


RESEARCH REVIEW

A review of methods for quantifying spatial predator–prey overlap

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Funding information

NOAA Fisheries and the Environment

Editor: Pedro Peres-Neto

Abstract

Background: Studies that attempt to measure shifts in species distributions often consider a single species in isolation. However, understanding changes in spatial overlap between predators and their prey might provide deeper insight into how species redistribution affects food web dynamics.

Predator–prey overlap metrics: Here, we review a suite of 10 metrics [range overlap, area overlap, the local index of collocation (Pianka's *O*), Hurlbert's index, biomass-weighted overlap, asymmetrical alpha, Schoener's *D*, Bhattacharyya's coefficient, the global index of collocation and the AB ratio] that describe how two species overlap in space, using concepts such as binary co-occurrence, encounter rates, spatial niche similarity, spatial independence, geographical similarity and trophic transfer. We describe the specific ecological insights that can be gained using each overlap metric, in order to determine which is most appropriate for describing spatial predator–prey interactions for different applications.

Simulation and case study: We use simulated predator and prey distributions to demonstrate how the 10 metrics respond to variation in three types of predator–prey interactions: changing spatial overlap between predator and prey, changing predator population size and changing patterns of predator aggregation in response to prey density. We also apply these overlap metrics to a case study of a predatory fish (arrowtooth flounder, *Atheresthes stomias*) and its prey (juvenile walleye pollock, *Gadus chalcogrammus*) in the Eastern Bering Sea, AK, USA. We show how the metrics can be applied to understand spatial and temporal variation in the overlap of species distributions in this rapidly changing Arctic ecosystem.

Conclusions: Using both simulated and empirical data, we provide a roadmap for ecologists and other practitioners to select overlap metrics to describe particular aspects of spatial predator–prey interactions. We outline a range of research and management applications for which each metric may be suited.

KEYWORDS

arrowtooth flounder, climate change, cold pool, Eastern Bering Sea, ecosystem models, predator–prey overlap, spatial overlap, species distribution models, species interactions, walleye pollock

1 | INTRODUCTION

Global environmental change is causing species distributions to shift at an accelerating rate, with species moving into new areas and disappearing from their former ranges (Lawing & Polly, 2011). However, species are not moving one at a time or in isolation. Instead, the distributions of entire communities are shifting, and there is a growing need to understand how these changes affect trophic interactions (Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010; Tylianakis, Didham, Bascompte, & Wardle, 2008). For example, climate-induced changes in habitat and phenology may drive differential responses in the distributions of predators and their prey (Durant, Hjermmann, Ottersen, & Stenseth, 2007; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Schweiger et al., 2012; Siddon et al., 2013). This may result in increased (Vors & Boyce, 2009) or reduced (Asch, 2015; Schweiger, Settele, Kudrna, Klotz, & Kühn, 2008) predation opportunities. These increased matches or mismatches in species distributions may have cascading effects, including directional changes in the abundance of predator or prey populations (Durant et al., 2007; Northfield, Barton, & Schmitz, 2017), predators switching prey types (Latham, Latham, Knopff, Hebblewhite, & Boutin, 2013), or changes in competition dynamics within predator guilds (Northfield et al., 2017). Understanding how predator–prey interactions respond to external pressures is therefore essential for predicting how ecosystems will respond to change (Araújo & Luoto, 2007) and for making informed ecosystem-based management decisions (Pikitch et al., 2004).

Indices that summarize spatial overlap between co-occurring species provide simple metrics that can describe the potential strength of their ecological interactions (Hurlbert, 1978). When applied to predictions of species distributions, information on changes in overlap can increase our ability to project realistic ecological outcomes for interacting species (Guisan & Thuiller, 2005; Schweiger et al., 2012), thereby better informing resource management and spatial conservation planning. Overlap metrics can also add time-varying and spatially explicit attributes to ecological and ecosystem models (e.g., size-spectrum models and multispecies stock assessment models). Within these models, spatial interactions between predator and prey species are often poorly resolved at resolutions most relevant to their ecology, which may complicate interpretations of how spatial overlap influences ecosystem dynamics (Greer & Woodson, 2016). Likewise, temporal changes in overlap between life stages of cannibalistic or competitive conspecifics could bias estimates of density-dependent controls on species productivity (Sigler et al., 2016). Incorporating an overlap metric can increase the capacity of these models to predict the impacts of future environmental change on ecosystem function more accurately (Greer & Woodson, 2016).

A number of overlap metrics have been developed for ecological applications. These metrics have been applied to diverse ecological questions, including the examination of niche equivalency of species in environmental space (Broennimann et al., 2012; Warren, Glor, & Turelli, 2008), overlap of animal home ranges (Fieberg & Kochanny, 2005), overlap in dietary niche among competitors (Woodward &

Hildrew, 2002), and changes in resource partitioning among species after environmental perturbations (Fattorini et al., 2017). Several reviews of overlap metrics have discussed their mathematical and biological properties and have investigated sources of bias and error (e.g., Hurlbert, 1978; Krebs, 1989; Rödder & Engler, 2011). However, there remains a clear need to understand the specific ecological insights that can be gained using each overlap metric, in order to determine which is most appropriate for describing spatial predator–prey interactions for different applications.

Here, we provide a review of metrics that can be used to quantify spatial overlap between two species. To determine how the metrics resolve spatial predator–prey dynamics, we examine the behaviour of the metrics when applied to simulations of varying predator and prey density distributions. Furthermore, we apply the metrics to spatial interactions between a predatory fish (arrowtooth flounder, *Atheresthes stomias*) and its prey (juvenile walleye pollock, *Gadus chalcogrammus*) in the Eastern Bering Sea, AK, USA. This case study demonstrates how the metrics can track changes in species overlap driven by differential responses to environmental variability. By summarizing the properties of available overlap metrics and illustrating their behaviour in response to various ecological scenarios, we aim to assist ecologists in the selection of appropriate metrics with which to quantify spatial predator–prey overlap for different purposes.

2 | METHODS

2.1 | Overlap metric description

Here we present 10 overlap metrics and their ecological interpretations (Table 1), separating them into descriptive categories to aid with ecological understanding. This is not a comprehensive suite of all available metrics, but instead represents a spectrum of metrics that are commonly used in ecology to measure horizontal overlap between two species distributions, including metrics that are particularly relevant for understanding predator–prey interactions. The metrics we have chosen provide population-level estimates of overlap for non-continuous survey data. Other scales of spatial overlap between species, such as patchiness, were not included within the scope of this paper (but see e.g., Fauchald & Erikstad, 2002; Greer, Woodson, Smith, Guigand, & Cowen, 2016; Saraux et al., 2014).

2.2 | Binary co-occurrence

For some applications, a metric of the co-occurrence of two species may be sufficient to describe changes in spatial overlap (Selden, Batt, Saba, & Pinsky, 2018). These metrics are particularly useful when data on occurrence but not biomass are available, such as for rare species. Co-occurrence can be described in many ways, including the proportion of one species' range where the other species also occurs ("range overlap"; Araújo, Rozenfeld, Rahbek, & Marquet, 2011; Kernohan, Gitzen, & Millsaugh, 2001), or the proportion of a predefined study area where both species

TABLE 1 Ecological description of each predator–prey overlap metric, ecological questions for which they are suitable, equations, types of data that are suitable for input, whether the metric returns a symmetrical result for predator and prey, whether the metric ranges from zero to one, and citations

