1 # The in situ light microenvironment of corals

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23 **In situ light microenvironment of corals**

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25 ## Acknowledgements

26 We thank Miriam Weber, Dirk De Beer, and Paul Faerber for technical
27 assistance and providing the profiling underwater microsensor system, Ponchalart
28 Chotikarn and Jim Franklin for logistical and technical assistance, and L. F. Rickelt
29 for manufacturing scalar irradiance microprobes. The technicians of the microsensor
30 group at the Max Planck Institute Bremen are thanked for constructing O_2
31 microsensors as are Kyra Hay and the staff at Heron Island Research Station for their
32 help during field work. The research was conducted under research permits for field
33 work on the Great Barrier Reef (G12/35118.1). This research was funded by grants
34 from the Australian Research Council (AWDL, PJR), the Danish Council for
35 Independent Research | Natural Sciences (MK), the Plant Functional Biology and
36 Climate Change Cluster (DW, MK, PJR), the Max Planck Institute for Marine
37 Microbiology (LP) and a postgraduate stipend from the University of Technology,
38 Sydney (DW).

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40

41 ## Abstract

42 We used a novel diver-operated microsensor system to collect the first in situ
43 spectrally resolved light fields on corals with a micrometer spatial resolution. The
44 light microenvironment differed between polyp and coenosarc tissues with scalar
45 irradiance (400-700 nm) over polyp tissue, attenuating between 5.1 to 7.8-fold from
46 top to base of small hemispherical coral colonies, whereas attenuation was at most
47 1.5-fold for coenosarc tissue. Fluctuations in ambient solar irradiance induced
48 changes in light and oxygen microenvironments, which were more pronounced and

faster in coenosarc as compared to polyp tissue. Backscattered light from the surrounding benthos contributed >20% of total scalar irradiance at the coral tissue surface and enhanced symbiont photosynthesis and the local O_2 concentration, indicating an important role of benthos optics for coral ecophysiology. Light fields on corals are species and tissue specific and exhibit pronounced variation on scales from micrometers to decimeters. Consequently, the distribution, genetic diversity, and physiology of coral symbionts must be coupled with the measurements of their actual light microenvironment to achieve a more comprehensive understanding of coral ecophysiology.

Introduction

The quantity and quality of light is one of the most important environmental factors affecting the ecology of reef-forming symbiont-bearing corals (e.g., Dubinsky et al. 1984; Falkowski et al. 1990; Iglesias-Prieto et al. 2004). Light drives photosynthesis of the endosymbiotic dinoflagellate microalgae of the genus *Symbiodinium* that are known as zooxanthellae and are harbored within the tissue of the cnidarian animal host. The coral host provides a protected environment for its symbionts with limited but constant nutrient availability in oligotrophic marine waters. Zooxanthellae photosynthesis generates O_2 and photosynthates that provide the coral host with organic carbon that can support >95% of its respiratory demand (Muscatine et al. 1981). Although zooxanthellate corals are dependent on sufficient light for photosynthesis, high solar radiation during summer-time in shallow waters can be stressful and cause the breakdown of the symbiosis through symbiont

73 expulsion or degradation, leading to visible paling of the colony, i.e., coral bleaching
74 (Glynn 1996; Hoegh-Guldberg 1999). Various physiological aspects of light
75 harvesting and light-related bleaching have been intensively studied over the past
76 decades. However, a detailed understanding of the actual light field experienced by
77 the photosymbionts in the coral tissue is limited, although such knowledge is a
78 prerequisite for a better understanding of coral photobiology (Falkowski et al. 1990;
79 Iglesias-Prieto and Trench 1994; Lesser and Farrell 2004) and ecophysiology (Rowan
80 et al. 1997).

81 Solar radiation takes many detours until it reaches the tissue surface of a coral
82 on a natural reef (Kirk 1994). The initial interaction of sunlight that has passed
83 through the atmosphere is largely determined by the refractive index difference
84 between air and seawater, causing refraction and reflection of incident radiation at the
85 air-water interface. Light that has entered the water column undergoes scattering and
86 absorption, which is caused by the inherent optical properties of the water and a major
87 contribution of dissolved substances and solid particles (e.g. dissolved organic matter,
88 plankton, suspended sediment etc.; Kirk 1994). The quantity of downwelling
89 irradiance reaching a coral reef at a certain depth could in principle be calculated by
90 the spectral attenuation coefficient of the given overlying water mass, which would
91 give a macroscale (i.e. m to km) approximation of irradiance over the area of interest
92 (Kirk 1994).

