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Density-dependent changes in effective area occupied for sea-bottom associated marine fishes
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Short title: Abundance and area-occupied for marine fishes

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Abstract

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). We estimate the average relationship using bottom trawl data for 92 fish species from six marine ecosystems spanning 1982-2014, 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 in a meta-analytic model 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), while only a small proportion of species-ecosystem combinations show a negative relationship (i.e., shrinking effective area when abundance increases). Approximately one-third of species-ecosystem combinations (and 34.6% in general) are predicted to increase in effective area by more than 1% with every 10% increase in population size. We therefore infer that population density generally changes faster than effective area occupied during abundance changes. Gadiforms 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 has a strong relationship 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 they may exhibit compressed range and become more efficiently fished.
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, foraging opportunities of top predators such as marine mammals and birds, and may also affect treaties and informal relationships 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, e.g., Atlantic cod (Gadus morhua) [8,9]. In support of these observations, the “basin model” for marine species predicts that the distribution of marine species will collapse towards preferred habitats as abundance decreases. This basin model 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 basin model, a species with declining abundance will shrink towards its core habitat rather than showing a proportional decrease in density throughout its range (Fig. 1). Due 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 hyper-stability 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 basin model, 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, and note that the proportional-density model (PDM) might be supported even when the assumptions of IFD theory are not met (Fig. 1). The proportional-density model 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 favor of both the basin model as supported by DDHS theory [9,5], and the proportional-density model 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 due 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 arises because total
abundance is treated as a predictor variable for area occupied, and abundance is generally estimated from a survey data or a population model with some error. Accounting for errors-in-variables bias has been shown to impact 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 the basin or proportional-density model 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 ecosystems, resulting in 120 species-ecosystem combinations (Fig. 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 D95) 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.

**Materials and Methods**

We estimate abundance as the total biomass (in kilograms) available to bottom trawl sampling gear (termed “total available biomass”), and area occupied (in square kilometers) as the total area necessary to contain the population at its average density (see later section titled “Defining area-occupied” for details). We use biomass rather than catch in 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-ecosystem
   combinations from six marine ecosystems. This model analyzes 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 is it present) and density (how much is present) [21]. Total abundance
   and area-occupied are predicted at the same time as model parameters, so that standard
   errors for abundance and area-occupied represent the predictive variance for each [22].
   By 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-ecosystem
combinations in the relationship between area-occupied and abundance (“parametric
variability”, see [17]).

Estimating spatio-temporal variation in population density
In the following, 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 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 previously-developed R package `SpatialDeltaGLMM` for estimating parameters for this model [26], and the software is publicly available ([https://github.com/nwfsc-assess/geostatistical_delta-GLMM](https://github.com/nwfsc-assess/geostatistical_delta-GLMM)).

**Defining area-occupied**

We quantify area occupied using a new metric termed “effective area occupied”, which measures the area (in units square kilometers) required to contain a population given its average population biomass density. 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 $D_t(s)$ for that year, so effective area occupied $h_t$ is simply their ratio as the average weight per individual cancels out in the estimation (see Appendix S1 for derivation and details):
\[ h_t = \frac{b_t}{m_t} = \frac{1}{\int D^2_t(s) ds} \]

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 (see Fig. 1). Other benefits of this metric are listed in Appendix S1.

**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 for each marine ecosystem included in the analysis, and for each individual species. 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 ecosystem:

\[
\log(h_t) = \gamma + \delta \log(b_t)
\]

where \( \gamma \) represents a species-ecosystem-specific intercept, and \( \delta \) 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, \( \delta \) can be interpreted as the proportion of abundance change that is explained by change in effective area occupied, while \( 1 - \delta \) 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 within the ecosystem (see Fig. 1).
However, both abundance and area occupied are estimated from the same data set 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 Appendix S2 for more details). We therefore use mixed-effects modeling techniques to account for correlated estimation error in both area occupied and abundance for each species (Appendix S3).

We also want to account for variation among species and ecosystems in the average relationship between abundance and area-occupied. We therefore specify that the relationship $\delta_e$ between abundance and area-occupied for species-ecosystem combination $c$ arises from a probability distribution, where this distribution represents the expected mean and variability in the abundance-area relationship:

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

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

1. **Constant** – The null hypothesis where the average abundance-area relationship ($\delta_e$) is constant for all stocks. In this case $X$ is an intercept (i.e., $X=1$), and $\boldsymbol{\theta}$ is a single parameter representing the average relationship between log-abundance and log-area-occupied.

