Depth distributions of benthic and pelagic species highlight the potential of mesophotic and deep habitats to serve as marine refugia

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ABSTRACT: Shallow marine ecosystems are threatened by human impacts. The prospect that deeper environments could serve as refugia is promising but remains uncertain, as it has been evaluated primarily in benthic taxa and on small spatial scales. We use a dataset of all biota from the Gulf of Mexico to evaluate the degree to which species' occurrences extend across shallow (0–30 m), mesophotic (>30–150 m), and deep (>150 m) environments. High percentages of species inhabit multiple depth zones: 70% of benthic and 81% of pelagic species occurring in the mesophotic zone are also found in the shallow zone, and 45% of benthic and 80% of pelagic species found in the shallow zone extend into mesophotic depths. After accounting for confounding effects using logistic regression, pelagic species have significantly higher odds of extending between depth zones than benthic species. Analyses of species in adjacent 20 m depth bands reveal taxonomically distinct communities of benthic species from 0 to 100 m and pelagic species from 0 to 200 m. Peaks in probability distributions show that pelagic species generally have broader depth ranges than benthic species. Depth ranges that overlap between deeper and shallower zones show that movement of individuals or propagules in one or both directions between these habitats is either occurring now or has occurred in the past. Over the long term, deeper habitats can allow species to escape regional extirpation, and can contribute to the resilience and persistence of coastal ecosystems in the face of increased disturbance in shallow water. This is particularly true when pelagic species are considered.

KEY WORDS: Marine refugia · Mesophotic · Pelagic · Benthic · Gulf of Mexico

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1. INTRODUCTION

Shallow seas and coastal ecosystems across the globe are heavily impacted by human activities (Jackson et al. 2001, Hughes et al. 2003, Halpern et al. 2008, Mele et al. 2020). Thus, the potential of regions beneath shallow ecosystems to act as refugia has become of great research interest (Lesser et al. 2009, Keppel et al. 2012, MacDonald et al. 2016, Semmler et al. 2017, Bongaerts & Smith 2019). While still susceptible to disturbances (Slattery et al. 2011,

Appeldoorn et al. 2016, Smith et al. 2016, Pinheiro et al. 2019), these deeper regions (>30 m below sea level) are further removed from adverse environmental impacts than shallow habitats (Bak et al. 2005, Bridge & Guinotte 2013, Pérez-Rosales et al. 2021). This lends hope that deeper regions could contribute to the resilience and persistence of the broader ocean ecosystem, including damaged shallow environments such as coral reefs (Glynn et al. 1996, Riegl & Piller 2003, Bak et al. 2005, Bongaerts et al. 2010, Baker et al. 2016). Their ability to do so,

however, hinges upon the degree to which species can inhabit, and, over short or long periods, move between shallower (≤30 m) and deeper (>30 m) waters. The degree and direction of movement between contemporary shallow and deeper habitats varies among taxa and sites (Serrano et al. 2014, Bongaerts et al. 2017, Studivan & Voss 2018, Kramer et al. 2019), making it difficult to ascertain whether species in deeper habitats can repopulate damaged shallow ecosystems on short, ecological time scales. However, if the distribution of a species spans shallow and deeper habitats, then the species is capable of living in both habitats, and movement of individuals or propagules between habitats (in one or both directions) is either occurring now, has occurred relatively recently, or has previously occurred—even intermittently—over geological time frames. Further, species with broad depth ranges can escape regional extirpation when environmental disturbances occur in shallow water, potentially allowing them to recolonize formerly occupied habitats over time and facilitating the long-term persistence of shallow species and communities (Smith et al. 2014, Bongaerts & Smith 2019, Pérez-Rosales et al. 2021).

Despite great advances in our understanding of environments >30 m below sea level, uncertainty remains surrounding their biotic resemblance to shallower depths and thus their potential to serve as refugia. Much of this uncertainty concerns the biology of the mesophotic depth zone (30–150 m below sea level) (Lesser et al. 2009, Andradi-Brown et al. 2016, Baker et al. 2016, Holstein et al. 2016, Semmler et al. 2017, Kramer et al. 2019). On the one hand, these ecosystems have ecologically distinct features (Morais & Santos 2018, Rocha et al. 2018), harboring unique species (Kane et al. 2014, Semmler et al. 2017) with distinct morphologies (Hurley et al. 2016), dietary preferences (Fukunaga et al. 2016), reproductive outputs (Turner et al. 2018, Shlesinger & Loya 2019), and photophysiology (Kahng et al. 2014, 2017, 2019, Einbinder et al. 2016). On the other hand, they resemble shallower regions in many of their reef-associated species (Bongaerts et al. 2010, Muir et al. 2015, Hurley et al. 2016, Semmler et al. 2017). Consequently, we do not yet have a full understanding of the degree to which species utilize the range of ecological conditions that exist between shallow and mesophotic environments.

The uncertainty as to how biotically unique deeper (>30 m below sea level) environments are exists at least in part because, despite recent advances in the geographic scale of our understanding of them (Loya et al. 2019), our knowledge of them often stems from studies of specific localities or taxa (Bridge et al. 2012, Bridge & Guinotte 2013, Bongaerts et al. 2015, Fukunaga et al. 2016, Hurley et al. 2016, Rosa et al. 2016, Asher et al. 2017, Reed et al. 2018, Turner et al. 2018, Laxmilatha et al. 2019, Quimpo et al. 2019). Furthermore, most studies focus only on benthic habitats (Bongaerts et al. 2015, Dumalagan et al. 2019, Laxmilatha et al. 2019) and do not include pelagic species. Spending most of their life cycle (except for larval stages) on or near the ocean floor, benthic taxa include sessile corals, sponges, bryozoans, macroalgae, and seagrasses, as well as motile annelids, mollusks, crustaceans, echinoderms, and fishes that do not venture high into the water column as adults (Semmler et al. 2017). Although many fishes and some invertebrates that spend most of their time near but above the ocean floor can be considered 'supra-benthic,' all 'benthic' and 'supra-benthic' species are referred to herein as 'benthic' for brevity. Their distributional ecology differs from their pelagic counterparts, which are open-ocean species (holoplankton, nekton) that spend their entire life in the water column and often are widely distributed, but frequently are ecologically coupled with benthic communities (Angel 1993, Norris 2000, Costa et al. 2012, Griffiths et al. 2017). Pelagic species thus are important components of marine communities from the coast to the continental slope and abyssal zones, making their inclusion essential in studies of the distributions of biota across depth.

