

1 **Ecosystem engineer morphological traits and taxon identity shape biodiversity across**
2 **the euphotic-mesophotic transition**

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16

17 **Abstract**

18 The euphotic-mesophotic transition is characterised by dramatic changes in environmental
19 conditions, which can significantly alter the functioning of ecosystem engineers and the
20 structure of their associated communities. However, the drivers of biodiversity change
21 across the euphotic-mesophotic transition remain unclear. Here, we investigated the
22 mechanisms affecting the biodiversity-supporting potential of free-living red coralline algae –
23 globally important habitat creators – towards mesophotic depths. Across a 73 m depth
24 gradient, we observed a general decline in macrofaunal biodiversity (fauna abundance,
25 taxon richness, and alpha diversity), but an increase in beta diversity (i.e. variation between
26 assemblages) at the deepest site (86 m depth, where light levels were <1% surface
27 irradiance). We identified a gradient in abundance decline rather than distinct ecological
28 shifts, driven by a complex interaction between declining light availability, declining size of
29 the coralline algal host individuals and a changing host taxonomy. However, despite
30 abundance declines, high between-assemblage variability at deeper depths allowed
31 biodiversity-supporting potential to be maintained, highlighting their importance as coastal
32 refugia.

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34

35 **Keywords:** maerl; rhodolith; biogenic habitat; mesophotic reef; ecosystem shift

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37

38 **Background**

39 Marine ecosystem engineers such as corals and macroalgae are of vast ecological
40 significance throughout the world's oceans [1, 2]. They support highly biodiverse, unique
41 and productive ecosystems [e.g. 3, 4], which can have positive spill-over effects into
42 neighbouring ecosystems [e.g. 5]. The ecological significance of ecosystem engineers is
43 especially large when, for example, extreme environmental conditions do not allow
44 alternative ecosystem engineers to persist [6].

45 The mesophotic oceanic zone – typically 30-150 m water depth, or the maximum depth
46 where corals can sustain photosynthetically-active symbionts [with a light limit of ~1%
47 surface irradiance; 7] – is characterised by diverse and unique benthic ecosystems [8].
48 Mesophotic ecosystem engineers create complex habitats in an environment where few
49 other photosynthetic organisms can survive through photosynthetic acclimation [e.g.
50 macroalgae; 7] and / or increased reliance on heterotrophy [e.g. corals; 9]. Despite facing
51 numerous anthropogenic disturbances at both local and global spatial scales [10],
52 mesophotic ecosystems are comparatively sheltered from shallow-water stressors,
53 suggesting they may be critical refugia for shallow-water communities [8, 11]. However,
54 fundamental questions about the ecological functioning of mesophotic reefs remain [7, 12],
55 especially in lesser studied macroalgal mesophotic habitats [e.g. 13, 14], including: 1) the
56 ecological community composition at mesophotic depths, 2) how these communities differ
57 from shallow depths, and 3) what key biotic and abiotic processes shape mesophotic
58 communities [12].

59 A myriad of environmental changes occur with increasing ocean depth, including reduced
60 irradiance, reduced temperature and altered water flow, driving significant alterations to the
61 physiological and ecological functioning of macroalgal ecosystem engineers [15]. Macroalgal
62 morphological traits are commonly found to change with depth, associated with e.g. light
63 acclimation, energy provision and environmental gradients [e.g. 16]. This can alter the
64 quantity and quality of biogenic habitat, with cascading effect on the diversity and
65 composition of supported communities [e.g. 17]. Depth-associated abiotic changes can also
66 directly alter associated communities [18]. Macroalgal-associated communities may
67 therefore be expected to significantly change through the euphotic to mesophotic [e.g. 19].

