WILEY

RESEARCH ARTICLE

Cold-water species deepen to escape warm water temperatures

Revised: 31 July 2021

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Funding information Israel Science Foundation, Grant/Award Number: 1356/15

Handling Editor: Aaron MacNeil

Abstract

Aim: Whether marine species can respond to ocean warming by changing their depth remains controversial. Some evidence suggests that species can deepen to cope with warming climates, whereas other studies have found ecologically constrained depth distributions. Our study focuses on generalizing the depth response of species to warming and elucidating whether some species display a larger change in depth than others. This might help us to understand the future distribution of marine species and communities.

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Location: The Mediterranean Sea.

Time period: 1985-2017.

Major taxa studied: Fish, malacostracans and cephalopods.

Methods: We compiled depth records of species from bottom-trawl surveys encompassing 236 marine species across the steep climatic gradient of the Mediterranean Sea. These data represent the largest assessment, to date, of the potential of species to modify their depth distribution in response to spatially varying climate. Using environmental variables (e.g., sea surface temperature, bottom temperature and salinity), we elucidate the change in depth of species across different climatic gradients. We then test whether species traits (e.g., thermal preference, depth affinity and taxonomic relationship) explain the variation in depth response.

Results: We reveal a significant deepening of minimum depths (shallow depth limits) with increasing sea temperatures across the Mediterranean Sea. Moreover, we show that this deepening is uneven among species, in that cold-water species and eurytherms deepen more than warm-water species and stenotherms. In addition, deep-water species deepen more than shallow-water species. We also find surprising changes toward shallower maximal depths (deep depth limits) with warming, but this pattern is not entirely supported by our sensitivity analyses.

Main conclusions: These large changes across the Mediterranean Sea imply that progressively warmer oceans will compress the vertical distribution of marine organisms. However, given that different species will respond differentially, the future vertical distribution of marine communities will change in complex ways.

KEYWORDS

fish, Mediterranean Sea, ocean warming, species distribution, species traits, thermal preference, thermal refuge, trawl

1 | INTRODUCTION

One of the most concerning drivers of change in the marine environment is the rapid warming of the oceans (Belkin, 2009; Hoegh-Guldberg et al., 2014; Levitus et al., 2000). This is indicated by increases in mean sea surface temperature (SST), ocean warming rates and the frequency and duration of marine heatwaves (Pörtner et al., 2019). Moreover, this warming encompasses both shallow- and deep-water environments (Giglio & Johnson, 2017; Meinen et al., 2020). A commonly predicted universal response of marine organisms to warming is to relocate (e.g., to shift distributions to higher latitudes; Chen et al., 2011; Cheung et al., 2010; Feary et al., 2014; Lejeusne et al., 2010; Murawski, 1993; Sunday et al., 2015). Given that water temperature decreases with depth (Lalli & Parsons, 1997), deeper waters might also serve as thermal refuges (Frade et al., 2018). Thus, in addition to latitudinal migration, it is also possible that marine species might deepen to cooler waters to escape the negative impacts of global warming.

Although climate-related latitudinal changes have received considerable support (see Chen et al., 2011; Last et al., 2011; Parmesan & Yohe, 2003; Poloczanska et al., 2013), evidence of changes in depth is more limited. On the one hand, several studies have found evidence for shifts in depth over time, often attributed to warming (Dulvy et al., 2008; Nye et al., 2009; Perry et al., 2005; Pinsky et al., 2013; Van Hal et al., 2016), although, for many species, deepening was not fast enough to keep up with the rapid pace of warming (Hiddink et al., 2015). On the other hand, deepening might be constrained ecologically owing to availability of habitats, appropriate food resources, light limitation, hydrostatic pressure and oxygen minimum zones (Brown & Thatje, 2015; Jorda et al., 2020; Rutterford et al., 2015; Spence & Tingley, 2020). In one case, species were found to shift into warmer and shallower waters over time, possibly attributable to a change in spawning phenology and transport of larvae (Fuchs et al., 2020). Hence, the generality of depth shifts in the marine realms remains unclear. Moreover, the above studies concentrated on depth change at high latitudes (e.g., the deepening of boreal species). It is not known whether temperate species that experience warming along the trailing edge of their distribution (i.e., the warmest region within their range) can deepen to escape the changes associated with warming.

It is likely that different species will display different depthrelated changes in relationship to warming. We propose four main patterns for species depth changes in response to warming seas (Figure 1): (1) depth conservatism, whereby minimum (shallow depth limits) and maximum (deep depth limits) depths do not change despite environmental changes (Figure 1a); (2) depth shift, whereby both minimum and maximum depths deepen to track climate change, potentially with less deepening of maximum depths owing to more mild environmental change at greater depths (Figure 1b); (3) depth compression, whereby minimum depths deepen while maximum depths remain constant (Figure 1c; Jorda et al., 2020); and (4) depth expansion, whereby minimum depths remain constant while maximum depths deepen, for example owing to changes in the ecology of the deep sea associated with warming (Figure 1d). Understanding which species follow each pattern is fundamental for elucidating the impacts of climate change on marine populations.

