven by other factors beyond spatial overlap, such as allometric
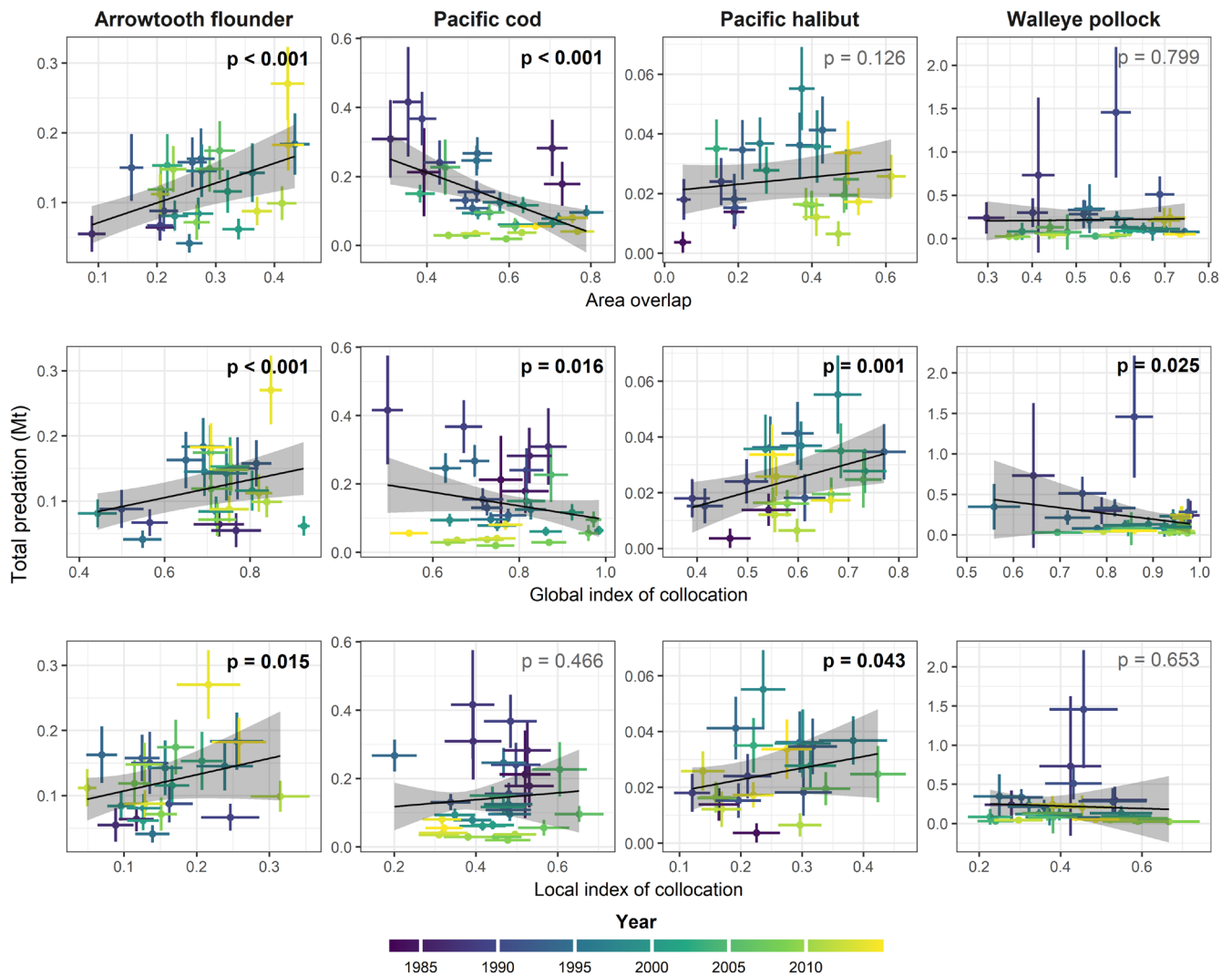
Figure 5. Bivariate scatterplots of predator–prey overlap metrics and total predation for each year, with vertical and horizontal error bars giving the standard deviation of the predictive distribution samples. Points are placed at the maximum-likelihood estimate. Regression lines represent the linear relationship between total predation and overlap at their respective annual maximum likelihood estimates, with 95% confidence bands computed using samples from the predictive distribution of each variable. p-values less than 0.05 are bolded.

