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Density-dependent changes in effective area occupied for sea-bottom-associated marine fishes

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The spatial distribution of marine fishes can change for many reasons, including density-dependent distributional shifts. Previous studies show mixed support for either the proportional-density model (PDM; no relationship between abundance and area occupied, supported by ideal-free distribution theory) or the basin model (BM; positive abundance–area relationship, supported by density-dependent habitat selection theory). The BM implies that fishes move towards preferred habitat as the population declines. We estimate the average relationship using bottom trawl data for 92 fish species from six marine regions, to determine whether the BM or PDM provides a better description for sea-bottom-associated fishes. We fit a spatio-temporal model and estimate changes in effective area occupied and abundance, and combine results to estimate the average abundance–area relationship as well as variability among taxa and regions. The average relationship is weak but significant (0.6% increase in area for a 10% increase in abundance), whereas only a small proportion of species–region combinations show a negative relationship (i.e. shrinking area when abundance increases). Approximately one-third of combinations (34.6%) are predicted to increase in area more than 1% for every 10% increase in abundance. We therefore infer that population density generally changes faster than effective area occupied during abundance changes. Gadiformes have the strongest estimated relationship (average 1.0% area increase for every 10% abundance increase) followed by Pleuronectiformes and Scorpaeniformes, and the Eastern Bering Sea shows a strong relationship between abundance and area occupied relative to other regions. We conclude that the BM explains a small but important portion of spatial dynamics for sea-bottom-associated fishes, and that many individual populations merit cautious management during population declines, because a compressed range may increase the efficiency of harvest.

1. Introduction

Recent studies have suggested that marine fish populations are shifting in response to climate impacts [1,2], but changes in spatial distributions can also be driven by variation in fishing and habitat alterations [3]. Shifts in distribution for marine species are likely to impact fishing opportunities for fishing communities, as well as foraging opportunities for top predators such as marine mammals and birds, and may also affect treaties and informal relationships

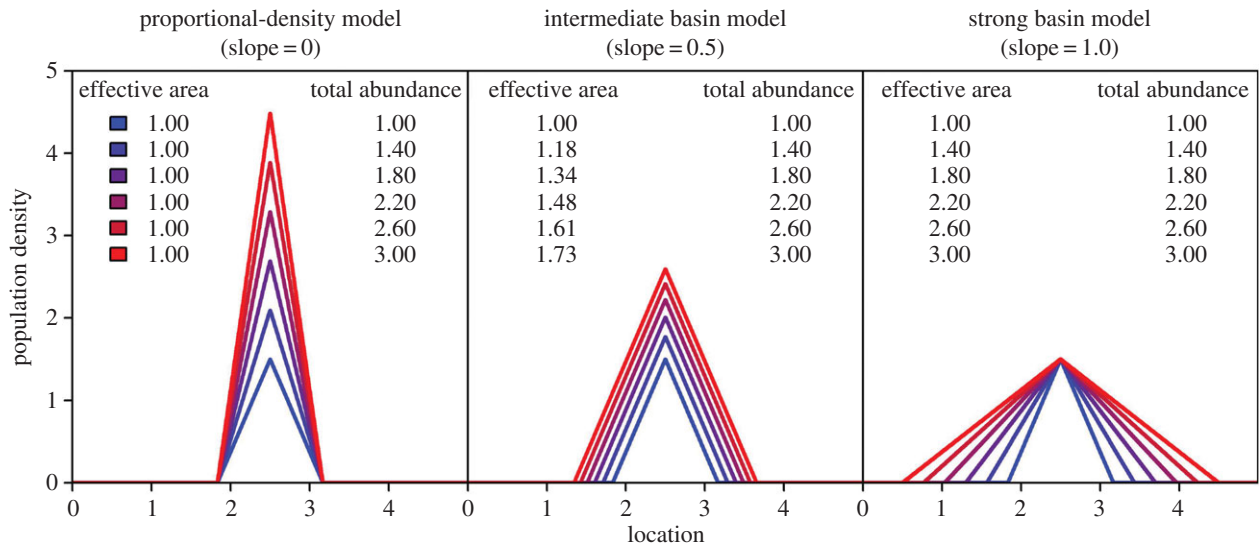


Figure 1. Conceptual diagram contrasting the proportional-density model (left panel, supported by IFD theory) and the basin model (middle and right panel, supported by density-dependent habitat selection theory). We define total abundance (b_t) as the product of average density (m_t) and effective area occupied (h_t), i.e. $b_t = m_t \times h_t$, and define a multiplicative relationship between effective area and abundance, $h_t \propto b_t^\delta$, where parameter δ governs this relationship. This implies that $m_t \propto b_t^{1-\delta}$, so δ is the proportion of abundance change attributable to range expansion/contraction, whereas $1 - \delta$ is the proportion owing to change in average density. In each panel, we show density (y -axis) along a one-dimensional spatial domain (x -axis) with optimal habitat at $x = 2.5$, subject to different levels of total abundance ($b_t = \{1, 1.4, 1.8, 2.2, 2.8, 3.0\}$). Panels differ in the parameter δ linking effective area and abundance (proportional-density model: $\delta = 0$; basin model: $\delta > 0$). When $\delta = 1$, abundance change is entirely attributable to change in effective area occupied. (Online version in colour.)

between countries near the boundary of moving populations [4]. Understanding the causes of these distribution shifts is vital for predicting future access to fish protein.

One much-discussed driver for changes in marine fish distribution is termed 'density-dependent distributional shift', and density-dependent shifts in distribution have been previously identified for several commercially important species [5]. For example, Japanese sardine and northern anchovy near California have historically exhibited a restricted range inshore during years with reduced population size [6,7]. Density-dependent distribution shifts have also been identified in sea-bottom-associated fishes, such as Atlantic cod (*Gadus morhua*) [8,9]. In support of these observations, the 'basin model' (BM) for marine species predicts that the distribution of marine species will collapse towards preferred habitats as abundance decreases. This BM has been justified by reference to the theory of density-dependent habitat selection (DDHS). DDHS theory predicts that habitat quality (i.e. measurements of *per capita* recruitment, individual growth or total productivity) will decrease with increasing density, such that individuals will seek to colonize unoccupied habitats during population increases.

