

Deeper than we thought: New depth records for northern Red Sea and eastern Mediterranean Sea fishes

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Abstract

The depth distribution of marine species is essential ecological information, especially within hotspots of biological invasions and given the increasing evidence of climate-driven depth shifts. Due to the scarcity of systematic surveys across depths, most studies rely on coarse-scale compilations of opportunistic data. High-quality depth estimates are particularly lacking in the eastern Mediterranean, a global hotspot of climate change and biological invasions, and the adjacent Red Sea, which serves as the source for most species introductions. Using baited remote underwater stereo-video systems to depths of 150 m, we report new depth records for fish species in the northern Red Sea and eastern Mediterranean Sea, and model their abundance patterns across depths. We found that 96 of the 230 studied species (42%) were found at novel depths compared to their previously known records, with 84 species showing deeper distributions. The mean deep border extension across these species was 22.4 m. Our results highlight the importance of *in-situ* observations across depths. We offer a comprehensive dataset including species' depth ranges, modeled central depth niches, abundance, body size, and associated habitat types. This dataset is useful for understanding the role of depth shifts in response to climate change and species introductions into the Mediterranean Sea.

Keywords: Fishes; depth distribution; non-indigenous species; stereo-BRUVs; species abundance; data.

Introduction

The vertical distribution of marine species is a fundamental ecological attribute, influencing community structure, trophic interactions, and habitat suitability (Priede, 2017). Accurate knowledge of depth distributions is essential for effective ecosystem characterization and wildlife management. While large-scale databases provide valuable and applicable compilations of species information (Humphries *et al.*, 2023), these resources usually contain depth records derived from disparate sources. Consequently, they carry a risk of introducing bias related to uneven sampling effort across depths (Meyer *et al.*, 2015; Wüest *et al.*, 2019; Ramírez *et al.*, 2022). The absence of systematically collected fine-grain data is especially pronounced in tropical environments and for depths exceeding traditional visual census (commonly down to 30m; Menegotto & Rangel 2018). This necessitates *in-situ* targeted surveys to refine species-specific depth boundaries.

The Mediterranean Sea and the Red Sea represent interconnected marine ecosystems, with the Suez Canal facilitating an ongoing influx of species predominantly

extending their range from the Red Sea into the Mediterranean (Streftaris & Zenetos, 2006; Edelist *et al.*, 2013; Golani, 2025). Understanding the ecological characteristics, including depth distributions, of Red Sea species is paramount for predicting the potential establishment and impact of future introductions in the Mediterranean. Further, the eastern Mediterranean Sea is undergoing rapid warming (Schroeder *et al.*, 2017; Ozer *et al.*, 2022), consequently altering species distributions (Hiddink *et al.*, 2012; Albouy *et al.*, 2013; Givan *et al.*, 2018; Schickele *et al.*, 2021). Across the Mediterranean, cold-water species deepen and warm-water species expand their depth ranges (Chaikin *et al.*, 2022; Chaikin & Belmaker, 2023). Depth redistributions may lead to altered species interactions and ecosystem functioning, underscoring the need for frequent depth monitoring. However, common demersal fish assessment methods have limitations: scientific bottom-trawl surveys (Tiralongo *et al.*, 2021; Maureaud *et al.*, 2024), do not sample hard-substrate habitats, and diving-based visual surveys are restricted to shallower depths. This leaves a gap in our knowledge of deeper communities and their depth zonation. Hence, a system-

atic census across depths encompassing both structurally complex hard substrate (e.g., coral reefs, rocky reefs) and less complex soft substrate (e.g., sand, silt) is lacking.