Here, we add new perspective to assessments of the potential of marine ecosystems beneath shallow waters to serve as refugia by analyzing the distributional ecology of both benthic and pelagic marine biota across an entire ocean basin. Specifically, we studied all species with documented depth and geographic distributions occurring in the Gulf of Mexico (GoMx), a well-defined, biodiverse basin rich in both benthic and pelagic species (Felder & Camp 2009, Brenner et al. 2010). We asked the following questions. (1) Overall, how expansive are the distributions of benthic and pelagic species across depth? We investigated the degree to which species extend from one to other depth zones, the vertical extents of benthic versus pelagic communities, and the total breadths of depth ranges for benthic and pelagic communities. This information is not generally known except in a few taxa. These results would help elucidate whether species assemblages can persist in potential areas of refuge when part of their range suffers disturbances in the short term, and whether biota from deeper water can potentially replenish communities in shallower damaged habi-

tats over the long term. (2) How do the distributions of under-studied pelagic species compare with those of more thoroughly investigated benthic species? We predicted that the distributions of pelagic species would be considerably more extensive than those of benthic species, as pelagic species are capable of great motility and spend their entire life in the water column (Angel 1993, Norris 2000, Costa et al. 2012). Previous work has demonstrated the long-term potential for mesophotic habitats to serve as refuge areas in the GoMx for benthic species alone (Semmler et al. 2017). That potential could be even greater if pelagic species generally exhibit more expansive ranges than benthic species. Then, more taxa than previously thought (i.e. than when only considering benthic taxa) could persist in refuge areas, and the hypothesis that deep environments can serve as marine refugia would be strengthened.

We analyzed these questions first by calculating the percentages of benthic and pelagic species that occur in, and extend between, shallow, mesophotic, and deep (below the mesophotic) zones. Then, in a series of logistic regression models, we compared the odds that pelagic species extend between zones to those of benthic species after accounting for confounding variables, including geographic distribution and endemism in the GoMx, taxonomic identity, and the numbers of species in each group. Further, we analyzed species occurrences across 20 m bands of depth to investigate the vertical extents and cohesiveness of benthic and pelagic communities over depth. Finally, we analyzed the frequencies and resulting probability distributions of the breadths of depth ranges for pelagic versus benthic species across depth.

2. MATERIALS AND METHODS

2.1. Data source

We conducted this study by organizing and statistically analyzing a large and taxonomically rigorous database that was derived and updated from a comprehensive re-analysis of the biodiversity of the GoMx (Felder & Camp 2009, Brenner et al. 2010, Moretzsohn et al. 2015, Semmler et al. 2017). The original database (Biodiversity of the Gulf of Mexico, or BioGoMx) was compiled between 2004 and 2009 by 140 leading taxonomists from 15 nations who documented all biota known for the GoMx using field observations; specimens archived in museums, research institutes, and private collections; and the

published literature (Felder & Camp 2009). BioGoMx includes all species observed from tidal wetlands and coastal waters to the abyssal plain, an area that covers a surface area of ~1.5 million square kilometers from 18°08'N to 30°40'N and 97°50'W to 80°26'W and incorporates partial coastlines of Cuba, Mexico, and the USA (TX, LA, FL, AL, and MS; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m700p039_supp.pdf) (Felder & Camp 2009). Horizontal species distributions were based on presence or absence of species in different octants of the GoMx (Felder & Camp 2009), and vertical distributions were based on minimum and maximum depths of species' occurrences. In most cases, the reported distributions were based on actual specimens observed in the GoMx. However, if such data were not available for a particular species, contributing taxonomists produced reliable estimations using known depth distributions of the species in other regions and their own expert knowledge of the taxon (Moretzsohn et al. 2015). In addition to taxonomic and distributional characteristics, the experts summarized the available information on the biological, ecological, and life-history traits of each species in the GoMx.

We obtained the BioGoMx data from GulfBase (https://www.gulfbase.org/project/biodiversity-gulf-mexico-biogomx-database), where it is maintained as a public database by Texas A&M University (Brenner et al. 2010). The database that we analyzed contains records for 16 023 species based on our most recent compilation in February 2020. Our analyses focused on the 12 291 of those species for which a depth range was recorded, as well as the attributes of species included in the database. Those attributes were as follows: species' taxonomic information, habitat and life-history characteristics, vertical depth ranges, occurrences in different geographic octants of the GoMx, and endemism, or lack thereof, to the GoMx. Of the 12 291 species, 27 exhibited maximum depths that exceeded 5203 m, the deepest depth in the GoMx (Broadus et al. 2022), because their vertical ranges were derived from their known distributions in other regions (see paragraph above). We set the maximum depths of these 27 species to 5203 m to reflect their likely distributions in the GoMx itself.

In analyzing species' vertical depth ranges, we divided the GoMx into 3 depth zones: shallow, mesophotic, and deep. The shallow depth zone extends from 9 m above mean sea level to 30 m below. It includes intertidal species that are found above mean sea level, such as the gastropods *Cenchritis muricata* and *Nerita versicolor*. The mesophotic zone

ranges from >30 m to 150 m, and the deep zone includes all waters below 150 m. Although recognizing that the extent of the mesophotic zone varies somewhat according to local oceanographic conditions (Baker et al. 2016), these designations stem from the general consensus that mesophotic coral ecosystems occur approximately 30–150 m below sea level, representing a region that is exposed to unique levels of light and other abiotic conditions (Kahng et al. 2010, Bridge & Guinotte 2013, Andradi-Brown et al. 2016, Asher et al. 2017, Loya et al. 2019).

2.2. Descriptive analysis of the depth ranges of species

We calculated the total numbers and percentages of the 12 291 species occurring within and across depth zones, using separate calculations for benthic and pelagic groups of species. To accomplish this, we designated each species as 'benthic' if the major portion of its life history is constrained to or near the ocean floor, or 'pelagic' if the major part or all of its life history occurs in the water column. We made those designations based upon each species' habitat and life-history characteristics that were documented by taxonomic experts for each taxon treated in Felder & Camp (2009) and in subsequent compilations, including our own knowledge and documentation. Species described in BioGoMx using any of the following keywords were considered pelagic: 'surface', 'epipelagic', 'coastal surface and epipelagic' or 'cep', 'nektonic' or 'nek', 'neustonic' or 'neu', 'oceanic', 'oceanic surface and epipelagic' or 'osp', 'pleustonic' or 'ple', 'pelagic' or 'plg', 'planktonic' or 'plk', or 'holoplanktonic'. All other species with depth and life-history data were considered benthic. With these designations made, we calculated the number and percentage of all benthic and, separately, all pelagic species that occur in each depth zone. For the benthic versus pelagic species that occur in each zone, we calculated the number and percentage of those species whose distributions extend into each of the other 2 zones.

