



Upwelling generates a unique refugium from climate change in the fast warming Eastern Mediterranean Sea

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Abstract

The identification of areas resistant to climate change is a strategy to support biodiversity conservation on a warming planet. Such ‘refugia’ are often detected by modeling future climate and species distributions. More rarely, refugia hypotheses are tested in the field. The easternmost sector of the Eastern Mediterranean is affected by the largest climate-driven collapse of native biodiversity hitherto documented. However, a 150-km-long upwelling system occurs along the south-western Cyprus coastline, keeping summer seawater temperatures 2–3 °C lower than at any other location in the whole sector. We here test the hypothesis that this area is an in-situ climate refugium. We sampled mollusks from 5 to 30 m depth along two transects with *Posidonia oceanica* meadows and on rocky substrates inside and outside the upwelling area. We reconstructed historical baselines from shelly death assemblages, that is, the accumulations of molluscan shells on the sea bottom. As expected, native species richness in the upwelling area was several fold higher than in the warmer site, irrespective of habitat type. Biodiversity loss was considerably lower in the upwelling area in *Posidonia* meadows. Rocky substrates showed significant biodiversity loss at both sites in shallow water (5–15 m) reflecting the loss of macroalgal cover. Deeper (20–30 m) rocky substrates were covered by macroalgae and showed considerably lower biodiversity loss, even at the warmer site. These results suggest to target also the lower photic zone when identifying refugia. The upwelling system of Cyprus is the only refugium for the collapsing eastern Mediterranean Sea biota and may prove the final stronghold of its endemic species.

Keywords Biodiversity · Cyprus · Historical baselines · Levantine sea · Marine protected areas · Mollusca · Upwelling

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Introduction

Global mean surface temperature has increased by 1.09 °C since the mid-19th century, with estimates between 1.4 °C and 4.4 °C by 2100 depending on the emission scenario (IPCC 2023). This magnitude of change has already caused numerous impacts on marine ecosystems, and future scenarios imply even greater biodiversity and biomass losses (Lotze et al. 2019; Poloczanska et al. 2013). In this context, the identification and protection of areas resistant to ongoing climate change is a strategy to support biodiversity conservation (Morelli et al. 2016). Such areas or ‘refugia’ – locations where species may retreat to and persist in during large-scale and long-term climatic change – will facilitate not only survival during anthropogenic climate warming, but also expansion into depleted surrounding areas should conditions become favorable again (Keppel et al. 2015). Refugia are often identified by comparing current to future climate and recognizing areas where suitable habitat persists (in situ refugia) or is generated (*ex situ* refugia) (e.g. Ban et al. 2016; Ben Rais Lasram et al. 2010; Cacciapaglia and van Woesik 2015; Davis et al. 2021; Doxa et al. 2022; Gallagher and Albano 2023; Sales and Pires 2023; van Hooedonk et al. 2013). Only rarely have potential refugia and their positive effects on biodiversity been assessed and quantified in the field. Indeed, areas where increasing seawater temperatures are already causing ecosystem shifts offer opportunities to detect refugia, identifying areas where structuring species (e.g. algae, corals) or a high biodiversity persist (e.g. Alabia et al. 2021; Arriaga et al. 2024; Barceló et al. 2018; Lourenço et al. 2016).