and thermal effects on metabolism and consumption rates. Additionally, estimated coefficients and confidence intervals remained largely unchanged after including juvenile pollock biomass in regressions of total and relative predation against overlap (Supporting information). Together, these results suggest that increases in total predation by arrowtooth flounder and Pacific halibut resulted from increased spatial overlap with juvenile pollock, and not solely from increases in the abundance of juvenile pollock along the EBS shelf, nor from changes in predator dietary composition.

Discussion

As marine species redistribute in a warming climate, changes in the extent of spatial overlap between species and their predators, prey and competitors are likely to alter ecological interactions, drive changes in abundance and have cascading impacts on food webs (Bindoff et al. 2019, Lotze et al. 2019, Reum et al. 2020, Whitehouse et al. 2021). In this study, we quantified the effect of shifts in species distributions on trophic interactions using more than three decades of abundance and diet data for predators of juvenile walleye pollock, an ecologically and commercially important groundfish species in the eastern Bering Sea, Alaska. We found that recent shifts in the distributions of groundfish in the EBS have increased the extent of spatial overlap between juvenile walleye pollock and their predators, and that for two such predators – arrowtooth flounder and Pacific halibut – increased overlap with juvenile walleye pollock has resulted in increased predation on pollock. In contrast, we found that even as the area of the EBS shelf in which Pacific cod and juvenile pollock co-occur increased, predation on pollock by cod has decreased. Our results suggest that current and future changes in spatial
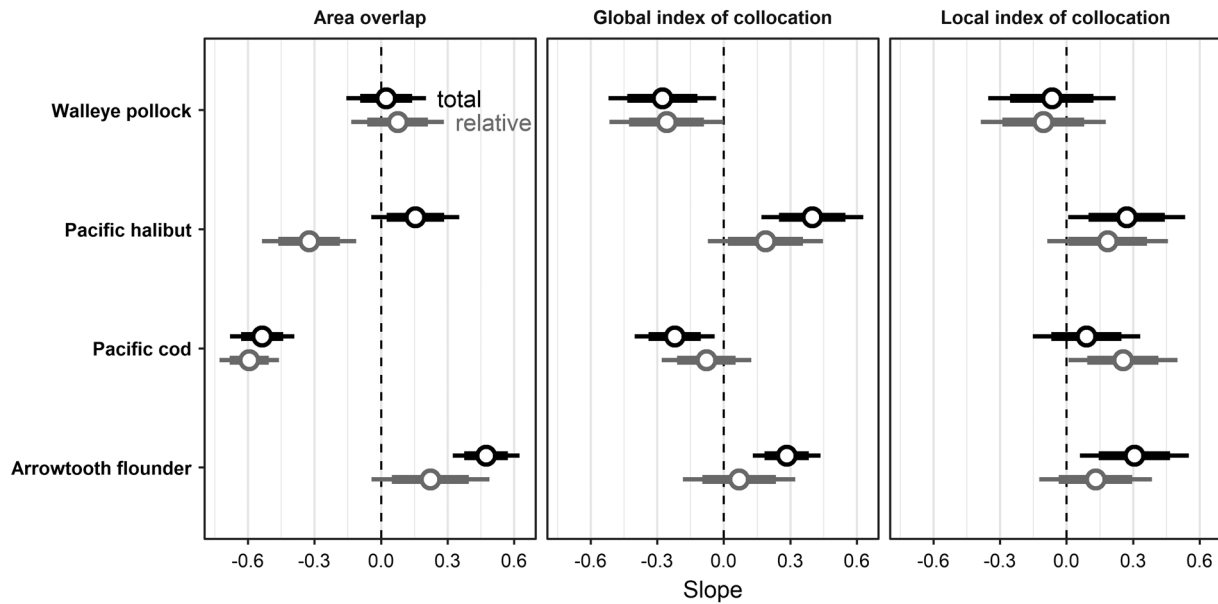
Figure 6. Standardized slope coefficients assessing the linear relationship of each overlap metric with total (black) and relative (grey) predation, estimated by aggregating samples from the predictive distribution. Points are placed at the maximum-likelihood estimate. 95% and 80% confidence intervals are given assuming a normal approximation to the sampling distribution.

overlap between predators and prey can, but may not always, drive changes in consumption.