2.3. Regression analysis of the depth ranges of species

We used a logistic regression approach to analyze benthic versus pelagic species' distributions across depth zones. Logistic regression is a powerful tool for comparing the depth ranges of benthic versus pelagic taxa while accounting for potential confounding variables that may also influence distributional patterns. A full description of our approach, including the mathematics underlying the logistic regression model, is available in Section S1 in the Supplement. Here, we provide a summary.

We used Harrell's 'rms' package in R v3.6.1 (R Core Team 2019, Harrell 2021) to optimize 6 logistic regression models. Each model addressed whether, for the species that occur in a given depth zone, the benthic versus pelagic lifestyle of those species influences whether their occurrences extend into one of the other 2 zones. In so doing, each model accounted for confounding variables, namely, species' taxonomic affiliations, minimum and maximum depths of vertical range, occurrences in different geographic octants of the GoMx, and endemism (or lack thereof) to the GoMx. These confounders were included in each model as independent variables, in addition to species' benthic or pelagic lifestyle. Independent variables were used to predict each model's dependent variable: a dichotomous outcome denoting whether or not each species extends into another depth zone. We obtained the odds ratio and associated p-value pertaining to species lifestyle from each model. An odds ratio >1 means that, among the species that occur in a given depth zone, the odds of a pelagic species extending into one of the other 2 zones is greater than the corresponding odds of a benthic species exhibiting that extension. Further, we plotted model-derived probabilities that benthic versus pelagic species occurring in one depth zone extend into another across varying minimum or maximum depths of species. To assess the goodness-of-fit for each model, we recorded its *C*-statistic and Brier score, and plotted its reliability diagram. A more robust model exhibits a *C*-statistic close to 1, a Brier score close to 0, and a reliability diagram in which its fitted curve resembles a line with a slope of 1 and a *y*-intercept of 0.

2.4. Analysis of the extents of communities across depth

We assessed the vertical extents and cohesiveness of benthic versus pelagic communities to determine whether they extend across depth zones. We divided the GoMx into 20 m depth bands, designating non-overlapping bands of 0–20, >20–40, >40–60 m, etc., to the abyssal floor of the GoMx. Using species' minimum and maximum depths of occurrence, we determined which species do and do not occur in

each depth band. We then used the 'vegan' package in R (Oksanen et al. 2019) to produce a matrix in which the off-diagonal elements store the Jaccard distances between all pairs of depth bands. The Jaccard distance between a pair of depth bands describes the dissimilarity in their community compositions. It is measured as 1 − (number of species that occur in both depth bands / total number of unique species found in the bands combined) (Semmler et al. 2017).

We employed hierarchical clustering to assemble depth bands into groups, where each group represents a taxonomically distinct ecological community. We first produced a clustering tree similar in structure to a phylogenetic tree, depicting how closely or distantly 'related' depth bands are in terms of their Jaccard distances from each other. The tree yielded an agglomerative coefficient close to 1, indicating that it exhibits a robust clustering structure (Kaufman & Rousseeuw 1990). To determine the optimal number of clusters to extract from the clustering tree, we used the silhouette method, a robust metric of the tightness and separation of clusters across space (Rousseeuw 1987) that can be applied to Jaccard distances.

With the clusters of depth bands formed, we performed permutational multivariate ANOVA (PERMANOVA), permutational analyses of multivariate dispersions (PERMDISP), and similarity percentages (SIMPER) to analyze differences in community structure among depths, and we produced non-metric multidimensional scaling (NMDS) ordinations to visualize the clusters. PERMANOVA is a permutation-based approach to MANOVA. It assesses whether clusters differ from each other in terms of the positions and/or dispersions of their depth bands in Jaccard distance space, and thus whether clusters represent taxonomically distinct communities with unique assemblage structures. PERMDISP more specifically determines whether pairs of clusters differ in the dispersions of their depth bands, and thus whether species turnover (i.e. the degree of taxonomic differences — see method of constructing Jaccard distances in the first paragraph of this subsection) is greater across the depth bands of one cluster compared to those of another. SIMPER ranks species by their contributions to the transitions that occur in the composition of communities across clusters. Finally, NMDS displays the Jaccard distances between depth bands in a 2-dimensional coordinate system. It can be used to visualize how relatively close or far clusters of depth bands are to each other in terms of Jaccard distances. The NMDS stress value is the degree to which the 2-dimensional distances between bands

preserve their original Jaccard distances, where a value < 0.2 denotes better preservation. We performed all 4 methods using the 'vegan' package in R (Oksanen et al. 2019), and we repeated this procedure for all, for only benthic, and for only pelagic species.

2.5. Analysis of breadths of depth range of species

To assess the degree of depth specialization of benthic versus pelagic species within the 3 depth zones, we analyzed the probability distributions of breadths of depth range (BDR) for all benthic, and separately pelagic, species. For each species, we calculated BDR as the species' maximum depth minus its minimum depth of occurrence, and subsequently categorized those calculations into 6 groups, based on each species' benthic versus pelagic lifestyle and occurrence in the 3 depth zones. For the species occurring in each zone, we visualized the distributions of their BDRs by creating probability density functions (PDFs), one for benthic and one for pelagic species in each of the 3 zones. While similar to frequency distributions, PDFs provide the probability that a certain BDR value is realized, thus showing more clearly which outcomes are expected. We produced all PDFs with a bandwidth parameter of 0.5. The bandwidth parameter, when closer to 0, leads to a PDF that captures finer detail, while a bandwidth parameter further from 0 leads to a PDF that is smoother and captures the general shape of the probability distribution. A parameter value of 0.5 balances these two extremes, and ensures that all PDFs are comparable. We visually assessed the magnitude of overlap between benthic and pelagic PDFs for each depth zone. We produced all PDFs and performed all analyses for this study in R v3.6.1 (R Core Team 2019).

