

Deep-sea climate futures are already observable in the Red Sea

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Abstract

The deep oceans are warming, but we lack reference systems for observing community restructuring without exploitation confounds. Here, we assess the deep Red Sea as a natural analogue for mesopelagic and upper-bathypelagic climate futures. Below 150 m, Red Sea temperatures stabilise at 21–22°C to the seafloor (3,040 m), conditions the global mesopelagic will not reach until at least 2100–2200. Deep-sea fisheries are effectively absent: over 70 years, catch composition has remained among the most coastally dominated globally (6th percentile). We identify 38 additional species, including conspicuous commercial taxa, potentially present but undocumented. Functional-space truncation relative to the Arabian Seas source pool is concentrated along axes of extreme depth-specialisation, while feeding and life-history diversity are retained. No other warm deep basin combines equivalent thermal extremity, oxygenation, and an unexploited baseline. The deep Red Sea is a globally unique, time-limited system for predicting mesopelagic restructuring under sustained ocean warming.

Introduction

The deep sea (broadly defined here as marine waters below 200 m) constitutes Earth's largest habitat by surface area and volume ¹, underpins global carbon cycling through the biological pump ², and harbours largely uncatalogued biodiversity shaped by hydrostatic pressure, low temperatures, perpetual darkness, and chronic oligotrophy ^{3,4}. It is also increasingly subject to direct human pressure. Deep-water fisheries commonly extend below 1,500 m ^{5–8}, and commercial seabed mining and deep-water hydrocarbon extraction continue to expand across continental slopes and abyssal plains ⁹. Simultaneously, accelerating climate change is reshaping the physical and chemical conditions on which these ecosystems depend. Climate predictions indicate substantial warming of the upper deep ocean within decades ¹⁰, compounded by deoxygenation, acidification, and reductions in the downward flux of organic material ^{11,12}. Many deep-sea taxa are vulnerable to these converging pressures because the conservative life-history traits that characterise them (slow growth, late maturity, low fecundity, and episodic reproduction) constrain population recovery ^{6,13}. Together, climate-driven environmental change and expanding exploitation risk restructuring deep-sea ecosystems before their current state is adequately documented, with cascading consequences for carbon sequestration, biogeochemical cycling, and emerging deep-water fisheries ^{14,15}.

Despite the urgency of these converging threats, predicting how deep-sea communities will respond to sustained warming remains challenging. Climate projections estimate future thermal and chemical conditions at depth with increasing resolution. Converting these physical projections into biological predictions requires reference systems with communities whose structure and functioning can be observed under conditions that the broader deep ocean has not yet reached. The interaction between climate-driven change and direct exploitation compounds this challenge; their effects are interlinked and often synergistic, making the disaggregation of their respective contributions to species and community change difficult where both are present ^{16–18}. Systems that exhibit minimal direct exploitation are

therefore especially valuable for isolating the effects of warming on community structure and for generating testable predictions of future change.

Natural analogue systems, environments where communities have persisted under conditions projected for the broader ocean under future warming, offer potential solutions to this constraint. Where such systems exist, they can function as *in situ* experiments, revealing which species, functional traits, and trophic configurations persist under sustained warmth and which do not. Here, we assess the deep Red Sea as a natural analogue for climate-driven restructuring of mesopelagic and upper-bathypelagic communities, examining its thermal context against global projections, its exploitation baseline, the composition and functional structure of its deep-water fish assemblage, and its position among comparable warm deep basins.

Main Text

The Deep Red Sea as a Thermal Analogue for Future Oceans

The Red Sea is an established analogue for shallow-water thermal biology. Its surface temperatures, among the highest of any semi-enclosed marine basin ^{19,20}, have been used to examine coral bleaching thresholds, the molecular basis of thermal tolerance, and the capacity of reef-associated species to persist under temperatures that would cause widespread mortality elsewhere ^{21,22}. Here, we extend this logic to deeper waters, where the case for the Red Sea as a climate analogue is, if anything, stronger. Below approximately 150 m, Red Sea temperatures stabilise at 21–22°C and remain near-constant through the water column to the seafloor at approximately 3,040 m (Fig. 1), making the Red Sea by far the warmest basin on Earth at equivalent depths. This near-isothermal deep profile is a consequence of restricted exchange with the Indian Ocean across the shallow Bab-el-Mandeb strait (maximum sill depths ~ 137–320 m), which limits the intrusion of cooler Gulf of Aden water to intermediate depths of the southern basin without meaningfully altering the deep thermal regime ^{23,24}.

Comparison with CMIP6 (Coupled Model Intercomparison Project Phase 6) ensemble projections under the worst-case SSP5-8.5 ¹⁰, a high-emissions scenario that is increasingly treated as an unrealistically severe upper-bound rather than a most-likely pathway ²⁵, reveals that the deep Red Sea occupies a thermal space that most of the global mesopelagic will not reach for decades to centuries (Fig. 1). Deep Red Sea temperatures exceed present-day sea surface temperatures across much of the subtropical and temperate ocean with global averages not exceeding them until approximately 2200. At depths of 200 m, most areas of the subtropical and tropical ocean do not approach current Red Sea conditions until beyond 2100 and many not until beyond 2200. The Red Sea's deep thermal profile therefore most closely approximates the projected future state of the global tropical and subtropical mesopelagic zone under sustained high-emission warming. However, this analogy does not extend to the bathyal or abyssal ocean zones, where projected warming lags far behind Red Sea conditions even by 2200. Though the

bathyal and abyssal zones of the Red Sea remain a uniquely extreme system for the exploration of evolution under extreme pressure and temperature. The deep Red Sea's value as a climate analogue is therefore strongest for the mesopelagic and upper bathypelagic (broadly 200–1,000 m), the deep-sea depth zone where climate-driven restructuring is most imminent.

While some *in situ* evolution may occur within the Red Sea ²⁶, including rare cases of within-basin diversification, most deep-water fish lineages are likely derived from Indian Ocean source populations that subsequently persisted, filtered, or adapted under the basin's unusually warm conditions. The Red Sea was originally connected to the Mediterranean before later desiccating, the modern basin was repopulated from the Indian Ocean through the Bab-el-Mandeb strait approximately 6.2 million years ago ²⁷. Most species currently present were therefore drawn from the waters of the Arabian Sea and wider Indian Ocean. The Red Sea's deep fauna therefore largely represents a community recruited from a historically cooler source pool that has persisted under elevated thermal conditions. Neither the rate at which the Red Sea warmed to its present deep-water temperatures nor the timeline over which deep-sea species entered the basin is well understood. It is therefore unclear whether the warming these lineages experienced was comparable in rate to the transient warming now unfolding under climate change, or whether the transition was rapid and followed by long-term thermal stability. This uncertainty does not diminish the Red Sea's value as an analogue; it refines the nature of the questions the system can answer. If the deep Red Sea assemblage represents a biological equilibrium reached under sustained warmth, it functions as an empirical endpoint: a window into what mesopelagic communities may look like once warming stabilises, independent of the trajectory by which they arrived. Whether communities under transient warming converge on that endpoint, or whether persistent and transient warmth produce structurally distinct assemblages, is itself a question of direct relevance to predicting deep-ocean futures that the Red Sea is uniquely positioned to address.

An Unexploited Deep Basin at a Fisheries Inflection Point

The value of a climate analogue is substantially enhanced when the system is free from direct exploitation, allowing community structure under sustained warmth to be observed without the confounding signal of fisheries' extractive pressures. The deep Red Sea meets this condition to a degree that is increasingly rare among the world's oceans, its deep and oceanic waters are currently essentially unexploited ^{28,29}. Analysis of functional group composition across all Large Marine Ecosystems (LMEs) reveals that the Red Sea has one of the most coastally dominated fisheries globally (Fig. 2). A principal component axis separating coastal and reef-dominated fisheries from those with substantial deep-water catch contributions (PC1; 27.2% of variance) places the Red Sea's average catch composition at the 6th percentile, with only the Indonesian Sea, Gulf of Thailand, Sulu-Celebes Sea, and Bay of Bengal averaging lower ²⁸. Further, the Red Sea has shown no meaningful movement along this axis across the 70-year period from 1950 to 2019, a period in which many comparable systems have shifted substantially toward deeper-water species (Fig. 2). Catches remain overwhelmingly composed of shallow-water, often reef-

associated taxa including mackerels, ponyfishes, emperors, anchovies, groupers, jacks, and snappers^{28,29}, with negligible contributions from oceanic pelagic or deep-water functional groups.