If depth shifts are associated with climatic refuge, we expect that differences among species could be explained by thermal



FIGURE 1 Theoretical patterns of depth shift by species in response to warming waters. Four main patterns are suggested. (a) Species do not change their depth preferences. (b) The minimum (shallow depth limits) and maximum (deep depth limits) depth of species deepens. (c) Species deepen their minimum depth while their maximum depth remains constant. (d) Species deepen their maximum depth while their minimum depth remains constant. The y axis represents depth. The colours represent water temperature, with shallow, warm waters at the top and deep, cold waters at the bottom. Climate warms from left to right, with deeper warm waters at the righthand end. Whiskers represent the depth range of species, with upper borders as minimum depth and bottom borders as maximum depth (see arrows and text in panel b)

preference. Hence, cold-water species are expected to avoid warm waters and display depth shift or compression patterns (Figure 1b,c). Conversely, for warm-water species, warming might allow depth expansion to hitherto unavailable deep-water habitats (Figure 1d).

We hypothesize further that the thermal range of a species (i.e., the range of temperature in which a species occurs; Afonso Silva et al., 2017) might impact depth change responses. For instance, species with a broad thermal range ("eurytherms") might be more likely to have the physiological thermal flexibility necessary to adjust to changing climate and be able to maintain their ecologically preferred depth (Figure 1a). In contrast, species with a narrow thermal range ("stenotherms") might be forced to change their depth distribution to maintain their thermal niche (Figure 1b,c). Alternatively, eurytherms might also be depth generalists and able to maintain their climatic optimum by changing to deeper waters (Figure 1d). If stenotherms are also depth specialists, their ability to shift to deeper waters might be more limited, hence a compression pattern might be observed (Figure 1c).

We hypothesize further that depth shifts (Figure 1b) will be more prominent for deep-water species compared with shallow-water species because they are already adapted to deep-water environments (e.g., slow metabolic rate, usage of piezolytes, sensory adaptation to low-light conditions; Gillett et al., 1997; Priede, 2017; Torres et al., 1979). Accordingly, in order for shallow-water species to survive in deeper waters, they must deal with relatively more biotic and abiotic changes than for a similar magnitude of deepening for deepwater species. Finally, given that depth generalists (i.e., species with a broad depth range) are pre-adapted to transitioning from shallow to deep environments, we hypothesize that they are likely to display greater deepening with warming waters than depth specialists (i.e., species with a narrow depth range). To date, the relative support for these hypotheses has not been evaluated empirically.

The Mediterranean Sea contains strong climatic gradients, with increasing water temperature and salinity and decreasing productivity from west to east (Figure 2c; Coll et al., 2010). These gradients can be used to test how climate impacts marine species (Lejeusne et al., 2010; Shapiro Goldberg et al., 2019; Van Rijn et al., 2017). The Mediterranean Sea represents the warmest distribution edge for many Atlantic species, meaning that many populations might already be close to their upper thermal limit in the Eastern Mediterranean, and the semi-enclosed nature of the Mediterranean hinders effective tracking of the preferred thermal niche through range redistributions (Albouy et al., 2013; Ben Rais Lasram et al., 2010; Bianchi & Morri, 2000; Gamliel et al., 2020). Examples already exist of shallow-water species found at unusual depths in the warm Levantine Basin of the Mediterranean Sea, including fish (Stern et al., 2018), polychaetes (Ben-Eliahu & Fiege, 1996) and sponges (Idan et al., 2020; Ilan et al., 1994). However, these records are anecdotal, and the extent of depth change across the Mediterranean Sea has never been quantified systematically.

In this study, we synthesize depth distributions of multiple species across the Mediterranean and ask:

1. Do marine species demonstrate change in their depth distribution across the Mediterranean Sea?

- 2. Are these patterns consistent with one of the suggested hypotheses (Figure 1)?
- 3. Are these changes associated with specific environmental gradients, such as minimal temperature, mean temperature or salinity?
- 4. Can climatic and depth affinities of species explain why some species change their depth distribution whereas others do not?

Answers to these questions will provide insights into the potential of species to escape future climatic warming by depth change.

2 | METHODS

2.1 | Data

We extracted data on the depth range of Mediterranean marine species from published literature based on bottom trawl surveys across multiple depths. We used the search terms "depth" and "Mediterranean" and "trawl*" on the "Web of Science" database in September 2020, resulting in 437 publications. These publications were screened for papers containing data on the depth ranges (minimum and maximum) of surveyed species. Publications were included if they focused on several species (more than five) and contained both deep (> 400 m) and shallow (< 100 m) samples. Additional criteria included trawl mesh size between 10 and 40 mm and habitat confined to sandy or muddy bottoms in continental shelves and slopes. If several publications relied on the same data, only one of the publications was used. The selected papers were supplemented by publications that either cited or were cited by these publications and other publications encountered. In total, this study was based on 12 publications spanning the Mediterranean Sea across three main taxonomic groups: fish (osteichthyes and chondrichthyes), cephalopods and malacostracans (Figure 2a; Supporting Information Figure S1; Table S1). Overall, the data are relatively recent, with a mean sampling year of 2011 (SE \pm 1.6 years) and mean study duration of 9 years (SE ± 2 years).

