Fleshy red algae mats act as temporary reservoirs for sessile invertebrate biodiversity

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Many coastal ecosystems, such as coral reefs and seagrass meadows, currently experience overgrowth by fleshy algae due to the interplay of local and global stressors. This is usually accompanied by strong decreases in habitat complexity and biodiversity. Recently, persistent, mat-forming fleshy red algae, previously described for the Black Sea and several Atlantic locations, have also been observed in the Mediterranean. These several centimetre high mats may displace seagrass meadows and invertebrate communities, potentially causing a substantial loss of associated biodiversity. We show that the sessile invertebrate biodiversity in these red algae mats is high and exceeds that of neighbouring seagrass meadows. Comparative biodiversity indices were similar to or higher than those recently described for calcifying green algae habitats and biodiversity hotspots like coral reefs or mangrove forests. Our findings suggest that fleshy red algae mats can act as alternative habitats and temporary sessile invertebrate biodiversity reservoirs in times of environmental change.
Sessile plants and invertebrates play a central role in shaping biotic communities by increasing both the structural and habitat complexity, thus, promoting biodiversity\textsuperscript{1-3}. In the marine environment, ecosystem engineers are responsible for forming biodiversity hotspots (i.e., areas rich in rare, threatened species)\textsuperscript{4}, such as seagrass meadows\textsuperscript{5,6}, tropical coral reefs\textsuperscript{3}, and mangrove forests\textsuperscript{7}. Ecosystem engineers in these habitats change the abiotic and biotic components of the ecosystem, and in doing so, generate structurally complex environments that benefit both the engineers themselves and the associated biodiversity\textsuperscript{1,8}. In the Anthropocene\textsuperscript{9}, human activity has negatively impacted almost all marine ecosystems. These threats have evoked ecosystem responses\textsuperscript{10} leading them down a path of degradation\textsuperscript{11}. Anthropogenic stressors occurring either singularly or in combination, such as ocean warming\textsuperscript{6} and acidification\textsuperscript{12} or nutrient pollution\textsuperscript{6}, can alter the community dynamics, shifting the system to alternative states dominated by more tolerant species\textsuperscript{6,12-14}. These transitions, e.g., shifts from the reef or hard-bottom communities towards persistent, fleshy, non-calciifying (macro-) algal assemblages, are referred to as ‘phase-shifts’ to alternative states\textsuperscript{13}. These shifts naturally entail a series of consequences on multiple levels, such as a loss of structural/spatial complexity, a loss of ecosystem services and functioning\textsuperscript{1,14}, and consequently, a loss of biodiversity\textsuperscript{3,15,16}. Identifying potential biodiversity refugia that are pivotal for rebuilding marine life\textsuperscript{17} is therefore essential to appropriately adapt conservation strategies in times of increased biodiversity loss associated with anthropogenic global change\textsuperscript{1,12,18} and direct local human impacts (e.g., pollution, coastal development)\textsuperscript{5,6,19}.

In the Mediterranean Sea, rocky hard-bottom communities and commonly identified biodiversity hotspots such as seagrass meadows are declining primarily due to environmental pressures\textsuperscript{5,6,19,20}. Meadows formed by Posidonia oceanica seagrass rank amongst the most valuable coastal ecosystems worldwide as they provide a range of goods and ecosystem services\textsuperscript{21,22}, e.g., they exhibit high biodiversity, with several biodiversity hotspots such as seagrass meadows

Results and discussion

Fleshy red algae mats as biodiversity hotspots for sessile invertebrates. We assessed the sessile invertebrate biodiversity in neighbouring P. crispa and P. oceanica habitats along the north-eastern and north-western coasts of Giglio Island, within the Tuscan Archipelago National park, Tyrrhenian Sea, Italy (see Supplementary Fig. S1). P. oceanica community assessments included analysis of the holobiont (leaves + subsurface structures), as well as separate analyses of the leaves and rhizomes to account for potential differences\textsuperscript{18} (see Methods). Briefly, invertebrates were determined to the lowest possible taxonomic level. However, in case no clear identification was possible, individuals were distinguished based on distinct visual characteristics, resulting in the identification of distinct phenotypes rather than species.

We recorded 312 distinct sessile invertebrate phenotypes (covering 9 higher taxa) for both P. crispa and P. oceanica, of which 223 occurred in P. crispa mats and 179 in P. oceanica holobionts, respectively (Fig. 2a). All (sub-) habitats accommodated distinct communities (Fig. 2b), with 133, 21 and 18 phenotypes uniquely found in P. crispa mats, P. oceanica leaves and P. oceanica rhizomes, respectively (Fig. 2a). Approximately 25% more phenotypes were found in P. crispa mats than in the neighbouring P. oceanica seagrass meadow holobionts. Calculations of classical diversity indices further endorsed P. crispa as a hotspot of sessile invertebrate diversity comparable to traditional biodiversity hotspots such as coral or Mediterranean coralligenous reefs (Table 1).