The basin model of marine biogeography (and the associated theory of DDHS) has been invoked in several famous narratives regarding the collapse of marine species. Under the BM, a species with declining abundance will shrink towards its core habitat rather than showing a proportional decrease in density throughout its range (figure 1). Owing to this range contraction, densities will decrease less in the core habitat than overall. As a consequence, fisheries catch rates can remain high in the core area even during population declines, a phenomenon also known as hyperstability in catch-per-unit-effort data obtained from fishers [10]. In spatially aggregated population models, this phenomenon will result in density-dependent catchability, which has been observed in a variety of marine species, including during the collapse of northern cod [11,12].

Despite frequent discussion of DDHS and the BM, there are alternatives for describing distribution changes in marine species. One example is the theory that predators will forage following an ideal-free distribution (IFD) [13]. When applied to species distributions, the IFD predicts that an increase in population size will be accompanied by a proportional increase in density for all portions of the population's distribution [14]. We therefore call this the 'proportional-density model' (PDM), and note that the PDM might be supported even when the assumptions of IFD theory are not met (figure 1). The PDM has been a useful description of distribution shifts for sea-bottom-associated fishes in the North Sea, near Newfoundland and in the Gulf of St Lawrence [15,16].

There is thus evidence in favour of both the BM as supported by DDHS theory [5,9], and the PDM as supported by IFD theory [15]. However, the relative importance of these theories in describing distribution shifts for marine fishes, in general, is unclear. Because negative results (lack of relationship) are reported in the literature less frequently (i.e. 'file drawer' bias [17]), published studies are unlikely to show the extent to which each theory describes a randomly selected species. Further, the previous analyses have potentially been biased owing to 'errors-in-variables' [18], which will generally bias statistical estimates towards zero whenever a predictor variable in a linear model is measured with some error [19]. In this case, errors-in-variables arise because total abundance is treated as a predictor variable for area occupied, and abundance is generally estimated from survey data or a population model with some error. Accounting for errors-in-variables bias has been shown to impact the results for analyses of population regulation [18] and life-history traits [20], but has not previously been accounted for in analyses of fish spatial distribution.

We seek to determine whether there is a general relationship between area-occupied and abundance for sea-bottom-associated marine fishes. Specifically, we estimate how often

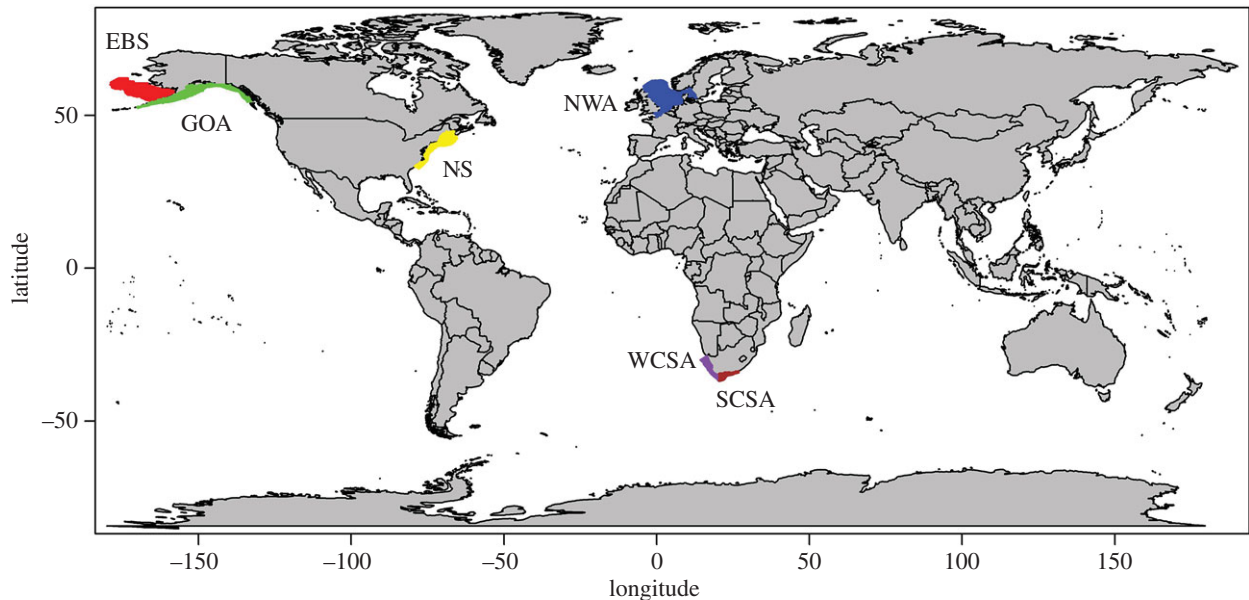


Figure 2. Map of six marine regions included in this study, each having data from multispecies bottom trawl surveys with standardized operations covering more than 20 years. Each survey corresponds to a shaded area and is labelled using region codes: red, Eastern Bering Sea (EBS); green, Gulf of Alaska (GOA); yellow, Northwest Atlantic (NWA); purple, West Coast of South Africa (WCSA); brown, South Coast of South Africa (SCSA); blue, North Sea (NS). (Online version in colour.)

the BM or PDM provides a better description of distribution shifts for sea-bottom-associated marine species, while accounting for the potential bias induced by errors-in-variables. We do so by conducting a meta-analysis of the relationship between total abundance and area occupied for 92 fish species across six region, resulting in 120 species–region combinations (figure 2). We specifically modify a previously developed spatio-temporal model for fish distributions, and estimate both abundance and a new metric of occupied area (termed ‘effective area occupied’). We use effective area occupied rather than the area occupied by $X\%$ of the population (e.g. 95%, sometimes termed D_{95}), because the results from the latter metric are sensitive to decisions about the value of X [8], whereas our new metric provides a single synoptic measure of concentration across the population’s range. We then develop a novel meta-analytic model that synthesizes estimates of total abundance and area occupied for individual species, while using errors-in-variables techniques to account for imprecise estimates of both.