While the compositional profile of Red Sea fisheries has remained static, total artisanal catches peaked between 1995 and 1999 and have since declined by approximately 35% (Fig. 2), despite increasing demand from a rapidly growing regional population. This pattern is consistent with observed progressive overexploitation of inshore and reef-associated stocks^{30–32}. Trajectories of LMEs with comparably coastal catch compositions at the time of their artisanal peak provide context for the Red Sea's current position (Fig. 2). Post-peak pathways diverge, with many systems showing substantial expansion into offshore and deep-water functional groups after an initial lag, while others continue to decline along the same coastal axis in a pattern consistent with unsustainable inshore intensification rather than compositional reorganisation. The Red Sea currently tracks the latter pathway, having passed its artisanal catch peak without meaningful compositional movement. This places the basin at a pivotal juncture: coastal fishing pressure may continue to intensify, or management and market pressures may drive expansion toward oceanic and deeper waters. An offshore and deep-water shift may become attractive as regional seafood demand grows but would compromise the unexploited deep-water baseline that underpins the Red Sea's scientific value as a climate analogue. Whether and how this transition unfolds will depend on decisions taken simultaneously across some of the wealthiest and some of the most food-insecure and governance-limited states in the world.

A less immediate but non-trivial additional threat is commercial interest in deep-sea mining of hydrothermal vent fields and metalliferous sediments in the Red Sea's axial rift zone, for which prospecting programmes and environmental risk assessments have a decades-long history^{9,33}. The consequences of seabed mining for deep-sea communities remain poorly characterised but are potentially severe in ecosystems defined by slow recovery rates and limited functional redundancy. Neither a fisheries transition to depth nor mining activity is guaranteed, but the incentives and enabling conditions for both are present. If extractive pressure reaches the deep Red Sea before a pre-disturbance biological baseline is established, the capacity to attribute community structure to temperature rather than exploitation will be substantially degraded. A shifted baseline³⁴ would compromise the basin's irreplaceable scientific value. Establishing that baseline is therefore not only a research priority but a time-sensitive one.

Undescribed Diversity and the Limits of Current Baselines

The shallow Red Sea is among the most biogeographically distinctive marine environments on Earth. Endemism among Red Sea fishes is estimated at ~ 14.2% and with invertebrates exhibiting comparable rates of in-basin diversification^{35,36}, reflecting the partial isolation imposed by the Bab-el-Mandeb strait. The same physical and environmental filtering that generates this shallow endemism is expected to operate at least as strongly at depth, where the sill's restriction on colonisation is more severe and the thermal contrast with the source pool more extreme. Yet systematic survey of deep-sea communities in

the Red Sea is sparse, assembled primarily through a small number of dedicated expeditions and opportunistic collections spread across several decades^{37–39}. The known deep-sea fish fauna (those known to occur at > 200 m) currently stands at 175 species, of which 35 (20%) are potentially endemic^{36,40}, but these figures almost certainly underestimate true richness. A secondary colonisation pathway from the Mediterranean via the Suez Canal (anti-Lessepsian migration) is established but rare for shallow-water taxa and the canal's minimum depth ~ 24 m effectively precludes it as a vector for deep-sea species⁴¹. The combined effects of physical isolation, environmental filtering at the Bab-el-Mandeb strait, and geographically uneven survey effort mean that both species richness and endemism in the deep Red Sea are substantially underestimated. Even greater gaps in knowledge exist for the invertebrate lineages that undoubtedly constitute most of the deep sea's animal diversity⁴².

Trait-based prediction modelling, applied to 175 known Red Sea deep-sea fish species and a further 194 deep-sea species recorded from the adjacent Arabian Seas and Somali Current, identified 38 additional species lineages with non-trivial occurrence probabilities in the Red Sea (Fig. 3). Across three confidence tiers (high: 95% credible interval > 0.5; moderate: 50% credible interval > 0.5; low: median > 0.5), predicted species include conspicuous, ecologically prominent, and commercially important taxa such as groupers (*Epinephelus chlorostigma*, *E. diacanthus*), amberjack (*Seriola rivoliana*), and bigeye tuna (*Thunnus obesus*) at high confidence; deep-water groupers (*Hyporthodus octofasciatus*, *H. chabaudi*), gamefish (*Etelis coruscans*, *Istiompax indica*, *Zeus faber*), and thresher and blue sharks (*Alopias vulpinus*, *A. superciliosus*, *Prionace glauca*) at moderate confidence. That so many readily detectable species have elevated predicted occurrence probabilities but remain absent from the Red Sea deep-sea record suggests that limited survey effort contributes substantially to current gaps, although genuine ecological exclusion cannot yet be ruled out. This conclusion is reinforced by the recent confirmation of wahoo and striped marlin in the basin, despite their large size and prominence as gamefish⁴³. These gaps, which are undoubtedly more severe for less conspicuous lineages, directly constrain the utility of baselines built from current records. A species inventory that is highly incomplete weakens any reference against which to evaluate future change. What the trait model does establish is that inclusion or exclusion from the Red Sea is not random but structured by identifiable traits, including reduced likelihood for species with deeper minimum depth ($\beta = -0.54$, 95%CI[-0.85, -0.25], $pd = 99.9\%$), wider depth range ($\beta = -0.27$, 95%CI[-0.56, 0.01], $pd = 96.8\%$), internal fertilisation ($\beta = -0.72$, 95%CI[-1.52, 0.17], $pd = 94.9\%$), and increasing distance of nearest record from the Bab-el-Mandeb strait ($\beta = -0.68$, 95%CI[-0.99, -0.39], $pd = 99.9\%$). Conversely, likelihood increased for species with wider latitudinal ranges ($\beta = 0.21$, 95%CI[-0.22, 0.65], $pd = 83.2\%$) and those at higher trophic levels ($\beta = 0.26$, 95%CI[-0.04, 0.57], $pd = 95.4\%$). There was also substantive variation in likelihood among body shapes and water column position. Species with short and deep bodies ($\beta = -0.37$, 95%CI[-1.13, -0.38], $pd = 83.6\%$), and elongated bodies ($\beta = -0.53$, 95%CI[-1.18, -0.13], $pd = 94.2\%$) had a decreased likelihood of occurrence relative to those with eel-like bodies. Benthopelagic ($\beta = -0.48$, 95%CI[-1.11, 0.16], $pd = 93.0\%$), and pelagic ($\beta = -0.57$, 95%CI[-1.18, 0.03], $pd = 96.8\%$), species had a lower likelihood of occurrence than benthic species. A more complete understanding of which species have established in the basin, and just as importantly which have not, will be essential for separating the physical filtering of the Bab-el-Mandeb sill from the environmental

filtering of the Red Sea's extreme thermal regime. Decoupling these two sources of community structuring is fundamental to the Red Sea's value as a climate analogue for the deep sea.

Sill Filtering Truncates Depth Specialists but Retains Mesopelagic Functional Diversity

The species composition of the deep Red Sea is shaped by the combined action of two selective filters: the extreme thermal regime of the basin and the shallow physical constraint of the Bab-el-Mandeb sill. A six-axis PCoA ordination of functional traits (AUC = 0.716; Fig. 4) quantifies deep-sea community trait-space truncation across nested spatial scales. The known and predicted Red Sea deep-sea fish assemblage occupies approximately 22.4% of global deep-water fish functional space; the Arabian Seas and Somali Current source pool occupies 33.6%; and the wider Indian Ocean 78.8% (Fig. 4). Not all this contraction is attributable to Red Sea-specific processes. Strong divergence from the Indian Ocean on axes loading primarily on geographic and bathymetric range breadth and on latitudinal range and habitat affinity is also shared by the Arabian Seas and Somali Current assemblage, with the Red Sea adding minimal further contraction beyond its source pool on these dimensions. This shared contraction most plausibly reflects the under-exploration of regional deep waters, particularly around Yemen and Somalia, combined with the exclusion of some species by one of the world's most intense oxygen minimum zones ⁴⁴.

The Red Sea assemblage covers only 66.8% of the Arabian Seas and Somali Current's functional convex hull. The primary truncation falls on an axis of deep-habitat specialisation, PCoA6, loading most strongly on median depth, body shape, and water column position (Fig. 4). This axis separates more depth-specialised species from shallower fauna, and its strong contribution to Red Sea–Arabian Sea and Somali Current divergence is a quantitative signature of the Bab-el-Mandeb acting as a bathymetric filter on species composition. By contrast, the axes most directly relevant to the climate analogue argument (PCoA1: feeding mode and water-column position, and PCoA2: the slow–fast life-history continuum) are not primary axes of divergence between the Red Sea and its source pool (Fig. 4). This pattern indicates that the trophic guilds and life-history strategies that structure mid-water communities are retained rather than systematically excluded by the sill filter. Despite its truncated overall extent, the Red Sea assemblage occupies a coherent region of functional trait space, with contraction concentrated on axes of depth specialisation rather than on the feeding and life-history dimensions that would undermine its utility as an analogue for mesopelagic futures. Whether this retained trait-space coverage translates into functional redundancy within guilds, a property that would further strengthen the analogue case, remains an open question that targeted functional analyses could address once Red Sea deep-sea diversity is better documented.