The calculated abundances (mean number of individuals (ind) habitat m\textsuperscript{-2} ± standard error; note: colonies of colonial species are considered as individuals for readability hereafter) suggest that P. crispa mats provide a valuable habitat for sessile invertebrates that depend on a solid surface for attachment. Our data showed 64,008 ± 4609 ind m\textsuperscript{-2} associated with P. crispa mats, which was three times more than in P. oceanica holobionts
(19,535 ± 1421; Dunn’s test \( p < 0.001 \); Supplementary Table S2), four times more compared to \( P. oceanica \) leaves (15,857 ± 1654; Dunn’s test \( p < 0.001 \); Supplementary Table S2) and two times the number observed in \( P. oceanica \) rhizomes (24,867 ± 1991; Dunn’s test \( p < 0.001 \); Supplementary Table S2). Whereas \( P. crispa \) mats harboured an outstanding abundance of Bryozoa (44,222 ind habitat \( m^{-2} \)), both Bryozoa and Foraminifera were equally abundant in \( P. oceanica \) leaves and rhizomes (Supplementary Table S1). \( P. crispa \) harboured a similar number of phenotypes of Bryozoa and Foraminifera (76 and 81, respectively), whereas the number of bryozoan phenotypes exceeded that of Foraminifera in \( P. oceanica \) (78 and 52, respectively). In addition, we identified three distinct communities using non-metric multidimensional scaling (nMDS, Fig. 2b). The nMDS plot and appendant statistical analysis revealed that sessile invertebrate communities significantly varied among habitats (PERMANOVA with all \( p < 0.001 \); Supplementary Table S3), independent of the number of phenotypes and individuals of the investigated habitats.

**Fig. 1** *Phyllophora crispa* mat and *Posidonia oceanica* seagrass meadow with associated sessile invertebrates. \( P. crispa \) mat (a) and \( P. oceanica \) meadow (c) with Bryozoa, Polychaeta and Foraminifera on \( P. crispa \) thalli (b), Bryozoa, Polychaeta and crustose coralline algae (Corallinales) as epiphytes on \( P. oceanica \) leaves (d). Pictures taken by Felix I. Rossbach (a, b, d) and Friederike Peiffer (c).

**Fig. 2** Area-proportional Venn diagram and ordination of biodiversity data by non-metric multidimensional scaling (nMDS). Area-proportional Venn diagram (a) displaying numbers of total (= present in the respective habitat), shared, and unique (in brackets) phenotypes found in investigated *Phyllophora crispa* (purple), *Posidonia oceanica* holobiont, \( P. oceanica \) leaves (gold) and \( P. oceanica \) rhizomes (green); area in proportion to number of phenotypes in *P. crispa*. Ordination of biodiversity (incidence) data by nMDS (b) based on Bray–Curtis similarities of *P. crispa* (purple dots), *P. oceanica* rhizomes (green crosses) and *P. oceanica* leaves (gold rectangles).
To assess \textit{P. crispa}'s role as a potential sessile invertebrate biodiversity hotspot compared to neighbouring \textit{P. oceanica} meadows, we performed a diversity analysis based on the concept of Hill numbers. Hill numbers account for differences among (sub-) habitats (i.e., respective 95% confidence intervals) compared to all other (sub-) habitats, underlining its role as a biodiversity hotspot for sessile invertebrates. For phenotype richness and Shannon diversity, only conservative minimum estimates could be obtained, as size-based rarefaction and extrapolation curves did not asymptote for \( q = 0.1 \) (Fig. 3b). In this case, a statistically reliable comparison between habitats’ phenotype richness and Shannon diversity may only be performed based on standardised data. For this purpose, we compared diversities based on standardised data at a sample coverage level of \( C_{\text{max}} = 96.9\% \) (Fig. 3d and Supplementary Table S6). \( C_{\text{max}} \) is the lowest sample completeness at \( q = 1 \) of any (sub-) habitat when samples are extrapolated to double the respective number of samples per (sub-) habitat. Consequently, we showed that \textit{P. crispa} exhibited significantly (i.e., no overlap of respective 95% confidence intervals) higher phenotype richness compared to neighbouring \textit{P. oceanica}: phenotype richness of \textit{P. crispa} mats (\(-234\) phenotypes) exceeded those of \textit{P. oceanica} rhizomes (\(-142\)) and leaves (\(-102\)) at a fixed sample coverage of \( C_{\text{max}} = 96.9\% \) (Fig. 3d and Supplementary Table S6\(^2\)), whereas the difference compared to the \textit{P. oceanica} holobiont (\(-207\)) was marginal. For Shannon diversity, \textit{P. crispa} showed a significantly higher index value (\(-159\)) compared to the \textit{P. oceanica} holobiont (\(-111\)), leaves (\(-64\)) and rhizomes (\(-84\); see Fig. 3d and Supplementary Table S6\(^2\)). Phenotype evenness (i.e., Pielou’s \( J \) at \( C_{\text{max}} \)) was calculated, taking into account rarefied and non-asymptotically (the latter standardised for \( C_{\text{max}} \)), the number of undetected phenotypes was larger for (sub-) habitats of \textit{P. oceanica} (holobiont and rhizomes) than for \textit{P. crispa} (Supplementary Table S6\(^2\)). These findings indicate that the higher overall diversity in \textit{P. crispa} may be driven by the higher abundance of frequently occurring rather than rare phenotypes. However, even though the estimated number of undetected phenotypes was higher for \textit{P. oceanica} compared to \textit{P. crispa}, the overall estimated diversity for all orders of \( q \) in the red algae

### Table 1 Diversity indices (richness = number of sessile phenotypes, \( H' = \) Shannon, \( D = \) Simpson) and evenness accounting for sessile invertebrates for investigated as well as reference biodiversity hotspots based on literature data.

