Capacity for short-term physiological acclimation to light does not control the lower depth distributions of branching corals

Lucas A. Langlois[*] [a] and Mia O. Hoogenboom [a]

[a] School of Marine Biology and Tropical Biology, James Cook University, Townsville 4811, Australia

[*] Corresponding author: lucas.langlois@my.jcu.edu.au

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Abstract

Light availability is a major constraint on the growth and physiological energetics of photosynthetic organisms such as reef-building corals. Despite extensive research on the mechanisms of coral photoacclimation the extent to which the depth distributions of different species are controlled by their capacity for physiological acclimation to light availability remains unclear. This study quantified the capacity for physiological acclimation to light intensity in four geographically widespread and locally abundant coral species (*Acropora digitifera*, *Acropora nasuta*, *Acropora millepora* and *Acropora muricata)*. We aimed to determine the extent of physiological plasticity of these coral species, and how variation in different physiological traits (including photosynthesis, particle feeding and symbiont density) contributed to determining their depth ranges. The results demonstrated that the capacity for short-term (9 d) physiological acclimation was generally limited for the four *Acropora* coral species. Indeed out of the 7 physiological traits that we measured, and which are known to contribute to photoacclimation in other species, 4 did not significantly vary with light under field and laboratory conditions. Collectively, this study indicates that light availability is unlikely to set the lower depth of occurrence for branching coral species that have relatively shallow depth distributions. Furthermore the capacity for reversible plasticity of theses corals appears not sufficient to cover the large changes in physiology that are required to enable corals to expand their depth distributions. This study suggests that processes such as selective recruitment, *Symbiodinium* type and inter-specific competition are important determinants of the habitat distribution of benthic marine organisms.

Keywords: Photoacclimation, Reaction norm, Fluorometry, *Symbiodinium*, Vertical distribution, Coral physiology.

Introduction

Understanding the factors that determine the habitat distribution of different species is a fundamental question in ecology. Although many factors, such as dispersal (Lessios et al. 1998) and geological events during a species evolutionary history (Hortal et al. 2011), are important determinants of species' distributions, variation in the physiological responses of organisms along environmental gradients remain a key component of models that predict 'who lives where' (Kearney & Porter 2004, Holt 2009). Early attempts to explain why certain species are most abundant in particular habitats focused on the concept of the niche. Although there are many different definitions of the niche (e.g., Pulliam 2000), the 'fundamental niche' was originally defined as a multi-dimensional space that represents the full range of conditions a species could live in, and the resources that it would use, in the absence of competition (Hutchinson 1957). The capacity for physiological acclimation (long term or short term adjustments in physiology in response to changes in a environmental variable under controlled laboratory conditions, Prosser 1991) and acclimatization (adjustments in physiology along an environmental gradient in the field, Prosser 1991) has been proposed as a mechanism underlying the breadth of the fundamental niche (Levins 1968, Chown & Terblanche 2007). For instance, capacity for physiological adjustment to different temperature regimes (i.e., thermal tolerance) is positively associated with geographic range size in ectothermic animals (Brattstrom 1968) and insects (Calosi et al. 2008, Calosi et al. 2010). Moreover, highly specialized species, that have a small niche and limited capacity to acclimatize to environmental variation, can be vulnerable to local extinction if environmental conditions change (e.g., Szabo et al. 2009).

The capacity to acclimatize to varying environmental conditions is beneficial for sessile organisms because they are unable to escape adverse conditions. In particular, sessile photosynthetic organisms are exposed to constant fluctuations in light intensity throughout

time (e.g., daily and seasonal cycles) and space (e.g., understory versus canopy or along a depth gradient). Given this variability, the capacity of photosynthetic organisms to acclimate to the local light environment (i.e., photoacclimatize) influences their growth and physiological energetics (Murchie & Horton 1997, Hoogenboom et al. 2009). Zooxanthellate reef building corals form symbioses with photosynthetic algae from the genus *Symbiodinium* that provide the coral host with the majority of its daily energy requirements (Muscatine 1980). Therefore, decreasing light availability and changes in light quality with depth generally constrains most coral species to relatively shallow waters (Dubinsky et al. 1984b). Nevertheless, some coral species do have very broad depth ranges (>100 m, Lesser et al. 2010, Kahng et al. 2012) and, in fact, more than 20% of extant coral species have depth distributions >30 m (Carpenter et al. 2008). The ability of certain coral species to grow in habitats that can differ in light availability by 3 orders of magnitude suggests that the observed among-species variation in coral depth distributions is associated with constraints on the capacity to acclimatize to light availability. The present study tested this hypothesis by quantifying the relative capacity for physiological acclimation (in the laboratory) and acclimatization (in the field) to light intensity for four geographically widespread and locally abundant coral species (*Acropora digitifera*, *Acropora nasuta*, *Acropora millepora* and *Acropora muricata)* that have different depth ranges.

The investigation of physiological plasticity is complex in reef-building corals because both the coral host and its photosymbionts have distinct processes of acclimatization to variation in light intensity. Studies of coral photoacclimation have demonstrated that *Symbiodinium* in corals from low-light habitats have increased light-absorption capacity (measured as the absorption coefficient of chlorophyll a, Dubinsky et al. 1984a), higher light harvesting pigment content (Falkowski & Dubinsky 1981, Dubinsky et al. 1984a, Titlyanov et al. 2001a, b) and higher photochemical efficiency (Hennige et al. 2008). The coral host

can also control their own intracellular light environment via changes in morphology (Falkowski & Dubinsky 1981, Willis 1985), tissue thickness (Kaniewska et al. 2011) or skeletal structure (Enriquez et al. 2005). The light protection mechanisms from the host are particularly important for high-light acclimatization and include the production of fluorescent pigments (Salih et al. 2000), mycosporine-like amino acids (Shick et al. 1999) and heat-shock proteins (Brown et al. 2002). Additionally, corals adjust their rates of feeding on plankton and suspended particulate and dissolved organic matter in seawater (Ferrier-Pagès et al. 2011), and can increase their rates of heterotrophic feeding when light intensity is reduced (Muscatine et al. 1984, Palardy et al. 2005, Lesser et al. 2010). Clearly, comparative studies of the overall capacity for physiological acclimatization of different coral species must account for potential plasticity in host- and symbiont-associated processes.

The aim of the present study was to quantify the magnitude of physiological plasticity of 4 common coral species across a light gradient, and to determine its potential influence on their depth distribution. We focus on branching corals from the genus *Acropora* that are highly abundant on reefs (Wallace 1999) and play a key role in the growth and productivity of reefs (Gattuso et al. 1996). We assessed overall physiological plasticity by monitoring variation in several physiological processes along a gradient of decreasing light intensity both in the laboratory and in the field.

Materials and methods

This study was conducted at Lizard Island in the northern region of Australia's Great Barrier Reef in August 2012. We quantified species' capacity for acclimation and acclimatization in 7 different physiological response variables for *Acropora digitifera*, *Acropora nasuta*, *Acropora millepora and Acropora muricata* (identified in the field based on Wallace 1999). The colonies identified as *A. digitifera* were all from a specific eco-morph of this species, known as "dig-gem", found at Lizard Island (Wolstenholme et al. 2003). This study was conducted on coral species from the same genus so that evolutionary and morphological factors (e.g., general stress tolerance, gross colony morphology and polyp size) would be approximately consistent for all species. These particular species were selected because they are locally abundant and, although they co-occur in upper reef crest habitats at the study location, they have different depth distributions (Carpenter et al. 2008). We note that a reciprocal transplant of deep and shallow colonies could not be used because two of the study species are restricted to the upper reef slope making 'deep' colonies extremely rare at the study site.

