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RESEARCH ARTICLE

Global phylogeography of hyperdiverse lanternfishes indicates sympatric speciation in the deep sea

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Abstract

Aim: Lanternfishes (Myctophidae) are one of the most species-rich families of mid-water fishes. They inhabit the mesopelagic zone, where physical barriers to dispersal and gene flow are permeable. Thus, modes of speciation that rely exclusively on geographical separation are potentially of less importance than those that rely more prominently on evolution of assortative mating through divergent habitat use and/or sexual signals, including visual signals from bioluminescent light organs. Here we used phylogenetic, ecological and morphological data to investigate the roles of geography, habitat use and lateral photophores in lanternfish speciation.

Location: Global.

Time period: Data collected between 1950 and 2015.

Major taxa studied: Lanternfishes (Myctophidae).

Methods: Ecological niche models (ENMs) were developed for 167 species, enabling the community composition of 33 mesopelagic ecoregions to be determined. Sequence data for seven protein-coding regions from 175 species were used to reconstruct a phylogenetic tree of Myctophidae. Age-overlap correlation tests were conducted using this phylogeny with outputs from ENMs (pairwise geographical overlap and pairwise ecological niche overlap, $n = 136$), in addition to matrices of pairwise depth overlap ($n = 158$) and photophore pattern dissimilarity ($n = 161$).

Results: Communities assembled according to nine broad climatic regions, and recently diverged species pairs possessed greater geographical and ecological niche overlap than more distantly related species, indicating that sympatric or parapatric speciation might be dominant modes of divergence. Differences in photophore patterns increased with the relative age of speciation events, suggesting that photophore patterns are largely constrained by phylogeny.

Main conclusions: Based on this evidence, we suggest that large-scale oceanographic features structure the diversity of lanternfish communities and that speciation within this family of deep-water fishes might not have required geographical isolation.

KEYWORDS
bioluminescence, divergence, ecological niche model, ecoregion, lanternfish, mesopelagic, photophore, phylogeny, speciation

1 | INTRODUCTION

Lanternfishes (Myctophidae) comprise over 250 species within 33 genera (Eschmeyer et al., 2018). They are distributed worldwide and typically occupy a large vertical range from the surface to mesopelagic depths ~200–1,000 m. Their global diversity makes them one of the few families of largely mesopelagic fishes that have diversified into a species-rich clade (Davis et al., 2014). As is typical of open-water species, lanternfishes are extremely abundant, geographically widespread and have planktonic larval dispersal (Catul et al., 2011; Gaither et al., 2016). Moreover, like many other pelagic species, lanternfishes have been found to be genetically homogeneous across large geographical regions (Kojima et al., 2009; Van de Putte et al., 2012), which has led to suggestions that dispersal is rarely a limiting factor to their distribution. Consequently, modes of speciation that rely upon the presence of physical dispersal barriers to limit genetic exchange between populations (i.e., allopatric speciation) are likely to be of less importance to oceanic species than to those on land (Norris, 2000; Palumbi, 1994).

In the absence of physical barriers, but where ecological gradients are present, "ecological speciation" can arise between populations through divergent adaptation to contrasting environmental regimes (Bowen et al., 2013; Puebla, 2009). As a population within a species is exposed to a novel environment or potential niche, it might experience new local selective pressures, potentially promoting reproductive isolation from the parent population despite gene flow (Nosil, 2012). Such adaptive evolution in response to ecologically distinct habitats is thought to have played an important role in divergence of several groups of marine fishes along depth, light (Ingram, 2011), salinity (Momigliano et al., 2017) and temperature (Teske et al., 2019) gradients, including within the deep sea (Gaither et al., 2018), but it has not yet been investigated as a speciation mechanism relevant to the hyperdiverse, mesopelagic lanternfishes.

Speciation is facilitated when traits under selection promote assortative mating (Nosil, 2012). In this way, bioluminescence might contribute to reproductive isolation among lanternfishes, particularly if used in sexual signalling. Lanternfishes have ventral photophores (light organs) that emit bioluminescent light, providing camouflage from predators below via counter-illumination (Hastings, 1971). Their lateral photophores, however, have species-specific patterning, which has been hypothesized to facilitate communication and recognition between conspecifics (Haddock et al., 2010; Paxton, 1972) and has been linked to their increased rate of speciation (Davis et al., 2014; Ellis & Oakley, 2016). If photophore patterns are important in speciation, we might expect to see selection favouring greater pattern dissimilarity when closely related species overlap in geographical space. This has been found in bioluminescent flash patterns (i.e., temporal differences in emissions) of sympatric *Photinus* firefly species (Stanger-Hall & Lloyd, 2015) and has been proposed to enable easier mate discrimination, reduce the time spent searching for a mate and reduce the risk of heterospecific copulation. Equally, it is possible that the positioning of lanternfish lateral photophores is determined by a conserved functional role, such as providing the optimal counter-illumination of a species' body shape (Denton & Adams, 2015).

To begin to investigate which mechanisms might have facilitated myctophid diversification, we compiled phylogenetic, distribution, ecological niche and photophore pattern data for up to 175 species. We used these data to test hypotheses related to the roles of geographical separation, ecological niche differences and photophore patterning in reproductive isolation. We first used ecological niche models (ENMs) to map the distribution of each species and asked whether assemblages associate with previously described mesopelagic ecoregions. Secondly, we asked whether geographical separation and ecological niche divergence are associated with speciation. Specifically, we investigated the predictions that if species have diverged in allopatry, then we might expect the most closely related species to show low levels of geographical and ecological niche overlap (Cardillo & Warren, 2016; Fitzpatrick & Turelli, 2006). Finally, we used binomial tests to infer whether sister-species pairs have greater geographical overlap, niche overlap, depth overlap and photophore similarity than expected relative to non-sister-species pairs.

2 | METHODS

2.1 | Ecological niche models

2.1.1 | Occurrence data

Occurrence records of 181 species of myctophid were downloaded from the Global Biodiversity Information Facility (GBIF; www.gbif.org) facilitated by the software ModestR v.4.6 (Garcia-Rosello et al., 2013). All occurrence records were then cleaned for unreliable data, including duplicate records, records with identical latitude and longitude, and records with a latitude and longitude corresponding to a terrestrial location. To ensure that records were spatially accurate, occurrences were also checked against the literature (Becker, 1983; Duhamel et al., 2005, 2014; Hulley, 1981, 1984; Hulley & Duhamel, 2009; Nafpaktitis, 1978; Nafpaktitis et al., 1995; Nafpaktitis & Nafpaktitis, 1970; Nafpaktitis & Paxton, 1968, 1978; Zahuranec, 2000). We retained 167 species and 62,590 occurrences for analyses. See the Data Accessibility Statement for information on both raw and cleaned occurrence datasets.

