A review of methods for quantifying spatial predator-prey overlap

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Biosketch

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

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Running title: Quantifying spatial predator-prey overlap

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 may give deeper insight into how species redistribution affects food web dynamics.

Predator-prey overlap metrics

Here we review a suite of ten 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, geographic similarity, and trophic transfer. We describe the specific ecological insights that can be gained using each overlap metric, 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 ten metrics respond to variation in three types of predator-prey interaction: 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, Alaska, 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.

Key words: Arrowtooth flounder, climate change, Eastern Bering Sea, predator-prey overlap, species distribution models, ecosystem models, spatial overlap, cold pool, species interactions, walleye pollock

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. Rather, the distributions of entire communities are shifting, and there is a growing need to understand how these changes affect trophic interactions (Tylianakis et al. 2008; Gilman et al. 2010). For example, climate-induced changes in habitat and phenology may drive differential responses in the distributions of predators and their prey (Durant et al. 2007; Schweiger et al. 2012; Pinsky et al.

2016; Siddon et al. 2016). This may result in increased (Vors & Boyce 2009) or reduced (Schweiger et al. 2008; Asch 2015) 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 et al. 2017), predators switching prey types (Latham et al. 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 (Araujo & Luoto 2007), and for making informed ecosystem-based management decisions (Pikitch et al. 2004).

Indices that summarise 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). Similarly, 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 more accurately predict the impacts of future environmental change on ecosystem function (Greer & Woodson 2016).

A number of overlap metrics have been developed for ecological applications. These metrics have been applied to diverse ecological questions, including examining niche equivalency of species in environmental space (Warren et al. 2008; Broennimann et al. 2011), 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 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. Further, 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, Alaska, USA. This case study demonstrates how the metrics can track changes in species overlap driven by differential responses to environmental variability. By summarising the properties of available overlap metrics and illustrating their behaviour in response to various ecological scenarios, we aim to assist ecologists to select appropriate metrics with which to quantify spatial predator-prey overlap for different purposes.

Methods

Overlap metric description

Here we present ten 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 rather 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 et al. 2002; Saraux et al. 2014; Greer et al. 2016).

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 et al. 2018). These metrics are particularly useful where data on occurrence but not biomass are available, such as for rare species. Co-occurrence can be described in multiple ways, including the proportion of one species' range where the other species also occurs ("range overlap"; Kernohan et al. 2001; Araújo et al. 2011), or the proportion of a pre-defined study area where both species co-occur ("area overlap"; Saraux et al. 2014). These metrics both range from 0 to 1. 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.

Encounter

Where biomass or abundance data are available from standardised surveys, an alternative approach to the co-occurrence metrics is the "local index of collocation" (also "Pianka's O", Pianka 1973; Bez & Rivoirard 2000). 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 give insight into the magnitude of predator biomass that can influence prey, or scaled to the maximum values for predator and prey in a given year, to keep the range between 0 and 1. 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, as it explicitly accounts for resources of unequal sizes. Hurlbert's overlap is 0 when species do not share space at all, 1 where both species occupy space in proportion to its availability and > 1 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.

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 modelled probability of occurrence data, or 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.

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 modelled probability of occurrence data, or on biomass-density values.

Geographic 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 & Revoirard 2000). This can be done using geographic coordinates weighted by biomass, 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).

Trophic transfer

Variability in predator density that can be explained by local prey density is a useful way of characterising overlap, as it accounts for potential trophic transfer between species ("AB ratio"; Greer & Woodson 2016). An AB ratio of 0 indicates that the mean densities of predator and prey across the whole survey area accurately represent predator-prey encounters, while a value of 1 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 -1 represents complete avoidance. This metric provides insight into how trophic processes are likely to translate local prey abundance into predator production.

Metric responses to simulated predator-prey interactions

Simulated populations

To illustrate how various overlap metrics respond to shifting predator-prey dynamics, we simulated interacting predator and prey populations on a 200 x 100 gridded spatial domain. We included two ways of manipulating predator density in relation 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 timescales 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 ($D_{prey,i}$) 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 ($D_{pred,i}$) to be influenced by three processes:

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

Where α is a coefficient (0-2) that controls the relationship between predator density and prey density (D_{prey}) in a given cell ($_i$). β is a coefficient (0-2) 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 ($\overline{D}_{prey}$) 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.

Scenarios of predator-prey interaction

1. △ Overlap window

After generating predator and prey distributions across the whole 200 x 100 spatial domain using the equation above, we clipped the spatial domain into two distinct distributions of predator and prey, with dimensions of 100 x 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 x 100, we then manipulated the proportion of the prey's distribution that was shared by the predator, from 0 (where the two species shared no common cells) to 1 (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 1, and fixed s ("search area") to a window of 9 cells (3 x 3), centred on the cell of interest.

2. △ Predator population size

To simulate the influence of uniformly increasing predator density, we manipulated α from 0 to 2 at intervals of 0.2. We left the overlap window constant at 0.5, search area at s = 9 and aggregation response at β = 1.

3. △ 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 1 to 2 at intervals of 0.1) within the overlap window, where predator and prey interacted directly. Simultaneously, we manipulated β from 1 to 0 in the area outside the overlap window, to ensure that the overall sum of predator densities were 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 predator's range, 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 α = 1, and the search window *s* at 9.

Application of overlap metrics

We applied the suite of ten 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 characterise patterns of overlap. Because 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 under each of the three scenarios.

Functions to implement the predator-prey overlap metric equations in R are included as supplementary material in the online version of this article.

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, Alaska. Arrowtooth flounder is a bottom-dwelling flatfish that has seen an 8-fold increase in abundance on the Eastern Bering Sea shelf over the past 36 years (Wilderbuer et al. 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 ^{o}C and varies greatly in size between years as a function of sea ice extent during the previous winter (Stabeno et al. 2008). 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), while arrowtooth flounder are constrained to warmer water and generally avoid the cold pool (Ciannelli et al. 2012, Spencer et al. 2016).

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

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 km^2, Alverson & Pereyra 1969) was determined for approximately 376 stations across the survey region using a standard trawl net (83 – 112 eastern otter trawl) towing for ~ 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-generalised linear mixed models using the Vector Autoregressive Spatiotemporal (VAST) package in R (https://github.org/james-thorson/VAST). VAST has become a widely used tool for fisheries scientists and managers, and we used default model settings for model parameterisation (Thorson and Barnett 2017; Thorson 2019). The delta model framework jointly estimated the probability of occurrence (binomial distribution) and the positive catch rate (log-normal 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 geographic locations that reflect survey sampling intensity (Thorson and Barnett, 2017). Environmental covariates were temperature at depth of trawl (°C; measured by trawl gear) and bottom depth (m), and were included as quadratic forms in the model to allow for non-linear responses (Thorson et al. 2017). Year was treated as a fixed effect (default VAST setting), while 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 modelling of multi-dimensional factors that are not directly included 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 (km^2) 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 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 et al. 2005).

Arrowtooth and pollock overlap

To illustrate differences in how the metrics characterise predator-prey overlap, we applied the suite of ten 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, 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 visualise how spatially-explicit overlap related to cold pool extent in 2012 and 2016, we mapped the position of the cold pool (bottom waters < 2 ^{o}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.

Results

Metric responses to simulated predator-prey interactions

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, predator density was four times greater in areas where it overlapped with prey, relative to its mean density across the whole arena (where both species were largely absent).

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 as both the area occupied by each species and their centres of gravity remained the same. Again, the AB ratio was the most sensitive in this scenario as predator density increased in areas where it overlapped with prey, relative to its mean across the domain.

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 in 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, as 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, as the size of the overlap window was held constant.

Metric responses to predator-prey dynamics in the Eastern Bering Sea

Pollock and arrowtooth overlap

The values of all metrics showed that the overlap between arrowtooth flounder and juvenile walleye pollock 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. 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. By 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 due to the absence of arrowtooth flounder from this area, or in the southeast portion of the shelf due 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 0, in places where the densities of both species were predicted to be low. Similarly, 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 toward the reduced cold pool area. Arrowtooth flounder shifted further up onto the shelf as it exploited a greater portion of available shelf habitat due 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 approximately 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 approximately 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 three years of the time series (2015 – 2017) showed higher overlap than the first three years (1982 – 1984), and overlap was relatively low and high in 2012 and 2016, respectively.

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

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 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 give important insight into how shifts in the spatial distribution of interacting species might be altering components of ecosystem function (Tylianakis et al. 2008; Gilman et al. 2010).