To estimate local population-level depth distributions, we extracted the minimum and maximum depth of occurrence for each species from each publication. In addition, we extracted the coordinates of each study. The data from a specific publication might cover multiple bottom trawl samples within a region [e.g., Lefkaditou et al. (2003) surveyed across the southern Aegean Sea]. For these cases, we used the coordinates of the centroid of the various trawl samples. Species with fewer than three occurrences across all publications (i.e., rare species) were excluded. Finally, our data contained 236 unique species, with 97 (*SE* ±21) species per publication. Across all species, the range of minimum depth was 10–780 m and maximum depth 11–878 m.

2.2 | Environmental variables

We extracted several environmental variables, including salinity (interpolation of *in situ* surface measurements; in practical salinity



FIGURE 2 Sampling locations, sampled depth range and Mediterranean Sea bottom temperature across depths. (a) Locations of publications included in the meta-analysis: (1) Massuti et al. (2017); (2) Massutí and Reñones (2005); (3) Fanelli et al. (2007); (4) Busalacchi et al. (2010); (5) Terribile et al. (2016); (6) Maiorano et al. (2010); (7) Krstulovic Sifner et al. (2005); (8) Tsagarakis et al. (2013); (9) Lefkaditou et al. (2003); (10) Keskin et al. (2011); (11) Dornelas et al. (2018) and Goren et al. (2019). Shapes represent the taxonomic groups reported. For Keskin et al. (2011), we used only data from the Mediterranean Sea because the Sea of Marmara is shallow. For Maiorano et al. (2010), we used only data from <900 m and excluded deeper hauls. (b) Sampled depths within each publication. The x axis represents the average longitude for each publication. Black vertical lines denote the sampled depth range. Deep (maximal) depths are at the bottom and shallow (minimal) depths at the top. Numbers above each line correspond to the identity of the publication (as shown in panel a). (c) Mediterranean bottom temperature against longitude at different depths. These data were extracted from the Bio-ORACLE database (Tyberghein et al., 2012) using the "sdmpredictors" R package (Bosch, 2018). Darker colours represent deeper seabeds. Bottom temperature decreases with depth but increases eastward with longitude even in deep water

units), maximum annual SST (SSTmax), minimum annual SST (SSTmin) and mean annual SST (SSTmean). These SST values were derived from monthly climatology estimates over the period 2002-2009 and were extracted from the Bio-ORACLE database (Asis et al., 2018; Bosch, 2018; Tyberghein et al., 2012) with a spatial resolution of 5 arcmin. To avoid complete reliance on the exact study centroid, we applied a 15 km buffer around the centroid from each publication and averaged the values within this range. In addition, we calculated the mean bottom temperature, also extracted from Bio-ORACLE, at a spatial resolution of 15 arcmin. The environmental changes throughout the time period examined are small relative to the large variability in these values across the Mediterranean. Thus, the SST range across the sites was found to be 5.1°C, whereas even for the fastest warming sites the change in temperature over the past 30 years was only 0.12°C (Ozer et al., 2017). We used averaged recent values of these environmental layers and did not aim to match these values to the time of sampling.

2.3 | Species traits

We were interested in understanding which traits can explain possible species-level depth changes. For this, we collected five specieslevel traits:

- 1. Taxonomic relationship (Cephalopoda, fish and Malacostraca).
- Depth affinity, which was calculated based on the mean depth from FishBase for fish (Boettiger et al., 2012; Froese & Pauly, 2019) and from SeaLifeBase (Palomares & Pauly, 2020) and Ocean Biodiversity Information System (OBIS; obis.org) for cephalopods and malacostracans.
- 3. Overall depth range, which was derived from the same databases as depth affinity (i.e., FishBase, SeaLifeBase and OBIS) but this time by calculating the difference between the maximum and minimum known depth values. Along this continuous axis, species

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with broad depth ranges were considered depth generalists and species with narrow depth ranges depth specialists.

- 4. Thermal preference, which was estimated at the species level based on known occurrence records. For this, we used the Global Biodiversity Information Facility (GBIF.org) to extract species occurrences, then cleaned the data by removing erroneous locations (e.g., points on land) using the "CoordinateCleaner" R package (Zizka et al., 2019) and locations that did not fit known species distributions [compared against FishBase for osteichthyes, chimaeriformes and selachimorpha; against the study by Last et al. (2016) for batoids; and against Sealifebase and OBIS for malacostracans and cephalopods]. After cleaning, the mean number of occurrences per species was 377 ± 11 (SE). For each species, occurrence records were overlapped with the SSTmean environmental layer to create two thermal preference indices: (a) the mean SST of each species for the locations in which it was observed; and (b) the mean SST across the species range, estimated using the convex hull (i.e., the smallest area that encompasses all species occurrence coordinates). The advantage of the latter index is that it can cover areas that contain few occurrences (e.g., owing to undersampling) and does not give greater weight to areas sampled intensively. However, results were generally similar for both indices, and we present results for the former index unless otherwise mentioned.
- 5. Finally, for each species, we calculated its thermal range (the difference between maximum and minimum SST values across occurrence locations). Similar to depth affinity, thermal range was used to estimate the degree of thermal generalism (i.e., eurythermality) of each species.