Our results demonstrate that it is essential to consider the ecology of individual predator–prey couplets when inferring species interaction rates from coupled species distribution shifts. Notably, while each of these species may be considered 'generalist' predators, stomach contents data indicate that juvenile pollock constitute the most common prey item for both arrowtooth flounder and Pacific halibut, but are (in most years) a relatively infrequent prey for Pacific cod and adult pollock (Buckley et al. 2016, Livingston et al. 2017). Thus, our results suggest that prey switching and the availability of other prey species may decouple predator–prey interactions from changes in spatial predator–prey overlap (sensu the oscillating control hypothesis; Coyle et al. 2011, Hunt et al. 2011), and that increases in overlap may best predict changes in predation for more 'specialist' predators for which specific predation rates are expected to be more closely tied to prey availability. For the predators considered, increases in overlap with juvenile pollock did not generally result in prey-switching to juvenile pollock (as evidenced by the lack of relationships between relative predation and overlap), possibly because of concurrent shifts in the distributions or abundances of other prey species. Practically, it is also possible that changes in spatial overlap, measured in two dimensions and at grid-scale resolutions, may not accurately reflect fine-scale rates of encounter in three dimensions due to predator foraging behavior, differences in the vertical distribution of predators and prey in the water column, and prey patchiness (Bergström and Englund 2004). For example, juvenile pollock display vertical migratory behavior which depends on several factors including light, temperature and body condition, such that the separation between juvenile

pollock and an opportunistic predator in the water column may have complex environmental dependencies (Francis and Bailey 1983, Bailey 1989, Olla et al. 1996, Sogard and Olla 1996). Finally, environmental changes may directly mediate trophic interactions through kinetic effects on consumption, driving both predator–prey overlap and changes in per-capita interaction rates (Englund et al. 2011, Holsman and Aydin 2015, Barnes et al. 2020). While our results highlight the importance of predator diet composition in mediating the relationship between spatial overlap and trophic interactions, factors beyond diet may interact to influence ecological outcomes from biogeographic range shifts.

The three spatial predator–prey overlap metrics employed in this study to estimate overlap between juvenile pollock and their predators (area overlap, the global index of collocation and the local index of collocation) describe overlap in fundamentally different ways yet each provide utility in predicting predation on juvenile pollock by both flounder and halibut. This is surprising because trophic interactions are dependent on the local density of both predators and prey (Holling 1959), but area overlap and other binary overlap metrics do not directly reflect changes in density (Carroll et al. 2019, Suraci et al. 2022) and there need not be overlap at fine scales for two species to have a high global index of collocation (Kotwicki and Lauth 2013). Still, the local index of collocation, which can be loosely interpreted as a proxy for predator–prey encounter rates (Carroll et al. 2019), is the only overlap metric used in this study which is positively correlated with both total and relative predation across three species of predators, indicating that it may most closely reflect the scale of spatial interactions necessary for enhancing predation opportunities. The shared utility of these metrics as proxies for predation may be unique to the

EBS shelf, and perhaps similar large marine ecosystems which show relatively little fine scale habitat structure (Laman et al. 2017). However, our results indicate that for some species and ecosystems, broad-scale distributional inferences using either encounter or abundance data may still provide useful approximations of trophic interactions.