2. **Varies among ecosystems** – An alternative hypothesis where $\delta_e$ varies by ecosystem. In this case, $X$ is a design-matrix where $x_c$ has a 1 for the ecosystem that contains the $c^{th}$
stock, and 0s otherwise, and $\theta$ is a vector representing the average relationship between
log-abundance and log-area-occupied in each ecosystem.

3. Varies among taxa – An alternative hypothesis where $\delta_c$ varies by taxonomic order,
where we have sufficient data to analyze Elasmobranchii (20 species-ecosystem
combinations), Gadiformes (24), Pleuronectiformes (28), Perciformes (13),
Scorpaeniformes (25), and other bony fishes (9), where $X$ and $\theta$ are defined similarly to
the “Varies among ecosystems” model.

4. Varies by ecosystem and taxa – An alternative hypothesis where $\delta_c$ varies by both
ecosystem and taxa. We specify that coefficients $\theta$ for each ecosystem must sum to zero
to ensure that ecosystem and taxa-effects are identifiable. The specification implies that
$\theta$ for each taxon is the expected value for $\delta_c$ across all six ecosystems.

We the use the Akaike Information Criterion to assess is the most parsimonious model, and
interpret parameter estimates to evaluate the evidence for either the basin or proportional-
change models. The proportional-change model predicts no change in effective area
occupied with changing density (i.e., $\hat{\theta} = 0$), while the basin model predicts some positive
relationship (i.e., $\hat{\theta} > 0$).

**Bottom trawl database**

We apply this meta-analytic technique to long-term data from six bottom trawl surveys (Fig.
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 timescale over which abundance and effective area occupied
have changed for many species. These surveys include:

1. A fixed-station survey operated by the Alaska Fisheries Science Center (AFSC) in the
Eastern Bering Sea from 1982 onward (data publicly available here:


4. A stratified random survey operated by South Africa’s Department of Agriculture, Forestry and Fisheries (DAFF) in the continental shelf (up to 500 m) of the South coast of South Africa during the Autumn from 1988-2010. We restrict data to autumn survey samples using the “old” gear type employed by the FRS Africana [27], and data are available upon request by DAFF.

5. A stratified random survey operated by DAFF on the continental shelf (up to 500 m) of the West coast of South Africa during the Summer from 1986-2010. We again restrict data to summer survey samples using the “old” gear as described for the south coast.

6. The North Sea international bottom trawl survey (NS-IBTS), a randomized survey operated by multiple countries in the North Sea. We restrict data to 1991 onward, collected during winter (quarter 1) and sampled using standardized sampling gear ("Gov" trawl configuration; data are available at https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx). For these data, survey lengths are converted to weights using annual weight-length relationships using the DATRAS R-package (https://www.rforge.net/DATRAS/Tutorial.html).

Sample sizes vary among surveys, and are greatest for the Gulf of Alaska (750 per year), lowest for South and West coast of South Africa (80-100 per year), and intermediate for the
others (300-400 per year). In general, we define “species-ecosystem 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-ecosystem 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 [28], and is reasonable given that each survey uses a randomized, probability sampling protocol where sampling probability is pre-defined 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 analyze data for the 20 fish species that are most frequently encountered during the course of the survey (i.e., have the highest proportion of survey tows that encountered at least one individual of that species) after excluding epipelagic fishes, e.g., shoaling forage fishes such as herring (*Clupea harengus*) or horse mackerel (*Trachurus trachurus*) (see Appendix S4 for species list). We exclude epipelagic fishes because they may not be captured consistently using bottom trawl sampling gear, and we analyze frequently encountered species because these species generally permit precise estimates of abundance and area occupied, and therefore are likely to be most informative about the average relationship between these variables. 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 ($\delta_c$) with the encounter rates for each species.