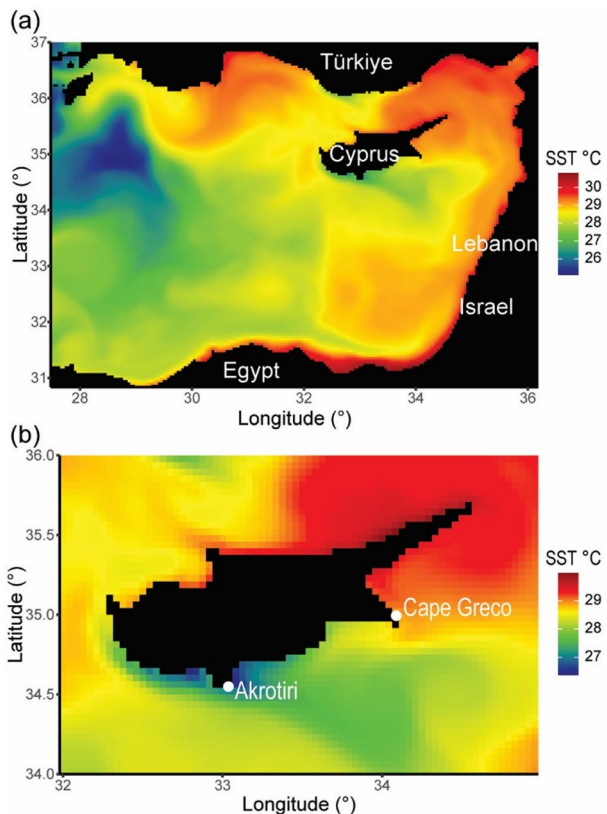
The Mediterranean Sea is a temperate semi-enclosed basin whose geographic location and hydrological regime cause a gradient of increasing seawater temperature from its north-western to south-eastern sectors (García-García et al. 2022). These features also increase its capacity to store heat and the basin is indeed warming at a rate of two to three times the global ocean average (IPCC 2022). The Levantine Sea, its easternmost sector of about 320,000 km², delimited by Türkiye in the north, the Middle East in the east, Egypt in the south and the Dodecanese islands in the west, has always been the warmest part of the entire basin and has warmed by ca. 3 °C in the last three decades (Ozer et al. 2017). Its thermal regime is now not dissimilar from the northern sectors of the Red Sea, facilitating the establishment of tropical non-indigenous species entering from the Suez Canal (Albano et al. 2021). Importantly, these temperatures, exacerbated by increasingly frequent and intense summer heatwaves (Garrahou et al. 2022), often exceed the thermal tolerance of most native species causing their regional-scale eradication from the shallow shelf (Albano et al. 2021; Rilov 2016). Indeed, 88–95% of native species known to occur historically on the Israeli shallow shelf were not detected during extensive surveys in 2016–2018, and most of the native species still found were non-reproductive individuals, indicating that this area has become a demographic sink for native species (Albano et al. 2021). This climate-driven collapse is the largest documented in the world’s oceans so far and may signal a more widespread pattern of biodiversity loss with continuing global warming in the Mediterranean Sea, which is characterized by a high share of endemic species (Costello et al. 2017; Schultz et al. 2023).

The dramatic decline of the native biota makes the Levantine Sea a priority area in the Mediterranean to locate refugia that can support the conservation of its biodiversity. Cyprus is a large (250 × 100 km) island located in the north-eastern Levantine Sea with a seawater temperature regime characterized by summers exceeding 30 °C along most of its coasts.

However, summer coastal upwelling occurs off its south-western coast along ca. 150 km of its 640 km coastline, keeping surface temperatures ca. 3 °C lower than the rest of the island and of the entire basin (Fig. 1). Coastal upwelling reduces thermal stress and such areas are thus considered candidates for refugia worldwide (Chollett and Mumby 2013; Jiménez et al. 2001; Podestá and Glynn 2001; Riegl and Piller 2003). Therefore, this is an excellent – and the only – candidate for a refugium in the Levantine Sea and a unique opportunity to test if upwelling areas may indeed safeguard threatened shallow-water biodiversity also in the Mediterranean Sea.

We thus tested two hypotheses related to the definition of this area as a refugium. Considering that the region has already been affected by climate-mediated biodiversity loss, the refugium is supposed to have higher native species diversity compared to biogeographically and ecologically similar areas outside. Additionally, the refugium is expected to have experienced less diversity loss than surrounding areas (Keppel et al. 2012). We tested these hypotheses by comparing native molluscan diversity in the two most diverse habitats of the Mediterranean Sea, *Posidonia oceanica* meadows and rocky substrates, along two depth transects from 5 to 30 m in two areas of Cyprus with contrasting seawater temperature regimes but separated by just 100 km and thus falling well within the same biogeographic realm. We quantified biodiversity loss by reconstructing baselines from shelly death assemblages, that is, accumulations of molluscan shells in the sediments that retain the signal of past species diversity and composition. Taken together, our results suggest that the upwell-

Fig. 1 Sea surface temperature (°C) in August 2022 (year of sampling) (data from the European Union Copernicus Marine Service). **(a)** Overview of the Levantine Sea showing the unique upwelling system in south-western Cyprus compared to other coastal areas in the region. **(b)** Close-up of Cyprus, with sampled sites indicated



ing system off south-western Cyprus and the deeper photic zone have a higher diversity and have experienced less diversity loss than Cyprus' much warmer eastern coasts, making it a priority area for conservation. The diverse thermal regimes of Cyprus make it a unique laboratory to inspect the processes behind diversity loss and to define strategies for conservation in warming oceans.