This short communication provides novel depth records for fishes in the northern Red Sea (northern Gulf of Aqaba) and the eastern Mediterranean Sea (in and around ‘Yam Rosh Haniqra’ protected area in the eastern Levantine Basin). Records are derived from a survey employing standardized Baited Remote Underwater stereo-Video systems (stereo-BRUVs; Langlois *et al.*, 2020). We further implement statistical tools to assess population-level depth distributions and central depth niches. By providing fine-grain depth information, we contribute timely data for assessing the ecological implications of ongoing biological invasions and the impacts of rapid warming on fish communities in a dynamic marine region.

Methods

Study areas

Our sampling focused on the continental shelves and upper slopes in the Red Sea and the Mediterranean Sea. Within the Red Sea, our sampling took place at the northern Gulf of Aqaba (Fig. 1). The general bathymetry in the northwestern tip of the Gulf of Aqaba is characterized by a relatively steep slope (Weinstein *et al.*, 2021), with hard substrate composed of live coral reefs and rocky substrate, as well as interspersed soft substrate (Fig. S1). The southern samples represent part of the “Yam Ha-Almogim” marine protected area (UNEP-WCMC, 2024a), while the northern samples can be subject to fishing; however, this is generally limited, and most coral-reef fishes

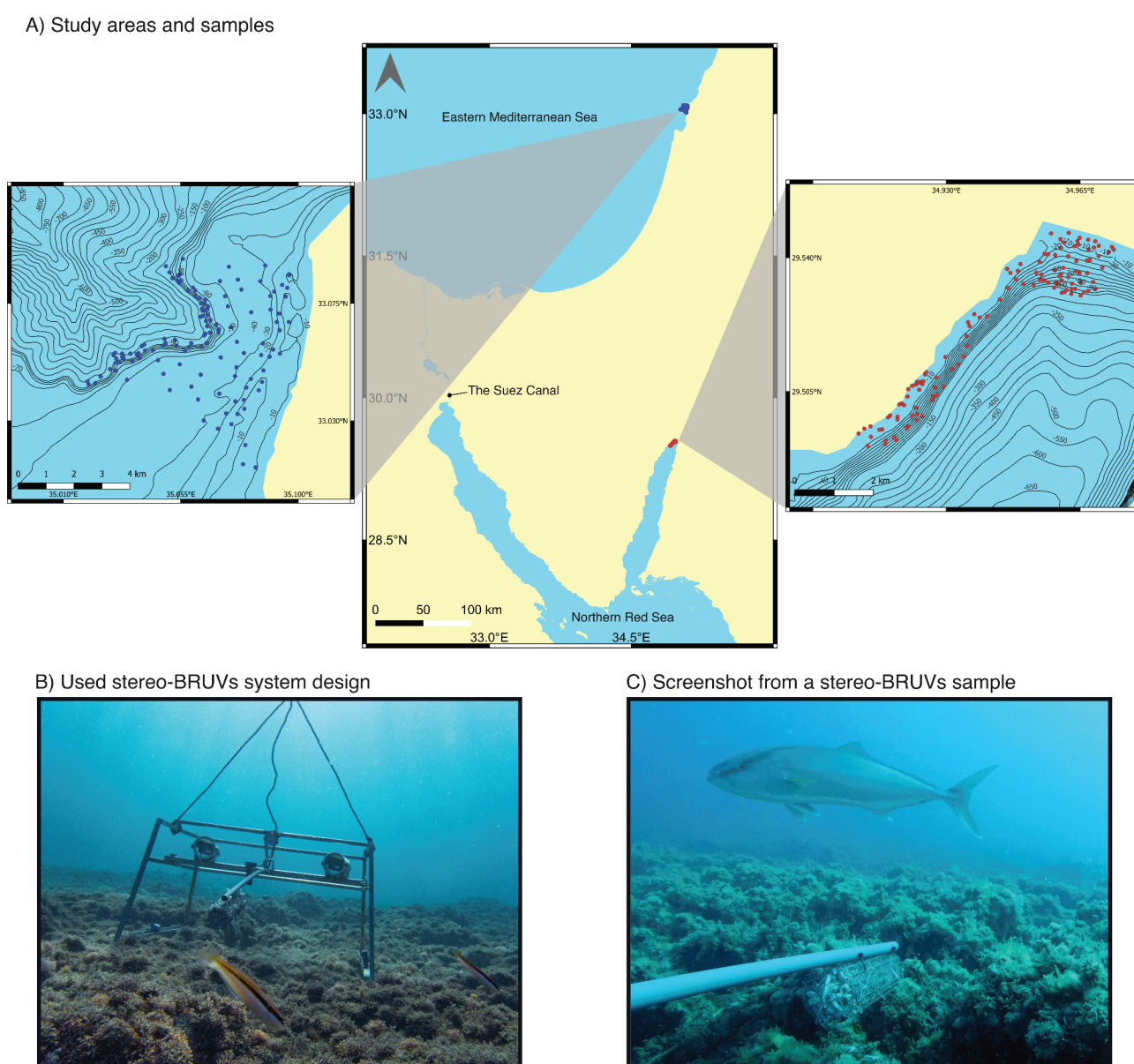


Fig. 1: Sampling areas and video surveys. A) Sampling maps. The stereo-BRUVs deployments occurred in the eastern Mediterranean Sea and the northern Red Sea. Blue points denote Mediterranean samples (i.e., deployments), and red points denote Red Sea samples. Red contours denote the survey area bathymetry. B) The stereo-BRUVs systems used in this study. Each system consisted of a metal frame, ballast, two video cameras, a barometer, and a bait arm. For more details on the system settings, view Table S1. C) An example screenshot from video analysis. Photo credit: Shahar Chaikin.