3. RESULTS

3.1. Benthic and especially pelagic species occur across multiple depth zones

Among all species in the GoMx and especially among those that are pelagic, many occur in multiple depth zones and extend from shallow to deep depths. Numbers of benthic species decrease with depth (Table 1a), whereas numbers of pelagic species remain relatively even across depth zones and increase slightly in deeper water (Table 1e). Close to 45% of benthic species that occur in the shallow zone also occur in mesophotic depths (Table 1c), while nearly 70%

Table 1. Distributions and extensions of benthic and pelagic species across depth zones. Percentages in (a) and (e) refer to the percentages of total benthic or pelagic species occurring in each depth zone. For example, 7515 out of 10 460 total benthic species occur in the shallow zone (71.8%). All other percentages refer to the percentages of total benthic or pelagic species occurring in each zone that extend into other zones. For example, 3364 out of 7515 benthic species found in the shallow zone extend into the mesophotic zone (44.8%). Percentages in rows do not sum to 100% because many species extend to multiple depth zones. Meso = mesophotic. Percentages are rounded in the text for brevity

	Shallow zone (0–30 m)	Mesophotic zone (>30–150 m)	Deep zone (>150 m)
Benthic species			
(a) Total no. of species (10 460)	7515 (71.8%)	4821 (46.1%)	3514 (33.6%)
(b) No. extending into shallow zone	–	Meso to shallow: 3364 (69.8%)	Deep to shallow: 1116 (31.8%)
(c) No. extending into mesophotic zone	Shallow to meso: 3364 (44.8%)	–	Deep to meso: 2027 (57.7%)
(d) No. extending into deep zone	Shallow to deep: 1116 (14.9%)	Meso to deep: 2027 (42.0%)	–
Pelagic species			
(e) Total no. of species (1831)	1178 (63.3%)	1157 (63.2%)	1297 (70.8%)
(f) No. extending into shallow zone	–	Meso to shallow: 940 (81.2%)	Deep to shallow: 665 (51.3%)
(g) No. extending into mesophotic zone	Shallow to meso: 940 (79.8%)	–	Deep to meso: 862 (66.5%)
(h) No. extending into deep zone	Shallow to deep: 665 (56.5%)	Meso to deep: 862 (74.5%)	–

of benthic species that occur in the mesophotic zone extend into shallow water (Table 1b). Corresponding percentages in pelagic species are higher and more equivalent: 80% of species that occur in the shallow zone extend into the mesophotic (Table 1g) and 81% of mesophotic species extend into shallow water (Table 1f). In both benthic and pelagic species, the extensions of those that are found in the mesophotic into the shallow zone represent the highest percentages of extension (70% and 81%, respectively; Table 1b,f).

Of species occurring in the shallow zone, only 15% of benthic but 57% of pelagic species range all the way to the deep zone (Table 1d,h). Similarly, a smaller percentage of deep benthic than pelagic species range all the way to the shallow zone (32% versus 51%; Table 1b,f). Among benthic and pelagic species found in the mesophotic zone, 42% and 75%, respectively, extend into deep habitats (Table 1d,h), while more than half of benthic and pelagic species occurring in those deep habitats are found in mesophotic waters as well (58% and 67%, respectively; Table 1c,g). These data demonstrate the prevalence of species, especially pelagic ones, that occur across multiple depth zones.

3.2. Pelagic species have more expansive ranges than benthic species

Whether species' depth distributions extend across depth zones is significantly associated with their benthic versus pelagic lifestyles (logistic regression; p < 0.05; Table 2), albeit to differing degrees for different types of depth range extensions. For all combinations of such extensions, the odds that a given pelagic species occurring in a given depth zone (rel-

Table 2. Ratios of the odds of pelagic versus benthic species extending across depth zones. Each dichotomous dependent variable was tested for an association with the benthic versus pelagic lifestyle of species after accounting for confounders (see Section S1 in the Supplement, www.int-res.com/articles/suppl/m700p039_supp.pdf). An odds ratio >1 signals that, among only the species occurring in a given depth zone, the odds that a pelagic species extends into another zone (relative to the total number of pelagic species) is higher than the corresponding odds for benthic species. A p-value <0.05 indicates that the associated odds ratio differs significantly from 1

Dependent variable	Odds ratio (95% CI)	p
Extension or non-extension of species that occur in the:		
(a) Shallow zone into the mesophotic zone	5.47 (4.48 – 6.67)	<0.001
(b) Shallow zone into the deep zone	11.26 (9.54 – 13.28)	<0.001
(c) Mesophotic zone into the deep zone	5.79 (4.48 – 7.47)	<0.001
(d) Mesophotic zone into the shallow zone	4.49 (2.67 – 7.56)	0.021
(e) Deep zone into the shallow zone	2.03 (1.53 – 2.70)	<0.001
(f) Deep zone into the mesophotic zone	1.17 (0.87 – 1.56)	0.006

ative to the total number of pelagic species in that zone) extends into another zone is greater than the corresponding odds for benthic species after accounting for confounding variables in logistic regression (all odds ratios >1; Table 2). However, this disparity between pelagic versus benthic species is lowest for species occurring in the deep habitat, since their associated odds ratios are closest to 1 (Table 2e,f). In particular, the odds that a pelagic species found in the deep zone is also found in the mesophotic zone is almost equal to the corresponding odds for benthic species (odds ratio = 1.17; Table 2f). By contrast, the disparity between pelagic versus benthic species is much greater in both mesophotic and shallow habitats, since odds ratios for those depth zones are further from 1 (Table 2a–d).

Most notably, the odds that a pelagic species occurring in the shallow zone exhibits a range that extends all the way to the deep zone is >11 times higher than that for benthic species (Table 2b). In summary, the depth distributions of pelagic species have significantly greater tendencies to extend across depth zones compared to those of benthic species, an asymmetry particularly pronounced in shallower habitats compared to deep environments.