More directly, our results provide novel insights into the EBS ecosystem and the implications of future environmental change. Previous studies have shown that warmer years, characterized by a less extensive cold pool, result in greater abundances of groundfish predators such as arrowtooth flounder along the middle EBS shelf (Spencer 2008, Ciannelli et al. 2012, Spencer et al. 2016), drive increases in overlap between arrowtooth flounder and other groundfish including juvenile pollock (Hollowed et al. 2012, Hunsicker et al. 2013, Carroll et al. 2019), and potentially drive increases in pollock predation mortality (Spencer et al. 2016). Across three metrics of overlap, our results confirm that spatial overlap between arrowtooth flounder and juvenile pollock has indeed increased in recent decades and indicate that increases in overlap have driven increased predation on juvenile pollock. As climate change continues to drive declines in winter sea ice and subsequent summer cold-pool extent (Wang et al. 2012, Hermann et al. 2016, 2019), arrowtooth flounder are expected to occupy a larger extent of the EBS shelf (Rooper et al. 2021), and are likely to become an increasingly important source of predation mortality for walleye pollock (Holsman et al. 2020b). As is the case for arrowtooth flounder, previous studies have implicated the extent of the EBS cold pool as a driver of increased overlap between juvenile and adult pollock (Mueter et al. 2007, Thorson et al. 2021) and, consequently, increased rates of cannibalism (Wespestad et al. 2000, Coyle et al. 2011, Boldt et al. 2012). While we did find that overlap between juvenile and adult pollock has increased in recent decades, in contrast to Wespestad et al. (2000), we found no general relationship between the degree of spatial overlap between juvenile and adult pollock and conspecific total and relative predation. While adult pollock typically predate upon juveniles at lower rates than other predators examined here, pollock biomass far exceeds that of other predators (Fig. 4), and cannibalism is therefore typically the greatest source of predation mortality (which we did not evaluate) on juvenile pollock (Holsman et al. 2020a, b). Thus, further research describing the combined conditions that promote pollock cannibalism, including (for example) climate-driven changes in the abundance of other prey species, will be crucial for predicting the future dynamics of this species in a warming climate (Coyle et al. 2011, Hunt et al. 2011). For example, future analyses could incorporate fine-scale environmental covariates such as temperature, and spatially-varying responses to broad-scale environmental indices such as cold-pool extent, to further discern the relationship between climate, overlap and predation on juvenile pollock in the EBS region (Boldt et al. 2012, Thorson 2019b, Holsman et al. 2020b).

That predation scales with overlap for two of the four predators studied here indicates that coupled species distribution shifts can have intuitive ecological consequences in some but not all cases. Determining how shifting species distributions shape trophic interactions across a suite of species and systems will require further research aimed at characterizing ecosystem dynamics in a changing climate. Process-based research coupling spatially-explicit models of species abundances with estimates of the parameters of the functional response (and, possibly, their dependence on the abiotic environment) may allow better, more realistic null hypothesis testing of the relationship between overlap and predation for various predator–prey couplets, and may provide better estimates of predation mortality with which to inform fisheries management. While it is apparent that local predator and prey densities influence trophic interaction rates, species interactions and foraging or predator avoidance behaviors can also have dramatic effects on observed species distributions, so advancements in joint species distribution modeling which incorporate 'teleconnections' among the ranges of different species may advance our understanding of the impacts of climate on predator–prey overlap and predation rates (Blanchet et al. 2020, Thorson et al. 2021). In cases where empirical assessments reveal clear relationships between predation and overlap (e.g. in this study, arrowtooth flounder and Pacific halibut), overlap indices may allow fisheries scientists to incorporate predator–prey overlap into multi-species and ecosystem models used for management (Holsman et al. 2020b), for which interaction rates are otherwise not informed by variability in species distributions (Greer and Woodson 2016). Where sufficient data exist, constructing models of three-dimensional spatial overlap may improve estimates of predator and prey densities, as well as estimates of overlap between predators and prey on fine scales (Bailey 1989, Link 2004).

Our results show that shifting species distributions in the EBS have driven changes in predation of juvenile pollock by at least two predators, that future changes in consumption driven by spatial overlap may be difficult to predict, and that even so, continued climate change is likely to have significant impacts on the population of walleye pollock in the EBS. We suggest that researchers attempting to infer ecological consequences from species distribution shifts should do so cautiously, because increases in spatial overlap between species are not, in and of themselves, evidential of increased predation. As climate change continues to drive changes in species distributions, impacts on interacting species and on their associated ecological communities will prove difficult to infer from species distribution models alone. However, with careful validation using process-based modeling approaches, simple metrics of spatial overlap between relatively specialized predators and their prey may offer promise as a means to incorporate the effects of species distribution shifts into climate-ready ecosystem-based fisheries management.

