Estimating circumpolar distributions of lanternfish using 2D and 3D ecological niche models

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ABSTRACT: Ecological niche models (ENMs) can be a practical approach for investigating distributions and habitat characteristics of pelagic species. In principle, to reflect the ecological niche of a species well, ENMs should incorporate environmental predictors that consider its full vertical habitat, yet examples of such models are rare. Here we present the first application of '3D' ENMs to 10 Southern Ocean lanternfish species. This 3D approach incorporates depth-specific environmental predictor data to identify the distribution of suitable habitat across multiple depth levels. Results were compared to those from the more common '2D' approach, which uses only environmental data from the sea surface. Measures of model discriminatory ability and overfitting indicated that 2D models often outperform 3D methods, even when accounting for reduced available sample size in the 3D models. Nevertheless, models for species with a known affinity for deeper habitat benefitted from the 3D approach, and our results suggest that species can track their ecological niche in latitude and depth leading to equatorward or poleward range extensions beyond that expected from incorporating only surface data. However, since 3D models require comprehensive depth-specific data, both data availability and the need for depth-specific model outputs must be considered when choosing the appropriate modelling approach. We advocate increased effort to include depth-resolved environmental parameters within marine ENMs. This will require collection of mesopelagic species occurrence data using appropriate temporal and depth-stratified methods, and inclusion of accurate depth information when occurrence records are submitted to global biodiversity databases.

KEY WORDS: 3D modelling · Ecological niche model · Species distribution model · Biogeography · Lanternfish · Myctophidae · Mesopelagic · Southern Ocean

1. INTRODUCTION

From the mid-20th century, the development of methods to sample organisms from discrete depths using midwater trawls (Isaacs & Kidd 1951, Clarke 1969, Baker et al. 1973) quickly helped to revolutionise mesopelagic biogeography. This is because studies were at last able to describe both fine-scale latitudinal and vertical patterns in species distributions, and begin to understand the processes main-

taining them (Sutton 2013). Increased access to these records via online global biodiversity databases has considerably enhanced our understanding of marine species distributions, and specifically the data have found an important role in underpinning modelling approaches such as ecological niche modelling or species distribution modelling. In general, these methods correlate records of species presence with biologically relevant environmental variables, enabling predictions of the probability of occurrence of

suitable habitat for a species across a region of interest (Peterson et al. 2011a). Examples of such methods being applied to mesopelagic fauna range from helmet jellyfish (Bentlage et al. 2013), giant squid (Coro et al. 2015), snipe eels (DeVaney 2016) and lanternfishes of the family Myctophidae (Loots et al. 2007, Flynn & Marshall 2013, Duhamel et al. 2014, Freer et al. 2018, 2019).

Ecological niche models (ENMs) of mesopelagic fishes have demonstrated that subsurface data (often conditions at 200 m or deeper) may be better predictors of distribution patterns than surface environmental conditions (Duhamel et al. 2000, Loots et al. 2007, Koubbi et al. 2011b). However, in marine ENMs, it is often the case that surface (or near-surface) environmental variables are paired with occurrence records of animals that were caught from a range of depths, despite the surface and deeper waters having very different environmental conditions. In such cases, the model may provide a poor representation of the normal environment of a species, and therefore their physical and ecological niche, ultimately leading to inaccurate predictions of suitable habitat (Duffy & Chown 2017).

A common method of including environmental information from multiple depths into an ENM is to treat data from each depth layer as a separate environmental predictor, for example, using both sea surface temperature and sea bottom temperature. Although such ENMs do not rely on surface data alone, they remain relatively simplistic (Duffy & Chown 2017) and do not fully account for variability in the association between depth and species occurrence throughout the pelagic environment, which plausibly may be relevant to species with pelagic life history stages.

Other methods exist to integrate a third (i.e. vertical/depth) dimension into ENMs such as the method described by Duffy & Chown (2017). This approach uses species occurrence records and their associated latitude, longitude and depth information, matching these records with environmental variables from a similar depth from which the animals were caught. For example, a record caught at 250 m would be matched to the temperature at 250 m (or the closest available depth level) rather than using temperature at the surface or any other depth level. As depth is considered as discrete (i.e. discontinuous) levels rather than as a continuous variable, a distinction can be made between this modelling approach and truly 3-dimensional models in which environmental data and species' depths of occurrence would be known in more detail. Nevertheless, this approach can be used

to create separate habitat suitability maps for each of the depth 'slices' used and, as only the most appropriate environmental data are paired with each occurrence record, the accuracy of the ENM can, in principle, be improved.

However, applying a vertical dimension in this way is rare (but see Bentlage et al. 2013), and models of deep sea species are often constrained by issues of low sampling effort, which can lead to problems of small sample sizes, spatial sampling bias and/or a poor representation of their environmental or geographic distribution (Robinson et al. 2011, Bentlage et al. 2013). Sub-selecting only those occurrence records that contain associated depth information may exacerbate these issues, meaning that trade-offs between data quantity and quality likely exist when choosing between 2D and 3D approaches (Duffy & Chown 2017).

Lanternfishes (Myctophidae) are the dominant family of offshore fish in the Southern Ocean in terms of biomass, abundance and diversity (Barrera-Oro 2002). As such they are key consumers of zooplankton and krill (Saunders et al. 2015, 2019), and are major components of the diets of predators such as birds, seals and fish (Guinet et al. 1996, Olsson & North 1997, Casaux et al. 1998, 2009, Collins et al. 2007, Cherel et al. 2008). Through their diel vertical migration behaviour, they also play a key role in the active transport of carbon to deeper waters (Collins et al. 2012). Whilst their latitudinal biogeography is well understood through large-scale modelling efforts (Loots et al. 2007, Koubbi et al. 2011b, Duhamel et al. 2014, Freer et al. 2019), their vertical distribution patterns remain less clear. The vertical habitat use of Southern Ocean lanternfish has been described from regional sampling efforts (Lancraft et al. 1989, Duhamel et al. 2000, Pusch et al. 2004, Collins et al. 2008, 2012, Hulley & Duhamel 2011, Koubbi et al. 2011a), yet vertical migration behaviour and a capability to evade net capture means that sampling can be prone to false negative results (Kaartvedt et al. 2012). Thus, 3D modelling approaches have the potential to bring novel insights to vertical distribution patterns and the complex use of the environment by these species.