The greater tendencies of pelagic species found in one depth zone to also occur in another is also evident from their probabilities of extension across depth zones for different minimum and maximum depths (Fig. 1). These probabilities are derived from each logistic regression model depicted in each row of Table 2. Across different minimum or maximum
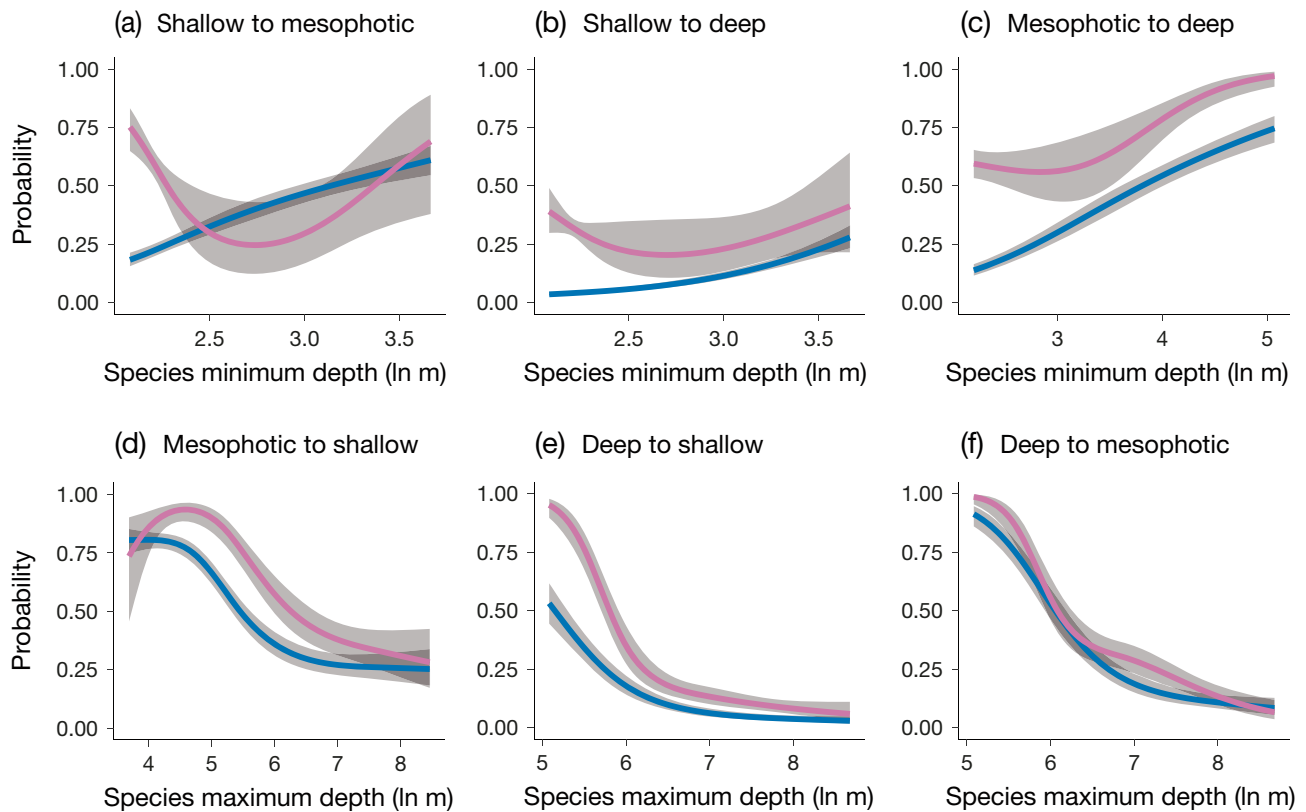

Fig. 1. Trends in benthic versus pelagic species' probabilities of extension across depth zones for different minimum or maximum depths of species' occurrences. Plots address extensions from (a) shallow to mesophotic, (b) shallow to deep, (c) mesophotic to deep, (d) mesophotic to shallow, (e) deep to shallow, and (f) deep to mesophotic zones. Values for depths of occurrence on the *x*-axes are natural log transformed as they are not normally distributed. Blue and pink curves refer to benthic and pelagic species, respectively, and grey areas provide 95% confidence limits. Plots addressing models of extensions of species that occur in shallower zones into deeper zones (a–c) focus only on minimum depths of species, because maximum depths are inappropriate predictors of each model's extension/non-extension outcome variable. Maximum depths are used to calculate whether a species occurring in a shallower zone extends into a deeper zone and thus have a direct relationship with each model's outcome variable. Their inclusion in these models would produce artificially high coefficients relating maximum depths and the outcomes. This would artificially reduce the relationship of the other predictors to the outcome, making the models less informative. The opposite is true for plots addressing models of extensions of depth ranges from deeper zones into shallower zones (d–f), so these employ only maximum depths of species

depths, pelagic species generally have an equal or higher probability of extending across depth zones compared to benthic species for 5 of the 6 possible extensions (Fig. 1b–f); this is most pronounced where species occurring in the mesophotic zone exhibit depth ranges that extend into deep habitats (Fig. 1c). The only major exception to this general pattern is in the extensions of species found in the shallow zone into the mesophotic, where benthic species with intermediate minimum depths have a slightly higher probability of extending into the mesophotic zone than pelagic species (mid-region of Fig. 1a). Extensions of depth ranges into shallower depths, e.g. from the mesophotic into the shallow zone (Fig. 1d) and from deep into shallow water (Fig. 1e), are more probable for pelagic than benthic species over most maximum depths of species, especially at shallower depths. There is, however, considerable overlap between pelagic and benthic species found in the deep zone in their probabilities of extension into mesophotic habitats (Fig. 1f) across most maximum depths. Thus, pelagic species generally have greater probabilities of extension across depth zones, albeit not in all cases. Additionally, the probabilities of extension of all species from shallower into deeper zones generally increase with increasing minimum depth (Fig. 1a–c), whereas from deeper into shallower zones, they decrease with increasing maximum depth (Fig. 1d–f).

The outcomes shown in Table 2 and Fig. 1 are validated by the robust predictive performance of all logistic regression models optimized. *C*-statistics and Brier scores for all models were >0.75 and <0.2, respectively, on a scale of 0–1, where a *C*-statistic closer to 1 and a Brier score closer to 0 signal greater predictive abilities of a given model (Table S1). Further, reliability diagrams of all models revealed consistent overlap between predicted and actual values related to each model's outcome variable (see Section S1 and Fig. S2).