Author contributions

Maurice C. Goodman: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (equal); Software (lead); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Gemma Carroll**: Conceptualization (equal); Methodology (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal). **Stephanie Brodie**: Conceptualization (equal); Methodology (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal). **Arnaud Grüss**: Data curation (lead); Formal analysis (supporting); Methodology (supporting); Writing – review and editing (equal). **James T. Thorson**: Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Software (equal); Writing – review and editing (equal). **Stan Kotwicki**: Data curation (equal); Writing – review and editing (supporting). **Kirstin Holsman**: Conceptualization (equal); Resources (equal); Writing – review and editing (equal). **Rebecca L. Selden**: Resources (equal); Writing – review and editing (equal). **Elliott L. Hazen**: Conceptualization (equal); Supervision (equal); Writing – review and editing (equal). **Giulio A. De Leo**: Conceptualization (equal); Supervision (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.06084>.

Data availability statement

Data are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.6596456> (Goodman et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Albouy, C. et al. 2014. From projected species distribution to food-web structure under climate change. – Global Change Biol. 20: 730–741.

Alexander, J. M. et al. 2015. Novel competitors shape species' responses to climate change. – Nature 525: 515–518.

Alverson, D. L. and Pereyra, W. T. 1969. Demersal fish explorations in the northeastern Pacific ocean – an evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecasts. – J. Fish. Res. Board Canada 26: 1985–2001.

Bailey, K. 1989. Interaction between the vertical distribution of juvenile walleye pollock *Theragra chalcogramma* in the eastern Bering Sea, and cannibalism. – Mar. Ecol. Prog. Ser. 53: 205–213.

Barnes, C. L. et al. 2020. Development of a predation index to assess trophic stability in the Gulf of Alaska. – Ecol. Appl. 30: 1–17.

Bergström, U. and Englund, G. 2004. Spatial scale, heterogeneity and functional responses. – J. Anim. Ecol. 73: 487–493.

Bindoff, N. L. et al. 2019. Changing ocean, marine ecosystems and dependent communities. – In: Pörtner, H.-O. et al. (eds), IPCC special report on the ocean and cryosphere in a changing climate. IPCC, pp. 477–587.

Blanchet, F. G. et al. 2020. Co-occurrence is not evidence of ecological interactions. – Ecol. Lett. 23: 1050–1063.

Boldt, J. L. et al. 2012. Factors influencing cannibalism and abundance of walleye pollock *Theragra chalcogramma* on the eastern Bering Sea shelf, 1982–2006. – Fish. Bull. 110: 293–306.

Boukal, D. S. et al. 2019. Species interactions under climate change: connecting kinetic effects of temperature on individuals to community dynamics. – Curr. Opin. Insect Sci. 35: 88–95.

Buckley, T. W. et al. 2016. Summer diet composition of walleye pollock and predator–prey relationships with copepods and euphausiids in the eastern Bering Sea, 1987–2011. – Deep. Res. Part II Top. Stud. Oceanogr. 134: 302–311.

Carroll, G. et al. 2019. A review of methods for quantifying spatial predator–prey overlap. – Global Ecol. Biogeogr. 28: 1561–1577.

Chyan-Huei Lo, N. et al. 1992. Indices of relative abundance from fish spotter data based on delta-lognormal models. – Can. J. Fish. Aquat. Sci. 49: 2515–2526.

Ciannelli, L. et al. 2012. Non-additive and non-stationary properties in the spatial distribution of a large marine fish population. – Proc. R. Soc. B 279: 3635–3642.

Coyle, K. O. et al. 2011. Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the oscillating control hypothesis. – Fish. Oceanogr. 20: 139–156.

Deslauriers, D. et al. 2017. Fish Bioenergetics 4.0: an R-based modeling application. – Fisheries 42: 586–596.

Domenici, P. et al. 2019. The effect of climate change on the escape kinematics and performance of fishes: implications for future predator–prey interactions. – Conserv. Physiol. 7: coz078.

Durant, J. M. et al. 2007. Climate and the match or mismatch between predator requirements and resource availability. – Clim. Res. 33: 271–283.