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, giving 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. Warren et al. 2008; Broennimann et al. 2012). 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, however 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 space use between two populations, they are not designed to give 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, however Hurlbert's index is sensitive to both the size of the area over which two species occur, as well as 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 prey's range (Hurlbert 1978).

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 type, 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 data are available, and 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 projecting spatial overlap under 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 a predator's future range 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 pre-defined 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 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 under 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; Persson et al. 2007; Eero et al. 2012).

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 species' biomass 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).

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 showing 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 Being 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, as juvenile walleye pollock is a species of great commercial importance for the United States, 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 under varying environmental conditions.

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 type of data available, and the desire to understand particular elements of ecological and spatial relationships between species (Figure 6). In many cases, employing 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 inter-specific encounter, accounting for variability in spatial resource availability. In such a combination, these metrics provide complementary information regarding shared space use and probability of interaction between predators and prey at nested scales of distribution and behaviour.

Data accessibility

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 supplementary material in the online version of this article.

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Figure and table legends

Table 1: Ecological description of each predator-prey overlap metric, ecological questions that they are suitable for, equations, data type that they can input, whether the metric returns a symmetrical result for predator and prey, whether the metric ranges from 0 to 1, and citations. In the equations, $pred_i$ and $prey_i$ are densities of predator and prey in a given area, p_pred_i and p_prey_i are the proportion of the total number of predator and prey in a given area, A_{pred} and A_{prey} are the total area occupied by the predator and prey, $\text{A}_{\text{pred,prey}}$ 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.

Table 2: Model parameter estimates and significance for the probability of occurrence and positive catch rate of pollock and arrowtooth flounder. μ is the mean and gives the average results for all years between 1982 - 2017; * indicates only some years were significant; σ is the standard deviation of the spatial and spatiotemporal processes. Modelled probability of occurrence and positive catch rate were estimated using a Vector Autoregressive Spatiotemporal (VAST) model, parameterized with a log-normal distribution, with spatial and spatiotemporal variation (FieldConfig=c(1,1,1,1)), and environmental covariates (temperature and depth) as quadratic functions.

Figure 1: Schematic 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; S3) incremental change in the aggregation response of the predator to prey (density of predator increases in relation to prey density only in the overlap window, while decreasing proportionally outside the overlap window), with 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.

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 (0-2) that controls predator density in relation to prey density), and C) changes in aggregative response (β is a coefficient (0-2) that controls 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.

Figure 3: A) Cold pool extent on the Eastern Bering Sea shelf in 2012, a cold year (grey areas reflect temperatures > 2 ^{o}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, local index of collocation, Schoener's D, area 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.

Figure 4: A) Cold pool extent on the Eastern Bering Sea shelf in 2016, an anomalously warm year (grey areas reflect temperatures > 2 ^{o}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, local index of collocation, Schoener's D, area 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.

Figure 5: 36-year time series (1982 – 2017) of overlap between juvenile walleye pollock and arrowtooth flounder in the Eastern Bering Sea, Alaska, calculated using ten 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). 2012 and 2016 (highlighted in spatial analyses) are shown with red triangles.

Figure 6: A decision tree to help readers select a predator-prey overlap metric based on considerations such as the type of species distribution data available and the type 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 = "geographic similarity", yellow = "trophic transfer", light blue = "encounter".

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 pre-defined area, where species co-occur	Suitable for estimating area of co-occurrence across a pre-defined 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	$\frac{\sum_i^n (p\_pred_i * p\_prey_i)}{\sqrt{\sum_i^n p\_pred_i^2 \sum_i^n p\_prey_i^2}}$	Biomass	Yes	Yes	Pianka 1973; Bez & Rivoirard 2000
Asymmetrical alpha	Encounter	Measures the competitive pressure of predator on prey	Suitable for estimating encounter rates relative to prey encounter	$\frac{\sum_i^n (p\_pred_i * p\_prey_i)}{\sqrt{\sum_i^n p\_prey_i^2}}$	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	$\frac{\sum_i^n (pred_i/\max(pred) * prey_i/\max(prey))}{\sum_i^n prey_i/\max(prey)}$	Biomass	No	No	J Thorson unpublished
Hurlbert's index	Encounter	Measures interspecific encounter rate between predator and prey	Suitable for estimating encounter rates where resources vary in abundance	$\sum_i^n \left(\frac{p\_pred_i * p\_prey_i}{A_i/A_{occupied}}\right)$	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	$1 - 0.5 * \sum_i^n \lvert p\_pred_i - p\_prey_i \rvert$	Biomass or occurrence	Yes	Yes	Schoener 1970
Bhattacharyya's Coefficient	Spatial independence	Measures statistical affinity between two distributions	Suitable for estimating independence in space use between two populations	$\sum_i^n \sqrt{p\_pred_i * p\_prey_i}$	Biomass or occurrence	Yes	Yes	Bhattacharyya, 1943

Global index of collocation	Geographic similarity	Measures geographic distinctness by comparing centres of gravity of populations with the dispersion of sampled individuals	Suitable for estimating spatial overlap at a regional scale	$$\frac{1-\ \Delta CG_{pred,prey}{}^{2}}{\Delta CG_{pred,prey}{}^{2}+I_{pred}+\ I_{prey}}$$ where: $$CG_{pred}=\frac{\sum_{n}^{i} i * pred_i}{pred_i}$$ and: $$I_{pred}=\frac{\sum_{i}^{n}(i-CG)^2 * pred_i}{pred_i}$$	Biomass	Yes	Yes	Bez & 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	$$\frac{pred_i-\ \overline{pred} *\ prey_i-\overline{prey}}{\overline{pred} * \overline{prey}}$$	Biomass	No	No	Greer & Woodson 2016

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Parameter	Pollock Occurrence Estimate	Pollock Occurrence Significance	Pollock Catch Rate Estimate	Pollock Catch Rate Significance	Flounder Occurrence Estimate	Flounder Occurrence Significance	Flounder Catch Rate Estimate	Flounder Catch Rate Significance
Year	μ = 1.8	p<0.05*	μ = 2.70	p<0.001	μ = -0.38	p<0.05*	μ = 1.13	p<0.05*
Temperature	-0.06	p=0.48	0.27	p<0.001	2.66	p<0.001	1.40	p<0.001
Temperature^2	0.07	p=0.06	-0.03	p=0.2	-1.14	p<0.001	-0.52	p<0.001
Depth	-0.11	p=0.49	-0.26	p<0.05	3.49	p<0.001	1.28	p<0.001
Depth^2	-0.42	p<0.001	-0.28	p<0.001	-0.89	p<0.001	-0.32	p<0.001
Spatial variation	σ = 1.01	p<0.001	σ = 0.61	p<0.001	σ = 1.48	p<0.001	σ = 0.73	p<0.001
Spatiotemporal variation	σ = 1.02	p<0.001	σ = 0.88	p<0.001	σ = 1.05	p<0.001	σ = 0.52	p<0.001