2.1.2 | Environmental data

Temperature, salinity and dissolved oxygen at 0 and 200 m were selected as predictor variables owing to their physiological importance for marine ectotherms and their significance in determining myctophid distributions (Duhamel et al., 2014; Flynn & Marshall, 2013; Koubbi et al., 2011). Temperature, salinity and dissolved oxygen at 1,000 m, and net primary productivity at the surface were also used, based on their importance for mesopelagic community biogeography (Sutton et al., 2017). Bathymetry was included to incorporate topographic preferences, and categorical variables for ocean basin (ten categories) and hemisphere (two categories) were included to constrain predictions to feasible geographical extents.

A summary of all predictor variables and data citations is given in Table 1. Owing to strong correlations between temperature and oxygen at both 0 and 200 m depth (Pearson's $r > 0.75$), Principal components analyses (PCAs) were used to obtain the first axis of variation for each of the two depths, and these were used in place of these two sets of variables. Bathymetric data (i.e., maximum water depth) had an original resolution of 30 arc-sec and were resampled to the same resolution as the other variables (0.25 × 0.25 decimal degrees at the equator) using the bi-linear resample tool in ArcGIS v.10.4.1 (ESRI, Redlands, CA, USA).

2.1.3 | MaxEnt ecological niche models

For each species, occurrence records and environmental predictors were fitted to the presence-only modelling algorithm MaxEnt v.3.3.3k (Elith et al., 2011; Phillips & Dudik, 2008). To avoid overfitting and to maximize model performance, only linear and quadratic feature classes were selected, which are more consistent with ecophysiological models than complex model functions (Elith et al., 2010). All ENMs were run using a five fold cross-validation method, with 20% of occurrence data reserved for model evaluation. To account for spatial sampling bias, a bias file was created using a Gaussian kernel density map of all myctophid occurrence points rescaled from 1 to 20 following Elith et al. (2010) and Fourcade et al. (2014). For each species, only one occurrence record per grid cell was used in the model, and all other MaxEnt settings were kept as default. Alternative values of the Regularisation Multiplier parameter (0-5) were tested but did not significantly improve evaluation metrics.

The performance of each ENM was evaluated by the Area Under the receiver operating characteristic Curve (AUC) and Continuous Boyce's Index (CBI). The AUC scores range from zero to one and can be interpreted as reporting the probability that a randomly chosen presence location is ranked higher than a randomly chosen background point (Merow et al., 2013). The CBI values were estimated using the R package "ecospat" (Di Cola et al., 2017). These can range between minus one and plus one, where positive values indicate a model where predictions of presence are consistent with the distribution of presences in the evaluation dataset, values close to zero mean that the model is not different from a random model, and negative values indicate counter-predictions (Hirzel et al., 2006). The degree of model overfitting was estimated using the minimum training presence omission rate (OR) and AUC_{diff} metrics. The OR reports the rate of occurrences within the evaluation dataset that fall outside the minimum prediction value of the calibration records, and AUC_{diff} is the difference between AUC scores from the calibration and evaluation datasets.

2.1.4 | Ecological niche and geographical overlap

The logistic output from MaxEnt was used to calculate pairwise ecological niche and geographical overlap values for each of the 167 species, using ENMTOOLS v.1.4 (Warren et al., 2010). Niche overlap used the similarity metric derived from Hellinger's distance, *I*, which calculated niche similarity by taking the difference between species' suitability scores at each grid cell, after suitabilities were standardized so that they summed to one over the geographical space being measured. Other similarity metrics (Schoener's *D* and relative rank) were tested and did not result in differences in the niche overlap patterns presented here. Geographical range overlap, as in the study by Fitzpatrick and Turelli (2006), was also calculated as $(N_{x,y}/\min[N_x, N_y])$, where $N_{x,y}$ is the number of grid cells in which both species are predicted to occur, and N_x and N_y are the number of grid cells in which X and Y, respectively, are predicted to be present (Warren et al., 2010).

TABLE 1 A summary of the predictor variables used to construct ecological niche models

Predictor	Units	Temporal period	Depth (m)	Source
Temperature	Degrees Celsius	1955–2012	0†, 200‡, 1,000	Locarnini et al. (2013)
Salinity	Practical salinity units	1955–2012	0, 200, 1,000	Zweng et al. (2013)
Dissolved oxygen	Millilitres per litre	1955–2012	0†, 200‡, 1,000	Garcia et al. (2014)
Primary productivity	Grams of carbon per metre cubed per day	2000–2014	0	Assis et al. (2018)
Bathymetry	Metres	–	–	Becker et al. (2009)
Ocean basin	–	–	–	Flanders Marine Institute (2021)
Hemisphere	–	–	–	–

Note: Full citations are given in the references. †‡Combined via first principal component owing to high collinearity.

2.2 | Lateral photophore mapping

The Interactive Individual Identification System (IS^3) software v.4.02 (Van Tienhoven et al., 2007) is a landmark-based, two-dimensional affine transformation method originally developed to identify individual animals from large image databases (for further background information on IS^3, see Supporting Information). Two hundred and sixty-six taxonomic drawings of 229 myctophid species were gathered from the published literature. If more than one drawing was available for a species, both were included. Three landmarks were identified and marked on each drawing: insertion of the operculum on the ventral lateral profile, anterior insertion of the dorsal fin, and posterior body extremity (Supporting Information Figure S1). The two-dimensional positions, relative to the dorsoventral and rostrocaudal axes of the fish, of the following homologous photophore groups were then mapped: pectoral lateral organ (PLO), pectoral ventral organs (PVO), ventral lateral organ (VLO), pectoral organs (PO), ventral organs (VO), supra-anal organs (SaO), posterior organ lateral (Pol) and precaudal organs (Prc) (Supporting Information Figure S1). Given that the accuracy of image comparison is highest when 12–30 spot pairs are used, only the first and last anterior anal organs (AOa) were included, and all of the posterior anal organs (AOp) were excluded. This decision was based on the AOp photophores being variable in number but less so in positioning; therefore, preference was given to other homologous groups that have greater potential to distinguish between species (J. Paxton, personal communication). For each image, IS^3 was used to obtain dissimilarity scores against other images for the first 250 matches, with higher scores indicating greater dissimilarity. Scores for each image were ranked from 0 to 249 and transformed into a species-level pairwise dissimilarity matrix (0 = most similar, 249 = most dissimilar).

