

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

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Short title: Coral responses to LAIW

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List of abbreviations:

LAIW: Large amplitude internal wave(s)

W: West

E: East

PAM: Pulse amplitude modulation

F_v/F_m : Maximum dark-adapted quantum yield of photosystem II

PSII: Photosystem II

DO: Dissolved oxygen

1 Summary:

2 Large amplitude internal waves (LAIW) cause frequent and severe changes in the physico-
3 chemical environment of Andaman Sea coral reefs and are a potentially important source of
4 disturbance for corals. To explore the coral response to LAIW, prey capture disposition and
5 photosynthesis were investigated in relation to changes in seawater temperature, pH, flow
6 speed, and food availability in LAIW simulation studies under controlled laboratory
7 conditions, using *Porites lutea* as a model organism. Although food presence stimulated polyp
8 expansion, we found an overriding effect of low temperature (19°C) causing retraction of the
9 coral polyps into their calices, particularly when pH was altered concomitantly. Decreases in
10 pH alone, however, caused the expansion of the polyps. The exposure history of the colonies
11 played a crucial role in coral responses: prior field exposure to LAIW yielded lower retraction
12 levels than in LAIW-inexperienced corals, suggesting acclimatization. Low temperature
13 (19°C) exposure did not seem to influence the photosynthetic performance, but LAIW-
14 experienced corals showed higher values of maximum dark adapted quantum yield (F_v/F_m)
15 of photosystem II (PSII) than LAIW-inexperienced controls. Collectively, these data suggest
16 that *P. lutea*, the dominant hermatypic coral in the Andaman Sea, can acclimatize to extreme
17 changes in its abiotic environment by modulating its mixotrophic nutrition through polyp
18 expansion and potential feeding as well as its photosynthetic efficiency.

1 Introduction:

2 The general perception of corals thriving in a benign tropical climate has masked the fact
3 that they are, by contrast, exposed to large variations in their natural environment, over a
4 range of scales. Coral evolution and diversity are in fact thought to be driven by large-scale
5 fluctuations in ocean circulation (Veron, 1995), glacial-interglacial changes in sea-level
6 (Pandolfi, 1996) and changes in sea surface temperature, $p\text{CO}_2$ and pH of $\sim 5^\circ\text{C}$ (Lea et al.,
7 2000), ~ 2000 ppm and 0.8, respectively (Pearson and Palmer, 2000) over the many years
8 they have inhabited the oceans. On a finer temporal scale, disturbances at decadal, inter-
9 annual, seasonal and daily time-scales have been shown to influence the diversity and
10 resilience of coral reefs (Connell, 1978; Lough, 1994; Brown, 1997). Seasonal variations in
11 temperature, current speeds and sedimentation are generated by fluctuations, durations and the
12 strength of the monsoon seasons (Naseer and Hatcher, 2000) as well as current or wind-driven
13 upwelling (Andrews and Gentien, 1982; Palardy et al., 2005).

14 Surface gravity waves and internal waves act on seconds to hours timescales (Leichter et
15 al., 2005). As opposed to surface waves which cause mainly mechanical impact on shallow
16 communities, internal waves may affect the physico-chemical environment of deeper
17 communities (15-30 m) (Leichter et al., 2005). A particular class of internal waves in stratified
18 macrotidal areas with abrupt topography are non-linear solitary large amplitude internal
19 waves (solitons or LAIW). They form when tidal flow acceleration across shallow topography
20 causes a depression of the pycnocline, separating light surface from dense deeper waters,
21 downstream of the obstacle. Flow reversal during slack tide causes this lee wave to detach and
22 transform, generating packets of internal waves propagating in the opposite direction. In deep
23 water, vertical displacements of the pycnocline may be more than 60 m, and in exceptional
24 cases, more than 100 m. These LAIW may propagate large distances across entire ocean
25 basins (Jackson, 2004). In the Andaman Sea, where LAIW were first discovered and their
26 soliton character established (Osborne and Burch, 1980), LAIW moving from deep waters
27 onto the shelf may cause strong vertical mixing (Vlasenko and Stashchuk, 2007), which can
28 cause drastic changes in the physico-chemical conditions of the water column. In the Similan
29 Islands (Fig. 1), an offshore archipelago in the Andaman Sea, where LAIW cause frequent
30 (several events per day) and sudden drops (within only minutes) in temperature and pH (of up
31 to 10°C and 0.6 pH units, respectively; Schmidt et al., 2012), and concomitant increases in
32 nutrient concentrations, the shallow water scleractinian coral communities are strongly
33 affected (Roder et al., 2011; Schmidt et al., 2012). While the LAIW disturbances appear to be
34 associated with higher coral diversity and the nutritional status relative to LAIW-protected

35 sites (Roder et al., 2011; Schmidt et al., 2012), a mechanistic understanding of LAIW impact
36 on coral nutrition is still lacking. Because scleractinian corals are mixotrophic, it is
37 conceivable that both the photoautotrophy of the endosymbiotic dinoflagellates (genus
38 *Symbiodinium*) and the heterotrophy of the coral-*Symbiodinium* holobiont are affected by the
39 severity of the LAIW-induced environmental changes. However, the effects of LAIW on the
40 expansion and retraction behavior of coral polyps and the photosynthetic performance of the
41 *Symbiodinium* are still unknown.

42 Polyp behavior has been well documented in tropical scleractinian corals, from studies on
43 feeding mechanisms (Lewis and Price, 1975; Porter, 1976), its effect on photosynthetic
44 productivity (Levy et al., 2006) and its response to radiation and current (Sebens and
45 DeRiemer, 1977; Levy et al., 2001). It has long been assumed that corals expand their
46 tentacles at night as a response to higher food availability and the lower risk of predation
47 (Lewis and Price, 1975). On the other hand, their retraction/expansion during the day is
48 supposed to enhance the planar density and photosynthetic performance of *Symbiodinium* as
49 more endosymbionts will be exposed to the light (Sebens and DeRiemer, 1977; Lasker, 1979).
50 However, polyp expansion and retraction also respond to a variety of other factors irrespective
51 of a light:dark cycle, such as differences in light intensities (Gladfelter, 1975; Levy et al.,
52 2003), current speed (Sebens et al., 1997), food availability (Levy et al., 2001), polyp size
53 (Lasker, 1981), interactions between the aforementioned, and the physiological needs of the
54 coral colony (Porter, 1976).