Species-specific physiological plasticity was quantified for a total of 156 coral fragments ('nubbins', 39 per species) that were collected from approximately 2 m depth in Mermaid Cove (Lizard Island, 14°38'47"S, 145°27'13"E). All nubbins were specifically collected at the same depth so that they had experienced similar environmental conditions prior to the experiment. The following traits were measured: maximum photochemical efficiency of photosystem II (F_v/F_m), maximum electron transport rate ($rETR_{max}$) and sub-saturation irradiance (E_K); heterotrophic feeding rate; *Symbiodinium* density; and chlorophyll *a* content. These particular physiological traits were selected because they are fundamental to coral energy acquisition and because they capture commonly measured photoacclimation processes that occur over timescales of days to weeks (Anthony & Hoegh-Guldberg 2003,

136 Palardy et al. 2005). Physiological traits were measured for corals that had been acclimated
137 (laboratory) or acclimatized (field) to light intensities across the ecologically relevant range
138 (i.e., daily maximum irradiance between 34 and 939 μmol photon m^{-2} s^{-1}, Hoogenboom et al.
139 2009).

140 In conjunction with assessment of species-specific physiological plasticity, we
141 conducted benthic surveys to confirm that the depth-distribution of each of the study species
142 at Lizard Island was broadly equivalent to the reported depth distribution of the species
143 throughout its geographic range (5-30 m for *A. muricata*, 3-15m for *A. nasuta*, 0-12 m for *A.*
144 *digitifera* and 2-12 m *A. millepora*, Carpenter et al. 2008). Belt transects (either 1 x 10 m or
145 1 x 15 m) were used to assess the relative abundance of the study species at sites, and line
146 intercept transects (10 m or 15 m long) were used to quantify benthic community
147 composition. In total, 1180 m^2 of reef (93 transects) was surveyed across shallow (<3 m),
148 intermediate (4-8 m) and deep (8-12 m) depths below lowest astronomical tide (LAT) at 11
149 locations around the island.

150 *Capacity for physiological acclimation: Laboratory experiment*

151 Nubbins from seven colonies of each species (3 fragments per colony, n = 84 in total)
152 were suspended into approximately 20 L plastic aquaria using fishing wire. Three light
153 acclimation treatments were established using the natural variation in sun exposure at
154 different positions along an outdoor (but undercover) bench, with addition of shade cloth as
155 required. The roof was partially transparent and allowed UV light to pass through. To
156 accommodate each species, 4 replicate tanks (12 tanks in total) were set-up for each of the
157 high, medium and low light treatments (hereafter referred to as HL, ML and LL
158 respectively). Light levels were measured in each treatment tank using a spherical quantum
159 sensor (Li-193, LI-COR Bioscience, USA) attached to a data logger (Li-1400, LI-COR
160 Bioscience, USA). Light intensity measurements from the spherical sensor were later

161 calibrated against a downwelling PAR sensor (Li-192) for direct comparison with the light
162 intensity data from the field (see below and Fig. S1 in Supplement 1 at 1 at www.
163 intres.com/articles/suppl/ m5008p149_supp. pdf for calibration). During the 9 d
164 photoacclimation period, the daily maximum irradiance in the different treatments averaged
165 939 μmol photon m^{-2} s^{-1} (HL, range 460 to 1750), 490 μmol photon m^{-2} s^{-1} (ML, range 375
166 to 550) and 34 μmol photon m^{-2} s^{-1} (LL, range 23 to 45). All aquaria received a constant flow
167 of seawater pumped directly from the adjacent coral reef lagoon. Temperature in the tanks
168 was measured using Hobo data loggers (HOBO Pendant, Onset, USA), and fluctuated
169 between 23.8 and 28.0 ºC (mean of 25.4 ºC) over the course of the experiment depending on
170 time of day and sun exposure. On average the LL treatment was slightly cooler
171 (approximately 0.5°C) than the other two treatments. The three fragments from each colony
172 were each dispatched into a different light treatment.

173 *Capacity for physiological acclimatization: Field experiment*

174 Nubbins from six colonies for each species (3 fragments per colony, n = 72 in total)
175 were glued onto 4 x 4 cm ceramic tiles using underwater epoxy (Selley's 'Knead-It') and
176 allowed to set overnight. The tiles (and nubbins) were then attached to mesh frames that
177 were secured onto concrete blocks at different depths in the field (at Horseshoe reef, Lizard
178 Island, 14°41'12S, 145°26'33E). Racks were placed onto open sand for the high- and
179 medium-light treatments, and on sand below an overhang in the deepest location to further
180 reduce the light intensity in the low-light treatment. This deployment situated the fragments
181 into three light acclimatization treatments with average maximum irradiance over the nine
182 days of 881 (range 484 to 980) μmol photon m^{-2} s^{-1} (~3 m depth below LAT), 670 (range
183 352 to 760) μmol photon m^{-2} s^{-1} (~ 4 m depth below LAT) and 142 (range 115 to 178) μmol
184 photon m^{-2} s^{-1} (~6 m depth below LAT). Light levels in the field were monitored using
185 'Odyssey' data loggers (cosine-corrected photosynthetic irradiance sensor, Dataflow

systems, New Zealand) that were attached to stakes hammered into the substratum immediately adjacent to each rack, and water temperature at each rack was also monitored using Hobo data loggers (HOBO Pendant, Onset, USA). Temperatures in the field averaged 24.7ºC (range 23.8 to 27.0), 24.9ºC (range 23.9 to 27.3) and 24.5ºC (range 23.8 to 25.3) for the high, medium and low light treatments respectively, and were similar to temperatures in the laboratory.

Physiological measurements

Immediately after the acclimation and acclimatization period, photosynthetic activity and heterotrophic feeding were measured for all the fragments. Photosynthetic activity was quantified using a pulse-amplitude-modulate (PAM) fluorometry technique (Ralph & Gademann 2005). This technique assesses photosynthetic capacity based on the variable fluorescence emitted by chlorophyll molecules when excited with light (Schreiber et al. 1986), and provides estimates of the photosynthetic yield of photosystem II (PSII maximum quantum yield, or F_v/F_m). Maximum photochemical efficiency (F_v/F_m) was measured during the night (after a 3 to 4h period of darkness) using a Diving-PAM fluorometer (Walz, Germany, see Table S1 in Supplement 1). In addition the $rETR_{max}$ and E_K (irradiance level at which photosynthesis starts to become saturated,) were derived from the analyses of "rapid light curves" (RLC). For this study the RLCs consisted of nine successive measurements of the effective quantum yield (F'_v/F'_m) where light intensity increases (0, 9, 31, 62, 114, 160, 235, 350 and 480 μmol photon m^{-2} s^{-1}).

Feeding rates were measured overnight using a standard incubation approach (e.g., Hoogenboom et al. 2010b). In summary, fragments were placed into custom-made feeding chambers filled with 1 L of seawater that contained a fixed initial number of freshly-hatched *Artemia salina* nauplii, and depletion of nauplii due to the grazing activity of the coral fragments was monitored at 3 sampling intervals during a 12 h incubation period. We used