2.3 | Molecular methods

2.3.1 | Sampling of genetic markers

Our phylogenetic reconstruction combined published sequence data (for accession numbers, see Supporting Information Table S1) and newly generated sequences for taxa with missing or incomplete sequence information (for details of new tissue samples, see Supporting Information Table S2). To integrate with the previous phylogenetic work, the following seven protein-coding loci were targeted for DNA sequencing: *histone H3* (*H3*), *glycosyltransferase* (*glyt*), *myosin heavy polypeptide 6* (*myh6*), *cytochrome c oxidase subunit 1* (*CO1*), *bone morphogenetic protein 4* (*bmp4*), *T-box brain 1 transcription factor* (*tbr1*) and *zinc finger protein ZIC 1* (*zic1*).

2.3.2 | DNA amplification and sequencing

Genomic DNA was extracted from each tissue sample using the DNeasy Blood and Tissue kit (Qiagen, Crawley, UK), following the manufacturer's instructions. PCRs were conducted using GoTaq Green Master Mix (Promega, Madison, WI, USA) in 20 μl volumes, with the following components: 10 μl Master Mix, 5 μl molecular biology grade water, 2 μl each of 2 μM forward and reverse primers, and 1 μl of DNA template. All reactions were carried out on a Techne Prime Thermal Cycler (Cole-Parmer, Stone, UK), and thermocycler protocols with primer sequence information for each genetic marker can be found in the Supporting Information (Table S3). The PCR products were visualized by gel electrophoresis. Band lengths were then checked against a 1 kb DNA ladder (Thermo Fisher Scientific, Waltham, MA, USA) to ensure that correct regions had been amplified. The PCR products were purified and sequenced in both forward and reverse directions by Eurofins Genomics (Wolverhampton, UK). Using GENEIOUS v.10.0.7 (Kearse et al., 2012), the resulting reads were assembled into contigs, the primer regions were trimmed, and the nucleotides were checked for stop codons and ambiguous or miscalled amino acids by examining translated protein sequences. Newly generated sequence data were archived on the National Center for Biotechnology Information (NCBI) GenBank nucleotide database under accessions MZ853123–MZ853141 (*CO1*) and OK181061–OK181106 (all other markers).

2.3.3 | Sequence alignment

For each of the seven genetic markers, we downloaded all relevant sequences of Myctophiformes (families Myctophidae and Neoscopelidae) from the NCBI nucleotide database (www.ncbi.nlm.nih.gov) using the R package TRAITS (Chamberlain et al., 2019). Alignments for each marker region were performed using MAFFT v.7.397 (Katoh & Standley, 2013). Sequence alignments were then concatenated into a single alignment using the R package PHYLOCH (Heibl, 2008) and poorly aligned regions were removed using GBLOCKS v.0.91b (Talavera & Castresana, 2007). See the Data Accessibility for the final concatenated alignment.

2.3.4 | Phylogenetic analysis

Phylogenetic relationships were estimated using maximum likelihood (ML) phylogenetic inference implemented in RAXML v.8.2.10 (Stamatakis, 2014) using the (GTR+G) nucleotide substitution model chosen by JMODELTEST v.2.1.10 (Darriba et al., 2012; Guindon & Gascuel, 2003) using Akaike's information criterion corrected for sample size (AICc). The best ML tree was determined from 1,000 randomized maximum-parsimony starting trees, and the statistical support values for ML branches were estimated from 1,000 bootstrap replicates.

2.4 | Statistical analyses

2.4.1 | Global species distributions and associations with mesopelagic ecoregions

Using MAXENT outputs, we calculated the number of cells occupied by each species within each of the 33 mesopelagic ecoregions of Sutton

et al. (2017). With the R package VEGAN (Dixon, 2003), non-metric multidimensional scaling (NMDS) was used to visualize differences in community composition across ecoregions. Measured distances between communities were constructed from a binary Bray–Curtis dissimilarity matrix, and NMDS iterations were repeated until stress was sufficiently minimized (<0.1). The resulting distance matrix was then used for model-based clustering within the R package MCLUST (Scrucca et al., 2016), enabling identification of the optimal number of clusters among all 33 ecoregions.

2.4.2 | Age-overlap correlation tests

The slope of the relationship between the relative age of species and the amount of overlap in a certain trait can reflect how overlap changes with time, accounting for independent, post-speciation range shifts. Shifting ranges can be accounted for by comparing the empirical relationship with those generated under a null hypothesis that overlap between species is uncorrelated with the length of time since their divergence (Fitzpatrick & Turelli, 2006). For example, when investigating the relationship between age and geographical overlap, a regression intercept >0.5 and a negative slope would be consistent with a dominant pattern of sympatric divergence, whereas the opposite would be consistent with a dominant pattern of allopatric divergence (Fitzpatrick & Turelli, 2006).

Age-overlap correlation tests were performed using the R package ENMTOOLS (Warren et al., 2021). A linear regression was fitted to the observed relationship between an overlap matrix (e.g., geographical overlap) and the time since divergence (phylogenetic branch lengths). One hundred Monte Carlo permutation tests were run by randomizing overlap values among species and re-computing the regression. Statistical significance was measured by comparing the empirical slope and intercept with the distribution of slopes and intercepts from the Monte Carlo replicates. Relative branch lengths were calculated by enforcing a molecular clock using the chronos function of the R package APE (Paradis et al., 2004), specifying an arbitrary branch length of one for the root. A strict molecular clock generated a smaller φIC (an information criterion for model selection in the presence of a penalized term; see Paradis, 2013) than correlated or relaxed clock parameters (ΔφIC = 1,013), hence the strict clock was used.

Age-overlap correlation tests were repeated using each of the four overlap matrices for species that had both genetic and trait information available (genetic distance derived from relative node age = 175, geographical overlap = 136 species, ecological niche overlap = 136 species, photophore pattern dissimilarity = 161 species, and depth overlap = 158 species). For heatmaps of all pairwise matrices, see the Supporting Information (Figures S2–S6).

2.4.3 | Sister species versus congener species

Age-overlap correlations can yield inconclusive results, because they require a single dominant mode of speciation across the clade of interest and post-speciation range shifts must not have obscured the information regarding the geography of speciation (Fitzpatrick & Turelli, 2006; Losos & Glor, 2003). Therefore, we also asked whether closest relatives (i.e., sister species) have greater similarity in geographical, ecological and photophore attributes than their next-closest species using pairwise distance analysis.