The clearest functional-space truncation in the Red Sea therefore occurs in the depth zones less central to the climate analogue argument. True bathyal and abyssal specialists are unlikely to have entered through the shallow Bab-el-Mandeb, and the deepest Red Sea strata represent the most severely filtered

component of the assemblage. The most imminent thermal exposure in the deep-sea applies to the global mesopelagic and upper bathypelagic (broadly 200–1000 m), where the Red Sea's sill-related restriction is substantially reduced. The apparent absence of deep-obligate lineages from the Red Sea does, however, generate niche vacancies that may be ecologically significant. Given that temperature does not meaningfully decrease with depth in the Red Sea, pressure becomes the more dominant physiological gradient. This unique feature may relax a key constraint on bathymetric range expansion, potentially allowing mid-depth species to occupy roles vacated by absent deep specialists, a hypothesis that targeted sampling could directly test. Fully disentangling filter-driven absences from survey-driven gaps remains a limitation that will require coordinated sampling both inside and outside the basin. Yet the distinct pattern of divergence along the depth-specialisation axis rather than the feeding and life-history axes provides a signal that is ecologically coherent, distinguishable from random under-sampling, and supportive of the Red Sea's utility as a climate analogue for the mesopelagic.

The Red Sea Among Warm Deep Basins: Unique Properties and Comparative Opportunities

The Red Sea is not the only semi-enclosed basin with deep waters substantially warmer than the open ocean at comparable depths. Comparison with the Mediterranean, Sulu Sea, and Black Sea, the three basins that most closely share this property, reveals that the Red Sea holds a unique combination of characteristics (Fig. 5). The Mediterranean, with its shallow ~ 280 m Gibraltar sill, has warm deep waters (~ 12.7–13.5°C⁴⁵) that approach projected mid-century conditions for parts of the Atlantic and Pacific mesopelagic¹⁰. However, its deep-sea fauna has been modified by a century of bottom trawling extending below 1,000 m⁴⁶, making thermal and exploitation signals more difficult to separate. The Black Sea, though also warmer at depth (~ 8.5–9°C) than much of the open ocean, is disqualified as an analogue for aerobic deep communities because of permanent anoxia below approximately 150–200 m⁴⁷. Its community structure is therefore dictated by the chemocline rather than temperature, and so the Black Sea's scientific value lies in biogeochemical and euxinic questions rather than in ocean warming. The Sulu Sea presents the most genuinely comparable case. Its deep-water column is oxygenated, bottom temperatures of ~ 10°C⁴⁸ are meaningfully warmer than the surrounding Indo-Pacific at equivalent depths, and the Sibutu Passage sill (~ 420 m) imposes weaker biogeographic filtering. Yet its weaker thermal contrast with the open ocean makes it a less extreme future analogue, and its deeper and less restrictive sill make the separation of thermal from dispersal effects substantially more difficult. Among these basins, the Red Sea alone combines the most extreme deep-water thermal profile (Fig. 1), strong and interpretable biogeographic filtering across a well-characterised shallow sill (Figs. 3, 4), an oxygenated water column, and negligible fishing pressure at depth (Fig. 2).

The heterogeneity among these basins is not a limitation of the comparative approach but a source of analytical strength. Paired with the Red Sea's unexploited baseline, the Mediterranean's combined record of warming and centuries of deep-water exploitation facilitate exploration of the independent and joint effects of these pressures on deep-sea community structure, a decomposition that neither system easily

permits alone. The Sulu Sea, positioned as an intermediate along both the thermal intensity and biogeographic filtering gradients, offers a system against which to disentangle the contribution of sill depth and temperature to functional truncation, an ambiguity that may be difficult to resolve within either basin individually. Finally, the Black Sea, disqualified as an aerobic warming analogue, represents the deoxygenated endpoint of a trajectory that ocean warming and stratification are projected to push other basins toward ⁴⁹. The functional comparison between the Black Sea's chemocline-structured communities and the oxygenated assemblages of the Red Sea and Sulu Sea could inform predictions about how warming-driven deoxygenation reshapes community structure independently of temperature. Together, these four basins span gradients of thermal intensity, exploitation history, oxygenation state, and sill geometry that no system captures in isolation. The Red Sea's value as a climate analogue is amplified, not diminished, by the existence of these complementary systems.

The Deep Red Sea as a Research Platform for Mesopelagic Futures

The deep Red Sea combines a thermal profile that approximates projected mesopelagic conditions under extreme sustained high-emission warming scenarios (21–22°C from 150 m to the seafloor; not reached globally at 200 m depth until 2100–2200 under SSP5-8.5 ^{10,50}, negligible deep-water exploitation across at least 70 years of catch records ^{5,28}, and a deep-water fish assemblage whose functional trait space is truncated along axes of depth specialisation but retains the feeding, trophic, and life-history diversity that structures mesopelagic communities. No other warm deep basin matches this combination: the Mediterranean's century of deep trawling confound its thermal signal, the Black Sea's permanent anoxia disqualifies it as an aerobic analogue, and the Sulu Sea's weaker thermal contrast and deeper sill reduce its discriminatory power. These properties position the deep Red Sea as a globally distinctive natural analogue for testing the effects of sustained warmth on mesopelagic ecosystems.

The Red Sea's value as a climate analogue rests not on the assumption that other ocean basins will converge on its current biological state, but on the testable questions its extreme conditions enable. Five lines of investigation are particularly tractable:

1. **Functional trait viability under warming.** Characterisation of the Red Sea's mesopelagic assemblage, and partitioning of community filtering between the Bab-el-Mandeb sill and the basin's thermal regime, can establish which functional trait configurations remain viable under the temperatures projected for global mid-depth oceans under climate change.
2. **Trait–vulnerability relationships.** Systematic comparison of which species and trait profiles have persisted in the Red Sea versus those absent from a cooler Indian Ocean source pool can yield empirical trait–vulnerability relationships for deep-sea taxa under sustained warming. If traits predicting exclusion from the Red Sea also predict sensitivity to warming in other systems, these relationships become transferable tools for conservation triage across the global mesopelagic,

enabling robust vulnerability assessment for deep-sea species in a future that cannot yet be directly observed.

3. **Cross-boundary thermal adaptation.** Species shared between the Red Sea and the adjacent Arabian Sea span a steep thermal gradient across a narrow geographic boundary, creating natural paired comparisons with which to examine the pace and mechanistic basis of thermal adaptation in deep-sea lineages. This includes determination of the relative contributions of plasticity and genetic adaptation, which trait axes respond earliest, and over what timescales measurable divergence accumulates.
4. **Life-history responses to sustained warmth.** The conservative life histories of deep-sea species (slow growth, late maturity, low fecundity) are conventionally attributed to cold-suppressed metabolic rates, yet Red Sea deep-water species experience temperatures far exceeding those at equivalent depths in any other basin. Whether sustained warmth accelerates these life histories, or whether they remain conservative because food limitation rather than temperature is the binding constraint, has direct implications for how fisheries reference points should be recalibrated as mesopelagic waters warm and exploitation expands to depth globally.
5. **Bathymetric zonation without a thermal gradient.** The Red Sea's near-isothermal water column largely removes the thermal gradient associated with depth partitioning. The Red Sea therefore offers a system in which to isolate whether bathymetric zonation is maintained primarily by temperature or by other mechanisms such as pressure, oxygen, or interspecific interactions, a question that is difficult to address in thermally stratified oceans.

If the patterns documented through these investigations (sustained trophic diversity, predictable trait–vulnerability relationships, relaxed depth zonation, adaptive divergence across the Bab-el-Mandeb thermal boundary, and life-history responses to warmth) begin to emerge in other mesopelagic systems as they warm, then the Red Sea provides an empirical reference point for the endpoints of mesopelagic restructuring worldwide.

Maximising this potential depends, however, on a single condition: the basin must be characterised before its defining properties erode. The preconditions for both a fisheries transition to depth and commercial seabed mining are present across the region. If extractive pressure reaches the deep Red Sea before a pre-disturbance baseline is established, the system's capacity to isolate temperature effects from exploitation will be substantially compromised. Yet the research programme required is not only urgent but achievable. The five lines of investigation outlined above are achievable with existing survey, genomic, and analytical technologies; the Red Sea's relative accessibility compared with open-ocean deep-sea systems reduces logistical barriers; and the basin's restricted spatial extent makes comprehensive characterisation feasible within a programme of coordinated expeditions rather than decades of incremental sampling. Realising its full potential will require scientific coordination across the diverse nations bordering the Red Sea, states that span a wide range of research capacity, governance structures, and development priorities. The deep Red Sea is an irreplaceable natural analogue for the future of the world's mid-depth oceans. The scientific capacity to characterise it exists; the question is whether the will to do so can be mobilised before the window closes.

