Vol. 508: 149–162, 2014
doi: 10.3354/meps10836

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published August 4

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

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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 4 geographically widespread and locally abundant coral species (*Acropora digitifera*, *A. nasuta*, *A. millepora* and *A. 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 4 *Acropora* coral species. 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 in these corals appears insufficient 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, depth-dependent uptake of different types of *Symbiodinium* and inter-specific competition are important determinants of the habitat distribution of reef corals.

KEY WORDS: 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 different definitions of 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 an environmental variable under controlled laboratory conditions; Prosser 1991) and ac-

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climatization (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 2006). 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, 2010). Moreover, highly specialized species, which 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 constrain most coral species to relatively shallow waters (Falkowski et al. 1984). 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 4 geographically widespread and locally abundant coral species (*Acropora digitifera*, *A. nasuta*, *A. millepora* and *A. 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 chl *a*; Dubinsky et al. 1984), higher light harvesting pigment content (Falkowski & Dubinsky 1981, Dubinsky et al. 1984, 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 reef growth and productivity (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 the capacity for acclimation and acclimatization in 7 different physiological response variables for the coral species *Acropora digitifera*, *A. nasuta*, *A. millepora* and *A. 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 'diggem' 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). A reciprocal transplant of deep and shallow colonies could not be used because 2 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 ~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 subsaturation irradiance (E_K); heterotrophic feeding rate; *Symbiodinium* density; and chl *a* per unit surface area and per *Symbiodinium* cell. 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, Palardy et al. 2005). Physiological traits were measured for corals that had been acclimated (laboratory) or acclimatized (field) to light intensities across the ecologically relevant range (i.e. daily maximum irradiance between 34 and 939 µmol photon m^{-2} s^{-1}; Hoogenboom et al. 2009).

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

Capacity for physiological acclimation

Laboratory experiment

Nubbins from 7 colonies of each species (3 fragments per colony, n = 84 in total) were suspended into ~20 l plastic aquaria using fishing wire, and were exposed to 3 light acclimation treatments (1 fragment per light treatment for each colony) using the natural variation in sun exposure at different positions along an outdoor (but undercover) bench, with the addition of a shade cloth as required. The roof was partially transparent and allowed UV light to pass through. To accommodate each species, 4 replicate tanks (12 tanks in total) were set up for each of the high, medium and low light treatments (hereafter referred to as HL, ML and LL respectively). Light levels were measured in each treatment tank using a spherical quantum sensor (Li-193, LI-COR Bioscience) attached to a data logger (Li-1400). Light intensity measurements from the spherical sensor were later calibrated against a downwelling photosynthetically active radiation (PAR) sensor (Li-192) for direct comparison with the light intensity data from the field (see below and Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m5008p149_supp.pdf for calibration). During the 9 d photoacclimation period, the daily maximum irradiance in the different treatments averaged 939, 490 and 34 µmol photon m^{-2} s^{-1} for HL (range: 460 to 1750), ML (375 to 550) and LL (23 to 45), respectively. All aquaria received a constant flow of seawater pumped directly from the adjacent coral reef lagoon. Temperature in the tanks was measured using Hobo data loggers (HOBO Pendant) and fluctuated between 23.8 and 28.0°C (mean: 25.4°C) over the course of the experiment depending on time of day and sun exposure. On average the LL treatment was slightly cooler (~0.5°C) than the other 2 treatments.

Field experiment

Nubbins from 6 colonies for each species (3 fragments per colony, n = 72 in total) were glued onto 4 × 4 cm ceramic tiles using underwater epoxy (Selley's 'Knead-It') and allowed to set overnight. The tiles (and nubbins) were then attached to mesh frames that were secured onto concrete blocks at different depths in the field (at Horseshoe reef, Lizard Island, 14° 41′ 12″ S, 145° 26′ 33″ E). Racks were placed onto open sand for the high- and medium-light treatments, and on sand below an overhang in the deep-