93 However, for a given coral reef, irradiance is highly variable in both space and
94 time. On a spatial scale, strong meso- (m to mm) and micro-scale (mm to μm) light-
95 matter interactions alter the light availability and quality for photosynthetic reef
96 organisms (e.g., Anthony and Hoegh-Guldberg 2003). Over time, irradiance varies on
97 scales ranging from yearly down to the smallest scales of milliseconds (Kirk 1994;

98 Darecki et al. 2011) . Optical phenomena such as wave focusing can be an important
99 source of variability in the underwater light field causing light flashes of high
100 amplitude and frequency (Stramski and Dera 1988). Especially in shallow water
101 environments, such as on coral reefs, wave focusing can induce light flashes at
102 frequencies of >100 times per minute with maximal amplitudes exceeding the mean
103 irradiance by more than fivefold (Darecki et al. 2011).
104 Studies dealing with the mesoscale light distribution on coral reefs show that
105 reef structures such as crevices and topographic elevations are important sources of
106 variability in the diffuse light component present within the coral reef framework
107 (Brakel 1979; Stimson 1985; Anthony and Hoegh-Guldberg 2003). Also,
108 characteristic features of the colony morphology (e.g. colony shape, branch length,
109 spacing, etc.) cause significant light attenuation and redistribution within a single
110 coral colony (Helmuth et al. 1997; Anthony et al. 2005; Kaniewska et al. 2011). For
111 instance, Kaniewska et al. (2011) showed that the incident downwelling irradiance
112 measured above the coral tissue surface varies about one order of magnitude from the
113 tip towards the base of a branch in the coral *Stylophora pistillata*. Although these
114 mesoscale studies have given invaluable insights, there are two major shortcomings
115 with regard to their relevance for microalgal physiology.
116 Previous in situ studies have mainly quantified available light in terms of the
117 incident downwelling irradiance (E_d). This parameter quantifies the downwelling
118 quantum flux from the upper hemisphere through a horizontal surface area, and does
119 not take backscattered light. However, light from all directions can be used for
120 microalgal photosynthesis and thus E_d measurements generally, underestimate the
121 light available for symbiont photosynthesis *in hospite* (Kühl et al. 1995). A more
122 appropriate parameter for quantifying light exposure relevant for microalgal

123 photosynthesis is the scalar irradiance, which is a measure of the total radiant flux
124 from all directions around a point (Kühl et al. 1995).
125 All in situ light field studies on corals have used sensors that detect light
126 variation only on a macro- or meso- (mm to m) scale. However, recent laboratory
127 studies have revealed that tissue and skeleton optics strongly alter coral light fields on
128 a microscale (Enriquez et al. 2005; Wangpraseurt et al. 2012*a*; Marcelino et al. 2013).
129 Light is strongly scattered at the water-tissue interface and within the coral
130 tissue, where photon trapping and redistribution leads to significant enhancement in
131 the local scalar irradiance in comparison with the incident downwelling irradiance
132 (Kühl et al. 1995; Wangpraseurt et al. 2012a). Light that has entered the tissue can be
133 laterally transferred, most likely through anisotropic scattering (Wangpraseurt et al.
134 2014). Additionally, reflective and/or fluorescent host pigments are synthesized by
135 many corals, which further alters the intensity and spectral quality of light due to e.g.
136 intense scattering and red-shifted emission (Salih et al. 2000). Finally, photons that
137 pass through the tissue are backscattered by the aragonite skeleton, further enhancing
138 tissue scalar irradiance and thus photon availability for zooxanthellae photosynthesis
139 (Enriquez et al. 2005; Marcelino et al. 2013). On a microscale, light is thus strongly
140 affected by the inherent optical properties of corals, which can vary between coral
141 species depending on their skeletal microstructure, tissue types and degree of polyp
142 contraction and expansion (Wangpraseurt et al. 2012*a*; Marcelino et al. 2013; Yost et
143 al. 2013). Microscale light-tissue interactions can thus not be neglected if one aims at
144 a detailed understanding of coral photobiology.
145 The assessment of microscale optics in corals in their natural habitats has until
146 now been limited by the lack of suitable technology, making it impossible to examine
147 the relationships between the macro-, meso- and microscale light distributions in coral

148 reefs. To bridge this gap, we developed here a submersible, fibre-optic based
149 spectrometer module that can be connected to a diver-operated microsensor system
150 (Weber et al. 2007) to measure the first spectrally resolved in situ microscale light
151 measurements in corals. We used this instrument to study in situ spectral scalar
152 irradiance at the coral tissue surface of various massive faviid corals and one
153 branching acroporid and compared the attenuation of light in a coral colony from top
154 to base, focusing on differences between coenosarc and polyp tissues. Additionally,
155 we quantified the contribution of the benthos surrounding the coral to the local scalar
156 irradiance at the coral surface, and assessed its role in coral photosynthesis. We
157 discuss our results in the context of microenvironmental controls of coral function and
158 *Symbiodinium* ecophysiology.
159