Methods

All analyses in this study were conducted using R v4.3.0 within RStudio 2023.03.1^{51,52}. Data manipulation used the *tidyverse* suite. Figures were produced using *ggplot2* with multi-panel layouts assembled using *cowplot*.

Red Sea Temperature Profiles

Observed temperature-depth profiles for the Red Sea were obtained from the CORA (Coriolis Ocean Dataset for Reanalysis) database, accessed via the CORIOLIS data portal (<https://data-selection.odatis-ocean.fr/coriolis>; downloaded 16 February 2026). All profiles falling within the Red Sea basin (32–43.5°E, 12.54–30°N) were retained. Where depth was not recorded directly, it was estimated from pressure using the TEOS-10 Gibbs SeaWater equation of state implemented in the *oce* R package. Profiles were filtered to retain only observations with position quality control flags indicating good or probably good data (CORIOLIS QC flags 1, 2, 5, and 8). For temperature, pressure, and depth QC variables, the same flags were accepted alongside NA values (reflecting unstandardised QC fields in some data providers), with the additional constraint that at least one of the four QC variables carried a non-missing flag for each observation. To ensure adequate vertical resolution, only profiles extending below 200 m with at least 10 valid temperature observations were retained. Temperature observations were binned at 10 m intervals and median temperature per bin was calculated across all retained profiles to characterise the basin's vertical thermal structure.

Global Climate Projections

To contextualise Red Sea deep-water temperatures against projected future ocean conditions, we extracted depth-resolved ocean temperature fields from CMIP6 (Coupled Model Intercomparison Project Phase 6) simulations¹⁰. We used the IPSL-CM6A-LR Earth system model⁵⁰ under the SSP5-8.5 scenario, which represents an aggressive upper-bound fossil-fuelled development pathway that is most probably implausible²⁵. This scenario was selected not as the most probable trajectory, but to identify the thermal envelope that the deep ocean may approach under the most extreme version of future conditions.

Decadal-mean potential ocean temperature (*thetao*) was extracted at three target depths (0, 200, and 1000 m) for four time horizons (2020, 2050, 2100, and 2200). The IPSL-CM6A-LR model outputs are stored on a curvilinear ORCA grid; to enable global mapping, fields at each depth–year combination were interpolated onto a regular 150 × 150 latitude–longitude grid using bilinear interpolation implemented in the *akima* R package. Duplicate coordinates arising from the curvilinear grid were resolved by averaging.

Because CMIP6 models do not resolve the Red Sea basin at sufficient spatial resolution to reproduce its anomalous deep thermal structure, a delta-change approach was applied. For grid cells falling within the Red Sea domain, the projected temperature anomaly (ΔT) relative to the 2020 baseline was computed at

each depth from the CMIP6 field. These anomalies were then added to observed Red Sea reference temperatures (27.88°C at 0 m, 22.10°C at 200 m, and 21.52°C at 1000 m; derived from CORA profile medians) to produce adjusted projections that preserve the basin's thermal structure while incorporating the projected rate of warming. For all non-Red Sea grid cells, CMIP6 temperatures were used directly. To facilitate global comparison with the Red Sea deep-water thermal regime, all temperatures were expressed as deviations from the Red Sea 1000 m reference temperature (21.52°C), such that grid cells with values near zero occupy a thermal space comparable to the present-day Red Sea deep basin.

Fisheries Compositional Analysis

To place the Red Sea's fisheries profile in a global context and assess the basin's exploitation trajectory, we analysed reconstructed catch data from the Sea Around Us database²⁸ for all Large Marine Ecosystems (LMEs). Catches were aggregated by LME, year, and functional group (as defined by Sea Around Us), summing across all fishing sectors and gear types. Krill were excluded as they occurred in only a single LME and introduced compositional instability. An artisanal and subsistence pressure index was constructed to characterise the trajectory of coastal small-scale fisheries catches in the Red Sea and comparator LMEs. Artisanal and subsistence catches were summed by LME and year, then smoothed using a trailing 5-year rolling mean to suppress interannual noise while preserving trend direction. The smoothed series was normalised to each LME's historical peak, yielding a pressure index ranging from 0 to 1, where 1 represents peak artisanal catch. This index provides a standardised basis for comparing the phase of artisanal exploitation across LMEs with very different absolute catch magnitudes. For each LME–year observation, catch tonnages by functional group were converted to proportions and analysed as compositional data, accounting for the unit-sum constraint. A pseudocount equal to half the minimum observed non-zero proportion was added to all zero entries to enable log-ratio transformation while minimising distortion of the compositional geometry. The centred log-ratio (CLR) transformation⁵³ was then applied using the *compositions* R package. CLR-transformed values were further smoothed with a trailing 5-year rolling mean (*zoo* R package) to align temporal resolution with the pressure index.

Principal components analysis (PCA) was performed on the CLR-transformed compositional data. Data were centred but not scaled, as the CLR transformation already places all functional groups on a comparable log-ratio scale. PCA loadings were examined to identify the functional groups driving compositional variation among LMEs, and loading magnitudes were compared against a null threshold of $1/\sqrt{z}$ (where $z = 29$ functional groups) to identify dominant contributors to each principal component. The Red Sea's position in global compositional space was characterised using 99% normal-theory standard ellipses in the PC1–PC2 plane, computed for each LME across all years. To assess the trajectory of fisheries composition following the peak of artisanal pressure, post-peak PC1 trajectories were extracted for all LMEs that occupied a compositional position within ± 35 PC1 units of the Red Sea at their respective artisanal peaks, and had peaked at least 5 years before the end of the time series, ensuring sufficient post-peak data for trend assessment. Individual LME trajectories were plotted

alongside the Red Sea's post-peak path to contextualise the direction and rate of compositional change following the artisanal inflection point.

Species Pool Compilation

The global species pool comprised all marine and brackish-water fish species with a recorded maximum depth exceeding 200 m, sourced from FishBase²⁸ via the *rfishbase* R package. This depth threshold was chosen to correspond to the conventional boundary of the continental shelf and the onset of the mesopelagic zone, consistent with the definition of “deep sea” adopted throughout this study. We therefore interpret this pool as fishes with documented use of waters deeper than 200 m, rather than as a set of obligate deep-sea specialists. For each species, the following trait data were extracted from FishBase: minimum and maximum recorded depth, maximum total length, trophic level, von Bertalanffy growth constant (*K*), feeding pathway, body shape, water column position, and fertilisation mode. Species were assigned to three nested geographic domains. Red Sea species were identified from a compiled regional checklist³⁶. Arabian Seas and Somali Current species were identified from FishBase distribution records and cross-referenced with regional occurrence databases. Indian Ocean membership was assigned to all species with at least one occurrence record in the Ocean Biodiversity Information System (OBIS) within the Indian Ocean basin (identified via spatial intersection with the IHO Global Oceans and Seas shapefile v1⁵⁴) or membership in the Arabian Seas and Somali Current or Red Sea pools.

Occurrence Data and Biogeographic Variables

Species occurrence records were obtained from OBIS⁵⁵, extracted 31 May 2026, using the World Register of Marine Species (WoRMS) AphiaIDs⁵⁶ as taxonomic identifiers, accessed via the *robis* R package. To avoid circularity in subsequent predictive modelling, all OBIS records falling within the Red Sea domain (32–43.5°E, 12.54–30°N) were removed prior to the calculation of biogeographic variables. Records intersecting land polygons (Natural Earth medium-scale coastlines) were excluded using spatial intersection in the *sf* R package.

Three biogeographic variables were derived from occurrence records. Latitudinal range (maximum minus minimum recorded latitude) and median latitude were calculated from the global OBIS dataset to characterise each species' climatic niche breadth and thermal affinity, respectively. The minimum great-circle distance from any Indian Ocean OBIS record to the Bab-el-Mandeb strait (12.54°N, 43.50°E) was calculated using the Haversine formula implemented in the *geosphere* R package as a proxy for geographic accessibility to the Red Sea. For Red Sea endemic species lacking OBIS records outside the basin, distance to Bab-el-Mandeb was set to 1 km. Total OBIS sighting count was retained as a proxy for discoverability.

Trait Standardisation and Derived Variables

FishBase water column positions were simplified into three categories to reduce sparsity: demersal (bathydemersal, demersal, and reef-associated), benthopelagic, and pelagic (bathypelagic, pelagic-neritic, pelagic-oceanic, and pelagic). Fertilisation mode was recoded as internal or external. Two derived variables were calculated: depth range (maximum minus minimum depth) and median depth (midpoint of depth range). Eight variables exhibiting strong right-skew (OBIS sighting count, minimum depth, maximum depth, maximum total length, K , median depth, depth range, and latitudinal range) were $\log_{10}(x + 1)$ -transformed prior to imputation to improve the linearity assumptions of subsequent imputation models.