est location to further reduce the light intensity in the low-light treatment. This deployment situated the fragments in 3 light acclimatization treatments with an average maximum irradiance over the 9 d of 881 (range: 484–980), 670 (352–760) and 142 (115–178) µmol photon m^{-2} s^{-1} for ~3, ~4 and ~6 m depth below LAT, respectively. Light levels in the field were monitored using 'Odyssey' data loggers (cosine-corrected photosynthetic irradiance sensor; Dataflow systems) that were attached to stakes hammered into the substratum immediately adjacent to each rack, and water temperature at each rack was monitored using Hobo data loggers (HOBO Pendant). Temperatures in the field averaged 24.7 (range: 23.8–27.0), 24.9 (23.9–27.3) and 24.5°C (23.8–25.3) 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 modulated (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 quantum yield (F_v/F_m) was measured during the night (after a 3 to 4 h period of darkness) using a Diving-PAM fluorometer (Walz; for settings, see Table S1 in Supplement 1). In addition, the $rETR_{max}$ and the 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 9 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). Feeding measurements were conducted over 7 nights, with a different chamber used as the control on each night. 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 freshly hatched nauplii every night to ensure that the size distribution of the prey would be the same. A gentle recirculating flow was generated inside each of 24 replicate chambers using an air stone at the base of the chamber that was connected to an aquarium air pump (Precision 12000, Aqua One). The chambers were specifically designed to prevent the nauplii from settling on the floor of the chamber whilst providing the conditions under which corals would expand their tentacles and feed normally. Corals were first placed in the chambers alone for 30 min to allow them to adjust to the conditions within the chamber and expand their tentacles. Subsequently, between 3490 and 5500 nauplii were added to each chamber, with slight variation in numbers between measuring days due to variation in the density of the *Artemia* culture. After 1 h, the number of nauplii within triplicate 10 ml subsamples of the solution taken with a glass pipette from each chamber was visually counted and used as the initial concentration of nauplii (time 0). After ~5 and 12 h, 2 subsequent counts were carried out and the grazing rate of each fragment was estimated using linear regression of nauplii concentration versus time during the incubation relative to control chambers that contained nauplii but not corals.

Once the fluorometry and feeding measurements were completed, the nubbins were frozen overnight, and tissue was subsequently removed from the skeleton using compressed air and collected and homogenised in 0.45 µm filtered seawater (GF/F filters, Whatman). The resulting tissue 'slurries' were centrifuged, and the supernatant was poured off, 2.5 ml of new filtered seawater was added, and the tubes were vortexed to re-suspend the symbionts in solution. The resulting symbiont suspension was then divided between 2 Eppendorf tubes. The symbionts in one tube were pelleted and then flash-frozen in liquid nitrogen for later chlorophyll extraction and measurement, and 1 ml of 10% formalin was added to the second 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 adding 1.5 ml of 100% ethanol to each sample and vortexing for 60 s to mix. Subsequently, chl *a* content was measured using spectrophotometry on a SpectraMax Plus^{384} Microplate Reader (Molecular Devices). Chl *a* (µg ml^{-1}) was calculated after Ritchie (2006) as:

chl a = 12.4380 (A_{665} − A_{750}) − 2.6094 (A_{629} − A_{750}) (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; therefore measurements of *Symbiodinium* density, feeding rates and chl *a* content were normalized by surface area and are reported per cm^2.

Data analyses

Non-linear regressions of an exponential function ($y = a \times e^{bx}$, 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 5 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, 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 weighted Akaike Information Criterion (wAIC) was used to determine which of the 5 models had the strongest support, as per Hoogenboom et al. (2011). This technique indicates which of a set of models (i.e. Models 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 were to be repeated (Burnham & Anderson 2002). We considered models with wAIC values greater than 0.95 (i.e. indicating 95% support for a single model among the set) to be strongly supported by the data. When several models have similar wAIC values, then those models are equally likely, given the data. Analogous to an ANOVA, 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 it 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:

$$rETR = rETR_{max} [1 - \exp(-x/E_K)] \quad (2)$$

where x is the light intensity at each step of the RLC.

To express changes in each physiological trait in a common currency, differences in physiology between high and low light were converted into carbon equivalents (µg C cm^{-2}). Species-specific data describing relationships between changes in particular physiological traits and overall carbon gain by the whole organism are generally lacking in the literature; therefore, the effect of the changes in chl *a* content on coral carbon acquisition was calculated based on published data describing the functional relationship between chl *a* and the maximum rate of photosynthesis (P_{max}) for *Acropora muricata* (Anthony et al. 2009), assuming colonies were photosynthesising for 8 h d^{-1}. The effect of the measured changes in symbiont density on carbon acquisition was determined from a previously published functional relationship between symbiont density and P_{max} (Hoogenboom et al. 2010a), again assuming colonies were photosynthesising for 8 h d^{-1}. Note that the data presented in Hoogenboom et al. (2010a) were here re-analysed with normalisation to surface area instead of protein (M. Hoogenboom unpubl. data; see Fig. S2 in Supplement 2 at www.int-res.com/articles/suppl/m508p149_supp.pdf). The effect of changes in heterotrophic feeding rates on coral carbon acquisition was calculated assuming that corals fed continuously for 12 h and acquired 0.15 µg C $prey^{-1}$ (Hoogenboom et al. 2010b). These conversions to carbon equivalents were conducted to provide a general approximation of the relative effects of changes in the measured traits on overall coral energy acquisition.