are protected. Within the eastern Mediterranean, our sampling took place in the eastern Levantine Basin in and around the major marine protected area of “Yam Rosh Haniqra” (UNEP-WCMC, 2024b). Within the protected area, offshore fishing is prohibited, while the southern sites outside the protected area are fished. This region is characterized by a moderate deepening to depths of 40 m, following a mild deepening to 60 m, which is later followed by a steeper slope. The samples were composed of rocky reef and soft substrates (Fig. S1). Other habitat features recorded in our samples included gravel, sand, silt, seagrass, macroalgae, and a few artificial objects such as marine litter (Fig. S2). The proportion of individuals per species occurring within each habitat feature is reported (Data S1).

Video surveys

Our sampling covered depths of 5 to 150 m using stereo-BRUVs (Langlois *et al.*, 2012; Santana-Garcon *et al.*, 2014; Goetze *et al.*, 2015; Whitmarsh *et al.*, 2017), which allowed us to estimate species abundance and depth distributions (Langlois *et al.*, 2020). We deployed stereo-BRUVs on both hard and soft substrates from November 2019 to July 2022, approximately every three months for each sea. Each sampling expedition lasted two consecutive days, during which we took 6–11 daily samples (mean of 7.9 ± 2.5 SD) from the entire depth range of the study area. Within each site, we sampled a depth gradient, maintaining intervals of approximately 15 m. Each standardized sample (i.e., a stereo-BRUVs deployment) consisted of a 60-minute video using ~800 g of mashed anchovies within a bait bag and mounted on a bait arm (details on system settings available in Table S1). Overall, we collected 247 samples (Red Sea = 123, Mediterranean Sea = 124; Fig. 1). To quantify species abundance, we used the video frame with the maximum number of individuals within a sample (i.e., MaxN). This conservative measure of abundance eliminates the overestimation of abundance from video-based census (Priede *et al.*, 1994; Whitmarsh *et al.*, 2017). We used observations of individuals that could be identified to the species level. As stereo-BRUVs are precalibrated systems, the dataset we provide is also complemented by accurate minimum, mean, and maximum fork-length estimates for the reported MaxN measurements (Harvey & Shortis 1995; Harvey *et al.*, 2001).