55 Although the effects of polyp expansion and contraction on the balance between
56 heterotrophy and autotrophy are still poorly known, the energetic costs associated with these
57 behavioral states have already been investigated. Specifically, polyp expansion increases the
58 rate of respiration due to the larger surface area available to dissipate the oxygen gradient
59 between the tissue and surrounding water (Levy et al., 2006). The hydrostatic skeleton also
60 entails an energetic cost of maintaining a pressure gradient between the coelenteron and
61 ambient seawater (Ruppert et al., 2004). Respiration rates are known to be lower in contracted
62 anthozoans compared to expanded ones (Shick et al., 1979), suggesting that contraction might
63 be a way to reduce the oxygen concentration in the coelenteron, lower the metabolic rates and
64 save energy (Sebens and DeRiemer, 1977; Sebens, 1987). On the other hand, polyp expansion
65 might help in the diffusion of excess oxygen resulting from hyperoxia in the gastrodermal
66 tissue layer, which is potentially detrimental to the photosymbiosis (Lesser and Shick, 1989).

67 Changes in certain physico-chemical parameters of the seawater surrounding reef corals
68 may affect not only the behavior of the host, but also the photosynthetic performance of the

69 *Symbiodinium*. These changes have been addressed with regard to temperature (Berkelmans
70 and van Oppen, 2006; Putnam and Edmunds, 2011), water flow (Carpenter and Patterson,
71 2007), and UV radiation (Ferrier-Pagès et al., 2007). The photosystem II complex (PSII) of
72 the photosynthetic apparatus is sensitive to thermal stress (Warner et al., 1996), as shown by a
73 decrease in the maximum quantum yield of PSII in pulse amplitude modulated (PAM)
74 chlorophyll *a* fluorometry (Schreiber et al., 1986). Damage to the PSII may lead to the
75 expulsion of the endosymbionts and a subsequent bleaching of the coral colony (Warner et al.,
76 1999). While the bulk of the work carried out so far has dealt with heat stress, similar
77 responses may be caused also by low temperature stress (Muscatine et al., 1991; Saxby et al.,
78 2003). The immediate response (seconds-several minutes), however, of the photosynthetic
79 efficiency to a low temperature shock is still unknown.

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

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

103 Methods:

104 Nubbins (4 – 5 cm diameter, 3 – 4 cm height) of the massive scleractinian coral *Porites*
105 *lutea* were collected from both LAIW-exposed west (W) and LAIW-sheltered east (E) sides of
106 two Andaman Sea Islands off the Thai coast (Ko Miang, 8°34'0"N, 97°37'60"E and Ko
107 Racha, 7° 34' 60"N, 98° 20' 60"E) at a depth of 15 m [N = 96 nubbins: 2 islands (i), 2 sides
108 (s), 3 colonies (c) per side, 8 nubbins (n) per colony; i and c were pooled, yielding 6 source
109 colonies for each (W and E) side with 8 nubbins, 1 for each of the 8 (4 factors, 2 levels)
110 experiments – see below]. The coral nubbins were chiseled from their mother colonies and
111 glued on individual acrylic holders using underwater cement (Silka waterplug, Thailand) and
112 taken back to the reef for 10 to 15 days to recover from the handling procedure. Thereafter,
113 they were taken to a reef water flow-through system in the aquaria facilities at the Phuket
114 Marine Biological Center (PMBC).

115 *Culturing conditions* - An aquaria system was built in order to maintain the coral nubbins at
116 specified conditions. During a 2-week acclimation period to the laboratory conditions, all
117 coral nubbins were supplied with a constant flow of unfiltered seawater from the nearby reef
118 at a rate of 43.2 ± 4.4 (S.D.) L/hr. An 11 hr light: 13 hr dark cycle was created with metal
119 halide lamps (5000 W), and photosynthetically active radiation (PAR) was measured once a
120 day with a 2π cosine corrected sensor (LI-COR LI-192, Lincoln, USA) connected to a data
121 logger (LI-COR LI-1400, Lincoln, USA). Light values ranged between 80 and 120 μmol
122 $\text{quanta m}^{-2} \text{s}^{-1}$ corresponding to the ambient light levels at 15 m water depth (Supplementary
123 material: Fig. S1). Temperature was monitored with TidbiT v2 temperature loggers (Onset
124 Computer, USA; logging interval 1 min). Mean temperature (\pm S.D.) of the unaltered reef
125 water was near ambient conditions at $29.8 \pm 0.6^\circ\text{C}$ and never exceeded 30.5°C (January
126 2011). Dissolved oxygen (DO) and pH were measured twice a day with a YSi ProODO
127 optical DO sensor (USA) and a WTW Routine Pt1000 Mettler Toledo Inlab pH sensor
128 (Germany), respectively, the latter of which was calibrated on a daily basis (NBS scale).
129 Values ranged between 246.9 and 284.4 $\mu\text{mol DO L}^{-1}$ and $\text{pH } 8.34 \pm 0.11$.