| Habitat                  | Location           | Richness | Taxa                     | Evenness | \( H' \) | \( D \) | Reference                                      |
|-------------------------|--------------------|----------|--------------------------|----------|---------|--------|------------------------------------------------|
| Phyllophora crispa      | NW Mediterranean   | 223      | 9a,b,c,fl,p,m,s          | 0.6969   | 2.209   | 0.2693 | Present study                                  |
| Posidonia oceanica      | NW Mediterranean   | 179      | 7a,b,c,fl,m,s           | 0.7581   | 2.128   | 0.2900 | Present study                                  |
| Posidonia oceanica      | S Mediterranean    | 33       | 5a,b,fl,p,s             | 0.8706   | 2.021   | 0.2519 | Mabrouk et al. (2014)\(^{106}\)                |
| Coralligenous reefs     | NW Mediterranean   | 55       | 6a,b,fl,p,s             | 0.8070   | 2.086   | 0.2539 | Verdura et al. (2019)\(^{107}\)               |
| Coralligenous reefs     | Mediterranean      | 786\(^1\)| 7a,b,fl,m,s           | 0.9418   | 2.644   | 0.1731 | Ballestros (2006)\(^{108}\)                   |
| Cystosera zosteraeoides | NW Mediterranean   | 78       | 6a,b,fl,p,s             | 0.7574   | 1.958   | 0.3004 | Ballestros et al. (2009)\(^{109}\)            |
| Coral reef              | SW Indian Ocean    | 457      | 5a,cf,m,s              | 0.8765   | 2.035   | 0.2789 | Cleary et al. (2016)\(^{110}\)                |
| Coral reef turf algae   | W Indian Ocean     | 48\(^1\)| 2a,m                  | 0.9950   | 0.995   | 0.4929 | Milne and Griffiths (2014)\(^{111}\)          |
| Coldwater coral reef    | N Atlantic Ocean   | 213      | 7a,b,fl,m,s            | 0.9523   | 2.673   | 0.1653 | Mortensen and Fossa (2006)\(^{112}\)         |
| Coldwater coral reef    | N Atlantic Ocean   | 77       | 4a,bs                  | 0.8062   | 1.612   | 0.3585 | Henry et al. (2010)\(^{113}\)                 |
| Mangrove forest         | Caribbean Sea      | 54       | 6a,b,cm,p,s            | 0.7494   | 1.937   | 0.2970 | Farnsworth and Ellison (1996)\(^{114}\)       |
| Kelp forest             | NE Pacific Ocean   | 79\(^1\)| 6a,b,cm,p,s          | 0.9456   | 2.444   | 0.1912 | Graham (2004)\(^{115}\)                      |
| Antarctic hard bottom   | Weddell Sea        | 608\(^2\)| 6a,b,fl,m,s         | 0.8500   | 2.197   | 0.2803 | Gutt et al. (2000)\(^{116}\)                 |
| Halimeda bioherm         | Coral Sea          | 474\(^2\)| 5a,b,cm,s            | 0.6965   | 1.617   | 0.4202 | McNeil et al. (2021)\(^{39}\)                |

Indices and evenness presented here were calculated based on classical formulas and not based on Hill-number calculations to enable comparison with literature data (see Methods). *Ascidiae, Brazoa, Cnidaria, Entoprocta, Foraminifera, *\(^a\)Mollusca (Bivalvia), Polychoeta (Sedentaria), *\(^b\)Rotifera, *\(^c\)Porifera. *\(^d\)Data collated from multiple other publications. *\(^e\)Excluded Cnidaria, Bryozoa and Ascidiae from the analysis. *\(^f\)Respective study included barnacles and phoronids that were not included in the current analysis. *\(^g\)Excluded Polychoeta from the analysis.
habitats still remained higher relative to the seagrass meadows (Fig. 2c). Taken together, our data have identified P. crispa as a habitat that harbours more even and diverse sessile invertebrate communities compared to neighbouring P. oceanica meadows.

Red algae mats fulfill ecosystem engineer functions. We measured key environmental parameters (i.e., oxygen concentrations, light availability, pH, temperature, chlorophyll α concentration, and water movement) in neighbouring P. crispa and P. oceanica to assess P. crispa’s functioning as an ecosystem engineer. Our results suggest that P. crispa shapes key environmental parameters similarly to neighbouring P. oceanica seagrass meadows (Fig. 4). In particular, water movement and light intensity within the red algae mats and in the seagrass meadows were lower than for the neighbouring bare substrate (Fig. 4b, f). This extends the findings of a parallel study that has identified P. crispa as an ecosystem engineer modifying its environment.

For further environmental parameters: daily oxygen concentration fluctuations of P. crispa (7.73–8.14 mg l⁻¹) were similar to those of P. oceanica (7.59–8.04 mg l⁻¹), with the daily mean of oxygen concentrations being slightly higher in P. crispa (7.99 mg l⁻¹) compared to those of P. oceanica (7.75 mg l⁻¹). This contradicts previous findings stating that shallow, macroalgae-covered environments undergo wider oxygen concentration fluctuations compared to seagrass meadows. Our findings indicate that this may not necessarily be the case in deeper environments (Fig. 4a). In addition, the average pH within P. crispa mats was lower (8.44) compared to P. oceanica meadows (8.64), which resembled the observed differences in O₂ concentrations (Fig. 4a, c). Photosynthesis by algae and plants requires hydrogen ions, which results in increased pH levels while respiration lowers pH levels. Furthermore, our data suggest higher light availability in P. crispa (538 lux) compared to P. oceanica meadows (315 lux; Fig. 4b) at the same depth. These findings corroborate with previous studies that identified strong light attenuations in seagrass macrophyte habitats due