Depth ranges and central depth niches

We report species depth range and MaxN across depths. To determine the depths most utilized by each species we estimated the central depth niches and optimum depths using Huisman-Olff-Fresco (HOF) models from the “eHOF” R package (Huisman *et al.*, 1993; Jansen & Oksanen, 2013). For the HOF models, the response was MaxN (including absences), and the predictor was the sampled depth; hence, each species’ model consisted of

123 samples in the Red Sea and 124 in the Mediterranean Sea. Estimates are provided for species with >3 occurrences (119 species) and are more robust for species that are more common in our data (Michaelis & Diekmann, 2017). We thus also clearly mark all species with < 10 occurrences for which we are less confident in the results (Data S1).

We fitted five hierarchical HOF models (i.e., I–V mentioned below; Huisman *et al.*, 1993) with a Poisson error distribution and selected the most appropriate model using Akaike’s Information Criterion (AIC) and 100 bootstraps. After each bootstrap run, the model having the lowest AIC score was chosen, and the final model selected was the one that appeared most often across all runs. Mean AIC weights across all bootstraps are reported and can directly inform the reader on the suitability of each model selected. The model output includes an optimum and a central depth niche. The optimum is the depth at which the expected MaxN is maximal. The central niche is the range of depths in which the expected MaxN is greater than 60% of the optimum value.

Following the HOF approach (Roberts *et al.*, 2019), model I represents species indifferent to the depth gradient. Model II represents species that monotonically increase or decrease in abundance with depth. Model III indicates species with abrupt abundance increases or decreases across depths. Finally, models IV and V denote species with unimodal or a skewed unimodal response curve, respectively. The categorization of species as non-indigenous was based on a recent checklist and published records (Ragkousis *et al.*, 2023; Golani, 2025).

Results and Discussion

Using 247 stereo-BRUVs samples, we report new depth borders for 96 out of 230 species (Fig. 2; Data S1). Specifically, 84 species extended their deep border. The mean deep border extension across these species was 22.4 m (lower and upper 95% CI: 18, 26.8). Additionally, 17 species showed previously undocumented shallow borders, with a mean extension of 11.2 m (7.5, 14.9). We also provide the first depth estimation for two mesophotic species: the Gulf of Aqaba endemic species, *Thamnanconus erythraeensis* Bauchot & Maugé 1978 (Golani & Fricke, 2018; Heemstra *et al.*, 2022), and the Red Sea species *Pseudanthias gibbosus* (Klunzinger 1884). These new depth records also provide novel information on 13 non-indigenous species in their native Red Sea range and 4 non-indigenous species in their introduced Mediterranean range (Fig. 2).

Ecologists often estimate depth ranges by using only the extreme depth values from occurrence data (Smith & Brown, 2002; Monk *et al.*, 2012; Duffy & Chown, 2017; Chaikin *et al.*, 2022). This can be problematic as the resulting depth range estimates from such data may increase with sampling effort and with species abundance (Brown, 1984; Chaikin & Belmaker, 2023). In this regard, model-based depth patterns, such as those generated using HOF models, may be more reliable (Jansen &