Metric	Metric type	Description	Suitability	Equation	Data type	Symmetry	0–1	Reference
Area overlap	Binary co-occurrence	Measures the proportion of all sampled locations across a predefined area where species co-occur	Suitable for estimating area of co-occurrence across a predefined region	$A_{pred, prey} / A_{total}$	Occurrence	Yes	Yes	Saraux et al. (2014)
Range overlap	Binary co-occurrence	Measures the proportion of one species' range where the other co-occurs	Suitable for estimating influence of one species on another based on their co-occurrence	$A_{pred, prey} / A_{prey}$	Occurrence	No	Yes	Araújo et al. (2011)
Local index of collocation	Encounter	Measures co-occurrence by estimating the correlation of predator and prey densities	Suitable for estimating encounter rates	$\frac{\sum_i (p_i \cdot pred_i + p_i \cdot prey_i)}{\sqrt{\sum_i p_i \cdot pred_i^2} \sqrt{\sum_i p_i \cdot prey_i^2}}$	Biomass	Yes	Yes	Pianka (1973), Bez and Rivoirard (2000)
Asymmetrical alpha	Encounter	Measures the competitive pressure of predator on prey	Suitable for estimating encounter rates relative to prey encounter	$\frac{\sum_i (p_i \cdot pred_i + p_i \cdot prey_i)}{\sqrt{\sum_i p_i \cdot pred_i^2}}$	Biomass	No	Yes	Levin (1968)
Biomass-weighted overlap index	Encounter	Measures amount of predator biomass interacting with prey (scaled to maximum prey density)	Useful where relative biomass of predator and prey is of interest	$\frac{\sum_i [pred_i / \max(pred_i + prey_i) \cdot \max(pred_i)]}{\sum_i pred_i / \max(pred_i)}$	Biomass	No	No	
Hurlbert's index	Encounter	Measures interspecific encounter rate between predator and prey	Suitable for estimating encounter rates where resources vary in abundance	$\sum_i \left(\frac{p_i \cdot pred_i + p_i \cdot prey_i}{A_i / A_{occupied}} \right)$	Biomass	Yes	No	Hurlbert (1978)
Schoener's D	Niche equivalency	Measures how equally predator and prey use space relative to its availability	Suitable to understand niche equivalency in spatial resource use	$1 - 0.5 * \sum_i p_i \cdot pred_i - p_i \cdot prey_i $	Biomass or occurrence	Yes	Yes	Schoener (1970)
Bhattacharyya's coefficient	Spatial independence	Measures statistical affinity between two distributions	Suitable for estimating independence in use of space between two populations	$\sum_i \sqrt{p_i \cdot pred_i * p_i \cdot prey_i}$	Biomass or occurrence	Yes	Yes	Bhattacharyya (1943)
Global index of collocation	Geographical similarity	Measures geographical distinctness by comparing centres of gravity of populations with the dispersion of sampled individuals	Suitable for estimating spatial overlap at a regional scale	where: $CG_{pred} = \frac{\sum_i i \cdot pred_i}{pred_i}$ and: $I_{pred} = \frac{\sum_i (i - CG)^2 * pred_i}{pred_i}$	Biomass	Yes	Yes	Bez and Rivoirard (2000)
AB ratio	Trophic transfer	Measures predator production that can be attributed to spatial overlap with prey	Suitable for understanding trophic implications of fine-scale predator–prey overlap	$\frac{pred_i - pred_i \cdot prey_i}{pred_i \cdot prey_i}$	Biomass	No	No	Greer and Woodson (2016)

Note: In the equations, $pred_i$ and $prey_i$ are densities of predator and prey in a given area, $p_i \cdot pred_i$ and $p_i \cdot prey_i$ are the proportions of the total number of predator and prey in a given area, A_{pred} and A_{prey} are the total areas occupied by the predator and prey, $A_{pred, prey}$ is the area occupied by both species, $A_{occupied}$ is the total area occupied by at least one of the species, A_{total} is the total size of the study area, CG is the centre of gravity, and I is inertia.

co-occur ("area overlap"; Saraux et al., 2014). These metrics both range from zero to one. Binary co-occurrence metrics are simple to interpret but do not discriminate between areas with high and low population density and therefore provide limited insight into the potential strength of interactions between species where they co-occur.

2.3 | Encounter

Where biomass or abundance data are available from standardized surveys, an alternative approach to the co-occurrence metrics is the "local index of collocation" (also "Pianka's O "; Bez & Rivoirard, 2000; Pianka, 1973). This metric assesses the co-occurrence of two populations using the proportion of their total biomass found at each sampling point and determines the degree of correlation between two density distributions. This can broadly be thought of as describing the ratio of the probability of interspecific (predator-prey) encounters to the probability of all intraspecific encounters (the product of both predator-predator and prey-prey encounters).

Similar metrics extend this approach, with the "asymmetrical alpha" reflecting the ratio of the probability of predator-prey encounters to the probability of prey-prey encounters only (Levins, 1968). This asymmetrical approach gives insight into the amount of pressure exerted by the predator on the prey. Another asymmetrical metric ("biomass-weighted overlap") is similar to the asymmetrical alpha but uses raw biomass rather than the proportion of total biomass located at each point. These values can be used to provide insight into the magnitude of predator biomass that can influence prey or can be scaled to the maximum values for predator and prey in a given year, in order to keep the range between zero and one. Biomass-weighted overlap may be useful when estimating potential consumptive demand (Chasco et al., 2017).

"Hurlbert's index" (Hurlbert, 1978) can be used to assess whether two species use space in proportion to its availability. Accounting for spatial availability is particularly relevant when considering spatial overlap across an arena where spatial units differ in area, because it accounts explicitly for resources of unequal sizes. Hurlbert's overlap is zero when species do not share space at all, one where both species occupy space in proportion to its availability, and more than one where species demonstrate preferences for particular spatial areas and these preferences coincide. Hurlbert's index is also the only encounter metric that explicitly accounts for the size of the area occupied by either species (rather than the size of the entire domain), making it sensitive to changes in the total area occupied by predator and prey.

2.4 | Spatial niche similarity

"Schoener's D " determines whether there is equivalency between the spatial niches occupied by two species (Schoener, 1970). This metric can be used either on the modelled probability of occurrence data or on estimates of abundance or density distributions to determine whether species occupy space in a similar way. In contrast to Hurlbert's index, a potential drawback of Schoener's D as

a predator-prey overlap metric is that it will return a high value of overlap in cases where both species co-occur across large areas at low densities or probabilities of occurrence, where their interaction is unlikely (i.e., their niche similarity is high because the absolute difference between their densities across these locations is low). Equally, this metric returns a low value of overlap in cases where predation pressure might be high, if there are many predators in some areas relative to the number of prey.

2.5 | Spatial independence

The "Bhattacharyya coefficient" is a statistical approach that can quantify the affinity between two probability density functions of spatial use, against the null assumption that the distributions are independent (Bhattacharyya, 1943). This approach is not derived from ecological theory but can be interpreted as assessing whether two populations use space independently of one another (Fieberg & Kochanny, 2005). In a similar fashion to Schoener's D , the Bhattacharyya coefficient can be applied to the modelled probability of occurrence data or on biomass-density values.

2.6 | Geographical similarity

An alternative to measuring overlap as the interaction between populations at the grid-cell level is to determine how geographically similar two distributions are across the entire study area ("global index of collocation"; Bez & Rivoirard, 2000). This can be done using geographical coordinates weighted by biomass, in order to determine the proximity of the centres of gravity of the two populations given the dispersion or "inertia" of individuals around that point. This approach describes spatial overlap at a regional scale, which may be useful for understanding broad patterns of overlap between two species, rather than fine-scale interactions. For example, a high global index of collocation for two species may not translate to high encounter or consumption rates if the species do not also co-occur at finer spatial scales (Saraux et al., 2014).

2.7 | Trophic transfer

Variability in predator density that can be explained by local prey density is a useful way of characterizing overlap, because it accounts for potential trophic transfer between species ("AB ratio"; Greer & Woodson, 2016). An AB ratio of zero indicates that the mean densities of predator and prey across the whole survey area accurately represent predator-prey encounters, whereas a value of one indicates 100% higher production of the predator as a result of fine-scale spatial overlap with prey, assuming a "Holling type I" functional response. Negative values can indicate different habitat preferences between species, or predator avoidance by the prey, where minus one represents complete avoidance. This metric provides insight into how trophic processes are likely to translate local prey abundance into predator production.