Materials and methods

We contrasted species richness and diversity loss off the Akrotiri Peninsula, in the middle of the upwelling system in south-western Cyprus, and at Cape Greco (Konnos Bay), an area characterized by warmer waters in eastern Cyprus (Fig. 1b). We focused on shelled mollusks due to their high taxonomic diversity and good representativeness of benthic community patterns (Tyler and Kowalewski 2017). Additionally, most species possess a durable shell, a feature that makes shelly death assemblages – the taxonomically identifiable, dead or discarded organic remains encountered in a seabed (Kidwell 2013) – effective recorders of past community and ecosystem states. Such death assemblages have repeatedly been used to faithfully reconstruct historical baselines where direct observational records were unavailable (Dietl et al. 2015; Kidwell and Tomašových 2013). Death assemblages can capture past ecosystem states occurring decades to centuries ago, depending on local conditions in terms of sedimentation rates, biogeochemistry of sediments, and durability of the skeletal remains of interest (e.g. Albano et al. 2016, 2023; Harnik et al. 2017). Here, we quantified current species richness by sampling living assemblages and we reconstructed past diversity by studying death assemblages because historical data for Cypriot waters are not available. We then measured the body size of live-collected native mollusks and contrasted it to historical values to detect any sub-lethal effects that may affect population persistence (Albano et al. 2021). To put our results into a rigorous temporal context, we determined the median age of death assemblages, a proxy for the extent of their “memory”, by radiocarbon dating. Below we offer greater detail for each step.

Data collection

The sampling design included three replicates (on 1-m² quadrats) of benthos samples taken at 5, 10, 15, 20 and 30 m depth in *Posidonia oceanica* meadows and on rocky substrates at each site (Table S1). We sampled the *Posidonia* leaves with a 20 × 40 cm hand-net (Russo et al. 1985), and the rhizomes and the rocky substrate with an airlift device (Templado et al. 2010), both equipped with a net of mesh size 0.5 mm. Datasets from leaves and rhizomes were merged to have a single dataset representative of the meadows. We sampled in spring and autumn 2022 to capture intra-annual variation and merged data into a single yearly data pool. This approach ensures robust comparisons between living and time-averaged death assemblages, avoiding any artificial overestimations of diversity loss that could have occurred by comparing single seasons (which likely have lower diversity due to e.g. phenological and demographic patterns). Samples were sieved in the field with a minimum mesh of 0.5 mm, then mollusks picked under stereomicroscopes and identified to species level. For living assemblages, we generally considered all live-collected shelled mollusks in a sample; 46 out of 634 (7.2%) sieved fractions were too voluminous for being picked entirely

and were thus subsampled. Abundances in the entirely picked fractions were adjusted proportionally to the subsampled fractions by analytically resampling species abundance matrices without replacement. For death assemblages, we extracted shells from the dried residue of suction samples after picking for living individuals. Due to the large number of shells, we split samples into smaller aliquots to obtain at least 500 empty shells at each depth $\times$ habitat combination. Abundances of loose valves of bivalves and polyplacophorans were divided by the respective number of their skeletal parts to obtain abundances comparable to gastropod shells and the living assemblage (Kowalewski et al. 2003). Overall, we based our study on 228 samples, 102,117 living specimens and 16,776 empty shells, representing 371 species (SI2–3).

Body size was measured for 41 species with at least 10 living individuals at each area/habitat, excluding taxa with unsettled taxonomy (seven species belonging to *Alvania*, *Vitreolina*, *Musculus*, Chamidae, Ostreidae, *Parvicardium*) using a ZEISS SteREO Discovery V.20 microscope (SI4). We obtained species historical maximum size from the literature and assumed half the maximum body size as the threshold for reproductive individuals as suggested by a review comparing reproductive and maximum adult size of shelled molluscs (reported in Electronic Supplementary Materials in Albano et al. 2021).

We quantified the age distribution of shells in death assemblages by radiocarbon dating five shells for each habitat and area at 5 and 20 m depth (details on dating and age calibrating procedures in SI1). We reported all calibrated ages in calendar years before 2022, the year of sample collection (SI5).

Temperature regime

We obtained monthly seawater temperature from the European Union Copernicus Marine Service. We used the 1987–2022 reanalysis (Escudier et al. 2020) and the analysis and forecast product for the Mediterranean for 2022–2024 (Clementi et al. 2021) with an horizontal spatial resolution of $1/24^\circ$ (~ 5 km at the equator). Temperatures were extracted at the surface (1 m) and at 30 m depth. The medians of the summer (August, the hottest month on average) and winter (February, the coldest month on average) temperatures were compared between sites with the Wilcoxon test.