RESULTS

Benthic surveys

Abundance of the study species varied between 0.1 to 2 colonies m^{-2}, and *Acropora nasuta* was the most widespread species overall, present on 57% of the transects compared to 34, 36 and 40% for *A. mille-*

pora, *A. digitifera* and *A. muricata*, respectively. The benthic surveys confirmed that the 4 study species had different depth distributions (see Fig. S3 in Supplement 3 at www.int-res.com/articles/suppl/m508p149_supp.pdf). Of the 4 species, *A. nasuta* and *A. muricata* had the broadest depth distributions (occurring down to ~7 m below LAT in our surveys), whereas *A. digitifera* was not found beyond ~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 chl *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). *A. muricata* showed the strongest decrease in chl *a* in response to increasing light intensity compared to the other 3 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 to 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 and 67 *Artemia salina* nauplii cm^{-2} per night (*Acropora 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 chl *a* 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 chl *a* per symbiont compared to those in the field except for *A. digitifera* (Fig. 5). For 2 of the study species, *A. digitifera* and *A. millepora,* chl *a* content per symbiont cell was approximately consistent across all light levels, whereas for *A. muricata* and *A. nasuta* there was a decrease in chl *a* per cell with increasing light both in the laboratory and the field.

Concerning the photosynthetic parameters measured using PAM fluorescence, maximum photochem-

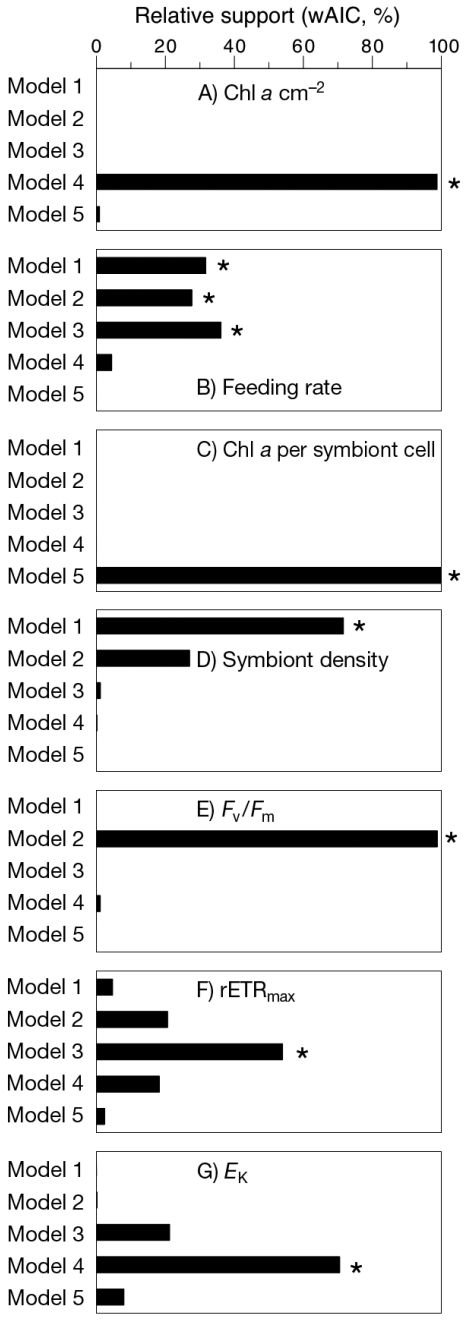

Fig. 1. Relative support for 5 models that describe, for 4 coral species, variation in 7 physiological traits with light intensity. Bars — weighted Akaike information criterion (wAIC) for each of the models fitted to the data for each of the traits. Models — (1) no effect (null model); (2) consistent 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 anaylses' 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 (F_v/F_m), (F) maximum electron transport rate ($rETR_{max}$), (G) subsaturation irradiance (E_K). *The model that is best supported by the data

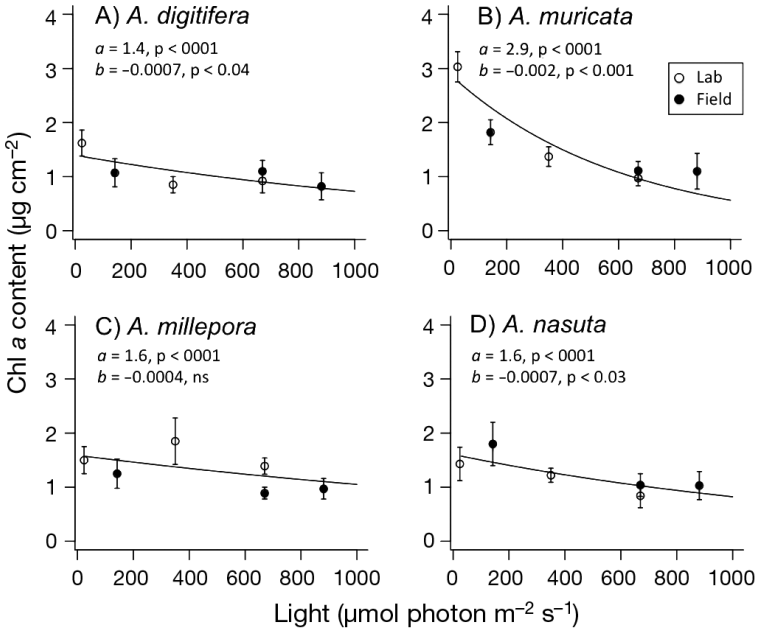

Fig. 2. Chl *a* content per cm^2 for (A) *Acropora digitifera*, (B) *A. muricata*, (C) *A. millepora* and (D) *A. nasuta* versus light intensity for corals deployed in the field (●) and in the laboratory (○). Lines: non-linear regression (exponential) fitted to all data. Data points: mean of 144 samples 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