211 freshly hatched nauplii every night to ensure that the size distribution of the prey would be
212 the same. A gentle re-circulating flow was generated inside each of 24 replicate chambers
213 using an air stone at the base of the chamber that was connected to an aquarium air pump
214 (Precision 12000, Aqua One, Australia). The chambers were specifically designed to prevent
215 the nauplii from settling on the floor of the chamber whilst providing conditions under which
216 corals expand their tentacles and feed normally. Corals were first placed in the chambers
217 alone for 30 minutes to allow them to adjust to the conditions within the chamber and
218 expand their tentacles. Subsequently, between 3490 and 5500 nauplii were added to each
219 chamber, with slight variation between measuring days due to variation in the density of the
220 *Artemia* culture. After an hour the number of nauplii within 3 replicate 10 mL sub-samples
221 of the solution within each chamber, that were removed from the chambers using a glass
222 pipette, was visually counted and used as the initial concentration of nauplii (time 0). After ~
223 5 h and 12 h, 2 subsequent counts were carried out and the grazing rate of each fragment was
224 estimated using linear regression of nauplii concentration versus time during the incubation
225 relative to control chambers that contained nauplii but not corals.
226 Once the fluorometry and feeding measurements were completed, the nubbins were
227 frozen overnight and tissue was subsequently removed from the skeleton using compressed
228 air, and collected and homogenised in 0.45 μm filtered seawater (GF/F filters, Whatman).
229 The resulting tissue 'slurries' were centrifuged and the supernatant was poured off, 2.5 ml of
230 new filtered seawater was added, and the tubes were vortexed to re-suspend the symbionts in
231 solution. The resulting symbiont suspension was then divided between two eppendorf tubes.
232 The symbionts in one tube were pelleted and then flash-frozen in liquid nitrogen for later
233 chlorophyll extraction and measurement and 1 mL of 10% formalin was added to the other
234 tube to preserve the symbionts for later counting. Coral skeletons were retained for later

quantification of fragment surface area using a wax coating technique (Stimson & Kinzie 1991).

Symbiodinium density was determined by 10 replicate counts of each sample using an improved Neubauer Haemocytometer (Weber). Chlorophyll was extracted by addition of 1.5 mL of 100% ethanol to each sample and vortexing for 60 s to mix. Subsequently, chlorophyll *a* content was measured using spectrophotometry on a SpectraMax Plus^{384} Microplate Reader (Molecular Devices). Chlorophyll concentration, Chl *a* (μg mL^{-1}), was calculated after Ritchie (2006) as:

$$\text{Chl } a = 12.4380\ (A_{665} - A_{750}) - 2.6094\ (A_{629} - A_{750}), \quad (1)$$

where A_{665}, A_{629} and A_{750} are the absorbance at 665, 629 and 750 nm. The coral fragments were not exactly the same size and therefore measurements of *Symbiodinium* density, feeding rates and chlorophyll content were normalized by surface area and are reported per cm^2.

Data analyses

Non-linear regressions of an exponential function ($y = a \bullet e^{(bx)}$ where y is a measured physiological variable, x is environmental light intensity, and a and b are fitted coefficients), were used to characterize how each of the different physiological traits varied in response to the light environment under which the fragments were grown. Regression analyses were performed in R using the "nls" routine (R Development Core Team, 2008). For each trait five different models were compared: 1) a null model (i.e., variation among fragments was not associated with either species identity or light regime) where a straight line was fitted to all the data; 2) a model with a consistent light effect for all species where the exponential function was fitted to all the data; 3) a model with no light effect but allowing for different mean trait values among species differ where a straight line was fitted to data separately for each species; 4) a model with a species specific light effect where the exponential function

was fitted to data separately for each species; and 5) a model with a treatment-specific light effect where the exponential function was fitted separately for each species under laboratory versus field conditions. A formal model selection procedure, based on the Akaike Information Criterion in the form of wAIC, was used to determine which of the five models had the strongest support, as per Hoogenboom et al. (2011). This technique indicates which of a set of models (i.e., model 1 through 5) is the most likely given the data, and estimates the probability that the chosen model would be the best model if the study was repeated (Burnham & Anderson 2002). Models with wAIC values greater than 0.95 (i.e., indicating 95% support for a single model among the set) were considered to be strongly supported by the data. In cases where several models have similar wAIC values, this indicates that those models are equally likely given the data. Analogously to an Analysis of Variance, but allowing consideration of non-linear and continuous variables, this approach enabled us to assess how strongly light intensity affected each physiological trait, and whether this effect was the same or different among species and among laboratory versus field treatments.

The RLCs were analyzed by non-linear regression to obtain estimates of the $rETR_{MAX}$ and E_K. To do so, the quantum yield was first multiplied by the light intensity increments to convert into a measure of relative electron transfer rate (Ralph & Gademann 2005). Subsequently, regressions were performed in R using the "nls" routine (R Development Core Team, 2008) by fitting the following photosynthesis/irradiance equation to the data:

$$rETR = rETR_{MAX} (1 - \exp (- x/E_K)), \quad \text{Eq 1}$$

where x is the light intensity at each step of the rapid light curve.

To express changes in each physiological trait in a common currency, differences in physiology between high and low light were converted into carbon equivalents ($\mu g\ C\ cm^{-2}$). Species-specific data describing relationships between changes in particular physiological

285 traits and overall carbon gain by the whole organism are generally lacking in the literature;
286 therefore, the effect of the changes in chlorophyll *a* content on coral carbon acquisition was
287 calculated based on published data describing the functional relationship between chl *a* and
288 the maximum rate of photosynthesis, P_{MAX}, for *A. muricata* (Anthony et al. 2009), assuming
289 colonies were photosynthesising for 8 h d^{-1}. The effect of the measured changes in symbiont
290 density on carbon acquisition was determined from a previously published functional
291 relationship between symbiont density and P_{MAX} (Hoogenboom et al. 2010a), again assuming
292 colonies were photosynthesising for 8 hours a day. Note that the data presented in
293 Hoogenboom et al. (2010a) were here re-analysed with normalisation to surface area instead
294 of protein (M. Hoogenboom, unpubl. data; see Fig. S2 in Supplement 2 at www.
295 intres.com/articles/suppl/ m508p149_supp. pdf). The effect of changes in heterotrophic
296 feeding rates on coral carbon acquisition was calculated assuming that corals fed
297 continuously for 12 h and acquired 0.15 μg C $prey^{-1}$ (Hoogenboom et al. 2010b). We note
298 that these conversions to carbon equivalents were conducted to provide a general
299 approximation of the relative effects of changes in the measured traits on overall coral
300 energy acquisition.
301

302 ## Results

303 ### *Benthic surveys*

304 Abundance of the study species varied between 0.1 to 2 colonies m^{-2} and *Acropora*
305 *nasuta* was the most widespread species overall, present on 57% of the transects compared
306 to 40%, 34% and 36% for *A. muricata*, *A. millepora* and *A. digitifera* respectively. The
307 benthic surveys confirmed that the four study species had different depth distributions (see
308 Fig. S3 in Supplement 3 at www. int-res.com/articles/suppl/ m508p149_supp. pdf). Of the
309 four species, *A. nasuta* and *A. muricata* had the broadest depth distributions (occurring to ~7

m below LAT in our surveys) whereas *A. digitifera* was not found below ~2 m below LAT. *A. millepora* had an intermediate depth range with a maximum of depth of ~5 m below LAT. The ranking of species as either generally restricted to shallow water (*A. digitifera* and *A. millepora*) or persisting to greater depths (*A. nasuta* and *A. muricata*) at Lizard Island were similar to previous observations (see Carpenter et al. 2008).

Physiological measurements

The model selection procedure revealed that the importance of light and species identity as drivers of variation in physiology varied among the different physiological traits (Fig. 1). Variation in chlorophyll *a* content per surface area was strongly associated with light intensity, and the shape of this response differed among species (i.e. Model 4, wAIC 0.99, Fig 1A). Indeed *A. muricata* showed the strongest decrease in chlorophyll in response to increasing light intensity compared to the other three species (Fig. 2). Conversely, neither symbiont density or feeding rate differed substantially in response to variation in light intensity, nor did these traits differ among coral species (model support was strongest for the null model [Model 1] for symbiont density, Fig 1D; and equivocal for Models 1 – 3 for feeding rate, Fig 1B). Overall, corals hosted an average of 0.9×10^6 symbionts per unit surface area (Fig 3) and consumed between 45 – 67 *Artemia* cm^{-2} per night (*A. digitifera* and *A. millepora*, mean feeding rates respectively) (Fig 4). The only trait for which there was evidence of a different response for colonies in the field versus the laboratory was for chlorophyll content per symbiont cell (Fig 1C, wAIC 0.99 for the model including the treatment effect [Model 5]). Overall, corals maintained in the laboratory tended to have more chlorophyll *a* per symbiont compared to the ones from the field except for *A. nasuta* (Fig. 5). For two of the study species, *A. nasuta* and *A. millepora,* chlorophyll *a* content per symbiont cell was approximately consistent across all light levels whereas for *A. muricata* and *A.*

digitifera there was a significant decrease in chlorophyll *a* per cell with increasing light both in the laboratory and the field.