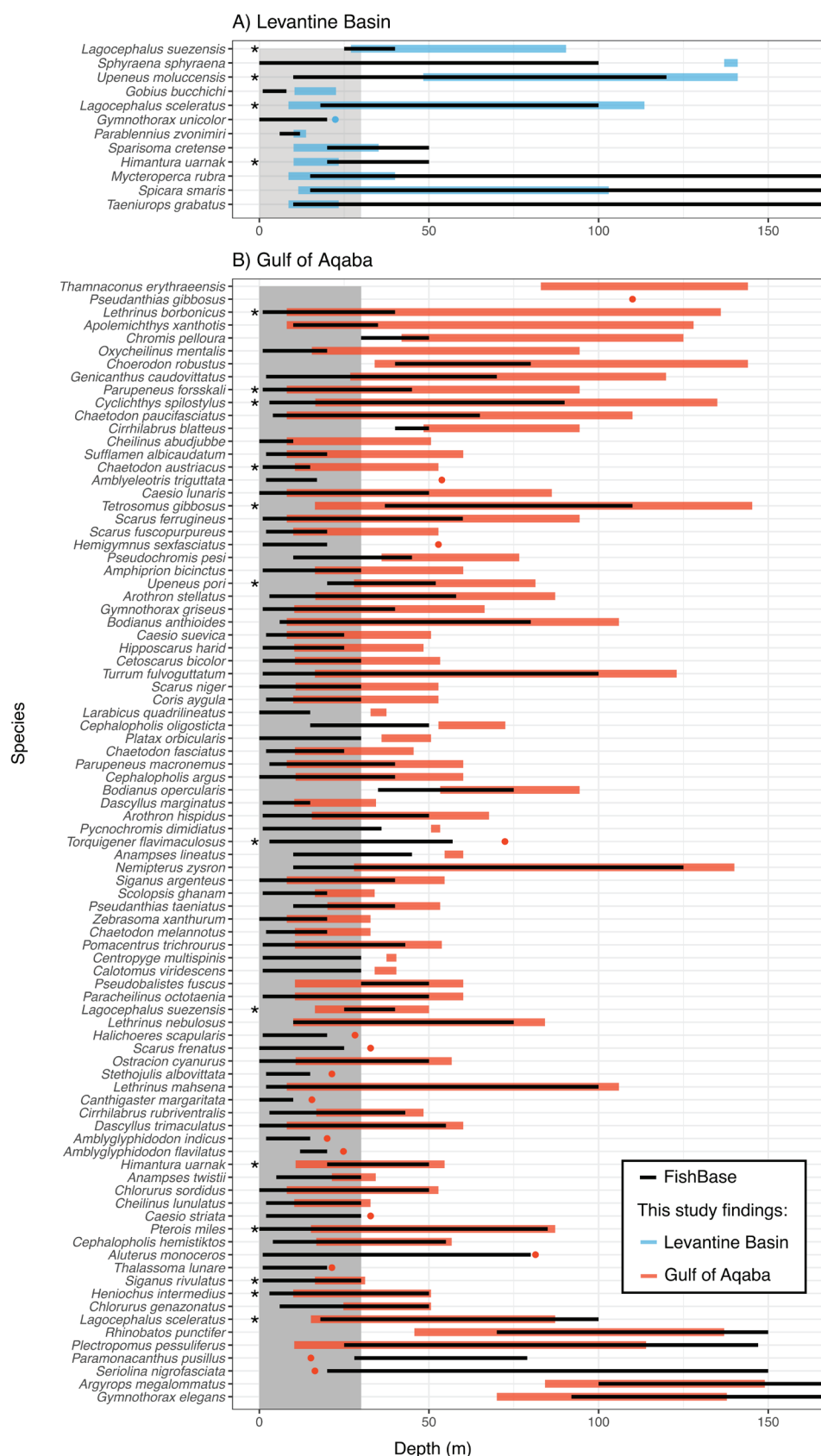


Fig. 2: New depth records compared with depth ranges published on FishBase. Previously known depth ranges are shown in black bars. The newly observed depth ranges are shown in blue for the Levantine Basin (eastern Mediterranean) and in red for the Gulf of Aqaba (northern Red Sea). Points denote rare species that occurred only once throughout the surveys. The grey vertical bars represent the common depth limits of SCUBA surveys (0-30 m). Three of the Mediterranean species, and 33 of the Red Sea species show FishBase-reported maximum depths shallower than 30 m. Species are ordered according to the difference between their maximum observed record and the FishBase-reported maximum depths. Asterisks (*) denote Red Sea species that were also recorded in the Mediterranean Sea. Note that *Thamnaconus erythraeensis* and *Pseudanthias gibbosus* lacked prior published depth information; their depth records are first reported in this study.