**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 Eastern Bering Sea and little skate (*Leucoraja erinacea*) in the Northwest Atlantic as examples (Fig. 3-4). Arrowtooth flounder has increased in abundance in the Eastern Bering Sea 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, while 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 (Appendix S5 and Fig. S1-S6) shows that only some species (e.g., bigmouth sculpin, *Hemitripterus bolini* the Eastern Bering Sea, EBS) have a discernable trend in abundance or effective area occupied over time. However, many other species (e.g., great sculpin, *Myoxocephalus polyacanthocephalus* in the EBS) have significant internannual 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, Fig. 5; 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, SE: 0.014; p<0.001 using a 2-sided Wald test). This provides support for the basin model (which predicts a non-zero relationship) relative to the proportional-density model. 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 (σδ = 0.10 vs. β = 0.061). On average across ecosystems, species-ecosystem 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 δ > 0.1), those showing a weak link between abundance and area (i.e., 38% having 0 < δ < 0.1), and those showing a negative impact of abundance on area occupied (i.e., 27% having δ < 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 than zero (as estimated using a 2-sided Wald test at a 0.05 level).

The Akaike information criterion indicates that the “Varies among ecosystems and taxa” model is most parsimonious (with the “Varies among ecosystems” a close second, ∆AIC = 0.78, see Table 1, Fig. 6). This model has a residual standard deviation σδ of 0.064 (compared with 0.099 for the “Constant” model), so ecosystem and taxon explain 58% (1 – 0.064²/0.099²) of variance in the abundance-area relationship among species. We identify strong and statistically significant relationships between abundance and effective area in Gadiforms (0.106; SE: 0.026), followed closely by Pleuronectiforms (0.076; SE: 0.025) and Scorpaeniforms (0.071; SE: 0.026). We find weaker relationships in Elasmobranchii (0.043; SE: 0.025) and Perciforms (-0.034; SE: 0.034), and neither is significant (see Table 1 for p-
Ecosystem 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 strongest ecosystem effect (after the model controls for differences in taxa among regions) is in the Eastern Bering Sea (mean: 0.107; SE: 0.025) and the weakest regional effect is in the Northwest Atlantic (mean: -0.086; SE: 0.030). The ecosystem effects in the Northwest Atlantic, South Africa west coast and South Africa south coast are not significantly different from zero. Ecosystem effects therefore play an important role in modifying the average abundance-area relationship for each taxon, where e.g., a Gadiform in the Eastern Bering Sea 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 change). The proportional-density model is generally a suitable description for most taxa in the Northwest Atlantic, while the basin model is important for all taxa except Perciformes in the Eastern Bering Sea, Gulf of Alaska, and North Sea regions. A comparison of the predicted abundance-area relationship for each species-ecosystem combination against encounter rates provides no evidence that less-encountered species have a different relationship than frequently-encountered species (Appendix S6 and Fig. S7). We therefore find evidence that the species in this database are likely to be representative of less-frequently encountered fishes in these regions.

**Discussion**

In this paper, we conduct the largest meta-analysis to date of two hypothesized models (the basin and proportional-density models) linking effective population area to population size in marine species. This analysis uses tow-by-tow survey data for 92 species from six marine ecosystems 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 $\delta$ 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 $1 - \delta$ (Fig. 1). While $\delta$ 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 basin-model is supported but has a small magnitude on average,
and that abundance changes for sea-bottom associated fishes are often not tightly linked to
shifts in effective area.

The theory of IFD (which underlies the proportional-density model) 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 among others: imperfect
information (i.e., the failure to move following changes in the optimal distribution); local
interference for resources (i.e., depletion of prey); unequal competitive abilities leading to
dominance hierarchies for space; and costs associated with movement [29]. Predictions
arising from the theory of IFD may also change when including interactions among species
[30]. 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 [31]. Similarly, juvenile Atlantic cod in the Gulf of St. Lawrence appeared to have
similar distribution regardless of population size, while adult cod had greater density-
dependent variation in area [32]. 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 [33]. 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 ecosystems in the average abundance-area relationship for sea 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 basin-model would presumably be more applicable when a wide range of suitable habitats are contiguous and therefore accessible to individuals as the abundance increases (e.g., [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 ecosystem. Specifically, high temporal variation could favor range expansion during pulses of productivity, while spatial variation would limit range expansion during population increases.