2. Material and methods

We estimate abundance as the total biomass (kg) available to bottom trawl sampling gear (termed ‘total available biomass’) and area occupied (square km) as the total area necessary to contain the population at its average density (see §2b for details). We estimate abundance in biomass rather than numbers to avoid disproportionate impacts of very large catches of small individuals, for which bottom trawl catchability tends to be variable. Further, when catches are large, the number of individuals is frequently measured for a subsample of catch even in cases where total weight is recorded for the species. Estimating the average relationship between abundance and area-occupied involves the following two steps.

1. We first fit a spatio-temporal model to survey data for each of 120 species–region combinations (drawn from six marine regions). This model analyses both occurrence (encounter or non-encounter on each survey occasion) and positive density (catch in weight per area when the species is encountered), and thereby accounts for both distribution (where it is present)

and density (how much is present) [21]. Total abundance and area occupied are predicted at the same time as model parameters, so standard errors for abundance and area occupied represent the predictive variance for each [22]. Using an appropriate statistical model, we use available data more efficiently than is achieved using a design-based or spatially stratified model [23].

2. We then fit a second-stage meta-analytic model to estimates of abundance and area occupied, as well as their estimated standard errors. This second-stage model uses error-in-variables techniques to account for the predictive variance arising from our use of model estimates of abundance and area occupied. The meta-analytic model also specifies that the relationship between abundance and area occupied varies among stocks, while estimating the average relationship and the magnitude of variation among stocks.

By using this approach, our meta-analysis accounts for both estimation errors arising from using noisy data (‘experimental variability’), and differences among species–region combinations in the relationship between area-occupied and abundance (‘parametric variability’ [17]).

(a) Estimating spatio-temporal variation in population density

We estimate a density function $D_t(s)$ that represents population density measured as biomass per area at any location s in year t (see electronic supplementary material, appendix S1). This function is decomposed into the probability of encountering the species at any location (P_t), and the expected density given that the species is encountered (R_t). Probability of encounter and expected density given encounter are in turn estimated as generalized linear-mixed models (GLMMs). Each of these two GLMMs involves estimating a spatial process (e.g. an increased or decreased probability of encounter at one location relative to another, on average across years), and a spatio-temporal process (e.g. an increased or decreased probability of encounter, where relative probability changes among years). The spatio-temporal process accounts for changes in spatial distribution over time.

In practice, we approximate all function-valued variables as if they were piecewise constant, and estimate parameters using

maximum marginal likelihood techniques. To do so, we use template model builder [24] called from within the R statistical platform [25]. We modify the R package ‘SpatialDeltaGLMM’ (https://github.com/nwfsc-assess/geostatistical_delta-GLMM) for estimating parameters for this model [26].

(b) Defining area-occupied

We then calculate ‘effective area occupied’, which measures the area (in units square km) required to contain a population given its average population density (kg km⁻²). This metric builds on the intuition that total abundance b_t is equal to average density m_t times the area occupied h_t ($b_t = m_t \times h_t$). Total abundance (in units biomass) and average density (in units biomass per area) are both easily calculated from the density function $\mathcal{D}_t(s)$ for that year, so effective area occupied h_t is simply their ratio (see electronic supplementary material, appendix S1 for derivation and details):

$$h_t = \frac{b_t}{m_t} = \frac{(\int \mathcal{D}_t(s) ds)^2}{\int \mathcal{D}_t^2(s) ds}.$$

We therefore interpret ‘effective area occupied’ as the area required to contain the population given the average density. Given that abundance increases (or decreases), an increase (decrease) in effective area occupied is in accordance with the DDHS model, whereas no change is in accordance with the IFD model (figure 1). Other benefits of this metric are listed in electronic supplementary material, appendix S1.

(c) Meta-analysis of the relationship between abundance and area-occupied

We seek to estimate the average relationship between total abundance in biomass (b) and effective area occupied (h) for sea-bottom-associated fishes. We approximate this relationship for a given species, using a linear model between the logarithm of abundance and the logarithm of area occupied for all years in a given region

$$\log(h_t) = \gamma + \delta \log(b_t),$$

where γ represents a species–region-specific intercept, and δ represents the average relationship. If $\delta = 0$, a change in abundance has no association on average with changes in area occupied, and this provides support for the ‘proportional-density’ model. Similarly, if $\delta > 0$, a 1% increase/decrease in abundance is associated with a $\delta\%$ increase/decrease in area occupied. Furthermore, we estimate $h_t = \exp(\gamma) \times b_t^\delta$, so this implies that $m_t = \exp(-\gamma) \times b_t^{1-\delta}$ (because $b_t = m_t \times h_t$ by definition). Therefore, δ can be interpreted as the proportion of abundance change that is explained by change in effective area occupied, whereas $1 - \delta$ is the proportion that is explained by increases in average density. For example, a value of $\delta = 0.5$ attributes increases in abundance equally to both range expansion and increases in density within the species range in that region (figure 1).

However, both abundance and area occupied are estimated from the same dataset for each species and year. Conventional linear models assume that the predictor variable (in this case, abundance) is known without error, and ‘error-in-variables bias’ arises whenever this assumption is violated [19]. There is a large literature regarding error-in-variables bias in statistics, fisheries and ecology [18,19]. Error-in-variables bias can be corrected in linear models by treating the latent (true but unobserved) variable as a random effect, and using the predictor variable as a noisy measurement of this random effect (see electronic supplementary material, appendix S2 for more details). We therefore use mixed-effects modelling techniques to account for correlated estimation error in both area occupied and

abundance for each species (electronic supplementary material, appendix S3).