130 Following the 2-week acclimation process and in order to maintain the original
131 acclimatization of coral nubbins originating from W island sides, they were treated with
132 simulated LAIW conditions in the laboratory, similar to their *in situ* experience
133 (Supplementary material: Fig. S2 – C). Thus, after the 2-week period, and while E tanks
134 remained with the regular reef water flow (Supplementary material: Fig. S2 –B), W rearing
135 tanks were flushed twice a day with temperature- and pH- manipulated seawater (incoming
136 water flow: $\sim 75 \pm 5$ L/hr). For that purpose the reef water was cooled down to 21°C

137 (AquaMedic Titan 1500 cooling unit, Germany), bubbled with pure CO₂ to a pH of 7.8
138 (LAIW temperature and pH conditions, Schmidt et al., 2012) and pumped into the coral tanks
139 using an aquarium pump (EHEIM, Germany). Cold and acidified seawater remained in the
140 coral basins for about 15 min before reopening the inflow valves for the warm, high pH water.
141 Ambient conditions were re-established within the following 15 - 20 min, which closely
142 mimics the arrival and departure of LAIW_s *in situ* (Schmidt et al., 2012). LAIW simulations
143 for the W rearing tanks started a week before the experiments took place and lasted for a total
144 of 20 days while the experiments were performed in parallel (Supplementary material: Fig. S2
145 - A).

146 *Experimental design* - To identify the relative importance of food, currents, temperature and
147 pH on polyp expansion and maximum quantum yield of PSII (F_v/F_m), their effects were
148 tested in isolation and in combination (Table 1). All experiments were performed in random
149 order using a flow-through chamber (25 × 10 × 15 cm) in which current flow of different
150 speeds could be created via a circulating pump (EHEIM, Germany) (Supplementary material:
151 Fig. S2). Two different flow speeds, 2 cm/s and 10 cm/s, were applied, representing the
152 natural flows on coral reefs under LAIW-free and LAIW conditions, respectively (Roder et
153 al., 2010). Flow speed was previously measured by following the movement of colored
154 particles that were added to the water. Particle movements were recorded using a video
155 camera (SONY HDR-XR520V).

156 In order to standardize the response of *Symbiodinium* to the PAM fluorometer
157 measurements, all experiments were conducted under crepuscular conditions. For that
158 purpose, a fiber optic lamp (Schott 1500, USA) was set to the minimal PAR level (~ 1.5 μmol
159 quanta m⁻² s⁻¹) to avoid any photosynthetic response while providing sufficient light for video
160 recording. Downwelling PAR was measured at the beginning of every experiment (LI-COR
161 LI-1400, Lincoln, USA). Temperature was recorded every 15 seconds with a TidbiT v2
162 temperature logger (Onset Computer, USA) placed in the flow-through chamber. DO levels
163 and pH were monitored hourly with the same instruments as described above (Supplementary
164 material: Table S1).

165 One out of 8 nubbins from each of the source colonies (6 from W and 6 from E, see
166 above) was used for each of the 8 different combinations of water flow, prey availability, pH
167 and temperature conditions (Table 1). Nubbins were used only once to minimize the risk of
168 acclimation to the experimental conditions. Preliminary experiments with triplicate nubbins
169 from different colonies showed no within-colony differences in the behavioral response of
170 coral nubbins to the factors above; hence within-colony variation was not considered relevant

171 in our experiments. The chamber and hoses were all thoroughly rinsed with distilled water
172 after each experiment. Because the flow-through chamber could only hold 3 fragments at a
173 time, repeated experiments were necessary to obtain a minimum of 6 observations per factor.
174 For each experiment (Control: ambient temperature and pH; Partial LAIW-Temp.:
175 temperature drop, ambient pH; Partial LAIW-pH: pH drop and ambient temperature; and Full
176 LAIW: temperature and pH drop) (Table 1), coral nubbins from the same island side were
177 placed into the flow-through chamber and left there untreated for 40 min under no light.
178 During this period of time, ambient-temperature (29°C), ambient-pH (8.3) seawater at 2 cm/s
179 was circulated through the system. Video recording and PAM fluorometer measurements
180 started 20 min prior to the treatment (time “0”). The actual experiment from the application of
181 the treatment (time “0”) lasted 180 min (Levy et al., 2001) during which polyp expansion
182 behavior of each nubbin in the flow-through chamber was recorded every 5 min for 1 minute
183 with a SONY HDR-XR520V video camera. In between the camera recordings, triplicate
184 *Fv/Fm* measurements were taken for each nubbin with a diving PAM fluorometer (Walz,
185 Germany) (Supplementary material: Table S2). Triplicate measurements were taken
186 randomized over the surface of each nubbin to minimize the risk of artefactual
187 photoinhibition by repeated PAM measurements. The mean of triplicate measurements was
188 used for subsequent analyses. After half of the experimental time (90 min) freshly hatched
189 *Artemia nauplii* were added to the chambers (0.3 individuals mL⁻¹). Visual observation
190 confirmed that the *Artemia* remained in suspension throughout the remainder of the
191 experiment. Tentacle expansion was scored on a percentage scale based on Lasker (1979),
192 ranging from 0% to 100%: with 0% representing complete retraction of the polyp with neither
193 tentacles nor oral disk visible, 25% indicating polyps expanded to the point that tentacles
194 were visible, though still retracted, 50% showing further expansion of the tentacles with the
195 oral disk visible, 75% representing polyp expansion up to the outer whorl of tentacles, and
196 100% indicating complete polyp expansion (Fig. 2). Each score referred to the whole coral
197 nubbin.

198 *Data analysis* – Almost 6000 min of video data polled across the 32 separate experiments
199 were analyzed. No significant differences were found within triplicate nubbins within a
200 chamber (i.e., no chamber effect, Table S3) nor were there significant differences between
201 islands (Table S6). Normality tests and Levene’s test (homogeneity of variances) were carried
202 out prior to parametric tests (ANOVA). The influence of the different treatments (Control,
203 Partial LAIW-Temp., Partial LAIW-pH and Full LAIW-Temp. & pH) on coral polyp behavior
204 was evaluated using the means of the behavioral responses over the 90 min time intervals.