Concerning the photosynthetic parameters measured using PAM fluorescence, maximum photochemical efficiency of PSII (F_v/F_m) decreased by ~8 to 14% across the measured light intensity gradient, and this response was generally consistent among the 4 species (wAIC for Model 2 = 0.99, Fig. 1E and Fig. 6). Maximum electron transport rate ($rETR_{MAX}$) was approximately consistent across the range of light intensities (and between field and laboratory treatments) but differed among the study species (Fig. 1F and Fig. 7). The sub-saturation irradiance (E_K) increased with increasing irradiance for all but *A. muricata,* suggesting that the effect of increasing light intensity was species-specific for this parameter (Fig. 1G, Fig. 8). On average, *A. muricata* had the highest $rETR_{MAX}$ (with 93 μmol electron m^{-2} s^{-1}) and the second highest E_k (223 μmol photon m^{-2} s^{-1}) while *A. millepora* had the highest E_K (235 μmol photon m^{-2} s^{-1}) and the second highest $rETR_{MAX}$ (91 μmol electron m^{-2} s^{-1}). Conversely, *A.nasuta* had the lowest $rETR_{MAX}$ and E_K (79 μmol electron m^{-2} s^{-1} and 194 μmol photon m^{-2} s^{-1} respectively).

Effects of photoacclimation on carbon acquisition

The variation in feeding rates, symbiont density and chlorophyll *a* content in response to variation in the light intensity at which colonies were maintained did lead to differences in carbon acquisition between the four species (Table 1). The species with the largest depth range, *A. muricata,* had the greatest change in carbon acquisition between high and low light with a gain of 112 μg C cm^{-2} associated with its ability acclimate to changes in light intensity. Changes in physiology associated with the same change in light intensity (i.e. between high and low light) led to overall gain in carbon acquisition of 36, 27 and 11 μg C cm^{-2} for *A. nasuta*, *A. millepora* and *A. digitifera*, respectively. Of the 3 processes considered here, the variation in chl a content had the largest influence on colony energy

359 acquisition (range 9 to 70 μg C cm^{-2} h^{-1}). Conversely, the observed variations in feeding
360 rates only caused a small change in colony energy acquisition (3 to 9 μg C cm^{-2} h^{-1}).
361

362 ## Discussion

363 Despite the differences in their depth ranges, the 4 *Acropora* species studied here had
364 approximately equivalent capacity to adjust their physiology in response to a change in
365 ambient light intensities. Additionally, our study indicates that, for *Acropora* species, short-
366 term photoacclimation and photoacclimatization is mainly driven by changes in chlorophyll
367 *a* content per cm^2 and in photochemical efficiency (F_v/F_m). The content of chlorophyll *a* per
368 symbiont cell also increased in response to decreasing light intensity for two of the four
369 study species, although the strength of this effect depended upon whether colonies were
370 deployed in the field or in the laboratory. Surprisingly, other physiological traits that have
371 been shown to vary with light intensity in other species, such as feeding rates (e.g., Lesser et
372 al. 2010) or *Symbiodinium* density (e.g., Titlyanov et al. 2001a, b), did not contribute to
373 photoacclimation for our study species during the experimental period.
374 Ecological theory suggests that environmental conditions can influence the assembly
375 of communities by filtering species into habitats based on their physiology, morphology and
376 life-history traits (Southwood 1988, Keddy 1992). However, there is on-going debate
377 regarding the relative importance of environmental tolerance as a determinant of species
378 habitat distributions compared with processes like dispersal limitation and biotic interactions
379 (e.g. Legendre et al. 2005). Few studies have explicitly quantified the relative importance of
380 environmental conditions compared with biological interactions as determinants of coral
381 distributions. One such study showed that intensity of competition had effects on tissue
382 quality (an index of coral health) that were comparable in magnitude to the effects of
383 environmental conditions (including light, temperature and flow, Hoogenboom et al. 2011).

384 At the reef sites surveyed in this study, coral cover generally declined with depth whereas
385 bare space increased (see Fig. S4 in Supplement 3), suggesting that competition is less
386 important in structuring coral communities in deeper waters. Our analyses of coral
387 physiology, however, do not support the hypothesis that species that are restricted to high
388 light environments are unable to persist in deeper waters (with lower light availability)
389 because they have limited capacity for photoacclimation. Instead, changes in colony
390 morphology (e.g., Anthony et al. 2005, Kaniewska et al. 2008) and/or very large changes in
391 physiology in the form of longer-term acclimatization process and/or genetic adaptation
392 appear to be required to cause an increase in a coral species' realised depth distribution.

393

394 *Changes in coral physiology along a light gradient*

395 By quantifying acclimation and acclimatization of multiple traits in response to a
396 light intensity gradient we were able to better estimate the overall capacity for physiological
397 plasticity of different species. Of the set of physiological traits measured in this study, the
398 increase in photochemical efficiency in response to decreasing light intensity is congruent
399 with responses observed in coral symbionts (Hennige et al. 2008), phytoplankton
400 (Kropuenske et al. 2010), seagrasses (Major & Dunton 2002) and higher plants (Demmig-
401 Adams et al. 1996). Such an adjustment is part of a common strategy among photosynthetic
402 organisms aiming at increasing the utilisation of light energy under light limiting (low
403 irradiance) condition (Perkins et al. 2006) while minimising damage to the photosynthetic
404 apparatus under high light conditions (e.g., Hoegh-Guldberg and Jones 1999). The increase
405 in sub-saturation irradiance with increasing light intensity was congruent with the decrease
406 in photochemical efficiency across the same light gradient, and was generally consistent with
407 observations for mound-shaped coral species (Hennige et al. 2008), and other branching
408 coral species (Frade et al. 2008). Conversely $rETR_{MAX}$, did vary between *Acropora* species

409 but not change significantly with light. This indicates that $rETR_{MAX}$ changes more slowly
410 following a change in light intensity than Fv/Fm or E_K do. Although further investigation is
411 needed to understand why E_K and $rETR_{MAX}$ vary with light intensity for some species but
412 not others, we propose that differences in *Symbiodinium* types, as well as host specific traits
413 relating to light regulation and photoprotection such as production of fluorescent proteins
414 and mycosporine-like amino acids (e.g., Shick et al. 1999, D'Angelo et al. 2008), are likely
415 to underlie these effects.