Data analysis

We contrasted species richness among sites, habitats and depths by coverage-standardized metrics (Chao and Jost 2012) with the iNEXT package (Hsieh et al. 2016). Such coverage-based estimators obey the replication principle and thus behave intuitively in ratio comparisons. Therefore, species diversity loss was quantified by computing the ratio between the current and the historical richness at equal coverage (completeness), using the observed richness of the assemblage with smallest and the rarefied richness of the sample with the largest coverage. Statistical significance of the difference between these ratios and perfect fidelity (i.e. ratio = 1) was tested by computing bootstrap-derived distributions. For each depth and habitat type, we merged abundances of living and death assemblages into a single dataset and resampled it to obtain a living and a death assemblage with the same original sample size (100 iterations). Under the null hypothesis that current and historic richness did not differ (ratio = 1), we estimated p-values by computing the proportion of bootstrapped

values smaller than the observed ratio, i.e. using a percentile approach (Kowalewski and Novack-Gottshall 2010). The difference between the adult size of individuals in the literature and the maximum size measured in our samples was divided by the literature adult size to standardize for variation in body size among species, and then box-plotted. We compared the group medians with the Wilcoxon rank-sum test, using the Holm-Bonferroni correction for pairwise tests. All analyses and plotting were conducted in the R statistical environment (R Development Core Team 2024).

Results

Temperature patterns

The two sites we investigated are characterized by markedly different seawater temperature regimes. As expected due to the occurrence of summer upwelling, sea surface temperatures in August – the warmest month of the year – were significantly lower at Akrotiri than at Cape Greco (Wilcoxon test, $W=54$, $p<<0.05$, Fig. 2a), with a difference of the medians of 2.3 °C. Significant differences persisted at 30 m depth (Wilcoxon test, $W=260$, $p<<0.05$, Fig. 2b), despite of lower magnitude (difference between medians = 1.3 °C) and much lower absolute values for temperature distributions (range: 25–29 °C and ca. 19–25.5 °C at the surface and 30 m, respectively, based on 5th –95th quantiles). Such differences did not occur in winter (Fig. 2c–d). In February, usually the coldest month of the year, no significant differences between sites could be detected at the surface and at 30 m (Wilcoxon test, $W=698$, $p=0.81$ and $W=689$, $p=0.74$, respectively, Fig. 2c–d).

Diversity patterns

The living assemblages contained 237 species, of which 204 (86.1%) are native to the Mediterranean Sea and are represented by 83,652 individuals (81.9%). Observed richness of non-indigenous species was considerably lower in the area influenced by upwelling: 13 (7.3%) species occurred at the cooler and 31 (16.3%) species at the warmer site. A similar pattern occurred for abundance (7.2% and 20.0%, respectively) (Table S1). The native component was remarkably richer at the cooler than at the warmer site, irrespective of the investigated habitat (species richness at a sample coverage of 0.907; Wilcoxon Test, $W=221$ and $W=224$ in *Posidonia oceanica* and on the rocky substrate, respectively, $p<<0.05$ in both cases; Fig. 3a, Table S2–S3).

Biodiversity loss was remarkably lower in the *Posidonia* meadow at the cooler site than at the warmer site (Wilcoxon test, $W=208$, $p<<0.05$), but no such differences could be detected on the rocky substrates (Wilcoxon test, $W=115$, $p=0.23$) (Fig. 3c, Table S3). Biodiversity loss declined with depth (Fig. 3d) with a clear step between 15 and 20 m. Median values of the current vs. historical species richness ratio within the shallow (i.e. 5–15 m) and the deep (20 and 30 m) layers did not differ, while a comparison of shallow and deep sites revealed differences, despite not always significant ($\alpha=0.05$, pairwise Wilcoxon test with Holm-Bonferroni correction, full results in Table S4). The range of the current vs. historical richness ratios increased considerably at deeper sites, even encompassing samples with perfect fidelity (i.e. ratio close or equal to 1). Death assemblages on rocky substrates