205 Polyp expansion percentage data were arcsine transformed to achieve normality (Martin and
206 Bateson, 2007). The effect of the independent factors (food, LAIW treatments, flow regime
207 and coral nubbin origin) on polyp expansion was tested initially with a backward stepwise
208 ANOVA. In case a term had non-significant effects on the dependent variable both for one
209 factor alone or for interactions of factors, that term was removed resulting in a minimal
210 adequate model. When ANOVA determined a significant difference, Tukey's post hoc tests
211 were used to attribute differences between treatments.

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

218 Results:

219 *Coral polyp expansion behavior* –The flow regime showed no significant effect on coral
220 polyp behavior, neither alone nor in combination with the other factors (backward stepwise
221 ANOVA; Table S4). For this reason, flow speed was not further considered as a factor and
222 data were pooled for further analyses.

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

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

239 When low temperature was combined with low pH (full LAIW), coral polyps retracted
240 their tentacles further into their calyxes ($p \leq 0.001$), in many cases entirely (from 100% before
241 time 0 to 0% when the temperature dropped). This effect was more noticeable and steady in E
242 ($p \leq 0.001$) than in W nubbins (Table 4; Fig. 4). Moreover, W corals showed a steady increase
243 in their expansion over the experimental period, with some of them responding to food
244 stimuli. E nubbins, however, remained retracted throughout the entire experimental time.
245 *Photosynthetic efficiency* – F_v/F_m values were highly variable in the different experiments as
246 well as in the control. Backward stepwise ANOVA showed no significant differences due to
247 flow or pH changes, neither alone nor in interactions (Table S5). For that reason these data
248 were pooled for further analyses, and the minimal adequate model is shown in Table 5.
249 Although temperature alone did not evoke differences in the yield values of the corals (Table
250 5), the inclusion of coral origin into the analysis revealed strong interaction effects, with W
251 nubbins showing higher F_v/F_m values than E nubbins ($p = 0.006$; Fig. 5; Table 5). Moreover,
252 while F_v/F_m values remained similar throughout the cold water treatments (Fig. 6, grey
253 lines), they appeared to decay in the ambient temperature over the 180 min of the experiment
254 (Fig. 6, black lines).

255 Discussion:

256 Low temperature had the strongest influence on coral polyp behavior and triggered the
257 retraction of the tentacles into the calices. Temperature is believed to constrain the latitudinal
258 distribution of coral species (Veron, 1995). Constant water temperatures below 18 °C (*in situ*)
259 limit tissue maintenance and growth, causing coral mortality unless heterotrophic nutrition
260 can supply the necessary metabolic requirements (Crossland, 1984). The results from this
261 study indicate that such heterotrophic nutrition might not be able to supply the corals'
262 energetic needs due to the fact that the tentacles of the coral polyps might not expand. Since
263 capture rates are directly related to the tentacle area exposed to the food particles (Sebens,
264 1987), contracted corals are unable to capture prey, unless other means of prey arrest are used,
265 such as mucus (Lewis and Price, 1975) or mesenteric filaments (Schlichter and Brendelberger,
266 1998). On this account Jokiel and Coles (1977) documented coral mortality after 2 weeks in
267 18 °C water, affirming that at the lower lethal limit (18 °C) mortality rate was initially low but
268 increased with time. Therefore, if other means for prey capture are used to supply the
269 energetic needs of the colony when confronted with low temperatures, they appear not to be
270 able to maintain metabolic rates for a long time, leading to the eventual death of the colony. In
271 our study we made preliminary observations (Fig. S6) of mucus filament production by
272 contracted colonies which may be involved in prey capture, but quantitative data on possible

273 food uptake in relation to mucus production are not available.

274 In the case of LAIW-exposed offshore islands in the Andaman Sea, where corals are
275 exposed to short-term temperature variations of up to 10 °C with temperature minima of 18.5
276 °C (Schmidt et al., 2012), the life history of the colonies played a crucial role in the respective
277 responses (Fig. 3 & 4). Low temperature exposure alone – corresponding to a partial LAIW
278 non-existent in nature and, hence, unfamiliar to both E and W corals – caused the retraction of
279 polyps with a slightly stronger response from E corals. However, the combination of low
280 temperature and low pH, a LAIW-induced scenario which is familiar to W but not to E corals,
281 showed stronger differences, with W corals showing only slight, if any, retraction, as opposed
282 to E corals, which showed a very strong response.

283 Organisms can display both phenotypic (acclimatization) and genotypic (adaptation)
284 mechanisms to deal with fluctuating temperatures (Cossins and Bowler, 1987). Phenotypic
285 mechanisms involve changes in the performance of the organism during its lifetime
286 (physiological adjustments) as a response to temperature fluctuations (Cossins and Bowler,
287 1987; Barshis et al., 2013). The cellular mechanisms that allow such adaptations are diverse,
288 from enzyme adaptations (Di Prisco, 1991), and stress proteins (Hoffmann and Parsons,
289 1991), to the saturation state of the membrane lipids (Tchernov et al., 2004), and the
290 interactions between them. Consequently, corals that experience large changes in their abiotic
291 environment on a regular basis will respond differently from non-acclimatized ones.
292 Accordingly, Coles and Jokiel (1978), Middlebrook et al. (2008), Edmunds (2009), among
293 others have found that corals which had been acclimatized to different temperature regimes
294 showed highest tolerance levels and survival rates to experimentally manipulated
295 temperatures when the conditions were not too different from the precedent acclimatization
296 temperatures. As evidenced by the present study, such acclimatization processes are not
297 restricted to long-term altered thermal exposures, but may also apply for naturally rapid
298 temperature changes (cf. Mayfield et al., 2012). Moreover this study shows that the
299 physiological adjustments that seem to allow the coral colony to stand this sudden change in
300 their abiotic environment are triggered in the first minutes of the exposure (Fig. 3).