We also want to account for variation among species and regions in the average relationship between abundance and area occupied. We therefore specify that the relationship δ_c between abundance and area occupied for species–region combination c arises from a probability distribution, where this distribution represents the expected mean and variability in the abundance–area relationship

$$\delta_c \sim \text{Normal}(\mathbf{X}\boldsymbol{\theta}, \sigma_\delta^2),$$

where \mathbf{X} is a design matrix, $\boldsymbol{\theta}$ is a vector of parameters and σ_δ^2 is the variance among species–region combinations in the area–abundance relationship. We specifically explore four models:

1. *Constant*—the null hypothesis where the average abundance–area relationship (δ_c) is constant for all stocks. In this case \mathbf{X} is an intercept (i.e. $\mathbf{X} = \mathbf{1}$), and $\boldsymbol{\theta}$ is a single parameter representing the average relationship between log-abundance and log-area-occupied.
2. *Varies among regions*—an alternative hypothesis where δ_c varies by region. In this case, \mathbf{X} is a design matrix where x_c has a 1 for the region that contains the c th stock, and 0 s otherwise, and $\boldsymbol{\theta}$ is a vector representing the average relationship between log-abundance and log-area-occupied in each region.
3. *Varies among taxa*—an alternative hypothesis where δ_c varies by taxonomic order, where we have sufficient data to analyse Elasmobranchii (20 species–region combinations), Gadiformes (24), Pleuronectiformes (28), Perciformes (13), Scorpaeniformes (25) and other bony fishes (9), where \mathbf{X} and $\boldsymbol{\theta}$ are defined similarly to the ‘varies among regions’ model.
4. *Varies among regions and taxa*—an alternative hypothesis where δ_c varies by both region and taxa. We specify that coefficients $\boldsymbol{\theta}$ for each region must sum to zero to ensure that region and taxa effects are identifiable. The specification implies that $\boldsymbol{\theta}$ for each taxon is the expected value for δ_c across all six regions.

We then use the Akaike information criterion to identify the most parsimonious model (the model with $\Delta\text{AIC} = 0$ is the most parsimonious, and values close to zero are more parsimonious than larger values), and interpret parameter estimates to evaluate the evidence for either the BM or PDM models. The PDM predicts no change in effective area occupied with changing density (i.e. $\hat{\theta} = 0$), whereas the BM predicts some positive relationship (i.e. $\hat{\theta} > 0$).

(c) Bottom trawl database

We apply this meta-analytic technique to long-term data from six bottom trawl surveys (figure 2). We choose these bottom trawl surveys because each has followed a standardized sampling protocol for over two decades (although not necessarily in every year), and therefore is likely to capture a time scale over which abundance and effective area occupied have changed for many species. These surveys comprise:

1. A fixed-station survey in the Eastern Bering Sea (EBS) from 1982 onwards.
2. A stratified random survey in the Gulf of Alaska from 1984 onwards.
3. A stratified random survey across the continental shelf of the eastern seaboard of the USA during the spring from 1985 to 2008.
4. A stratified random survey in the continental shelf (up to 500 m) of the south coast of South Africa during the autumn from 1988 to 2010.
5. A stratified random survey on the continental shelf (up to 500 m) of the west coast of South Africa during the summer from 1986 to 2010.

6. The North Sea international bottom trawl survey (NS-IBTS), a randomized survey operated by multiple countries in the North Sea from 1991 onwards.

For each survey, we restrict analysis to data collected using standardized vessels and sampling gear (electronic supplementary material, appendix S4). In general, we define ‘species–region combination’ as a fish species occurring within each individual survey. In some regions (e.g. the Bering Sea), the species in the survey may represent a small portion of the total contiguous range for that species, but our definition of ‘species–region combination’ is generally consistent with the scale at which these species are managed.

We make several assumptions by using these data for our analysis. First, we assume that detectability (the proportion of fishes within the surveyed area that are observed) is constant spatially for each survey (but differs between surveys). Second, we assume that the probability of sampling at a given location is statistically independent of density at that location. This assumption is common in spatio-temporal statistics [27], and is reasonable given that each survey uses a probability sampling protocol where sampling probability is predefined independently of expected population density. Together, these assumptions imply that spatial variation in survey catch rates is an informative measure of spatial variation in fish density.

For each survey, we analyse data for the 20 fish species that are most frequently encountered during the survey (i.e. have the highest proportion of survey tows that encountered that species) after excluding epipelagic fishes (e.g. shoaling forage fishes such as herring *Clupea harengus* or horse mackerel *Trachurus trachurus*; electronic supplementary material, appendix S5). We exclude epipelagic fishes because they may not be captured consistently using bottom trawl sampling gear, and we analyse frequently encountered species because these species generally permit precise estimates of abundance and area occupied. This decision raises the possibility that our results are only representative of frequently encountered species in each survey. We therefore include a *post hoc* analysis where we compare the predicted abundance–area relationship for each species (δ_i) with the encounter rates for each species.

3. Results

We first illustrate the effect of a negative or positive relationship between abundance and effective area occupied, using arrowtooth flounder (*Atheresthes stomias*) in the EBS and little skate (*Leucoraja erinacea*) in the Northwest Atlantic as examples (figures 3 and 4). Arrowtooth flounder has increased in abundance in the EBS since 1982, and effective area has also increased somewhat during this time. Notably, the greatest peak in abundance (2004) coincides with the greatest effective area. By contrast, little skate exhibits high fluctuations in abundance over time, where the highest and lowest abundance estimates (1998 and 2006, respectively) coincide with the smallest and largest effective area. Inspection of the estimated density function for each species in evenly spaced years shows that little skate in 2008 (a year with greater-than-average abundance) has density concentrated in a small, inshore portion of the population’s range, whereas 1995 (a year with lower-than-average abundance) has little change in low-density areas but a large decrease in density in the core of the range. Conversely, arrowtooth flounder shows a gradual movement from offshore towards inshore habitats as the population size has grown over time. Inspection of estimates for all species in the database (electronic supplementary material, appendix S6 and figures

S2–S7) shows that only some species (e.g. bigmouth sculpin, *Hemitripterus bolini* the EBS) have a discernible trend in abundance or effective area occupied over time. However, many other species (e.g. great sculpin, *Myoxocephalus polyacanthocephalus* in the EBS) have significant interannual variation (i.e. non-overlapping confidence intervals but without a long-term trend) in one or both variables, and this interannual variation still provides statistical contrast for estimating the relationship between variables.