2.4 | Statistical analyses

Our first aim was to explore how minimum depth, maximum depth and depth range of species change across the Mediterranean. These were treated as separate response variables and were Intransformed. We then regressed these values, using linear mixed effect (LME) models ("glmer" function in the "Ime4" R package; Bates et al., 2015), against each of the environmental variables (bottom temperature, SSTmean, SSTmin, SSTmax and mean salinity) and longitude (for the correlation between these predictors, see Supporting Information Figure S2). Here, species was treated as a random intercept term to allow for species-level variation in depth. To allow for species-level variation in response to the environmental variables, we also treated species as a full random term (both intercept and slopes). However, the above model did not converge; hence, we performed these analyses with mean-centred depth (i.e., the observed depth estimate was subtracted from the mean depth for each species). These two options (random intercepts, and random intercepts and slopes after centring) gave similar results overall. To ensure that the number of hauls in a publication did not bias results, because better-studied locations will have more precise depthrange estimates, we weighed each study by the number of hauls (In-transformed, under the weights argument). Regardless, we found that the number of hauls in each study was not significantly related to publication location (linear model relating hauls to longitude, t = -0.28, p > .05). All models were found to meet the statistical assumptions. We used the Akaike information criterion (AIC; Burnham & Anderson, 2002) to make comparisons among models using different environmental variables.

To examine how species traits impact the association between depth and the environmental variables, we also tested explicitly for an interaction between species traits and the environment. For this, we used highly supported single environmental variables selected during the analysis described above. Thus, an interaction between *SSTmin* and species-level thermal preference was modelled as depth ~ *SSTmin* × thermal preference + (1|species), with Intransformed number of hauls for weighting. A significant interaction term would mean that depth change with minimal SST differs according to the thermal preference of the species.

For additional support, given that such interactions are sometimes hard to visualize and interpret, we also took a meta-analytical approach. In this model, we used the slope of the regression between the depth of each species and the selected environmental variable as a species-level effect size (Supporting Information Table S2). For instance, negative effect sizes imply deepening of species with increasing temperature. We then tested whether this effect size changes with species traits. For this, we used the "rma" function in the "metafor" R package (Viechtbauer, 2010). The estimate for each species was weighted by the inverse of the variance of the slope (under the vi argument in the "rma" function).

2.5 | Sensitivity analysis

To ensure that the results were not derived by sampling biases or variation in the sampling design between publications, we performed the following sensitivity analyses:

- Forcing the depth range in all sites to be identical. This was done using the publication with the shallowest (for maximal depth) and deepest (for minimal depth) samples (depth range of 63-401 m). Records beyond these depths in other publications were re-assigned to the truncated depth values.
- Given that the maximum sampled depths in the Levant and North Aegean Sea were relatively shallow (Figure 2b, lines 10 and 11), we examined our models without these locations and tested whether the patterns held.
- We removed species from a publication if its minimum or maximum depths were equal to the sampled depth range. This was done to reduce cases in which species with depth limits that exceeded the sampled depths received a truncated depth-range estimate.
- 4. Finally, it was possible that deeper hauls might catch mid-water species while the net was descending or ascending, thus overestimating maximum depths. To deal with this potential bias, we

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excluded pelagic species [representing 27 (11%) of all species]. We would like to emphasize that even if some overestimation or underestimation of depth was present, this was not expected to change our results because this bias was not expected to vary along environmental gradients. Model settings in all sensitivity analyses were identical to those detailed in the sections above.

3 | RESULTS

We collected data from 12 publications representing both the western and eastern Mediterranean: the Balearic Sea, Tyrrhenian Sea, Ionian Sea, Adriatic Sea, Aegean Sea and the Levantine Basin (Figure 2a). After excluding rare species (fewer than three occurrences across publications), our data contained 236 species (162 fishes, 40 malacostracans and 34 cephalopods) of various thermal preferences (10–28°C), from cold water (e.g., Atlantic mackerel, *Scomber scombrus*) to warm water (e.g., greater amberjack, *Seriola dumerili*; Supporting Information Table S2; Supporting Information Figure S3).

3.1 | Prominent deepening response across the Mediterranean Sea

We found strong changes in the minimum depth, maximum depth and depth range of species across the Mediterranean Sea. Longitude, *SSTmin* and *SSTmean* were the variables that were best supported by the data (Supporting Information Table S3). Bottom temperature received support in some models (Supporting Information Table S3).

Minimum depth is ecologically related to SST estimates owing to its relatively high proximity to the water surface. Therefore, for minimum depth we chose to investigate SSTmin further as the main environmental predictor (see also Clark et al., 2020). We found that minimum depth deepened with increasing SSTmin (Figure 3a,d; Supporting Information Table S4). Maximum depth was best explained by longitude (Supporting Information Table S3), and bottom temperature was the second best predictor (longitude and bottom temperature were strongly correlated; r = .95, p < .0001; Figure 2c; Supporting Information Figure S2). Therefore, we chose to use bottom temperature as the main environmental predictor for maximum depth and depth range. Surprisingly, we found that maximum depth became shallower (Figure 3b,e; Supporting Information Table S4) and depth range decreased (Figure 3c,f; Supporting Information Table S4) with increasing bottom temperature (Figure 3).