All six ecosystems 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 [34]. 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 ecosystem. 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, while 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 basin or proportional-density models per se. Opportunities for survival, growth, and
reproduction are often affected by temperature in ectotherms such as insects [35] and fishes [36], so the optimal distribution (and the strength of abundance-area relationship) may in fact change during changes in the distribution of temperature for marine ecosystems [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 for species like Atlantic cod [37]. We therefore encourage future research that seeks to predict distribution shifts for marine species, including simultaneous impacts of temperature and density, rather than analyzing temperature-induced range shift in isolation [2,22]. The modeling 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 [38,39] 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 complicated to analyze 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 [12,40,41]. However, it is increasingly feasible to account for spatial adjustments in fishing effort via spatio-temporal models [42], and fishing efficiency can sometimes be estimated by inferring relationships between measured variables (e.g., gear) and vessel
performance [43]. We therefore foresee a time when fishery-dependent and –independent catch rates will be simultaneously analyzed 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.

**Authors’ Contributions**

JT and AR planned the research, JT conducted the research, JT, AR, JG, DH, and HW analyzed results, and all authors contributed writing and editing.

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Table 1 – Estimated hyper-parameters for the four meta-analytic models described in the section *Meta-analysis of the relationship between abundance and area-occupied* (p-values are calculated using a two-sided Wald test).

<table>
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<td><strong>Constant (AIC = -7.42)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average: general</td>
<td>$\theta$</td>
<td>0.061</td>
<td>0.014</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Variation among species</td>
<td>$\sigma_\delta$</td>
<td>0.099</td>
<td>0.016</td>
<td>-</td>
</tr>
<tr>
<td><strong>Varies among regions (AIC = -17.51)</strong></td>
<td></td>
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</tr>
<tr>
<td>Average: EBS</td>
<td>$\theta_1$</td>
<td>0.159</td>
<td>0.028</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Average: GOA</td>
<td>$\theta_2$</td>
<td>0.089</td>
<td>0.031</td>
<td>0.005</td>
</tr>
<tr>
<td>Average: NS</td>
<td>$\theta_3$</td>
<td>0.066</td>
<td>0.031</td>
<td>0.033</td>
</tr>
<tr>
<td>Average: NWA</td>
<td>$\theta_4$</td>
<td>-0.030</td>
<td>0.036</td>
<td>0.417</td>
</tr>
<tr>
<td>Average: SCSA</td>
<td>$\theta_5$</td>
<td>0.026</td>
<td>0.028</td>
<td>0.350</td>
</tr>
<tr>
<td>Average: WSCSA</td>
<td>$\theta_6$</td>
<td>0.043</td>
<td>0.028</td>
<td>0.133</td>
</tr>
<tr>
<td>Variation among species</td>
<td>$\sigma_\delta$</td>
<td>0.080</td>
<td>0.015</td>
<td>-</td>
</tr>
<tr>
<td><strong>Varies among taxa (AIC = -7.38)</strong></td>
<td></td>
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<td></td>
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<tr>
<td>Average: Elasmobranch</td>
<td>$\theta_1$</td>
<td>0.024</td>
<td>0.027</td>
<td>0.368</td>
</tr>
<tr>
<td>Average: Gadiform</td>
<td>$\theta_2$</td>
<td>0.093</td>
<td>0.029</td>
<td>0.001</td>
</tr>
<tr>
<td>Average: Pleuronectiform</td>
<td>$\theta_3$</td>
<td>0.095</td>
<td>0.027</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Average: Other bony</td>
<td>$\theta_4$</td>
<td>0.026</td>
<td>0.053</td>
<td>0.619</td>
</tr>
<tr>
<td>Average: Perciform</td>
<td>$\theta_5$</td>
<td>-0.014</td>
<td>0.037</td>
<td>0.703</td>
</tr>
<tr>
<td>Average: Scorpaeniform</td>
<td>$\theta_6$</td>
<td>0.095</td>
<td>0.028</td>
<td>0.001</td>
</tr>
<tr>
<td>Variation among species</td>
<td>$\sigma_\delta$</td>
<td>0.087</td>
<td>0.016</td>
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<tr>
<td><strong>Varies by region and taxa (AIC = -18.29)</strong></td>
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<tr>
<td>Average: Elasmobranch</td>
<td>$\theta_1$</td>
<td>0.043</td>
<td>0.025</td>
<td>0.081</td>
</tr>
<tr>
<td>Average: Gadiform</td>
<td>$\theta_2$</td>
<td>0.106</td>
<td>0.026</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Average: Pleuronectiform</td>
<td>$\theta_3$</td>
<td>0.076</td>
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<td>0.002</td>
</tr>
<tr>
<td>Average: Other bony</td>
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<td>0.049</td>
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<td>Average: Perciform</td>
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<td>0.034</td>
<td>0.317</td>
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<tr>
<td>Average: Scorpaeniform</td>
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<tr>
<td>Average: EBS</td>
<td>$\theta_7$</td>
<td>0.107</td>
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<td>&lt;0.001</td>
</tr>
<tr>
<td>Average: GOA</td>
<td>$\theta_8$</td>
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<td>0.027</td>
<td>0.367</td>
</tr>
<tr>
<td>Average: NS</td>
<td>$\theta_9$</td>
<td>-0.008</td>
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<td>0.753</td>
</tr>
<tr>
<td>Average: NWA</td>
<td>$\theta_{10}$</td>
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<td>0.030</td>
<td>0.005</td>
</tr>
<tr>
<td>Average: SCSA</td>
<td>$\theta_{11}$</td>
<td>-0.019</td>
<td>0.024</td>
<td>0.444</td>
</tr>
<tr>
<td>Average: WSCSA</td>
<td>$\theta_{12}$</td>
<td>-0.019</td>
<td>0.025</td>
<td>0.454</td>
</tr>
<tr>
<td>Variation among species</td>
<td>$\sigma_\delta$</td>
<td>0.064</td>
<td>0.015</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure Legends