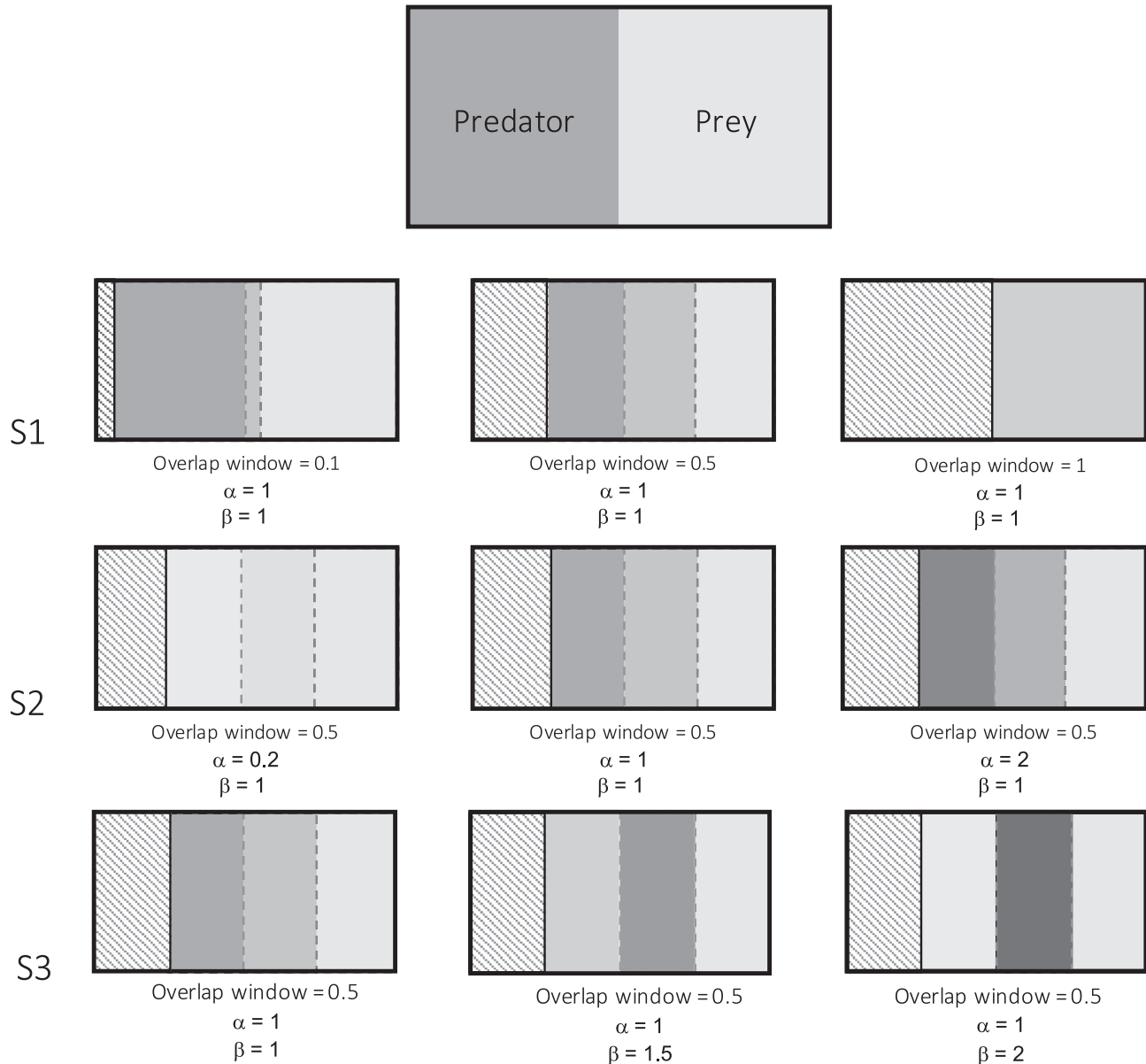


FIGURE 1 Schematic diagram showing three scenarios of spatial interaction between simulated populations of predator and prey: (S1) incremental change in the area of overlap between predator and prey (dashed lines), with predator density and aggregation response held constant; (S2) incremental change in predator density in response to prey density, with the overlap window and aggregation response held constant; and (S3) incremental change in the aggregation response of the predator to prey (density of predator increases in relationship to prey density only in the overlap window, while decreasing proportionally outside the overlap window), with the size of the overlap window and overall predator density held constant. In each panel, the predator is on the left and the prey on the right. The prey is shown in light grey, and the shade of the predator is manipulated to show increases or decreases in density. Areas where the predator and prey overlap are depicted using shades that are intermediate between the two densities, and hatched areas are where both species are absent

2.8 | Metric responses to simulated predator–prey interactions

2.8.1 | Simulated populations

To illustrate how various overlap metrics respond to shifting predator–prey dynamics, we simulated interacting predator and prey populations on a 200×100 gridded spatial domain. We included two ways of manipulating predator density in relationship to prey

density: changing “predator population size”, where predator density increased uniformly, and changing “predator aggregation”, where predator biomass shifted from areas where there were no prey into areas of high prey density, keeping total predator abundance constant across the domain. Although these ecological processes occur at different time-scales in the real world, we use the resulting distributions as snapshots to determine how different types of spatial interactions between predator and prey influence metric values.

On the gridded arena, we simulated unconditional Gaussian densities of a prey population ($D_{\text{prey},i}$) with moderate spatial autocorrelation (patchiness), using a spherical variogram model (sill = 0.35, nugget = 0.05, range = 10) in the R package *gstat* (Pebesma, 2004). We took the exponent of these values to obtain a lognormal distribution, to match right-skewed densities observed in natural populations. We then allowed predator density ($D_{\text{pred},i}$) to be influenced by three processes:

$$D_{\text{pred},i} = \alpha D_{\text{prey},i} + \beta \bar{D}_{\text{prey},s} + \delta_i$$

where α is a coefficient (ranging from zero to two) that controls the relationship between predator density and prey density ($D_{\text{prey},i}$) in a given cell (i), and β is a coefficient (ranging from zero to two) that controls the response of predator density to mean prey density within a specified search area, representing the "aggregation" response of predators to mean prey density ($\bar{D}_{\text{prey},s}$) within a neighbourhood of s grid cells around the cell of interest (i). The spatial variance term (δ_i) is a second log-density value generated using a spherical variogram model (sill = 0.2, nugget = 0.1, range = 9), added to represent spatial processes, such as habitat selection, that influence predator density independently of prey density.

2.8.2 | Scenarios of predator–prey interaction

Δ Overlap window

After generating predator and prey distributions across the whole 200×100 spatial domain using the above equation, we clipped the spatial domain into two distinct distributions of predator and prey, with dimensions of 100×100 each (Figure 1). We designated species as absent in the portion of the spatial domain outside their distribution. Keeping the size of the predator and prey distributions constant at 100×100 , we then manipulated the proportion of the distribution of the prey that was shared by the predator, from zero (where the two species shared no common cells) to one (where the two species overlapped completely), in 10% spatial increments. While changing the size of this overlap window, we left α ("population size" parameter) and β ("aggregation response" parameter) constant at one, and fixed s ("search area") to a window of nine cells (3×3), centred on the cell of interest.

Δ Predator population size

To simulate the influence of uniformly increasing predator density, we manipulated α from zero to two at intervals of 0.2. We left the overlap window constant at 0.5, search area at $s = 9$ and aggregation response at $\beta = 1$.

Δ Aggregation response of predator to prey

To simulate a change in the aggregative effect of prey on predator density, we manipulated the predator aggregation response from weaker to stronger (β from one to two at intervals of 0.1) within the overlap window, where predator and prey interacted directly. Simultaneously, we manipulated β from one to zero in the area

outside the overlap window, to ensure that the overall sum of predator densities was unchanged. For example, where predator density increased relative to prey density by a factor of 1.1 in the overlap window, it decreased by a factor of 0.9 across the rest of the range of the predator, to simulate the predator moving from areas of no prey to areas of high prey density. We fixed the overlap window at 0.5, "bottom-up" density response at $\alpha = 1$, and the search window, s , at nine.

2.8.3 | Application of overlap metrics

We applied the suite of 10 overlap metrics to the predator and prey distributions in each of the three scenarios (changing overlap window, changing predator population size and changing aggregation response) to characterize patterns of overlap. Given that the overlap metrics were influenced by the random variation in biomass distribution in each spatial model run, we calculated the mean value for each overlap metric for each of 500 iterations of predator and prey distributions in each of the three scenarios.

Functions to implement the predator–prey overlap metric equations in R are included as Supporting Information.

2.9 | Metric responses to predator–prey dynamics in the Eastern Bering Sea

To evaluate the performance of the overlap metrics on real ecological data, we present a case study of spatial dynamics between a predator (arrowtooth flounder, *Atheresthes stomias*) and prey (juvenile walleye pollock, *Gadus chalcogrammus*) in the Eastern Bering Sea, AK, USA. The arrowtooth flounder is a bottom-dwelling flatfish that has seen an eightfold increase in abundance on the Eastern Bering Sea shelf over the past 36 years (Wilderbuer, Nichol, & Aydin, 2010). It is a key predator of juvenile walleye pollock, an abundant forage fish in the Eastern Bering Sea ecosystem (Springer, 1992). The distributions of both species are influenced by the Eastern Bering Sea "cold pool" (Kotwicki & Lauth, 2013), a water mass on the seafloor that is defined by temperatures $< 2^\circ\text{C}$ and varies greatly in size between years as a function of sea ice extent during the previous winter (Stabeno et al., 2001). The study species have contrasting responses to the cold pool: juvenile pollock are more tolerant of cold water (Kotwicki & Lauth, 2013) and may use the cold pool as a refuge to avoid predation (Hollowed et al., 2012), whereas arrowtooth flounder are constrained to warmer water and generally avoid the cold pool (Ciannelli, Bartolino, & Chan, 2012; Spencer et al., 2016).

Previous work has demonstrated a potential increase in overlap between these two species as the biomass of flounder increases and the extent of the cold pool decreases (Hunsicker, Ciannelli, Bailey, Zador, & Stige, 2013). This results in increased predation pressure by arrowtooth flounder on juvenile pollock, affecting pollock recruitment and abundance, which creates a complex management issue for the Eastern Bering Sea (Hunsicker et al., 2013; Spencer et al., 2016). This relatively well-characterized example of changes

in predator–prey dynamics over a 36-year time series provides an opportunity to explore the behaviour of the overlap metrics when estimating real-world changes in spatial predator–prey dynamics.