68 Free-living, non-geniculate red coralline algae (Corallinaceae, Rhodophyta) – commonly
69 known as rhodoliths or maerl – are macroalgal ecosystem engineers with a cosmopolitan
70 global distribution and are the deepest known macroalga, with coralline algal beds recorded
71 at 270 m depth [20]. Aggregations of free-living red coralline algae create a complex, three-
72 dimensional substrate in otherwise dimensionless soft-bottom seafloors [21]. In turn,

73 shallow-water free-living coralline algal beds have comparable biodiversity other marine
74 biodiversity hotspots such as kelp forests or coral reefs [22]. Morphological traits such as
75 their thallus size and shape are known to affect associated faunal communities through
76 niche provision [e.g. 23], and also change with depth [e.g. 24]. The interaction between free-
77 living coralline algal morphology and water depth may therefore be crucial in determining the
78 biodiversity provision of coralline algal beds at mesophotic depths.

79 Here, we tested the hypothesis that the interaction between the physical and environmental
80 factors of habitat morphology and water depth drive a significant biodiversity transition
81 through the euphotic-mesophotic zones. By comparing coralline algal-associated
82 macrofaunal biodiversity between and within community assemblages across a 73 m depth
83 gradient, we gained insights into the key environmental, morphological and taxonomic
84 drivers shaping biodiversity patterns and their potential for biodiversity provision across the
85 euphotic-mesophotic transition.

86

87 **Methods**

88 **Field sampling**

89 Free-living coralline algal thalli were collected by hand using SCUBA at five sites spanning a
90 73 m depth gradient (13, 40, 56, 65 and 86 m depths) around the Fernando de Noronha
91 archipelago (Figure S1) across a 5 day period in September/October 2018. At each site,
92 coralline algal thalli (n = 7 – 27 per site, 65 total) were non-intentionally targeted in intervals
93 of five diver fin kicks, apart from the deepest site where all samples were collected within a 4
94 m² area due to SCUBA time restrictions. Thalli covered by large fleshy algae (e.g.
95 Dictyotales) were avoided. Thalli were immediately transferred to individual nylon mesh bags
96 (500 µm mesh size) at the seabed to minimise macrofaunal loss. All thalli were returned to
97 the surface within 1 hour of collection and stored in the dark at ambient water temperature
98 before transfer to shore. Thalli were returned to the laboratory within two hours of reaching
99 the surface and immediately fixed in a 10% formalin/seawater solution. In situ
100 photosynthetically active radiation (PAR) at the seabed was recorded at each site
101 (Supplementary Methods 1).

102

103 **Coralline algal species identification**

104 Taxonomic identification of the coralline alga from each free-living coralline algal sample was
105 based on morphoanatomical analyses using the histological methods described in [25] and
106 comparison to known species of the region [13, 26-28].

107

108 **Coralline algal morphology**

109 The volume of each coralline algal thallus sampled for biodiversity was measured via liquid
110 displacement. Sphericity (ψ) [29] was determined by measuring the x, y and z axes using
111 digital calipers (± 0.01 mm resolution, FisherScientific) [30]. Due to the destructive nature of
112 biodiversity assessment (below), surface complexity could not be conducted on the same
113 samples. Instead, additional thalli ($n = 5-16$ per site) were collected for determination of
114 surface complexity: air-dried thalli were 3D scanned at ~ 100 μm resolution (NextEngine, Inc.,
115 USA). Surface complexity was calculated as the average of the three-dimensional surface
116 area of three randomly chosen 1 cm^2 areas from each thallus.

117

118 **Assessment of associated faunal biodiversity**

119 Coralline algal-associated faunal assemblages from each thallus were determined by
120 breaking up the thallus and removing all fauna. The washing water was also filtered using a
121 $500\text{ }\mu\text{m}$ mesh. Vagile macrofauna were preserved in 70% ethanol and identified to Class
122 level. Fauna were counted only when: the cephalic region was preserved (Maxillopoda,
123 Malacostraca, Polychaeta and Sipuncula); the central disc was preserved (Ophiuroidea and
124 Echinoidea); soft body parts were present (Mollusca). Unidentifiable individuals accounted
125 for only 0.32% of total faunal abundance.