416 The general trends of increasing chlorophyll *a* content with decreasing light were
417 consistent with previous studies (Falkowski & Dubinsky 1981, Dubinsky et al. 1984a).
418 Interestingly in our study there was no significant evidence of increasing *Symbiodinium*
419 density with decreasing light unlike previous findings (Titlyanov et al. 2001a, Titlyanov &
420 Titlyanova 2002). Similar to our findings with respect to the fluorescence traits (F_v/F_m, E_K
421 and $rETR_{MAX}$) these findings indicate that changes in *Symbiodinium* population density
422 occur more slowly in response to changes in light intensity (e.g., over a period of 30 to 90
423 days, Titlyanov et al. 2001a, Hoogenboom et al. 2010b) than do changes in chlorophyll
424 content. Hence, the 9 day photoacclimation period used in this study might have been too
425 short to observe a significant effect of light on symbiont density. Our results also reveal that
426 chlorophyll *a* content per *Symbiodinium* cell varies during photoacclimation to low light for
427 some species (i.e., for *A. muricata* and *A. digitifera*), but that the production of chlorophyll a
428 per cell is highly sensitive to small differences in light-quality and/or water quality.
429 Although we cannot definitively explain why this result occurred, the treatment effect on
430 chlorophyll *a* per *Symbiodinium* suggests that environmental conditions in the field
431 compared with the laboratory limited the production of chlorophyll *a* per symbiont cell.
432 Given that seawater used in the experimental aquaria was obtained directly from the lagoon
433 less than 500 m away from the site at which colonies were deployed in the field, it is

434 unlikely that differences in water quality are responsible for this trend. Instead, we suggest
435 that differences in the light spectrum experienced in the field compared with the laboratory
436 (i.e., due to light wavelength specific attenuation with depth below the water surface) may
437 have contributed to this finding (e.g., Mass et al. 2010).

438 There is growing evidence that different types of *Symbiodinium* have different
439 capacity for photophysiological adjustments (Rodriguez-Roman & Iglesias-Prieto 2005), and
440 that the scope for variation in photosynthetic processes can be strongly influenced by the
441 types of symbionts hosted by coral species (Iglesias-Prieto et al. 2004, Frade et al. 2008b).
442 Therefore the ability to harbour a broad range of *Symbiodinium* types might help corals
443 expand their depth distribution as there are evidence of strong genetic structuring both host
444 and symbiont along the depth (Rowan & Knowlton 1995, Frade et al. 2008a, Bongaerts et al.
445 2010). Indeed differences in the *Symbiodinium* type composition have been linked to
446 irradiance gradients (Iglesias-Prieto et al. 2004). Our work suggests that changes in
447 *Symbiodinium* type are required for corals to increase their depth range as physiological
448 plasticity alone is insufficient. Although we did not identify the specific types of symbionts
449 present within our samples, previous research into symbiont specificity on the Great Barrier
450 Reef has revealed that most *Acropora* species harbour type C3 (ITS2, see Tonk et al. 2013)
451 under normal conditions, although low concentrations of other symbiont types can also be
452 present (LaJeunesse et al. 2004). Furthermore several other studies pointed out that
453 *Symbiodinium* types present within colonies of the same species are generally consistent for
454 colonies present at the same depth (Bongaerts et al. 2010, Silverstein 2012).

455 Heterotrophic feeding can act as an alternate source of carbon for corals when the
456 capacity for photosynthesis becomes limited (Anthony & Fabricius 2000, Grottoli et al.
457 2006). However, our study showed that light intensity did not influence the feeding rates of
458 corals either from the laboratory or from the field. Interestingly, throughout the experiment,

459 *A. millepora* was the only species to have expanded tentacles during the day and night
460 suggesting this species might rely more on heterotrophic feeding than the other species, as
461 indicated by (Anthony 1999, Anthony 2000). The availability of particulate food during
462 laboratory experiments can affect how coral grazing rates differ in response to variation in
463 irradiance (Hoogenboom et al. 2010b). However, even though corals used in the laboratory
464 experiment versus the field experiment had different food availability during the
465 photoacclimation period, feeding rates were generally consistent between these two groups
466 and no treatment effect was detected after data analyses. More broadly, the absence of a
467 general up-regulation in grazing rate in response to declining light availability suggests that
468 *Acropora* species are unlikely to be able to rely solely on heterotrophy as food source during
469 coral bleaching events (see Grottoli et al. 2006).
470

471 *Physiological plasticity and carbon acquisition*

472 In order to better understand how changes in individual physiological processes
473 influence energy acquisition of coral colonies, some of the traits measured here were
474 converted into carbon units. Unfortunately the conversion could not be done accurately for
475 F_v/F_m and E_K due to limitations associated with fluorescence data (Enríquez & Borowitzka
476 2010). Nevertheless, this analysis clearly showed that the observed variation in the different
477 traits had different implications for carbon gain. In particular, the variation in feeding rates
478 had a smaller effect on colony carbon acquisition compared with variation in chlorophyll
479 concentration and *Symbiodinium* density. When converted into units of carbon acquisition,
480 the species with the largest depth range (*A. muricata*) did have the greatest
481 photoacclimation-associated total change in carbon acquisition across the experimental light
482 gradient. Although these conversions to carbon equivalents only approximate the relative
483 effects of changes in the measured traits on overall coral energy acquisition, these analyses

484 indicate that the observed change in chlorophyll content has a larger effect on energy
485 acquisition of coral colonies than the observed change in particle feeding. Therefore,
486 converting variation in physiological traits into common units of energy acquisition is
487 important for understanding how overall coral health varies along environmental gradients.
488 Research on species-specific traits relating to carbon use efficiency, carbon translocation
489 from symbiont to host, and carbon and nutrient allocation to host and symbiont tissue is
490 required to confirm the relationship between physiological plasticity in carbon acquisition
491 and coral depth distributions.

492

493 *Beyond "reversible plasticity"*

494 Although our study provides a useful contribution towards elucidating the role of
495 physiological tolerance in shaping the habitat distributions of reef-building corals, we
496 measured only the 'reversible plasticity' (sensu Angilletta 2009) of adult corals to changes in
497 light intensity. This type of plasticity encompasses only the short-term physiological changes
498 that enable individual coral colonies to cope with, for instance, weekly or seasonal
499 fluctuations in environmental conditions. Extrapolating from our results, we suggest that the
500 capacity for physiological plasticity of coral colonies may be greater in juvenile corals
501 compared with adults. Such 'developmental plasticity' is common in both terrestrial and
502 marine species (Beck 1983, Newman 1989) but, to our knowledge, has not yet been
503 investigated in reef corals. However, consistent with our interpretation, juvenile corals, at the
504 end of their pelagic larval phase, are able to recognize habitat-specific cues from the
505 substratum to actively choose the depth of their settlement (Baird et al. 2003), and exhibit
506 light dependent settlement patterns that match the vertical distribution of adults (Mundy &
507 Babcock 1998). This suggests that coral larvae have enhanced physiological plasticity that
508 enables them to successfully establish in diverse environments, and that the early stage of the

509 coral life-cycle is critical for determining species' depth distributions. Quantitative studies of
510 the relationship between the physiological plasticity and recruitment success of coral larvae
511 in different environments are required to determine whether depth-selection by coral larvae
512 establishes the depth distribution of coral colonies, and whether the physiological tolerance
513 of adult corals is established early in their life-cycle.

514 Our study provides a new assessment of the light intensity reaction norms for
515 photophysiology of four common coral species based on a multi-trait analysis. Previous
516 studies (Lesser et al. 2000, Frade et al 2008a, Frade et al 2008b) measured physiological
517 traits of corals after collection of colonies from different depths, therefore targeting long-
518 term acclimatization responses. Instead this study included corals from same light regimes to
519 novel light levels in the laboratory and in the field, therefore comparing short-term
520 acclimation and acclimatization potential. The results showed that the capacity for
521 physiological plasticity was generally limited for the four *Acropora* species. Indeed out of
522 the 7 physiological traits that we measured, that are known to contribute to photoacclimation
523 in other species, 4 did not significantly vary with light suggesting that plasticity in these
524 particular traits is strongly species-specific, or occurs in response to longer-term changes in
525 the environment than those investigated here. Collectively, the lack of evidence of a link
526 between depth distribution and physiological plasticity indicates that light availability is
527 unlikely to set the lower depth of occurrence for branching coral species that have relatively
528 shallow depth distributions. Although short-term reversible plasticity is important for corals
529 to cope with short-term (diurnal or weekly) changes in environmental conditions, larger
530 changes in photophysiology over a longer time period appear to be required to enable corals
531 to expand their depth distributions. Furthermore, the results of this study suggest that other
532 biological processes such as selective recruitment, depth-related variation in *Symbiodinium*

533 types, and inter-specific competition are important determinants of the habitat distribution of
534 sessile marine organisms.
535

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540

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747

748

Tables

Table 1. Difference in carbon acquisition (μg C cm^{-2}) between coral adapted to low light and high light as a result of the changes in feeding rate, symbiont density and chlorophyll *a* content. The different species are ordered based on decreasing depth range.