To ensure that the results were not derived exclusively from the variation in sample design, we performed several sensitivity analyses. Using equal sampling depth ranges, we found complete support for the abovementioned results (minimum depth: slope = 0.09, t = 8.75, p < .0001; maximum depth: slope = -0.07, t =-3.22, p < .01; depth range: slope = -0.26, t = -5.26, p < .0001; Supporting Information Figure S4a-c). Likewise, the results did not change when we excluded observations with minimum or maximum depths equal to the sampled depth range (minimum depth: slope = 0.14, t = 6.3, p < .0001; maximum depth: slope = -0.17, t =-5.2, p < .0001; depth range: slope = -0.34, t = -5.32, p < .0001; Supporting Information Figure S4g-i) or when we excluded pelagic species (minimum depth: slope = 0.15, t = 7.48, p < .0001; maximum depth: slope = -0.16, t = -5.62, p < .0001; depth range: slope = -0.32, t = -6.08, p < .0001; Supporting Information Figure S4j–I). However, when we excluded the North Aegean and the Levant, we still found deepening of the minimum depth (slope = 0.37, t = 5.98, p < .0001; Supporting Information Figure S4d), but the changes in maximum depth and depth range disappeared (maximum depth: slope = -0.01, t = -0.22, p > .05; depth range: slope = -0.05, t =-0.86, p > .05; Supporting Information Figure S4e,f). Thus, deepening minimum depth with temperature seemed to be more robust than shallowing maximum depth and depth range decrease. This suggested that the depth response of species to increasing water temperature generally followed a pattern of depth compression (Figure 1c).

3.2 | Species traits explain depth changes

Next, we tested how depth patterns were modified by species-level traits. For minimum depth, we did not find an interaction between *SSTmin* and thermal preference (interaction term using *SSTmin*: t = -1.42, p > .05). Nonetheless, we found a significant interaction between bottom temperature and thermal preference (Figure 4a; t = -2.42, p < .05). Thus, cold-water species deepened their minimum depth with increasing bottom temperatures (Figure 1b,c), whereas the depth of warm-water species remained relatively constant (Figure 1a). The meta-analytical approach supported these findings (Supporting Information Figure S5a; z = 3.08, p < .01). We did not find a significant interaction between *SSTmin* (or bottom temperature) and thermal preference with species maximum depth (*SSTmin*: t = -0.9, p > .05; bottom temperature: t = 0.29, p > .05; Figure 4d) or depth range (*SSTmin*: t = -0.66, p > .05; bottom temperature: t = 0.21, p > .05; Figure 4g).

We also found that eurytherms deepened their minimum depth with increasing temperature more than stenotherms (the interaction was marginally significant when estimating thermal range using observed occurrences: t = 1.85, p = .06; Figure 5a; and significant when using thermal range calculated over the entire species distribution: t = 2.53, p = .01).

Moving to depth-related traits, we found that deepening of minimum depth with increasing temperature occurred for both shallow- and deep-water species, but was stronger for deep water species (interaction term using *SSTmin*: t = 2.45, p < .05; bottom temperature: t = 3.53, p < .001; Figure 4b). Once again, a meta-analytical analysis supported these results (Supporting Information Figure S5b; z = -4.74, p < .0001). The maximum depth change with increasing temperature was not significantly related to depth affinity (*SSTmin*: t = 0.81, p > .05; bottom temperature:



FIGURE 3 Depth change response of species to increasing minimum sea surface temperature (SSTmin) and bottom temperature. (a-c) Overall depth changes for minimum depth (shallow depth limit), maximum depth (deep depth limit) and depth range, respectively. (d-f) Species-level slopes and intercepts (colours represent taxonomic groups). For these panels, depth is mean centred (relative depth). Black trend lines are the predicted values from the linear mixed effect models. In a,b,d,e, shallower depths are at the top and deeper depths at the bottom of the y axes. In c,f, smaller depth ranges are at the top and larger depth ranges at the bottom of the y axes. Generally, minimum depth deepens while maximum depth becomes shallower and depth range decreases with warming

t = -0.25, p > .05; Figure 4e). Depth range decreased more dramatically for deep-water species than for shallow-water species (bottom temperature: t = -2.4, p < .05; Figure 4h). This pattern was less pronounced when using SSTmin instead of bottom temperature (SSTmin: t = -1.33, p > .05). We also found that depth generalists demonstrated greater minimum depth deepening with increasing temperature in comparison to depth specialists (bottom temperature: t = 3.64, p < .001; SSTmin: t = 2.34, p < .05; Figure 5b).