2.9.1 | Arrowtooth and pollock distributions

Annual summer distributions of juvenile walleye pollock (<25 cm, approximate age classes 1–2) and adult arrowtooth flounder (>30 cm) in the Eastern Bering Sea were estimated between 1982 and 2017, during annual summer fisheries-independent trawl surveys conducted by the National Oceanic and Atmospheric Administration. These length classes reflect the size above which arrowtooth flounder begins to predate intensively on pollock (Livingston et al., 2017). Catch per unit effort (CPUE; number of fish per square kilometre; Alverson & Pereyra, 1969) was determined for c. 376 stations across the survey region using a standard trawl net (83–112 eastern otter trawl) towing for c. 30 min at 1.54 m/s. Length classes were determined by measuring the fork length of a subsample of fish from each tow and expanding this to the entire catch in a given tow based on the ratio of sampled weight to total towed weight for each species.

We estimated the distribution and density of juvenile pollock and arrowtooth flounder using the Eastern Bering Sea shelf CPUE data, while accounting for sampling effort that was uneven in space and time. To do this, we applied two separate delta-generalized linear mixed models using the vector autoregressive spatio-temporal (VAST) package in R (<https://github.com/james-thorson/VAST>). VAST has become a widely used tool for fisheries scientists and managers, and we used default model settings for model parameterization (Thorson, 2019; Thorson & Barnett, 2017). The delta model framework jointly estimated the probability of occurrence (binomial distribution) and the positive catch rate (lognormal distribution) for each species for each survey year (1982–2017). Model parameters were estimated for 250 locations (“knots”) that were selected by applying a k-means clustering algorithm to the CPUE data to identify geographical locations that reflect survey sampling intensity (Thorson & Barnett, 2017). Environmental covariates were the temperature at the depth of trawl (in degrees Celsius; measured by trawl gear) and bottom depth (in metres) and were included as quadratic forms in the model to allow for nonlinear responses (Thorson, Ianelli, & Kotwicki, 2017). Year was treated as a fixed effect (default VAST setting), whereas spatial variation (which does not change among years) and spatio-temporal variation (which is estimated independently in each year) were treated as random effects described by a Gaussian process. These random fields allow the modelling of multi-dimensional factors that are not included directly in the model but that affect the density and distribution of the modelled species. Including spatial variation in the model allowed for correlations in CPUE between nearby locations, with spatial correlation declining with increasing distance. Species density was predicted at each knot by multiplying the probability of occurrence with positive catch rate estimates. Density estimates for each knot were then multiplied by

the knot area (in square kilometres) to create annual surfaces of species abundance across the entire Eastern Bering Sea shelf.

In order to create “absences” for the binary cooccurrence metrics, we determined that species were absent at knots where the probability of occurrence was less than the lower quartile of probability of occurrence values across the total sampled area for that species in a given year. This approach to defining absences based on the distribution of probability values results in lower bias than using an arbitrary probability threshold, such as 0.5 (Liu, Berry, Dawson, & Pearson, 2005).

2.9.2 | Arrowtooth and pollock overlap

To illustrate differences in how the metrics characterize predator–prey overlap, we applied the suite of 10 metrics to the estimated density surfaces for arrowtooth flounder and juvenile pollock for 2012 and 2016, years when the cold pool extent was high and low, respectively. Given the contrasting preferences of each species for the cold pool, the overlap between flounder and pollock might be expected to be low in 2012 and higher in 2016 (Hunsicker et al., 2013). We present spatially explicit estimates of each overlap metric, by decomposing the global metric values into their grid-cell-level components (i.e., we map the value for each cell without integrating or taking means across the whole spatial domain). For the global index of collocation, we map the position of the centre of gravity and inertia axes. Along with spatially explicit estimates, we show total metric values. We also present the full annual time series (1982–2017) of overlap values for each metric.

To visualize how spatially explicit overlap related to cold pool extent in 2012 and 2016, we mapped the position of the cold pool (bottom waters < 2°C) from the bottom temperatures measured during the trawl surveys. We used ordinary kriging in the R package *gstat* (Pebesma, 2004) to estimate these temperatures at the same knots as the species abundance data.

3 | RESULTS

3.1 | Metric responses to simulated predator–prey interactions

3.1.1 | Sensitivity to changes in spatial overlap

Most overlap metrics demonstrated an increase in response to a larger window of overlap between the predator and prey populations (Figure 2a). These responses were predominantly linear. However, the global index of collocation demonstrated a sigmoidal curve, and Hurlbert's index reached an asymptote as the overlap window shared by the distributions neared one. The AB ratio was by far the most sensitive metric to changes in the size of the overlap window because it has the largest range. This simulation showed that when the distributions reached complete overlap, the predator density was four times greater in areas where it overlapped with

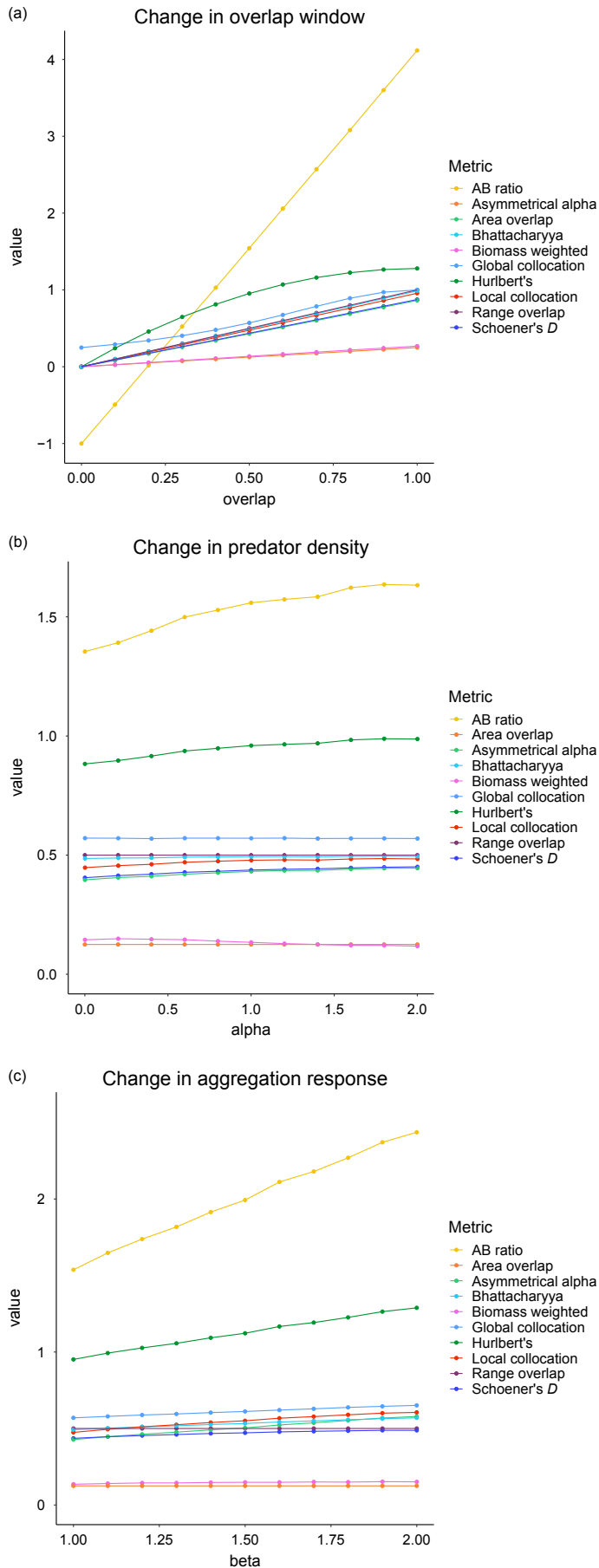


FIGURE 2 Overlap metric behaviour in response to different scenarios of predator–prey interaction: (a) change in area of overlap; (b) change in predator density [α is a coefficient (ranging from zero to two) that controls predator density in relationship to prey density]; and (c) changes in aggregative response [β is a coefficient (ranging from zero to two) that controls the aggregation response of the predator such that predator biomass moves from areas of no prey into areas of high overlap with prey]. Metric values are means taken over 500 simulations of predator–prey distribution [Colour figure can be viewed at wileyonlinelibrary.com]

prey, relative to its mean density across the whole arena (where both species were largely absent).