Edwards, E. K. et al. 2015. The impact of high temperatures on foraging behaviour and body condition in the Western Australian magpie *Cracticus tibicen dorsalis*. – Ostrich 86: 137–144.

Englund, G. et al. 2011. Temperature dependence of the functional response. – Ecol. Lett. 14: 914–921.

Evans, M. R. and Moustakas, A. 2018. Plasticity in foraging behaviour as a possible response to climate change. – Ecol. Inform. 47: 61–66.

Francis, R. C. and Bailey, K. M. 1983. Factors affecting recruitment of selected gadoids in the northeast Pacific and east Bering Sea. – In: Wooster, W. S. (ed.), From year to year: interannual variability of the environment and fisheries of the Gulf of Alaska and the Eastern Bering Sea. Washington Sea Grant, Univ. of Washington Press, pp. 17–29.

Fredston, A. et al. 2020. Range edges of North American marine species are tracking temperature over decades. – Global Change Biol. 27: 3145–3156.

Gilman, S. E. et al. 2010. A framework for community interactions under climate change. – Trends Ecol. Evol. 25: 325–331.

Goodman, M. C. et al. 2022. Data from: Shifting fish distributions impact predation intensity in a sub-Arctic ecosystem. – Zenodo Digital Repository, <https://doi.org/10.5281/zenodo.6596456>.

Gravel, D. et al. 2019. Bringing Elton and Grinnell together: a quantitative framework to represent the biogeography of ecological interaction networks. – Ecography 42: 401–415.

Greer, A. T. and Woodson, C. B. 2016. Application of a predator–prey overlap metric to determine the impact of sub-grid scale feeding on ecosystem productivity. – ICES J. Mar. Sci. 73: 1051–1061.

Grüss, A. et al. 2018. Producing distribution maps for informing ecosystem-based fisheries management using a comprehensive survey database and spatio-temporal models. – ICES J. Mar. Sci. 75: 158–177.

Grüss, A. et al. 2020. Spatio-temporal analyses of marine predator diets from data-rich and data-limited systems. – Fish Fish. 21: 718–739.

Grüss, A. et al. 2021. Synthesis of interannual variability in spatial demographic processes supports the strong influence of cold-pool extent on eastern Bering Sea walleye pollock *Gadus chalcogrammus*. – Prog. Oceanogr. 194: 102569.

Harley, C. D. G. 2003. Abiotic stress and herbivory interact to set range limits across a two-dimensional stress gradient. – Ecology 84: 1477–1488.

Hermann, A. J. et al. 2016. Projected future biophysical states of the Bering Sea. – Deep. Res. Part II Top. Stud. Oceanogr. 134: 30–47.

Hermann, A. J. et al. 2019. Projected biophysical conditions of the Bering Sea to 2100 under multiple emission scenarios. – ICES J. Mar. Sci. 76: 1280–1304.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. – Can. Entomol. 91: 293–320.

Hollowed, A. B. et al. 2012. Effects of climate variations on pelagic ocean habitats and their role in structuring forage fish distributions in the Bering Sea. – Deep. Res. Part II Top. Stud. Oceanogr. 65–70: 230–250.

Holsman, K. K. and Aydin, K. 2015. Comparative methods for evaluating climate change impacts on the foraging ecology of Alaskan groundfish. – Mar. Ecol. Prog. Ser. 521: 217–235.

Holsman, K. K. et al. 2016. Multi-species stock assessment for walleye pollock, Pacific cod and arrowtooth flounder in the eastern Bering Sea. – NPFMC Bering Sea and Aleutian Islands stock assessment and fishery evaluation, pp. 181–218.

Holsman, K. K. et al. 2019. Climate effects and bottom–up controls on growth and size-at-age of Pacific halibut *Hippoglossus stenolepis* in Alaska (USA). – Fish. Oceanogr. 28: 345–358.

Holsman, K. K. et al. 2020a. Ecosystem-based fisheries management forestalls climate-driven collapse. – Nat. Commun. 11: 4579.

Holsman, K. K. et al. 2020b. Climate-enhanced multi-species stock assessment for walleye pollock, Pacific cod and arrowtooth flounder in the South Eastern Bering Sea. – NPFMC Bering Sea and Aleutian Islands stock assessment and fishery evaluation, pp. 1–42.