126 Univariate diversity matrices of species abundance (N), number of taxa (richness, S), and
127 Shannon-Wiener (H') diversity were calculated using the "Vegan" package in R v3.5.1 [31].
128 Differences between depths were analysed using ANOVA and a post hoc Least Square
129 Means comparisons with Bonferroni adjustment ("LsMeans" package [32]). ANOVA
130 assumptions of normality and homogeneity of variances were tested using the "gvlma"
131 package [33], and data transformed as necessary.

132

133 **Relationship between faunal assemblage, morphological traits and abiotic variables**

134 Faunal-habitat relationships were investigated by constrained additive ordination (CAO) [34]
135 and reduced-rank vector generalized linear models (RR-VGLMs) [35] using the VGAM 1.1-5
136 R package [36]. Details on model fitting is provided in Supplementary Methods 2. All
137 statistical analyses were performed using R 4.1.2.

138

139 **Results**

140 **Potential abiotic and biotic drivers of biodiversity**

141 Light intensity decreased by two orders of magnitude across the sampling depth range, from
142 524 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ PAR at 13m to 6.89 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ PAR at 86m (Figure 1a),
143 equivalent to 26% (13 m) to 0.3% (86 m) of maximum surface irradiance.

144 Biometric traits of thallus size (volume and diameter) significantly declined with depth (Figure
145 1b,c & Table S2), with thalli significantly larger at 13m compared to all deeper depths
146 (except for 65 m where thallus volume did not differ). Thallus sphericity did not significantly
147 vary with depth (Figure 1d, Table S2), but was characterised by high variability at 86 m.

148 Thallus complexity significantly declined with depth, with two groupings: 13-56 m and 65-86
149 m (Figure 1e, Table S2). Taxonomically, the thalli were each composed of single
150 representatives from the Orders Corallinales, Hapalidiales, Peyssonneliales and
151 Sporolithales (Figure S2).

152

153 ***Macrofaunal biodiversity associated with free-living coralline algae***

154 88% of the taxa were accounted for by Malacostraca (35% of total abundance), Gastropoda
155 (29%), Polychaeta *lato sensu* (16%) and Ostracoda (8%), with limited depth specificity
156 (Figure 1). Ten other faunal classes each comprised <4% of the total recorded faunal
157 abundance and demonstrated higher site specificity (Figure 1). Ophiuroidea and Sipuncula
158 were only recorded at the shallowest site. The rarest taxa (<0.5% total abundance) –
159 Pycnogonida, Echinoidea, Monoplacophora and Actinopterygii – were not observed at 86 m.
160 A single Cephalopoda was recorded at the 56 m site.

161 There was a tenfold and significant decline in faunal abundance with depth (Figure 3a, Table
162 S3). The highest abundance in a single thallus was 129 individuals (13 m site). A similarly
163 significant decline was observed for taxon richness (Figure 3b, Table S3). Shannon-Wiener
164 alpha diversity (H') also declined with depth, with a significant difference between the
165 shallowest and deepest sites (Figure 3c, Table S3). Beta-diversity (i.e. variation between
166 assemblages) was similar at 13-56 m, highest at 86 m and lowest at 65 m (Figure 3d, Table
167 S3).

168

169 **Abiotic and biogenic drivers of macrofaunal biodiversity**

170 Increasing mean abundance of all classes was characterised by a fitted gradient comprising
171 a negative relationship with depth, PAR and some host taxa (particularly Peyssonneliaceae)
172 and a positive relationship with thallus diameter (Figure S3, S4, Table S4). Thallus
173 sphericity, complexity and volume were not important explanatory variables (Figure S3,
174 Table S4). These interacting drivers were integrated into a positive log-linear relationship
175 along the CLO ordination gradient – indicated by consistently positive values of \hat{A} (Figure
176 S5, Table S5). Optimum conditions for an abundance maximum could not be defined for
177 seven of the 14 classes (Table S5). The ordination curves for Bivalvia, Maxillopoda and
178 Echinoidea suggest an abundance decline at intermediate gradient values (the composite of
179 the abiotic and biogenic explanatory variables), whilst Pycnogonida, Monoplacophora and
180 Cephalopoda exhibited an abundance maximum at intermediate gradient values (Figure S5).
181 Low total abundances led to Ophiuroidea, Sipuncula and Actiniopterygii being most sensitive
182 to driver change - indicated by the highest coefficients of \hat{A} (Table S5).