Across taxa, we found that deepening of minimum depth with increasing bottom temperatures was stronger for malacostracans than for fish (interaction term using bottom temperatures: t = 2.56, p = .01; Figure 4c; Supporting Information Figure S5c). In addition, malacostracans and fish decreased their maximum depth with increasing temperature, whereas cephalopods significantly deepened it (compared with fish: t = 4.38, p < .0001; compared with malacostracans: t = -2.19, p < .05; Figure 4f). These differences suggested a depth shift pattern for cephalopods (Figure 1b) and an unexpected pattern of depth shrinkage for fish and malacostracans. Finally, all groups reduced their depth range with temperature, but with a weaker effect in cephalopods than in fish (t = 3.74, p < .001; Figure 4i).

Within fish, we found that both chondrichthyes (n = 21) and osteichthyes (n = 141) deepened their minimum depth with increasing SSTmin (Supporting Information Figure S6a). However, chondrichthyes deepened their maximum depth with increasing SSTmin, whereas osteichthyes transitioned to shallower depths (Supporting Information Figure S6b). Overall, the depth range of chondrichthyes increased, whereas the depth range of osteichthyes decreased with increasing SSTmin (Supporting Information Figure S6c). These differences suggested a depth shift pattern for chondrichthyes (Figure 1b) and an unexpected pattern of depth shrinkage (i.e., minimum depth deepened while maximum depth becomes shallower) for osteichthyes.



FIGURE 4 Minimum depth (a-c, shallow depth limit), maximum depth (d-f, deep depth limit) and depth range (g-i) plotted against bottom temperature for species across different traits. (a,d,g) Predictions for species of cold (10°C), intermediate (17.5°C) and warm (25°C) thermal preferences. (b,e,h) Predictions for shallow (50 m), medium (400 m) and deep (800 m) water species. (c,f,i) Predictions for the three taxa. In a-f, shallower depths are at the top and deeper depths at the bottom of the y axes. In g-i, smaller depth ranges are at the top and larger depth ranges at the bottom of the y axes. The *p*-values within panels represent the interaction terms. The *p*-values for panels c,f,i are reported in the Results, section 3.2. We find that with warming bottom temperatures, the minimum depth of cold-water species deepens more than that of warm-water species. Along the same gradient, the minimum depth and depth range of deep-water species deepened more than the minimum depth of shallow-water species. Overall, taxa decreased their minimum depth and depth range at higher temperatures, whereas the maximum depth response was more variable

4 | DISCUSSION

The ability of marine organisms to change depths in order to cope with changing environmental conditions is still under debate. Some studies have found warming-associated depth changes (Dulvy et al., 2008; Fuchs et al., 2020; Hiddink et al., 2015; Nye et al., 2009; Perry et al., 2005; Pinsky et al., 2013; Van Hal et al., 2016), whereas others have found that depth changes are ecologically constrained (Brown & Thatje, 2003; Jorda et al., 2020; Rutterford et al., 2015; Spence & Tingley, 2020). In this study, we compiled data on 236 marine species across the Mediterranean Sea and report a clear and significant pattern of minimum depth deepening associated with warming. Importantly, we found that the extent of deepening was strongly dependent on species traits, including the climatic and depth affinities of species. Thus, cold-water species and eurytherms deepened more than warm-water species and stenotherms. This study reconciles previous findings and reveals generalities in the tendency of species either to retain their depth distributions or to change to deeper water. This has important implications for predicting the future response of marine species and communities to a warming climate.



FIGURE 5 Minimum depth (shallow depth limit) response of specialist and generalist species to increasing bottom temperatures. (a) Thermal range. Predictions for eurytherms (thermal range of 25°C) versus stenotherms (thermal range of 5°C). (b) Overall depth range. Predictions for depth generalists (depth range of 800 m) versus depth specialists (depth range of 50 m). Shallower minimum depths are at the top and deeper minimum depths at the bottom of the *y* axes. Depth generalists and eurytherms respond to warming waters by greater minimum depth deepening when compared with depth specialists and stenotherms. Shaded areas represent 95% confidence intervals. The *p*-values within panels represent the interaction terms

4.1 | Thermal preference reveals uneven depth deepening

We found a strong and significant pattern of minimum depth deepening across the Mediterranean Sea (Figure 3). This effect was best explained by predictors associated with SST (Supporting Information Table S3). This pattern is similar to temporal patterns described in the North Sea and north-west Atlantic Ocean (Dulvy et al., 2008; Nye et al., 2009; Perry et al., 2005). Apart from climaterelated effects, the Mediterranean Sea has been impacted greatly by the increasing invasion of Indo-Pacific migrants via the Suez canal ("Lessepsian species"; Golani & Appelbaum-Golani, 2010; Por, 2012). Theoretically, these warm-water species might competitively exclude the Mediterranean indigenous fauna into deeper, suboptimal habitats. Nevertheless, a large number of invasive species are found only in the extreme eastern Mediterranean (Levant), whereas depth change is observed even when this region is excluded from the analyses (Supporting Information Figure S4d-f). Moreover, the fact that we observed a deepening of cold-water species while warm-water species maintained depth hints that alien species are unlikely to cause the observed depth shifts across the Mediterranean. Finally, several studies have found that alien Lessepsian species do not compete strongly with indigenous species (Arndt et al., 2018; Azzurro et al., 2014; Buba & Belmaker, 2019; Givan et al., 2018). Together, these findings provide evidence for climate as the main driver of the deepening pattern observed.