3.3. Communities of benthic and pelagic species extend across depth zones

When considering all species, clusters of 20 m bands of depth (i.e. taxonomically distinct communities) exist at 0–100, 100–200, 200–380, 380–600, 600–1000 m, and at 10 additional depth ranges beyond 1000 m (Fig. 2a). Within benthic species alone, these clusters occur at 0–100, 100–200, 200–380, 380–740, 740–1180 m, and at 11 deeper depth ranges (Fig. 2b). Within pelagic species, clusters exist at 0–200, 200–

500, 500–1000 m, and at 6 deeper depth ranges (Fig. 2c). All 3 visualizations of clusters in Fig. 2 exhibit a stress value of ≤0.02, indicating that they largely preserve the original Jaccard distances
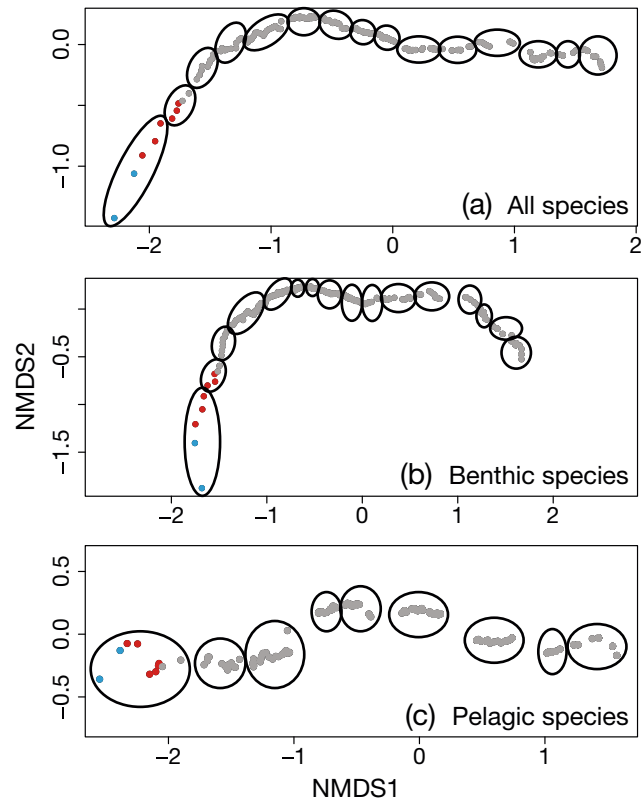

Fig. 2. Non-metric multidimensional scaling (NMDS) plots depicting clusters of taxonomically distinct communities across depth. Plots represent clusters of 20 m bands of depth, where each data point represents a depth band, when considering (a) all species together, as well as (b) benthic and (c) pelagic species alone. NMDS displays the Jaccard distances between depth bands, where a greater distance between 2 depth bands means that they are less similar in their component species than 2 depth bands in closer proximity. Ellipses encompass clusters of depth bands, where the degree of species turnover among depth bands within clusters is lower than the turnover among depth bands between clusters. Data points are colored based on the depth zone within which their upper depth boundary occurs (e.g. the 20–40 m depth band is associated with the shallow zone), where blue = shallow, red = mesophotic, and grey = deep. In this case, depth bands are generally ordered sequentially from the left (shallower) to the right (deeper) of the first NMDS axis. The shallowest (furthest left) cluster of depth bands encompasses 0–100 m for all species (a) and for benthic species (b), and includes 0–200 m for pelagic species (c). Distinct taxonomic clusters occur on the lower continental shelf/upper continental slope (100–200, 200–380, and 380–740 m) for benthic species (b) and on the upper continental slope (200–500 m and 500–1000 m) for pelagic species (c). Many unique taxonomic assemblages are found across the remainder of the bathyal and abyssal depths of the Gulf of Mexico (GoMx)

between clusters and their component depth bands. Clusters in Fig. 2a,b are largely contiguous, indicating that among all species, and within benthic species alone, the structure of communities exhibits change that is less abrupt as depth increases. Conversely, clusters in Fig. 2c are more isolated, denoting changes that are more abrupt in the structure of pelagic communities across depth. In all cases, the clusters explain a high proportion of the variance in the Jaccard distances between depth bands (PERMANOVA; $p < 0.05$, $R^2 = 0.96$ for all species, 0.95 within benthic species, and 0.95 within pelagic species). Further, the shallowest clusters (0–100 m among all species and benthic species, 0–200 m among pelagic species) are notable for the relatively high dispersion of their depth bands (PERMDISP; $p < 0.05$ for 35 of 37 pair-wise comparisons; Fig. 2, left-most clusters). This indicates that adjacent depth bands in shallower waters exhibit greater differences in their taxonomic compositions than adjacent depth bands in deeper zones. Although there is a generally consistent pattern of change in community structure across depth (i.e. along one NMDS axis), the more surprising and evolutionarily interesting result is the large number of clusters that occur all across the deeper environments in both benthic and pelagic species.

Based on the SIMPER analysis of all species, a diversity of taxa contributes to community transitions across depth. Benthic species are primarily responsible for community transitions occurring across the shallow, mesophotic, and deep zones, but pelagic species play an increasingly important role in community transitions in deeper water. From the shallow to the mesophotic zone, the primary contributors to community transitions are benthic mollusks, crustaceans, and chordates (e.g. the gastropod *Conus arangoi*, the majid decapod crab *Tyche emarginata*, and the scarid actinopterygian *Scarus iseri*). From the mesophotic to the deep zone, the primary contributors are benthic mollusks and crustaceans (e.g. the gastropod *Olivella mutica* and the stomatopod mantis shrimp *Squilla empusa*), as well as pelagic ciliophoran protistans (e.g. the spirotrich *Metacylis conica*). The taxa that contribute most to differences in community composition between 0–100 m and 100–200 m (the first 2 clusters) are benthic mollusks, crustaceans, and chordates (e.g. the gastropod *Lodderena pulchella*, the copepod *Cletodes macrura*, and the balistid actinopterygian triggerfish *Balistes vetula*), as was the case between the shallow and mesophotic zones. These same 3 taxonomic groups are also primary contributors in deeper waters, e.g. between 600–1000 m and 1000–1480 m, although

their associated species are more often pelagic than benthic (e.g. the cephalopod squid *Histioteuthis corona*, the hyperiid amphipod *Vibilia stebbingi*, and the barbourisiid actinopterygian whalefish *Barbourisia rufa*).