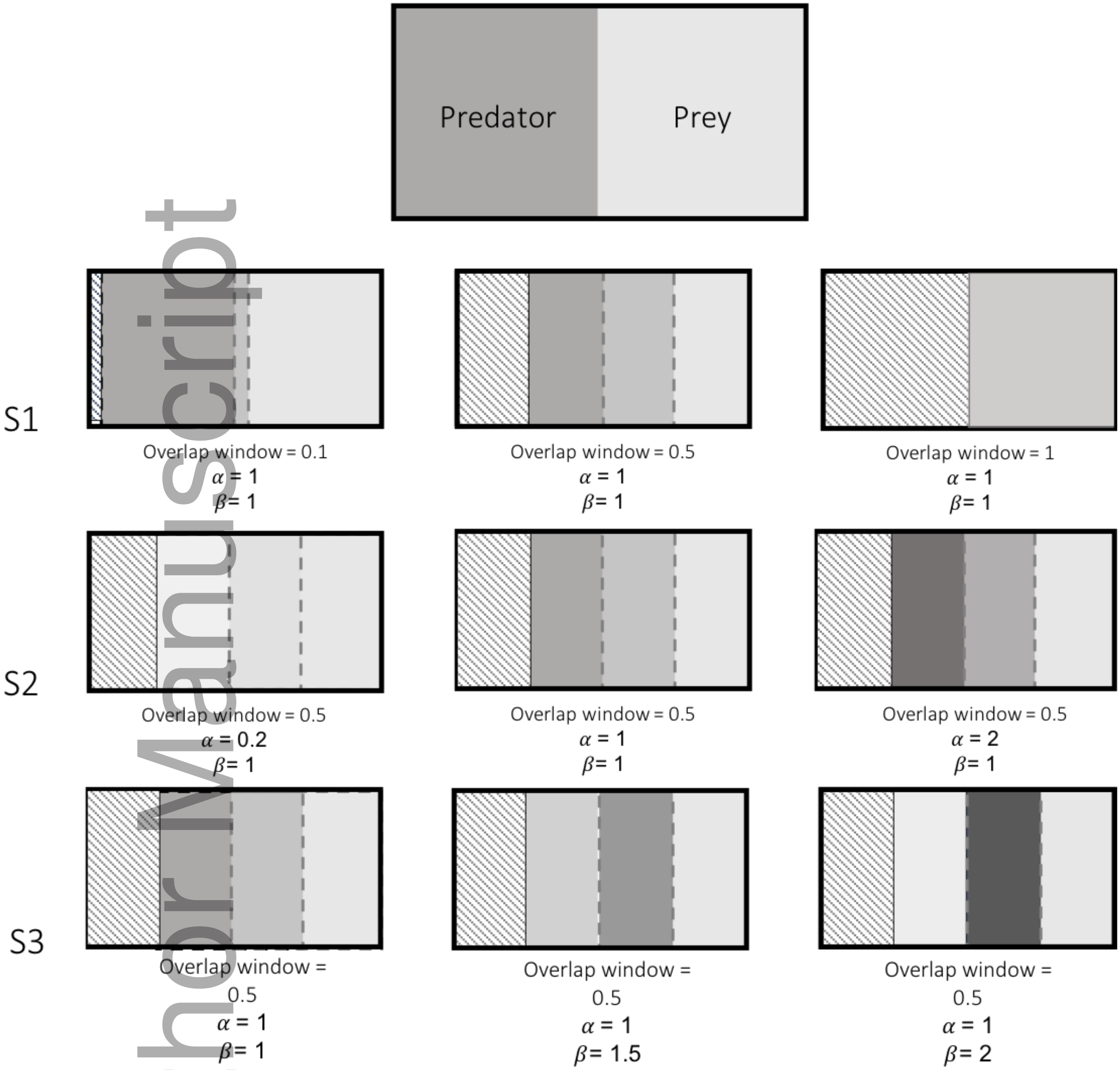

Predator
Prey
S1
Overlap window = 0.1
α = 1
β= 1
Overlap window = 0.5
α = 1
β= 1
Overlap window = 1
α = 1
β= 1
S2
Overlap window = 0.5
α = 0.2
β= 1
Overlap window = 0.5
α = 1
β= 1
Overlap window = 0.5
α = 2
β= 1
S3
Overlap window = 0.5
α = 1
β= 1
Overlap window = 0.5
α = 1
β= 1.5
Overlap window = 0.5
α = 1
β= 2

Figure 1

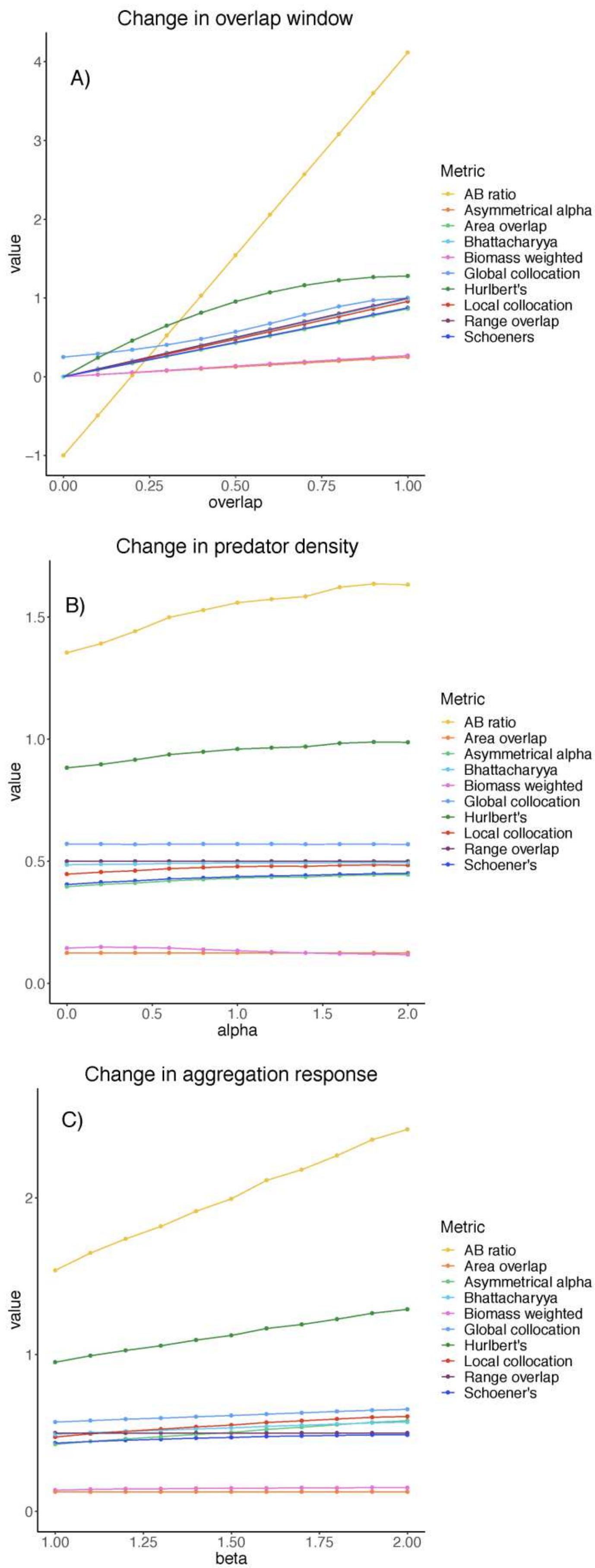

Change in overlap window
A)
value
overlap
0.00
0.25
0.50
0.75
1.00
−1
0
1
2
3
4
Metric
AB ratio
Asymmetrical alpha
Area overlap
Bhattacharyya
Biomass weighted
Global collocation
Hurlbert's
Local collocation
Range overlap
Schoeners
Change in predator density
B)
value
alpha
0.0
0.5
1.0
1.5
2.0
0.0
0.5
1.0
1.5
Metric
AB ratio
Area overlap
Asymmetrical alpha
Bhattacharyya
Biomass weighted
Global collocation
Hurlbert's
Local collocation
Range overlap
Schoener's
Change in aggregation response
C)
value
beta
1.00
1.25
1.50
1.75
2.00
0
1
2
Metric
AB ratio
Area overlap
Asymmetrical alpha
Bhattacharyya
Biomass weighted
Global collocation
Hurlbert's
Local collocation
Range overlap
Schoener's