301 Under the impact of low pH alone, *P. lutea* polyps showed an enhancement in their
302 expansion state with no difference between W and E colonies. Even though the effects of a
303 long term exposure to low pH on coral development are a topic of great interest in an era of
304 ocean acidification (reviewed by Hoegh-Guldberg, 2005), this study is the first to address the
305 immediate effect of low pH on coral polyp expansion behavior. The findings herein suggest
306 that low pH does not have a deleterious effect on the coral polyp itself, in line with the results

307 of Fine and Tchernov (2007) who reported even positive effects of low pH on tissue growth
308 and polyp size after a year of exposure to acidified water. The short-term effect of pH on
309 polyp expansion in our study, however, proved to be very sensitive to temperature and nubbin
310 origin, particularly in the first minutes of the thermal shock (Fig. 3). The results suggest that,
311 although the direct effects of low pH waters on polyp size and behavior may be neutral or
312 positive (Fine and Tchernov, 2007), low pH may have an amplifying effect on other
313 disturbances such as low temperatures in our study as the contraction of the polyps is greater,
314 among E colonies, when pH was lowered together with temperature in comparison with
315 lower temperature alone. The reasons of this sensitizing influence of low pH require further
316 research since the results found here suggest interactions on the cellular level as the effects of
317 low pH waters over coral tissue are not yet fully understood.

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

324 The presence of food exerted a strong effect over the expansion/contraction behavior of
325 the polyps of *P. lutea*, but this effect was not always positive, as opposed to previous studies
326 (Elliott and Cook, 1989; Levy et al., 2001). In some cases food availability caused polyps to
327 retract rather than expand their tentacles. Moreover, a stimulating effect was almost entirely
328 restricted to the control and partial LAIW-pH treatments. At partial LAIW-temperature and
329 full-LAIW conditions, food presence did not elicit polyp expansion, apart from a few
330 exceptions notably among the W colonies (Fig. S3, S4). These results confirm the hypothesis
331 that the mechanical and chemical cues triggering polyp expansion in the presence of food
332 particles (McFarlane 1978; Elliott and Cook, 1989) are superseded by the behavioral reaction
333 in response to full-LAIW conditions.

334 The flow speed of the surrounding water did not seem to be an important element ruling
335 over the polyp expansion state of *P. lutea*, independent of any combination with other factors
336 (temperature and pH). These results are in contrast with the findings of Levy et al. (2001) who
337 showed that under low light levels the expansion behavior of *Favia favaus* depended on the
338 flow speed and prey availability, with prey presence being secondary to flow speed as polyps
339 expanded their tentacles further at intermediate and high flow regimes (10 and 15 cm/s), even
340 without the presence of food. As LAIW may reach coastal reefs with free-stream flow

341 velocities of 10 to 40 cm/s (Roder et al., 2010), we cannot rule out the possibility that higher
342 flow speeds may have played a role in controlling expansion states of *P. lutea*. However,
343 given the much lower flow velocities in the benthic boundary layer near the sea-bed (Shashar
344 et al., 1996), an upper margin of 10 cm/s near the coral colony under LAIW conditions seems
345 more realistic, as shown in this study. So far only Levy et al. (2001) studied polyp expansion
346 behavior of scleractinian corals in response to water flow and food presence. However,
347 several studies on other anthozoan species exist, demonstrating higher expansion states with
348 higher flow speeds and consequently higher capture rates (Anthony, 1997; Bell et al., 2006).
349 Nevertheless direct comparisons are difficult since flow regimes in these studies were much
350 more turbulent and strong (40 – 60 cm/s) than in our study.

351 The F_v/F_m of the coral colonies during the experiments was in the range of the responses
352 of healthy corals to dark conditions (Saxby et al., 2003; Berkelmans and van Oppen, 2006;
353 Middlebrook et al., 2008). Results show that the sensitivity of the F_v/F_m to low temperatures
354 depended on the coral's origin, suggesting acclimation to disturbance (Putnam and Edmunds,
355 2011; Mayfield et al., 2012), where LAIW-experienced *P. lutea* colonies from the exposed W
356 side showed higher F_v/F_m values at low temperature than LAIW-inexperienced E corals.

357 Although the temperature effect was not reflected in the overall F_v/F_m values, it showed
358 an influence over the experimental time with a steady decay of the yield during the treatments
359 in which temperature was not altered in contrast to constant values throughout the low
360 temperature treatments (Fig. 6). The fact that the yield decreased over time under control
361 temperature conditions (28 °C) may be an artifact of the experimental design where, in spite
362 of the precautionary randomizing of measurements across the coral surface, the high
363 frequency of repeated excitations with the PAM fluorometer (every 10 min) may have added
364 up to a cumulative photoinhibition in the *Symbiodinium*. Previous studies on continuous
365 recordings of F_v/F_m over a short period of time (4 h) under control (28 °C) conditions did not
366 demonstrate such a decay (Jones et al., 1998), yet the recovery phases for the *Symbiodinium*
367 between the measurements in that case were longer (20 min) than in our study. The fact that
368 F_v/F_m was steadier in the cold water treatments raises the question about its effects on
369 mitigating the possible cumulative photoinhibition under light stress. It is not likely that the
370 expansion state of the polyps played a role in this response since Levy et al. (2003) found no
371 differences in the maximum quantum yield of expanded versus contracted tentacles in
372 different coral species. Given the intermittent nature of the stress, the lower cumulative
373 photoinhibition in corals subjected to low temperature might be related to an enhanced
374 photoprotection (Krämer et al., 2012) and/or repair (Hill et al., 2011) at lower temperature.