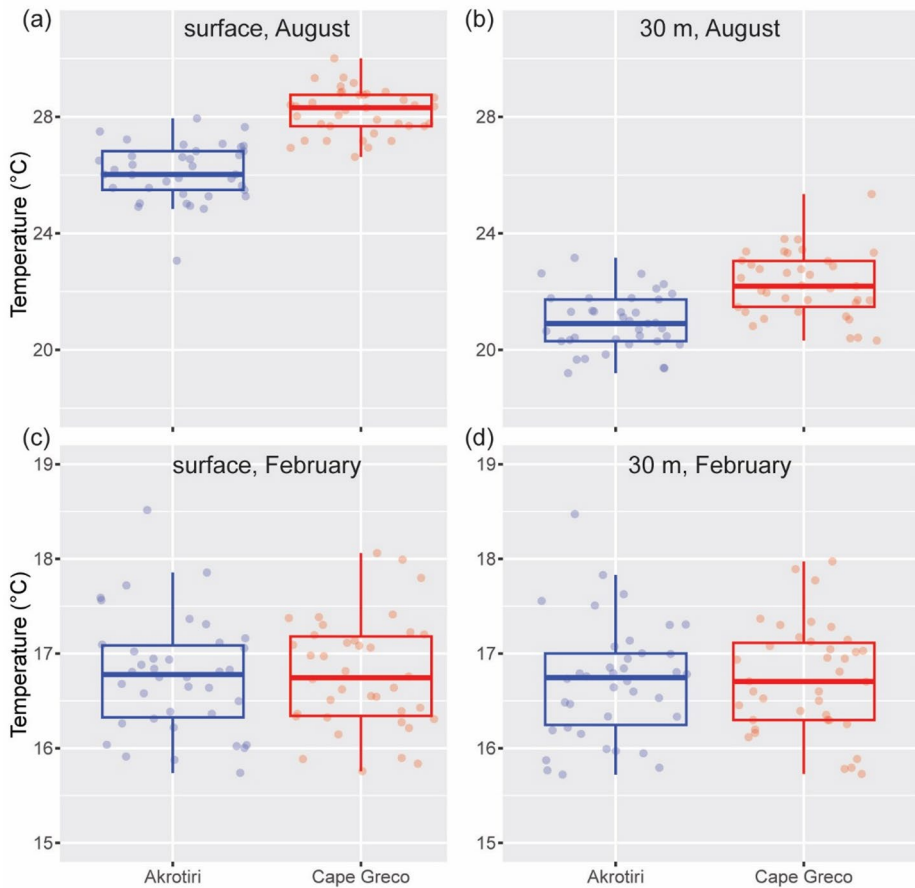


Fig. 2 Seawater temperature regimes (average monthly temperatures) in 1987–2024 at the two investigated locations in Cyprus: Akrotiri (SW Cyprus, colder site with summer coastal upwelling, in blue) and Cape Greco (E Cyprus, warmer site, in red). **(a)** Sea surface temperature (at 1 m depth) in August. **(b)** Sea water temperature at 30 m depth in August. **(c)** Sea surface temperature (at 1 m depth) in February. **(d)** Sea water temperature at 30 m depth in February. Differences in temperatures between the two sites in August (boreal summer) are statistically significant but not in February (boreal winter) (data from the European Union Copernicus Marine Service)

were extremely young, with median ages of 6–12 years and maximum age not exceeding 25 years at three of the four dated sites, whereas *Posidonia oceanica* meadows had older assemblages with median age between 7 and 261 years and maximum ages reaching 4579 years at one site (Table S4).

Most native species (67.6% and 61.9% at Akrotiri and Cape Greco, respectively) had specimens exceeding half the historical adult size, a proxy of reproductive size, with no significant differences between the two sites (Wilcoxon test, $W=380$, $p=0.897$) (Fig. 3b).

