

RESEARCH ARTICLE

Autotrophic and heterotrophic responses of the coral *Porites lutea* to large amplitude internal waves

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SUMMARY

Large amplitude internal waves (LAIW) cause frequent and severe changes in the physico-chemical environment of Andaman Sea coral reefs and are a potentially important source of disturbance for corals. To explore the coral response to LAIW, prey capture disposition and photosynthesis were investigated in relation to changes in seawater temperature, pH, flow speed and food availability in LAIW simulation studies under controlled laboratory conditions, using *Porites lutea* as a model organism. Although food presence stimulated polyp expansion, we found an overriding effect of low temperature (19°C) causing retraction of the coral polyps into their calices, particularly when pH was altered concomitantly. Decreases in pH alone, however, caused the expansion of the polyps. The exposure history of the colonies played a crucial role in coral responses: prior field exposure to LAIW yielded lower retraction levels than in LAIW-inexperienced corals, suggesting acclimatization. Low temperature (19°C) exposure did not seem to influence the photosynthetic performance, but LAIW-experienced corals showed higher values of maximum dark-adapted quantum yield (F_v/F_m) of photosystem II than LAIW-inexperienced controls. Collectively, these data suggest that *P. lutea*, the dominant hermatypic coral in the Andaman Sea, can acclimatize to extreme changes in its abiotic environment by modulating its mixotrophic nutrition, through polyp expansion and potential feeding, as well as its photosynthetic efficiency.

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INTRODUCTION

The general perception of corals thriving in a benign tropical climate has masked the fact that they are, by contrast, exposed to large variations in their natural environment, over a range of scales. Coral evolution and diversity are in fact thought to be driven by large-scale fluctuations in ocean circulation (Veron, 1995), glacial–interglacial changes in sea level (Pandolfi, 1996), and changes in sea surface temperature, partial pressure of CO₂ (P_{CO_2}) and pH of ~5°C (Lea et al., 2000), ~2000 ppm and 0.8, respectively (Pearson and Palmer, 2000), over the many years they have inhabited the oceans. On a finer temporal scale, disturbances at decadal, inter-annual, seasonal and daily time scales have been shown to influence the diversity and resilience of coral reefs (Connell, 1978; Lough, 1994; Brown, 1997). Seasonal variations in temperature, current speeds and sedimentation are generated by the fluctuations, durations and strength of the monsoon seasons (Naseer and Hatcher, 2000), as well as currents or wind-driven upwelling (Andrews and Gentien, 1982; Palardy et al., 2005).

Surface gravity waves and internal waves act on time scales of seconds to hours (Leichter et al., 2005). As opposed to surface waves, which cause mainly mechanical impact on shallow communities, internal waves may affect the physico-chemical environment of deeper communities (15–30 m) (Leichter et al., 2005). A particular class of internal waves in stratified macrotidal areas with abrupt topography is the non-linear solitary large amplitude internal waves (solitons or LAIW). They form when tidal flow acceleration across shallow topography causes a depression of

the pycnocline, separating the light surface from dense deeper waters, downstream of the obstacle. Flow reversal during slack tide causes this lee wave to detach and transform, generating packets of internal waves propagating in the opposite direction. In deep water, vertical displacements of the pycnocline may be more than 60 m, and in exceptional cases, more than 100 m. These LAIW may propagate large distances across entire ocean basins (Jackson, 2004). In the Andaman Sea, where LAIW were first discovered and their soliton character established (Osborne and Burch, 1980), LAIW moving from deep waters onto the shelf may cause strong vertical mixing (Vlasenko and Stashchuk, 2007), which can cause drastic changes in the physico-chemical conditions of the water column. In the Similan Islands (Fig. 1), an offshore archipelago in the Andaman Sea, where LAIW cause frequent (several events per day) and sudden (within only minutes) drops in temperature and pH [of up to 10°C and 0.6, respectively (Schmidt et al., 2012)], and concomitant increases in nutrient concentrations, the shallow-water scleractinian coral communities are strongly affected (Roder et al., 2011; Schmidt et al., 2012). While the LAIW disturbances appear to be associated with higher coral diversity and the nutritional status relative to LAIW-protected sites (Roder et al., 2011; Schmidt et al., 2012), a mechanistic understanding of LAIW impact on coral nutrition is still lacking. Because scleractinian corals are mixotrophic, it is conceivable that both the photoautotrophy of the endosymbiotic dinoflagellates (genus *Symbiodinium*) and the heterotrophy of the coral–*Symbiodinium* holobiont are affected by the severity of the LAIW-induced environmental changes. However,