160
Methods

161
Study site and coral species

162 In situ microsensor measurements were done in November 2012 on the shallow
163 reef flat next to the Heron Island Research station (152°06'E, 20°29'S), Southern
164 Great Barrier Reef, Australia. Measurements were performed between 09:00 h and
165 17:00 h at water depths ranging from 0.5 m to 2.5 m (as measured from the benthos to
166 the water surface). Low and high tide measurements were done by snorkeling and
167 SCUBA diving, respectively.

168 Massive corals of the family Faviidae (*Goniastrea asprea, Platygyra*
169 *lamelinna, Favites pentagona*) were chosen because of their microscale tissue optical
170 properties, as previously measured with microsensors under laboratory conditions
171 (Wangpraseurt et al. 2012*a*). The branching *Acropora millepora* specimens were

172 additionally selected to compare light attenuation over massive corals with the more
173 pronounced light attenuation known to occur in branching growth forms (Kaniewska
174 et al. 2011).
175
176 **Underwater microsensor system**
177 Ambient scalar irradiance of photosynthetically active radiation (PAR, 400-700 nm)
178 was measured with a miniature scalar irradiance sensor (3 mm diameter; Walz
179 GmbH) connected to an underwater microsensor meter (UnderWater Meter system,
180 Unisense A/S). Spectrally resolved scalar irradiance was measured with a fibre-optic
181 scalar irradiance microsensor prepared as previously described (Lassen et al. 1992).
182 The microsensor had a spherical light-collecting tip with a diameter of ~80 µm and an
183 isotropic angular response. Both sensors were linearly calibrated against a calibrated
184 spherical quantum sensor (US-SQS/L; Heinz Walz GmbH) connected to a PAR light
185 meter (Li-250A, Li-COR); calibration was done during mid-day in a white seawater-
186 filled container. The sensors were aligned next to each other (2-3 cm distance) and
187 submersed in the container (depth of ~15 cm) such that the angle between the sun and
188 the sensor axis was 45°. Subsequently, the sensor readings were taken at 50% and
189 100% solar radiation (blue sky), the former achieved by a neutral density filter with
190 50% transmittance.
191 Oxygen measurements were done with a Clark-type O_2 microsensor (Revsbech
192 1989). The sensor had a tip diameter of ~50 µm, response time of <2 s, stirring
193 sensitivity of <1.5%, and was adapted for underwater use as previously described
194 (Wangpraseurt et al. 2012*b*). Linear calibrations before and after each dive were done
195 using readings in air-saturated and anoxic seawater, the latter achieved by flushing
196 with N_2 gas.

197 In situ microsensor measurements were performed using a diver-operated
198 motorized microsensor (DOMS) profiler operated as previously described (Weber et
199 al. 2007). The O_2 microsensor and the PAR minisensor meter were connected to the
200 analogue inputs of the DOMS, whereas the fibre-optic based scalar irradiance
201 microsensor was connected to a separate water-proof module. This module contained
202 a spectrometer (USB 4000, Ocean Optics) and a custom-made board that allowed
203 acquisition and storage of spectra at time intervals of 1 s or more as triggered by a
204 digital signal provided externally by the DOMS (Fig. 1). The integration time
205 intervals of the spectral acquisition were adjusted interactively during the
206 measurements to optimize the dynamic range of the sensor. The spectral signal output
207 was followed during the measurements via a custom-made underwater PC module
208 (Fig. 1). At the end of each deployment, the raw spectral data were read out via a
209 custom-built circuit connected to a computer, and processed as described below.
210

211 **In situ measurements of the scalar irradiance distribution**

212 To identify differences between coral species and different tissue types with respect to
213 their light microenvironment, spectral scalar irradiance was first measured on the
214 upper light-exposed surface of the corals and compared to the incident downwelling
215 spectral irradiance (Fig. 2a). This was done for coenosarc and polyp tissue of each of
216 the three massive faviid corals (*P. lamellina*, *F. pentagona*, and *G. aspera*). For each
217 measurement, the microsensor was carefully positioned at the corresponding tissue
218 surface with the aid of a magnifying glass. The angle between the sensor and the
219 coral-sun line was 45° to avoid self-shading. Scalar irradiance spectra were recorded
220 in 5 s intervals over a period of 0.5–1 min and averaged. The incident downwelling
221 spectral irradiance (E_d) was determined by measuring the signal above a black non-