In this study, we investigated the 3-dimensional distribution of 10 Southern Ocean lanternfish species by building depth-specific ENMs following the method of Duffy & Chown (2017). We also compared the predictive performance of models and the spatial overlap of 3D ENMs to those built using the less complex '2D' approach. Therefore, as well as improving our understanding of the vertical habitat of these

species, we aimed to evaluate the relative utility of 2D and 3D approaches when modelling suitable habitat of mesopelagic species.

2. MATERIALS AND METHODS

2.1. Species occurrence records

Occurrence records of the family Myctophidae were downloaded from the Global Biodiversity Information Facility (GBIF; www.gbif.org/). The 10 species with the highest number of records in the Southern Ocean were retained for analyses: *Electrona antarctica, E. carlsbergi, Gymnoscopelus bolini, G. braueri, G. fraseri, G. nicholsi, G. opisthopterus, Krefftichthys anderssoni, Protomyctophum bolini* and *P. tenisoni*. All occurrence records were subject to quality assurance and control processes. Unreliable data, which included records with identical latitude and longitude, and records with a latitude and longitude corresponding to a terrestrial location, were removed. Due to high sampling bias towards austral spring and summer seasons, only records from the months October–March were kept for analyses. Furthermore, only occurrence records from 1960–2010 were retained, to correspond to a similar baseline period of available environmental data. Along with latitude and longitude, depth-of-catch information was retained for each occurrence record, obtained from the 'depth' field of the GBIF database, when this was available. It is possible that some records reflect only the maximum depth that the net reached, and not the actual depth that the fish was caught. Hence, only records falling within the expected vertical bounds for these fishes (i.e. 0–1500 m) were retained.

2.2. Environmental predictors

Five environmental predictors were selected on which to build the ENMs. These comprised temperature, salinity, dissolved oxygen, primary productivity and bathymetry, and were chosen based on their physiological importance for marine ectotherms and on previous results demonstrating their importance for determining marine species distributions (Loots et al. 2007, Koubbi et al. 2011b, Flynn & Marshall 2013, Duhamel et al. 2014). Climatological means for temperature, oxygen and salinity predictors were extracted from the World Ocean Atlas 2013 database (Locarnini et al. 2013, Zweng et al. 2013, Garcia et al. 2013, 2014) at a resolution of 0.25° × 0.25° (~27.75 km

at the equator) for the months October–March across the baseline temporal period 1956–2005. These data were extracted from 7 vertical depth layers: sea surface, 50, 100, 200, 500, 800 and 1000 m, with the greater resolution at shallow depths representing increased variability in conditions within the epipelagic zone. Primary productivity data represent the primary organic carbon production by all types of phytoplankton (nmol m^{-2} s^{-1}) in the upper 150 m for the months October–March from 1956–2005. Bathymetric data correspond to maximum water depth, and had an original spatial resolution of 30 arc seconds (Becker et al. 2009), being re-sampled to the same resolution as the other variables (i.e. 0.25° × 0.25°) using the bi-linear resample tool in ArcGIS v.10.5.1 (ESRI). All data were delimited to 35–75° S, as this region encompasses the known geographic extent of these species (Duhamel et al. 2014) and environmental data south of 75° S are often missing or imprecise.

We acknowledge that some environmental predictors (e.g. oxygen and temperature) are highly correlated, having Pearson's r > 0.9 (Table S1 in the Supplement at www.int-res.com/articles/suppl/m647 p179_supp.pdf), and that including correlated predictors can make it difficult to assess the relative importance of each due to issues of collinearity. Nevertheless, there is evidence to suggest that, when dealing with correlated variables that are each biologically meaningful, including all predictors can produce models with better predictive performance, in addition to a better fit, than a model parameterized on only one of the correlated predictors (Braunisch et al. 2013). MaxEnt (Phillips et al. 2006, 2017), the maximum entropy modelling approach we used here, is (1) particularly effective in dealing with collinearity through its iterative model fitting approach, which can consider variables independently, (2) can include non-linear interactions between variables and (3) has a robust ability to rank variables according to their importance (Braunisch et al. 2013).

2.3. Building 2D and 3D models

The 2D ENMs were built with no reliance on depth-of-catch information from occurrence records. The 5 environmental predictors (sea surface temperature, sea surface salinity, sea surface dissolved oxygen, primary productivity and bathymetry) were matched to the longitude and latitude fields of each occurrence record. These models, that include all available species presence data, are hereafter referred to as '2D*all*' models.

Many occurrence records were missing the depth-of-catch information required for the 3D models. To enable direct comparisons between 2D and 3D models based upon the same sample size, a '2D*sub*' model was fitted for each species, which only used the occurrence records that are available for the 3D models.

To build the 3D models, occurrence records with associated depth-of-catch information were used in combination with the 5 environmental predictors from each of the 7 depth layers; 0, 50, 100, 200, 500, 800 and 1000 m. Data were extracted from each environmental predictor raster and were matched to occurrence records based upon their longitude, latitude and depth fields, following the methodology of Duffy & Chown (2017). Specifically, the depth field from each occurrence record was used to identify the closest depth layer from which to extract the most appropriate environmental data. Primary productivity data were assigned to all occurrences regardless of vertical position. The resulting ENMs were then projected spatially onto each of the aforementioned depth layers. This resulted in habitat suitability maps for each modelled species and each depth layer, each representing a 2-dimensional slice within a 3-dimensional environment.