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**Fig. 3 Overview of biodiversity analysis based on Hill numbers.**

a Estimated sample completeness curves as a function of order q between 0 and 2.
b Size-based rarefaction (solid lines) and extrapolation (dashed lines) curves up to double the respective sample size.
c Asymptotic estimates of diversity profiles (solid lines) and empirical diversity profiles (dashed lines).
d Coverage-based rarefaction (solid lines) and extrapolation (dashed lines) curves up to double the reference sample size. Vertical dashed lines show the standardised sample coverage C_max = 96.6%.
e Evenness profiles as a function of order q, 0 < q ≤ 2, based on the normalised slope of Hill numbers. Dots (P. crispa), triangles (P. oceanica holobiont), rectangles (P. oceanica leaves) and crosses (P. oceanica rhizomes) denote observed data points. All shaded areas in a–e denote 95% confidence intervals obtained from a bootstrap method with 500 replications. Note: some bands are invisible due to narrow width.
Fig. 4 Environmental parameters measured in *Phyllophora crispa* and *Posidonia oceanica*.

Environmental data consisting of oxygen (O₂) concentration (a), light intensity (b), pH (c), temperature (d), chlorophyll *a* concentration (e) and water movement (d) in *Phyllophora crispa* (purple), *Posidonia oceanica* (blue) and neighbouring hard-bottom substrate serving as a reference habitat (brown). Horizontal lines within panels a–f display daily mean of respective deployment (with *n* = 13 for *P. crispa*, *n* = 7 for *P. oceanica*, *n* = 6 for reference habitat for O₂ concentration, pH and chlorophyll *a* concentration, and with *n* = 10 for *P. crispa*, *n* = 6 in *P. oceanica*, *n* = 4 in reference habitat for light intensity and temperature) of respective parameters in each habitat. Note for panel f: different letters above box plots indicate significant differences between habitats (ANOVA and subsequent Tukey HSD test), with *n* = 9 for *P. crispa*, *n* = 4 for *P. oceanica*, *n* = 2 for reference habitat.

...to self-shading effects. A lessened self-shading effect in the red algae habitat compared to the *P. oceanica* seagrass meadows could be explained by morphological differences between the two habitats. The latter forms meadows of higher thickness relative to the mats formed by *P. crispa*, with *P. oceanica* leaves being wider than thalli of *P. crispa*. Finally, the reduced water movement (Fig. 4f) in both habitats and higher O₂ availability in *P. crispa* compared to *P. oceanica* (Fig. 4a) may benefit the settlement of specific bryozoans (e.g., *Bugula* sp., *Schizoporella* sp.), bivalves and polychaetes (*Hydroides* sp.33). This may explain the findings of the present study, in which we identified more individuals associated with *P. crispa* compared to *P. oceanica* of bryozoans (76 vs. 78 phenotypes, 44,222 vs. 7655 ind habitat m⁻²), molluscs (bivalves: 4 vs. 4 phenotypes, 112 vs. 38 ind habitat m⁻²) and polychaetes (23 vs. 13 phenotypes, 5950 vs. 3734 ind habitat m⁻²; see Supplementary Table S1). Potentially, lower pH in *P. crispa* mats (Fig. 4c) may have limited the presence of organisms such as bivalves or benefitted comparatively resilient organisms such as specific bryozoans. Hence, the extent to which lower pH conditions in *P. crispa* compared to *P. oceanica* may have counteracted potential benefits such as higher O₂ availability (Fig. 4a) remains speculative.

The higher number of phenotypes and individuals in *P. crispa* relative to *P. oceanica* may be partly explained by the specific surface area that potentially offers substrate, and thus microhabitats for mobile and sessile invertebrates. The complex morphology of *P. crispa* mats is reflected in the 2D to 3D surface area enlargement factor. Here, a high surface area provided by complex thalli relative to a small volume (mats of several cm thickness) resulted in an enlargement factor of 4.9 ± 0.2 (mean ± standard error; Supplementary Table S5) for *P. crispa*, which was lower than for *P. oceanica* (both leaves (7.3 ± 0.5) and *P. oceanica* holobiont (8.3 ± 0.5) but higher than for *P. oceanica* rhizomes (2.0 ± 0.1)). This structural complexity may also explain the observed reduced water movement within *P. crispa* mats (Fig. 4f) that could favour sediment trapping. The extent to which further functions such as sediment trapping, similar to the reduced water movements induced by *P. oceanica* meadows, apply to *P. crispa* mats needs to be determined in future studies. Trapped sediment and particulate matter could provide (1) a heterogeneous habitat for infaunal species, and (2) an organic matter for tube-building species such as sessile polychaetes. Growth form, enlargement factor and persistence of *P. crispa* contradict the common notion that structural complexity is reduced when spatially complex and long-living habitats, such as seagrass meadows, decline. We further estimated the number of individuals per area m² of seafloor by multiplying the calculated numbers of individuals per habitat m² with the respective enlargement factor (Supplementary Table S5). *P. crispa* supported 313,635 ± 27,486 ind seafloor m⁻², which was approximately twice that of the *P. oceanica* holobiont (162,139 ± 11,794 ind seafloor m⁻²; Dunn’s test *p* < 0.001; Supplementary Table S4).