Pairwise distances between the pairs of tips on the ML phylogeny were computed using its branch lengths, with mean distances used when a species was represented by two or more specimens. We identified 46 pairs of sister species, and the most recently diverged species from each pair (non-sister species). Values of geographical range, ecological niche, depth overlap, photophore pattern dissimilarity and relative age were then extracted for each pair of sister and non-sister species. Both sister species were compared with the non-sister species, and an average of their distances were used. The difference between the sister pair and averaged non-sister pair was calculated for each metric, and an exact binomial test was used to infer whether the observed frequency (*f*) of sister pairs that have greater geographical overlap, niche overlap, depth overlap and photophore similarity relative to their averaged non-sister pair was greater than expected owing to chance.

3 | RESULTS

3.1 | Global patterns of myctophid biogeography

Ecological niche models were built for 167 species. The predictor variable sea surface temperature/dissolved O_2 (combined via first principal component owing to high collinearity) had the highest average importance for model permutation at 38.98 ± 21.30%, followed by ocean basin (15.85 ± 20.72%) and temperature/dissolved O_2 at 200 m (12.63 ± 13.09%). See the Supporting Information (Table S4) for MAXENT summary metrics per species and the Data Accessibility Statement for maps of ENM outputs per species.

Combining outputs from the ENMs, we analysed species composition within the previously described mesopelagic ecoregions of Sutton et al. (2017). Globally, nine clusters of myctophid communities were identified using a binary Bray–Curtis dissimilarity index of species presence (Figure 1). These clusters demonstrated a high degree of community similarity within the Atlantic Ocean and North Pacific Ocean basins. In the Southern Hemisphere, Atlantic, Indian and Pacific Ocean ecoregions clustered together, separated predominantly by latitude (Figure 1b). Community shifts were detected where broad and persistent oceanographic features are present, for example between ocean gyre systems (e.g., regions 4–6 and 6–8 in Figure 1a), oxygen-minimum zones (e.g., regions 14 and 15) and frontal regions, such as at the polar and subtropical fronts (regions 32 and 33).

We found that the distributions of individual species were rarely contained within one ecoregion, with species typically having ≥10% of their total distribution within one to five ecoregions. The most diverse ecoregions were found to be the Southern Central Pacific

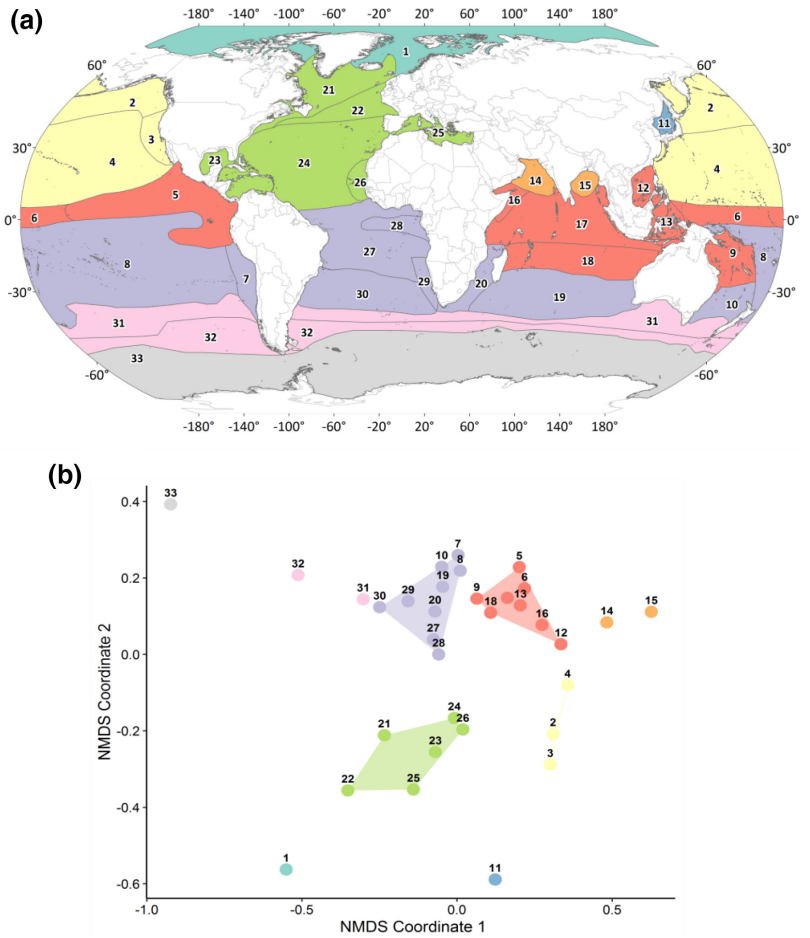

FIGURE 1 (a) Global mesopelagic ecoregions of Sutton et al. (2017), coloured by myctophid community cluster as identified from model-based clustering of a Bray–Curtis dissimilarity matrix generated from ecological niche model outputs. (b) Non-metric multidimensional scaling (NMDS) ordination plot of the dissimilarity matrix, with each ecoregion coloured by myctophid community cluster. The NMDS coordinate labels and colours correspond to the ecoregion labels in (a).

and Tropical-West Equatorial Atlantic (regions 8 and 27 in Figure 1a), with 138 and 131 species, respectively, predicted to have suitable habitat within these ecoregions.

3.2 | Phylogenetic analysis

A total of 1,184 sequences from 255 specimens were used to reconstruct phylogenetic relationships of 175 myctophiformes. The structure of the phylogeny was consistent with previous phylogenetic reconstructions (Denton, 2014, 2018; Martin et al., 2018), with the family Myctophidae and five of the seven tribes–Electronini, Gymnoscopelini, Diaphini, Lampanyctini and Notolychnini–recovered as monophyletic while the Myctophini + Gonichthyini collectively formed a monophyletic group, but were not respectively monophyletic within that group (Figure 2). Regarding intertribal relationships, our phylogeny was in agreement with Martin et al. (2018) in the placement of Notolychnini as sister group to Lampanyctini (vs. nested in Lampanyctini as in the study by Denton, 2014), but reflected the phylogeny of Denton (2014) in the position of Diaphini as sister group to Notolychnini + Lampanyctini + Gymnoscopelini (vs. Myctophini + Gonichthyini + Electronini as in the study by Martin et al., 2018). The position of Diaphini was poorly supported both here and in the analysis by Martin et al. (2018), with a bootstrap value of <75%.

3.3 | Sister species versus congener species

By comparing 46 pairs of sister species with 46 congener, non-sister species pairs, we found that a significant proportion of sister species pairs had greater overlap in geographical range and ecological niche and greater similarity in photophore pattern relative to non-sister species pairs (Table 2). Sister species pairs were found to have a mean geographical overlap of 76%, compared with 63% within the non-sister species pairs (Table 2). The mean depth overlap was similar between groups, and a binomial test was non-significant (Table 2).