2.4. MaxEnt ecological niche models

For each species, occurrence and environmental data were fitted to the presence-only ecological niche modelling algorithm MaxEnt v. 3.4.1. MaxEnt estimates the conditional probability of presence of a species relative to locations where the species has been observed by sampling the environment at a range of locations across the study region ('background sites') and discriminating these from locations and environments where species are known to be present ('presence sites'). MaxEnt assumes background locations adequately cover areas accessible to the species and that presence localities are unbiased and cover important environmental gradients (Jarnevich et al. 2015). While a lack of absence data prevents probability estimates of a species presence and predictions of species' realised distributions, presence-only outputs can be interpreted as showing the existing, fundamental niche and the potential distribution of a species (sensu Hutchinson 1957) (Peterson et al. 2011b). MaxEnt was chosen for its repeatedly high performance against other ENM algorithms (Elith et al. 2006, Ortega-Huerta & Peterson 2008, Monk et al. 2010). Moreover, MaxEnt's capacity to use presence-only data is partic-

ularly appropriate for mesopelagic species given the high potential for errors under a presence–absence approach, due to the low sampling effort relative to the potential habitat area (or volume) available, as well as the net-avoidance behaviour common among lanternfishes (Collins et al. 2008, Kaartvedt et al. 2012). Using an ensemble of model algorithms rather than relying on a single approach can be the best methodological practice when the aim is to gain robust predictions of a species distribution (Araújo & New 2007, Araújo et al. 2019). However, as the main aim of this work was to understand the appropriateness and utility of 3D models in comparison to traditional 2D methods, we give emphasis to this methodological comparison rather than comparing between algorithms.

All ENMs were fitted using the 'SDMtune' R package (Vignali et al. 2019). Occurrence data were partitioned into 'calibration' and 'evaluation' data using 3 sub-samples, with 30% of data used for model evaluation each time. Only linear, quadratic and hinge feature classes were selected in order to avoid fitting overly complex responses (Elith et al. 2010). We selected 10 000 background data points from within 2 degrees of all mesopelagic fish records within the study region. This ensures that both the background and presence sites have the same spatial and environmental bias (Phillips et al. 2009). Similarly, for 3D models, the depth distribution of background points reflected the same depth sampling bias as occurrence records. We used 5000 model iterations, and all other MaxEnt settings were kept as default, including the use of the complementary log-log (cloglog) transformed output for estimating probability of presence (Phillips et al. 2017).

2.5. Comparing 2D and 3D modelling approaches

The outputs of the 2D*all*, 2D*sub* and 3D modelling approaches were compared in terms of their discriminatory ability, calibration and overfitting. Discriminatory ability was determined by the area under the receiver operating characteristic curve (AUC) calculated on the evaluation data (AUC_{TEST}). The AUC score is a widely used rank-based measure of predictive accuracy that can be interpreted in the context of MaxEnt as the probability that a randomly chosen presence location is ranked higher than a randomly chosen background point (Merow et al. 2013). A model with no discriminatory power will have an AUC value equal to 0.5 (no better than random), whilst a model with perfect fit would have an AUC value of 1.0. Discriminatory accuracy of each model

was also measured using the true skill statistic (TSS) (Allouche et al. 2006). TSS values range from −1 to 1, with 0 reflecting a model that is no different than random and values closer to 1 being better at discerning presence and background points. Overfitting was measured using AUC_{DIFF} (Warren & Seifert 2011, Bohl et al. 2019), the difference between the AUCs calculated with calibration records (AUC_{TRAIN}) and evaluation records (AUC_{TEST}). This metric is based on the notion that overfitted models generally perform well on training data but poorly on test data, and will therefore yield relatively high AUC_{DIFF} values. Lastly, Akaike's information criterion corrected for small sample size (AICc) was used as a metric of calibration performance, as it has been demonstrated that information criterion-based approaches to model selection may be particularly useful when sample sizes are small (Warren & Seifert 2011, Lawson et al. 2014).

We also compared how model outputs differed across environmental space by reporting the permutation importance of each environmental predictor for 2D*all*, 2D*sub* and 3D model outputs. Response curves, which describe the relationship between a modelled species occurrence and an individual environmental predictor, were also compared between all model outputs. Finally, the niche overlap between the 2D*all* or 2D*sub* output and each of the 7 depth predictions of the 3D model (e.g. 2D*all* vs. 3D 0 m, 2D*all* vs. 3D 50 m etc.) were calculated using the 'niche overlap' tool in the software ENMTools v.1.3 (Warren et al. 2010). Both the Spearman rank correlation coefficient and *I* metrics are reported for comparison. The *I* metric reflects the similarity of environmental suitability predicted by the ENMs, yet tends to overestimate similarity when many grid cells are of similar value. Rank correlation is more reflective of similarity between ENMs in their underlying response to environmental gradients.

To quantify how model outputs differed geographically, range overlap scores were also calculated between the 2D*all* or 2D*sub* output and each of the 7 depth predictions of the 3D model using ENMTools. This requires a threshold value over which a species is classified as present, rather than using a continuous score between 0 and 1. To transform outputs into binary maps, we used the 'Equal test sensitivity plus specificity' threshold criteria. Selecting threshold criteria is somewhat arbitrary, and each approach can generate different results. Our selection was based on the results of Liu et al. (2016), who found that sensitivity–specificity approaches performed best compared to others.

3. RESULTS

3.1. Comparing model predictive performance

A total of 2918 unique occurrence records were used in analyses. For 5 out of the 10 species (*Electrona carlsbergi*, *Gymnoscopelus bolini*, *G. fraseri*, *G. opisthopterus*, *Protomyctophum tenisoni*), the total number of occurrence records available for the 3D approach fell below 90 records per species due to absence of depth information for the occurrence records (Table 1). Depending on species, between 21.4 and 74.5% of records did not have associated depth information.

Highest-scoring metrics of model performance varied greatly between species and model approaches (Table 1). In comparing overall performance between 2D*all* and 3D models, 2D*all* models had, on average, higher AUC_{TEST} and lower AUC_{DIFF} scores, whilst 3D models had higher TSS and lower AICc scores (Table 1). Three of the 4 metrics were stronger in the 2D*all* approach for *G. fraseri*, *G. nicholsi* and *Kreftichthys anderssoni*, whilst the opposite was found for *E. antarctica*, *G. braueri* and *G. opisthopterus*. In comparing performance between 2D*sub* and 3D models, AUC_{TEST}, AUC_{DIFF} and TSS scores were all stronger, on average, for the 2D*sub* approach (Table 1). Whilst the 2D*sub* approach yielded higher performing metrics for most species, indicators of discrimination accuracy (AUC_{TEST} and TSS) remained higher under the 3D approach for *E. antarctica* and *G. opisthopterus.*

3.2. Comparing predictions in environmental space

Temperature was the variable with highest permutation importance for *E. antarctica*, *G. bolini*, *G. braueri*, *G, fraseri*, *G. opisthopterus* and *K. anderssoni* regardless of modelling approach. 2D*all* and 3D approaches both found primary productivity to be the most important variable for *E. carlsbergi*, whilst bathymetry was highest for *G. nicholsi* under both 2D*sub* and 3D models (Table S2).