183

184 **Discussion**

185 Fundamental questions remain on the ecological role and mechanistic drivers of mesophotic
186 macroalgal habitats [12]. Here, we identified how mesophotic macrofaunal biodiversity is
187 driven by both depth-associated changes in the environment and by biogenic variability of
188 the underlying ecosystem engineer. Despite a marked decline in macrofaunal biodiversity
189 with depth, beta diversity was highest well into the mesophotic zone – indicative of an
190 ecological ‘poise’ for community biodiversity across the euphotic-mesophotic transition.

191

192 **Free-living coralline algal beds are a globally consistent hotspot for biodiversity**

193 Molluscs, crustaceans and polychaetes appear to be consistently abundant in many free-
194 living coralline algal ecosystems worldwide [e.g. 37, 38], and sometimes dominated by
195 Echinodermata [e.g. 39]. In terms of total fauna abundance, the maximum mean abundance
196 (53 individuals per thallus at 13 m depth) is comparable to other shallow-water beds in Brazil
197 and other structurally complex ecosystems such as seagrass meadows [14]. However, we
198 observed a marked decline in faunal abundance with depth. Based on known coralline algal
199 thallus densities at Fernando de Noronha [13], our data suggests at least ~15,700 – 1,000
200 individuals m⁻² at 13 - 86 m respectively, plus additional organisms living between thalli and /
201 or in the underlying sediment. This is an order of magnitude higher than other mesophotic
202 sites (e.g. Malta, Mediterranean Sea - up to 814 macroinvertebrates m⁻² at 46 m) [38]. Given
203 the prevalence of free-living coralline algal beds around the Fernando de Noronha

204 archipelago to at least 100 m depth [13, 14], this study demonstrates their ecological
205 importance throughout the euphotic and mesophotic zones of the region.

206

207 **Biodiversity transition through the mesophotic**

208 Coralline algal bed biodiversity typically exhibits a negative relationship with depth [38, 24,
209 14]. However, these observations have almost all been restricted to non-mesophotic (<30 m)
210 depths, often with only 2-3 depth comparisons and with a focus on fish assemblages [e.g.
211 40], limiting our understanding of euphotic-mesophotic biodiversity transitions. Distinct
212 biodiversity shifts between the euphotic and mesophotic were not evident - perhaps due to
213 the continued capacity for photoautotrophy by the coralline algal hosts via low-light
214 acclimation. Coralline algae in shallow waters are typically light saturated. The consequent
215 gradual change in the ecosystem niche provision may allow for a continuous general
216 transition in faunal communities rather than ecological 'zones' [41], albeit with taxon-specific
217 sensitivities. A recurring challenge in depth-associated coralline algal biodiversity studies is
218 the co-occurrence of algal morphological and taxonomic changes, which makes it difficult to
219 tease apart the individual role of each biogenic trait, nor the role of biogenic habitat vs the
220 environment [e.g. 38, 14]. Our analysis indicates that host diameter and taxonomy are
221 important in describing associated biodiversity, likely via habitat niche provision and
222 hydrodynamic regulation. The negative effect of PAR and host taxonomy on biodiversity may
223 be explained by species-specific production of chemical attractants and / or inhibitors (such
224 as dimethylsulphoniopropionate), perhaps driven by high rates of coralline algal non-
225 photochemical quenching and antioxidant cascade in shallower waters [42]. Experimental
226 investigation using 'discrete habitat units' [e.g. 43] might enable mechanistic understanding
227 of the relative and combined role of environmental and habitat drivers on biodiversity.