Figure 2

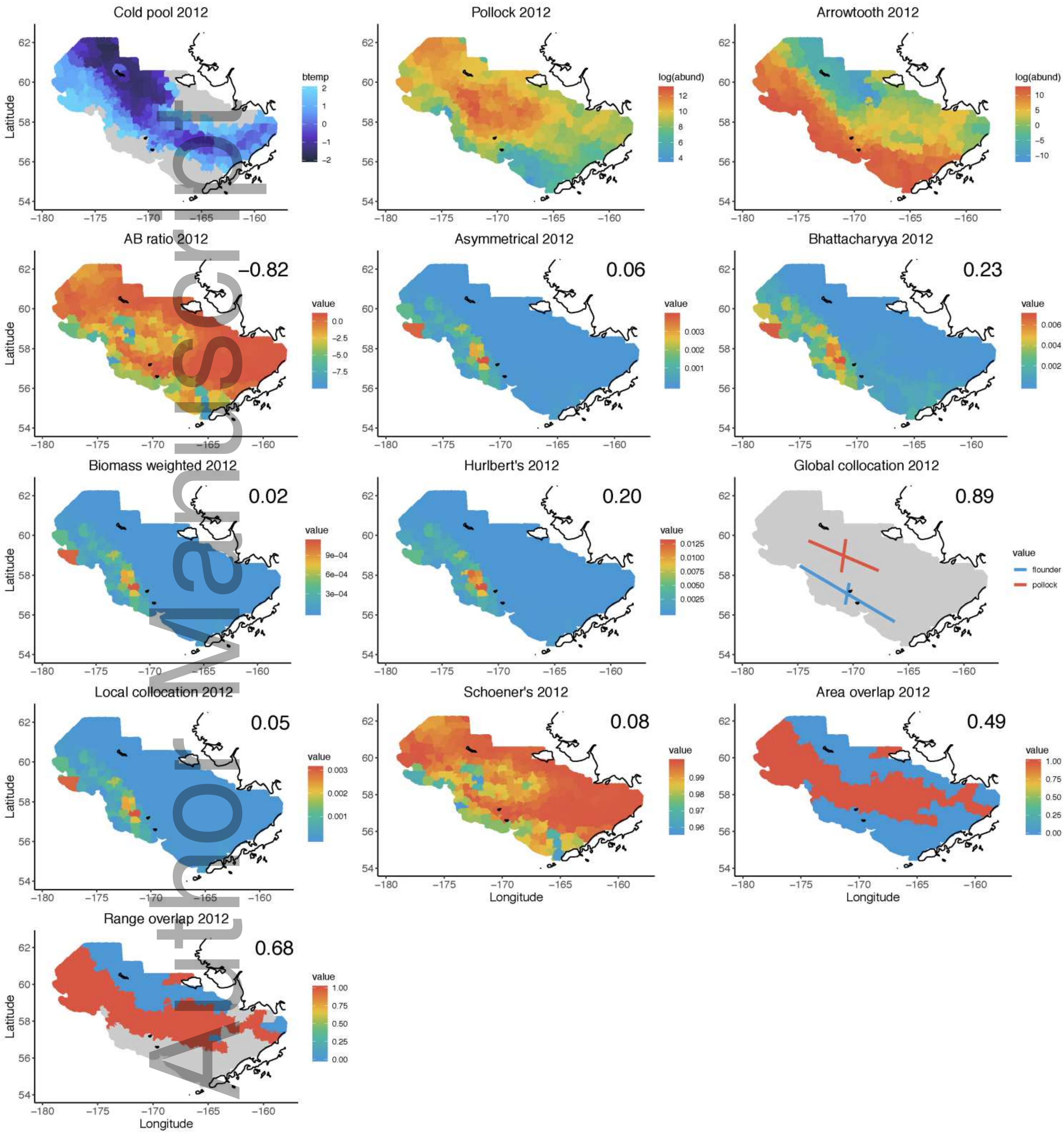


Figure 3

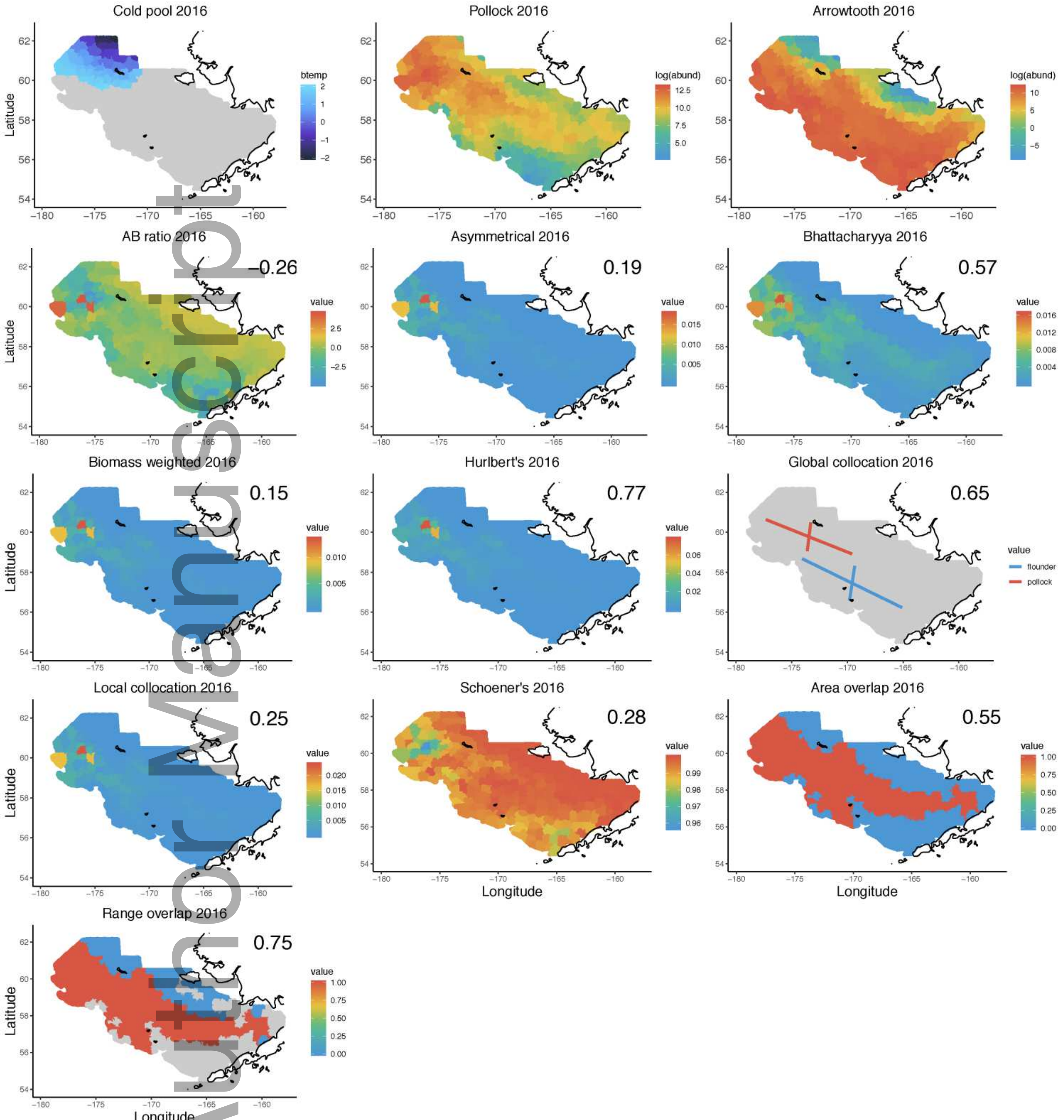
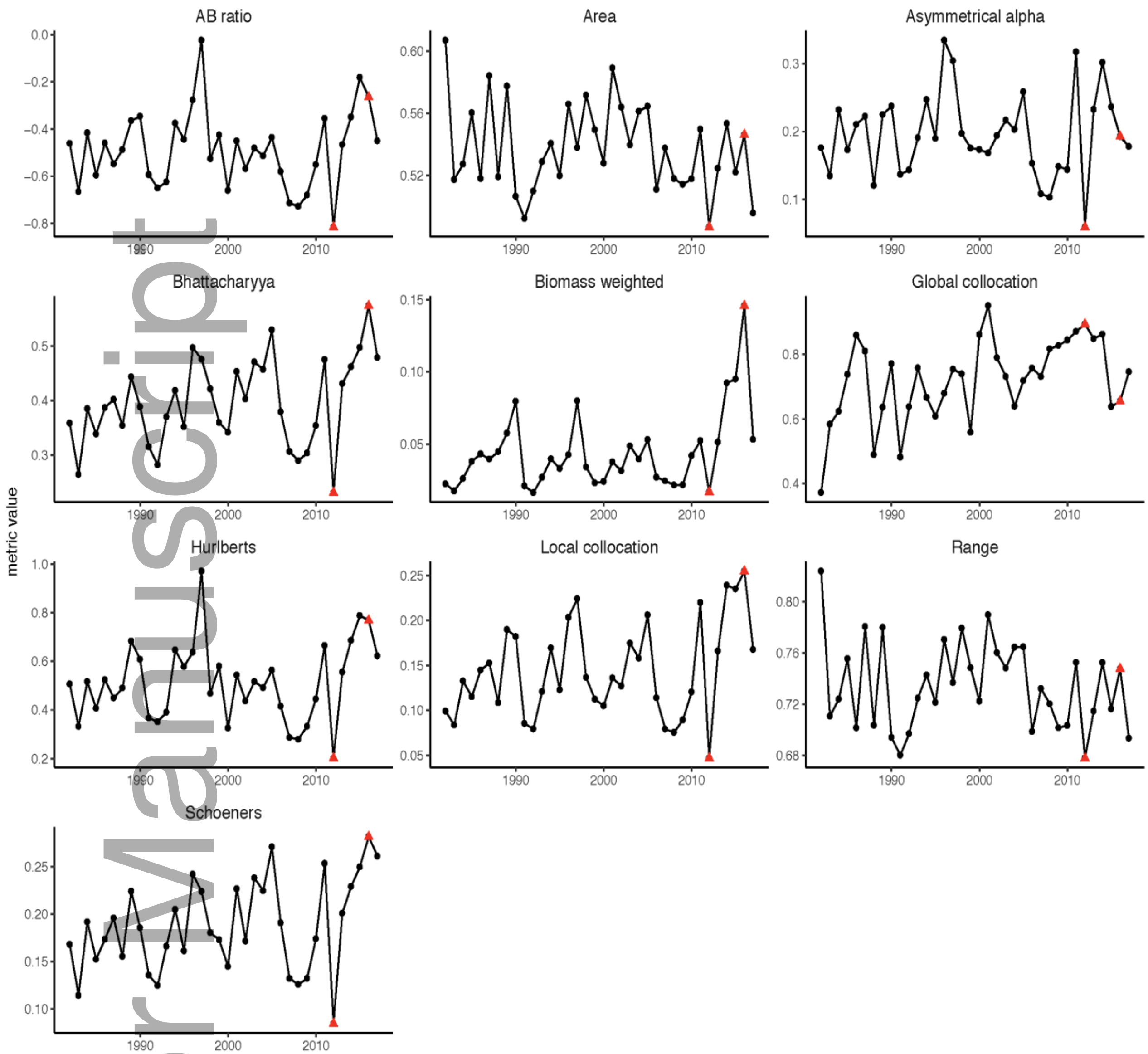