Multiple Imputation of Species Traits

Missing trait values are pervasive in global fish trait databases, particularly for life-history parameters of deep-sea species. Little's missing-completely-at-random (MCAR) test⁵⁷ rejected the null hypothesis of missing completely at random ($p < 0.05$), indicating that missingness was related to observed variables and supporting the use of multiple imputation under a missing-at-random (MAR) assumption. Multiple imputation was performed using multivariate imputation by chained equations (MICE) implemented in the *mice* R package.

Continuous variables were imputed using predictive mean matching (PMM), which preserves the distributional properties of observed data by drawing imputed values from observed donors rather than from a parametric distribution. Categorical variables (body shape, water column position, fertilisation mode, feeding pathway) were imputed using logistic regression or polytomous logistic regression as appropriate. Two variables required non-standard imputation strategies. Minimum depth was imputed using a custom bounded PMM algorithm that resampled from valid observed donors whenever the standard PMM draw violated the constraint that minimum depth cannot exceed maximum depth. This constraint-aware imputation prevents biologically implausible values that would propagate into derived variables and downstream analyses. Median depth and depth range were imputed passively as deterministic functions of imputed minimum and maximum depth, with transformations accounting for the $\log_{10}(x + 1)$ scale of the parent variables.

The prediction matrix was configured to include all variables intended for downstream analysis as predictors during imputation, following the congeniality principle⁵⁸, which requires that the imputation model be at least as rich as the analysis model to avoid bias. The taxonomic class was included as a categorical predictor to capture broad phylogenetic structure in trait covariance. Other taxonomic levels (phylum, order, family, genus) and species identity were excluded as predictors to avoid overfitting and rank-deficiency. Derived variables (median depth, depth range) were excluded as predictors for their parent variables (minimum and maximum depth) to prevent circular conditioning.

The number of imputations was determined empirically using the von Hippel quadratic rule⁵⁹. A pilot imputation with $m = 20$ datasets (25 iterations each) was run and the fraction of missing information (FMI) was estimated from a pooled frequentist logistic regression fitted to the pilot imputations using the same predictor structure as the final Bayesian model. At a target coefficient of variation of 0.05, the quadratic rule indicated that $m = 50$ imputations were required, assessed using the *howManyImputations* R package. The final imputation used $m = 50$ datasets with 25 iterations per chain. Convergence was assessed visually using trace plots of imputed values and density overlays of imputed versus observed distributions.

Imputation was performed on the full global species pool, including species from outside the Arabian Seas and Somali Current region. These species were subsequently excluded from the prediction model but were retained during imputation to preserve the global trait covariance structure. Excluding them prior to imputation would have biased the imputation model toward the trait distributions of a geographically restricted subset.

Bayesian Species Prediction Occurrence Model

To identify deep-sea fish species plausibly present in the Red Sea but not yet recorded, we fitted a Bayesian phylogenetic logistic regression model predicting the probability of Red Sea occurrence as a function of species traits, biogeographic accessibility, and discoverability. The model was designed not as a powerful predictive classification tool but as a hypothesis-generating framework. The model aims to estimate the plausibility of Red Sea presence for each species in the regional pool, conditional on functional traits, geographic proximity, and sampling effort.

A taxonomy-based phylogeny was constructed for all species in the Arabian Seas and Somali Current pool using the *ape* R package. The tree was built from the Linnaean hierarchy (phylum, class, order, family, genus, species) and branch lengths were assigned using Grafen's method⁶⁰ to produce an ultrametric tree. This approach captures broad taxonomic non-independence but should not be interpreted as a time-calibrated evolutionary history. A phylogenetic variance–covariance matrix was computed from this tree and incorporated as a random effect to account for phylogenetic non-independence in species' propensity to colonise the Red Sea.

For the Bayesian species prediction model the response variable was binary Red Sea occurrence (0/1). Fixed effects were grouped into three inferential categories reflecting distinct mechanisms: accessibility (minimum depth, median latitude, and minimum distance to Bab-el-Mandeb), which encode the physical and biogeographic filters governing entry into the Red Sea; tolerance (depth range and latitudinal range), which encode tolerance of environmental variation and niche breadth; and ecology (maximum total length, trophic level, body shape, water column position, and fertilisation mode), which encode functional attributes potentially relevant to persistence under the Red Sea's thermal and bathymetric constraints. A fourth term, OBIS sighting count ($\log_{10}$ -transformed), was included as a discoverability covariate to

separate the effect of detection probability from genuine ecological filtering. All continuous predictors were scaled (zero-mean, unit-variance) prior to model fitting.

Weakly informative priors were specified to regularise estimation while permitting the data to dominate inference. Fixed-effect slopes were assigned $\text{Normal}(0, 0.7)$ priors, providing moderate shrinkage toward zero on the logit scale. The intercept was assigned a $\text{Normal}(0, 1)$ prior, centred on a logit-scale value corresponding to equal prior probability of presence and absence; this reflects the expectation that the true proportion of Red Sea species in the Arabian Seas and Somali Current pool may be higher than the observed ratio of ~ 0.39 but without strong prior commitment to a specific value. The phylogenetic standard deviation was assigned an $\text{Exponential}(2)$ prior, which places most prior mass on small phylogenetic effects while permitting larger values if strongly supported by the data, thereby regularising the model toward trait-based rather than clade-based prediction unless the phylogenetic signal is strong.

The model was fitted across all 50 imputed datasets using *brms*, fitting a separate Bayesian model to each imputed dataset and pooling posterior draws using Rubin's rules⁶¹. Each model was fitted with 4 chains of 6,000 iterations (4,000 warmup), an adapted delta of 0.99, and a maximum tree depth of 15 to ensure adequate exploration of the posterior geometry. Model performance was assessed using posterior predictive checks and Pareto-smoothed importance-sampling leave-one-out cross-validation (PSIS-LOO). Posterior collinearity was assessed by examining pairwise correlations among fixed-effect posterior draws; only latitudinal range and sighting count exhibited moderate correlation, consistent with the shared information content of range breadth and detection probability. Bayesian R^2 was 0.20.

Counterfactual Prediction of Occurrence

To separate ecological filtering from sampling artefact, we generated counterfactual predictions under a scenario of high discoverability. For all species in the Arabian Seas and Somali Current pool, the OBIS sighting count was set to the 95th percentile of the observed distribution (25,304 records), simulating a hypothetical state in which all species have been sampled with equivalent high effort. Posterior expected predictions (conditional mean probabilities; 1,000 draws per species, with new phylogenetic levels permitted) were generated from the pooled model applied to this counterfactual dataset using the *tidybayes* R package. Species were classified into confidence tiers based on their posterior predictive distributions: high-confidence colonisers (entire 95% credible interval above 0.5), moderate-confidence colonisers (entire 50% credible interval above 0.5) and low confidence colonisers (median probability > 0.5). Posterior probabilities were interpreted as calibrated plausibility estimates rather than hard classification outputs.

Functional Trait Analysis

To characterise the functional structure of the Red Sea deep-sea fish assemblage relative to the broader species pool, we performed a principal coordinates analysis (PCoA) on species-level functional traits.

Trait selection followed established functional ecology frameworks⁶², aiming to represent five core dimensions of species' ecological roles: food acquisition (trophic level, feeding pathway, maximum total length), mobility (body shape, maximum total length, latitudinal range, median depth, depth range, water column position), nutrient budget (maximum total length, *K*), reproduction (fertilisation mode, maximum total length), and defence against predation (maximum total length). Gregariousness and mouth position were excluded due to extreme data sparsity (available for ~1% and ~12% of species, respectively). Trait values were averaged across the 50 imputations at the species level prior to ordination. For continuous traits, this was the arithmetic mean; for categorical traits, the modal category across imputations was assigned. This approach captures central tendencies in trait space while avoiding artificial inflation of trait volume that would result from treating each imputation as an independent observation.

Gower distances⁶³ were computed using *cluster* R package, chosen for its ability to handle mixed continuous and categorical trait data with appropriate distance scaling for each data type. PCoA was performed on the Gower distance matrix with Cailliez correction for negative eigenvalues⁶⁴, implemented in *ape*. The number of retained axes was determined using the AUC of the co-ranking R^{NX} curve⁶⁵, computed using the *coRanking* R package. This metric quantifies how well the reduced-dimension representation preserves the neighbourhood structure of the original high-dimensional distance matrix. Six PCoA axes were required to achieve $AUC > 0.7$ ⁶⁶, and these were retained for all subsequent analyses. Trait–axis correlations were quantified using the *envfit* function in the *vegan* R package, which fits each trait vector (continuous) or centroid (categorical) to each PCoA axis independently and assesses significance using 999 permutations. This per-axis approach (rather than fitting all axes simultaneously) provides an interpretable decomposition of which functional dimensions each ordination axis captures.