228

229 **Mesophotic coralline algal beds as a depth refugium**

230 Despite reduced abundance, richness and alpha diversity at 86 m, dispersion among
231 communities (beta-diversity) was highest at this depth. The observed increase in beta-
232 diversity combined with the observation that the pool of taxa remained largely unchanged
233 with depth indicates that the carrying capacity of the thalli declined at depth [44]. Mesophotic
234 community assemblages were therefore likely restricted by ecological limits rather than the
235 availability of species [45], driven by a reduction in thallus size and a shift in host taxonomy.
236 However, the ecological role of the habitat (as beta-diversity) was not impacted to the same
237 extent. The limited depth specificity for all major taxa (in terms of presence/absence),

238 combined with the limited motility of these fauna in the adult stage, suggests that deeper
239 sites may therefore act as a long-term depth refugium (as opposed to a short-term depth
240 refuge) [46]. This contrasts to the high depth-specificity in reef fish communities [10],
241 suggesting coralline algal biodiversity dynamics and / or invertebrate biodiversity may
242 respond differently to the euphotic-mesophotic transition. Faunal identification to a higher
243 taxonomic resolution would enable deeper functional insight into the refugium potential of
244 these mesophotic communities.

245

246 **Conservation implications**

247 Coralline algal beds have significant economic resource value for industries including
248 carbonate extraction and commercial fisheries; mesophotic beds in particular often coincide
249 with oil and gas activities [47]. Quantitative determination of predictive variables to identify
250 high biodiversity regions (and therefore of high conservation priority) is therefore important
251 for their conservation, particularly where coralline algal beds are extensively distributed.
252 Contrasting community patterns within and between depths highlights a complexity that
253 enables these habitats to be one of the most biodiverse marine ecosystems. Shallow-water
254 coralline algal beds are well known to be threatened by a wide range of environmental
255 stressors [48]. Our results indicate that their deep-water counterparts hold the potential to
256 act as an ecological 'buffer'. We therefore recommend consideration of the euphotic-
257 mesophotic transition as an ecological gradient rather than as distinct 'zones', with formal
258 integration of mesophotic ecosystems into marine protection policies and conservation
259 initiatives [49].

260

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417 **Figure legends**

418 **Figure 1.** Changes in abiotic and biogenic drivers of biodiversity across a 73 m depth range.
419 a) photosynthetically active radiation (PAR) at the seabed, and free-living coralline algal
420 morphological traits: b) thallus volume (cm³), c) diameter (cm), d) sphericity (ψ) and e)
421 surface complexity (dimensionless). Data in b-e presented as mean \pm SE. Letters above
422 symbols indicate statistically different groupings (c.f. Table S2). For a: n = 1; for b-d: n = 27,
423 11, 12, 8 and 7 for sites 13, 40, 56, 65 and 86 m respectively, except for c) where n = 10 at
424 40 m; for e: n = 10, 5, 5, 16 and 15 for sites 13, 40, 56, 65 and 86 m respectively.

425

426 **Figure 2.** Heatmap of macrofaunal abundance associated with free-living coralline algae
427 across a 73 m depth range. Data presented as % contribution to total faunal abundance and
428 as % abundance per site. N = 27, 11, 12, 8 and 7 thalli for sites 13, 40, 56, 65 and 86 m,
429 respectively; total N = 2170 organisms. White colouring indicates zero observed abundance.

430

431 **Figure 3.** Macrofaunal diversity associated with free-living coralline algae across a 73 m
432 depth range. a) abundance (number of individuals per thallus), B) taxon richness (number of
433 taxa per thallus), C) alpha diversity measured using the Shannon-Wiener (H') index, and D)
434 beta diversity (as multivariate dispersion based on a Bray-Curtis similarity index on square
435 root transformed abundance data). Data presented as mean \pm SE. Letters above symbols
436 indicate statistically different site groupings (c.f. Table S3). N = 27, 11, 12, 8, and 7 for
437 depths 13m, 40m, 56m, 65m and 86m respectively.

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