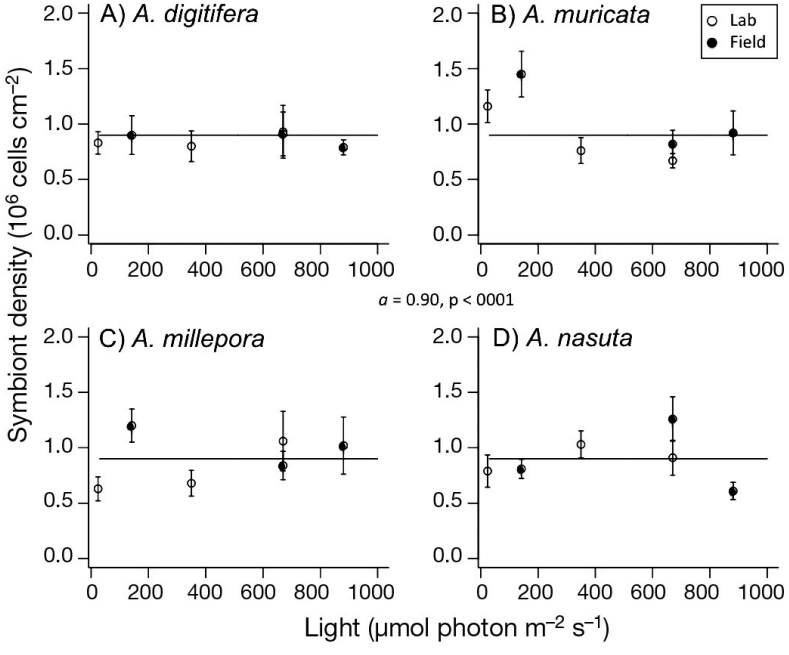

Fig. 3. Symbiont density for (A) *Acropora digitifera*, (B) *A. muricata*, (C) *A. millepora* and (D) *A. nasuta* versus light intensity for corals deployed in the field (●) and in the laboratory (○). Lines: linear regression fitted to all data ($y = a$). Data points: mean of 155 samples with error bars (SE). Fitted coefficient of linear regression ($y = a$) and the statistical significance of its difference from zero are shown

ical 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 (Figs. 1F & 7). The subsaturation 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 chl *a* content in response to variation in the light intensity exposure lead to differences in carbon acquisition between the 4 species (Table 1). The species with the largest depth range, *A. muricata*, had the greatest change in carbon acquisition between high and low light, a gain of 112 µg C cm^{-2}, associated with its ability to 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 acquisition (range 9 to 70 µg C cm^{-2} h^{-1}). Conversely, the observed variations in feeding rates only caused a small change in colony energy acquisition (3 to 9 µg C cm^{-2} h^{-1}).

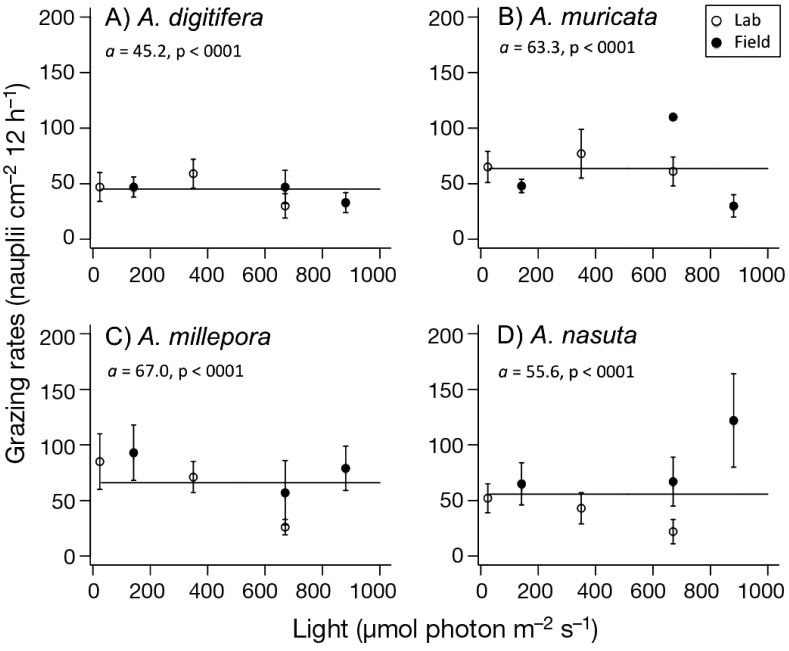

Fig. 4. Feeding rates for (A) *Acropora digitifera*, (B) *A. muricata*, (C) *A. millepora* and (D) *A. nasuta* versus light intensity for corals deployed in the field (●) and in the laboratory (○). Lines: linear regression fitted to all the data ($y = a$). Data points: mean of 117 samples with error bars (SE). Fitted coefficient of linear regression ($y = a$) and the statistical significance of its difference from zero are shown