Difference in carbon acquisition (μg C cm^{-2})	*A. muricata*	*A. nasuta*	*A. millepora*	*A. digitifera*
Feeding rate	8	3	-3	-1
Symbiont density	34	8	6	3
Chlorophyll *a* content	70	25	24	9
Total	112	36	27	11
Depth range (m) observed	8	8	6	3
Depth range (m) from Carpenter et al. 2008	25	12	12	10

Figure Legends

Fig. 1. Relative support for 5 models that describe, for 4 coral species, variation in 7 physiological traits with light intensity. Bars—weighted Akaike information criterion (wAIC) for each of the models fitted to the data for each of the traits. Models—(1) no effect (null model); (2) consistent light effect for all species; (3) no light effect, but different trait values among species; (4) species-specific light effect; (5) treatment-specific light effect (see 'Materials and methods: Data analyses' for full descriptions of the models). Traits—(A) chl a content, (B) coral feeding rate, (C) chl a per symbiont cell, (D) symbiont density, (E) maximum photochemical efficiency of PSII (Fv/Fm), (F) maximum electron transport rate (rETRmax), (G) subsaturation irradiance (EK).*The model that is best supported by the data.

Fig. 2. Chl a content per cm^2 for (A) *Acropora digitifera*, (B) *A. muricata*, (C) *A. millepora* and (•) *A. nasuta* versus light intensity for corals deployed in the field (D) and in the laboratory (o). Lines: non-linear regression (exponential) fitted to all data. Data points: mean of 144 samples with error bars (SE). Fitted coefficients of non-linear regression ($y = a \times e^{bx}$) and the statistical significance of their difference from zero are shown.

Fig. 3. Symbiont density for *Acropora digitifera* (A), *A. muricata* (B), *A. millepora* (C) and *A. nasuta* (D) versus the light intensity for corals deployed in the field (•) and in the laboratory (o). Lines represent the linear regression fitted to all the data ($y = a$) and points are average of 155 samples with error bars representing standard error. Values within panels indicate fitted coefficient of linear regression ($y=a$), and whether this coefficient is significantly different from zero.

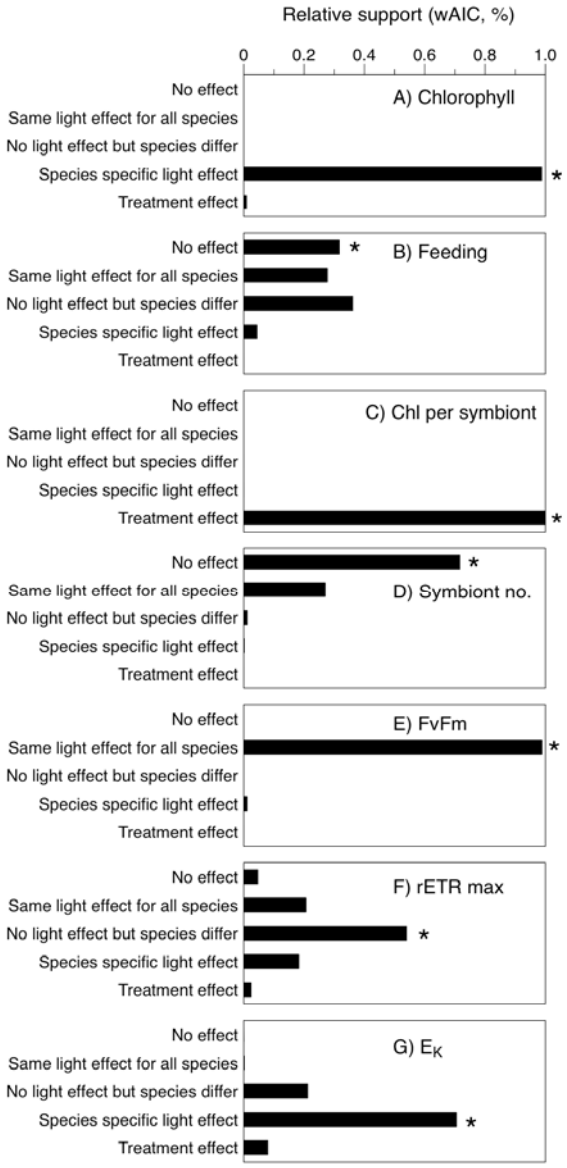
781 Fig. 4. Feeding rates for (A) *Acropora digitifera*, (B) *A. muricata*, (C) *A. millepora* and (D)
782 *A. nasuta* versus light intensity for corals deployed in the field (•) and in the laboratory (o).
783 Lines: linear regression fitted to all the data (y = a). Data points: mean of 117 samples with
784 error bars (SE). Fitted coefficient of linear regression (y = a) and the statistical significance
785 of its difference from zero are shown.
786
787 Fig. 5. Chl a content per 10^6 symbiont cells for (A) *Acropora digitifera*, (B) *A. muricata*, (C)
788 *A. millepora* and (D) *A. nasuta* versus light intensity for corals deployed in the field (•) and
789 in the laboratory (o). Lines: non-linear regression (exponential) fitted to laboratory (solid) or
790 field (dashed) data. Data points: mean of 144 samples with error bars (SE). Fitted
791 coefficients of non-linear regression ($y = a \times e^{bx}$) for the laboratory and field and the
792 statistical significance of their difference from zero are shown.
793
794 Fig. 6. Maximum photochemical efficiency of PSII (Fv/Fm) ($\times 10^3$) for (A) Acropora
795 *digitifera*, (B) *A. muricata*, (C) *A. millepora* and (D) *A. nasuta* versus light intensity for
796 corals deployed in the field (•) and in the laboratory (o). Lines: non-linear regression
797 (exponential) fitted to all the data. Data points: mean of 151 samples with error bars (SE).
798 Fitted coefficients of non-linear regression ($y = a \times e^{bx}$) and the significance of their
799 difference from zero are shown. Note that the same regression applies to data for all 4
800 species.
801
802 Fig. 7. Relative maximum electron transfer rates ($rETR_{max}$) for (A) *Acropora digitifera*, (B)
803 *A. muricata*, (C) *A. millepora* and (D) *A. nasuta* versus light intensity for corals deployed in
804 the field (•) and in the laboratory (o). Lines: linear regression fitted to all the data (y = a).

Data points are average of 151 samples with error bars (SE). Fitted coefficient of linear regression (y = a), and the statistical significance of its difference from zero are shown.

Fig. 8. Sub-saturation irradiance (E_K) for *Acropora digitifera* (A), *A. muricata* (B), *A. millepora* (C) and *A. nasuta* (D) versus the light intensity for corals deployed in the field (•) and in the laboratory (o). Lines: non-linear regression (exponential) fitted to all the data. Data points: mean of 144 samples with error bars (SE). Fitted coefficients of non-linear regression ($y=a \times e^{bx}$), and statistical significance of their difference from zero are shown.