Inspection of meta-analytic results for all species, while assuming that species from all regions share the same distribution for the abundance–area relationship (the ‘constant’ model; figure 5 and table 1) shows that there is a positive relationship on average between abundance and area occupied, and this average relationship is statistically significant (mean: 0.061, s.e.: 0.014; $p < 0.001$ using a two-sided Wald test). This provides support for the basin model (which predicts a non-zero relationship) relative to the PDM. However, the average magnitude of this effect is weak, such that a 10% increase in abundance is associated with a 0.61% increase in effective area. Furthermore, variation among stocks is larger than the mean effect ($\sigma_\delta = 0.10$ versus $\beta = 0.061$). On average, across regions, species–region combinations are evenly split between those showing a greater than 1% increase in effective area for every 10% increase in abundance (i.e. 35% of the predictive distribution having $\delta > 0.1$), those showing a weak link between abundance and area (i.e. 38% having $0 < \delta < 0.1$, and those showing a negative impact of abundance on area occupied (i.e. 27% having $\delta < 0$). We note that none of these population-specific estimates of a negative relationships (e.g. as seen in little skate in the Northwest Atlantic) are significantly different from zero (as estimated, using a two-sided Wald test at a 0.05 level).

The Akaike information criterion indicates that the ‘varies among regions and taxa’ model is most parsimonious ($\Delta\text{AIC} = 0$), whereas the ‘varies among regions’ model is a close second ($\Delta\text{AIC} = 0.78$; table 1 and figure 6). The ‘varies among regions and taxa’ model has a residual standard deviation σ_δ of 0.064 (compared with 0.099 for the ‘constant’ model), so region and taxon explain 58% ($1 - (0.064^2/0.099^2)$) of variance in the abundance–area relationship among species. We identify strong and statistically significant relationships between abundance and effective area in Gadiformes (0.106; s.e.: 0.026), followed closely by Pleuronectiformes (0.076; s.e.: 0.025) and Scorpaeniformes (0.071; s.e.: 0.026). We find weaker relationships in Elasmobranchii (0.043; s.e.: 0.025) and Perciformes (−0.034; s.e.: 0.034), and neither is significant (see table 1 for p -values). Region estimates for this model are specified to have a mean of zero, and represent offsets of each region from the average for each taxon. The EBS has a significantly stronger-than-average relationship between abundance and effective area (after the model controls for differences in taxa among regions; mean: 0.107; s.e.: 0.025) and the Northwest Atlantic has a significantly weaker-than-average relationship (mean: −0.086; s.e.: 0.030). The region effects in the Northwest Atlantic, South Africa west coast and South Africa south coast are not significantly different from zero. Region effects therefore play an important role in modifying the average abundance–area relationship for each taxon, where a gadiform in the EBS, for example, has a substantial relationship on average (a 2.1% increase in area for a 10% abundance increase), but in the Northwest Atlantic has a very weak relationship (0.2% increase in area for the same abundance