Comparing the niche overlap between 2D*all* and 3D model predictions, we found that overlap values were high across all species, although relative rank values were lower and more variable (mean ± SD across all comparisons = 0.8 ± 0.04) than the *I* similarity metric (mean across all comparisons = 0.93 ± 0.01; Table 2). Per species, niche overlap values remained stable across the 3D model predictions at different depth bands and often peaked at mid depths

Table 1. Comparison of 2D*all*, 2D*sub* and 3D model performance for each species indicated by metrics of area under the receiver operating characteristic curves (AUC$_{TEST}$ and AUC$_{DIFF}$), true skill statistic (TSS) and Akaike's information criterion corrected for small sample size (AICc). Better performance is indicated by high AUC$_{TEST}$ and TSS scores and low AUC$_{DIFF}$ and AIC$_c$ scores. Sample sizes reflect the number of occurrence records per species and modelling approach. See Sections 2.3 and 2.5 for details of the models and the performance metrics, respectively. NA: not available

Species	Sample size		2D*all*				2D*sub*				3D			
	2D	3D	AUC test	AUC diff	TSS	AICc	AUC test	AUC diff	TSS	AICc	AUC test	AUC diff	TSS	AICc
Electrona antarctica	876	688	0.833	0.007	0.514	13155	0.860	0.007	0.575	10049	0.870	0.007	0.588	10239
E. carlsbergi	141	87	0.759	0.034	0.409	2392	0.754	0.058	0.459	1613	0.751	0.050	0.435	2293
Gymnoscopelus bolini	106	75	0.824	0.032	0.532	1669	0.830	0.044	0.566	1427	0.782	0.053	0.482	1234
G. braueri	356	242	0.745	0.033	0.387	5709	0.760	0.032	0.428	3842	0.750	0.031	0.396	3933
G. fraseri	124	81	0.857	0.018	0.584	2059	0.833	0.039	0.628	NA	0.776	0.081	0.531	1791
G. nicholsi	228	151	0.850	0.020	0.548	3617	0.830	0.029	0.525	2667	0.812	0.033	0.491	2456
G. opisthopterus	152	65	0.810	0.031	0.493	3358	0.864	0.017	0.596	2815	0.869	0.021	0.616	NA
Krefftichthys anderssoni	436	256	0.779	0.015	0.437	6878	0.780	0.019	0.471	4068	0.731	0.030	0.370	4208
Protomyctophum bolini	362	135	0.802	0.015	0.461	5597	0.822	0.020	0.505	2142	0.804	0.026	0.492	2339
P. tenisoni	137	35	0.877	0.015	0.624	2113	0.939	0.015	0.744	NA	0.895	0.034	0.704	NA
Mean	292	182	0.814	0.022	0.499	4655	0.827	0.028	0.550	3578	0.804	0.037	0.511	3562
SD	237	193	0.043	0.010	0.076	3483	0.055	0.016	0.093	2781	0.057	0.020	0.103	2879

(100–500 m; Table 2). A similar pattern was found when comparing the 2D*sub* and 3D model predictions (Table S3).

Response curves describing the relationship between a modelled species occurrence and an individual environmental predictor were compared across the modelling approaches (Figs. S1–S30). The 3D models demonstrate a slightly lower optimal temperature and narrower thermal tolerance ranges. Most species were predicted to tolerate a broader range of salinity and dissolved oxygen under the 3D models.

3.3. Comparing predictions in geographic space

Examples of suitable habitat predicted by the different model approaches are shown for *G. opisthopterus* (Fig. 1) and *G. fraseri* (Fig. 2) while all other outputs are given in Figs. S31–S40. Comparisons of geographic range overlap between 2D*all* and 3D model outputs varied considerably, but were found to have higher overlap in the upper 200 m depth bands than at deeper depths (Table 2). Spatial overlap was consistently high at all depth bands for *E. antarctica*, *G. opisthopterus* and *G. braueri* (Table 2). A similar pattern was found when comparing the 2D*sub* with 3D model predictions, and overlap values were slightly elevated in these comparisons (Table S3).

For some species, the 3D outputs revealed vertical distribution features that were not resolved by the 2D*all* or 2D*sub* approaches. For example, *E. antarctica* (Fig. S31) was estimated to have greater suitable habitat in the upper 200 m, whilst *G. opisthopterus* was estimated to have greater suitable habitat below 500 m (Fig. 1). The 3D outputs also suggest that the habitat suitability of some species, notably *E. carlsbergi*, *G. bolini*, *G. fraseri* and *K. anderssoni*, extends equatorward at deeper depths (Figs. S32, S33, S35, S38, respectively). *P. tenisoni* had the highest loss of occurrence records, and the resulting habitat suitability maps under the 3D approach have low estimates of presence throughout the study region compared to the circumpolar prediction under the 2D approach (Fig. S40).

4. DISCUSSION

In this study we present results of Southern Ocean lanternfish distributions obtained from both simplistic (2D*all*, 2D*sub*) and depth-integrated (3D) ENMs. In comparing metrics of model performance, and how outputs differ in geographic and environmental niche space, we have gained valuable knowledge of the benefits and trade-offs presented by each approach and how to interpret the ecological information they provide.