3.1.2 | Sensitivity to changes in predator population size

Most overlap metrics increased slightly as predator density increased relative to prey density, in the absence of an aggregative response. These increases generally reached an asymptote as the ratio of predator density to prey density neared one (Figure 2b). Exceptions were the area and range overlaps and the global index of collocation, which remained constant because both the areas occupied by each species and their centres of gravity remained the same. Again, the AB ratio was the most sensitive in this scenario because predator density increased in areas where it overlapped with prey, relative to its mean across the domain.

3.1.3 | Sensitivity to changes in aggregative response of predator to prey

Most overlap metrics increased slightly in response to changes in the aggregative response of predator to prey within the area of overlap (Figure 2c). Unlike the previous scenario, the global index of collocation increased, because the centre of gravity of the predator shifted incrementally towards that of the prey as its biomass in the overlap window increased. Hurlbert's index was sensitive to changes in this parameter, because the predator distribution became increasingly less uniform and coincided more with the spatial niche occupied by the prey. The AB ratio was also sensitive to changes in this parameter, because predator density increased in areas where it overlapped with prey, relative to its mean across the domain. The biomass-weighted overlap did not vary in response to this scenario, because predator density is scaled to its maximum value across the range, which did not increase. The binary co-occurrence metrics did not change in response to this scenario either, because the size of the overlap window was held constant.

3.2 | Metric responses to predator–prey dynamics in the Eastern Bering Sea

3.2.1 | Pollock and arrowtooth overlap

The values of all metrics showed that the overlap between the distributions of arrowtooth flounder and juvenile walleye pollock (as determined by spatio-temporal models, Table 2) was low in 2012, when the cold pool covered most of the shelf area (Figure 3). However, the overlap metrics demonstrated some differences in patterns of spatially explicit overlap. The centre of gravity and inertia for pollock (key components of the global index of collocation) showed that its distribution was centred in the middle of the shelf, in the cold pool. In contrast, the distribution of arrowtooth flounder was centred on the lower portion of the shelf, outside the cold pool. The co-occurrence metrics showed that during this year, the species co-occurred across

the centre of the shelf, but did not co-occur in shallower waters, owing to the absence of arrowtooth flounder from this area, or in the southeast portion of the shelf, owing to the absence of pollock from this area. Most other metrics (asymmetrical overlap, Bhattacharyya's coefficient, biomass-weighted overlap, Hurlbert's index and the local index of collocation) showed that the highest area of overlap occurred in the northwest corner of the Eastern Bering Sea shelf, where relatively high densities of both flounder and pollock coincided. The AB ratio returned mostly negative values, indicating that there was general avoidance between juvenile pollock and arrowtooth, probably caused by their different relationships with the cold pool rather than direct avoidance of arrowtooth by juvenile pollock. Values of the AB ratio were lower in areas where arrowtooth density was most negatively associated with pollock density (e.g., where flounder density was high but pollock density was low). The highest values of the AB ratio were around zero, in places where the densities of both species were predicted to be low. Likewise, Schoener's *D* showed higher values in areas where the difference in the proportion of flounder and pollock abundance was lower (i.e., where niche similarity was high), including large portions of the shelf where both species were present at very low densities.

During 2016, an unusually warm year in the Eastern Bering Sea, overlap between arrowtooth flounder and juvenile pollock was much higher than in 2012 (Figure 4). The centre of gravity and inertia of the distributions showed a shift westward by pollock towards the reduced cold pool area. Arrowtooth flounder shifted further up onto the shelf as it exploited a greater portion of available shelf habitat, owing to the absence of the cold pool, and potentially experienced a density-dependent expansion (Spencer, 2008). The co-occurrence metrics showed the least change between the two years, with only slightly more overlap in the middle portion of the shelf in 2016, where arrowtooth flounder had expanded its occupation. The encounter metrics showed a small region of intense overlap in the westernmost part of the shelf on the periphery of the cold pool, with spatially explicit metric values in those cells an order of magnitude greater in 2016 than in 2012. In several cells in this part of the shelf region, the AB ratio indicated that the density of arrowtooth flounder was 2.5 times greater than the mean, potentially as a result of its overlap with juvenile pollock.

The 36-year time series showed substantial variability in the values of the metrics between years (Figure 5). Perhaps unsurprisingly, the binary cooccurrence metrics showed the smallest range of variation across the time series, with changes of c. 10% in the amount of the shelf area occupied by both arrowtooth flounder and juvenile pollock. The most sensitive metrics included the global index of collocation, which showed a relative shift in the weighted centres of gravity of both species of c. 20% of the total metric range. A general increasing trend in overlap was seen in some metrics, including Bhattacharyya's coefficient, Schoener's *D* and the global index of collocation. For most metrics, the last 3 years of the time series (2015–2017) showed higher overlap than the first 3 years (1982–1984), and overlap was relatively low and high in 2012 and 2016, respectively.

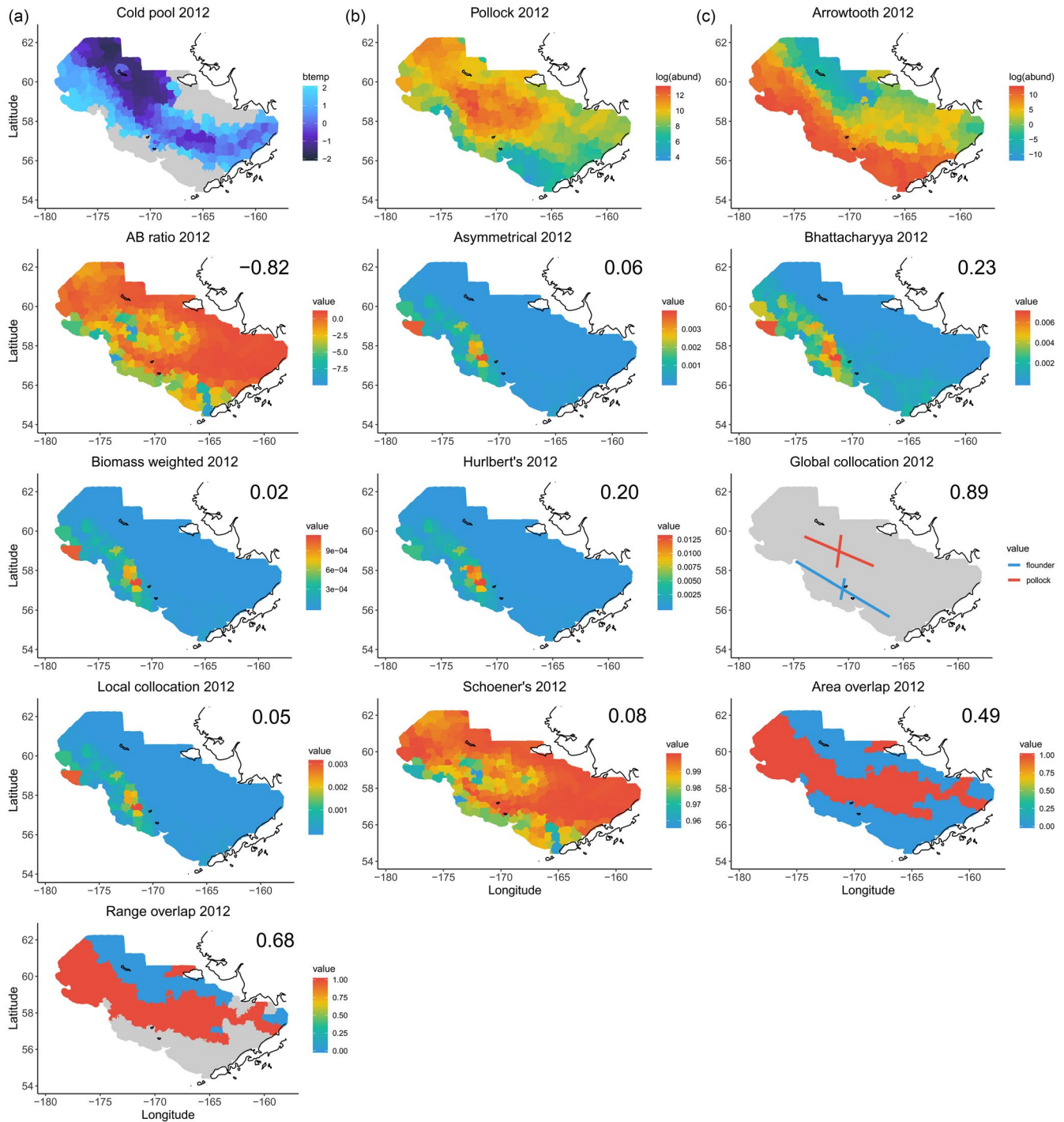


FIGURE 3 (a) Cold pool extent on the Eastern Bering Sea shelf in 2012, a cold year (grey areas reflect temperatures $> 2^{\circ}\text{C}$); (b) estimate of arrowtooth flounder (predator) density distribution in 2012; and (c) estimate of juvenile walleye pollock (prey) distribution in 2012. Densities at locations where the probability of occurrence was less than the lower quartile across the survey area were deemed to be absences and are greyed out. Spatially explicit overlap calculated by the 10 overlap metrics (AB ratio, asymmetrical overlap, Bhattacharyya coefficient, biomass-weighted overlap, Hurlbert's index, global index of collocation, local index of collocation, Schoener's D , area overlap and range overlap) are shown below. Total values of overlap for each metric for this period are displayed in the top right corner of each map [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Discussion