222 reflective surface next to the coral at approximately the same height as the coral
223 measurement spots; this was done for each coral after the microscale scalar irradiance
224 mapping (every 20 min).
225 To quantify the distribution of light at the coral surface over a larger scale,
226 spectral scalar irradiance was additionally mapped from top to bottom of the coral
227 colonies. This was done at 3-4 positions over the coral colony (Fig. 2b) and for each
228 position over one coenosarc and one polyp tissue area. During all measurements, the
229 ambient PAR photon scalar irradiance next to the coral was monitored using the
230 miniature spherical PAR sensor, arranged in the same direction and at about the same
231 height as the scalar irradiance microsensor. This data was used to account for small
232 variations (generally <10%) in the ambient light field by multiplying the values
233 measured with the light microsensor on the coral with the factor by which the ambient
234 light field had changed.
235
236 **Effect of backscattered light on coral light and O_2 microenvironments**
237 The relevance of diffuse light for scalar irradiance and O_2 levels at the coral tissue
238 surface was studied for *G. aspera*. The scalar irradiance and oxygen microsensors
239 were positioned on the tissue surface close to each other, both oriented at an angle of
240 45º relative to the coral-sun line. The measured locations were on a coral surface
241 oriented at about 45º relative to the benthos surface and about 5 cm away from the
242 benthos. Subsequently, a thick black cloth (0.5 x 0.5 m) was placed above the coral or
243 above the benthos next to the coral to block, respectively, the direct sunlight or
244 backscattered light from the benthos (Fig. 2c-d) while measuring the scalar irradiance
245 and oxygen concentrations. Measurements were done at solar noon and both on

246 coenosarc and polyp tissues. During all measurements, the ambient PAR was recorded
247 to ensure comparable ambient irradiance regimes.
248
249 **In situ dynamics of microscale scalar irradiance and O_2**
250 Using the same arrangement of microsensors as above, spectral scalar irradiance and
251 O_2 concentrations in coenosarc and polyp tissues of *F. pentagona* were continuously
252 monitored during early afternoon on a partially cloudy day. Ambient scalar irradiance
253 was recorded during all measurements.
254
255 **Data analysis**
256 Data were analysed with routines written in Matlab (MathWorks, version 2012a).
257 Spectral data were either normalised to the incident downwelling irradiance or
258 converted to photon spectral scalar irradiance (μmol photons m^{-2} s^{-1} nm^{-1}). The latter
259 conversion involved two steps. The raw USB4000 spectrometer data was corrected
260 for spectral sensitivity (µmol photons count^{-1}), which was done based on sensitivity
261 data acquired previously (Finke et al. 2013) using a calibrated spectrometer (Jazz,
262 Ocean Optics). The spectra acquired during the calibration experiment (*see* above)
263 were then integrated over wavelengths in the PAR region and plotted against the
264 corresponding output of the PAR sensor. This resulted in a calibration line whose
265 slope was subsequently used to convert all spectral sensitivity-corrected spectra to
266 μmol photons m^{-2} s^{-1} nm^{-1}. When relevant, spectra were also integrated over the 400-
267 700 nm wavelength range to quantify the total photon scalar irradiance of PAR.
268
269 ## Results

270 ***In situ* spectral scalar irradiance at the upper surface of faviid corals**

271 Spectral scalar irradiance at the upper surfaces of faviid corals (E_0) differed markedly
272 from the incident downwelling irradiance (E_d, Fig. 3). Depending on the wavelength
273 in the PAR region, the E_0:E_d ratio varied between 0.8 and 2.4, with the most
274 pronounced enhancement at wavelengths 500-640 nm and >680 nm (Fig. 3a-c).
275 Coenosarc and polyp tissues had characteristic spectral signatures, which differed
276 between the studied coral species (Fig. 3a-c). Contributions of fluorescent host
277 pigments could be clearly seen in the scalar irradiance spectra of the polyp tissue in *P.*
278 *lamellina* and *F. pentagona* (arrows in Figs. 3a, 1c). Light in the far-red region (685
279 nm to 700 nm) was enhanced by about 40% and 80% in the polyp tissue compared to
280 coenosarc tissue in *F. pentagona* and *P. lamellina*, respectively, while such
281 enhancement was not present in *G. aspera*.

282 The relative enhancement of integrated PAR (400-700 nm) differed at the tissue
283 surface between coral species and tissue types (Fig. 3d). For instance, for *P.*
284 *lamellina*, PAR was enhanced by about 36% in polyp tissue as compared to 15% in
285 coenosarc tissue, whereas this trend was reversed for *G. aspera* (42% in coenosarc vs.
286 6% in polyp).