4.1. Distribution patterns

Using a variety of model performance metrics, we have shown that, even after accounting for sample size differences, 2D ENMs can perform better than

Table 2. Comparison of 2D*all* and 3D model predictions (see Section 2.3 for model details) in relation to their spatial range overlap and niche overlap as measured by relative rank and I metrics. 'n records' indicates the number of occurrences available for 3D models. Mean and SD values for each depth band are also given. See Table 1 for full species names

| 3D model depth band (m)	Metric	E. ant-arctica	E. carls-bergi	G. bo-lini	G. brau-eri	G. fra-seri	G. ni-cholsi	G. opis-thopterus	K. anders-soni	P. bolini	P. teni-soni	Mean	SD
0	n records	106	3	0	24	3	4	7	23	11	2	18	32
	Range overlap (%)	0.90	0.60	0.99	0.73	0.94	0.99	0.89	0.67	0.66	0.77	0.81	0.15
	Niche overlap (rel.rank)	0.93	0.75	0.85	0.86	0.85	0.84	0.87	0.79	0.81	0.69	0.82	0.07
	Niche overlap (I)	0.95	0.95	0.95	0.95	0.97	0.93	0.90	0.94	0.89	0.74	0.92	0.07
50	n records	73	4	6	14	10	13	0	34	11	1	17	22
	Range overlap (%)	0.91	0.59	0.99	0.69	0.95	0.96	0.90	0.73	0.73	0.80	0.82	0.14
	Niche overlap (rel.rank)	0.93	0.75	0.87	0.83	0.85	0.83	0.85	0.80	0.83	0.71	0.83	0.06
	Niche overlap (I)	0.96	0.95	0.96	0.94	0.98	0.94	0.89	0.95	0.91	0.75	0.92	0.07
100	n records	69	6	4	16	7	8	2	15	6	3	14	20
	Range overlap (%)	0.83	0.59	0.91	0.75	0.95	0.79	0.95	0.80	0.80	0.88	0.83	0.11
	Niche overlap (rel.rank)	0.91	0.76	0.86	0.82	0.86	0.83	0.84	0.83	0.85	0.72	0.83	0.06
	Niche overlap (I)	0.96	0.96	0.97	0.95	0.98	0.94	0.90	0.97	0.94	0.77	0.93	0.06
200	n records	192	24	8	39	10	55	1	38	20	3	39	57
	Range overlap (%)	0.88	0.69	0.66	0.83	0.93	0.65	0.97	0.77	0.81	0.73	0.79	0.11
	Niche overlap (rel.rank)	0.89	0.78	0.81	0.85	0.83	0.81	0.88	0.87	0.85	0.70	0.83	0.05
	Niche overlap (I)	0.95	0.96	0.97	0.98	0.95	0.96	0.94	0.98	0.96	0.74	0.94	0.07
500	n records	113	35	37	60	31	52	12	78	61	25	50	29
	Range overlap (%)	0.98	0.49	0.75	0.89	0.93	0.71	0.93	0.68	0.79	0.83	0.80	0.15
	Niche overlap (rel.rank)	0.86	0.78	0.81	0.83	0.83	0.75	0.86	0.81	0.82	0.78	0.81	0.03
	Niche overlap (I)	0.94	0.97	0.97	0.98	0.94	0.94	0.94	0.97	0.96	0.81	0.94	0.05
800	n records	96	14	18	66	16	17	34	49	24	1	34	29
	Range overlap (%)	0.99	0.37	0.70	0.86	0.72	0.48	0.93	0.55	0.61	0.78	0.70	0.20
	Niche overlap (rel.rank)	0.83	0.72	0.77	0.82	0.79	0.64	0.85	0.73	0.75	0.78	0.77	0.06
	Niche overlap (I)	0.96	0.96	0.96	0.97	0.92	0.90	0.95	0.95	0.93	0.79	0.93	0.05
1000	n records	39	1	2	23	4	2	9	19	2	0	10	13
	Range overlap (%)	0.98	0.34	0.59	0.81	0.47	0.38	0.92	0.31	0.49	0.69	0.60	0.24
	Niche overlap (rel.rank)	0.80	0.69	0.70	0.77	0.74	0.57	0.85	0.62	0.67	0.76	0.72	0.08
	Niche overlap (I)	0.92	0.95	0.94	0.94	0.89	0.88	0.96	0.92	0.90	0.75	0.91	0.06
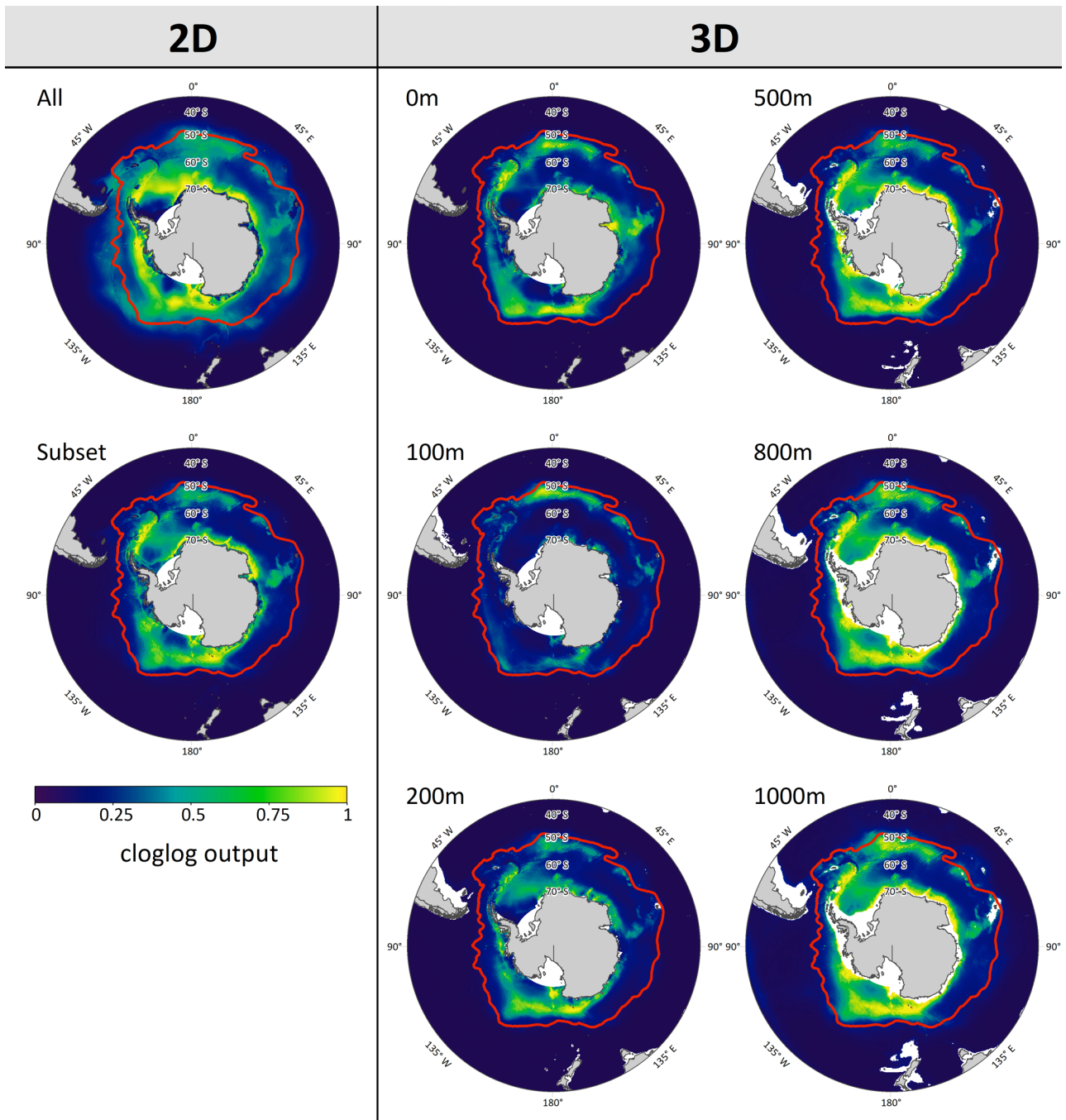
Fig. 1. Comparison of estimated conditional probability of presence (cloglog output) for *Gymnoscopelus opisthopterus* using 2D*all* (using all available occurrence records and sea surface environmental data), 2D*sub* (as 2D*all*, but built using only the same occurrence records as in the 3D model) and 3D (matches occurrence records with environmental variables from a similar depth from which the animals were caught) approaches. The red line denotes the position of the Polar Front from Orsi & Harris (2015)