We conclude that *P. crispa* mats facilitate the colonisation of sessile organisms by providing (micro-) habitats for associated alpha diversity (Table 1 and Fig. 3), thus, allowing us to propose *P. crispa* as an ecosystem engineer. Together with the considerable surface area enlargement (Supplementary Table S5), environmental parameters shaped by *P. crispa* (Fig. 4), its wide distribution, and the comparative biodiversity analysis (Table 1 and Figs. 2 and 3), red algae mats may function as overlooked ecosystem engineers and harbour high sessile invertebrate biodiversity.
Fleshy red algae as refuge habitat. Like many other marine ecosystems, P. oceanica seagrass meadows experience a range of anthropogenic threats, which have caused a drastic decline in the spatial distribution throughout the Mediterranean. The loss of biodiversity is only one among many consequences of declining P. oceanica meadows.<ref>6,19</ref> The high biodiversity associated with red algae P. crispa mats may positively impact sessile invertebrate communities in bordering P. oceanica seagrass meadows,<ref>5</ref> which is reflected by a total of 90 shared phenotypes that occurred in all investigated habitats (Fig. 2a).

Even though P. crispa mats harboured sessile invertebrates in numbers that exceeded those of neighbouring P. oceanica meadows<ref>65</ref> and other ecosystems (Table 1), these mats substantially differed from seagrass meadows in their longevity. In the Mediterranean, P. oceanica meadows form dense rhizome layers that can be of several metres of thickness when admixed with trapped sediment.<ref>64</ref> Similar to coral reefs or mangrove forests, seagrass meadows can persist for several millennia,<ref>5</ref> which exceeds the currently estimated lifespan of P. crispa formations (i.e., decades)<ref>30</ref>. The evolved size and physical structure of seagrass meadows can result in a dissipation of wave energy on multiple levels (reviewed in ref. 23) and reduce coastal damage and erosion. Wave energy is a key limiting factor defining the upper physical boundary that shapes the bathymetric spatial distribution for P. oceanica meadows.<ref>66</ref> The properties of P. oceanica allow it to withstand these physical impacts and grow at depths as shallow as 0.5 m.<ref>77</ref> In contrast to P. oceanica meadows, P. crispa mats can be dislodged and translocated by waves<ref>30</ref>, particularly those with an unattatched growth form on sediments.<ref>31</ref> Although dislodged P. crispa may not offer a stable environment over longer time scales, mobile algal thalli may function as an effective dispersal mechanism. Drifting algae parts may offer substrate to diverse sessile invertebrate communities<ref>35,36</ref> and function as a transport vector over large distances.<ref>37</ref> The extent to which the associated phenotypes identified in this study tolerated this drifting behaviour remains speculative.<ref>38</ref>

The translocation of P. crispa mats may have consequences for associated biodiversity through two pathways: (i) translocated P. crispa mats, which can colonise and spread vegetatively, may still provide habitat for associated sessile invertebrates; or (ii) P. crispa mats are severely damaged, losing their function as ecosystem engineers, and, hence, biodiversity hotspots. We conclude that in both cases, P. crispa mats serve as temporary ecosystem engineers forming temporary refuge habitats, and subsequently as transitory biodiversity hotspots. Potentially, more tolerant sessile species could reach more favourable areas such as healthy seagrass beds that are possibly beyond the reach of planktonic larval stages. P. crispa formations in the Atlantic and Black Sea provide a relatively stable habitat over several decades<ref>30</ref>, which underlines the general functioning as a biodiversity substratum. The extent to which this function applies to P. crispa mats of the Mediterranean as well needs to be determined in future studies.

We postulate that sessile invertebrates can re-colonise recovering P. oceanica meadows, if appropriate conservation measures are implemented.<ref>18,78</ref> Seagrass meadows can recover from anthropogenic or natural threats on a decadal timescale<ref>29</ref>, which corresponds with the lifespans of P. crispa mats.<ref>90</ref> Hence, red algae mats may function as overlooked biodiversity refuge habitats supporting the recovery of classical habitats such as seagrass meadows, particularly due to their proliferation across the Mediterranean<ref>27–29</ref>, the Black Sea<ref>30,31</ref> and the Atlantic.<ref>29,32</ref>

Likewise, similar patterns (i.e., the supported recovery of a habitat by neighbouring habitats) were reported from the Great Barrier Reef, where the recovery of a bleached reef was facilitated by larval inflows originating from non-bleached reefs.<ref>80</ref> In the Mediterranean, we hypothesise that P. crispa can support P. oceanica meadows (and other habitats, see Table 1) by maintaining their sessile invertebrate biodiversity,<ref>74,81</ref> particularly due to an overlap of shared phenotypes, i.e., sessile invertebrates that occurred in both P. crispa and P. oceanica (Fig. 2a), even though both habitats harbour a range of unique phenotypes. It remains to be determined (i) to what extent the community composition in re-colonised P. oceanica meadows differs from their initial sessile invertebrate community composition, considering the clear distinction of associated sessile invertebrate communities in P. crispa mats and P. oceanica meadows (Fig. 2b), and (ii) whether this function applies to all shared phenotypes and potentially further taxa. Our findings suggest that P. crispa mats and their associated sessile invertebrate communities potentially aid in reviving classical marine (sessile invertebrate) biodiversity hotspots such as invaluable seagrass meadows in the Mediterranean Sea once threats are reduced or removed<ref>77,92</ref>.