Cold pool 2016
btemp
Pollock 2016
log(abund)
Arrowtooth 2016
log(abund)
AB ratio 2016
−0.26
Asymmetrical 2016
0.19
Bhattacharyya 2016
0.57
Biomass weighted 2016
0.15
Hurlbert's 2016
0.77
Global collocation 2016
0.65
flounder
pollock
Local collocation 2016
0.25
Schoener's 2016
0.28
Area overlap 2016
0.55
Range overlap 2016
0.75
value
Latitude
Longitude

Figure 4



AB ratio
Area
Asymmetrical alpha
Bhattacharyya
Biomass weighted
Global collocation
Hurlberts
Local collocation
Range
Schoeners
metric value
1990
2000
2010

Figure 5

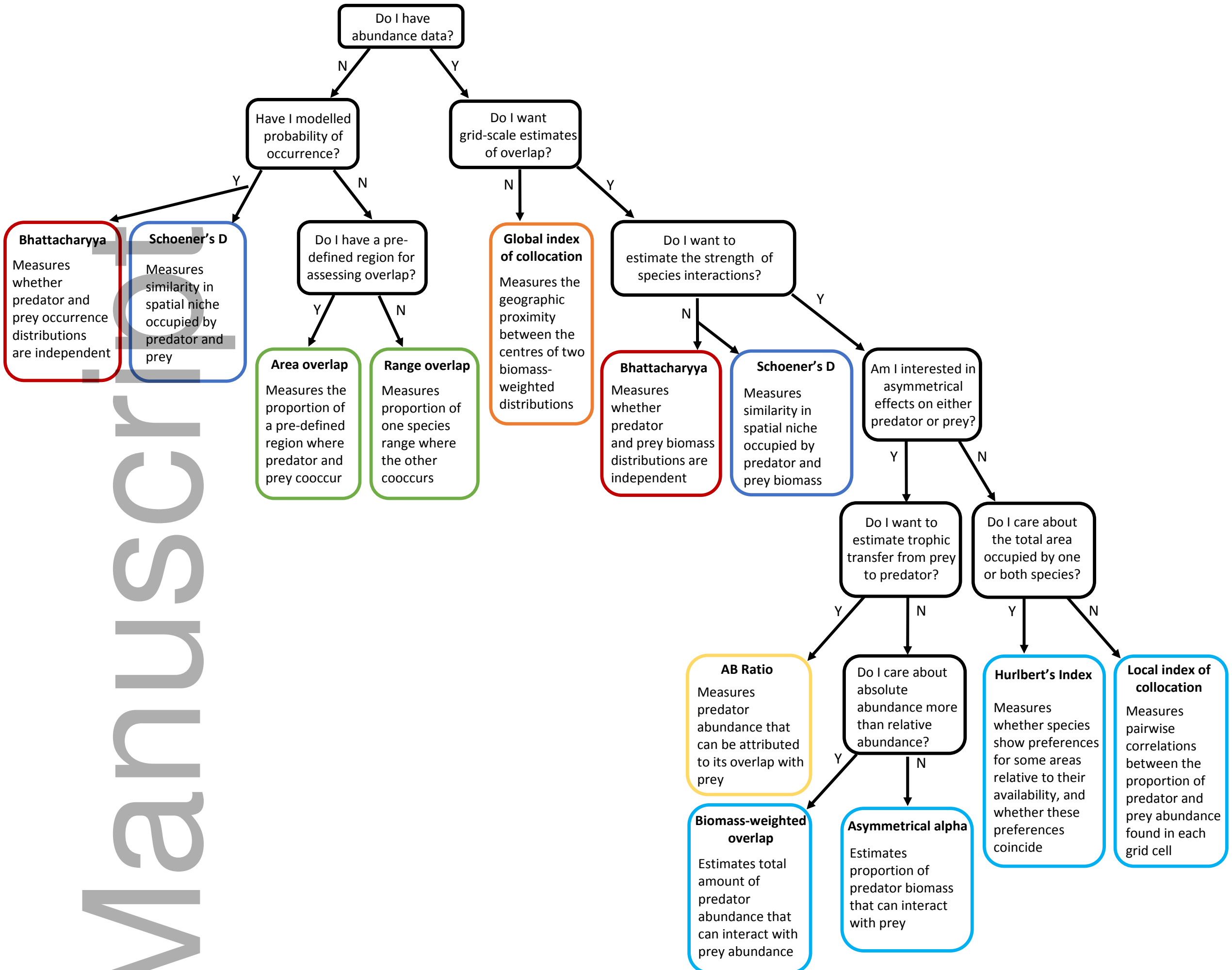
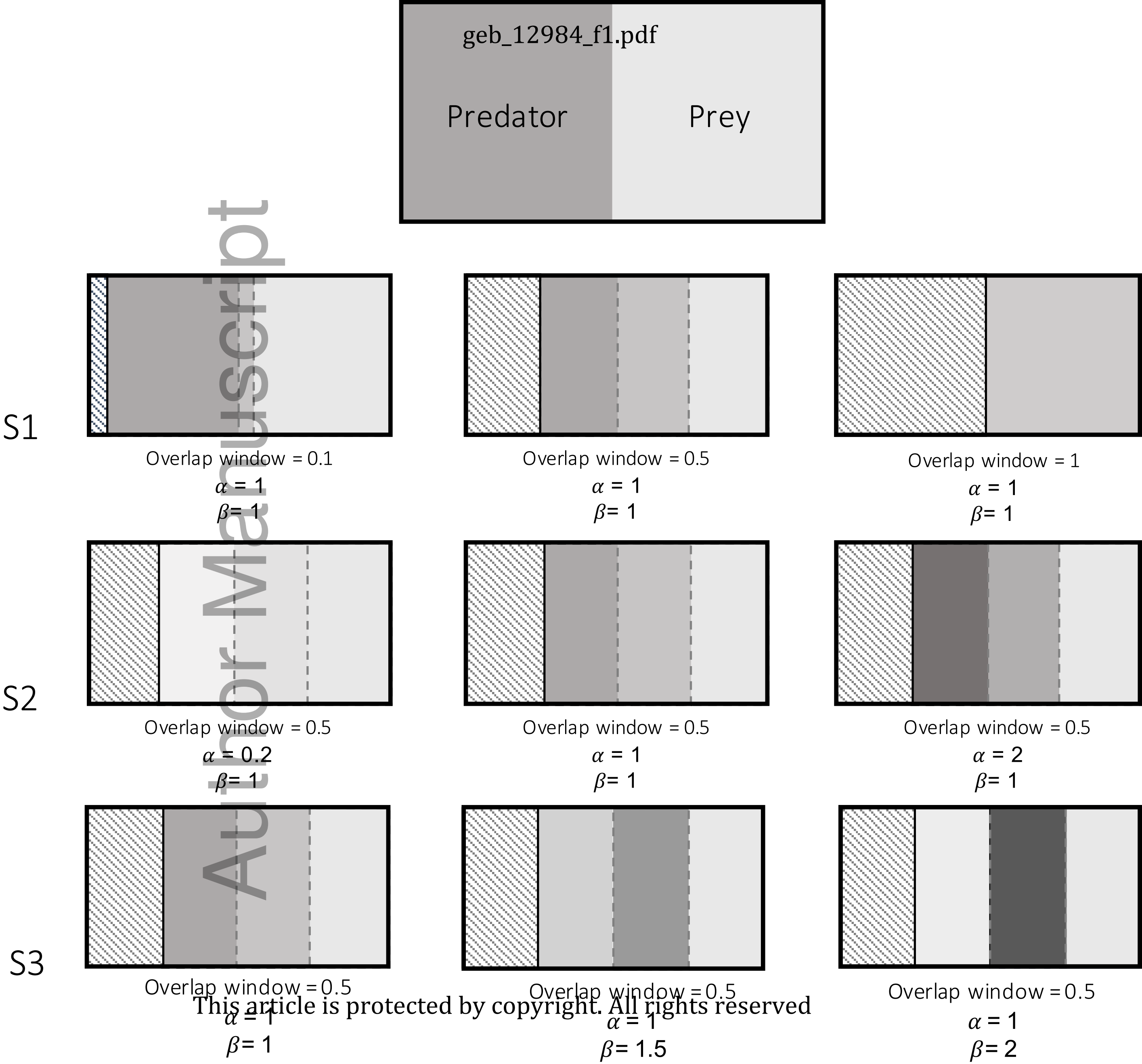
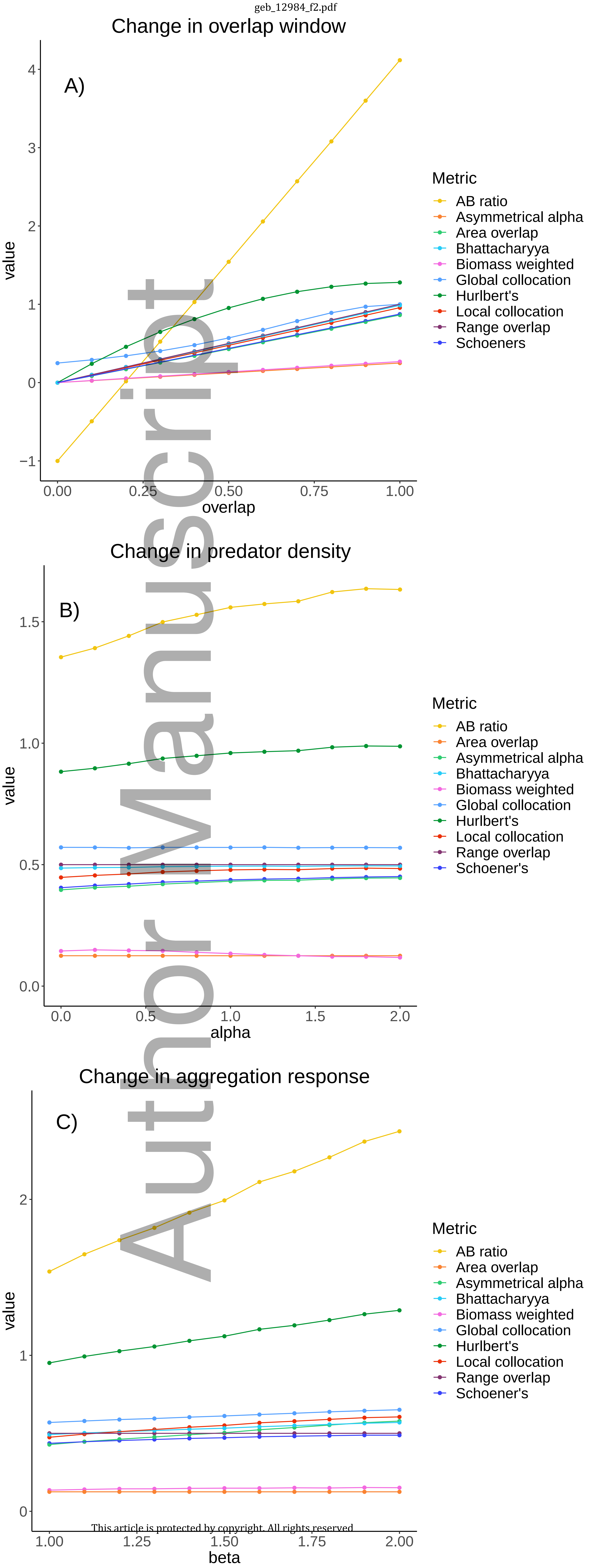
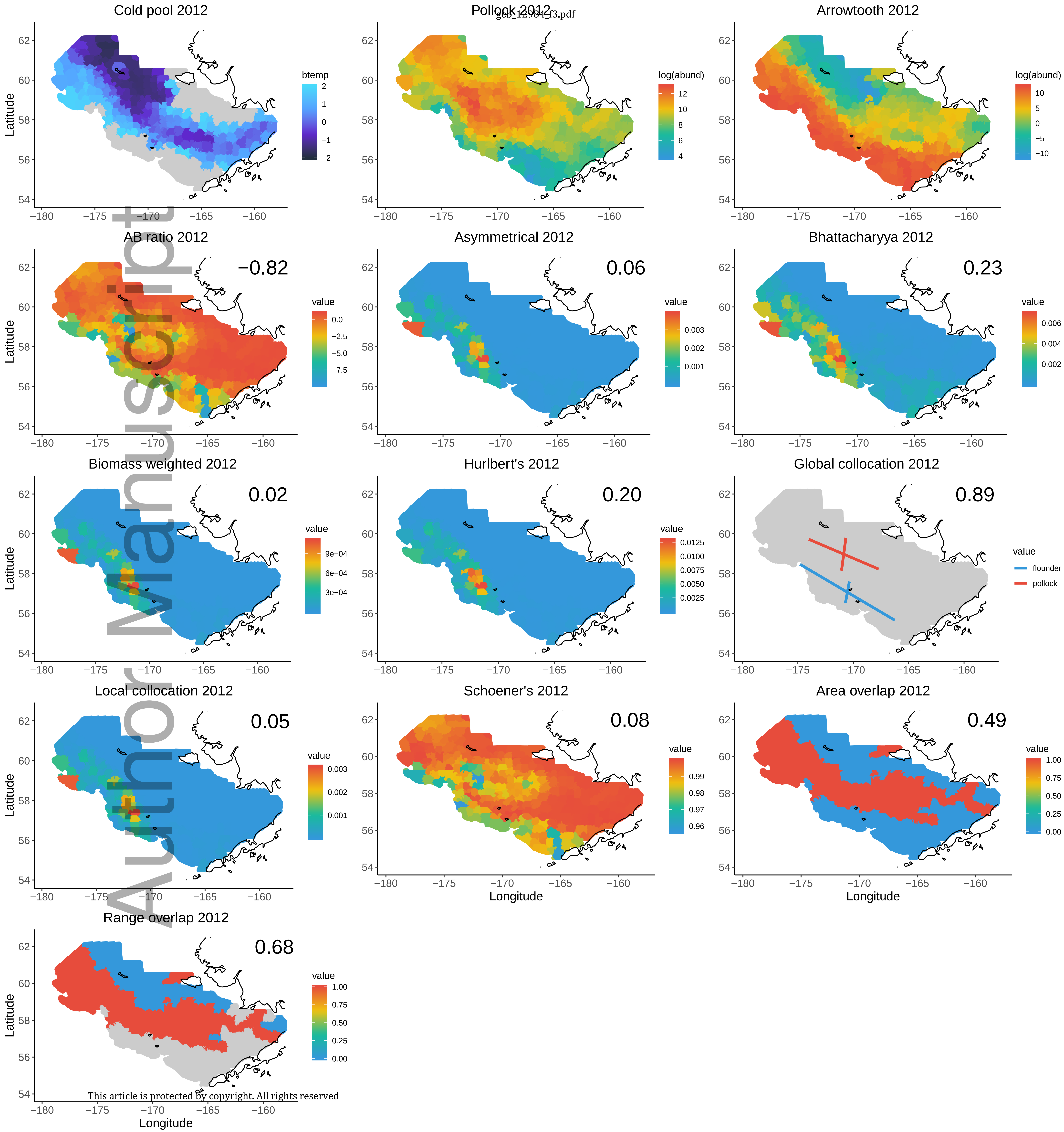
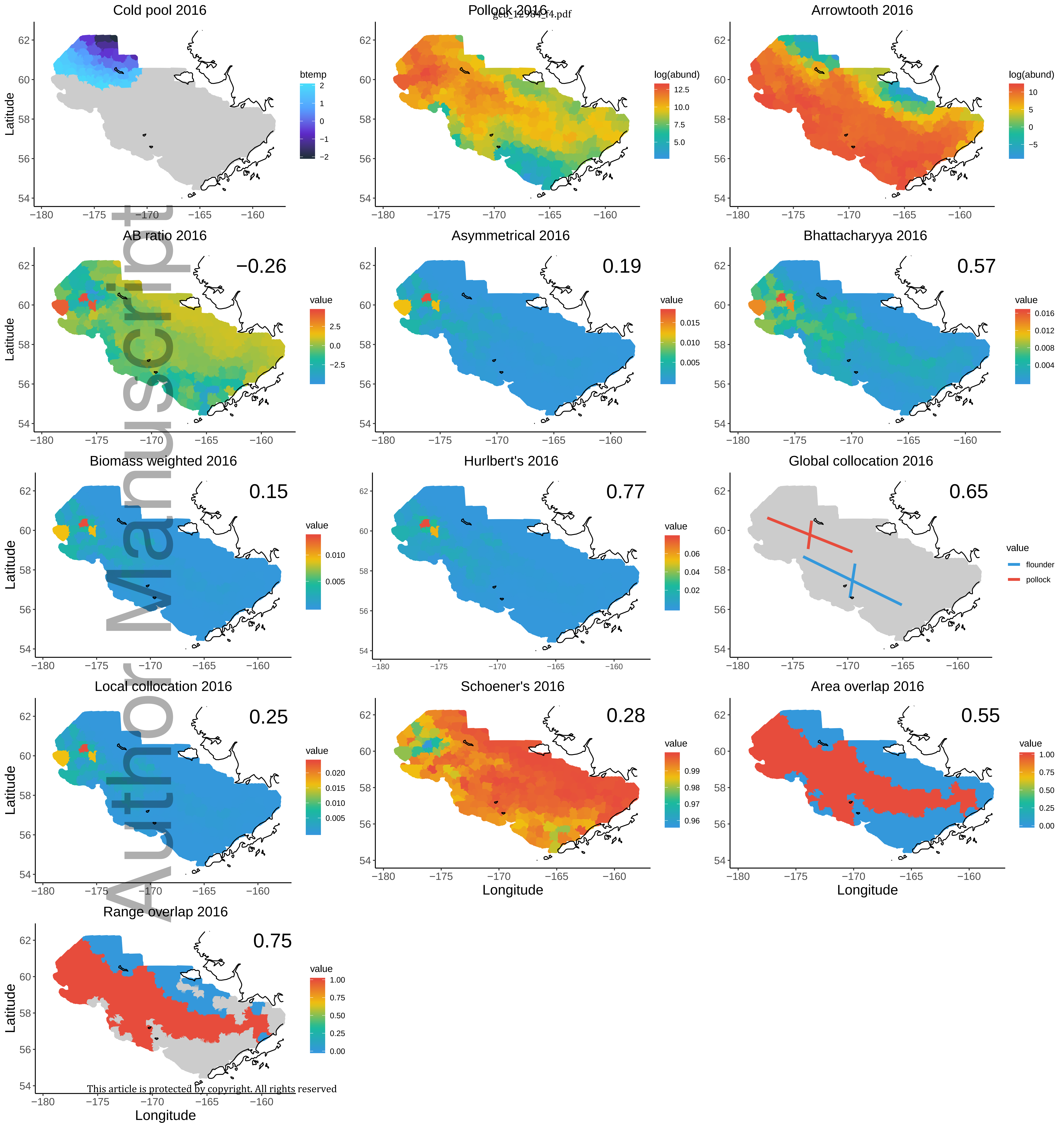