Oksanen, 2013).

Using HOF models (Fig. 3, Data S1), we find that 37 species exhibit a model V pattern, meaning that their expected depth-abundance pattern tends to have a skewed unimodal curve. Then, 30 species follow a monotonous (model II) pattern and thus increase or decrease in abundance with depth, which may indicate a depth-specific specialization at one end of the depth gradient. An abrupt response curve (model III) was chosen for 33 species, which may indicate the presence of a biotic or abiotic threshold (e.g., changes in levels of light exposure). Lastly, 21 species follow a symmetric unimodal curve (model IV), while 3 species follow a uniform response (model I), indicating an indifferent response to the depth gradient examined. These patterns establish a detailed baseline that is important for understanding how depth distributions may change due to the diverse impacts of global change, such as ocean warming, species introductions, fishing pressure, and extreme climatic events.

As a caveat, our study reports detailed depth distributions to depths of 150 m at two local regions, in and around the “Yam Rosh Haniqra” protected area in the eastern Levantine Basin and the northern Gulf of Aqaba. Hence, it remains unclear how well these populations represent the depth distribution over the entire eastern Mediterranean or Red Sea. Further, the maximum depth we examined was 150 m. In our case, 59 species have a deep-range limit larger than 150 m (based on FishBa-

se). These species’ deeper depth limits are likely to be only partially represented in our data. Lastly, HOF depth niches produced in this study should be cautiously interpreted for species represented by few non-zero records, although the exact cutoff below which models are non-robust remains debatable.

Using the data for ecology, biogeography, and conservation

Our depth distribution data, encompassing 230 fish species across two distinct regions and extending to 150 m, provides useful information for stakeholders and ecologists. The reported new depth limits, coupled with rare depth estimations for two mesophotic species, offer a fine-grained understanding of fish ecology along depth gradients. These data, including the reported abundance, body size, and habitats, provide a baseline to address timely ecological questions. For instance, examining to what extent introduced and native species overlap in their depth distributions can be used to assess whether native species are displaced to deeper waters by introduced species (Edelist *et al.*, 2013; Golani & Galil, 1991; Givan *et al.*, 2017). More generally, the provided data can be utilized for comparisons of habitat preferences and depths between species of tropical (Red Sea) and temperate (Mediterranean) seas. Finally, the data can also serve