We found that depth changes were not uniform for all species. We found larger minimum depth deepening for cold-water species in comparison to warm-water species (Figure 4a; Supporting Information Figure S5a). Similar species-level responses were explained by thermal preference in the North Sea (Van Hal et al., 2016). In addition, we found that deepening was mainly observed for species with a broad thermal range (Figure 5a). This result suggests that eurytherms are able to track their climatic niche, whereas stenotherms are depth conservatives. This result can be explained if stenotherms are also depth specialists, which is a pattern we observed in our data (Supporting Information Figure S7). Indeed, other studies have found that shifts in species distributions are associated with thermal generalism (Belmaker et al., 2013; Sunday et al., 2015). In the context of climate change, this would mean that depth might serve as a refuge for eurytherms, but that stenotherms might not have the ecological flexibility to deepen.

Our findings might have several implications for the future of marine communities. First, warming will cause reshuffling of depth distributions, with some species maintaining their depth and other species that respond to warming by deepening. This will change biotic interactions and produce novel communities (Clark et al., 2020). Second, ecosystems with mostly cold-water species might experience attrition of the shallow-water communities as more and more species deepen, a process similar to that suggested to occur in tropical terrestrial communities moving up mountains (Colwell et al., 2008). This might pose an unrecognized threat for the biodiversity in warming waters.

4.2 | Deep-water species deepen

Deep-water species demonstrated stronger climate-related deepening than shallow-water species (Figure 4b). We also found that depth generalists were more likely to shift into deeper waters than depth specialists (Figure 5b). These patterns might have two mutually nonexclusive explanations. First, bottom temperature decreases steeply with depth within shallow waters, but temperature differences at larger depths are relatively mild (Figure 2c). Thus, deep-water species might need to deepen more than shallow-water species to track their preferred temperature. Consequently, deep-water species might be at risk because, eventually, even the deepest regions might be too warm, leaving no refuge from warming seas (similar to mountaintop extinctions on land; Freeman et al., 2018). In addition, descending to deeper waters might pose other barriers, such as oxygen ILEY-

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minimum zones, which might compress the depth ranges of deepwater species (Jorda et al., 2020; Mavropoulou et al., 2020; Stramma et al., 2012). Second, change in depth is correlated with multiple biotic and abiotic changes (light, pressure, food availability, habitat suitability, etc.). Like temperature, these factors change rapidly with deepening in shallow waters but more moderately in deeper waters. Thus, in comparison to deep-water species, shallow-water species might be constrained ecologically in their ability to adjust to warming seas by deepening (i.e., as environmental barriers are more prominent; Jorda et al., 2020; Priede, 2017; Rutterford et al., 2015). Although we cannot differentiate between these two hypotheses, we note that their implications are very different. Thus, according to the former explanation, deep-water species might experience a decrease in abundance and fitness with warming, whereas according to the latter suggestion, shallow-water species are at greater risk.

4.3 | Depth range shrinkage

In addition to deepening the minimum depth of species, we found shallower maximum depth with elevated sea temperatures, causing a shrinkage of depth range (Figure 3c,f). This represents an unexpected result that was not part of our a priori hypotheses (Figure 1). We note that this pattern is much weaker than the decrease in minimum depth with warming, because when we excluded two samples in which maximum depth was shallow, this trend disappeared (Supporting Information Figure S4d-f). Therefore, we cannot exclude the possibility that this trend is spurious and driven by the sampling design. If further research confirms this trend, we suspect it might be caused by a general contraction of the depth range towards the central niche owing to harsher conditions. For instance, warming-induced decreases in abundance (Givan et al., 2018) might limit each species exclusively to the depths that represent optimal environmental suitability. Alternatively, specific oceanographic conditions, such as the vertical distribution of oxygen minimum zones, which are common at intermediate depths within the Mediterranean (Mavropoulou et al., 2020), might drive this pattern.

4.4 | Intertaxa comparisons

Three main groups were compared in this study (cephalopods, fish and malacostracans), and all showed a deepening of minimum depth with increasing water temperature (Figure 4c; Supporting Information Figure S6a). This implies that warming has a strong and broad impact across the marine realm. Nonetheless, we did find some differences between taxa. Although all taxa deepened their minimum depths, cephalopods and chondrichthyes also deepened their maximum depths, whereas other taxa had shallower maximum depths with warmer temperature (Figure 4f; Supporting Information Figure S6b). Hence, cephalopods and chondrichthyes showed a pattern consistent with depth shift (Figure 1b). The ability of chondrichthyes and cephalopods to shift depth might indicate that these taxa

have fewer physiological and ecological constraints that prevent deepening in comparison to osteichthyes and malacostracans. For example, chondrichthyes are known to have relatively high pressure tolerance (e.g., by having "chemical chaperones"; Priede, 2017).