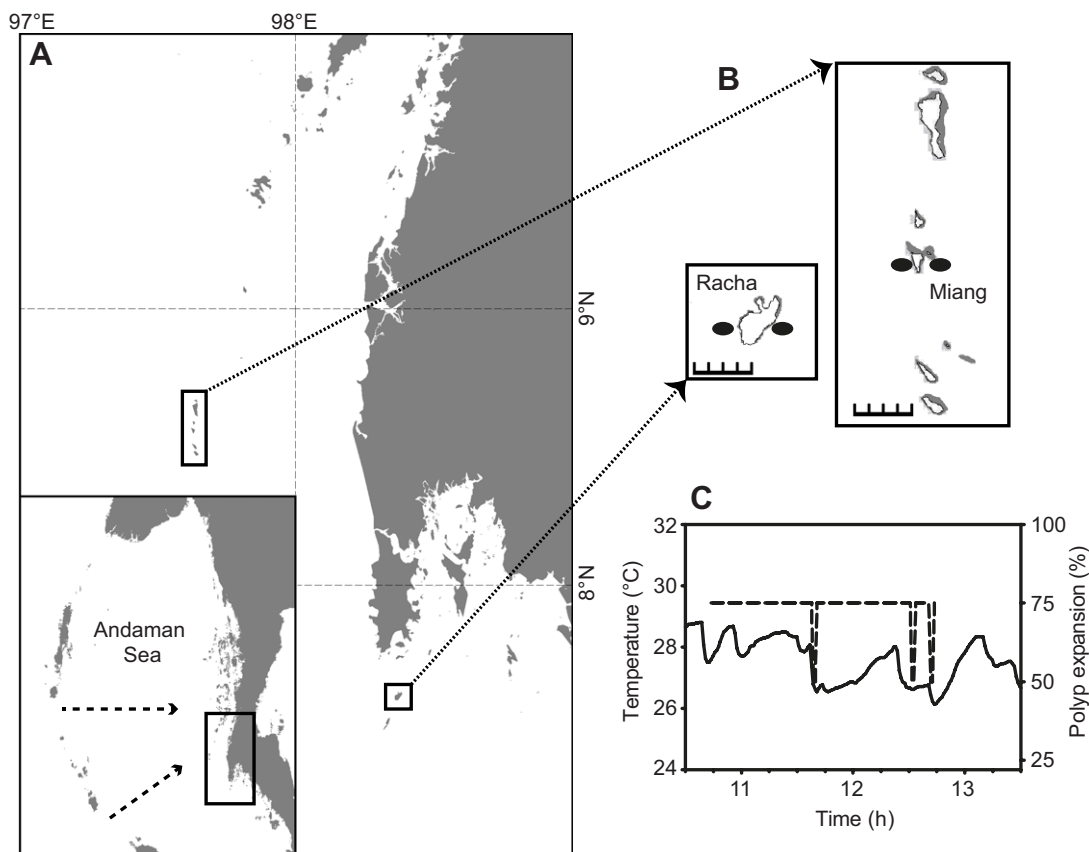


Fig. 1. (A) Map of the Andaman Sea off the western coast of Thailand, with inset showing the direction of the large amplitude internal waves (LAIW) formed along the Andaman–Nicobar Island Arc (dashed arrows) [map source (Wessel and Smith, 1996)]. (B) Close-up map of Racha Island (small rectangle) and the Similan Islands (large rectangle), showing the central island of Miang, where the preliminary *in situ* experiments took place (UNEP Coral Millennium Project). Scale bars, 4 km. Black circles represent nubbin collection locations for the laboratory experiments. (C) Results of the preliminary *in situ* experiment showing polyp expansion behavior (dashed line) in response to the temperature (solid line) of a *Porites lutea* colony at the LAIW-exposed west side of the island. Notice the drop in polyp expansion as the water temperature drops.

the effects of LAIW on the expansion and retraction behavior of coral polyps and the photosynthetic performance of the *Symbiodinium* are still unknown.

Polyp behavior has been well documented in tropical scleractinian corals, from studies on feeding mechanisms (Lewis and Price, 1975; Porter, 1976) to its effect on photosynthetic productivity (Levy et al., 2006) and its response to radiation and current (Sebens and DeRiemer, 1977; Levy et al., 2001). It has long been assumed that corals expand their tentacles at night as a response to higher food availability and the lower risk of predation (Lewis and Price, 1975). However, the retraction/expansion of polyps during the day is supposed to enhance the planar density and photosynthetic performance of *Symbiodinium*, as more endosymbionts will be exposed to the light (Sebens and DeRiemer, 1977; Lasker, 1979). However, polyp expansion and retraction also respond to a variety of other factors irrespective of the light:dark cycle, such as differences in light intensities (Gladfelter, 1975; Levy et al., 2003), current speed (Sebens et al., 1997), food availability (Levy et al., 2001), polyp size (Lasker, 1981), interactions between the aforementioned factors, and the physiological needs of the coral colony (Porter, 1976).

Although the effects of polyp expansion and contraction on the balance between heterotrophy and autotrophy are still poorly known, the energetic costs associated with these behavioral states have already been investigated. Specifically, polyp expansion increases

the rate of respiration because of the larger surface area available to dissipate the oxygen gradient between the tissue and surrounding water (Levy et al., 2006). The hydrostatic skeleton also entails an energetic cost of maintaining a pressure gradient between the coelenteron and ambient seawater (Ruppert et al., 2004). Respiration rates are known to be lower in contracted anthozoans compared with expanded ones (Shick et al., 1979), suggesting that contraction might be a way to reduce the oxygen concentration in the coelenteron, lower the metabolic rates and save energy (Sebens and DeRiemer, 1977; Sebens, 1987). However, polyp expansion might help in the diffusion of excess oxygen resulting from hyperoxia in the gastrodermal tissue layer, which is potentially detrimental to the photosymbiosis (Lesser and Shick, 1989).

Changes in certain physico-chemical parameters of the seawater surrounding reef corals may affect not only the behavior of the host, but also the photosynthetic performance of the symbionts. These changes have been addressed with regard to temperature (Berkelmans and van Oppen, 2006; Putnam and Edmunds, 2011), water flow (Carpenter and Patterson, 2007) and UV radiation (Ferrier-Pagès et al., 2007). The photosystem II complex (PSII) of the photosynthetic apparatus is sensitive to thermal stress (Warner et al., 1996), as shown by a decrease in the maximum quantum yield of PSII in pulse amplitude modulated (PAM) chlorophyll *a* fluorometry (Schreiber et al., 1986). Damage to PSII may lead to the expulsion of the endosymbionts and a subsequent bleaching of

the coral colony (Warner et al., 1999). While the bulk of the work carried out so far has dealt with heat stress, similar responses may be caused by low temperature stress (Muscatine et al., 1991; Saxby et al., 2003). The immediate response (seconds to several minutes), however, of the photosynthetic efficiency to a low temperature shock is still unknown.

Colonies of the massive coral *Porites lutea* Milne Edwards and Haime 1851, one of the most abundant and dominant coral species in the Andaman Sea, and the most important reef-building coral along the Thailand coast (Phongsuwan and Chansang, 1992), are frequently exposed to LAIW, particularly along the exposed western island sides (Roder et al., 2011; Schmidt et al., 2012). Preliminary *in situ* video observations performed at a depth of 18 m on the west side of Koh Miang (8°34'0"N, 97°38'60"E) in the Similan Islands showed a clear behavioral retraction and recovery of the polyps of *P. lutea* in response to sudden changes in the seawater brought on by a LAIW (Fig. 1). These observations gave rise to the hypothesis that corals may show behavioral and/or metabolic responses to the frequent changes in water conditions brought on by the waves (temperature drops, lower pH, stronger currents and higher food availability), and that there may be differences in the type and magnitude of response between LAIW-habituated and LAIW-sheltered colonies on the western (W) and eastern (E) sides of the islands, respectively. Similar W–E differences were observed in coral nutritional status (Roder et al., 2010; Roder et al., 2011), but a mechanistic understanding of the underlying autotrophic and/or heterotrophic processes is so far lacking.