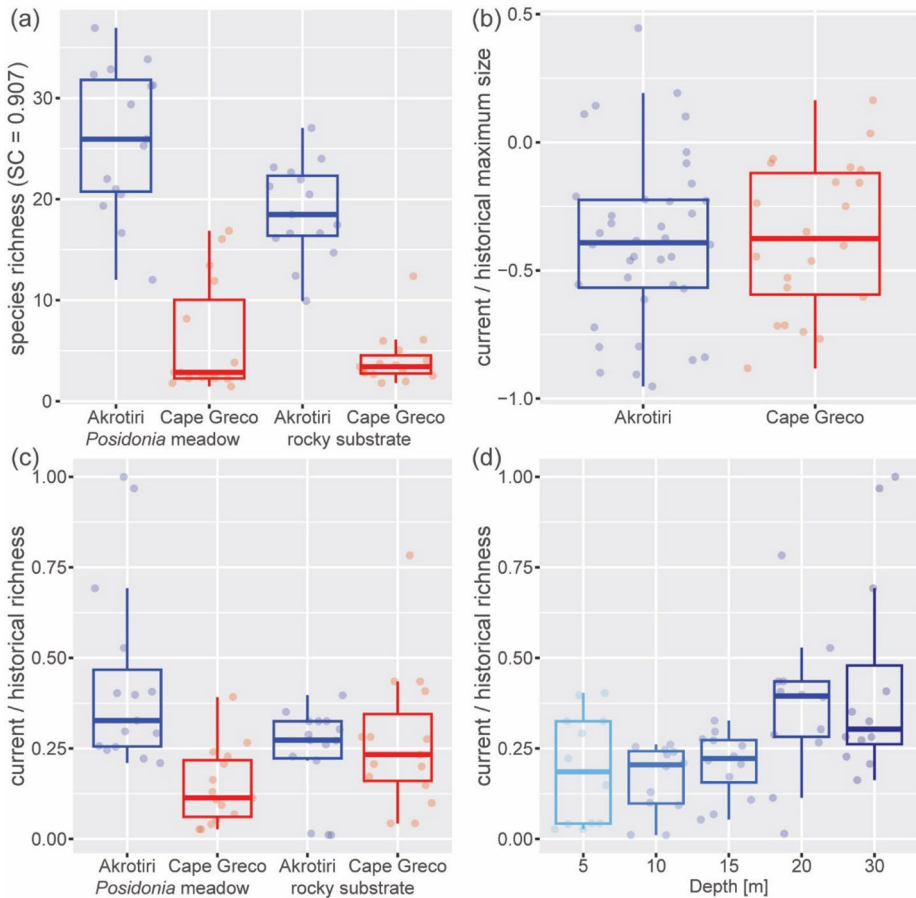


Fig. 3 (a) Coverage-standardized (sample coverage (SC) of 0.907) native species richness in *Posidonia oceanica* meadows and on rocky substrates at Akrotiri (SW Cyprus, colder site with summer coastal upwelling, in blue) and Cape Greco (E Cyprus, warmer site, in red). The richness at Akrotiri is much higher than at Cape Greco, irrespective of the investigated habitat. (b) Ratio between the maximum current and historical size of native molluscs at Akrotiri (in blue, $n=38$) and Cape Greco (in red, $n=22$). We assumed half the maximum historical adult size (value of -0.5 on y axis) as threshold for reproductive size (see Methods). (c–d) Diversity loss estimated with the ratio between current (from living assemblage) and historical (from death assemblage) species richness. The higher the ratio, the lower the diversity loss, (c) contrasting *Posidonia oceanica* meadows and rocky substrates at Akrotiri (in blue) and Cape Greco (in red), and (d) arranging samples per depths (sampling locations and habitats pooled, with darker blue indicating greater depth). The *Posidonia* meadow at the cooler site experienced the least diversity loss, which was significantly lower than in the same habitat at the warmer site. No significant difference could be detected on rocky substrates. Diversity loss is more severe at shallow (5–15 m) depths than in the deeper photic zone (20 to 30 m)

Discussion

A unique refugium in the Eastern Mediterranean Sea

The upwelling system off south-western Cyprus hosts a native molluscan species richness that is several folds higher than in the warmer Cape Greco, irrespective of the investigated habitat (Fig. 3a). The magnitude of this difference is striking considering the comparatively short distance between the two areas (ca. 100 km), which belong to the same biogeographic province and are similar in terms of nutrient regime (Fyttis et al. 2023) and coastal morphology (e.g. rocky coast, gradually deepening bottoms with a mosaic of hard, soft and seagrass substrates, absence of major freshwater input). The main difference lies in the temperature of shallow subtidal waters that are ca. 2–3 °C cooler in the upwelling area than in the rest of the Cypriot coastline, as well as in any other coastal area of the Levantine Sea in summer (Figs. 1 and 2). Indeed, in-situ measurements with temperature loggers placed at 12 m depth at both Akrotiri and Cape Greco between June and September 2021 showed Akrotiri to be 2.10–2.61 °C cooler (P. Stipcich, unpublished data). These results suggest the existence of an ‘avoidance’ (*sensu* McClanahan et al. 2024; West and Salm 2003) *in-situ* (*sensu* Ashcroft 2010) refugium, that is, an area that prevents the deleterious effects of excessively warm waters by buffering summer temperature peaks and by counteracting the effects of regional heatwaves. Indeed, native Mediterranean species do not survive the current summer temperatures in the Levantine Sea that often exceed their thermal tolerance (Noè et al. 2024; Rilov et al. 2022) causing the collapse of native biodiversity (Albano et al. 2021; Steger et al. 2024). In contrast, non-indigenous species of tropical origin are well adapted to these conditions (see also Marras et al. 2015; McKnight et al. 2021), explaining why they were more diverse and abundant in the warmer Cape Greco (Table S1).

The comparison of current diversity against the historical baseline reconstructed from death assemblages clearly showed that the cooler site experienced lower biodiversity loss than the warmer site in *Posidonia oceanica* meadows (Fig. 3c). In particular, at 5 m depth in the warm Cape Greco, we found only 2.7–4.1% of the species historically present, as inferred from their presence in the death assemblage. On the rocky substrate, such differences were less marked. However, at this site and at 5 m depth – the space × depth combination with the highest temperatures – we found alive only 4.3–14.9% of the species present in the death assemblage. Such low proportions closely matched those recorded from the Israeli shelf, where in the shallow subtidal only 5–12% of the native species that occurred historically were still found alive in 2016–2018 (Albano et al. 2021), suggesting that indeed such a collapse is affecting also the warmest areas of Cyprus. The process seems at its initial stages, because two thirds of the native species encountered still reach reproductive size with no appreciable differences between sites, in stark contrast with the situation reported from the Israeli shelf where ca. 60% of the few still extant native species were not reproductive (Albano et al. 2021).