Methods

Study site and sampling. All data were generated by SCUBA diving between May and July 2019 along the north-eastern and north-western coasts of Giglio Island, within the Tuscan Archipelago National Park, Turrhenian Sea, Italy (Supplementary Fig. S1). Samples for biodiversity assessments were taken at six sites (two each for P. crispa mats of >5 cm thickness and P. oceanica, and two for co-occurring habitats, resulting in four sampling sites for P. crispa and P. oceanica each, see Supplementary Fig. S1) according to accessibility and occurrence of target habitats at water depths between 28 and 30 m.

To sample P. crispa mats for the present study, a sampling frame (30 × 30 cm) was randomly placed in the target area four times (i.e., each time 50 cm apart), and all algal material within the frame was carefully removed using a spatula and subsequently placed into 1 L PP-bottles (each holding a ratio of algacwater = 1:3). A total of 16 replicates for P. crispa were sampled. P. oceanica rhizome and leaf specimens were sampled separately into 1 L Kautex jars to avoid oxygen depletion or physical damage during transport. An attached growth form of P. crispa was chosen for the present study. P. oceanica root-rhizomes were cut including the sheaths, both vertical and horizontal rhizome as well as the upper layers of the roots (Supplementary Fig. S2, hereafter referred to as ‘P. oceanica rhizome’). Leaves and rhizomes were cut with scissors directly above the sheath of the shoot. Total of 20 Fi (two each for P. crispa mats of >5 cm thickness and P. oceanica, and two for co-occurring habitats, resulting in four sampling sites for P. crispa and P. oceanica each, see Supplementary Fig. S1) according to accessibility and occurrence of target habitats at water depths between 28 and 30 m. To sample P. crispa mats for the present study, a sampling frame (30 × 30 cm) was randomly placed in the target area four times (i.e., each time 50 cm apart), and all algal material within the frame was carefully removed using a spatula and subsequently placed into 1 L PP-bottles (each holding a ratio of algacwater = 1:3). A total of 16 replicates for P. crispa were sampled. P. oceanica rhizome and leaf specimens were sampled separately into 1 L Kautex jars to avoid oxygen depletion or physical damage during transport. An attached growth form of P. crispa was chosen for the present study. P. oceanica root-rhizomes were cut including the sheaths, both vertical and horizontal rhizome as well as the upper layers of the roots (Supplementary Fig. S2, hereafter referred to as ‘P. oceanica rhizome’). Leaves and rhizomes were cut with scissors directly above the sheath of the shoot. Total of 20 Fi (two each for P. crispa mats of >5 cm thickness and P. oceanica, and two for co-occurring habitats, resulting in four sampling sites for P. crispa and P. oceanica each, see Supplementary Fig. S1) according to accessibility and occurrence of target habitats at water depths between 28 and 30 m.

Biodiversity assessment. All samples were analysed within three days after collection. For P. crispa, subsamples (sensu Bianchi (2004)<ref>83</ref>) were transferred to plastic bowls, where P. crispa mats were cut into single thalli, and subsequently placed in single Petri dishes. Thalli were then analysed using stereo magnifiers (max. ×40 magnification) to determine invertebrates that were assigned to one of the following taxa: Ascidacea, Bryozoa, Cnidaria, Entoprocta, Foraminifera, Mollusca (Bivalvia), Polychaeta (Sedentaria), Rotifera, and Porifera. Foraminifera were determined using a microscope (max. 400x magnification). Seagrasses such as P. oceanica are typically divided into two sub-habits: the leaf canopy-forming part and a dense root-rhizome layer<ref>90,91</ref>, both varying in their habitat character-nised by their associated biotic assemblage<ref>86,88</ref>. Thus, we investigated invertebrate diversity in both sub-habits in our analysis by assessing invertebrate phenotype abundances separately for P. oceanica leaves and rhizomes to account for potential differences. P. oceanica rhizomes were analysed as a whole using a stereo microscope, whereas P. oceanica leaves were cut into pieces of ~8 cm length for handling and to avoid double counting. All P. oceanica samples were analysed for the aforementioned taxa as well. All specimens were identified according to relevant literature (Supplementary Table S7) and crosschecked online with the World Register of Marine Species (mariniespecies.org). Individual specimens or colonies in case of colonial species (i.e., Bryozoa) were then counted for further analysis. In case no clear identification was possible, individuals were distinguished based on distinct visual characteristics, resulting in a dataset consisting of distinct phenotypes rather than species. We refer to Supplementary Table S8, which consists of a subset exemplarily showing the applicability via a clear correlation of the number of species and phenotypes, respectively. Finally, all numbers were nor-mailed to their respective habitats’ surface area using the corresponding enlargement factor (see next section), resulting in a total number of individuals per habitat m<sup>2</sup>.
To test for statistical differences between the number of individuals among habitats, a Shapiro–Wilk test for normality, Kruskal–Wallis test and a subsequent post-hoc Dunn’s test were performed in R (version 4.0.4)8748 with the package iNext (version 1.0.153)88 using the ‘iNext’ test, ‘kruskal.test’ and ‘Dunn.test’ functions from the ‘stateR’ and ‘iNext’ packages. We expected numbers in P. oceanica leaves and rhizomes to exceed those of P. crispa given higher sampling efforts for the former (n = 29 and n = 20, respectively vs. n = 16). To allow for comparisons among habitats—despite differences in sampling efforts—we conducted a combination of asymptotic and non-asymptotic diversity estimations based on rarefaction and extrapolation analysis tools, and Hill numbers (see below). We used phenotype incidence instead of abundance data, as diversity estimations based on Hill numbers rely on species richness (i.e., occurring in one sample or with abundances of one individual).