Figures

Fig 1



821 Fig 2

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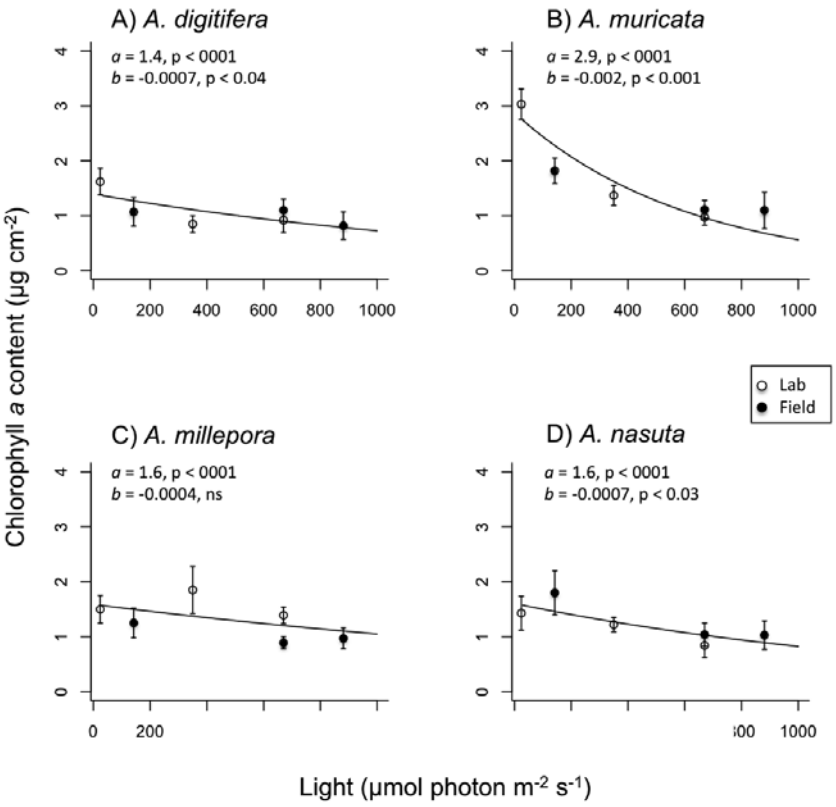

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827 Fig 3

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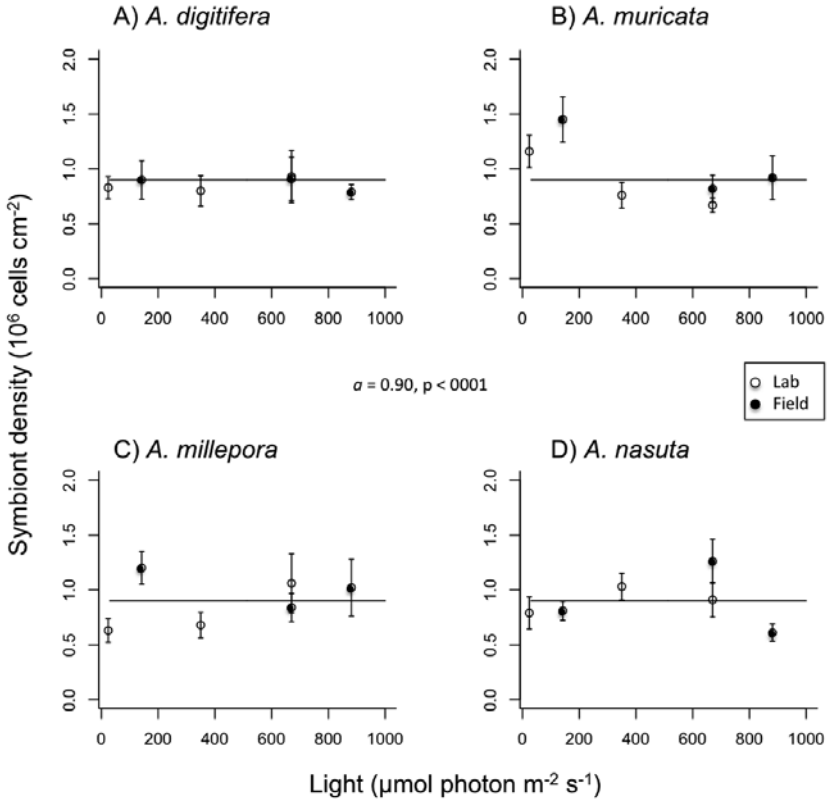

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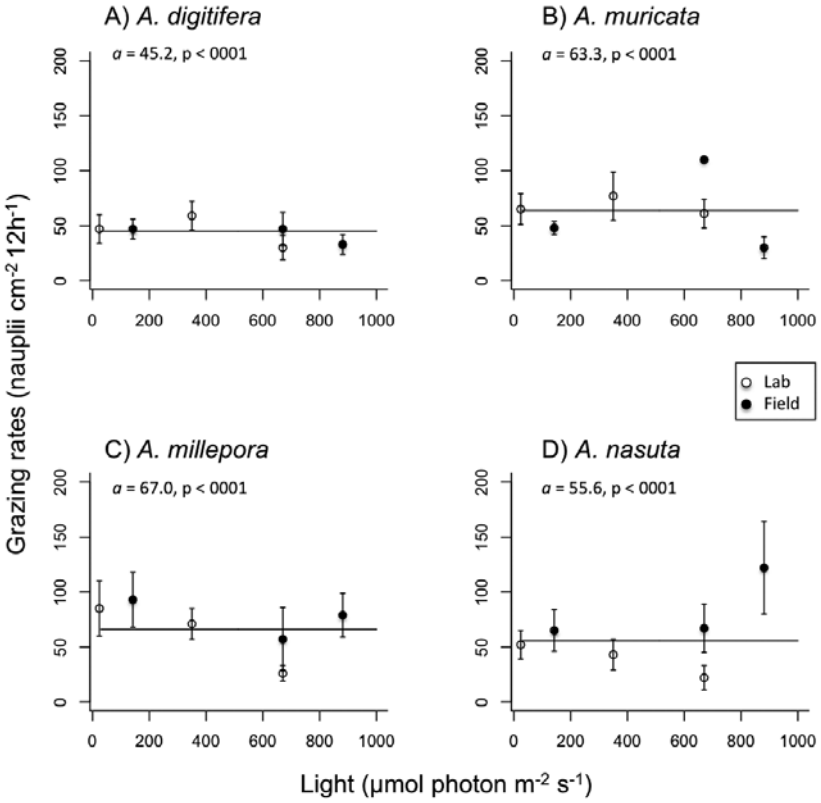
833 Fig 4



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836 **Fig 5**

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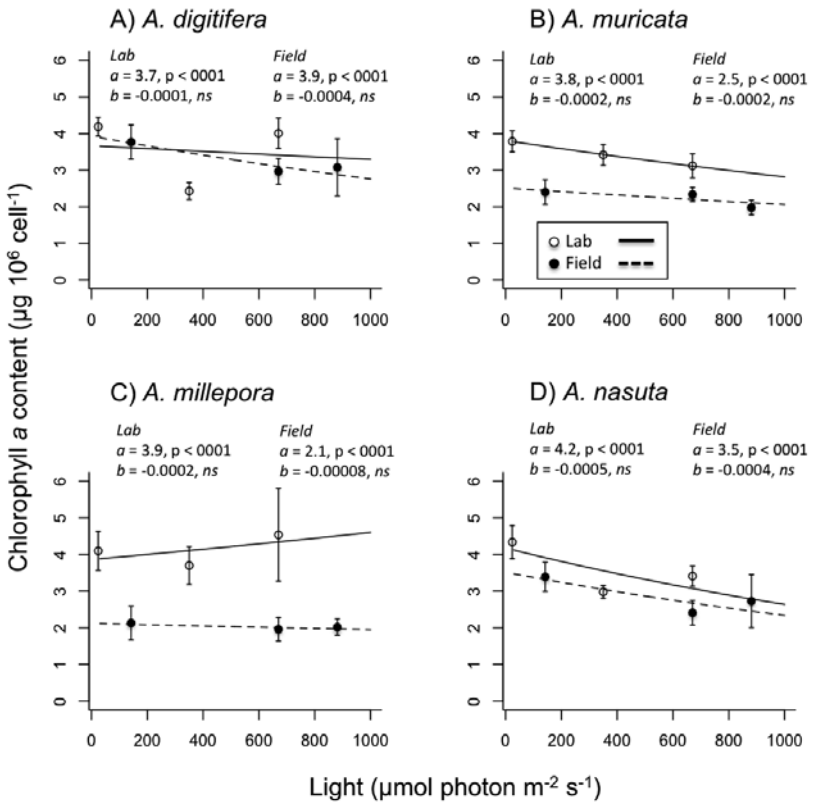