Thus, the aim of this study was to experimentally explore the potential role of LAIW on coral mixotrophy, using *P. lutea* as a model organism. The experiment involved the following steps: (1) collection of colonies from LAIW-exposed and LAIW-sheltered sides, (2) rearing under controlled laboratory conditions that mimic the *in situ* environment, (3) exposure to simulated LAIW (i.e. sudden drops in temperature and pH under different current regimes and food supply levels), and (4) monitoring of polyp expansion and retraction behavior, as well as the maximum dark-adapted quantum yield of their resident *Symbiodinium* populations in response to simulated LAIW.

MATERIALS AND METHODS

Nubbins (4–5 cm diameter, 3–4 cm height) of the massive scleractinian coral *Porites lutea* were collected from both LAIW-exposed W and LAIW-sheltered E sides of two Andaman Sea islands off the Thailand coast (Ko Miang, 8°34'0"N, 97°37'60"E and Ko Racha, 7°34'60"N, 98°20'60"E) at a depth of 15 m [$N=96$ nubbins: two islands (I), two sides (S), three colonies (C) per side, eight nubbins (N) per colony; I and C were pooled, yielding six source colonies for each (W and E) side with eight nubbins, one for each of the eight (four factors, two levels) experiments – see below]. The coral nubbins were chiseled from their mother colonies and glued on individual acrylic holders using underwater cement (Silka Waterplug, Baar, Switzerland) and taken back to the reef for 10 to 15 days to recover from the handling procedure. Thereafter, they were taken to the aquarium facilities at the Phuket Marine Biological Center.

Culturing conditions

An aquarium system was built in order to maintain the coral nubbins at specified conditions. During a 2-week acclimation period to the laboratory conditions, all coral nubbins were supplied with a constant flow of unfiltered seawater from the nearby reef at a rate of $43.2 \pm 4.4 \text{ l h}^{-1}$ (mean \pm s.d.). An 11 h:13 h light:dark cycle was

created with metal halide lamps (5000 W), and photosynthetically active radiation (PAR) was measured once a day with a 2π cosine corrected sensor (LI-COR LI-192, Lincoln, NE, USA) connected to a data logger (LI-COR LI-1400). Light values ranged between 80 and 120 $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$, corresponding to the ambient light levels at 15 m water depth (supplementary material Fig. S1). Temperature was monitored with TidbiT v2 temperature loggers (Onset Computer Corporation, Bourne, MA, USA; logging interval 1 min). Mean (\pm s.d.) temperature of the unaltered reef water was near ambient conditions at $29.8 \pm 0.6^\circ\text{C}$, and never exceeded 30.5°C (January 2011). Dissolved oxygen (DO) and pH were measured twice a day with a YSI ProODO optical DO sensor (YSI, Yellow Springs, OH, USA) and a WTW Routine Pt1000 Inlab pH sensor (Mettler-Toledo, Columbus, OH, USA), respectively, the latter of which was calibrated on a daily basis (NBS scale). Values of DO ranged between 246.9 and 284.4 $\mu\text{mol DO l}^{-1}$ and pH was 8.34 ± 0.11 .

Following the 2-week acclimation process and in order to maintain the original acclimatization of coral nubbins originating from W island sides, nubbins were treated with simulated LAIW conditions in the laboratory, similar to their *in situ* experience (supplementary material Fig. S2C). Thus, after the 2-week period, and while E tanks remained under regular reef water flow (supplementary material Fig. S2B), W rearing tanks were flushed twice a day with temperature- and pH-manipulated seawater (incoming water flow: $\sim 75 \pm 5 \text{ l h}^{-1}$). For that purpose, the reef water was cooled down to 21°C (AquaMedic Titan 1500 cooling unit, Bissendorf, Germany), bubbled with pure CO_2 to a pH of 7.8 [LAIW temperature and pH conditions (Schmidt et al., 2012)] and pumped into the coral tanks using an aquarium pump (EHEIM, Deizisau, Germany). Cold and acidified seawater remained in the coral basins for ~ 15 min before the inflow valves were reopened for the warm, high pH water. Ambient conditions were re-established within the following 15–20 min, which closely mimics the arrival and departure of LAIW *in situ* (Schmidt et al., 2012). LAIW simulations for the W rearing tanks started a week before the experiments took place and lasted for a total of 20 days while the experiments were performed in parallel (supplementary material Fig. S2A).

Experimental design

To identify the relative importance of food, currents, temperature and pH on polyp expansion and maximum quantum yield of PSII (F_v/F_m), their effects were tested in isolation and in combination (Table 1). All experiments were performed in random order using a flow-through chamber ($25 \times 10 \times 15 \text{ cm}$) in which current flow of different speeds could be created *via* a circulating pump (EHEIM) (supplementary material Fig. S3). Two different flow speeds, 2 and 10 cm s^{-1} , were applied, representing the natural flows on coral reefs under LAIW-free and LAIW conditions, respectively (Roder et al., 2010). Flow speed was previously measured by following the movement of colored particles that were added to the water. Particle movements were recorded using a video camera (Sony HDR-XR520V, Minato, Tokyo, Japan).