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

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

References:

- Andrews, J. C. and Gentien, P.** (1982). Upwelling as a source of nutrients for the Great Barrier Reef ecosystems: A solution to Darwin's question? *Mar Ecol Prog Ser* **8**, 257-269.
- Anthony, K. R. N.** (1997). Prey capture by the sea anemone *Metridium senile* (L.): Effects of body size, flow regime, and upstream neighbors. *Biol Bull (Woods Hole)* **192**, 73-86.
- Barshis, D. J., Ladner, J. T., Oliver, T. A., Seneca, F. O., Traylor-Knowles, N. and Palumbi, S. R.** (2013). Genomic basis for coral resilience to climate change. *Proc Natl Acad Sci U S A*, (in press).
- Bell, J. J., Shaw, C. and Turner, J. R.** (2006). Factors controlling the tentacle and polyp expansion behaviour of selected temperate Anthozoa. *J Mar Biol Assoc U K* **86**, 977-992.
- Berkelmans, R. and van Oppen, M. J. H.** (2006). The role of Zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. *Proc R Soc Biol Sci Ser B* **273**, 2305-2312.
- Brown, B. E.** (1997). Adaptations of reef corals to physical environmental stress. In *Adv Mar Biol*, vol. Volume 31 eds. J. H. S. Blaxter and A. J. Southward), pp. 221-299: Academic Press.
- Carpenter, L. W. and Patterson, M. R.** (2007). Water flow influences the distribution of photosynthetic efficiency within colonies of the scleractinian coral *Montastrea annularis* (Ellis and Solander, 1786); implications for coral bleaching. *J Exp Mar Biol Ecol* **351**, 10-26.
- Coles, S. L. and Jokiel, P. L.** (1978). Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. *Mar Biol* **49**, 187-195.
- Connell, J. H.** (1978). Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302-1310.
- Cossins, A. R. and Bowler, K.** (1987). Temperature biology of animals: Chapman and Hall.
- Crossland, C. J.** (1984). Seasonal variations in the rates of calcification and productivity in the coral *Acropora formosa* on a high-latitude reef. *Mar Ecol Prog Ser* **15**, 135-140.
- Di Prisco, G.** (1991). Life under extreme conditions: biochemical adaptations: Springer.
- Edmunds, P.** (2009). Effect of acclimatization to low temperature and reduced light on the response of reef corals to elevated temperature. *Mar Biol* **156**, 1797-1808.
- Elliott, J. and Cook, C. B.** (1989). Diel variation in prey capture behavior by the Corallimorpharian *Discosoma sanctithomae*: Mechanical and chemical activation of feeding. *Biol Bull (Woods Hole)* **176**, 218-228.
- Ferrier-Pagès, C., Richard, C., Forcioli, D., Allemand, D., Pichon, M. and Shick, J. M.** (2007). Effects of temperature and UV radiation increases on the photosynthetic efficiency in four scleractinian coral species. *Biol Bull (Woods Hole)* **213**, 76-87.
- Fine, M. and Tchernov, D.** (2007). Scleractinian coral species survive and recover from decalcification. *Science* **315**, 1811.
- Gladfelter, W. B.** (1975). Sea anemone with Zooxanthellae: Simultaneous contraction and expansion in response to changing light intensity. *Science* **189**, 570-571.
- Hill, R., Brown, C. M., DeZeeuw, K., Campbell, D. A. and Ralph, P. J.** (2011). Increased rate of D1 repair in coral symbionts during bleaching is insufficient to counter accelerated photo-inactivation. *Limnol Oceanogr* **56**, 139-146.
- Hoegh-Guldberg, O.** (2005). Low coral cover in a high-CO₂ world. *J Geophys Res* **110**, 1-9.
- Hoffmann, A. A. and Parsons, P. A.** (1991). Evolutionary genetics and environmental stress: Oxford Univ. Press.
- Jackson, C. R.** (2004). An atlas of internal solitary-like waves and their properties. Alexandria, Virginia: Global Ocean Associates.
- Jokiel, P. L. and Coles, S. L.** (1977). Effects of temperature on the mortality and growth of Hawaiian reef corals. *Mar Biol* **43**, 201-208.
- Jones, R. J., Hoegh-Guldberg, O., Larkum, A. W. D. and Schreiber, U.** (1998).