Do I have abundance data?
N
Y
Have I modelled probability of occurrence?
Do I want grid-scale estimates of overlap?
Y
N
N
Y
Bhattacharyya
Measures whether predator and prey occurrence distributions are independent
Schoener's D
Measures similarity in spatial niche occupied by predator and prey
Do I have a pre-defined region for assessing overlap?
Y
N
Area overlap
Measures the proportion of a pre-defined region where predator and prey cooccur
Range overlap
Measures proportion of one species range where the other cooccurs
Global index of collocation
Measures the geographic proximity between the centres of two biomass-weighted distributions
Do I want to estimate the strength of species interactions?
N
Y
Bhattacharyya
Measures whether predator and prey biomass distributions are independent
Schoener's D
Measures similarity in spatial niche occupied by predator and prey biomass
Am I interested in asymmetrical effects on either predator or prey?
Y
N
Do I want to estimate trophic transfer from prey to predator?
Do I care about the total area occupied by one or both species?
Y
N
Y
N
AB Ratio
Measures predator abundance that can be attributed to its overlap with prey
Do I care about absolute abundance more than relative abundance?
Y
N
Biomass-weighted overlap
Estimates total amount of predator abundance that can interact with prey abundance
Asymmetrical alpha
Estimates proportion of predator biomass that can interact with prey
Hurlbert's Index
Measures whether species show preferences for some areas relative to their availability, and whether these preferences coincide
Local index of collocation
Measures pairwise correlations between the proportion of predator and prey abundance found in each grid cell