The ratio between current and historical diversity is influenced by the time over which skeletal parts of organisms accumulate into a single death assemblage. Death assemblages of rocky substrates had median ages between 7 and 15 years, with three samples out of four being entirely composed of shells younger than 25 years. *Posidonia* meadows hosted slightly older death assemblages with median ages between 7 and 261 years and some shells being centuries or even millennia old (Table S4). These orders of magnitude match results

from other locations in the eastern Mediterranean Sea (Albano et al. 2023) and may have been exacerbated in Cape Greco by the extreme production of *Amphistegina lobifera* tests. This foraminifer, whose native or non-indigenous status is still debated (Albano et al. 2022; Stulpinaite et al. 2020), constituted most of the sediment in Cape Greco and buried substrates and older shells, similarly to southern Türkiye where 30–60 cm thick layers of such deposits have been observed in the last decade (Yokeş et al. 2014). Such young death assemblages imply that these historical baselines were likely already shifted from pristine states because global warming has accelerated in the last few decades (IPCC 2023; Steger et al. 2024). Consequently, the major species richness loss documented at 5 m in Cape Greco is likely a recent event that occurred in the last 10 to 20 years. Additionally, the comparison with a shifted baseline implies that our quantification of biodiversity loss may be an underestimate.

Depth as a third dimension of shallow subtidal refugia

Depth proved to be an important predictor of biodiversity loss (Fig. 3d). Samples collected at depths equal to or deeper than 20 m showed a better match between current and historical diversity, with some samples even showing perfect fidelity (i.e. present vs. past species richness ratio = 1). In contrast, shallow water samples consistently showed much lower ratios, often below 0.30. On rocky substrates, these differences certainly reflected habitat complexity. In shallow water and irrespective of site, rocky substrates appeared devoid of algal cover and sessile organisms ('barrens', Fig. 4a–b), whereas deeper sites had a richer assemblage of structuring species including macroalgae and sponges (Fig. 4c–d). Barrens develop in the Eastern Mediterranean due to over-grazing by the non-indigenous rabbitfishes *Siganus luridus* and *S. rivulatus* (Sala et al. 2011). These fishes graze not only on adult stands but also on the epilithic algal matrix that typically contains macroalgal recruits, hindering recovery (Vergés et al. 2014). The grazing pressure, compounded by the deleterious physiological effects of warming on the algae and by over-fishing that removes rabbitfish' predators, eventually leads to the disappearance of algal forests, consequently their habitat complexity and associated biodiversity (Bianchi et al. 2012; Harley et al. 2012; Vergés et al. 2014). The disappearance of algal cover and the resulting barrens have been observed in the north-western Mediterranean since the early 2000s and are attributed to multiple factors including overgrazing by sea urchins, competitive displacement by mussels, increased water turbidity, chemical pollution and their combination (Thibaut et al. 2005). However, in the eastern Mediterranean such barrens are the effect of global warming and biological invasions working in synergy: the thermophilic rabbitfishes thrive as temperatures increase, contributing to the eradication of macroalgae from increasingly large areas (Vergés et al. 2014).

The hypothesis that deeper waters, for example at mesophotic depths (30–150 m depth), may be a refugium for species occurring in shallower water has been widely debated. On the one hand, such depths are less vulnerable to heatwaves and seawater temperature increases, avoiding the exposure of the resident organisms to potentially fatal conditions (Glynn 1996). While this concept stemmed from coral reef ecology, it can be applied also to temperate ecosystems. For example, in the subtropical–temperate biogeographical transition zone of Western Australia, a marine heatwave that occurred in 2011 caused a shift in composition of structuring species down to 15 m depth, but had a much reduced effect in deeper communities down to 40 m (Giraldo-Ospina et al. 2020). On the other hand, fully mesophotic waters (i.e. below 60 m) may harbor a taxonomically distinct species pool (Albano et al.