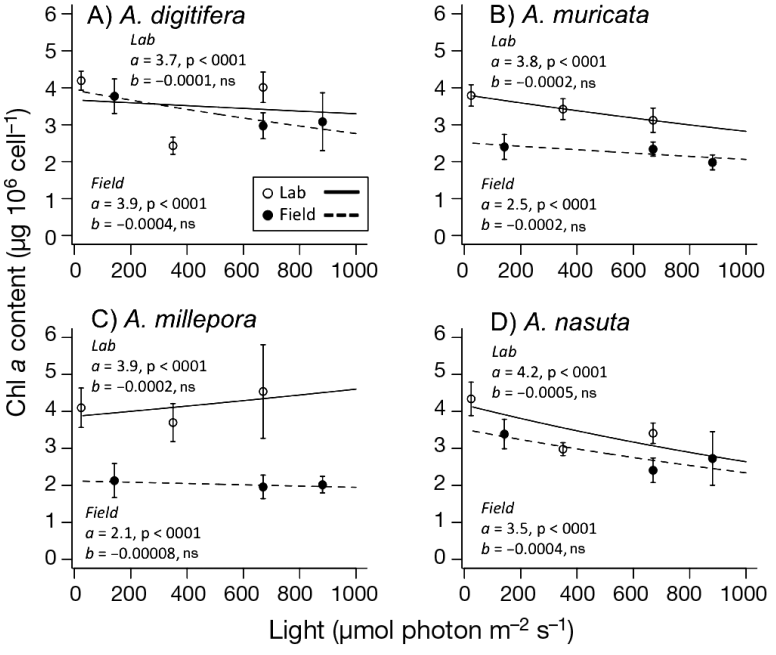

Fig. 5. Chl *a* content per 10^6 symbiont cells for (A) *Acropora digitifera*, (B) *A. muricata*, (C) *A. millepora* and (D) *A. nasuta* versus light intensity for corals deployed in the field (●) and in the laboratory (○). Lines: non-linear regression (exponential) fitted to laboratory (solid) or field (dashed) data. Data points: mean of 144 samples with error bars (SE). Fitted coefficients of non-linear regression ($y = a \times e^{bx}$) for the laboratory and field and the statistical significance of their difference from zero are shown

DISCUSSION

Despite the differences in their depth ranges, the 4 *Acropora* species studied here had approximately equivalent capacity to adjust their physiology in response to a change in ambient light intensity. Additionally, our study indicates that, for *Acropora* species, short-term photoacclimation and photoacclimatization is mainly driven by changes in chl *a* content per cm^2 and in photochemical efficiency (F_v/F_m). The content of chl *a* per symbiont cell also increased in response to decreasing light intensity for 2 of the 4 species, although the strength of this effect depended upon whether colonies were deployed in the field or in the laboratory. Surprisingly, other physiological traits that have been shown to vary with light intensity in other species, such as feeding rates (e.g. Lesser et al. 2010) or *Symbiodinium* density (e.g. Titlyanov et al. 2001a,b), did not contribute to photoacclimation for our study species during the experimental period.

Ecological theory suggests that environmental conditions can influence the assembly of communities by filtering species into habitats based on their physiology, morphology and life-history traits (Southwood 1988, Keddy 1992). However, there is on-going debate regarding the relative importance of environmental tolerance as a determinant of species habitat distributions compared with processes like dispersal limitation and biotic interactions (e.g. Legendre et al. 2005). Few studies have explicitly quantified the relative importance of environmental conditions compared with biological interactions as determinants of coral distributions. One such study showed that intensity of competition had effects on tissue quality (an index of coral health) that were comparable in magnitude to the effects of environmental conditions (including light, temperature and flow; Hoogenboom et al. 2011). At the reef sites surveyed in this study, coral cover generally declined with depth whereas bare space increased (see Fig. S4 in Supplement 3), suggesting that competition is