In order to standardize the response of *Symbiodinium* to the PAM fluorometer measurements, all experiments were conducted under crepuscular conditions. A fiber-optic lamp (Schott 1500, Elmsford, NY, USA) was set to the minimal PAR level ($\sim 1.5 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$) to avoid any photosynthetic response while providing sufficient light for video recording. Downwelling PAR was measured at the beginning of every experiment (LI-COR LI-1400). Temperature was recorded every 15 s with a TidbiT v2 temperature logger (Onset Computer Corporation) placed in the flow-through chamber. DO levels and pH were monitored hourly

Table 1. Abiotic characteristics of the seawater for each experiment

Treatment	Flow rate	Fragment origin	Temperature (°C)	pH
Control	Low	East	28.60±0.46	8.23±0.03
		West	29.70±0.25	8.25±0.01
	High	East	28.59±0.43	8.16±0.05
		West	29.60±0.17	8.28±0.01
Partial LAIW–temperature	Low	East	19.36±0.40	8.31±0.04
		West	19.56±0.76	8.29±0.04
	High	East	19.57±0.58	8.23±0.11
		West	19.38±0.22	8.31±0.05
Partial LAIW–pH	Low	East	29.31±0.22	7.80±0.03
		West	29.29±0.13	7.80±0.04
	High	East	29.48±0.22	7.80±0.02
		West	29.55±0.14	7.83±0.05
Full LAIW–temperature + pH	Low	East	19.09±0.38	7.82±0.02
		West	19.19±0.41	7.82±0.03
	High	East	19.12±0.24	7.86±0.08
		West	19.27±0.32	7.80±0.04

Flow rate: low=2 cm s⁻¹; high=10 cm s⁻¹. LAIW, large amplitude internal wave. Values are given as means ± s.d.

with the same instruments as described above (supplementary material Table S1).

One out of eight nubbins from each of the source colonies (six from W and six from E, see above) was used for each of the eight different combinations of water flow, prey availability, pH and temperature conditions (Table 1). Nubbins were used only once to minimize the risk of acclimation to the experimental conditions. Preliminary experiments with triplicate nubbins from different colonies showed no within-colony differences in the behavioral response of coral nubbins to the factors above; hence within-colony variation was not considered to be relevant in our experiments. The chamber and hoses were all thoroughly rinsed with distilled water after each experiment. Because the flow-through chamber could only hold three fragments at a time, repeated experiments were necessary to obtain a minimum of six observations per factor. For each

experiment (control: ambient temperature and pH; partial LAIW–temperature: temperature drop, ambient pH; partial LAIW–pH: pH drop and ambient temperature; and full LAIW: temperature and pH drop; Table 1), coral nubbins from the same island side were placed into the flow-through chamber and left there untreated for 40 min under no light. During this period, ambient-temperature (29°C), ambient-pH (8.3) seawater was circulated through the system at 2 cm s⁻¹. Video recording and PAM fluorometer measurements started 20 min prior to the treatment (time 0). The actual experiment from the application of the treatment (time 0) lasted 180 min (Levy et al., 2001), during which polyp expansion behavior of each nubbin in the flow-through chamber was recorded every 5 min for 1 min with a Sony HDR-XR520V video camera. In between the camera recordings, triplicate F_v/F_m measurements were taken for each nubbin with a diving PAM fluorometer (Walz,

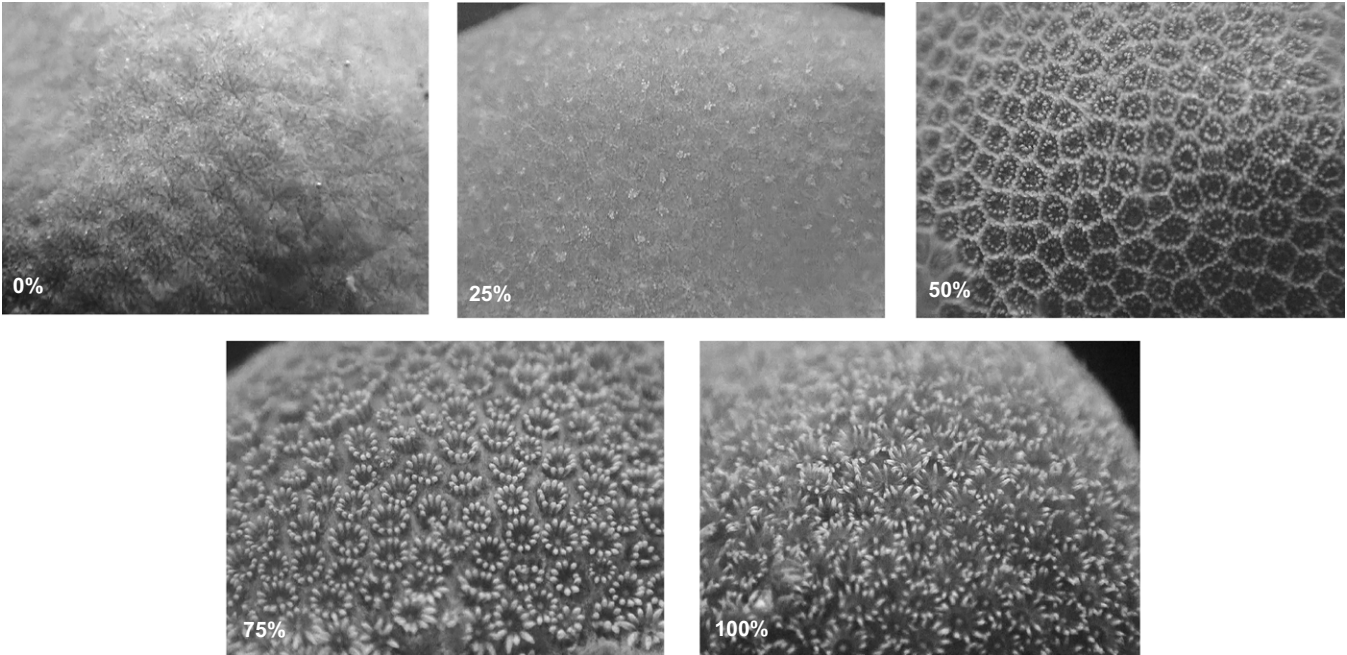


Fig. 2. Photographs illustrating the percentage of polyp expansion of colonies of *Porites lutea*. The five levels were designated by Lasker (Lasker, 1979). The different scores are the visual average for the entire coral nubbin in the treatment. Polyp size, ~0.1 cm. See Materials and methods for complete description of the expansion states.