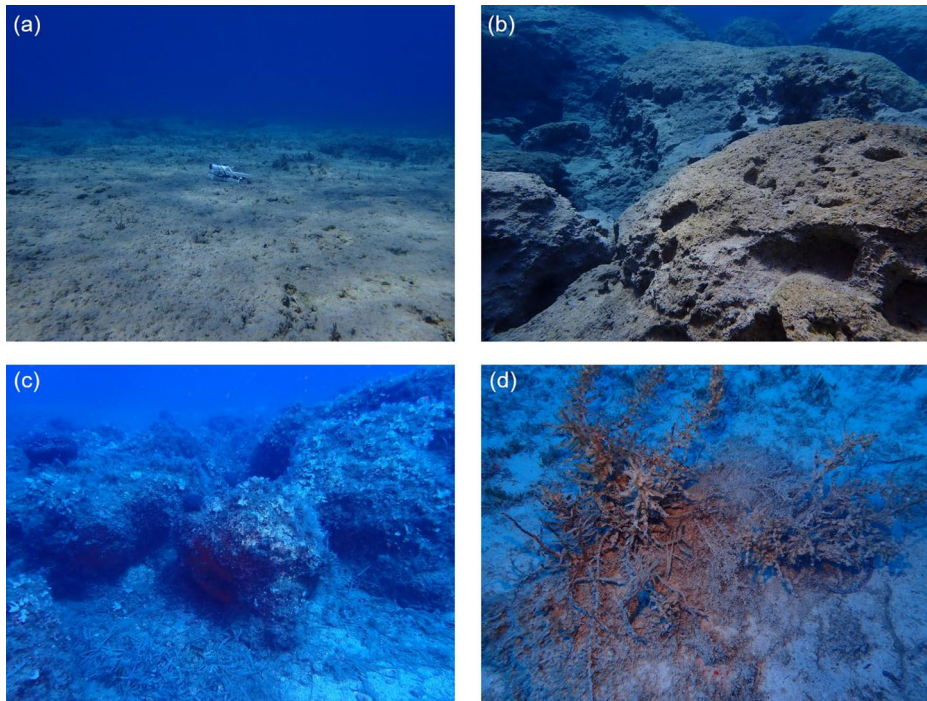


Fig. 4 Rocky substrates at different sites and depths in Cyprus. **(a)** Barren rocks off Akrotiri at 5 m depth (the white object is a data logger). **(b)** Barren rocks at Cape Greco at 5 m depth. **(c)** Rocks off Akrotiri at 30 m depth, covered by *Padina pavonica* and other algae. Near the top-left corner of the photograph, a large black sponge (*Sarcotragus* sp.) is visible on a rock, adding to habitat complexity. **(d)** Rocks at Cape Greco at 30 m depth, covered by *Sargassum* sp. (photo credits: V. Resaikos)

2011; Rocha et al. 2018; Semmler et al. 2017) and thus not serve as a reservoir of propagules to recolonize shallower waters. Still, in the Mediterranean Sea, increasing sea temperatures caused the deepening of the shallowest limit of depth ranges, especially for species of temperate-cold affinity and eurytherms (Chaikin et al. 2022). Additionally, some species such as gorgonians showed connectivity between shallow and upper mesophotic populations (Bramanti et al. 2023; Padrón et al. 2018; Pilczynska et al. 2016), and the highest seawater warming rates during heatwaves and heatwave-related mortality events were recorded at 10 m and 15–25 m depth, respectively (Garrahou et al. 2022). This evidence supports that the 20–30 m depth range where we documented less biodiversity loss may constitute a third dimension of the refugium, also considering that this depth range still harbors truly photic species, particularly in oligotrophic and transparent waters.

The way ahead

The Mediterranean Sea is a basin with 45% of its species being endemic (Costello et al. 2017). The boundaries between closely related species are still being defined by integrative taxonomy (e.g. Aissaoui et al. 2016; Calvo et al. 2009), but it is clear that the Eastern Mediterranean has a high number of endemic species and more are likely to be identified as

taxonomic work progresses. This very same basin is experiencing regional-scale native biodiversity collapses, so far described in detail from Israel but most likely occurring elsewhere in the Levantine Sea (Albano et al. 2021; Crocetta et al. 2013). Our results suggest that the upwelling system in south-western Cyprus, extending for approximately 150 km from Paphos in the west to Larnaca in the east, represents a unique area in the entire 320,000 km² of the Levantine Sea where species richness is high, biodiversity loss is comparatively lower and non-indigenous species are still not dominant. Therefore, such upwelling systems as well as other sites where oceanographic conditions keep coastal waters cooler than nearby areas are candidates for refugia also in the Mediterranean Sea. Additionally, the deeper photic zone (20–30 m depth) experienced lower diversity loss than shallower waters, suggesting the importance of large-scale protection measures for this depth range that probably extends deeper in basins with high water transparency like the oligotrophic eastern Mediterranean. This depth range between the shallowest waters and the proper mesophotic zone still hosts truly photic species and thus deserves greater consideration in conservation plans.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-025-03228-1>.

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Data availability The datasets generated during the current study are available as supplementary information.

Declarations

Competing interests The authors declare no competing interests.

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