3D ENMs for the same species. For certain species, this suggests that surface data alone can largely determine the abiotic drivers of their fundamental geographic distributions. This is also reflected in the high niche overlap between modelling approaches, and the similar, broadscale patterns in habitat suitability they generate. Given that many myctophids and other mesopelagic species spend time feeding in
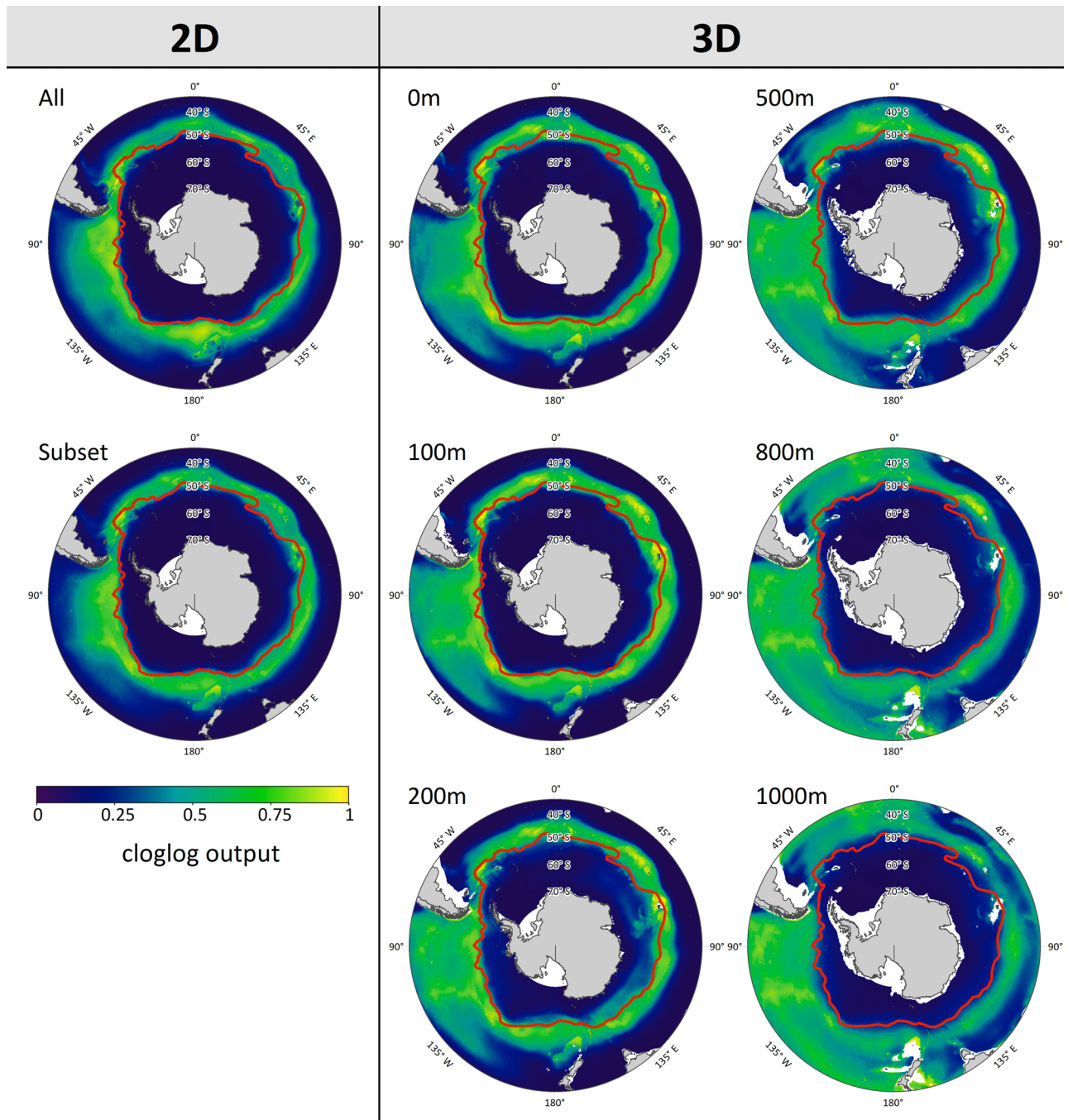
Fig. 2. Comparison of estimated conditional probability of presence for *Gymnoscopelus fraseri* (cloglog output); details as in Fig. 1

surface zones, and that their prey depend upon surface productivity, high performance of 2D ENMs in comparison to 3D methods could be anticipated and is reassuring for previous ENM predictions that have not used fully depth-resolved methods for these species (Loots et al. 2007, Duhamel et al. 2014, Freer et al. 2018) and other mesopelagic fishes (DeVaney 2016).