Table 2. Results of three-way ANOVA after model simplification on the effects of nubbin origin (W and E), food and treatment (control, partial LAIW–temperature, partial LAIW–pH and full LAIW–temperature + pH) on the polyp expansion behavior of *Porites lutea*

Source of variation	Sum of squares	d.f.	Mean square	F	P
Origin	0.211	1	0.211	1.84	0.176
Food	0.890	1	0.889	7.78	0.006**
Treatment	7.479	3	2.493	21.80	0.000***
Origin × Treatment	1.222	3	0.407	3.56	0.015*

Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Germany) (supplementary material Table S2). Triplicate measurements were taken, randomized over the surface of each nubbin to minimize the risk of artefactual photoinhibition by repeated PAM measurements. The mean of triplicate measurements was used for subsequent analyses. After half of the experimental time (90 min) had elapsed, freshly hatched *Artemia* nauplii were added to the chambers ($0.3 \text{ individuals ml}^{-1}$). Visual observation confirmed that the *Artemia* remained in suspension throughout the remainder of the experiment. Tentacle expansion was scored on a percentage scale based on Lasker (Lasker, 1979), with 0% representing complete retraction of the polyp, with neither tentacles nor oral disk visible; 25% indicating polyp expansion to the point that tentacles were visible, though still retracted; 50% showing further expansion of the tentacles with the oral disk visible; 75% representing polyp expansion up to the outer whorl of tentacles; and 100% indicating complete polyp expansion (Fig. 2). Each score referred to the whole coral nubbin.

Data analysis

Almost 6000 min of video data polled across the 32 separate experiments were analyzed. No significant differences were found within triplicate nubbins within a chamber (i.e. no chamber effect; supplementary material Table S3), nor were there significant differences between islands (supplementary material Table S6). Normality tests and Levene's test (homogeneity of variances) were carried out prior to parametric tests (ANOVA). The influence of the different treatments on coral polyp behavior was evaluated using the means of the behavioral responses over the 90 min time intervals. Polyp expansion percentage data were arcsine transformed to achieve normality (Martin and Bateson, 2007). The effect of the independent factors (food, LAIW treatments, flow regime and coral nubbin origin) on polyp expansion was tested initially with a backward stepwise ANOVA. In case a term had non-significant effects on the dependent variable both for one factor alone or for interactions of factors, that term was removed, resulting in a minimal adequate model. When ANOVA determined a significant difference, Tukey's *post hoc* tests were used to attribute differences between treatments.

A simplified, repeated-measures ANOVA was also performed for the F_v/F_m measurements made over the 180 min experiment. Food availability did not appear to have an immediate effect on photosynthesis, and the corresponding F_v/F_m values for the two food levels were pooled. The sphericity of the data was proven with Mauchly's test using the corrected degrees of freedom from the Greenhouse–Geisser epsilon values (Keren and Lewis, 1993). If not stated otherwise, data are presented as means \pm s.d.

RESULTS

Coral polyp expansion behavior

The flow regime showed no significant effect on coral polyp behavior, neither alone nor in combination with the other factors (backward stepwise ANOVA; supplementary material Table S4).

For this reason, flow speed was not further considered as a factor and data were pooled for further analyses.

Polyp expansion ranged from 25 to 100% under control conditions and did not vary between W and E corals ($P = 0.175$; Table 2). The addition of food resulted in an increased expansion of the coral polyps ($P = 0.006$; Table 2) from $\sim 55 \pm 25\%$ in the absence of food to $61 \pm 27\%$ when food was present. This increase was independent of temperature, pH and the origin of the coral nubbins.

Even though the origin of the colony did not influence the coral's behavior under control conditions, it did play an important role in the behavioral response to the LAIW simulation treatments ($P = 0.015$; Table 2), with generally stronger responses from E nubbins than W ones (Fig. 3). Multiple comparisons were performed to identify the isolated and combined effects of temperature and pH on coral expansion (Table 3). Low temperature had a significant effect on polyp behavior ($P = 0.002$; Table 3), triggering a retraction of the coral polyps, a response that was more pronounced among E nubbins ($P = 0.006$) than W ones (Table 4, Fig. 4). The opposite effect was caused by low pH, in which case polyps expanded their tentacles further (reaching 100% expansion in some instances) than those of the polyps under control (no LAIW) conditions (Table 3). Under these seawater conditions, this increase in polyp expansion was documented at similar levels between W and E nubbins (Table 4, Fig. 4).

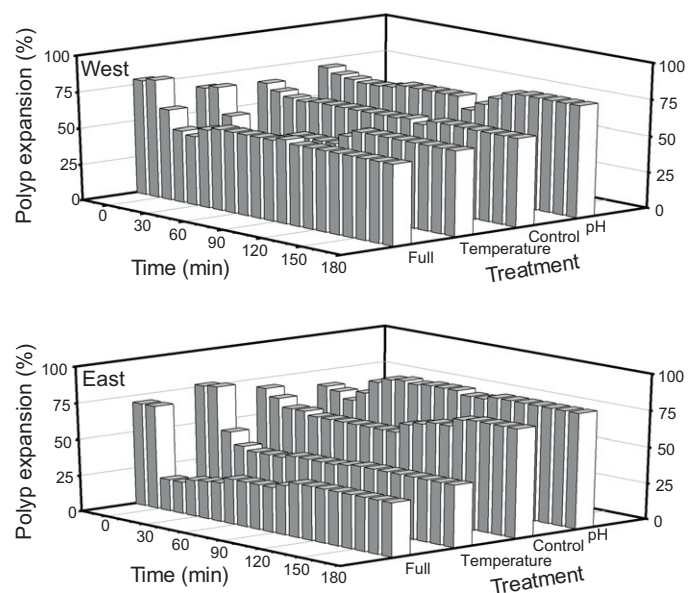


Fig. 3. Mean polyp expansion across colonies and flow regimes plotted at 10 min intervals for each experimental treatment over the experimental period: control, pH [partial large amplitude internal wave (LAIW)–pH], temperature (partial LAIW–temperature) and full (full LAIW–temperature and pH). Responses to the treatments are shown for colonies originating from the west and east island sides (see Table 1 for seawater quality data). *Artemia* nauplii were added at 90 min in all experiments.