Here, we demonstrated the properties of a suite of overlap metrics and showed how they can describe different types of predator-prey

interactions. Below, we briefly review the specific ecological insights that we gained from the metrics using the simulated populations and the Eastern Bering Sea case study. Based on these insights, we discuss various applications for which the metrics may be suitable and

TABLE 2 Model parameter estimates and significance terms for the probability of occurrence and positive catch rate of juvenile walleye pollock and arrowtooth flounder. Modelled probability of occurrence and positive catch rate were estimated using a vector autoregressive spatio-temporal (VAST) model, parameterised with a lognormal distribution, and spatial and spatio-temporal variation. Environmental covariates (temperature and depth) were defined as quadratic functions

Parameter	Pollock occurrence		Pollock catch rate		Flounder occurrence		Flounder catch rate	
	Estimate	Significance	Estimate	Significance	Estimate	Significance	Estimate	Significance
Year	$\mu = 1.8$	$p < .05^*$	$\mu = 2.70$	$p < .001$	$\mu = -0.38$	$p < .05^*$	$\mu = 1.13$	$p < .05^*$
Temperature	-0.06	$p = .48$	0.27	$p < .001$	2.66	$p < .001$	1.40	$p < .001$
Temperature ²	0.07	$p = .06$	-0.03	$p = .2$	-1.14	$p < .001$	-0.52	$p < .001$
Depth	-0.11	$p = .49$	-0.26	$p < .05$	3.49	$p < .001$	1.28	$p < .001$
Depth ²	-0.42	$p < .001$	-0.28	$p < .001$	-0.89	$p < .001$	-0.32	$p < .001$
Spatial variation	$\sigma = 1.01$	$p < .001$	$\sigma = 0.61$	$p < .001$	$\sigma = 1.48$	$p < .001$	$\sigma = 0.73$	$p < .001$
Spatio-temporal variation	$\sigma = 1.02$	$p < .001$	$\sigma = 0.88$	$p < .001$	$\sigma = 1.05$	$p < .001$	$\sigma = 0.52$	$p < .001$

Note: The mean (μ) gives the average results for all years between 1982 and 2017.

*Indicates that only some years were significant; and σ is the standard deviation of the spatial and spatio-temporal processes.

include a decision tree to help readers select a metric based on data types and ecological question (Figure 6).

3.3.1 | Insights into ecological interactions

The overlap metrics give a range of insights into spatial interactions between predators and their prey. This is important because there are different types of predator–prey interactions that practitioners may wish to quantify, such as total predation pressure exerted by a predator on a prey population (Spencer et al., 2016), spatial hotspots of predation (Eero et al., 2012) or the productivity of a predator population that can be attributed to its overlap with a key prey species (Greer & Woodson, 2016). Understanding the specific insights that the metrics give into predator–prey interactions can allow appropriate metrics to be selected for different applications (Figure 6) and for metric values to be interpreted appropriately. Furthermore, tracking changes in metric values through time can provide important insight into how shifts in the spatial distribution of interacting species might be altering components of ecosystem function (Gilman et al., 2010; Tilyanakis et al., 2008).

Using our simulation and case study, we show that the binary co-occurrence metrics (area and range overlap) provide a simple and interpretable way of measuring spatial overlap between two species. However, these metrics cannot be used to quantify fine-scale interspecific interactions, such as predation, which are a function of factors including species density and aggregation patterns (Hurlbert, 1978). Specifically, because species can be designated “present” even at very low densities, the co-occurrence metrics are likely to overestimate the probability of interspecific interactions. In most cases, using habitat models to calculate a spatially explicit probability of occurrence surface provides more information than simply a “presence” or “absence” and can deal with biases associated with the detection of species or variability in sampling. Estimated probability values can then be fed into overlap metrics, such as Schoener's

D or Bhattacharyya's coefficient, providing insight into the relative preferences of both species for shared spatial resources (Fieberg & Kochanny, 2005).

Many studies have demonstrated the efficacy of Schoener's *D* for understanding niche overlap between species in environmental space (e.g., Broennimann et al., 2012; Warren et al., 2008). We took a purely spatial approach to understanding overlap between predator and prey without explicitly testing the underlying environmental mechanisms driving their distributions. Used in this way, Schoener's *D* provides insight into whether species share preferences for particular areas, which is important for understanding whether they might be affected in similar ways by anthropogenic or environmental processes. Bhattacharyya's coefficient is not derived from either ecological or spatial theory, but it provides an objective statistical approximation of whether two populations use space independently of one another. Although Schoener's *D* and Bhattacharyya's coefficient quantify similarities and differences in the use of space between two populations, they are not designed to provide insight into the strength of potential interactions between two species. They may therefore be more appropriate for quantifying overlap in general, rather than as tools to understand specific elements of spatial predator–prey dynamics.

The encounter metrics (asymmetrical alpha, biomass-weighted overlap, Hurlbert's index and the local index of collocation) provide the most intuitive definition of overlap as a proxy for predator–prey interactions. The insights from each of the encounter metrics are similar, but Hurlbert's index is sensitive to both the size of the area over which two species occur and the variability in the size of spatial sampling units. Explicitly accounting for changes in the size of the area occupied by predator and prey incorporates useful information on species' range expansions or contractions and better captures the potentially increasing impacts of a predator on its prey as it occupies a larger proportion of the range of the prey (Hurlbert, 1978).