By comparing geographical range maps of the identified sister species, we found that a number of possibilities exist: they might be separated geographically between or within ocean basins; they might occupy adjacent regions whilst overlapping extensively at range edges; one might occupy an area within the range of the sister species; or they might display extensive co-occurrence (Figure 3).

3.4 | Age-overlap correlation tests

Age-overlap correlation tests quantify the association between the relative age of each node of the phylogeny and the extent of trait overlap observed for descendent lineages. When analysing correlations between relative age and geographical overlap, the intercept

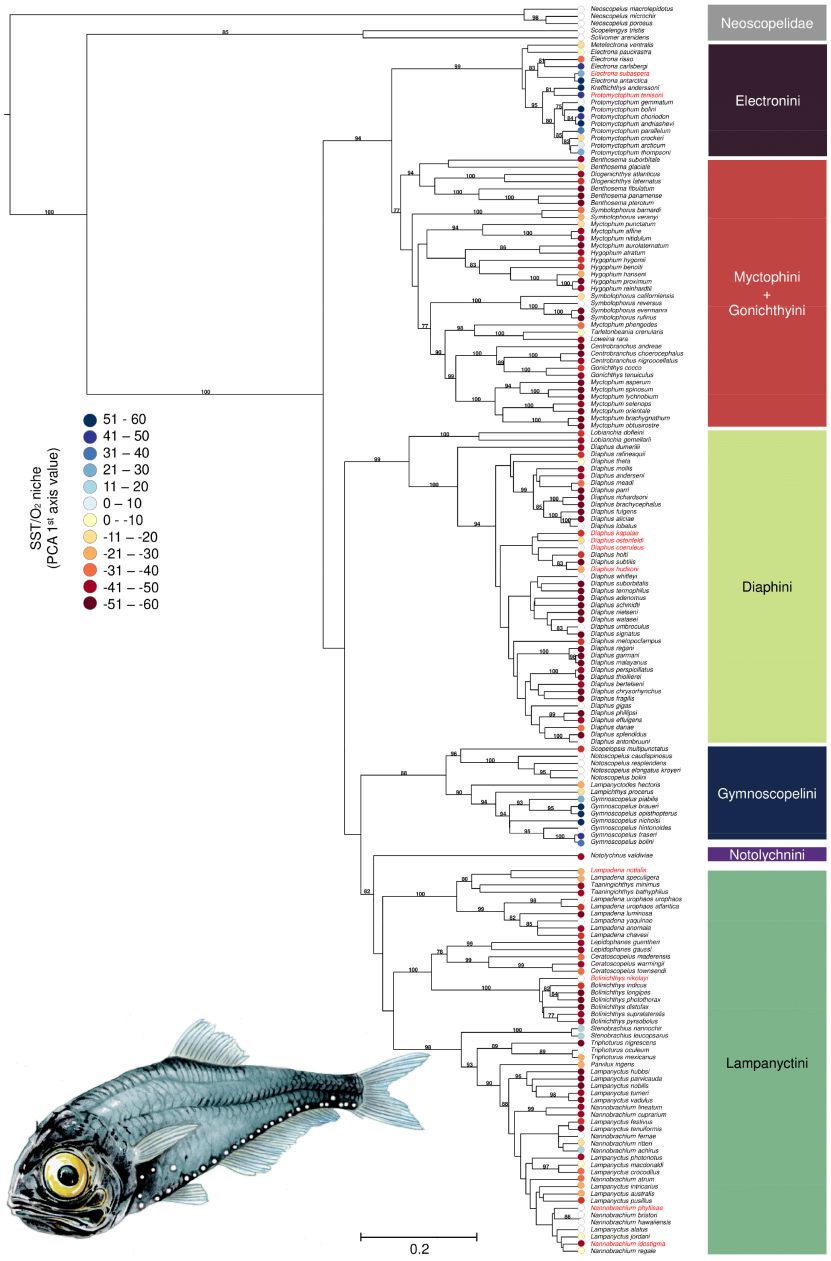

FIGURE 2 Phylogenetic relationship of Myctophiformes based on a maximum likelihood analysis of seven protein-coding genes. Branch lengths and scale bar indicate genetic distance, scaled to a maximum of one at the root. Branch bootstrap support values ≥75 are shown. Nine species highlighted in red are newly sequenced for this study. Tribal relationships *sensu* Paxton (1972) are given on the right-hand side. Coloured tips of the phylogram for each species indicate sea surface temperature (SST)/O_2 niche categories [principal components analysis (PCA), first axis], taken as the average from species occurrence records. Extremely negative values reflect high-temperature/low-oxygen conditions, extremely positive values reflect cold-temperature/high-oxygen conditions, and blank nodes indicate no niche information available. The image of *Electrona antarctica* is reproduced with the kind permission of the Administration of the British Antarctic Territory.

value of the empirical slope was significantly greater than expected from null model iterations (intercept coefficient = .68, p = .01; slope coefficient = −.38, p = .09; Figure 4a). This suggests that the level of geographical overlap in more recently diverged species is greater than expected under a null model.

For the correlation between relative age and ecological niche overlap, both the empirical intercept and the slope were significantly different from those generated under the null model iterations (intercept coefficient = .54, p = .01; slope coefficient = −.65, p = .01; Figure 4c). This suggests that closely related species have greater ecological niche overlap than expected and that a negative relationship between relative age and niche overlap exists, similar to that between relative age and geographical overlap.

We found no significant difference between the empirical and null model iterations when analysing the correlation between relative age and depth overlap (intercept coefficient = .62, p = .58; slope coefficient = .12, p = .30; Figure 4b), suggesting no association between species relatedness and the extent of overlap in their known vertical distributions.

IS^3 returned photophore dissimilarity results that showed high similarity of photophore patterns within genera and subfamilies (Supporting Information Figure S6). In 70% of cases where species had two images available for photophore mapping, the second image was ranked within the top 15 matches. In agreement with the binomial test results, we found a significant positive relationship when analysing the correlation between relative age and photophore dissimilarity (intercept coefficient = 20.47, p = .02; slope coefficient = 255.20, p = .02; Figure 4d), which indicates that photophore patterns are more similar between recently diverged species than between distantly related species.