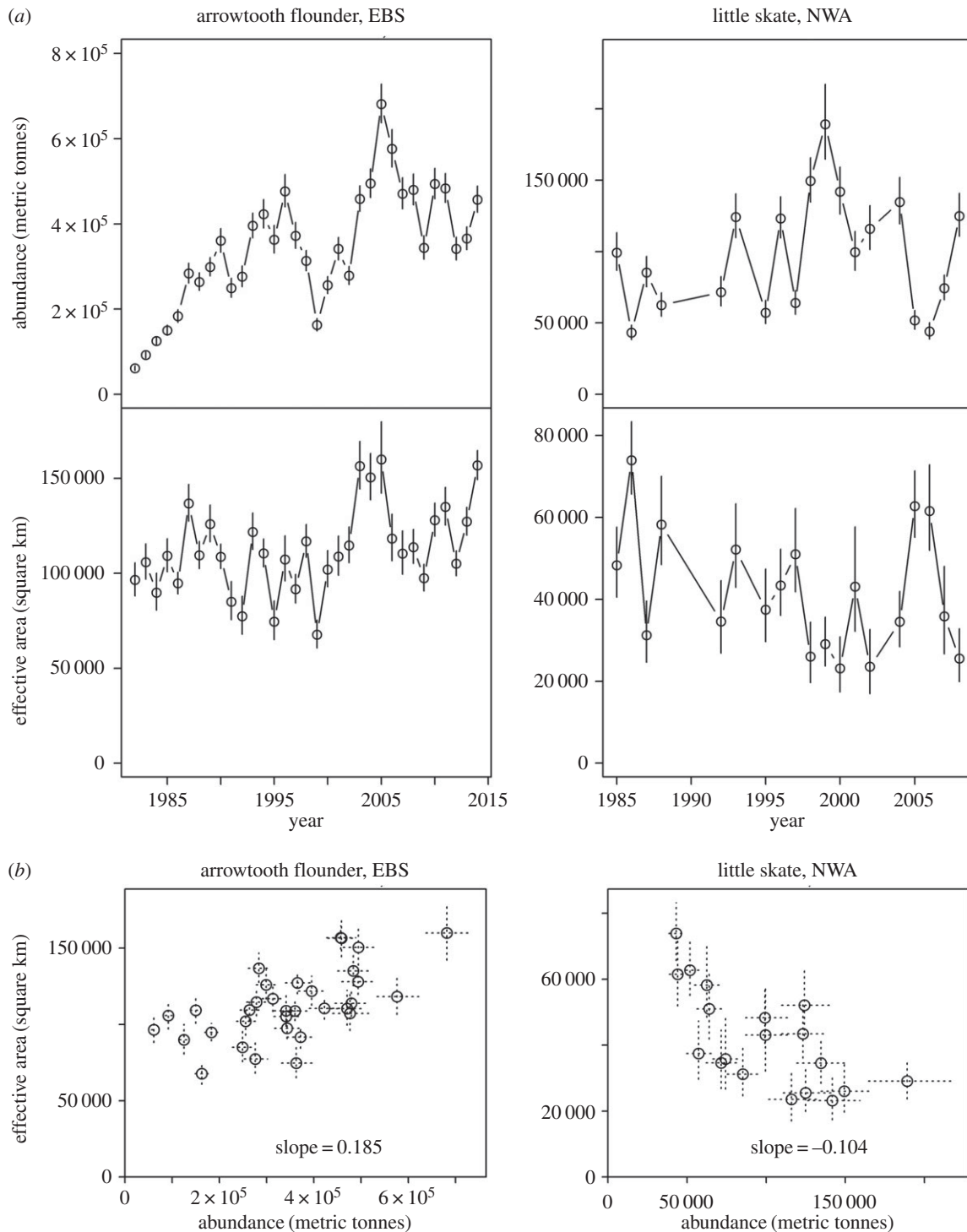


Figure 3. (a) Example species show positive (first column: arrowtooth flounder in the Eastern Bering Sea) or negative (second column: little skate in the Northwest Atlantic) responses of effective area to increases in species abundance over time. Each panel shows the estimate (circle) and confidence interval (± 1 s.e.; y-axis) against year (x-axis). (b) The same example species showing effective area and species abundance, where points and dotted whiskers are the estimate ± 1 s.e. for both variables in each year. Each panel lists the estimated slope (δ_c) from the meta-analysis model that includes differences among regions in the average area–abundance relationship (i.e. where expected δ_c differs systematically among regions).

change). The PDM is generally a suitable description for most taxa in the Northwest Atlantic, whereas the basin model is important for all taxa except Perciformes in the EBS, Gulf of Alaska and North Sea regions. A comparison of the predicted abundance–area relationship for each species–region combination against encounter rates provides no evidence that less-encountered species have a different relationship than frequently encountered species (electronic supplementary material, appendix S7 and figure S8). We therefore find

evidence that the species in this database are likely to be representative of less frequently encountered fishes in these regions.

4. Discussion

In this paper, we conduct the largest meta-analysis to date of two hypothesized models (the BM and PDM) linking effective population area to population size in marine fishes. This

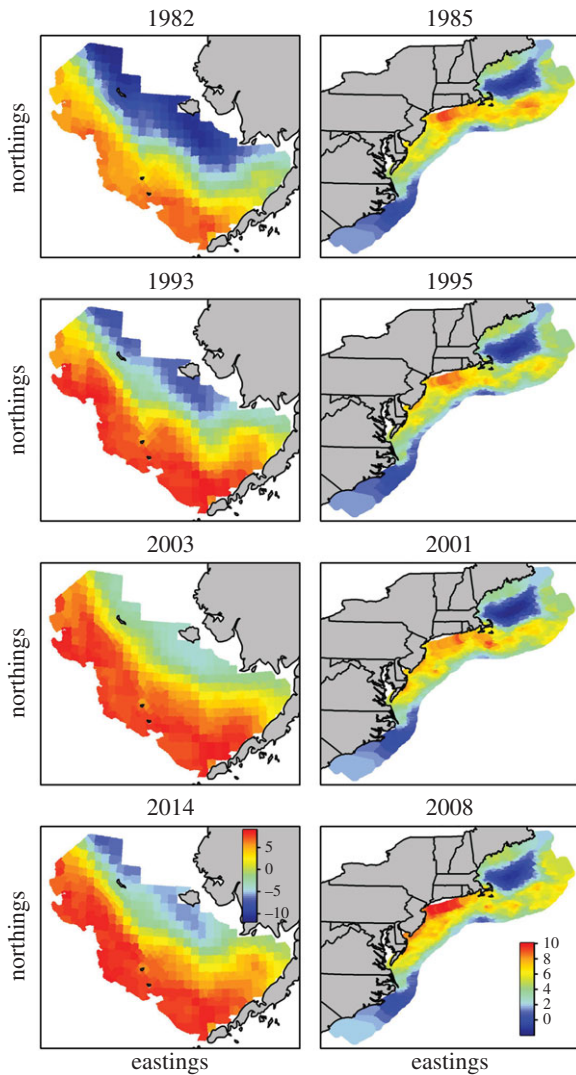


Figure 4. Predicted density relative to maximum observed (inset colour bars show range in $\ln(\text{kg km}^{-2})$, which differ between columns/species) for example species (see figure 3a caption), illustrating changes in abundance and area occupied among four years (the first and last years with available data for each species, and 2 years in between).

analysis uses tow-by-tow survey data for 92 species from six marine regions near three continents, and is the first to properly account for errors-in-variables bias arising from using a noisy variable (abundance estimates) as a predictor variable in a linear regression. We estimate a parameter δ representing the proportion of abundance change that is attributable to range expansion/contraction, where the proportion attributable to density changes within the population's range is $1 - \delta$ (figure 1). While δ is significantly positive on average, our results suggest that the majority (80–100%) of variation in population abundance is explained by changes in average density within the population's range. We therefore conclude that the BM is supported but has a small magnitude on average, and that abundance changes for most sea-bottom-associated fishes are not strongly attributed to shifts in effective area.

The theory of IFD (which underlies the PDM) generally predicts that animals will distribute themselves in proportion to the suitability of available habitat. This prediction can be violated in many different ways, including imperfect information (i.e. the failure to move following changes in the optimal distribution), local interference for resources (i.e.