287

288 **Light distribution along colony architecture**

289 Variation of scalar irradiance across massive corals differed strongly between polyp
290 and coenosarc tissues (Fig. 4). While the decrease in scalar irradiance from top to base
291 of the coral colonies was strong at the surface of polyp tissues (up to a 7-fold
292 decrease), for coenosarc tissues the scalar irradiance was fairly homogenously
293 distributed for *F. pentagona*, decreased up to 1.5-fold for *P. lamellina*, or even
294 increased by about 10% towards the base for *G. aspera*. For the branching species *A.*

295 *millepora*, scalar irradiance at the tissue surface decreased by about one order of
296 magnitude from the apical tip towards the base of the branch (Fig. 4m-o). For all
297 studied coral species, these trends were similar for all wavelengths in the PAR region.
298

299 **Environmental effects of benthos optics on coral light and O_2 levels**

300 For coenosarc tissue located about 5 cm from the benthos and oriented at about
301 45° relative to the benthos surface, blocking of direct sunlight led to a decrease in the
302 scalar irradiance at the tissue surface by 80-90%, whereas the reduction was 15-20%
303 when the light backscattered from the sediment surrounding the coral was blocked
304 (Fig. 5a). Thus, about 10-20% of the light exposure was perceived as indirect light at
305 the given spot. Simultaneous microscale measurements of spectral scalar irradiance
306 and O_2 revealed that O_2 concentrations at the tissue surface changed immediately
307 upon blocking of the light backscattered from the sediment surrounding the coral (Fig.
308 5b-c), implying that indirect light plays a significant role in coral photosynthesis. For
309 coenosarc tissue, light blocking led to a decrease in local scalar irradiance by 250-500
310 μmol photons m^{-2} s^{-1} (20-30% of total irradiance) and a corresponding reduction in O_2
311 concentration by >25 μmol L^{-1} (i.e. >12% air saturation; Fig 5b). The effect was
312 stronger for polyp tissue, where the same blocking decreased the local scalar
313 irradiance by about 50% and led to a decrease in O_2 concentration by >50 μmol L^{-1}
314 (Fig 5c). When the sensor was placed towards the top of the coral those effects were
315 no longer visible (data not shown).
316

317 **In situ dynamics of light and O_2 on coral surfaces**

318 Simultaneous in situ measurements of O_2 and spectral scalar irradiance at the tissue
319 surface of *G. aspera* revealed highly dynamic microenvironmental conditions (Fig. 6).

320 For coenosarc tissue, O_2 concentrations reached up to 450 μmol L^{-1} (about 200% air
321 saturation) when the tissue surface scalar irradiance was around its peak value of 980
322 μmol photons m^{-2} s^{-1}. Upon cloud cover, the tissue surface scalar irradiance dropped
323 within seconds from 950 to 150 μmol photons m^{-2} s^{-1}, resulting in a gradual decrease
324 in O_2 concentrations by about 60 μmol L^{-1} (Fig. 6a).

325 Maximal O_2 concentrations at the surface of polyp tissue were ~25% lower than
326 on coenosarc tissue (350 vs. 450 µM O_2), consistent with the observed trend for the
327 tissue surface scalar irradiance (compare Fig. 6a and b). The O_2 dynamics at the
328 surface of polyp tissue did not closely follow changes in the tissue surface scalar
329 irradiance (Fig. 6a). Interestingly, changes in the scalar irradiance at the surface of
330 polyp tissue appeared somewhat 'buffered' in comparison to the dynamic changes in
331 the ambient scalar irradiance. For instance, a 4.4-fold decrease in ambient scalar
332 irradiance (from 1750 to 400 μmol photons m^{-2} s^{-1}) led to only a 2.4-fold decrease in
333 scalar irradiance at the polyp tissue (126 to 53 μmol photons m^{-2} s^{-1}; Fig. 6b). In
334 contrast, the relative changes in microscale and ambient scalar irradiance were equal
335 for coenosarc tissue.

336 Discussion

337 We used a novel diver-operated microsensor system for the first in situ
338 characterisation of coral spectral light fields with µm spatial resolution. Our study
339 provides evidence for the occurrence of different optical niches in different spatial
340 compartments of corals under natural reef conditions and highlights the importance of
341 microscale optics in controlling coral light exposure.