To quantify functional-space truncation across spatial scales, convex hull volumes were computed in the six-dimensional PCoA space for four nested assemblages: the global deep-sea species pool, the Indian Ocean subset, the Arabian Seas and Somali Current pool, and the Red Sea assemblage (including both confirmed and probable colonists as identified by the prediction model). Convex hulls were calculated using the Quickhull algorithm implemented in the *geometry* R package. The ratio of Red Sea to Arabian Seas and Somali Current hull volume quantifies the proportion of regional functional space retained after the combined environmental and physical filtering imposed by the Red Sea basin.

Declarations

Author Contributions

AJT: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, visualisation, writing – original draft, writing- review & editing. **MLB**: funding acquisition, project administration, writing- review & editing.

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Competing Interests

The authors declare no competing interests.

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Figures

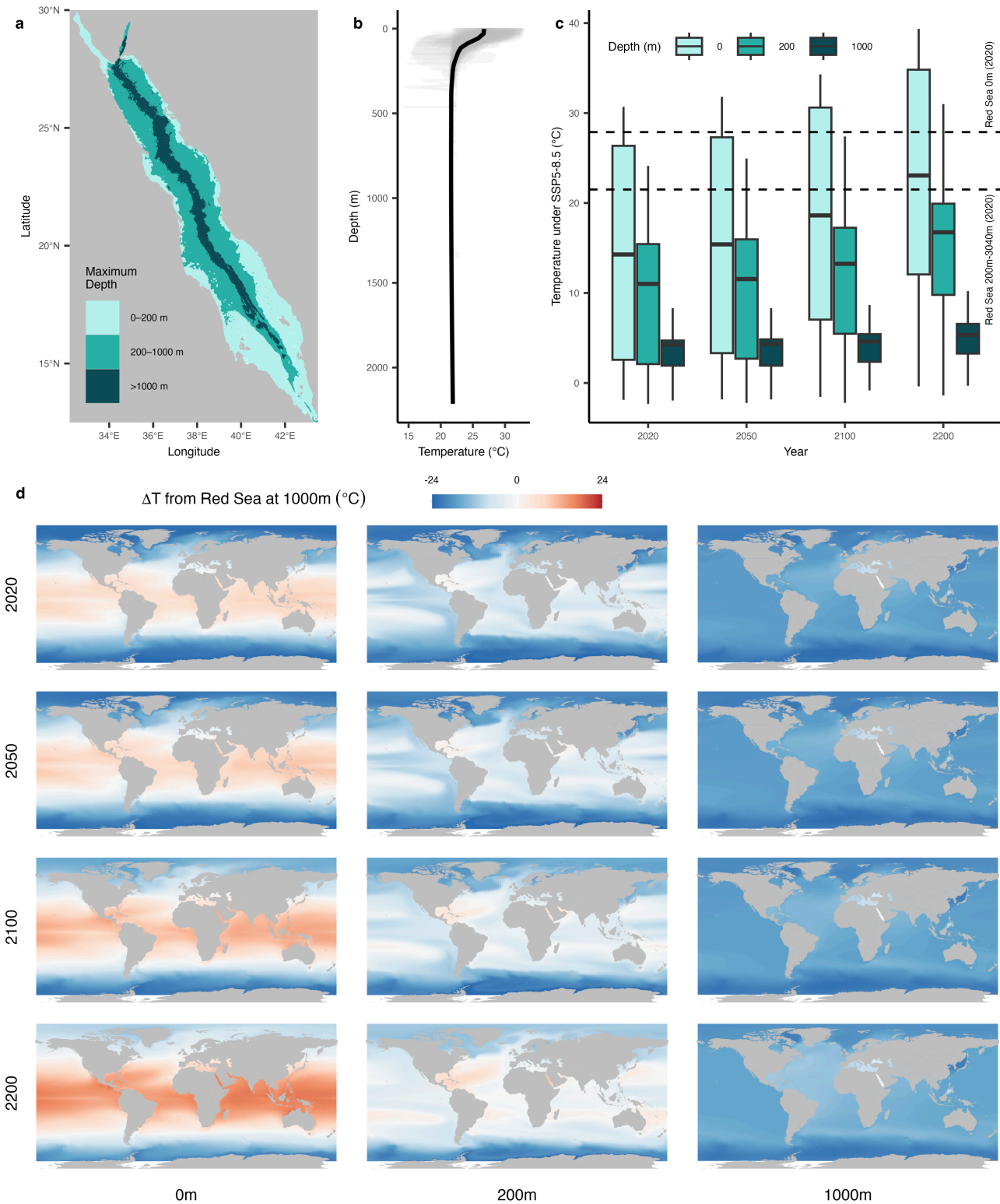


Figure 1

The deep Red Sea already occupies the thermal space projected for the global mesopelagic under sustained warming. **a** Depth profile of the Red Sea. **b** Median temperature–depth profile for the Red Sea (black line) compiled from CORA hydrographic profiles ($n = [X]$ profiles; 10 m depth bins), showing near-isothermal conditions of 21–22 °C from ~150 m to the seafloor (~3,040 m). **c** Global ocean temperature distributions relative to current Red Sea surface and deep water temperatures for four time horizons under

SSP5-8.5 (IPSL-CM6A-LR). Global average upper mesophotic temperatures do not approach current Red Sea temperatures until 2200. **d** Global ocean temperature distributions relative to predicted Red Sea 1,000 m temperature at three depths for four time horizons (2020, 2050, 2100, 2200) under SSP5-8.5 (IPSL-CM6A-LR). Grid cells near zero (white) occupy a thermal regime comparable to the deep Red Sea. At 200 m depth, most tropical and subtropical regions do not approach current Red Sea deep-water temperatures until beyond 2100, and many not until beyond 2200.