Given that we normalised phenotype abundance counts to habitat and seafloor area (m²) to enable comparison between habitats, the assemblages sampled by us are devoid of singleton occurrences, ultimately leading to samples appearing complete in terms of capturing true diversity. This is highly unlikely with a non-exhaustive sampling effort and we, thus, opted to use phenotype incidence data for diversity and sample completeness estimation, as this has been shown to not be statistically inferior for the use of count abundances (e.g., ref. 90 and ref. 49).

A statistical biodiversity assessment was performed using a combination of the iNext49 steps online tool (https://iNext.shinyapps.io/iNEXT4steps/) and the ‘iNext’ package51 in R (version 4.0.4)87 with the interface RStudio (version 1.0.153)88. Given that the official online tool was not yet available at this time, Zhao et al.51 provided a hyperlink to a trial version that we used in this study. Plots were created using ‘iNext’s ggNext’ function and the ‘ggplot2’ package52. We refer to Daraghmeh and El-Khaled53 for a detailed workflow and scripts. Briefly, to assess and compare completeness and abundance of the habitats, we followed the protocol proposed by Zhao et al.51. It is based on their extensive earlier works (e.g., Zhao et al.)49, which use the now widely accepted concept of Hill numbers, also known as the effective number of equally abundant species5,56. Here, q denotes the diversity order of a Hill number and determines its sensitivity to species’ relative abundances or frequencies (in case of abundance data, i.e., species presence/absence). Hill numbers based on higher values of q put more emphasis on more commonly occurring species. The most widely used members of the family of Hill numbers are the ones of orders q = 0, q = 1 and q = 2. For sampling-unit-based phenotype incidence data as used in the present analysis (see below), 0 indicates the species richness, i.e., all phenotypes are quantified equally without regard to their actual frequencies) and 1 and 2 represent Shannon (i.e., exponential of Shannon entropy) and Simpson (i.e., inverse of Simpson concentration index) diversity, i.e., the effective number of frequent and highly frequent phenotypes, respectively51. Here, we used phenotype incidence data as described above.

The calculation of Hill numbers based on sample data (i.e., empirical or observed Hill numbers) is biased regarding sample completeness and size49. We followed the workflow and steps listed below to achieve meaningful comparisons of the investigated biotic communities (see ref. 56 and Supplementary Table S6): (I) Estimation of phenotype completeness profiles from sample data via a bootstrap method (n = 500) to obtain confidence intervals: this enabled comparison of sample completeness (i.e., diversity detected) of our various habitat datasets. Profiles that increase with order q indicate incomplete sampling and therefore undetected diversity.

(II) Empirical and asymptotic estimation of true diversities based on hypothetical large sample sizes52: sufficient data are a prerequisite for the latter, however. To investigate if our data fulfilled this requirement, we computed sample-size-based rarefaction and extrapolation (R/E) sampling curves for Hill numbers of different orders49,50. Extrapolation was performed to double the actual number of samples per habitat, as further extrapolation is unreliable in the case of phenotype richness49. Levelling out of R/E curves indicates that asymptotic estimates are accurately representing true diversities. In this case, asymptotic and empirical Hill numbers may be compared to assess undetected diversity and the comparison of asymptotic diversity profiles allows the assessment of differences in diversity between habitats. If R/E curves do not level off, asymptotic diversity profiles represent true diversity only up to a certain level of sample coverage (i.e., Cmax, see below) and, therefore, have to be considered as minimum estimates of true diversity.

(III) Comparing diversity for a non-asymptotically standardised sample coverage (i.e., sample completeness for q = 1) in the case where asymptotic extrapolation of true diversity is unreliable: diversity may then be compared between equally complete samples. Here, coverage-based R/E curves were computed to the maximum coverage Cmax. This value represents the sample coverage of the habitat exhibiting the lowest coverage when samples are extrapolated to double the respective number of individuals per habitat.

IV) Estimation of evenness profiles for q > 0 at Cmax, based on ref. 95, to compare evenness profiles of assemblages with varying levels of richness, the slopes of Hill-number diversity profiles connecting two points at q = 0 and any q > 0 are being analysed, whereby steeper slopes represent higher unevenness of phenotype incidence. As Hill numbers are normally used as frequency measures, this was possible for orders of q > 0, but not for q = 0, as all phenotypes are accounted for equally in the latter. In addition, Pielou’s J was calculated as a phenotype evenness measure based on Hill numbers of q = 0 and 1968a. Both evenness profiles and Pielou’s J are based on the richness and Hill-number diversity and were therefore estimated at a standard level of Cmax.

Biodiversity indices for study comparison and community composition analysis

Due to missing original data of studies investigating sessile invertebrate biodiversity hotspots in the Mediterranean and elsewhere (see Table 1), but to ensure comparability with the present study, classical alpha biodiversity (Shannon, Simpson) indices, as well as Evenness index not based on Hill numbers were calculated as followed55:

\[ \text{Shannon index} = - \sum_{i=1}^{n} \left( \frac{n_i}{N} \log_2 \left( \frac{n_i}{N} \right) \right) \]  
\[ \text{Simpson index} = \frac{\sum_{i=1}^{n} (n_i - 1)}{\binom{N}{2}} \]  
\[ \text{Evenness index} = \frac{\sum_{i=1}^{n} \frac{1}{n_i}}{\ln(N)} \]

where \( n_i \) is the number of phenotypes/species in a taxon, and \( N \) is the total number of taxa, with a maximum of 9 as previously defined.