Table 3. Comparisons between the effects of the different LAIW treatments *versus* the control treatment on the polyp expansion of *Porites lutea*, regardless of coral nubbin origin

Comparison	Difference	Lower limit	Upper limit	P
Control <i>versus</i> partial LAIW–temperature	−0.249	−0.428	−0.07	0.002**
Control <i>versus</i> partial LAIW–pH	0.183	0.004	0.362	0.042*
Control <i>versus</i> full LAIW–temperature + pH	−0.309	−0.488	−0.13	0.000***

See Table 1 for seawater quality data. Results are shown in Fig. 4, upper asterisks. Significance levels: * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

When low temperature was combined with low pH (full LAIW), coral polyps retracted their tentacles further into their calyxes ($P\leq0.001$), in many cases entirely (from 100% before time 0 to 0% when the temperature dropped). This effect was more noticeable and steady in E than in W nubbins ($P\leq0.001$; Table 4, Fig. 4). Moreover, W corals showed a steady increase in their expansion over the experimental period, with some of them responding to food stimuli. E nubbins, however, remained retracted throughout the entire experimental period.

Photosynthetic efficiency

F_v/F_m values were highly variable in the different experiments as well as in the control. Backward stepwise ANOVA showed no significant differences due to flow or pH changes, neither alone nor in interactions (supplementary material Table S5). For that reason, these data were pooled for further analyses, and the minimal adequate model is shown in Table 5. Although temperature alone did not evoke differences in the yield values of the corals (Table 5), the inclusion of coral origin into the analysis revealed strong interaction effects, with W nubbins showing higher F_v/F_m values than E nubbins ($P=0.006$; Fig. 5, Table 5). Moreover, while F_v/F_m values remained similar throughout the cold water treatments (Fig. 6, gray lines), they appeared to decay in the ambient temperature over the 180 min of the experiment (Fig. 6, black lines).

DISCUSSION

Low temperature had the strongest influence on coral polyp behavior and triggered the retraction of the tentacles into the calices. Temperature is believed to constrain the latitudinal distribution of coral species (Veron, 1995). Constant water temperatures below 18°C (*in situ*) limit tissue maintenance and growth, causing coral mortality unless heterotrophic nutrition can supply the necessary metabolic requirements (Crossland, 1984). The results from the present study indicate that such heterotrophic nutrition might not be able to supply the corals’ energetic needs because the tentacles of the coral polyps might not expand. As capture rates are directly related to the tentacle area exposed to the food particles (Sebens, 1987), contracted corals are unable to capture prey, unless other means of prey arrest are used, such as mucus (Lewis and Price,

1975) or mesenteric filaments (Schlichter and Brendelberger, 1998). Jokiel and Coles (Jokiel and Coles, 1977) documented coral mortality after 2 weeks in 18°C water, affirming that at the lower lethal limit (18°C) mortality rate was initially low but increased with time. Therefore, if other means of prey capture are used to supply the energetic needs of the colony when confronted with low temperatures, they appear not to be able to maintain metabolic rates for a long time, leading to the eventual death of the colony. In our study we made preliminary observations (supplementary material Fig. S6) of mucus filament production by contracted colonies, which may be involved in prey capture, but quantitative data on possible food uptake in relation to mucus production are not available.

In the case of LAIW-exposed offshore islands in the Andaman Sea, where corals are exposed to short-term temperature variations of up to 10°C with temperature minima of 18.5°C (Schmidt et al., 2012), the life history of the colonies played a crucial role in the respective responses (Figs 3, 4). Low temperature exposure alone – corresponding to a partial LAIW non-existent in nature and, hence, unfamiliar to both E and W corals – caused the retraction of polyps with a slightly stronger response from E corals. However, the combination of low temperature and low pH, a LAIW-induced scenario that is familiar to W but not to E corals, showed stronger differences, with W corals showing only slight, if any, retraction, as opposed to E corals, which showed a very strong response.

Organisms can display both phenotypic (acclimatization) and genotypic (adaptation) mechanisms to deal with fluctuating temperatures (Cossins and Bowler, 1987). Phenotypic mechanisms involve changes in the performance of the organism during its lifetime (physiological adjustments) as a response to temperature fluctuations (Cossins and Bowler, 1987; Barshis et al., 2013). The cellular mechanisms that allow such adaptations are diverse, from enzyme adaptations (Di Prisco, 1991) and stress proteins (Hoffmann and Parsons, 1991) to the saturation state of the membrane lipids (Tchernov et al., 2004), and are not mutually exclusive. Consequently, corals that experience large changes in their abiotic environment on a regular basis will respond differently from non-acclimatized ones. Accordingly, previous researchers (e.g. Coles and Jokiel, 1978; Middlebrook et al., 2008; Edmunds, 2009) have found that corals that had been acclimatized to different temperature regimes showed the highest tolerance levels (and subsequent

Table 4. Comparisons between the effects of the different LAIW treatments *versus* the control treatment on the polyp expansion behavior of *Porites lutea* according to coral nubbin origin

Origin	Comparison	Difference	Lower limit	Upper limit	P
East	Control <i>versus</i> partial LAIW–temperature	−0.364	−0.663	−0.064	0.006**
	Control <i>versus</i> partial LAIW–pH	0.213	−0.086	0.512	0.367
	Control <i>versus</i> full LAIW–temperature + pH	−0.473	−0.772	−0.173	0.000***
West	Control <i>versus</i> partial LAIW–temperature	−0.134	−0.433	0.165	0.868
	Control <i>versus</i> partial LAIW–pH	0.153	−0.146	0.453	0.767
	Control <i>versus</i> full LAIW–temperature + pH	−0.145	−0.444	0.154	0.814

See Table 1 for seawater quality data. Results are shown in Fig. 4, lower asterisks. Significance levels: ** $P<0.01$; *** $P<0.001$.