342 Photon scalar irradiance of PAR was enhanced over the incident PAR and the
343 magnitude of light enhancement differed between the investigated coral colonies and

344 their tissue types (Fig. 3). Such modulation of microscale irradiance with respect to
345 incident irradiance is attributable to skeleton and tissue-type specific scattering and
346 absorption properties (Wangpraseurt et al. 2012*a*; Marcelino et al. 2013). For
347 instance, spectral signatures of host pigments in polyp tissue of *P. lamellina* (Fig. 3a,
348 c) likely explained the ~ 20% enhancement of PAR in polyp vs. coenosarc tissue, as
349 fluorescent host pigments around the polyp mouth can scatter light and lead to longer
350 wavelength emission (Salih et al. 2000). Corals show a plastic response to the ambient
351 light field by altering pigment content (Dubinsky et al. 1984), tissue structure
352 (Winters et al. 2009) and growth morphology (Muko et al. 2000), all of which will
353 likely affect the optical environment for corals. Therefore, and as our measurements
354 are from a limited number of corals, the absolute values of light enhancement cannot
355 be considered as unique to a certain species. However, the observed in situ
356 differences in the coral microscale light field (Fig. 3) suggest that despite identical
357 regimes of incident irradiance, a given symbiont population is exposed to different in
358 vivo light fields, as a result of light modulation by the optical properties of the animal
359 host environment and surrounding benthos.
360 The in situ light distribution around the faviid corals points to a central role of
361 corallite architecture in controlling irradiance levels. Studies on colony-level light
362 redistribution have focussed on branching and foliose corals (Helmuth et al. 1997;
363 Hoogenboom et al. 2008) and only recently, a light capture model was developed for
364 a massive coral, but without any support from direct light measurements at the
365 corallite level (Ow and Todd 2010). We show that PAR at the surface of polyp tissue
366 was reduced >7-fold from colony top to base during mid-day, while no substantial
367 attenuation occurred over coenosarc tissue (Fig. 4). Light is thus redistributed by the
368 skeleton and efficiently absorbed by adjacent coenosarc tissue, thereby inducing

369 optical micro niches in polyp tissue even on small hemispherical colonies (<30 cm)
370 under high solar radiation during mid-day. The magnitude of light attenuation found
371 on massive corals is similar to the attenuation observed due to branch shading in *A.*
372 *millepora* (Fig. 4) and other branching corals (Kaniewska et al. 2011) supporting the
373 role of tissue optics and corallite architecture in regulating colony level light capture
374 of massive corals.

375 We found that diffuse backscattered light from the sediment contributed
376 considerably to the microscale light field of corals (Fig. 5). Light reflection from the
377 reef benthos has previously been proposed to control coral photophysiology (Brakel
378 1979; Colvard and Edmunds 2012; Fine et al. 2013), but hitherto no quantification of
379 backscattered light effects on local O_2 evolution have been reported. Diffuse
380 backscattering from the reef sediment was found to contribute as much as 10-50% of
381 the total scalar irradiance at the tissue surface and such diffuse light can stimulate
382 photosynthesis and enhance local O_2 concentrations by >50 μM (~25% air saturation;
383 Fig. 5). This identifies a central role of indirect diffuse light on coral reefs. The
384 contribution of indirect light to local irradiance and photosynthesis will depend on the
385 distance and orientation of the coral surface relative to the benthos. Also,
386 backscattering of light from the benthos will differ between benthos types such as
387 sediment (Kühl and Jørgensen 1994), macroalgae (Colvard and Edmunds 2012) and
388 coral types (Marcelino et al. 2013) and will thus likely influence estimates of coral
389 productivity on ecosystem scales .

390 Coral reef light fields are not static but are modulated by temporal fluctuations
391 in solar radiation that operate on temporal scales ranging from annual (Kirk 1994) to
392 millisecond fluctuations (Darecki et al. 2011). Cloud formation was found to induce
393 fluctuations in light exposure of coenosarc tissue by up to 6-fold within a minute (Fig.

394 6a), while light fields of polyp tissue were less fluctuating and exhibited an apparent
395 dampening of light fluctuations in relation to shifts in the ambient irradiance (Fig. 6b).
396 Such differences might be related to an enhanced contribution of diffuse over direct
397 radiation induced by cloud cover (Kirk 1994). For terrestrial forests, it is known that
398 diffuse light penetrates deeper into understory canopies than direct light does (Urban
399 et al. 2007). We speculate that diffuse light likewise penetrates deeper into the
400 corallite microtopography (*see* structure in Fig. 3) and reaches the polyp tissue surface
401 as compared to direct light, which gets more easily attenuated due to the corallite
402 structure (e.g., polyp walls; Figs. 3, 4). Thus enhanced penetration of diffuse light into
403 the corallite matrix may counterbalance a decrease in the intensity of light during
404 cloud cover and could thus explain observed dampening of temporal fluctuations in
405 light capture present over polyp tissue. The dynamics reported are limited by the
406 temporal resolution of our underwater meter, which operates on the scale of seconds.
407 High amplitude, millisecond pulses of light due to wave focusing (Darecki et al.
408 2011), could thus not be captured. Future in situ studies combining light microsensors
409 with systems capable of capturing high frequency irradiance fluctuations are thus
410 needed to resolve the importance high frequency light pulses in coral
411 photophysiology.
412 Additionally, we found that the O_2 microenvironment was highly dynamic in
413 coenosarc tissue and fluctuated closely with changes in the ambient irradiance, while
414 the O_2 microenvironment of polyp tissue was less dynamic and did not fluctuate
415 simultaneously with changes to the ambient irradiance (Fig. 6b). Such decoupling of
416 O_2 vs. irradiance fluctuations in polyp tissue is likely related to the intricate polyp
417 topography and associated flow patterns forming complex patterns of O_2 exchange
418 with the environment (Wangpraseurt et al. 2012*b*). These observations highlight that