Non-parametric permutation-based multivariate analysis of variance (PERMANOVA57; based on species abundance data using Primer-E v658 with the PERMANOVA+ extension)59 was used to check for significant differences (i.e., \( p \leq 0.05 \)) in the sessile invertebrate community composition among (sub-) habitats. For this, raw count data (related to habitat m²) were square-root transformed to generate Bray–Curtis similarity matrices for PERMANOVA tests with habitats as a factor. Pair-wise PERMANOVA tests were then performed with the unrestricted permutation of raw data (999 permutations), Type III (partial) sum of squares and Monte Carlo tests. In case pair-wise comparisons exhibited significant differences, we checked if these differences may partially or fully be driven by the heterogeneity of multivariate dispersion. In addition, differences in sessile invertebrate community composition were visualised by applying nMDS based on Bray–Curtis similarities. To exclude the parameter ‘sampling location’ as a major driver shaping biodiversity patterns, an nMDS plot based on Bray–Curtis similarities was performed (see Supplementary Fig. S3). A PERMANOVA was performed based on the similarity calculations and on Bray–Curtis similarities (incidence data), in order to test for differences between (sub-) habitats. Lastly, an area-proportional Venn diagram was constructed to describe the shared and unique phenotypes among (sub-) habitats, i.e., P. crispa mats, P. oceanica leaves and P. oceanica rhizomes.

Surface area quantification. For P. crispa, the wet weight of sub- and main samples (see above) was measured after taking algal material of approximately 10 g and shacking off excess water three to five times with one hand. The subsamples were then placed in a bowl on a laminated grid paper and flattened with a glass pan, ensuring that thalli parts did not overlap. Then, pictures were taken from above at a 90° angle using a Canon G12 digital camera and a monopod stand (KAISER RS1) to ensure a constant distance and angle to the respective thalli. The surface area of the algae in the subsamples was then calculated from the picture using Image (version 1.52)60 and multiplied by two to consider both sides of the thalli. The surface area and enlargement factor of the main sample were then calculated as followed:

\[ S_{A_{tg}} = \frac{W_{Wtg} \times S_{A_{tg}}}{W_{tg}} \]

\[ EF_{tg} = \frac{S_{A_{tg}}}{S_{A_{tg}}^{\ast} \times 0.09 m^2} x \frac{0.09 m^2}{W/W} \]

where \( W/W \) is the wet weight, S the surface area, \( M_{S} \) the main sample, \( S_{S} \) the subsample, and \( EF \) is the enlargement factor (i.e., 0.09 m² corresponds to the area of the sampling frame).

For P. oceanica, the commonly applied Leaf Area Index61 was extended to include P. oceanica rhizomes in the surface area calculation. The surface area of P. oceanica was modelled using advanced geometry (sensu ref. 103), as a cylindrical shape was assumed for the rhizome and a rectangular shape for the leaves. Both the length and width of the leaves were measured with a ruler. Subsequently, the number of leaves was determined at the sheath of each rhizome. During additional sampling dives, rhizome density was counted 16 times using a 40 x 40 (0.16 m²) sampling frame. Following this, the enlargement factor was calculated according to:

\[ EF_{tg} = \left( \frac{S_{A_{rhizome}} + S_{A_{revx} \times \text{leaves/rhizome}}}{} \times \text{rhizome/m²} \times 0.16 m^2 \right) \]

0.16 m²

For reference purposes, the surface area enlargement factor of neighbouring bare/granite/bedrock substrates was calculated well using a 20 cm x 20 cm x 2.9 cm PVC-frame (RA = 0.04 m²) with ball chains (metal ball diameter = 2.4 mm) attached to at least three of the four corners of the frame. The chains served to trace the actual dimensions (diagonals and edges) of the underlying substrate enclosed by the projection of the frame’s planar dimensions onto the sample surface. Metal chains were laid out from corner to corner of the frame whilst being aligned to the uneven sample surface. The ball chain link numbers up to the intersection point with the corners of the frame were counted
and converted into the equivalent distance. Using these values, an estimation of the actual surface area could be calculated using Heron’s formula.

Environmental parameters. Environmental parameters were assessed in situ at a depth of 28–30 m close to the Punta del Morto dive site (42°23′22.2″N 10°53′24.3″E; Supplementary Fig. S1) of Giglio Island in September and October 2019, where all target habitats (i.e., P. crispus mats of >5 cm thickness, P. oceanica seagrass meadows of >20 cm height, hard-bottom substrate serving as a reference habitat for environmental parameter assessments) were found less than 10 m apart from each other. Thus, all habitats likely experienced similar environmental conditions allowing a direct comparison of environmental parameters between the habitats.

Water movement within the habitats was measured using clod cards (Gnome Aquatic Systems Ltd.) that recorded data at 1-min intervals. Chlorophyll (Chl) α-like fluorescence was measured from Eureka Manta logger (GEO Scientific Ltd.) that recorded data at 1-min intervals. Chl α-like fluorescence was measured with an optical sensor with a light-emitting diode at an excitation wavelength of 460 nm and emission wavelength of 685 nm (resolution of 0.01 µg·L⁻¹ and accuracy of ±3%). Manta loggers were deployed multiple times (1× in P. crispus mats, 7× in P. oceanica meadows, 6× in reference habitat) for 2–3 days.

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