3.4. BDR changes across depth for benthic versus pelagic species

Several trends exist across a depth gradient for BDRs, or the difference between species' maximum and minimum depths of occurrence. These trends emerge from PDFs of the BDRs of benthic versus pelagic species occurring within each depth zone. First, a broader range of BDRs exists among all benthic and all pelagic species in shallower than in deeper zones (Fig. 3). Second, in shallow water, the total range of BDR values is equivalent in benthic and pelagic species, but the shapes of their PDFs differ (Fig. 3a). A large proportion of benthic species have very narrow to moderately narrow BDRs, while a large proportion of pelagic species have wider BDRs, such that BDRs are generally wider in pelagic than in benthic species in the shallow zone (Fig. 3a).
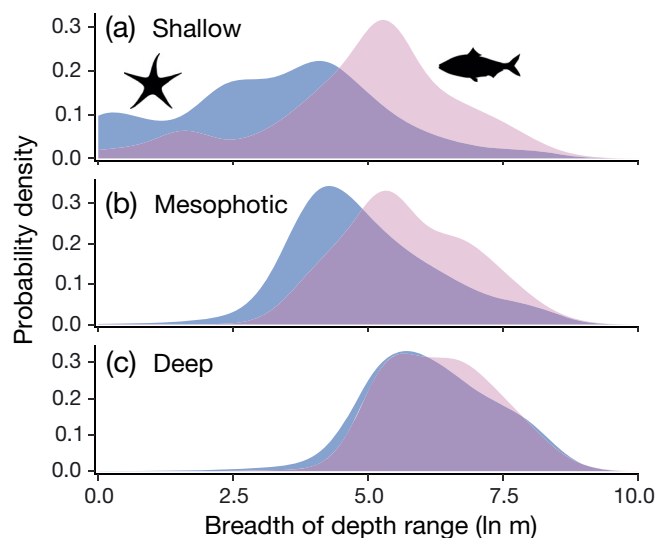

Fig. 3. Probability density functions (PDFs) of the breadths of depth range (BDRs) of benthic versus pelagic species occurring in the 3 depth zones. BDR refers to the difference between the maximum and minimum depth of occurrence of a species. We constructed the distributions of the BDRs of all species in the (a) shallow, (b) mesophotic, and (c) deep zones with a bandwidth parameter of 0.5 to provide consistency across all distributions (see Materials and Methods Section 2.5 for an explanation of this parameter). BDR values are natural log transformed as they are not normally distributed. Blue and pink PDFs refer to benthic and pelagic species (represented by a seastar and a fish), respectively

Third, among species occurring in mesophotic habitats (Fig. 3b), the shapes of the PDFs for benthic and pelagic species are generally similar to those in shallow habitats, with peaks at similar breadths, but, unlike shallow habitats, many fewer species with narrow BDRs exist, particularly among benthic species (Fig. 3a versus b). Finally, the BDRs of benthic versus pelagic species increasingly overlap as one progresses from shallower into deeper water, until in deep water (Fig. 3c) the PDFs of benthic and pelagic species are almost completely congruent.

4. DISCUSSION

Marine species occurring throughout the GoMX, especially those that are pelagic, exhibit extensive depth ranges that encompass multiple depth zones. For instance, 70% of benthic and 81% of pelagic species that are found in the mesophotic zone extend upward into shallow depths (Table 1). Further, a taxonomically distinct pelagic community extends across the shallow, mesophotic, and deep zones from 0 to 200 m (Fig. 2c). Overall, then, there is considerable potential for species to occur and move between habitats at different depths over the long term. Understandably, there is a lower incidence of range connection between shallow and deep habitats, particularly among benthic species. Of species occurring in the shallow zone, the depth ranges of only 15% of benthic species but 57% of pelagic species extend all the way into deep habitats, while 32% of deep benthic species and 51% of deep pelagic species reach all the way into shallow depths (Table 1).

A few patterns are visible in the extensions of depth ranges depicted in Table 1. (1) The percentages of extensions from deeper into shallower water are always higher than those from shallower into deeper water, reflecting the greater dominance of depth specialists in progressively shallower water, especially in benthic species. Thus, it is important to record the origin of the species pool from which the percentage overlap is derived to make comparisons of the magnitude of overlap between shallow and mesophotic depths among studies. (2) These reciprocal relationships (e.g. from shallow to deep versus deep to shallow) are much more equivalent in pelagic species than they are in benthic species, suggesting much greater vertical movement in pelagic than benthic species over the long term. For example, the depth ranges of 80% of shallow pelagic species extend into the mesophotic zone and 81% of mesophotic pelagic species extend into the shallow zone; however, the depth ranges of only 45% of shallow benthic species extend into mesophotic depths, but the depth ranges of 70% of mesophotic benthic species extend into shallow water (Table 1). (3) In every one of the 12 types of depth zone extensions, pelagic species have a higher incidence of extension into other depth zones than benthic species. This provides a preliminary answer to our second question regarding how the distributions of the less studied pelagic species compare to those of more thoroughly investigated benthic species.

Although a number of studies have evaluated the overlap between depth zones relative to total number of species considered rather than the number of species present in each habitat, we sought to highlight the potential of species within each habitat to also occur in other depth regions. Nevertheless, our results are of similar magnitude to those found in other studies of depth distributions for benthic biota. Bridge et al. (2013) reported that 77 and 40% of Caribbean and Indo-Pacific coral species, respectively, extend from shallow into mesophotic depths (>30 m), and Muir et al. (2015) found that 43% of shallow staghorn coral in northeastern Australia extended into the mesophotic zone. In the southwestern GoMx, visual inspection of data in Fig. 2a,c of Quiroz-Martínez et al. (2022) suggests that the depth ranges of a large proportion of the species of polychaete annelids on the southwestern shelf (259 species) and those inhabiting carbonate substrates (234 species) extend from shallow (≤30 m) into mesophotic (>30–150 m) depths, and that the depth distributions of a considerably smaller proportion of species from these areas extend from shallow to deep (>150 m) water. In the eastern GoMX, 52 out of the 86 fish species (60.5%) that occur in the mesophotic environments of Pulley Ridge are also found in the shallow water reefs of the Florida Keys (Reed et al. 2019, Sponaugle & Cowen 2019).

Inclusion of pelagic species is one of the keys to understanding the overall potential for deep-water refugia to enhance the persistence of damaged shallow ecosystems. It is understandable that pelagic species have been given less focus than benthic species in prior studies of marine refugia since benthic species are more diverse than pelagic species globally (Angel 1993, Norris 2000), as they are in the GoMx (Table 1a,e). Benthic species also are the main components of some of the most widely recognized ecosystems on earth (Duarte et al. 2008), such as coral reefs, which are concentrated in relatively accessible shallow environments (Table 1a) where human activities occur. Pelagic species, by con-

trast, are more evenly spread across a wide range of depths (Table 1e), often in relatively inaccessible regions of the world's oceans (Angel 1993, Norris 2000). However, pelagic species are nonetheless critical components of marine environments. They help shape marine food webs and nutrient flows (Roman et al. 2014), and comprise important fisheries (Tommasi et al. 2017), making their consideration essential to a full understanding of the resilience and persistence of coastal ecosystems in a changing environment.