Fig. 1 – Conceptual diagram contrasting the proportional-density model (left panel, supported by Ideal Free Distribution 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 \( \delta \) governs this relationship. This implies that \( m_t \propto b_t^{1-\delta} \), so \( \delta \) is the proportion of abundance change attributable to range expansion/contraction while \( 1-\delta \) is the proportion due 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 \( \delta \) 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.

Fig. 2 – Map of six marine ecosystems included in this study, each having data from multispecies bottom trawl surveys with standardized operations covering more than twenty years (each survey corresponds to a shaded area and is labeled using region codes; red: Eastern Bering Sea; green: Gulf of Alaska, yellow: Northwest Atlantic; purple: West Coast of South Africa; brown: South Coast of South Africa; blue: North Sea).

Fig. 3a – Example species showing positive (1\textsuperscript{st} column: arrowtooth flounder in the Eastern Bering Sea) or negative (2\textsuperscript{nd} 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 (+/- one standard error; y-axis) against year (x-axis).
Fig. 3b – Example species showing effective area and species abundance (see Fig. 3a caption for details), where points and dotted whiskers are the estimate +/- one standard error for both variables in each year. Each panel lists the estimated slope ($\delta_c$) from the meta-analysis model that includes differences among ecosystems in the average area-abundance relationship (i.e., where expected $\delta_c$ differs systematically among regions).

Fig. 4 – Predicted density relative to maximum observed (insert colorbars showing range in units ln(kilograms/kilometer$^2$)) for example species (see Fig. 3a caption), illustrating changes in abundance and area-occupied among four years (the first and last years with available data for each species, and two years in between).

Fig. 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 ($\delta_c$, e.g., slopes listed in Fig. 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).

Fig. 6 – Distribution for relationship between abundance and effective area occupied from the “Varies by ecosystem 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 ecosystem (panels with no histogram represent combinations that are not observed in our database).
Fig. 1 – Conceptual diagram contrasting the proportional-density model (left panel, supported by Ideal Free Distribution 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 \( \delta \) governs this relationship. This implies that \( m_t \propto b_t^{1-\delta} \), so \( \delta \) is the proportion of abundance change attributable to range expansion/contraction while \( 1-\delta \) is the proportion due 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 \( \{1, 1.4, 1.8, 2.2, 2.8, 3.0\} \). Panels differ in the parameter \( \delta \) 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.
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215x114mm (100 x 100 DPI)
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96x177mm (100 x 100 DPI)
Fig. 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 Fig. 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).