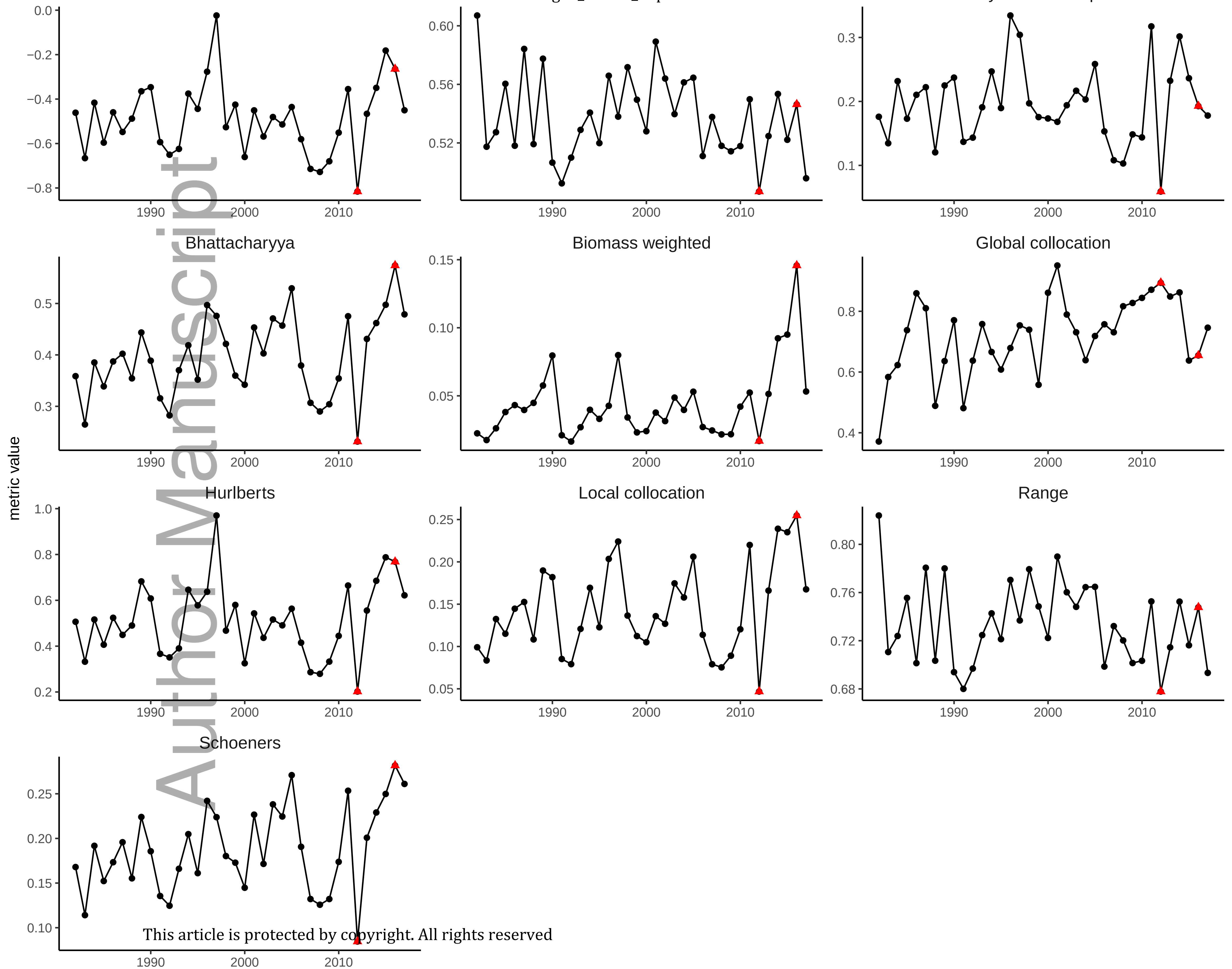
Figure 6

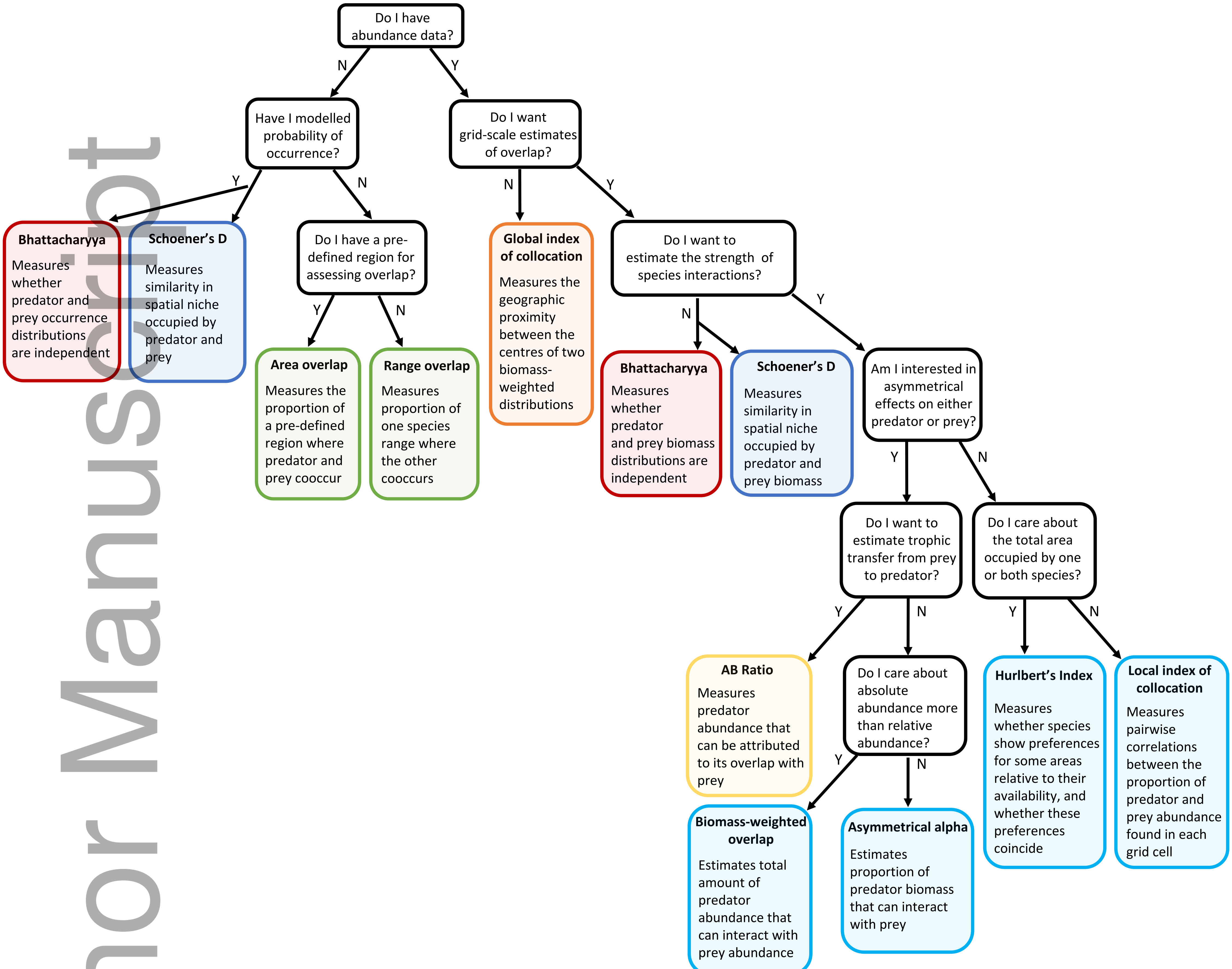

Predator
Prey
S1
Overlap window = 0.1
α = 1
β= 1
Overlap window = 0.5
α = 1
β= 1
Overlap window = 1
α = 1
β= 1
S2
Overlap window = 0.5
α = 0.2
β= 1
Overlap window = 0.5
α = 1
β= 1
Overlap window = 0.5
α = 2
β= 1
S3
Overlap window = 0.5
α = 1
β= 1
Overlap window = 0.5
α = 1
β= 1.5
Overlap window = 0.5
α = 1
β= 2


Change in overlap window
A)
value
overlap
4
3
2
1
0
−1
0.00
0.25
0.50
0.75
1.00
Metric
AB ratio
Asymmetrical alpha
Area overlap
Bhattacharyya
Biomass weighted
Global collocation
Hurlbert's
Local collocation
Range overlap
Schoeners
Change in predator density
B)
value
alpha
1.5
1.0
0.5
0.0
0.0
0.5
1.0
1.5
2.0
Metric
AB ratio
Area overlap
Asymmetrical alpha
Bhattacharyya
Biomass weighted
Global collocation
Hurlbert's
Local collocation
Range overlap
Schoener's
Change in aggregation response
C)
value
beta
2
1
0
1.00
1.25
1.50
1.75
2.00
Metric
AB ratio
Area overlap
Asymmetrical alpha
Bhattacharyya
Biomass weighted
Global collocation
Hurlbert's
Local collocation
Range overlap
Schoener's


Cold pool 2012
btemp
Pollock 2012
log(abund)
Arrowtooth 2012
log(abund)
AB ratio 2012
−0.82
Asymmetrical 2012
0.06
Bhattacharyya 2012
0.23
Biomass weighted 2012
0.02
Hurlbert's 2012
0.20
Global collocation 2012
0.89
flounder
pollock
Local collocation 2012
0.05
Schoener's 2012
0.08
Area overlap 2012
0.49
Range overlap 2012
0.68
value
Latitude
Longitude


Cold pool 2016
btemp
Pollock 2016
log(abund)
Arrowtooth 2016
log(abund)
AB ratio 2016
−0.26
Asymmetrical 2016
0.19
Bhattacharyya 2016
0.57
Biomass weighted 2016
0.15
Hurlbert's 2016
0.77
Global collocation 2016
0.65
flounder
pollock
Local collocation 2016
0.25
Schoener's 2016
0.28
Area overlap 2016
0.55
Range overlap 2016
0.75
value
Latitude
Longitude


AB ratio
Asymmetrical alpha
Bhattacharyya
Biomass weighted
Global collocation
Hurlberts
Local collocation
Range
Schoeners
metric value
1990
2000
2010


Do I have abundance data?
N
Y
Have I modelled probability of occurrence?
Do I want grid-scale estimates of overlap?
Y
N
N
Y
Bhattacharyya
Measures whether predator and prey occurrence distributions are independent
Schoener's D
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Measures the proportion of a pre-defined region where predator and prey cooccur
Range overlap
Measures proportion of one species range where the other cooccurs
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Measures the geographic proximity between the centres of two biomass-weighted distributions
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Y
Bhattacharyya
Measures whether predator and prey biomass distributions are independent
Schoener's D
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Y
N
Do I want to estimate trophic transfer from prey to predator?
Do I care about the total area occupied by one or both species?
Y
N
Y
N
AB Ratio
Measures predator abundance that can be attributed to its overlap with prey
Do I care about absolute abundance more than relative abundance?
Y
N
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Asymmetrical alpha
Estimates proportion of predator biomass that can interact with prey