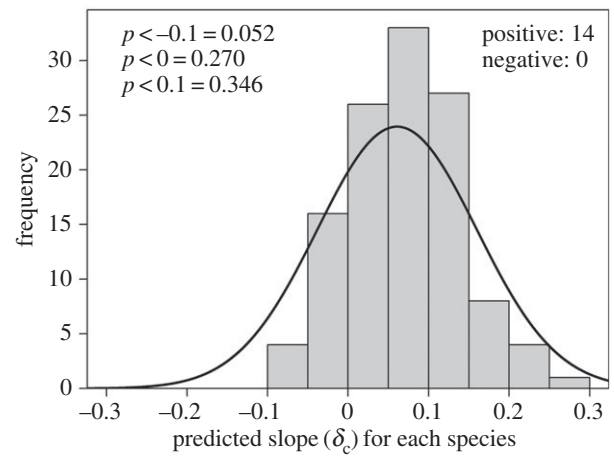


Figure 5. Distribution for relationship between abundance and effective area occupied (e.g. where a positive slope signifies a positive relationship between abundance and area occupied) from the 'constant' meta-analysis model. We show the frequency of predicted slopes (δ_c , e.g. slopes listed in figure 3b), the predictive distribution for a species not included in the analysis, the probability that a given slope value is below or above a given value (listed in the top-left), and the proportion of stocks that have a positive or negative predicted slope that is significantly different from zero (using a two-sided Wald test and the estimated standard error).

depletion of prey), and unequal competitive abilities leading to dominance hierarchies for space and costs associated with movement [28]. Predictions arising from the theory of IFD may also change when including interactions among species [29]. For fishes, we hypothesize that ontogenetic habitat partitioning is particularly important for limiting shifts in distribution during stock decline or recovery. For example, haddock (*Melanogrammus aeglefinus*) on the southwestern Scotian Shelf were not distributed in proportion to variation in juvenile growth rates, supporting a rejection of the IFD for that stock [30]. Similarly, juvenile Atlantic cod in the Gulf of St Lawrence appeared to have similar distribution, regardless of population size, whereas adult cod had greater density-dependent variation in area [31]. More generally, others have hypothesized that density-dependent range shift occurring at some life stages but not others may be an important element to population regulation for many marine fishes [32]. However, estimating the strength of density-dependent distributional shift at different ages, while accounting for errors-in-variables bias, has not previously been attempted and remains a topic for future research.

Importantly, our study also uncovered important variation among marine regions in the average abundance–area relationship for sea-bottom-associated fishes. The North Sea, Bering Sea and Northwest Atlantic regions all have wide shelf habitats relative to the Gulf of Alaska and the west and south coast of South Africa. The BM would presumably be more applicable when a wide range of suitable habitats are contiguous and therefore accessible to individuals as the abundance increases [7]. However, the prediction of a stronger abundance–area relationship in the North Sea, Bering Sea and Northwest Atlantic was not supported here. An alternative explanation is that the magnitude of spatial and temporal variation in productivity affects the abundance–area relationship for each region. Specifically, high temporal variation could favour range expansion during pulses of productivity, while spatial variation would limit range expansion during

Table 1. Estimated hyper-parameters for the four meta-analytic models described in S2c (p -values are calculated using a two-sided Wald test; Δ AIC measures model parsimony; see figure 2 caption for region codes).

parameter name	symbol	estimate	s.e.	p -value
<i>constant</i> (Δ AIC = 10.87)				
average: general	θ	0.061	0.014	<0.001
variation among species	σ_δ	0.099	0.016	—
<i>varies among regions</i> (Δ AIC = 0.78)				
average: EBS	θ_1	0.159	0.028	<0.001
average: GOA	θ_2	0.089	0.031	0.005
average: NS	θ_3	0.066	0.031	0.033
average: NWA	θ_4	-0.030	0.036	0.417
average: SCSA	θ_5	0.026	0.028	0.350
average: WCSA	θ_6	0.043	0.028	0.133
variation among species	σ_δ	0.080	0.015	—
<i>varies among taxa</i> (Δ AIC = 10.91)				
average: Elasmobranchii	θ_1	0.024	0.027	0.368
average: Gadiformes	θ_2	0.093	0.029	0.001
average: Pleuronectiformes	θ_3	0.095	0.027	<0.001
average: other bony	θ_4	0.026	0.053	0.619
average: Perciformes	θ_5	-0.014	0.037	0.703
average: Scorpaeniformes	θ_6	0.095	0.028	0.001
variation among species	σ_δ	0.087	0.016	—
<i>varies among regions and taxa</i> (Δ AIC = 0)				
average: Elasmobranchii	θ_1	0.043	0.025	0.081
average: Gadiformes	θ_2	0.106	0.026	<0.001
average: Pleuronectiformes	θ_3	0.076	0.025	0.002
average: other bony	θ_4	0.063	0.049	0.200
average: Perciformes	θ_5	-0.034	0.034	0.317
average: Scorpaeniformes	θ_6	0.071	0.026	0.006
offset: EBS	θ_7	0.107	0.025	<0.001
offset: GOA	θ_8	0.024	0.027	0.367
offset: NS	θ_9	-0.008	0.027	0.753
offset: NWA	θ_{10}	-0.086	0.030	0.005
offset: SCSA	θ_{11}	-0.019	0.024	0.444
offset: WCSA	θ_{12}	-0.019	0.025	0.454
variation among species	σ_δ	0.064	0.015	—

population increases. All six regions have greater chlorophyll a concentrations (a proxy for productivity) in shallow waters near shore, with the North Sea and west coast of South Africa showing perhaps the greatest spatial variation within the sampled domains [33]. However, comparative analyses regarding temporal variation in productivity are generally scarce at the scales considered here. Finally, abundance–area relationships might vary depending upon exploitation history for each region. However, the North Sea and Gulf of Alaska differ greatly in exploitation history (the former has a long history of exploitation, including overfishing of many species, whereas the latter has less overfishing and a shorter history of exploitation) but very similar estimates of the abundance–area relationship.