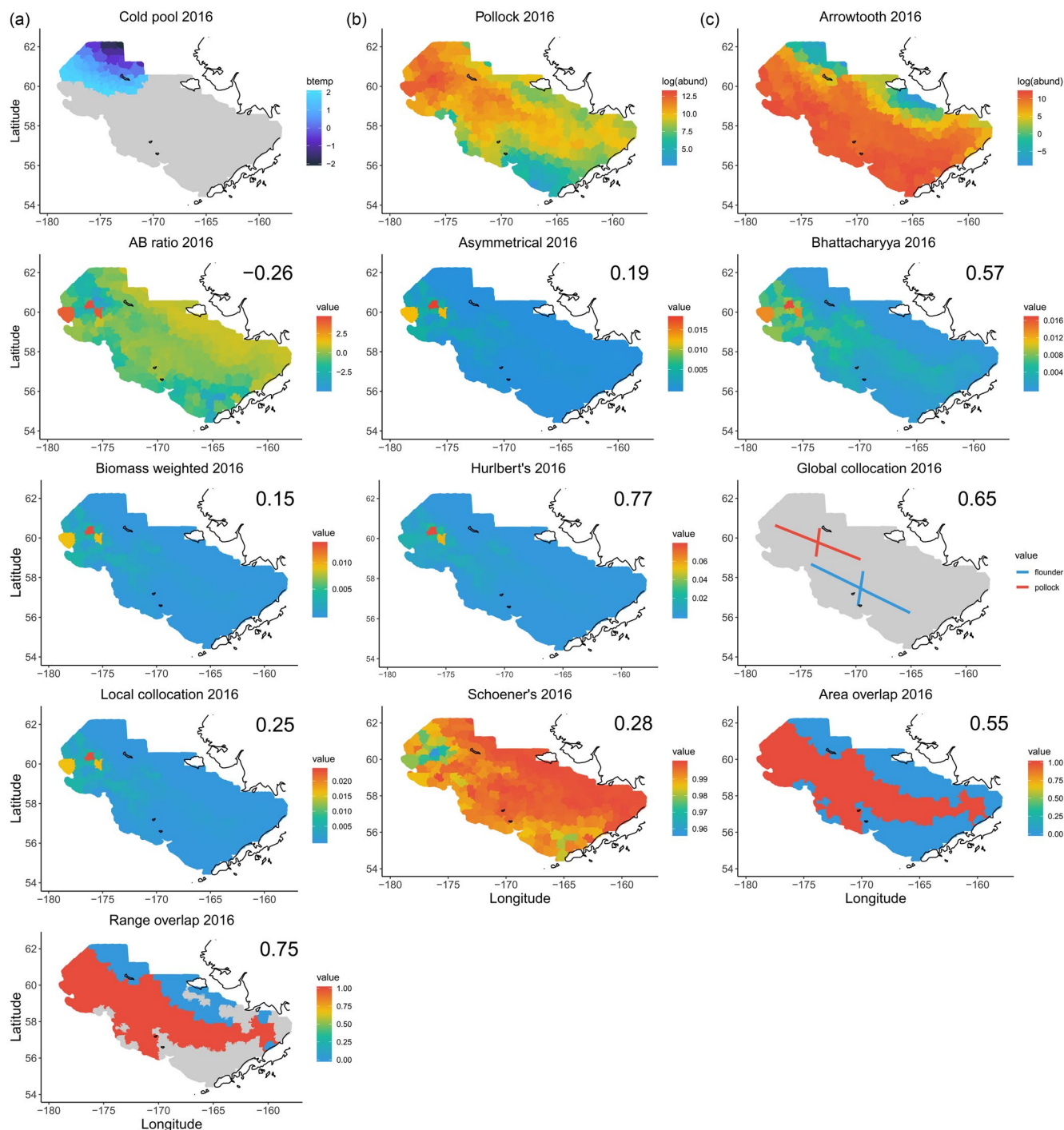


FIGURE 4 (a) Cold pool extent on the Eastern Bering Sea shelf in 2016, an anomalously warm year (grey areas reflect temperatures > 2°C); (b) estimate of arrowtooth flounder (predator) density distribution in 2016; and (c) estimate of juvenile walleye pollock (prey) distribution in 2016. Densities at locations where the probability of occurrence was less than the lower quartile across the survey area were deemed to be absences and are greyed out. Spatially explicit overlap calculated by the 10 overlap metrics (AB ratio, asymmetrical overlap, Bhattacharyya coefficient, biomass-weighted overlap, Hurlbert's index, global index of collocation, local index of collocation, Schoener's *D*, area overlap and range overlap) are shown below. Total values of overlap for each metric for this period are displayed in the top right corner of each map [Colour figure can be viewed at wileyonlinelibrary.com]

3.3.2 | Applications of overlap metrics

There are many applications for which overlap metrics can provide important information about spatial relationships between predators and their prey. The choice of overlap metric for each application

depends on both the data types and the scale of inference that is required (Figure 6).

The binary co-occurrence metrics describe broad spatial patterns relating to the potential for two populations to be in the same area. This may be desirable for some applications where only occurrence

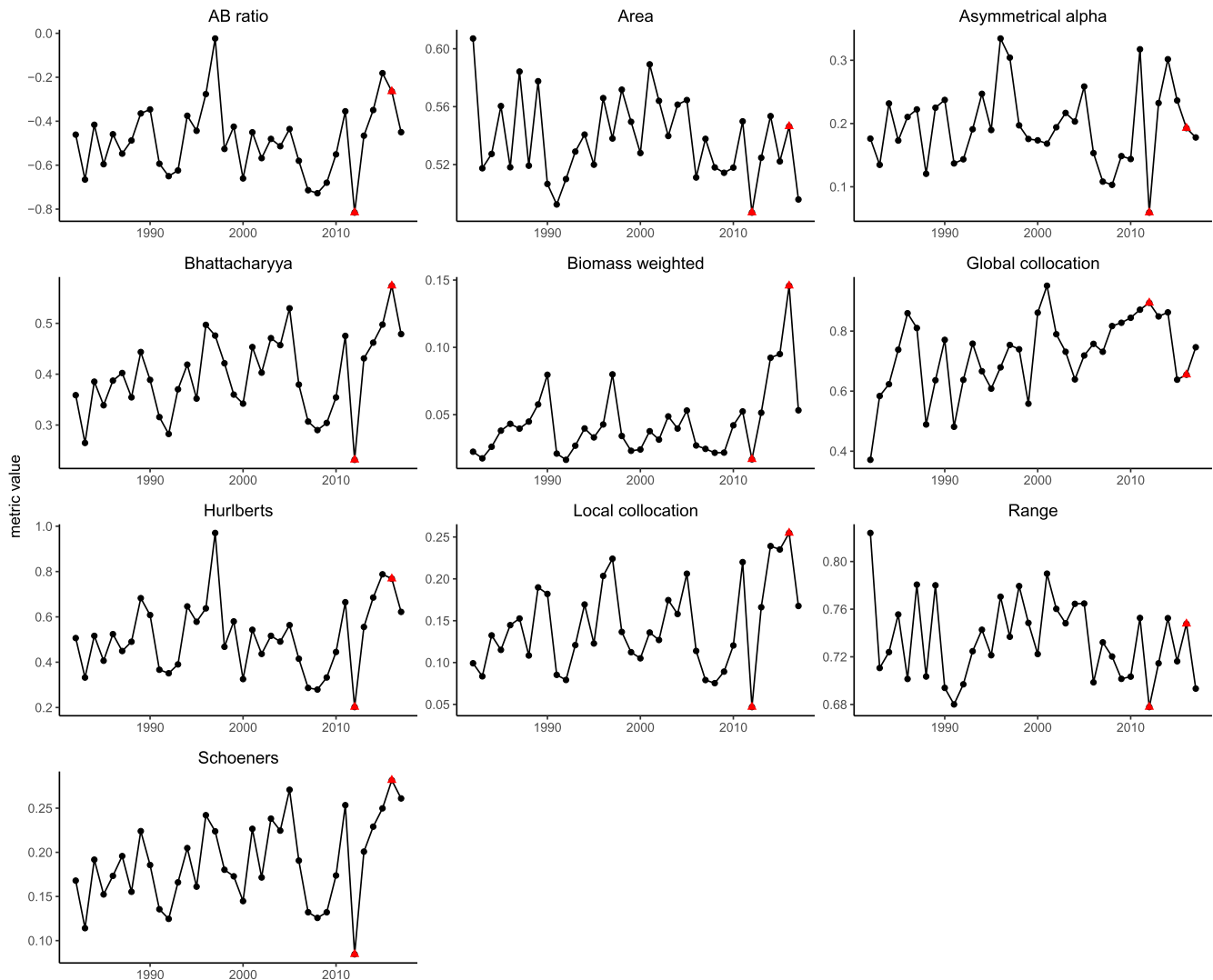


FIGURE 5 Thirty-six-year time series (1982–2017) of overlap between juvenile walleye pollock and arrowtooth flounder in the Eastern Bering Sea, Alaska, calculated using 10 overlap metrics (AB ratio, asymmetrical overlap, Bhattacharyya's coefficient, biomass-weighted overlap, global index of collocation, Hurlbert's index, local index of collocation, Schoener's *D*, area overlap and range overlap). The years 2012 and 2016 (highlighted in spatial analyses) are shown with red triangles [Colour figure can be viewed at wileyonlinelibrary.com]

data are available and where a simple approach is required for defining spatial boundaries. For example, binary metrics may be appropriate for conservatively managing interactions with rare species (Hazen et al., 2018) or for projecting spatial overlap in future environmental conditions where the precision of estimated distribution shifts is assumed to be low (Selden et al., 2018).

Within this category of metrics, the choice of whether the area or range overlap metric is preferred depends on whether a study aims to determine the directional influence of one species on another (range overlap) or the overlap between two species across a given spatial area (area overlap) (Figure 6). For example, the range overlap metric could be used to quantify how much of the future range of a predator will overlap with that of its prey, using predictions of species distributions made onto climate forecasts (e.g., Schweiger et al., 2008; Selden et al., 2018). The area overlap metric could be used to quantify the proportion of a predefined management area (e.g., park,

region, state or continent) that might continue to see the co-occurrence of two species under future conditions.

The encounter metrics and the AB ratio can be used to add spatial information to non-spatial models. For example, non-spatial ecosystem models (e.g., *Ecosim*) aggregate information about species' biomass and calculate estimates of consumption and mortality across a whole region. However, these models often assume constant proportions of prey biomass available to a predator (e.g., 100%), which may result in overestimates of consumption rates if two species do not overlap at ecologically relevant spatial or temporal scales (Greer & Woodson, 2016). Conversely, consumption rates can be underestimated in cases where prey is highly aggregated and therefore more readily accessible to predators, such as at fronts in the open ocean (Bost et al., 2009) or at water sources in terrestrial systems (de Boer et al., 2010). The encounter metrics and the AB ratio provide information about correlations between the densities of two species