TABLE 2 Summary of sister species versus non-sister species comparison tests using each of four trait metrics described in the Methods

Metric	Sister-species pair mean	Non-sister-species pair mean	Number of pairs	*f*	*p*-value	Interpretation
Percentage geographical overlap	76 ± 25	63 ± 26	46	70	.003	Sister pairs have greater range overlap than non-sister pairs
Percentage depth overlap	69 ± 21	67 ± 13	42	59	.06	Sister pairs and non-sister pairs have no difference in depth overlap
Percentage ecological niche (*I*) overlap	57 ± 27	42 ± 24	46	61	.04	Sister pairs have greater niche overlap than non-sister pairs
Rank photophore dissimilarity	45 ± 46	50 ± 43	44	68	.006	Sister pairs have more similar photophore patterns than non-sister pairs

Note: The mean value (±1 *SD*) of each metric is given for sister- and non-sister species pairs. The frequency (*f*) of sister species pairs with greater overlap or similarity than the corresponding non-sister species pairs is given as a percentage. The *p*-value denotes significance after a binomial test of probability. The fewer species pairs for depth and photophore tests are attributable to missing data.

4 | DISCUSSION

In this study, we integrated multiple sources of data to investigate the roles of geographical separation, ecological niche differences and photophore patterning in reproductive isolation and speciation of lanternfishes. Our findings provide novel insights into the patterns of myctophid biogeography and phylogeography within a global context.

4.1 | Global patterns of myctophid biogeography

There have been several attempts to classify the geographical zonation of the epi- and mesopelagic ocean layers based upon oceanographic (Oliver & Irwin, 2008), biogeochemical (Reygondeau et al., 2018) and biogeographical (Spalding et al., 2012; Sutton et al., 2017) approaches. When our ENM outputs were allocated to the 33 ecoregions identified by Sutton et al. (2017), myctophid communities clustered into nine distinct groupings based upon major climatic zones and large-scale physical features. These groupings align most closely with the biogeographical approaches to ocean classification, because they account for the distinct assemblages within different hemispheres. Most notably, large-scale oceanographic features are found to be important delineations of communities that match well to previously recognized "biomes" or "provinces" (Longhurst, 2007). This includes the mid-ocean gyres, equatorial and polar regions. Nevertheless, the separation of subpolar and polar groupings in the Southern Hemisphere closely matches classification based on remotely sensed variables (Oliver & Irwin, 2008).

The majority of lanternfish species were found to have wide-ranging distributions that encompass multiple ecoregions. The number of clusters we obtained was markedly fewer than found by other methods, especially within the North Atlantic (e.g., Spalding et al., 2012). Fragile zooplankton of the mesopelagic zone, such as tunicates, siphonophores and ctenophores, were also found to have broad-scale (e.g., ocean basin) spatial structuring (Stemmann et al., 2008). Costello et al. (2017) also found that deep-sea and pelagic species often have broader ranges than coastal species, owing to relatively greater habitat homogeneity and the dominance of planktonic larval dispersal.

Many lanternfish species, such as *Diaphus effulgens*, *Lampanyctus festivus* and *Myctophum selenops*, were predicted to have circumglobal distributions but were generally absent from oxygen-minimum regions of the Pacific and Indian Oceans and high-latitude regions that are typically populated by specialist species (e.g., *Lampanyctus parvicauda*, *Nannobrachium idostogma* and *Electrona antarctica*). These ecoregions are characterized by either very low-oxygen conditions or powerful Circumpolar and Subarctic fronts (Sutton et al., 2017), suggesting that conditions within these regions require specific physiological adaptations (Childress & Seibel, 1998). Such distinct changes in water mass properties can limit species distributions (Angel, 1993; Sutton et al., 2017; Vecchione et al., 2015), and around these boundary regions, limits to species distributions are likely to be dependent on their physiological tolerances, the spatial