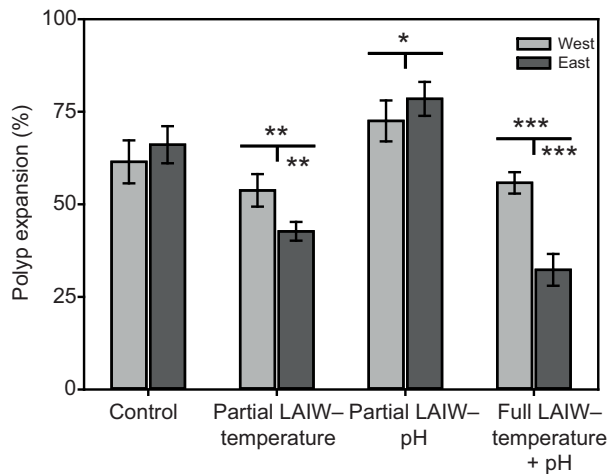


Fig. 4. Effect of large amplitude internal wave (LAIW) treatments (partial LAIW-temperature, partial LAIW-pH and full LAIW-temperature and pH) on the polyp expansion behavior of west and east *Porites lutea* nubbins versus the control group (see Table 1 for seawater quality data). Error bars represent \pm s.e.m. Upper asterisks indicate the significance of the general effect of the treatment against the control; lower asterisks correspond to the origin differences within a treatment against the respective control. Significance levels: * P <0.05; ** P <0.01; *** P <0.001.

survival rates) to experimentally manipulated temperatures when the conditions were not too different from the precedent acclimatization temperatures. As evidenced by the present study, such acclimatization processes are not restricted to long-term altered thermal exposures, but may also occur in response to naturally rapid temperature changes (cf. Mayfield et al., 2012). Moreover, the present study shows that the physiological adjustments that seem to allow the coral colony to withstand this sudden change in the abiotic environment are triggered in the first minutes of the exposure (Fig. 3).

Under the impact of low pH alone, *P. lutea* polyps showed an enhancement in their expansion state, with no difference between W and E colonies. Even though the effects of a long-term exposure to low pH on coral development are a topic of great interest in an era of ocean acidification (reviewed by Hoegh-Guldberg, 2005), this study is the first to address the immediate effect of low pH on coral polyp expansion behavior. The findings herein suggest that low pH does not have a deleterious effect on the coral polyp itself, in line with the results of Fine and Tchernov (Fine and Tchernov, 2007), who reported even positive effects of low pH on tissue growth and polyp size after a year of exposure to acidified water. The short-term effect of pH on polyp expansion in our study, however, proved to be very sensitive to temperature and nubbins origin, particularly in the first minutes of the thermal shock (Fig. 3). Our results suggest that, although the direct effects of low pH waters on polyp size and behavior may be neutral or positive (Fine and Tchernov, 2007), low

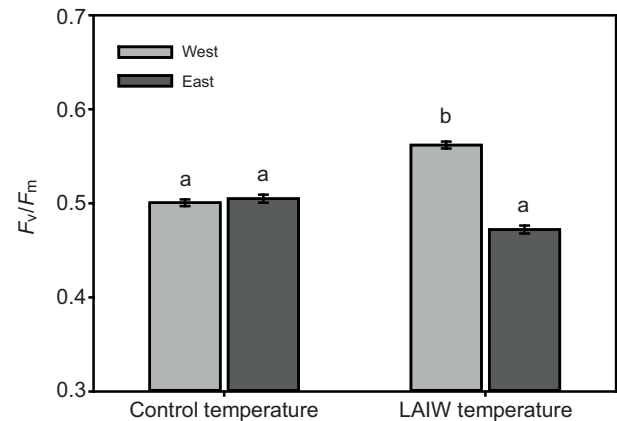


Fig. 5. Maximum quantum yield of photosystem II (F_v/F_m) of *Symbiodinium* within west and east *Porites lutea* nubbins at control ($29.11 \pm 0.62^\circ\text{C}$) and large amplitude internal wave (LAIW) temperatures ($19.48 \pm 0.56^\circ\text{C}$). Error bars represent \pm s.e.m. Letters on top of the bars represent Tukey's honestly significant difference groups (α <0.05) (supplementary material Table S7).

pH may have an amplifying effect on other disturbances such as low temperatures, as the contraction of the polyps was greater, among E colonies, when pH was lowered together with temperature in comparison with lower temperature alone. The reasons for this sensitizing influence of low pH require further research as the results found here suggest that interactions occur on the cellular level, and the effects of low-pH water on coral tissue are not yet fully understood.

Even though the experiments were conducted under low light for the reasons already mentioned, our field observations suggest similar results regarding the polyp expansion reaction under natural light. As shown in Fig. 1C, which illustrates the response of a colony from the W side of Ko Miang to the arrival of a LAIW, coral polyps experience a decrease in their expansion state immediately after the arrival of the low temperature front, with rapid recovery, similar to our experiments with W nubbins.

The presence of food exerted a strong effect over the expansion/contraction behavior of the polyps of *P. lutea*, but this effect was not always positive, as opposed to previous studies (Elliott and Cook, 1989; Levy et al., 2001). In some cases, food availability caused polyps to retract rather than expand their tentacles. Moreover, a stimulating effect was almost entirely restricted to the control and partial LAIW-pH treatments. At partial LAIW-temperature and full LAIW conditions, food presence did not elicit polyp expansion, apart from a few exceptions, notably among the W colonies (supplementary material Figs S4, S5). These results confirm the hypothesis that the mechanical and chemical cues triggering polyp expansion in the presence of food particles (McFarlane, 1978; Elliott and Cook, 1989) are superseded by the behavioral reaction in response to full LAIW conditions.

Table 5. Repeated-measures ANOVA with interactions after model simplification between fragment origin and temperature on F_v/F_m of *Porites lutea*

Source of variation	Sum of squares	d.f.	Mean square	F	P
Origin	0.791	1	0.791	6.67	0.011*
Temperature	0.088	1	0.088	0.74	0.391
Origin \times Temperature	0.958	1	0.958	8.08	0.006**

Significance levels: * P <0.05; ** P <0.01.

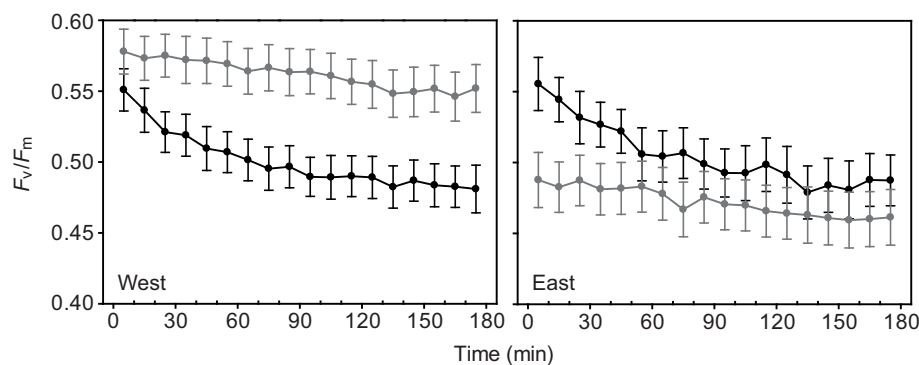


Fig. 6. Influence of temperature on the maximum quantum yield of photosystem II (F_v/F_m) of *Symbiodinium* within *Porites lutea* at 10 min intervals over the course of the experiment. Responses are shown for the nubbins originating from the west and east island sides. Black, control temperature ($29.11 \pm 0.62^\circ\text{C}$); gray, LAIW temperature ($19.48 \pm 0.56^\circ\text{C}$). Error bars represent \pm s.e.m.