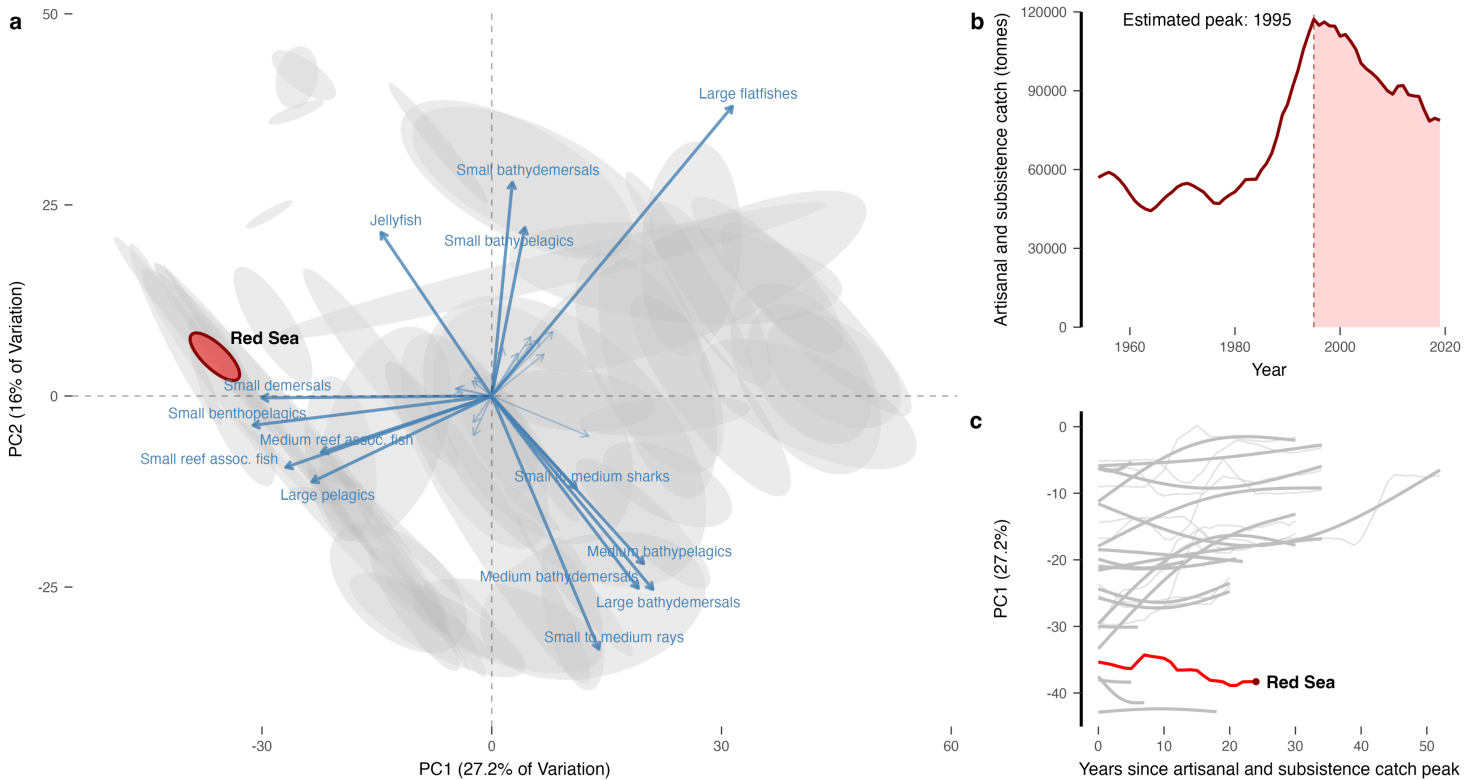


Figure 2

Red Sea fisheries remain among the most coastally dominated globally despite decades of artisanal overexploitation. **a** Principal component analysis of centred log-ratio transformed catch composition across all Large Marine Ecosystems (LMEs), based on Sea Around Us reconstructed catch data (1950–2019). PC1 (27.2% of variance) separates coastal and reef-dominated fisheries (negative values) from those with substantial deep-water and oceanic catch contributions (positive values). Ellipses represent 99% normal-theory standard ellipses for each LME; the Red Sea (highlighted) occupies the 6th percentile on PC1. **b** Artisanal and subsistence catch pressure index (5-year trailing mean, normalised to each LME's historical peak) for the Red Sea and comparator LMEs with similarly coastal catch composition at their respective artisanal peaks. The Red Sea peaked between 1995 and 1999 and has since declined by ~35% without meaningful compositional movement along PC1. **c** Post-peak PC1 trajectories for LMEs occupying a comparable compositional position at their artisanal peak, illustrating divergent post-peak pathways, expansion into offshore and deep-water functional groups versus continued coastal focus.

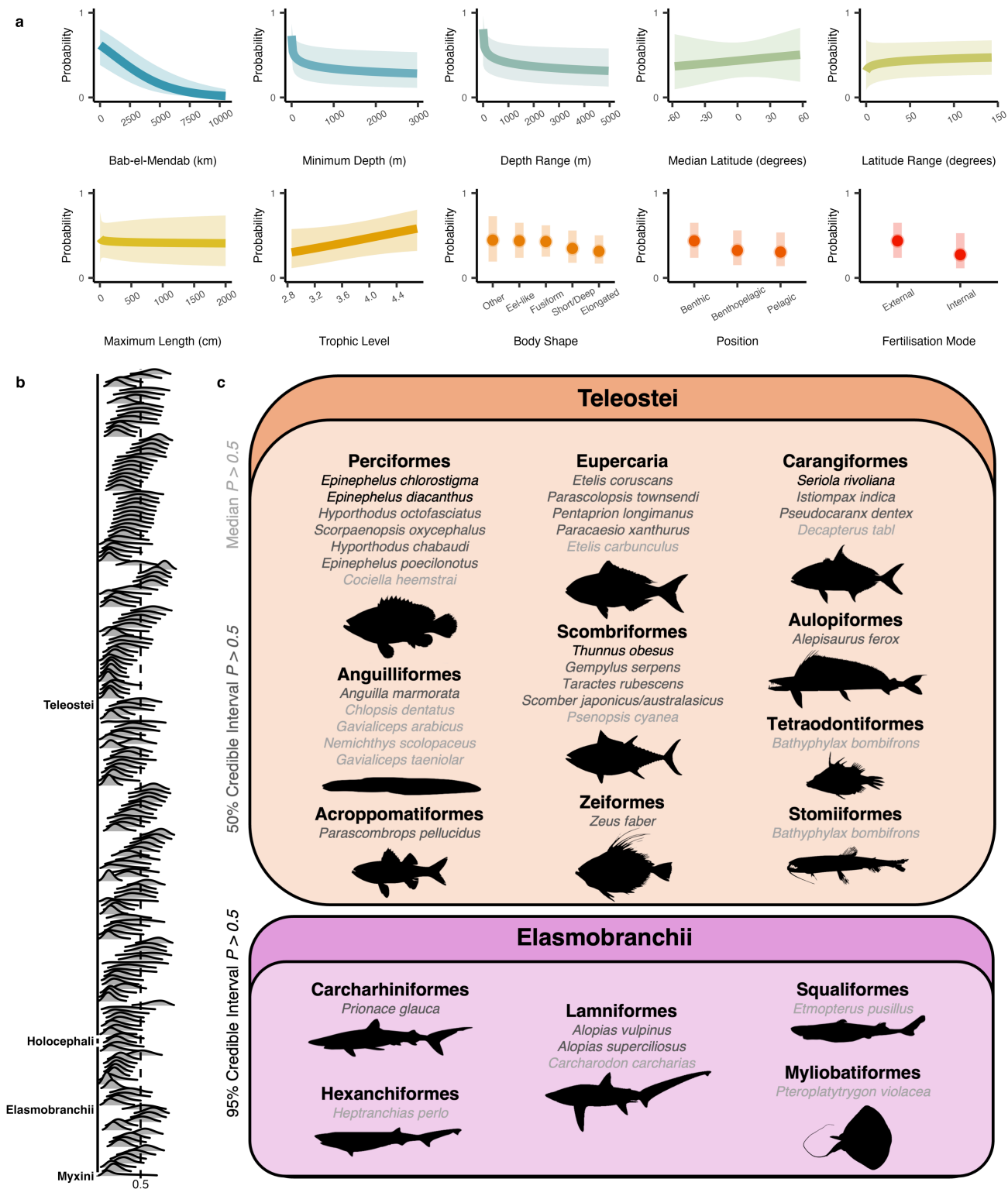


Figure 3

Trait-based prediction identifies fish species plausibly present but unrecorded in the deep Red Sea.
a Standardised posterior coefficient estimates (mean $\pm$ 95% credible interval) for fixed effects in the Bayesian phylogenetic logistic regression model, pooled across 50 multiply imputed datasets using Rubin's rules. Negative coefficients for minimum depth, distance to Bab-el-Mandeb, and internal fertilisation indicate reduced likelihood of Red Sea occurrence. Positive coefficients for trophic level and latitudinal

range indicate increased likelihood. **b** Posterior predicted probabilities of Red Sea occurrence for all species in the Arabian Seas and Somali Current deep-sea pool ($n = 194$ non-Red Sea species), under a counterfactual high-discoverability scenario. Species are classified into three confidence tiers: high (entire 95% credible interval > 0.5), moderate (entire 50% credible interval > 0.5), and low (median > 0.5). **c** Thirty-eight species across 15 orders meet at least the low-confidence threshold for potential occurrence in the Red Sea.