Density may act interactively with other processes to affect distribution. Our results suggest that there is substantial variation in effective area occupied beyond that explained by either the BM or PDM *per se*. Opportunities for survival, growth and reproduction are often affected by temperature in ectotherms such as fishes [34], so the optimal distribution (and the strength of abundance–area relationship) may in fact change during changes in the distribution of temperature for marine regions [3]. Ideally, each individual would distribute itself to maximize fitness given its opportunities for growth, survival and reproduction across a landscape. However, direct measurement of survival, growth and reproduction is generally difficult for marine species, so temperature and depth have often been used as proxies for habitat suitability

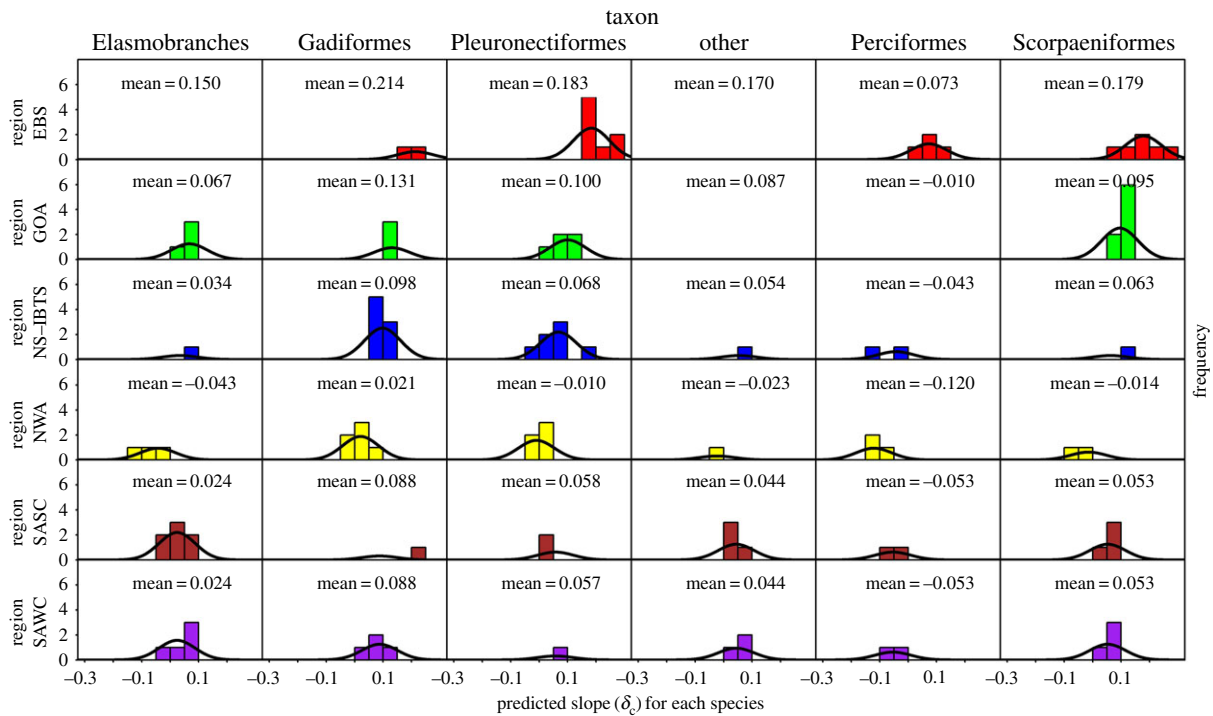


Figure 6. Distribution for relationship between abundance and effective area occupied from the ‘varies among regions and taxa’ meta-analysis, where each row corresponds to a different region and each column to a different taxon. For each taxon-region pair, we show the average abundance–area relationship, as well as a histogram of estimates for all species with that taxon and region (panels with no histogram represent combinations that are not observed in our database). (Online version in colour.)

for species like Atlantic cod [35]. We therefore encourage future research that seeks to predict distribution shifts for marine species, including simultaneous impacts of temperature and density, rather than analysing temperature-induced range shift in isolation [2,22]. The modelling framework presented here could incorporate covariates collected on these trawl surveys (e.g. bottom temperature measurements), and we encourage future research that combines multiple hypotheses (e.g. density dependence and temperature) in driving distribution shifts. We also envision future research using size-structured spatio-temporal models [36,37] to assess whether changes in size or age distribution could explain the remaining variation in effective area occupied. However, future meta-analyses using size-structured spatio-temporal models will require improved sharing and documentation of regional size and age sampling data.

We also encourage further research to estimate changes in the spatial distribution of fish populations from fishery-dependent data. There are many reasons why fishery-dependent catch rates are difficult to analyse for estimating fishing density, including small-scale fishery targeting, large-scale redistribution of fishing effort in response to fish densities, changes in fishing efficiency over time and fisheries management actions that impact catch rates [12,38]. However, it is increasingly feasible to account for spatial adjustments in fishing effort

via spatio-temporal models [39], and fishing efficiency can sometimes be estimated by inferring relationships between measured variables (e.g. gear) and vessel performance [40]. We therefore foresee a time when fishery-dependent and -independent catch rates will be simultaneously analysed to estimate range shifts for a wide range of marine species. This will be particularly useful when estimating within-year shifts in distribution, given that fisheries usually operate over a larger proportion of the calendar year than planned surveys.

Data accessibility. Sources for all data are described in detail in electronic supplementary material, appendix S4.

Authors’ contributions. J.T.T. and A.R. planned the research, J.T.T. conducted the research, J.T.T., A.R., J.G., D.H.H. and H.W. analysed results, and all authors contributed writing and editing.

Competing interests. We declare we have no competing interests.

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