419 different spatial compartments within a single coral colony also exhibit different
420 temporal fluctuations of the local physico-chemical microenvironment adding further
421 complexity to the landscape of ecological micro niches in corals.

422 Our results shed new light onto the control of *Symbiodinium* ecophysiology.
423 The distribution of *Symbiodinium* geno- and phenotypes can be controlled by
424 irradiance across water depth gradients (Rowan and Knowlton 1995) and within a
425 single colony (Rowan et al. 1997). However, often such spatial distribution patterns of
426 *Symbiodinium* in relation to irradiance are ambiguous (Warner et al. 2006; Ulstrup et
427 al. 2007) and thus the role of light vs. e.g., host specificity (Lajeunesse et al. 2004) in
428 regulating *Symbiodinium* distribution within corals has remained disputed. If it is true
429 that irradiance controls *Symbiodinium* distribution (Rowan et al. 1997; Iglesias-Prieto
430 et al. 2004), then any detailed patterns will be masked by the spatial and temporal
431 complexity of the light microenvironment reported here. Our results thus call for a
432 reassessment of *Symbiodinium* distribution in relation to its actual light
433 microenvironment. As a first step it will be useful to compare differences between
434 coenosarc and polyp tissue as they differ in total light exposure and spectral quality
435 (Figs. 3, 4; Wangpraseurt et al. 2012*a*) and can exhibit different patterns of
436 photoacclimation (Ralph et al. 2002).

437 The presence of different optical microniches in different spatial compartments
438 within corals supports the suggestion that such niches can serve as refugia during
439 light-related bleaching conditions (Hoegh-Guldberg 1999; Loya et al. 2001). For
440 instance, polyp tissue at the sides of massive corals will be effectively sheltered (Fig.
441 4) thereby alleviating local light stress during bleaching conditions. It is thus possible
442 that minor symbiont populations are harbored within those niches and can play an

443 important role for the repopulation and redistribution of symbionts after a bleaching
444 event.
445 It has long been reported that an organism's capacity to adapt to environmental
446 change depends on its previous exposure to a given environmental parameter (e.g.,
447 temperature or irradiance; Brown et al. 2002). Whilst initially only the role of the
448 organism's exposure to the average of that parameter has been considered, more
449 recently, it has been proposed that adaptive capacity is determined by the degree of
450 environmental variability (i.e. differences in the magnitude of fluctuation) the
451 organism has been exposed to (Deutsch et al. 2008). The differences in fluctuation of
452 the physico-chemical microenvironment (i.e. light and O_2) reported here thus suggest
453 that symbionts harbored within different spatial compartments (e.g., coenosarc vs
454 polyp, Fig. 6) have a different exposure history of environmental variability. Such
455 different exposure history could translate to and explain differential patterns of
456 adaptation and/or acclimation capacity observed in corals (Loya et al. 2001). While
457 the detailed ecological implications remain to be investigated, we show here that
458 corals harbor complex light microenvironments that can now be characterised at μm
459 resolution under in situ conditions. Such optical microniches show pronounced spatio-
460 temporal variation and differ strongly from the incident underwater irradiance regime
461 both in terms of intensity and spectral quality. The optical properties of the
462 surrounding benthos also affect local light fields and photosynthesis in corals and
463 such interaction needs further attention in coral photobiology studies. A detailed
464 understanding of the in situ microenvironmental ecology of healthy corals will thus be
465 a key to better interpret the spatio-temporal complexity of stress related patterns
466 observed on reefs.
467

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Figure legends

Fig. 1. Diver-operated microsensor system (DOMS) with(1) the measurement control and data storage module, (2) the battery, (3) the motorized micromanipulator equipped with the spectral scalar irradiance microsensor (orange fiber), (4) the