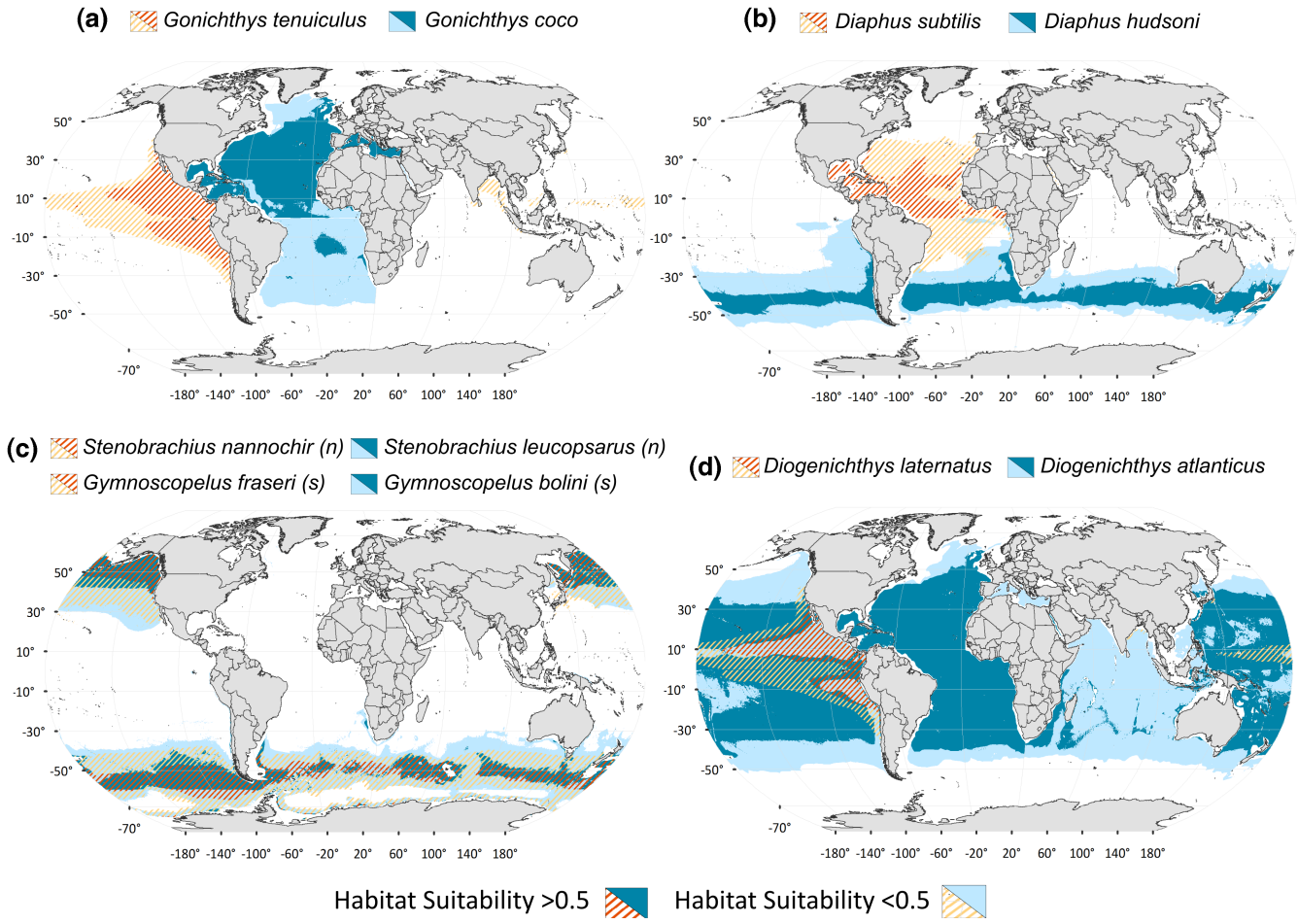

FIGURE 3 Examples of geographical overlap found among myctophid sister species. Sister species may be separated (a) between ocean basins or (b) within ocean basin, and may (c) have extensive spatial overlap or (d) occupy adjacent regions whilst overlapping at range edges. In panel (c), letters in parentheses indicate whether the species occurs in the southern (s) or northern (n) hemisphere.

gradient of environmental change, and the nature of the oceanographic features present.

In contrast, some of the most diverse ecoregions were found to be associated with boundary currents, such as the Benguela Upwelling, Humboldt Current and Agulhas Current. Similar patterns exist for Atlantic coastal fishes (Macpherson, 2002), oceanic species of predatory fishes, cetaceans, squid and euphausiids (Tittensor et al., 2010; Worm et al., 2003), pelagic cephalopods (Rosa et al., 2008) and foraminifera (Rutherford et al., 1999). Heightened diversity in these areas might be attributable to the fact that, in productive regions, the thermal structure of the near-surface ocean increases vertical niche availability (Rutherford et al., 1999) or that boundary currents act as ecotones, transitional zones between faunas of different origins (Beamish et al., 1999; Worm et al., 2003). For example, the Benguela Current contains both pseudo-oceanic and oceanic species owing to its proximity to the continental shelf (Hulley & Lutjeharms, 1989), and Olivar et al. (2017) found mesopelagic fish richness in the central Atlantic to peak in the Cape Blanc upwelling region (Mauritania/Cape Verde ecoregion) because these fauna contains relict populations of North Atlantic species, species of temperate and tropical origin, and endemic species.

From our findings, habitat suitability across multiple ecoregions is common and might be enhanced by boundary currents acting as transitional zones between assemblages. Separating the influences of temperature, primary productivity and habitat heterogeneity on lanternfish distributions, in addition to historical processes, is a necessary next step to determine how species–energy relationships function in the mesopelagic zone and how they each contribute to global biogeographical patterns.

4.2 | Phylogenetic insights into the geography of speciation

The potential dominance of sympatric and parapatric speciation in marine fishes has been speculated (Bowen et al., 2013; Norris, 2000; Palumbi, 1994), with perhaps the strongest evidence for these mechanisms coming from Pacific rockfishes (Ingram, 2011) and tropical reef fishes (Bowen et al., 2013). A negative relationship between species age and geographical overlap, as found by the present study, is expected when speciation is occurring in the face of gene flow

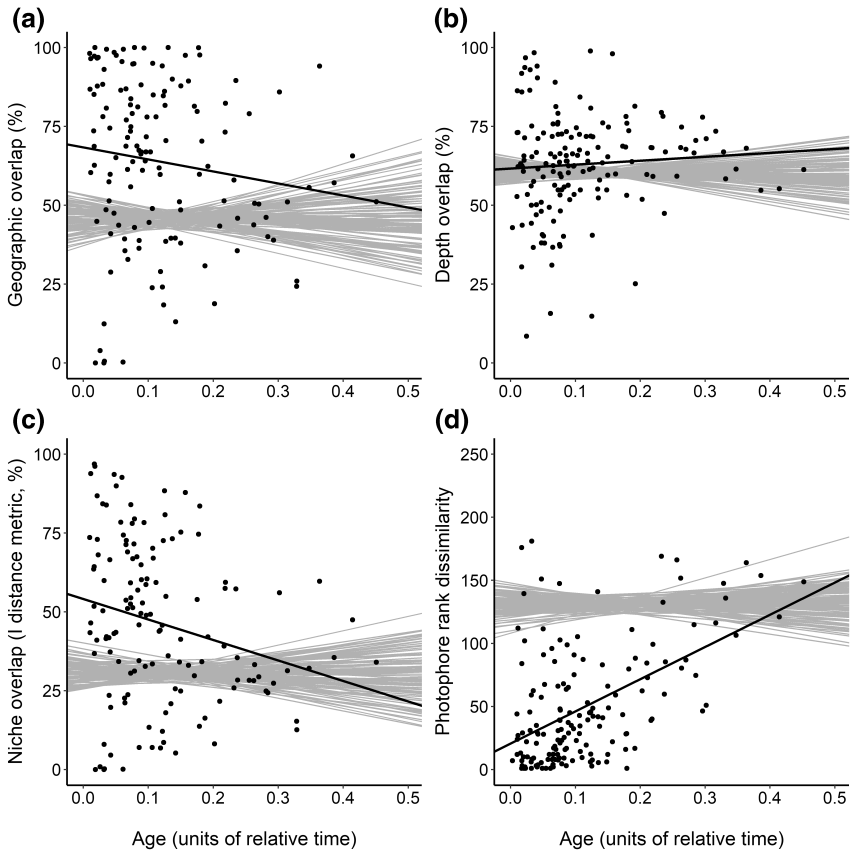

FIGURE 4 Associations between relative age of species divergence and trait overlap, for the following traits: (a) geographical overlap; (b) depth overlap; (c) ecological niche overlap; and (d) photophore pattern dissimilarity. Grey lines are the slopes of the 100 null model replicates, and black lines are the slopes of the empirical age-overlap regression. Points are the nodal values from the phylogenetic tree and overlap matrices. Empirical regression values are significantly different from null model expectations in (a) (intercept only) and in (c,d) (slope and intercept). This suggests that closely related species have greater geographical overlap, ecological niche overlap and photophore similarity than more distantly related species.

and in the absence of substantial geographical barriers to dispersal (Anacker & Strauss, 2014; Fitzpatrick & Turelli, 2006).