Hunsicker, M. E. et al. 2013. Climate and demography dictate the strength of predator–prey overlap in a subarctic marine ecosystem. – PLoS One 8: e66025.

Hunt, G. L. et al. 2011. Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the oscillating control hypothesis. – ICES J. Mar. Sci. 68: 1230–1243.

Hurlbert, S. 1978. The measurement of niche overlap and some relatives. – Ecology 59: 67–77.

Kharouba, H. M. et al. 2018. Global shifts in the phenological synchrony of species interactions over recent decades. – Proc. Natl Acad. Sci. USA 115: 5211–5216.

Kordas, R. L. et al. 2011. Community ecology in a warming world: the influence of temperature on interspecific interactions in marine systems. – J. Exp. Mar. Biol. Ecol. 400: 218–226.

Kotwicki, S. and Lauth, R. R. 2013. Detecting temporal trends and environmentally-driven changes in the spatial distribution of bottom fishes and crabs on the eastern Bering Sea shelf. – Deep. Res. Part II Top. Stud. Oceanogr. 94: 231–243.

Kotwicki, S. et al. 2014. Correcting density-dependent effects in abundance estimates from bottom-trawl surveys. – ICES J. Mar. Sci. 71: 1107–1116.

Kristensen, K. et al. 2016. TMB: automatic differentiation and laplace approximation. – J. Stat. Softw. 70: 1–21.

Laman, E. A. et al. 2017. Model-based essential fish habitat definitions for bering sea groundfish species. – NOAA Fisheries.

Lauth, R. R. et al. 2019. Results of the 2017 Eastern and Northern Bering Sea continental shelf bottom trawl survey of groundfish and invertebrate fauna. – NOAA Tech. Memo.

Lemoine, N. P. et al. 2013. Increased temperature alters feeding behavior of a generalist herbivore. – Oikos 122: 1669–1678.

Lindgren, F. et al. 2011. An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. – J. R. Stat. Soc. Ser. B Stat. Methodol. 73: 423–498.

Link, J. S. 2004. Using fish stomachs as samplers of the benthos: integrating long-term and broad scales. – Mar. Ecol. Prog. Ser. 269: 265–275.

Livingston, P. A. et al. 2017. Quantifying food web interactions in the North Pacific – a data-based approach. – Environ. Biol. Fish. 100: 443–470.

Lotze, H. K. et al. 2019. Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. – Proc. Natl Acad. Sci. USA 116: 12907–12912.

Martin, T. G. et al. 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. – Ecol. Lett. 8: 1235–1246.

Mueter, F. J. and Litzow, M. A. 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. – Ecol. Appl. 18: 309–320.

Mueter, F. J. et al. 2007. Recruitment and survival of Northeast Pacific Ocean fish stocks: temporal trends, covariation and regime shifts. – Can. J. Fish. Aquat. Sci. 64: 911–927.

Mueter, F. J. et al. 2011. Expected declines in recruitment of walleye pollock *Theragra chalcogramma* in the eastern Bering Sea under future climate change. – ICES J. Mar. Sci. 68: 1284–1296.

Northfield, T. D. et al. 2017. A spatial theory for emergent multiple predator–prey interactions in food webs. – Ecol. Evol. 7: 6935–6948.

Olla, B. L. et al. 1996. Behavioral determinants of distribution and survival in early stages of walleye pollock, *Theragra chalcogramma*: a synthesis of experimental studies. – Fish. Oceanogr. 5: 167–178.

Ortiz, I. et al. 2016. Climate to fish: synthesizing field work, data and models in a 39-year retrospective analysis of seasonal processes on the eastern Bering Sea shelf and slope. – Deep. Res. Part II Top. Stud. Oceanogr. 134: 390–412.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change. – Nature 421: 37–42.

Pecl, G. T. et al. 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. – Science 355: eaai9214.

Pepi, A. et al. 2018. As temperature increases, predator attack rate is more important to survival than a smaller window of prey vulnerability. – Ecology 99: 1584–1590.

Pinsky, M. L. et al. 2013. Marine taxa track local climate velocities. – Science 341: 1239–1243.