Table 1 shows that high percentages of benthic and especially pelagic species extend across depth zones, but our logistic regression models were necessary to statistically compare the prevalence of extensions across depth zones in pelagic versus benthic species. These models show that pelagic species have greater odds than benthic species of extending from each depth zone into the others (Table 2). In almost every combination of depth zone extensions, and for almost every minimum or maximum depth of species' occurrences, pelagic species consistently have higher probabilities of extension across zones compared to benthic species (Fig. 1). SIMPER analysis also shows that the species primarily responsible for community transitions across depth zones are benthic. Additionally, when considered across the entire depth range of the basin, the shallowest taxonomically distinct benthic community extends from 0 to 100 m, considerably more constrained than the taxonomically distinct pelagic community at 0−200 m (Fig. 2b,c). Finally, particularly in shallower water, pelagic species generally have greater BDRs than benthic species (peaks in Fig. 3a). Altogether, this suggests that pelagic species may offer greater potential for repopulating damaged shallow areas than benthic species. Compared to consideration of benthic species alone, this means that more species than previously thought could contribute to the resilience of shallow communities, strengthening the interpretation that deeper waters can serve as refugia (Glynn et al. 1996, Riegl & Piller 2003, Bongaerts et al. 2010, Baker et al. 2016, Bongaerts & Smith 2019).

However, benthic species also can display expansive ranges, comparable to or even greater than pelagic species in specific cases. In shallow waters, benthic species display a higher probability of extension into the mesophotic zone across intermediate minimum depths of species than do pelagic species (Fig. 1a). When all depths in the ocean basin are considered, a taxonomically distinct benthic community extends from the shallow well into the mesophotic

zone (0−100 m; Fig. 2b). Furthermore, the odds that the distribution of a deep pelagic species extends into the mesophotic zone is only 1.17 times higher than for benthic species (Table 2f), and the probability of such extension across different maximum depths of species' occurrence is similar in both lifestyles (Fig. 1f). Finally, deep benthic versus deep pelagic species have comparable BDR distributions (Fig. 3c). Taken together, it is evident that even benthic species display instances in which they have extensive ranges, sometimes comparable to the highly range-generalized pelagic biota.

Despite the broad depth ranges of both benthic and pelagic species and the relative homogeneity of many deep-water habitats, our NMDS analysis of species across the entire depth of the GoMx basin (5203 m) shows an unexpectedly large number of taxonomically distinct assemblages (i.e. clusters of depth bands where there is less taxonomic turnover within clusters compared to that between clusters in Fig. 2) in bathyal and abyssal depths. This may reflect multiple independent invasions followed by subsequent radiation of particular lineages in the deeper habitats, as was found in fishes by Tornabene et al. (2016), which could be important in understanding the evolution of biodiversity in the deep sea. Evidence of clustering is particularly strong in pelagic species, whose unique assemblages in deep water are further separated and thus more distinct from one another (Fig. 2c). Conversely, among benthic species, clusters are more contiguous (Fig. 2b), indicating more continuous change in the taxonomic composition of benthic communities across depth.

Regardless of taxon and benthic or pelagic lifestyle, the ecological and behavioral dynamics of the threatened shallow-water biota are worth noting. A considerable number of species in the shallow zone have BDRs that are close to or equal to zero (Fig. 3a), and these species are unlikely to be able to survive in deeper environments. The predominance of these species with reduced BDRs in shallow water is not a tautology due to limited depth available in shallow waters, since there is no reason that shallow species could not occur over large depth ranges (as some do) and that deeper-dwelling species could not have narrow BDRs (as some do; Fig. 3). In addition, while many shallow species have lower BDRs than species in mesophotic or deep zones, the BDRs of some shallow species nonetheless reach the same deep extremes as those of species in mesophotic and deeper regions (Fig. 3). The predominance of depth specialists in shallow water does not negate the idea that some species, regardless of benthic or pelagic

lifestyle, are capable of living across a great expanse of depths and localities, and thus may be able to escape or tolerate disturbances in at least parts of their range.

To fully understand the capacity of marine taxa to persist despite disturbance, however, future work must consider more nuanced patterns as more data become available. Relatively few studies consider how factors such as population density, behavioral ecology, reproductive biology, and life history vary across depth. These factors are important because, for deeper habitats to replenish disturbed shallow communities, they must maintain sufficiently large source populations that can deliver viable larvae to shallow environments (Bongaerts et al. 2010, Sponaugle & Cowen 2019). However, empirical evidence of such source populations across many taxa remains limited (Bongaerts & Smith 2019), and varies among taxa and geographical areas. In the coral *Agaricia fragilis*, for example, vertical connectivity from mesophotic to shallow populations is weak (Bongaerts et al. 2017), implying that mesophotic environments may be more of a sink than a source. In contrast, rockfishes such as *Sebastes pinniger* move into deeper regions as they reach reproductive maturity (Keller et al. 2018), allowing mesophotic and deep populations to serve as sources of larvae that move into shallow water (Love et al. 2002). In many species of coral-dwelling stomatopods (e.g. *Neogonodactylus oerstedii*), reproduction occurs almost exclusively in shallow habitats (Reaka 1987, Reaka et al. 1989). However, competitive success and benthic predation are largely determined by relative body size, and heavy adult–juvenile predation decreases survival and prevalence of juveniles in shallow habitats. Body size distributions suggest that the larvae disperse offshore and settle in deep fore-reef waters, then migrate up the reef into shallow water as they grow, reaching the shallow habitat at larger sizes, which allows them to more successfully compete for limited protective cavities, avoid predation, and reproduce (Reaka 1987). We encourage future studies to expand upon this approach in many more taxa to determine whether mesophotic assemblages can increase the overall resilience of coastal communities. This is particularly of interest for under-studied pelagic species, whose extensive depth ranges and high motility lead us to hypothesize that they could, in fact, make major contributions to damaged shallow communities.

In conclusion, we find broad-scale evidence that the distributions of species often overlap multiple depth zones. Ranges that overlap depth zones indicate that individuals can survive in both shallower and deeper habitats, and that some individuals or propagules have made or are making successful depth transitions either in the past or present, even if these transitions are intermittent, such as during El Niño events or glacial cycles. Thus, there is considerable potential for species to persist across broad depths over the long term. Parts of these broad depth ranges can provide refugia where populations can survive and eventually replenish damaged shallower habitats, contributing to the resilience and long-term persistence of coastal ecosystems in the face of increased anthropogenic disturbance. The strength of that conclusion grows significantly when under-studied pelagic species are taken into consideration.

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