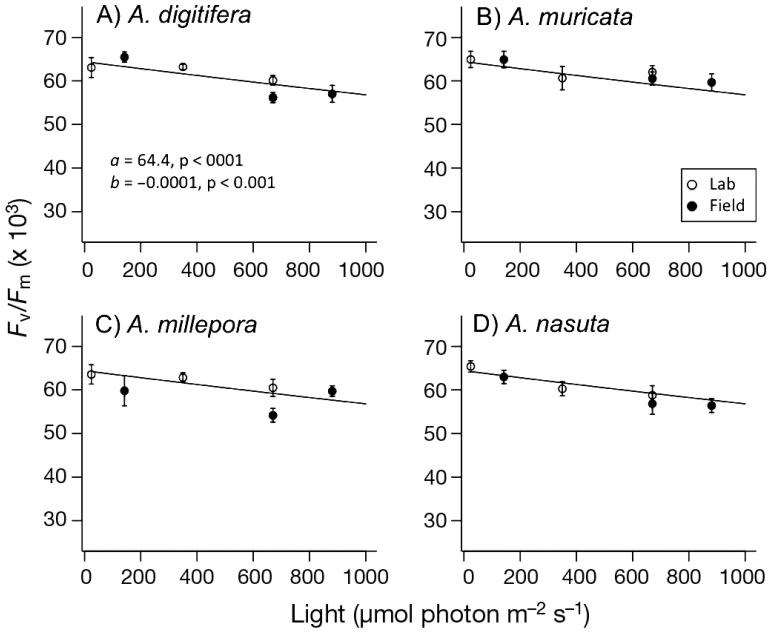

Fig. 6. Maximum photochemical efficiency of PSII (F_v/F_m) (×10^3) for (A) *Acropora digitifera*, (B) *A. muricata*, (C) *A. millepora* and (D) *A. nasuta* versus light intensity for corals deployed in the field (●) and in the laboratory (○). Lines: non-linear regression (exponential) fitted to all the data. Data points: mean of 151 samples with error bars (SE). Fitted coefficients of non-linear regression ($y = a \times e^{bx}$) and the significance of their difference from zero are shown. Note that the same regression applies to data for all 4 species

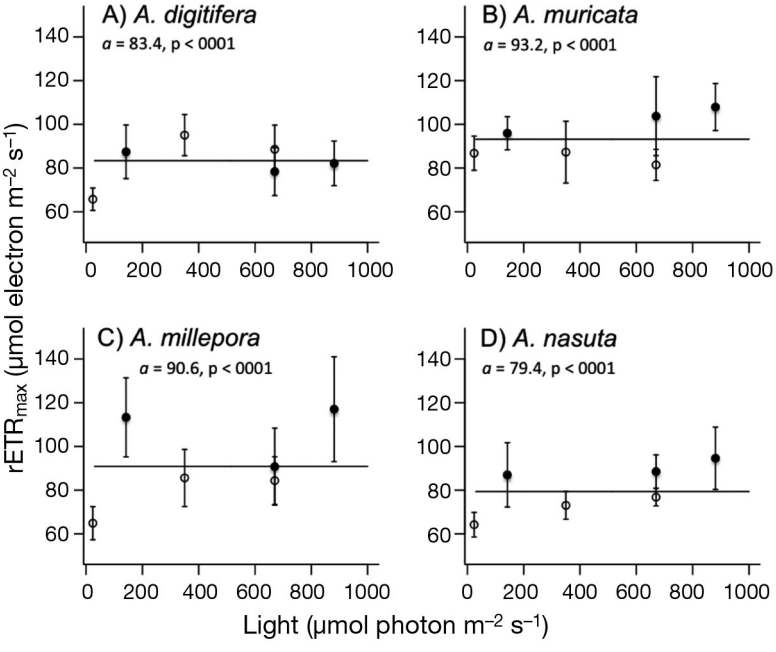

Fig. 7. Relative maximum electron transfer rates ($rETR_{max}$) for (A) *Acropora digitifera*, (B) *A. muricata*, (C) *A. millepora* and (D) *A. nasuta* versus light intensity for corals deployed in the field (●) and in the laboratory (○). Lines: linear regression fitted to all the data ($y = a$). Data 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

less important in structuring coral communities in deeper waters. Our analyses of coral physiology, however, do not support the hypothesis that species that are restricted to high light environments are unable to persist in deeper waters (with lower light availability) because they have limited capacity for photoacclimation. Instead, changes in colony morphology (e.g. Anthony et al. 2005, Kaniewska et al. 2008) and/or very large changes in physiology in the form of longer-term acclimatization processes and/or genetic adaptation appear to be required to cause an increase in a coral species' realised depth distribution.

Changes in coral physiology along a light gradient

By quantifying acclimation and acclimatization of multiple traits in response to a light intensity gradient, we were able to better estimate the overall capacity for physiological plasticity of different species. Of the set of physiological traits measured in this study, the increase in photochemical efficiency in response to decreasing light intensity is congruent with responses observed in coral symbionts (Hennige et al. 2008), phytoplankton (Kropuenske et al. 2010), seagrasses (Major & Dunton 2002) and higher plants (Demmig-Adams et al. 1996). Such an adjustment is part of a common strategy among photosynthetic organisms aiming at increasing the utilisation of light energy under light limiting (low irradiance) conditions (Perkins et al. 2006) while minimising damage to the photosynthetic apparatus under high light conditions (e.g. Hoegh-Guldberg & Jones 1999). The increase in subsaturation irradiance with increasing light intensity was congruent with the decrease in photochemical efficiency across the same light gradient, and was generally consistent with observations for mound-shaped coral species (Hennige et al. 2008) and other branching coral species (Frade et al. 2008a). Conversely, $rETR_{max}$ did vary between *Acropora* species but did not