- Temperature-induced bleaching of corals begins with impairment of the CO₂ fixation mechanism in zooxanthellae. *Plant Cell Environ* **21**, 1219-1230.
- Keren, G. and Lewis, C.** (1993). A handbook for data analysis in the behavioral sciences. New York: Erlbaum.
- Krämer, W. E., Caamaño-Ricken, I., Richter, C. and Bischof, K.** (2012). Dynamic regulation of photoprotection determines thermal tolerance of two phylotypes of Symbiodinium clade A at two photon fluence rates. *Photochem Photobiol* **88**, 398-413.
- Lasker, H. R.** (1979). Light dependent activity patterns among reef corals: *Montastrea cavernosa* *Biol Bull (Woods Hole)* **156**, 196-211.
- Lasker, H. R.** (1981). Phenotypic variation in the coral *Montastrea cavernosa* and its effects on colony energetics. *Biol Bull (Woods Hole)* **160**, 292-302.
- Lea, D. W., Pak, D. K. and Spero, H. J.** (2000). Climate impact of late Quaternary Equatorial Pacific sea surface temperature variations. *Science* **289**, 1719-1724.
- Leichter, J. J., Deane, G. B. and Stokes, M. D.** (2005). Spatial and temporal variability of internal wave forcing on a coral reef. *J Phys Oceanogr* **35**, 1945-1962.
- Lesser, M. P. and Shick, J. M.** (1989). Effects of irradiance and ultraviolet radiation on photoadaptation in the Zooxanthellae of *Aiptasia pallida* primary production, photoinhibition, and enzymic defenses against oxygen toxicity. *Mar Biol* **102**, 243-255.
- Levy, O., Dubinsky, Z. and Aчитuv, Y.** (2003). Photobehavior of stony corals: responses to light spectra and intensity. *J Exp Biol* **206**, 4041-4049.
- Levy, O., Mizrahi, L., Chadwick-Furman, N. E. and Aчитuv, Y.** (2001). Factors controlling the expansion behavior of *Favia fava* (Cnidaria: Scleractinia): Effects of light, flow, and planktonic prey. *Biol Bull (Woods Hole)* **200**, 118-126.
- Levy, O., Dubinsky, Z., Aчитuv, Y. and Erez, J.** (2006). Diurnal polyp expansion behavior in stony corals may enhance carbon availability for symbionts photosynthesis. *J Exp Mar Biol Ecol* **333**, 1-11.
- Lewis, J. B. and Price, W. S.** (1975). Feeding mechanisms and feeding strategies of Atlantic reef corals. *J Zool (Lond)* **176**, 527-544.
- Lough, J. M.** (1994). Climate variation and El Niño-Southern Oscillation events on the Great Barrier Reef: 1958 to 1987. *Coral Reefs* **13**, 181-185.
- Martin, P. and Bateson, P.** (2007). Measuring behaviour. Cambridge: Cambridge University Press.
- Mayfield, A. B., Chan, P.-H., Putnam, H. M., Chen, C.-S. and Fan, T.-Y.** (2012). The effects of a variable temperature regime on the physiology of the reef-building coral *Seriatopora hystrix*: results from a laboratory-based reciprocal transplant. *J Exp Biol* **215**, 4183-4195.
- McFarlane, I. D.** (1978). Multiple conducting systems and the control of behaviour in the brain coral *Meandrina meandrites* (L.). *Proc R Soc Biol Sci Ser B* **200**, 193-216.
- Middlebrook, R., Hoegh-Guldberg, O. and Leggat, W.** (2008). The effect of thermal history on the susceptibility of reef-building corals to thermal stress. *J Exp Biol* **211**, 1050-1056.
- Muscatine, L., Grossman, D. and Doiño, J.** (1991). Release of symbiotic algae by tropical sea anemones and corals after cold shock. *Mar Ecol Prog Ser* **77**, 233-243.
- Naseer, A. and Hatcher, B. G.** (2000). Assessing the integrated growth response of coral reefs to monsoon forcing using morphometric analysis of reefs in Maldives. *Proc 9th Int Coral Reef Symp* **1**, 75-80.
- Osborne, A. R. and Burch, T. L.** (1980). Internal solitons in the Andaman Sea. *Science* **208**, 451-460.
- Palardy, J. E., Grottoli, A. G. and Matthews, K. A.** (2005). Effects of upwelling, depth, morphology and polyp size on feeding in three species of Panamanian corals. *Mar Ecol Prog*

Ser **300**, 79-89.

Pandolfi, J. M. (1996). Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea: constancy during global change. *Paleobiology* **22**, 152-176.

Pearson, P. N. and Palmer, M. R. (2000). Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature* **406**, 695-699.

Phongsuwan, N. and Chansang, H. (1992). Assessment of coral communities in the Andaman Sea (Thailand). *Proc 7th Int Coral Reef Symp* **1**, 114-121.

Porter, J. W. (1976). Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building coral. *Am Nat* **110**, 731-742.

Putnam, H. M. and Edmunds, P. J. (2011). The physiological response of reef corals to diel fluctuations in seawater temperature. *J Exp Mar Biol Ecol* **396**, 216-223.

Roder, C., Fillinger, L., Jantzen, C., Schmidt, G. M., Khokiattiwong, S. and Richter, C. (2010). Tropic response of corals to large amplitude internal waves. *Mar Ecol Prog Ser* **412**, 113-128.

Roder, C., Jantzen, C., Schmidt, G., Kattner, G., Phongsuwan, N. and Richter, C. (2011). Metabolic plasticity of the corals *Porites lutea* and *Diploastrea heliopora* exposed to large amplitude internal waves. *Coral Reefs* **30**, 57-69.

Ruppert, E. E., Fox, R. S. and D., B. R. (2004). Invertebrate zoology: a functional evolutionary approach. London: Thomson, Brooks/Cole.

Saxby, T., Dennison, W. C. and Hoegh-Guldberg, O. (2003). Photosynthetic responses of the coral *Montipora digitata* to cold temperature stress. *Mar Ecol Prog Ser* **248**, 85-97.

Schlichter, D. and Brendelberger, H. (1998). Plasticity of the scleractinian body plan: Functional morphology and trophic specialization of *Mycedium elephantotus* (Pallas, 1766). *Facies* **39**, 227-241.

Schmidt, G. M., Phongsuwan, N., Jantzen, C., Roder, C., Khokiattiwong, S. and Richter, C. (2012). Coral community composition and reef development at the Similan Islands, Andaman Sea, in response to strong environmental variations. *Mar Ecol Prog Ser* **456**, 113-126.

Schreiber, U., Schliwa, U. and Bilger, W. (1986). Continuous recording of photochemical and non-photochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. *Photosynth Res* **10**, 51-62.

Sebens, K. P. (1987). Coelenterata. In *Animal energetics*, vol. 1. Protozoa through Insecta (eds. T. J. Pandian and F. J. Vernberg), pp. 55-120. California: Academic Press.

Sebens, K. P. and DeRiemer, K. (1977). Diel cycles of expansion and contraction in coral reef anthozoans. *Mar Biol* **43**, 247-256.

Sebens, K. P., Witting, J. and Helmuth, B. (1997). Effects of water flow and branch spacing on particle capture by the reef coral *Madracis mirabilis* (Duchassaing and Michelotti). *J Exp Mar Biol Ecol* **211**, 1-28.

Shashar, N., Kinane, S., Jokiel, P. L. and Patterson, M. R. (1996). Hydromechanical boundary layers over a coral reef. *J Exp Mar Biol Ecol* **199**, 17-28.

Shick, J. M., Brown, W. I., Dolliver, E. G. and Kayar, S. R. (1979). Oxygen uptake in sea anemones: Effects of expansion, contraction, and exposure to air and the limitations of diffusion. *Physiol Zool* **52**, 50-62.