The flow speed of the surrounding water did not seem to be an important element ruling over the polyp expansion state of *P. lutea*, independent of any combination with other factors (temperature and pH). These results are in contrast with the findings of Levy et al. (Levy et al., 2001), who showed that under low light levels the expansion behavior of *Favia fava* depended on the flow speed and prey availability, with prey presence being secondary to flow speed as polyps expanded their tentacles further at intermediate and high flow regimes (10 and 15 cm s^{-1}), even without the presence of food. As LAIW may reach coastal reefs with free-stream flow velocities of 10 to 40 cm s^{-1} (Roder et al., 2010), we cannot rule out the possibility that higher flow speeds may have played a role in controlling expansion states of *P. lutea*. However, given the much lower flow velocities in the benthic boundary layer near the seabed (Shashar et al., 1996), an upper margin of 10 cm s^{-1} near the coral colony under LAIW conditions seems more realistic, as shown in this study. So far, only Levy et al. (Levy et al., 2001) have studied polyp expansion behavior of scleractinian corals in response to water flow and food presence. However, several studies on other anthozoan species exist, demonstrating higher expansion states with higher flow speeds and consequently higher capture rates (Anthony, 1997; Bell et al., 2006). Nevertheless, direct comparisons are difficult because flow regimes in these studies were much more turbulent and strong ($40\text{--}60\text{ cm s}^{-1}$) than in our study.

The F_v/F_m of the coral colonies during the experiments was in the range of the responses of healthy corals to dark conditions (Saxby et al., 2003; Berkemans and van Oppen, 2006; Middlebrook et al., 2008). Results show that the sensitivity of the F_v/F_m to low temperatures depended on the coral's origin, suggesting acclimation to disturbance (Putnam and Edmunds, 2011; Mayfield et al., 2012), where LAIW-experienced *P. lutea* colonies from the exposed W side showed higher F_v/F_m values at low temperature than LAIW-inexperienced E corals.

Although the temperature effect was not reflected in the overall F_v/F_m values, it showed an influence over the experimental period, with a steady decay of the yield during the treatments in which temperature was not altered in contrast to constant values throughout the low temperature treatments (Fig. 6). The fact that the yield decreased over time under control temperature conditions (28°C) may be an artifact of the experimental design where, in spite of the precautionary randomizing of measurements across the coral surface, the high frequency of repeated excitations with the PAM fluorometer (every 10 min) may have added up to a cumulative photoinhibition in the *Symbiodinium*. A previous study on continuous recordings of F_v/F_m over a short period of time (4 h) under control (28°C) conditions did not demonstrate such a decay (Jones et al., 1998), yet the recovery phases for the *Symbiodinium* between the measurements in that case were longer (20 min) than in our study.

The fact that F_v/F_m was steadier in the cold-water treatments raises the question about its effects on mitigating the possible cumulative photoinhibition under light stress. It is not likely that the expansion state of the polyps played a role in this response, as Levy et al. (Levy et al., 2003) found no differences in the maximum quantum yield of expanded *versus* contracted tentacles in different coral species. Given the intermittent nature of the stress, the lower cumulative photoinhibition in corals subjected to low temperature might be related to an enhanced photoprotection (Krämer et al., 2012) and/or repair (Hill et al., 2011) at lower temperature.

The results of this study highlight the importance of acclimatization in corals and their ability to withstand changes in their abiotic environment. Yet the cellular pathways that allow corals to acclimatize and the possible energetic costs and effects (e.g. on coral growth) are still unknown. The reduced coral development along the exposed W side of the islands (Schmidt et al., 2012) indicates that the costs in response to the frequency and intensity of LAIW disturbance may be substantial, as suggested previously (Wall et al., 2012). The fact that LAIW-exposed corals present higher tissue biomass and protein content compared with sheltered E specimens (Roder et al., 2010) suggests that, in the case of LAIW-experienced colonies, energy allocation might be directed more towards LAIW acclimatization, rather than skeletal growth, especially if a whole array of thermal tolerance genes and enzymes is activated at the arrival of the thermal shock (Barshis et al., 2013).

Nevertheless, coral acclimatization potential is no insurance against a changing environment: the frequency and intensity of the natural disturbances described, along with the anthropogenic stressors in many places, may overwhelm the corals' resistance to disturbance. As the pH and temperature effects on coral polyp expansion have demonstrated, given independent variables may have very different effects on dependent variables investigated alone or in combination, suggesting that interactions between factors may cause nonlinearities, which are very difficult to predict. Our multifactorial study on the natural co-variation of various stressors including temperature and pH may thus have important repercussions on the interpretation of laboratory-based largely single-factor approaches dominating many large-scale programs, including ocean acidification research.

LIST OF SYMBOLS AND ABBREVIATIONS

DO	dissolved oxygen
E	east
F_v/F_m	maximum dark-adapted quantum yield of photosystem II
LAIW	large amplitude internal wave(s)
PAM	pulse amplitude modulation
PAR	photosynthetically active radiation
PSII	photosystem II
W	west

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AUTHOR CONTRIBUTIONS

C.O.P., G.M.S. and C.R. created the setup for the behavioral experiments *in situ* and in the laboratory. C.O.P. and G.M.S. conducted the *in situ* experiments. C.O.P. conducted all the experiments in the laboratory and analyzed the video data. C.O.P. and G.M.S. created all figures. C.O.P., G.M.S. and C.R. contributed to the interpretation of the collected data, and conceived and wrote the manuscript.

COMPETING INTERESTS

No competing interests declared.

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