Nevertheless, we also found examples of species whose model performance benefitted from including depth-resolved environmental parameters and, for all 10 species investigated, the 3D model predictions

gave novel insights into their vertical habitat suitability, which until now was only described from trawl data covering areas between 100 and 1000 km (Lancraft et al. 1989, Duhamel et al. 2000, Pusch et al. 2004, Collins et al. 2008, 2012, Hulley & Duhamel 2011, Koubbi et al. 2011a).

The apparent preferences for shallow or deep habitat in our study species largely follow expectations from observed data. For example, the prediction of higher suitability of *E. antarctica* habitat in the upper 200 m matches previous observational records (Hulley 1981, 1990, Lancraft et al. 1989). Suitable habitat for *Gymnoscopelus bolini* and *G. nicholsi*, both benthopelagic as adults, is increased along shelf regions at depths below 200 m and between 100 and 500 m, respectively. This reflects patterns from catch data at similar depths (Duhamel et al. 2014). *G. braueri* and *Krefftichthys anderssoni* display suitable habitat throughout the water column, which may reflect the extensive vertical migrations known in these species (Collins et al. 2012, Duhamel et al. 2014). As adults, *G. opisthopterus* inhabit deeper (>600 m) waters associated with eastern slope regions of the Kerguelen Plateau (Hulley & Duhamel 2011), the continental slope of Antarctica (Koubbi et al. 2011a) and the southern Scotia Sea (Collins et al. 2012), which reflects our findings of suitable habitat throughout these shelf and slope regions at depths below 500 m. The suitable habitat predicted in shallow water regions may be explained by the upwelling of deeper water masses towards the surface in these areas (Hulley & Duhamel 2011).

Overall, there was a tendency for 3D model predictions at shallow depths to identify suitable habitat further south than the 2D*all* or 2D*sub* model predictions, particularly noticeable at the polar front boundary within the Scotia Sea. This is likely due to the 3D models occupying niche space with lower optimal temperature and higher optimal salinity than the equivalent 2D models, as identified by model response curves. Despite this, the 2D and 3D approaches were found to have high overlap in environmental niche space across all depth predictions, but their overlap in geographic space generally declined at deeper depths. This highlights the potential for 3D models to reveal how the latitudinal habitat of a species may change with depth. For example, comparisons amongst 3D model predictions at different depths show that suitable habitat for *Electrona carlsbergi* extends further south at shallow depths and is extended equatorward at deeper layers. Similar patterns are found for *G. bolini, K. anderssoni* and *G. fraseri,* which all have extended equatorward distributions that reach into the region of the Subtropical Convergence at depths greater than 500 m. This suggests that these species may follow Antarctic Intermediate Water as it moves from shallow depths in the Antarctic Convergence to deep waters around the Subtropical Convergence (Pardo et al. 2012). Such a hypothesis was first put forward by Hulley (1981) following the disparate vertical ranges of these species from different latitudes.

3D model outputs for some species also suggest suitable habitat in areas previously unrecorded or thought to be unsuitable based upon the outputs of the 2D models. For example, *Protomyctophum bolini* has an oceanic distribution that is bounded to the south by the South Antarctic Circumpolar Current Front (SACCF) (Saunders et al. 2019), and is generally absent inshore of shelf breaks (Duhamel et al. 2014). Results from the 3D model would suggest that regions of the Western Antarctic Peninsula and continental slope approximately 90–140°E are also potential suitable habitats, not dissimilar from the results of Duhamel et al. (2014) that also predict suitable habitat south of the SACCF.

4.2. Challenges of modelling in 3 dimensions

Integrating a vertical dimension into an ENM brings with it additional challenges. Diel vertical migrations, by their nature, will result in differences in recorded depth between daytime and night-time sampling efforts (Robison 2003). Extreme seasonal changes in light conditions, as is found in polar regions, may also alter the pattern, timing or extent of vertical migrations (Cisewski et al. 2010, Dypvik et al. 2012). Diel, seasonal and ontogenetic variability in depth distributions are confounded by net avoidance issues, as species are more likely to evade nets deployed above 400 m in daylight resulting in higher catch rates at night (Collins et al. 2012). Overall, light conditions at the time of sampling likely influence the depth at which a fish is caught, which can in turn can affect the vertical component of a model that has incorporated this information. Authors should acknowledge that the vertical distribution patterns described by a 3D niche model are specific to a particular set of diel and seasonal light conditions.

To control for these issues of vertical sampling bias, data from a wide range of diel and temporal sampling times are required. One solution is to have sampling protocols that are standardised across day/night cycles and multiple depth bands. The need for systematic sampling across environmental and

spatial gradients echoes previous calls for well-designed surveys to obtain the high quality data needed for better performing ENMs (Fei & Yu 2016, Leroy et al. 2018, Araújo et al. 2019). For mesopelagic species, factoring in an additional temporal dimension is necessary to generate a more informative sample of presences, as well as non-detections, which would refine our ability to predict and interpret patterns of vertical habitat use in light of diel migratory behaviour.

4.3. Data quantity versus quality

Since many occurrence records do not have associated depth data, they must be excluded from 3D ENMs (Duffy & Chown 2017), or else alternative solutions must be sought; for example, it may be possible to assign assumed depths to occurrence records through a hierarchical modelling approach with certain expectations about the distribution-at-depth of the missing data. In the examples considered in our study, the sample size for half the species of 3D ENMs dropped to fewer than 90 occurrence records, and to only 35 records in the case of *P. tenisoni*. This dropout highlights the need to consider the availability of depth-specific presence data when choosing the most appropriate modelling approach for marine species.