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842 Fig 6

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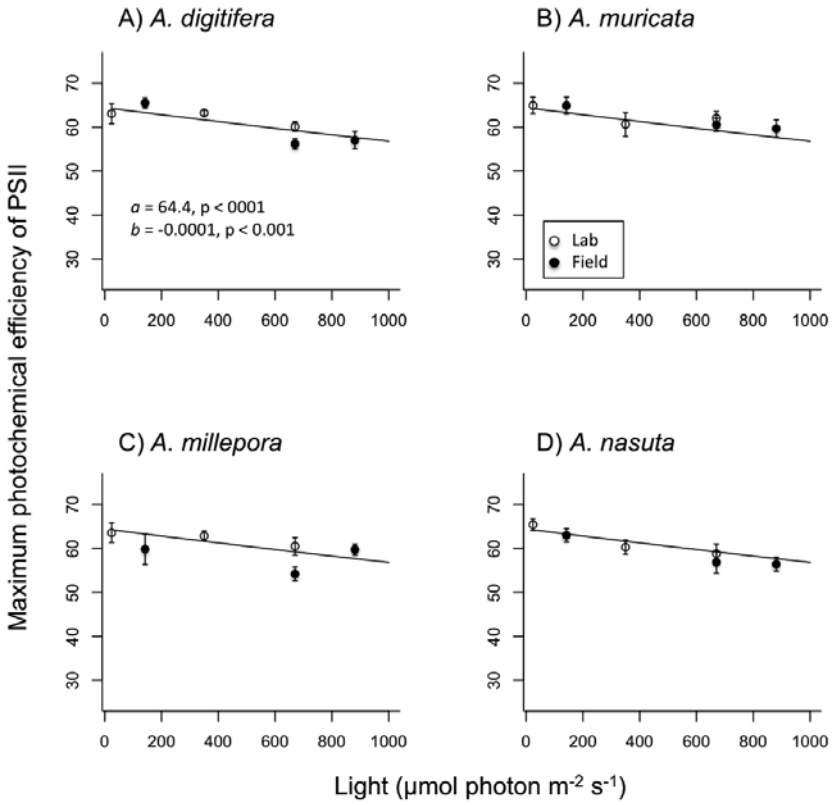

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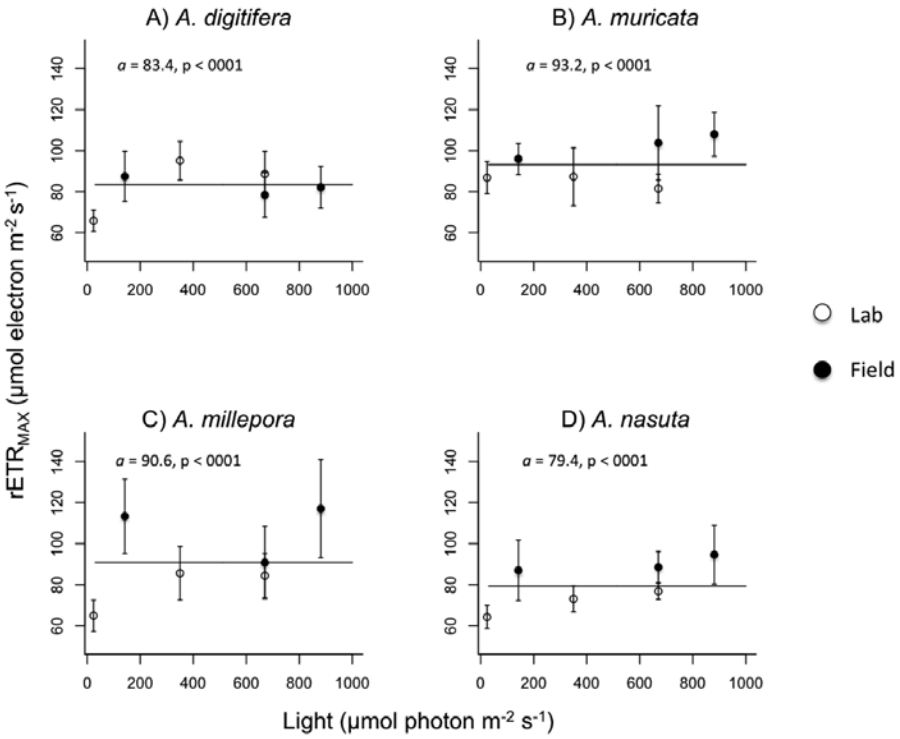
Fig 7


A) A. digitifera
a = 83.4, p < 0001
B) A. muricata
a = 93.2, p < 0001
C) A. millepora
a = 90.6, p < 0001
D) A. nasuta
a = 79.4, p < 0001
rETR_MAX (µmol electron m-2 s-1)
Light (µmol photon m-2 s-1)
Lab
Field

853

854 Fig 8

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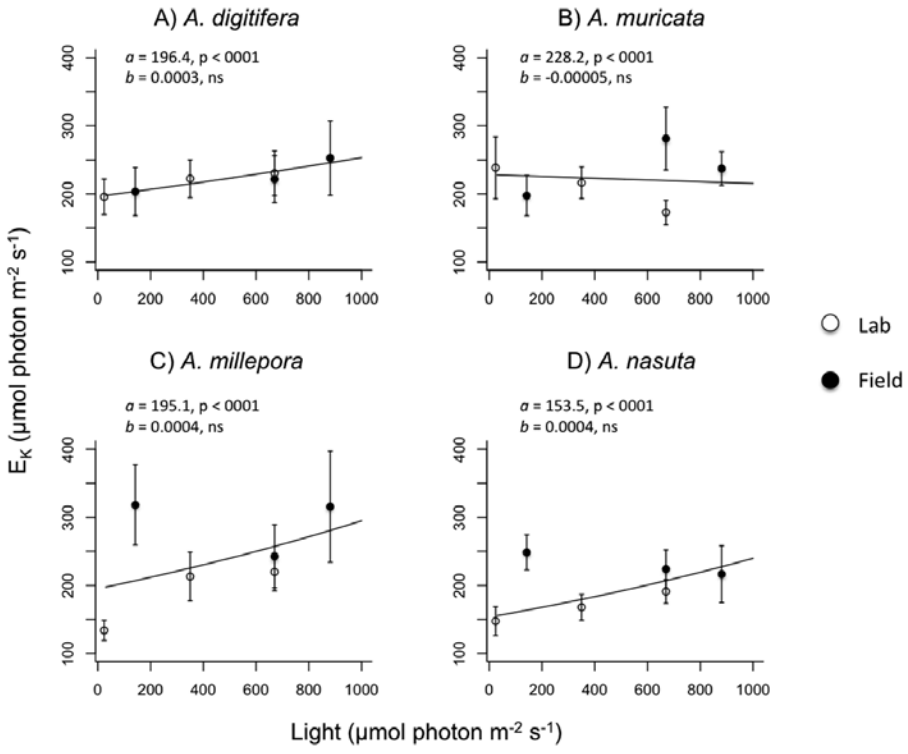

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