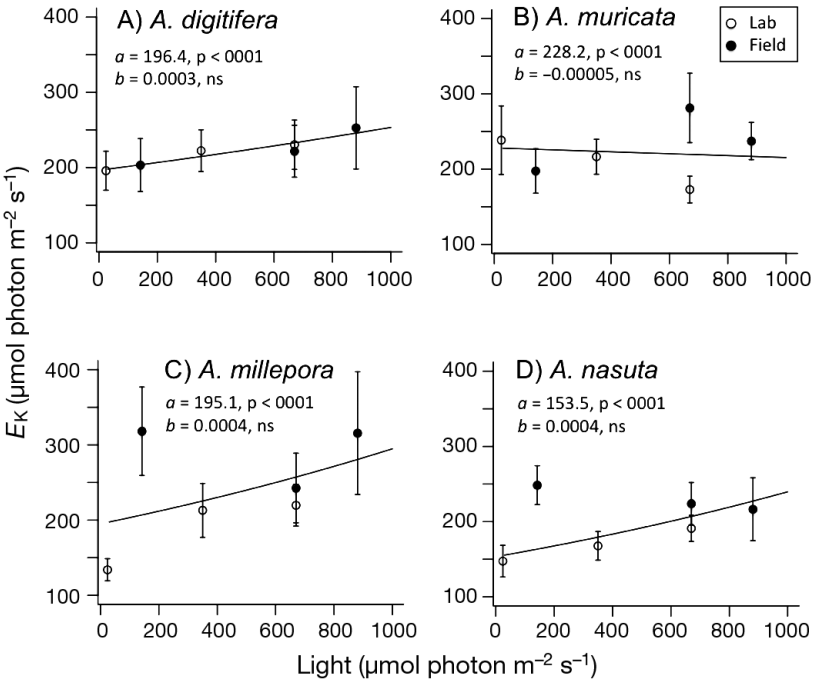

Fig. 8. Subsaturation irradiance (E_K) for (A) *Acropora digitifera*, (B) *A. muricata*, (C) *A. millepora* and (D) *A. nasuta* versus light intensity for corals deployed in the field (●) and in the laboratory (○). Lines: non-linear regression (exponential) fitted to all the data. Data points: mean of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

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

The general trend of increasing chl *a* content with decreasing light was consistent with previous studies (Falkowski & Dubinsky 1981, Dubinsky et al. 1984). Interestingly in our study there was no significant evidence of increasing *Symbiodinium* density with decreasing light unlike previous findings (Titlyanov et al. 2001a, Titlyanov & Titlyanova 2002). Similar to our findings with respect to the fluorescence traits (F_v/F_m, E_K and $rETR_{max}$), these findings indicate that changes in *Symbiodinium* population density occur more slowly in response to changes in light intensity (e.g. over a period of 30 to 90 d; Titlyanov et al. 2001a, Hoogenboom et al. 2010b) than do changes in chlorophyll content. Hence, the 9 d photoacclimation period used in this study might have been too short to observe a significant effect of light on symbiont density. Our results also reveal that chl *a* content per *Symbiodinium* cell varies during photoacclimation to low light for some species (i.e. for *A. muricata* and *A. digitifera*), but that the production of chl *a* per cell is highly sensitive to small differences in light-quality and/or water quality. Although we cannot definitively explain why this result occurred, the treatment effect on chl *a* per *Symbiodinium* suggests that environmental conditions in the field compared with the laboratory limited the production of chl *a* per symbiont cell. Given that seawater used in the experimental aquaria was obtained directly from the lagoon less than 500 m away from the site at which colonies were deployed in the field, it is unlikely that differences in water quality are responsible for this trend. Instead, we suggest that differences in the light spectrum experienced in the field compared with that in the laboratory (i.e. due to light wavelength specific attenuation with depth below the water surface) might have contributed to this finding (e.g. Mass et al. 2010).

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 chl *a* content. *Acropora* species are ordered based on decreasing depth range

Taxon	Difference in carbon acquisition (µg C cm^{-2})				Depth range (m)	
	From change in feeding rate	From change in symbiont density	From change in chl *a* content	Total	Observed	Carpenter et al. (2008)
A. muricata	8	34	70	112	8	25
A. nasuta	3	8	25	36	8	12
A. millepora	–3	6	24	27	6	12
A. digitifera	–1	3	9	11	3	10

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

Heterotrophic feeding can act as an alternate source of carbon for corals when the capacity for photosynthesis becomes limited (Anthony & Fabricius 2000, Grottoli et al. 2006). However, our study showed that light intensity did not influence the feeding rates of corals either in the laboratory or in the field. Interestingly, throughout the experiment, *A. millepora* was the only species to have expanded tentacles during the day and night, suggesting this species might rely more on heterotrophic feeding than the other species, as indicated by Anthony (1999, 2000). The availability of particulate food during laboratory experiments can affect how coral grazing rates differ in response to variation in irradiance (Hoogenboom et al. 2010b). However, even though corals used in the laboratory experiment versus the field experiment had different food availability during the photoacclimation period, feeding rates were generally consistent between these 2 groups and no treatment effect was detected after data analyses. More broadly, the absence of a general upregulation in grazing rate in response to declining light availability suggests that *Acropora* species are unlikely to be able to rely solely on heterotrophy as their food source during coral bleaching events (see Grottoli et al. 2006).