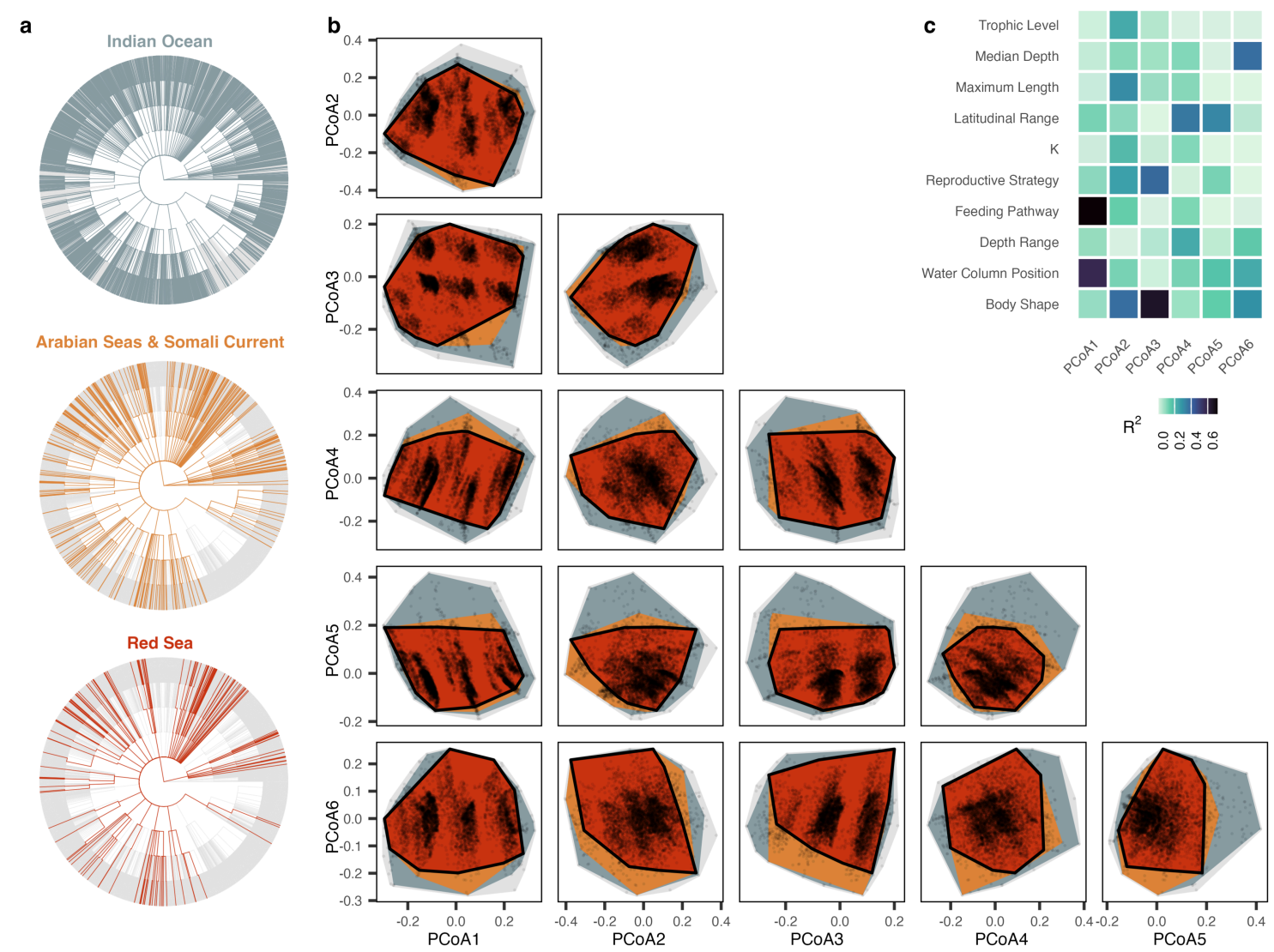
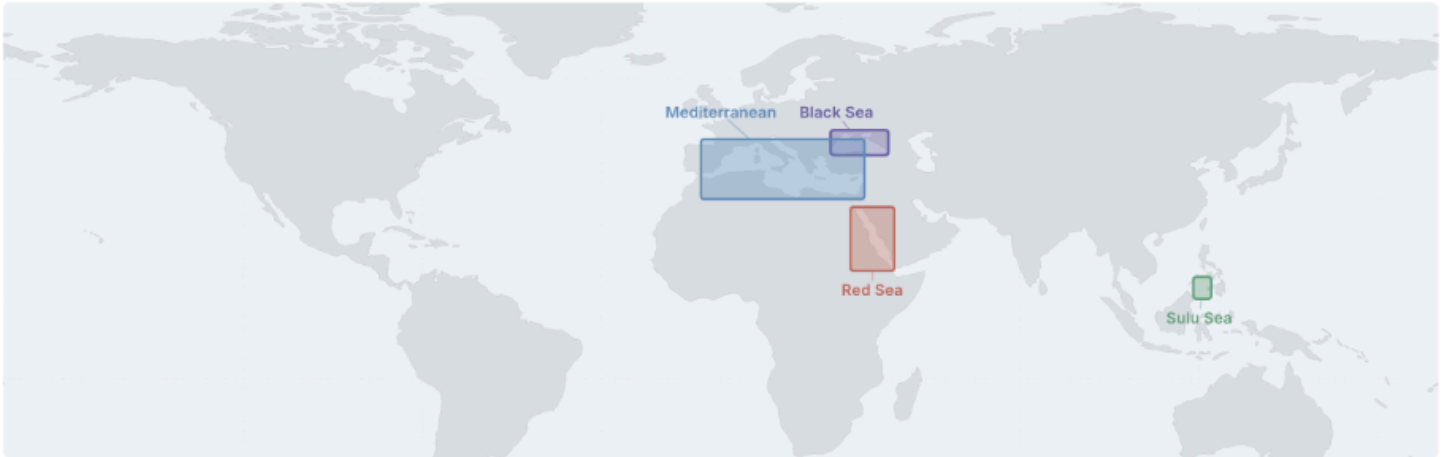


Figure 4

Sill filtering truncates depth-specialist functional space but retains mesopelagic feeding and life-history diversity. **a** taxonomic tree of all known deep-water species (light grey) and those from the Indian Ocean, the Arabian Seas and Somali Current, and the Red Sea (including predicted species). **b** Pairwise projections of the six-axis principle coordinates analysis (PCoA) ordination of functional traits for global deep-sea fishes. Convex hulls delineate the four nested assemblages: global pool, Indian Ocean, Arabian Seas and Somali Current, and Red Sea. The Red Sea assemblage occupies 22.4% of global and 66.8% of Arabian Seas and Somali Current functional space. **c** PCoA analysis axis loadings. PCoA6, loading on median depth, body

shape, and water column position, is the primary axis of Red Sea–source pool divergence, consistent with bathymetric filtering by the Bab-el-Mandeb sill. PCoA1 (feeding mode, water column position) and PCoA2 (slow–fast life-history continuum), the axes most relevant to the climate-analogue argument, show minimal divergence between the Red Sea and its source pool, indicating retention of mesopelagic trophic and life-history diversity.

a Semi-enclosed deep-sea basins



b Basin profiles

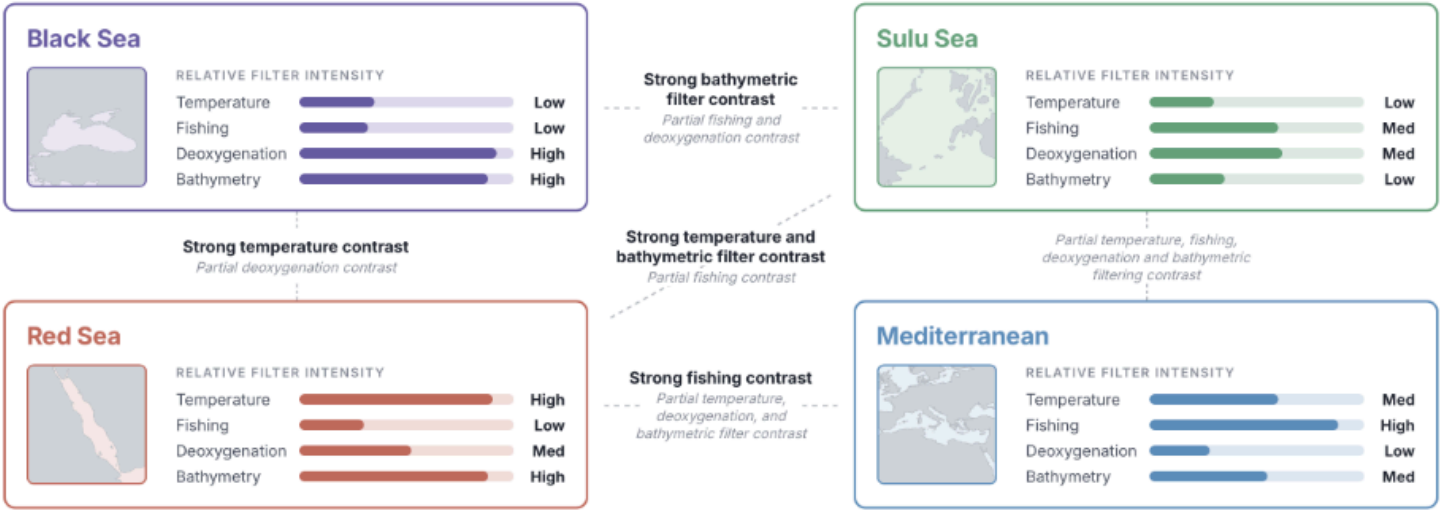


Figure 5

The Red Sea holds a unique combination of thermal extremity, oxygenation, and exploitation-free baseline among warm deep basins. Comparative summary of semi-enclosed basins with anomalously warm deep waters. **a** Geographic locations of the Red Sea, Mediterranean Sea, Sulu Sea, and Black Sea. **b** Key properties governing each basin's utility as a climate analogue for aerobic deep-sea communities. The Mediterranean's century of deep trawling confounds thermal and exploitation signals; the Black Sea's permanent anoxia below ~150–200 m precludes aerobic community comparison; the Sulu Sea's weaker thermal contrast (+10 °C versus open Indo-Pacific) and deeper sill (~420 m) reduce discriminatory power. Only the Red Sea combines the most extreme deep thermal regime, oxygenated water column, strong

biogeographic filtering across a shallow sill (~137–320 m), and negligible deep-water fisheries exploitation. Together, these four basins span complementary gradients of thermal intensity, exploitation history, oxygenation, and sill geometry that enable decomposition of drivers no single system can isolate.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [01ClimateProjections.txt](#)
- [Specieslist.csv](#)
- [02FisheriesComparisons.txt](#)
- [03SpeciesFunction.txt](#)
- [finalspeciesdata.csv](#)
- [RS4.pdf](#)