4.5 | Fitness implications of changing depth distributions

In this study, we found strong spatial associations between depth change of species and warmer climates. These redistributions might affect the fitness and abundances of species and therefore have an important ecological impact. For example, deepening might indicate a deep-water thermal refuge (Bongaerts et al., 2010; Frade et al., 2018; Iden at el., 2020; Kramer et al., 2019), which could allow species to thrive despite worsening climatic conditions (Keppel et al., 2012). Nonetheless, it might be that deepening cannot compensate completely for the costs of descending into ecologically suboptimal conditions (Hiddink et al., 2015). This would mean that there would still be negative effects of warming on population sizes or breeding potential. Likewise, it remains unclear what the fitness consequences might be for remaining at the same depth. It is possible that species displaying a conservative depth distribution with warming are those that are least sensitive to warming and that might be considered "winners" in a future warm ocean. However, it is also possible that depth-conservative species simply lack the ecological flexibility to deepen and might suffer fitness consequences from maintaining their depth distribution.

The data available in this study do not allow us to detect fitness consequences, which would require detailed abundance data across depths. However, examples of a warming-associated decrease in abundance of cold-water species and increase in abundance of warm-water species are widely reported in the literature (Beare et al., 2004; Brander et al., 2003; Simpson et al., 2011). Nye et al. (2009) found, across the north-west Atlantic continental shelf, that southern species increased in abundance with warming, whereas northern species (i.e., cold-water species) experienced deepening in tandem with range contraction and stock size reduction. Similar patterns of decreases in the abundances of cold-water species were also reported from the eastern Mediterranean Sea (Givan et al., 2018). Given the existing knowledge, it seems likely that the deepening response of cold-water species to a warming climate might drive species to suboptimal conditions.

4.6 | Caveats

Several caveats should be acknowledged. First, the bottom trawl data used here differ across publications in sampling effort (number of hauls), sampling depth range and the sampling depth intervals. Greater sampling effort increases the chances of detection, especially at the depth extremes where a species is less likely to be found. We tackled this issue by weighting each sampling point according to the number of hauls per study and found that this weighting did not alter our main findings. To control for variability in sampling depth range, we performed several sensitivity analyses. Although we found that most patterns were robust to this variability, the shallowing of maximal depth and decreasing depth range disappeared when controlling for sampling depth range (Supporting Information Figure S4d-f). Finally, publications differ in the depth intervals sampled. We believe this should not be a problem for the minimal depth estimates, because all studies had relatively dense sampling intervals in shallow waters (i.e., samples were close together in terms of depth). However, at deeper depths some studies used relatively sparse sampling. This might have biased the maximal depth estimate in ways that are hard to predict. We note that if we had data on the entire catch record of each species by depth, it would have been possible to model the depth distribution explicitly accounting for sampling variability (e.g., using Huisman-Olff-Fresco models; Huisman et al., 1993; Jansen & Oksanen, 2013). We also did not control explicitly for seasonality in depth distributions (Clay, 1991; Hyndes et al., 1999; Kallianiotis et al., 2000) or diel shifts in depth (Neilson & Perry, 1990). We expect that with the future availability of large-scale trawl data (Maureaud et al., 2021), more refined analyses will be possible.

4.7 | Conclusions

Using the Mediterranean Sea as a "natural experiment" (Lejeusne et al., 2010), we found strong depth changes associated with warming. These changes were consistent across multiple taxonomic groups, attesting to the generality of the pattern. Moreover, these depth changes were explained by the climatic and depth affinities of species. The trait-specific depth changes observed imply largescale reshuffling of marine communities, which will be likely to include new biotic interactions. Shallow-water species seem to have fewer options than deep-water species to deepen in order to escape warming. In addition, stenotherms and depth specialists show less depth changes than eurytherms and depth-generalists. Therefore, specialists might suffer disproportionately from climate change. It is possible to identify these species using large-scale occurrence data (such as GBIF and FishBase), as done here. Hence, it might be possible to predict the "winners" and "losers" in the future warmer oceans on a vertical axis, similar to the predictions made across space (Albouy et al., 2013; Ben Rais Lasram et al., 1997; Feary et al., 2014; Sunday et al., 2015). Such predictions can have large implications for understanding the way in which climate change will impact commercial stocks (Brander, 2010; Cheung et al., 2013), protected areas and future conservation efforts (Bruno et al., 2018).

ACKNOWLEDGMENTS

We are grateful to Tal Gavriel, Mai Lazarus and Daphna Shapiro Goldberg for providing valuable insights. This research was partially supported by the Israel Science Foundation (ISF) grant number 1356/15 to J.B.

CONFLICT OF INTEREST

The authors declare that this study was conducted without any commercial or financial relationship that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

All authors conceived and planned the study. SD and SC conducted literature review. SD performed data screening and data extraction. SC performed the analyses and edited the manuscript. SC and JB wrote the text. JB provided valuable insights throughout the study. All authors contributed to revisions. All authors consented to the manuscript being submitted in its final form.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Dryad Digital Repository at: https://doi.org/10.5061/dryad.stqjq 2c46

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BIOSKETCHES

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SUPPORTING INFORMATION

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How to cite this article: Chaikin, S., Dubiner S., & Belmaker J. (2021). Cold-water species deepen to escape warm water temperatures. *Global Ecology and Biogeography*, 00, 1–14. https://doi.org/10.1111/geb.13414