Thus, our results showing that closely related species have greater overlap in geographical range than expected by chance support the concept that speciation in the absence of geographical boundaries might have played a dominant role in the diversification of mesopelagic fishes on a global scale. Nevertheless, examples of geographically isolated sister species were also found. For example, the sister pair *Gonichthys cocco–Gonichthys tenuiculus* is a case where the closing of the Isthmus of Panama might have caused vicariant speciation. It is also possible that, as only 70% of myctophid species were included, some sister pairings could be missing and/or misassigned to others in their absence. The ENM outputs on which the geographical and niche overlap values depend are also subject to limitations and assumptions. Although we followed general guidelines for developing ENMs (Jarnevich et al., 2015; Merow et al., 2013), model outputs should be validated and improved continually, as future sampling and model iterations allow.

4.3 | Evidence of assortative mating via bioluminescent photophores

Examples of marine sympatric speciation are typically associated with divergent natural selection overwhelming the homogenizing effects of gene flow (Bowen et al., 2013), which can readily occur when selection acts on characters that directly facilitate assortative mating. For example, divergence in reproductive timing and breeding colours (Crow et al., 2010), body size (Jones et al., 2003) and sound production (Rocha et al., 2005) has potentially influenced mate choice, hence prezygotic reproductive isolation, in sympatric marine fishes. Contrary to previous research (Davis et al., 2014; Ellis & Oakley, 2016), we found no clear evidence that lateral photophore patterns are under strong divergent selection for more efficient conspecific mate-recognition purposes.

However, we found a strong positive association between lateral photophore pattern dissimilarity and phylogenetic age. This indicates a conserved functional role, such as in counter-illumination to disguise body silhouettes seen from below against remnant downwelling sunlight, in which case photophore position is likely to be determined largely by body shape (Denton & Adams, 2015; Haddock et al., 2010). Although located on the lateral flanks of the fish, the anatomy of myctophid non-ventral photophores could still result in the direction of light primarily downwards. However, anecdotal evidence suggests that photophore luminescence might vary in flash timing, pulse rate, intensity or colour (Paxton, 1972), and these additional signalling dimensions could increase differences between species, but such variables were not accounted for in the present study. Other luminous organs, including the headlight organs in *Diaphus* and *Gymnoscopelus* and the supra- and infracaudal organs of many genera, can be sexually dimorphic and are also speculated to be involved in signalling (Herring, 2007). Notably, Mensinger and Case (1990, 1997) observed significant differences in the caudal flash duration of three *Lampanyctus* species, two of which have

overlapping distributions and similar lateral photophore patterns. Future observational studies will enhance our knowledge of how these traits are used in intra- and interspecific communication and help us fully to appreciate any role of bioluminescence in the speciation process. Nevertheless, as a caveat, understanding the salience of any signal requires not only an appreciation of the signal properties, but also of the sensory system of the receiver. Testing for signals inherent in the spatial positioning of photophores, for instance, requires a clear understanding of the ability of the intended receiver to resolve the generated spatial signal visually.

4.4 | Ecologically based divergent selection

Ecological speciation is characterized by niche divergence among separating taxa, either in sympatry or along parapatric clines (Rundle & Nosil, 2005; Schluter, 2009). We found that many sister species pairs occupied adjacent habitats that are abiotically distinctive, such as oxygen-limited and non-oxygen-limited water masses (*Diogenichthys atlanticus–Diogenichthys laternatus*, *Triphoturus mexicanus–Triphoturus nigrescens* and *Diaphus thiollierei–Diaphus perspicillatus*), upwelling equatorial and oligotrophic gyre (*Diaphus schmidti–Diaphus signatus*), boreal and temperate-tropical regions (*Benthosema glaciale–Benthosema suborbital* and *Electrona carlsbergi–Electrona risso*) or between the California Current and Pacific Subarctic waters (*Protomyctophum crockeri–Protomyctophum thompsoni* and *Lampanyctus jordani–Nannobrachium ritteri*). In general, the ecological niche overlap of sister species was lower than their geographical overlap, often accompanied by pronounced differences in average temperature/O_2 niches, which might indicate adaptation to specific abiotic conditions, as has been found for tropical wrasses in adjacent habitats (Rocha et al., 2005). This is in line with the conclusions drawn by Denton (2018), who used a time-calibrated phylogenetic tree of myctophiformes to conclude that diversification patterns of this clade have overlapped with, and responded positively to, major oceanic perturbations, including anoxic events in the Cretaceous, the elimination of marine predators at the Cretaceous–Palaeogene boundary, and the onset of Northern Hemisphere glaciation. Key next steps in understanding niche divergence within this group will be in extending geographical and niche overlap estimates to include multiple resolutions (Cardillo & Warren, 2016), in addition to exploring the niche similarity and equivalency of individual sister species pairs (Warren et al., 2008).

Divergent selection could also be acting upon niche axes that were not considered in this study, for example in resource acquisition, reproductive habitat or the timing of reproduction, all of which are poorly known and seldom reported for deep-sea pelagic species. Recent studies have reported high morphofunctional variability in myctophid body and otolith shape (Tuset et al., 2018), jaw size (Martin & Davis, 2016) and dentition (Martin & Davis, 2020). Coupled with evidence of low overlap in the diet of sympatric species (Zavala-Munoz et al., 2019), these studies also suggest that co-existing lanternfishes can undergo niche differentiation by adapting morphologically and behaviourally to their environment. Obtaining comprehensive data on species traits, bioluminescent signal properties, vertical distributions and ecological niche characteristics might require the development of methods to observe midwater species behaviour, and the use of contemporary genomic techniques for dietary analysis, or for detection of species via environmental DNA. Together, these techniques might uncover the adaptations to local-scale environmental conditions and the mechanisms that have promoted speciation and maintained co-occurrence in this globally important group of fishes. Such methods will be important for building on the findings of the present study, which adds to the growing evidence that ecological speciation without physical barriers to genetic exchange might have an important role in generating marine species diversity.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Newly generated sequence data were archived on the NCBI GenBank nucleotide database under accessions MZ853123-MZ853141 (CO1) and OK181061-OK181106 (all other markers). Raster layers of environmental predictors are available from Satellite Geodesy (https://topex.ucsd.edu/WWW_html/srtm30_plus.html), World Ocean Atlas 2013 (www.nodc.noaa.gov/OC5/woa13/), Bio-ORACLE (www.bio-oracle.org/) and Marine Regions (www.marineregions.org). All other data generated during the study (e.g. species occurrence records and overlap/dissimilarity matrices) can be accessed at the following DOI: [https://doi.org/10.5281/zenodo.6903802].

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BIOSKETCH

Jennifer J. Freer is a postdoctoral researcher at the British Antarctic Survey. With a particular interest in pelagic and polar environments, her work applies ecological models to investigate the ecological and evolutionary processes driving species distributions and to help predict their response to environmental change.

SUPPORTING INFORMATION

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

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