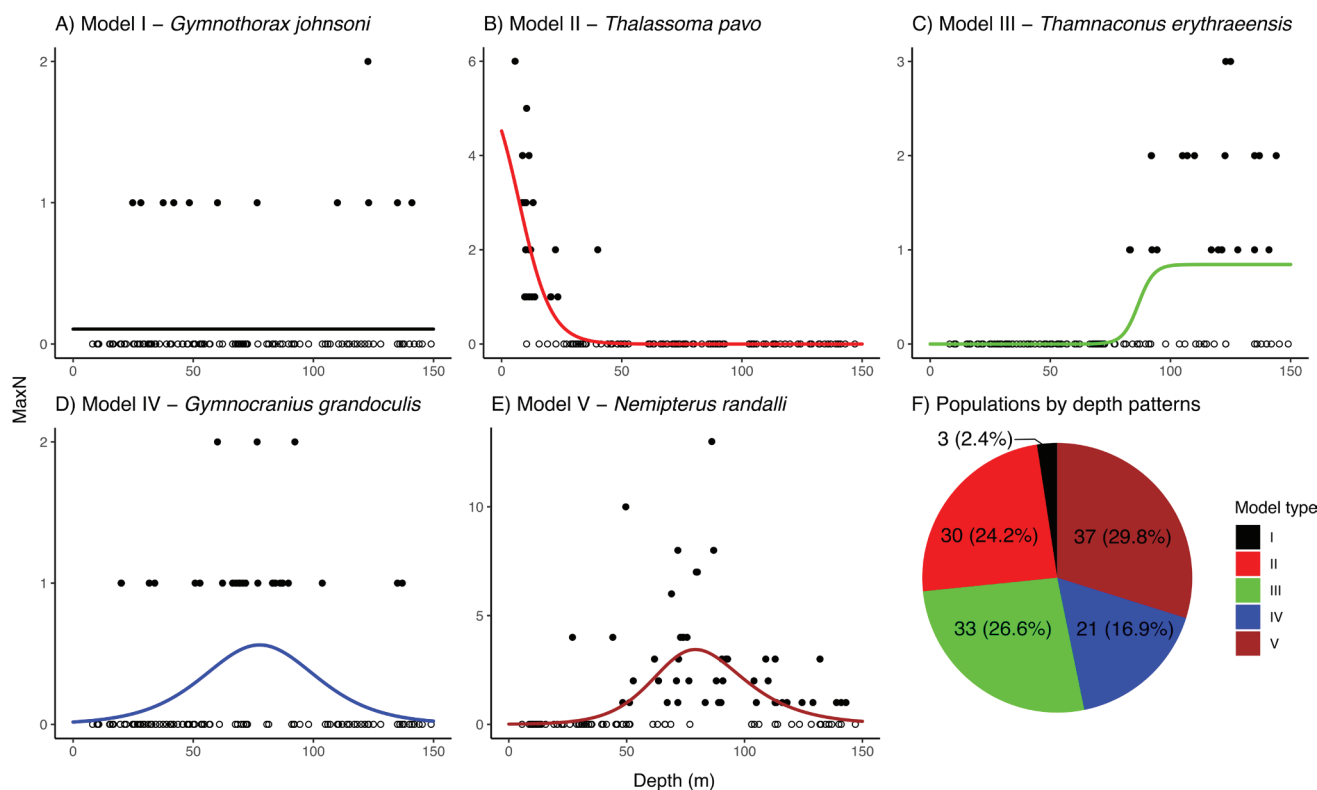


Fig. 3: Modeled depth patterns. A-E) HOF model predictions for selected species. The y-axis represents MaxN (abundance), and the x-axis represents the studied depth gradient. Each point represents a sample, with white points indicating absences and black points indicating presences. Colored lines represent the chosen HOF model predictions. Distributions A, C, and D represent Red Sea populations, and distributions B and E are of Mediterranean populations. Panel F represents the number of populations across both seas and their percentages within each selected HOF model type. Note that some introduced species may have different selected models in the native range compared to the invaded range. Additional response curves can be viewed in Data S3.

as a baseline to examine climate-driven depth shifts, as increasing evidence suggests that ocean warming may drive the expansion of warm-water species into deeper waters (Dulvy *et al.*, 2008; Pinsky *et al.*, 2013; Chaikin *et al.*, 2022). The depth estimates are readily accessible in Data S1-S3, and the raw data are deposited in figshare (see “Data availability statement”). The data can be extended employing a standard protocol (Langlois *et al.*, 2020). Taken together, this information can aid in resolving questions related to ecology and biogeography and inform effective conservation and management strategies across depths in these dynamic marine ecosystems.

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Supplementary Data

The following supplementary information is available online for the article:

Data S1. HOF model selection table.

Data S2. Population-level depth summary and habitat use.

Data S3. Population-level depth niche plots.

Fig. S1: Histogram plots showing the substrate type distribution across depth within the study regions. The studied sites within the Gulf of Aqaba are characterized by a relatively uniform spread of hard substrate, except for a partial gap between 60-90m. The studied sites within the Levantine Basin are mainly characterized by hard substrate to depths of 40m and a more dispersed occurrence between 80-140m. Hard substrate samples refer to deployments showing the hard substrate in parts of the frame.

Fig. S2: Histogram plots showing substrate features across depth within the study regions. Note that multiple habitat features can occur within an individual sample.

Table S1. System setup and camera settings.