613 commercial underwater PAR meter, (5) the underwater module containing the Ocean
614 Optics spectrometer, and the (6) the underwater personal computer module. Modules
615 (1-3) were part of the original design developed by Weber et al. (2007); modules (5-6)
616 were designed and developed during this study.
617
618 Fig. 2. Schematic representation of measurement geometry for a) Upper surface
619 mapping of different faviid coral species, where E_0 was measured exclusively at the
620 upper light-exposed surfaces for coenosarc and polyp tissue (*n=3*). (b) Colony surface
621 mapping, where E_0 was mapped from top to base around the colony; one coenosarc
622 and polyp tissue area were mapped each. (c) Contribution of direct (0º zenith angle)
623 and indirect light (180º zenith angle) to E_0 measured at ~45º from hemispherical
624 colony center (around 5 cm from the benthos). We used a black cloth to block out
625 light from the different zenith angles. (d) Microscale O_2 and E_0 measurements
626 following repeated darkening of the sediment benthos. (e) Temporal O_2 and E_0
627 dynamics on polyp and coenosarc tissue measured on a cloudy day. The hemisphere
628 represents the idealised structure of the massive faviid corals. The thick arrow
629 represents the incident solar radiation (at 0° zenith angle, or varying angles over time
630 if not specified) and the small white arrows represent indirect, diffuse light. Black and
631 white dots show relative measurement positions of tissue scalar irradiance, E_0, and O_2
632 concentration, respectively.
633
634 Fig. 3. Microscale spectral scalar irradiance (E_0) measured in situ on the surface of
635 polyp and coenosarc tissues located on the colony top of (a) *Favites pentagona,* (b)
636 *Goniastrea aspera,* (c) *Platygyra lamellina*. Measurements were normalised to the

637 downwelling spectral irradiance, E_d, to allow easier comparison between coral species
638 and tissue types. Solid lines show means (E_0 in % of E_d), dashed lines represent mean
639 ± SE (*n*=3). Measurements were done around noon when the sun was close to zenith.
640 Insets illustrate the structure of the corals and different coenosarc (black circles) and
641 polyp tissues (red circles; scale bar = 1 cm). Grey areas represent spectral regions
642 where in vivo Chlorophyll *a* absorption is insignificant and thus the scalar irradiance
643 is affected mainly by light scattering on coral skeleton. (d) photon scalar irradiance
644 integrated over the PAR region (400-700 nm) normalized to the PAR-integrated
645 incident downwelling irradiance (*n=3*).
646
647 Fig 4. Macroscale in situ distributions of spectral scalar irradiance over coral colonies
648 and branches measured separately on the surface of polyp (dashed lines) and
649 coenosarc (solid lines) tissues in locations marked by circles in the coral images. For
650 *A. millepora*, polyp and coenosarc were not differentiated due to the small polyp size.
651 Also, because the position 4 was deeper along the branch of this coral, it is not
652 marked in the image. Bar graphs on the right show scalar irradiance integrated over
653 three wavelength bands in the PAR region (*see* legend in panel O). Note the different
654 y-axis scales. During the measurements, the PAR photon scalar irradiance above the
655 sediment next to the coral was 2500 (*F. pentagona*), 2400 (*G. aspera*), 1700 (*P.*
656 *lamellina*), and 1300 μmol photons m^{-2} s^{-1} (*A. millepora*). Scale bar = 2cm.
657
658 Fig. 5. (a) Spectral scalar irradiance (E_0) was measured when direct light (0° zenith
659 angle; dashed line) and indirect diffuse light backscattered from the benthos (180°
660 zenith angle; solid line) was blocked, and is expressed in per-cent of the scalar
661 irradiance measured without blocking. Measurements were performed on coenosarc

662 tissue of *Favites pentagona* (*see* Fig. 2 for details of the measurement approach). (b-c)

663 Variation of the local PAR photon scalar irradiance and O_2 concentration induced by

664 artificial blocking of the diffuse backscattered light (indicated by gray areas), as

665 measured at coenosarc (b) and polyp (c) tissue of *Goniastrea aspera*. For both

666 measurements, the microsensor tips were about 5 cm from the sediment. The ambient

667 downwelling irradiance remained stable during blocking, as checked by simultaneous

668 light measurements next to the coral.

669

670 Fig. 6. In situ dynamics of scalar irradiance (PAR, black line) and O_2 concentration

671 (dotted line) at the surface of polyp (lower panel) and coenosarc tissue (upper panel)

672 of the upper colony surface of *P. lamellina* during a sunny day with many

673 intermittent passings of clouds (onsets marked by arrows). Ambient scalar irradiance

674 (grey line) was measured next to the coral above strongly reflecting sediment.

675