Physiological plasticity and carbon acquisition

In order to better understand how changes in individual physiological processes influence energy acquisition of coral colonies, some of the traits measured here were converted into carbon units. Unfortunately the conversion could not be done accurately for F_v/F_m and E_K due to limitations associated with fluorescence data (Enríquez & Borowitzka 2010). Nevertheless, this analysis clearly showed that the observed variation in the different traits had different implications for carbon gain. In particular, the variation in feeding rates had a smaller effect on colony carbon acquisition compared with variation in chl *a* concentration and *Symbiodinium* density. When converted into units of carbon acquisition, the species with the largest depth range (*Acropora muricata*) did have the greatest photoacclimation-associated total change in carbon acquisition across the experimental light gradient. Although these conversions to carbon equivalents only approximate the relative effects of changes in the measured traits on overall coral energy acquisition, these analyses indicate that the observed change in chl *a* content has a larger effect on energy acquisition of coral colonies than the observed change in particle feeding. Therefore, converting variation in physiological traits into common units of energy acquisition is important for understanding how overall coral health varies along environmental gradients. Research on species-specific traits relating to carbon use efficiency, carbon translocation from symbiont to host, and carbon and nutrient allocation to host and symbiont tissue is required to confirm the relationship between physiological plasticity in carbon acquisition and coral depth distributions.

Beyond 'reversible plasticity'

Although our study provides a useful contribution towards elucidating the role of physiological tolerance in shaping the habitat distributions of reef-building corals, we measured only the 'reversible plasticity' (sensu Angilletta 2009) of adult corals to changes in light intensity. This type of plasticity encompasses only the short-term physiological changes that enable individual coral colonies to cope with, for

instance, weekly or seasonal fluctuations in environmental conditions. Extrapolating from our results, we suggest that the capacity for physiological plasticity of coral colonies may be greater in juvenile corals compared with adults. Such 'developmental plasticity' is common in both terrestrial and marine species (Beck 1983, Newman 1989) but, to our knowledge, has not yet been investigated in reef corals. However, consistent with our interpretation, juvenile corals at the end of their pelagic larval phase are able to recognize habitat-specific cues from the substratum to actively choose the depth of their settlement (Baird et al. 2003), and exhibit light dependent settlement patterns that match the vertical distribution of adults (Mundy & Babcock 1998). This suggests that coral larvae have enhanced physiological plasticity that enables them to successfully establish in diverse environments, and that the early stage of the coral life-cycle is critical for determining species' depth distributions. Quantitative studies of the relationship between the physiological plasticity and recruitment success of coral larvae in different environments are required to determine whether depth-selection by coral larvae establishes the depth distribution of coral colonies, and whether the physiological tolerance of adult corals is established early in their life-cycle.

Our study provides a new assessment of the light intensity reaction norms for photophysiology of 4 common coral species based on a multi-trait analysis. Previous studies (Lesser et al. 2010, Frade et al. 2008b,c) measured physiological traits of corals after collection of colonies from different depths, therefore targeting long-term acclimatization responses. Instead this study included corals from same light regimes to novel light levels in the laboratory and in the field, thereby comparing short-term acclimation and acclimatization potential. The results showed that the capacity for physiological plasticity was generally limited for the 4 *Acropora* species. Indeed out of the 7 physiological traits that we measured, which are known to contribute to photoacclimation in other species, 4 did not significantly vary with light, suggesting that plasticity in these particular traits is strongly species-specific or occurs in response to longer-term changes in the environment than those investigated here. Collectively, the lack of evidence of a link between depth distribution and physiological plasticity indicates that light availability is unlikely to set the lower depth of occurrence for branching coral species that have relatively shallow depth distributions. Although short-term reversible plasticity is important for corals to cope with short-term (diurnal or weekly) changes in environmental conditions, larger changes in photophysiology over a longer time period appear to be required to enable corals to expand their depth distributions. Furthermore, the results of this study suggest that other biological processes such as selective recruitment, depth-related variation in *Symbiodinium* types, and inter-specific competition are important determinants of the habitat distribution of sessile marine organisms.

Acknowledgements. This work was funded by James Cook University. We thank J. Jeans, M. Rocker and the staff of Lizard Island Research Station for their valuable assistance with the field work. This research was conducted under GBR Marine Park Authority permit number G12/35052.1.

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Editorial responsibility: Peter Edmunds, Northridge, California, USA

Submitted: June 18, 2013; Accepted: April 24, 2014
Proofs received from author(s): July 14, 2014