ENMs built using a small sample size tend to be less powerful because their parameter estimates have higher uncertainty, outliers have a higher weight, and there may not be enough records to comprehensively represent the complexity of an ecological niche (Wisz et al. 2008). Previous studies have explored the performance of multiple ENM algorithms with different sample sizes. These studies found that, whilst MaxEnt can be less sensitive to changes in sample size than other algorithms (Hernandez et al. 2006, Wisz et al. 2008), (1) depending on the type of data available, a minimum of 50−100 occurrences are needed to characterise a species' niche (Meynard et al. 2019), though some studies have produced useful models with as few as 10 records (Stockwell & Peterson 2002, Soultan & Safi 2017); (2) model performance tends to increase with additional presences, but can plateau after reaching a certain threshold where additional records add little to model accuracy (Stockwell & Peterson 2002); and (3) characteristics of a species, e.g. niche breath, specialisation (Mateo et al. 2010, Soultan & Safi 2017) and the size of the study area (van Proosdij et al. 2016), can influence minimum prior information needed about a species. Taken together, these studies

are a strong indicator that low sample size can affect model performance and may help to explain the subtle differences we observed between the performance of 2D*all*, 2D*sub* and 3D models presented here.

That our results have signs of better fit with larger sample size, as measured by the AUC_{DIFF} metric, is consistent with this literature. However, the AUC_{TEST} (Lobo et al. 2008) and recently the TSS (Leroy et al. 2018) metrics have been shown to be prevalence-dependent; i.e. they are dependent on the proportion of the data representing species presence (Phillips et al. 2006, Raes & ter Steege 2007). When there is a strong imbalance between presence and absence, the model is very likely to have a higher probability of occurrence at a random presence point than at a random absence point, resulting in an AUC value that is falsely inflated by statistical artefacts caused by the lower sample size (McPherson et al. 2004, van Proosdij et al. 2016). Here, several models showed slightly higher AUC_{TEST} and TSS values under the 2D*sub* and 3D approaches, which had lower sample size, and thus lower prevalence, than comparative 2D*all* models. Thus, it is unclear whether these indicators of performance are a statistical artefact, or a true reflection of a better model performance. Nevertheless, these metrics are able to give an indication of model discriminatory ability and, used in tandem with other methods, such as niche and range overlap tools, the ecological realism of model outputs can be compared (Fourcade et al. 2014).

Data quality can be determined by several characteristics of the presence data, including the reliability of species identifications, spatial accuracy and the degree to which they represent the true distribution of the species (Kadmon et al. 2003). By utilising depth-of-catch information, the 3D method employed here matches presence data to abiotic values, which more accurately reflect the conditions at the depth at which they were caught. In doing so, 3D methods theoretically provide an improvement in the spatial accuracy of the presence data and also in the completeness of the representation of the environmental niche provided by the model training data, which is important for obtaining reliable models with good calibration (Jimenez-Valverde et al. 2009, Meynard et al. 2019). Our results demonstrate that this may be particularly relevant for species that are known to prefer deep ocean environments. *G. opisthopterus* can be characterised as being a deeper-living (400−1000 m), bathypelagic species (Hulley & Duhamel 2011, Saunders et al. 2019). Performance metrics agree that the 3D model for this species is better performing than 2D models, supporting the

idea that, in some cases, the quality of ecological information provided by the presence (and absence/pseudo-absence) data can be more important than the quantity of information (Mateo et al. 2010).

At depths below the surface, environmental climatologies, particularly for biochemical variables such as dissolved organic carbon or chlorophyll, which are often derived from satellite products, are not as readily available as in surface layers. Global ocean models can provide estimates of carbon and nutrient parameters subject to their own model-based uncertainties (Allen et al. 2007, Aumont et al. 2015), yet overcoming the limitations of creating depth-resolved predictor information will also be important to address the uptake, quality and performance of future 3D ENM techniques.

In reality, both the quantity and quality of data will influence model predictions, alongside sampling biases (Fei & Yu 2016) and the distribution characteristics of the modelled species (Kadmon et al. 2003). The choice of the most appropriate modelling approach will depend upon all of these factors and the intended use of the model. While a large, representative sample size should be favoured in studies interested in defining environmental conditions of a species or complex conservation applications, a smaller sample size may be tolerated when the aims of an ENM are to identify potential sampling locations or to explore macroecological patterns of poorly known regions or taxa (Wisz et al. 2008, Soultan & Safi 2017).

Here we have shown that 3D approaches can give results that are insightful and comparable to the more simplistic 2D models for some species. However, the utility of these 3D approaches are limited by the paucity of depth-of-catch data associated with online-sourced occurrence records, at least for the species considered here. We emphasise the need for mesopelagic species data to be collected using appropriate temporal and depth-stratified methods, and for providers to upload full and accurate records of occurrence, including depth-of-catch, when submitting data to global biodiversity databases such as GBIF. This should also include the type of net used, deployment method (e.g. oblique or stratified depth), and non-detections of species, as this information gives researchers a fuller understanding of the data and its limitations. Future studies aiming specifically to integrate a third dimension into ENMs should consider the data quality, quantity, the ecological characteristics of the species and the objectives of the study to clarify the suitability of such methods.

4.4. Concluding remarks

We have found that 3D ENMs developed for mesopelagic species have a higher and more consistent overlap to 2D ENMs in environmental space than geographic space. However, this rarely resulted in differences to inferred broad-scale patterns of habitat suitability. 3D models may outperform models based on 2D approaches depending on the metrics used and species of interest, yet trade-offs are required between the quality and quantity of occurrence records, which will determine the subsequent choice of ENM (2D or 3D). In particular, the paucity and added uncertainty of depth-of-catch data may limit the widespread use of 3D if this is not corrected through an increased effort of appropriate collection and documentation. 3D models could be a valuable addition to the researcher's toolbox when investigating deep pelagic biogeography, and we advocate their continued use and development, where data are appropriate.

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