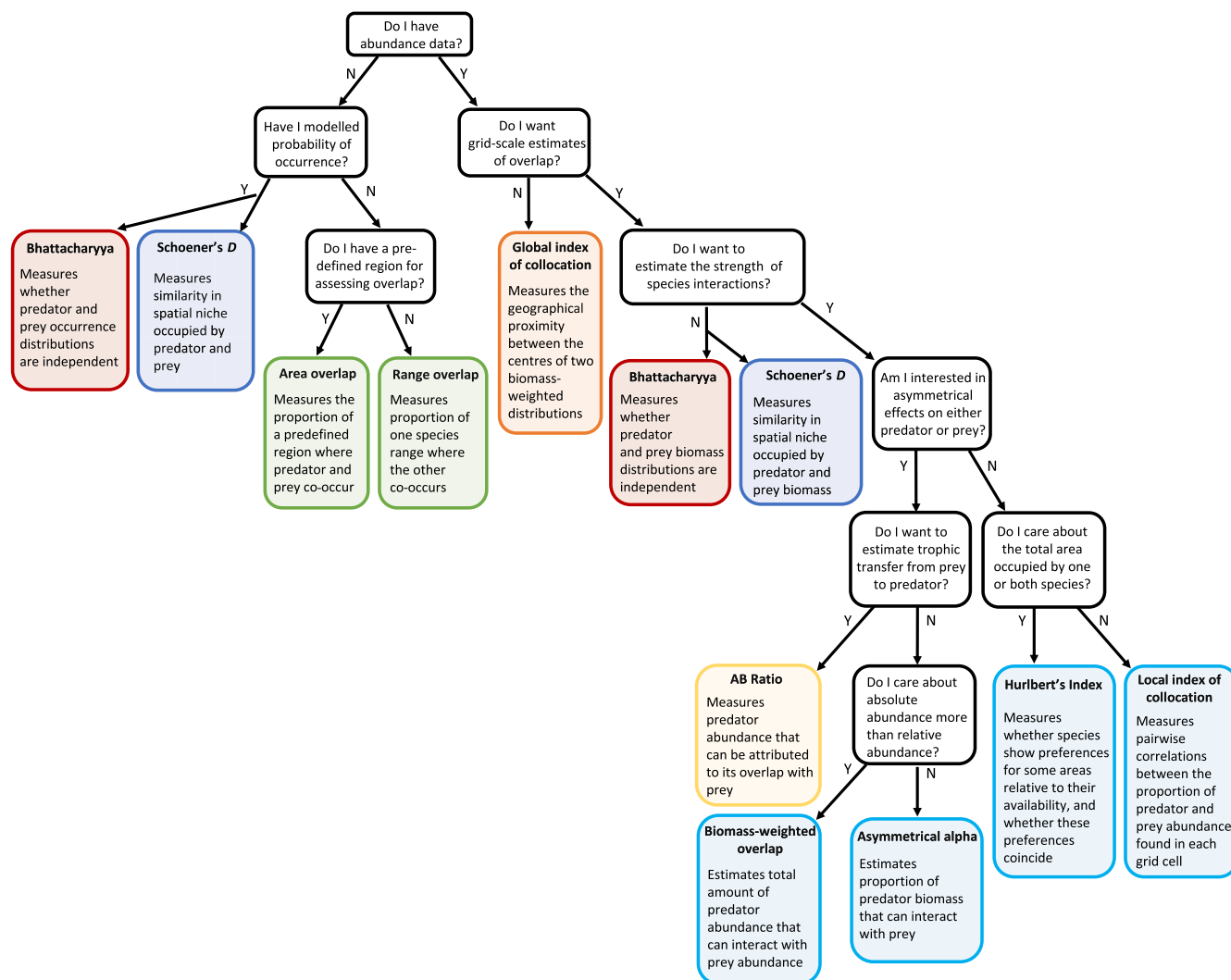


FIGURE 6 A decision tree to help readers select a predator–prey overlap metric based on considerations such as the types of species distribution data available and the types of predator–prey interactions that are of interest. Colours represent the metric categories, with red = “spatial independence”, dark blue = “niche similarity”, green = “binary co-occurrence”, orange = “geographical similarity”, yellow = “trophic transfer” and light blue = “encounter” [Colour figure can be viewed at wileyonlinelibrary.com]

across sampling points, which relates to the probability of their interaction or production. These metrics therefore provide a useful time-varying estimate of the potential strength of predator–prey interactions that can be included in ecological models.

Spatially, the encounter metrics can illustrate areas of more or less intense interaction between predator and prey. In our Eastern Bering Sea case study, the northwest portion of the survey area demonstrated high overlap between arrowtooth flounder and juvenile pollock using the encounter metrics, with overlap increasing in this area in warmer conditions (Figures 3 and 4). This information may be useful for managing resources in a spatially explicit way, in cases where mitigation of the influence of one species on another is desired for ecosystem-based management. For example, targeted culling of a “problem” predator in areas of high overlap (i.e., high putative predation pressure) may prove an efficient and cost-effective means of boosting the abundance of a prey species that is

commercially important or of conservation concern (Burrows et al., 2003; Eero et al., 2012; Persson et al., 2007).

The global index of collocation can be applied to define overlap at the broad scale of the ranges of stocks, populations or species; the scales at which spatial conservation and management decisions are usually made. Furthermore, the centre of gravity and inertia, from which the global index of collocation is calculated, provide simple and interpretable spatial metrics that can aid in understanding the mechanisms underlying changes in patterns of spatial overlap. For example, these can be used to highlight differential rates of poleward shifts by predator and prey in response to climate change (Le Roux & McGeoch, 2008). Unlike any of the other metrics examined in this paper, the global index of collocation does not include information on co-occurrence or the correlation of the biomass of species at the grid-scale level, making it less useful for understanding interactions between species at scales that are more relevant to their

ecology. However, the global index of collocation can provide a useful complement to the encounter metrics, to understand processes governing the overlap of species at nested spatial scales (Saraux et al., 2014).

3.4 | Overlap between arrowtooth flounder and juvenile pollock

The metrics that we investigated gave new insight into changes in spatial overlap between juvenile walleye pollock and adult arrowtooth flounder, a predator that has been growing in abundance in the Eastern Bering Sea over the past 30 years. We showed that spatial overlap between these two species was very low in 2012, when the presence of an intense Eastern Bering Sea cold pool restricted flounder from moving up onto the shelf. We then showed that in an anomalously warm year (2016), overlap estimated using all 10 metrics was much higher than in 2012, mirroring previous work that showed an increase in predation pressure by arrowtooth flounder on juvenile pollock associated with warm conditions (Hunsicker et al., 2013; Spencer et al., 2016).

By mapping areas of high and low overlap of these species, we show how the metrics can identify important shared habitat. We also highlight areas that may be of management interest during the stanzas of anomalously warm temperatures that have increasingly been impacting the Eastern Bering Sea ecosystem (Stabeno et al., 2017). The full 36-year time series of overlap between juvenile pollock and flounder showed an overall increasing trend in overlap for some metrics. This trend is of concern to managers, because juvenile walleye pollock is a species of great commercial importance for the USA, and predation pressure may have an increasing effect on the population as the Eastern Bering Sea warms (Hunsicker et al., 2013; Spencer et al., 2016). This case study highlights how overlap metrics can be used to track species interactions both in space and through time in varying environmental conditions.

3.5 | Conclusions

The diverse suite of overlap metrics examined in this paper quantify spatial predator–prey interactions and can track how these interactions change through time. Our simulations and case study show that no single metric emerges as being most useful across all scenarios. Instead, we recommend that the overlap metric(s) chosen for a particular study should reflect the types of data available and the desire to understand particular elements of ecological and spatial relationships between species (Figure 6). In many cases, the use of a combination of several metrics may deliver the most comprehensive assessment of spatial predator–prey overlap. For example, the global index of collocation could be chosen to give insight into broad patterns of distribution, Schoener's *D* to understand niche equivalency across habitat types that may drive overlap, and Hurlbert's index to estimate interspecific encounter, accounting for variability in spatial resource availability. In such a combination, these metrics provide complementary information regarding the use of shared space and

probability of interaction between predators and prey at nested scales of distribution and behaviour.

ACKNOWLEDGMENTS

Funding for this project was provided by NOAA's Fisheries and the Environment (FATE) programme for a grant titled, "Creating and evaluating indices of climate-induced changes in spatial distributions and predator–prey overlap for North Pacific fishery resources" to E.L.H., R.L.S., S.B., J.S., K.K.H. and M.A.H. We thank Eastern Bering Sea ground trawl survey participants for their hard work in collecting the data used in the case study. We also thank Nick Tolimieri for comments on a previous draft.

DATA AVAILABILITY STATEMENT

We used bottom trawl data collected by the Eastern Bering Sea bottom trawl survey, publicly available at: http://www.afsc.noaa.gov/RACE/groundfish/survey_data/data.htm

Functions to implement the predator–prey overlap metric equations in R are included as Supporting Information.

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BIOSKETCH

Gemma Carroll is an ecologist with an interest in understanding how predator–prey dynamics are shaped by changing environments.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Carroll G, Holsman KK, Brodie S, et al. A review of methods for quantifying spatial predator–prey overlap. *Global Ecol Biogeogr*. 2019;28:1561–1577. <https://doi.org/10.1111/geb.12984>