Pinsky, M. L. et al. 2020. Climate-driven shifts in marine species ranges: scaling from organisms to communities. – Ann. Rev. Mar. Sci. 12: 153–179.

Rall, B. C. et al. 2010. Temperature, predator–prey interaction strength and population stability. – Global Change Biol. 16: 2145–2157.

Reum, J. C. P. et al. 2020. Ensemble projections of future climate change impacts on the eastern Bering Sea food web using a multispecies size spectrum model. – Front. Mar. Sci. 7: 124.

Rooper, C. N. et al. 2021. Predicted shifts of groundfish distribution in the eastern Bering Sea under climate change, with implications for fish populations and fisheries management. – ICES J. Mar. Sci. 78: 220–234.

Saraux, C. et al. 2014. Spatial structure and distribution of small pelagic fish in the northwestern Mediterranean Sea. – PLoS One 9: e111211.

Schleuning, M. et al. 2020. Trait-based assessments of climate-change impacts on interacting species. – Trends Ecol. Evol. 35: 319–328.

Selden, R. L. et al. 2018. Diversity in thermal affinity among key piscivores buffers impacts of ocean warming on predator–prey interactions. – Global Change Biol. 24: 117–131.

Sogard, S. M. and Olla, B. L. 1996. Diel patterns of behavior in juvenile walleye pollock, *Theragra chalcogramma*. – Environ. Biol. Fish. 47: 379–386.

Somerton, D. A. and Weinberg, K. L. 2001. The affect of speed through the water on footrope contact of a survey trawl. – Fish. Res. 53: 17–24.

Spencer, P. D. 2008. Density-independent and density-dependent factors affecting temporal changes in spatial distributions of eastern Bering Sea flatfish. – Fish. Oceanogr. 17: 396–410.

Spencer, P. D. et al. 2016. Modelling spatially dependent predation mortality of eastern Bering Sea walleye pollock, and its implications for stock dynamics under future climate scenarios. – ICES J. Mar. Sci. 73: 1330–1342.

Suraci, J. P. et al. 2022. Beyond spatial overlap: harnessing new technologies to resolve the complexities of predator–prey interactions. – Oikos 2022: e09004.

Thorson, J. T. 2018. Three problems with the conventional delta-model for biomass sampling data, and a computationally efficient alternative. – Can. J. Fish. Aquat. Sci. 75: 1369–1382.

Thorson, J. T. 2019a. Guidance for decisions using the vector autoregressive spatio-temporal (VAST) package in stock, ecosystem, habitat and climate assessments. – Fish. Res. 210: 143–161.

Thorson, J. T. 2019b. Measuring the impact of oceanographic indices on species distribution shifts: the spatially varying effect of cold-pool extent in the eastern Bering Sea. – Limnol. Oceanogr. 64: 2632–2645.

Thorson, J. T. et al. 2016. Model-based inference for estimating shifts in species distribution, area occupied and centre of gravity. – Methods Ecol. Evol. 7: 990–1002.

Thorson, J. T. et al. 2021. Forecasting community reassembly using climate-linked spatio-temporal ecosystem models. – Ecography 44: 612–625.

Wang, M. et al. 2012. Future climate of the Bering and Chukchi Seas projected by global climate models. – Deep. Res. Part II Top. Stud. Oceanogr. 65–70: 46–57.

Weinberg, K. L. and Kotwicki, S. 2008. Factors influencing net width and sea floor contact of a survey bottom trawl. – Fish. Res. 93: 265–279.

Wespestad, V. G. et al. 2000. On relationships between cannibalism, climate variability, physical transport and recruitment success of Bering Sea walleye pollock *Theragra chalcogramma*. – ICES J. Mar. Sci. 57: 272–278.

Whitehouse, G. A. et al. 2021. Bottom–up impacts of forecasted climate change on the eastern Bering Sea food web. – Front. Mar. Sci. 8: 624301.

Woillez, M. et al. 2007. Indices for capturing spatial patterns and their evolution in time, with application to European hake *Merluccius merluccius* in the Bay of Biscay. – ICES J. Mar. Sci. 64: 537–550.

Yang, L. H. and Rudolf, V. H. W. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. – Ecol. Lett. 13: 1–10.