Tchernov, D., Gorbunov, M. Y., de Vargas, C., Narayan Yadav, S., Milligan, A. J., Häggblom, M. and Falkowski, P. G. (2004). Membrane lipids of symbiotic algae are diagnostic of sensitivity to thermal bleaching in corals. *Proc Natl Acad Sci U S A* **101**, 13531-13535.

Veron, J. E. N. (1995). Corals in Space and Time. Sydney: UNSW Press.

Vlasenko, V. and Stashchuk, N. (2007). Three-dimensional shoaling of large-amplitude

internal waves. *J Geophys Res* **112**, C11018.

Wall, M., Schmidt, G. M., Janjang, P., Khokiattiwong, S. and Richter, C. (2012). Differential impact of monsoon and large amplitude internal waves on coral reef development in the Andaman Sea. *PLoS ONE* **7**, e50207.

Warner, M. E., Fitt, W. K. and Schmidt, G. W. (1996). The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae in hospite from four different species of reef coral: a novel approach. *Plant Cell Environ* **19**, 291-299.

Warner, M. E., Fitt, W. K. and Schmidt, G. W. (1999). Damage to photosystem II in symbiotic dinoflagellates: A determinant of coral bleaching. *Proc Natl Acad Sci U S A* **96**, 8007-8012.

Table 1. Abiotic characteristics of the seawater for each experiment. Flow rate: Low = 2 cm/s, High= 10 cm/s. Fragment origin: E = East; W = West. LAIW = Large amplitude internal wave. Values are given as mean (S.D.).

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

Table 2. Three-way ANOVA after model simplification on the effects of nubbin origin (W and E), food and treatment (control, partial LAIW-Temp., partial LAIW-pH and full LAIW-Temp. & pH) on the polyp expansion behavior of *Porites lutea*. Significance levels: (*) $0.05 > p \geq 0.01$, (**) $0.01 > p \geq 0.001$, (***) $p \leq 0.001$.

Source of variation	Sum of squares	DF	Mean square	F	<i>p</i>
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*

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. 1 = control; 2 = partial LAIW-Temp.; 3 = partial LAIW-pH; 4 = full LAIW-Temp. & pH (see Table 1 for seawater quality data). Results can be seen in Fig. 4, upper asterisks. Significance levels: (*) $0.05 > p \geq 0.01$, (**) $0.01 > p \geq 0.001$, (***) $p \leq 0.001$.

Comparison	Difference	Lower limit	Upper limit	<i>p</i>
1 vs. 2	-0.249	-0.428	-0.07	0.002**
1 vs. 3	0.183	0.004	0.362	0.042*
1 vs. 4	-0.309	-0.488	-0.13	0.000***

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. East (E), West (W). 1 = control; 2 = partial LAIW-Temp.; 3 = partial LAIW-pH; 4 = full LAIW-Temp. & pH (see Table 1 for seawater quality data). Results can be seen in Fig. 4 lower asterisks. Significance levels: (**) $0.01 > p \geq 0.001$, (***) $p \leq 0.001$.

Origin	Comparison	Difference	Lower limit	Upper Limit	<i>p</i>
E	1 vs. 2	-0.364	-0.663	-0.064	0.006**
	1 vs. 3	0.213	-0.086	0.512	0.367
	1 vs. 4	-0.473	-0.772	-0.173	0.000***
W	1 vs. 2	-0.134	-0.433	0.165	0.868
	1 vs. 3	0.153	-0.146	0.453	0.767
	1 vs. 4	-0.145	-0.444	0.154	0.814

Table 5. Repeated Measures ANOVA with interactions after model simplification between fragment origin and temperature on *Fv/Fm* of *Porites lutea*. Significance levels: (*) $0.05 > p \geq 0.01$, (**) $0.01 > p \geq 0.001$.

Source of Variation	Sum of squares	DF	Mean square	F	<i>p</i>
Origin	0.791	1	0.791	6.67	0.011*
Temperature	0.088	1	0.088	0.74	0.391
Origin × Temperature	0.958	1	0.958	8.08	0.006**

Fig. 1. A) Map of the Andaman Sea off the western coast of Thailand, with inset showing the direction of the LAIW formed along the Andaman-Nicobar Island Arc (dashed arrows) (Mainland: 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 bar represents 4 km. Black dots represent the locations of the nubbin collection for the laboratory experiments. C) Results of the preliminary *in situ* experiment showing polyp expansion behavior 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.

Fig. 2. Photographs illustrating the percentage of polyp expansion of colonies of *Porites lutea*. The 5 levels were designated by Lasker (1979). The different scores are the visual average for the entire coral nubbin in the treatment. Polyp size = ~ 0.1 cm. See text for complete description of the expansion states.

Fig. 3. Mean of the polyp expansion percentage across colonies and flow regimes plotted at 10 min intervals for each experimental treatment over the experimental time: Control, pH (Partial LAIW-pH), temp. (Partial LAIW-Temp.) and full (Full LAIW-Temp. & pH). (W) Response to the treatments of colonies originated from the west island sides. (E) Response to the treatments of colonies originated from the east island sides (see Table 1 for seawater quality data). *Artemia nauplii* was added at min 90 in all experiments.

Fig. 4. Effect of large amplitude internal wave (LAIW) treatments; partial LAIW-Temp., partial LAIW-pH and full LAIW-Temp. & pH on the polyp expansion behavior of W (west) and E (east) *Porites lutea* nubbins versus the control group (see Table 1 for seawater quality data). Vertical lines = standard error of the mean. Upper (*): General effect of the treatment against the control; lower (*) correspond to the origin differences within a treatment against the respective control. Significance levels: (*) $0.05 > p \geq 0.01$, (**) $0.01 > p \geq 0.001$, (***) $p \leq 0.001$.

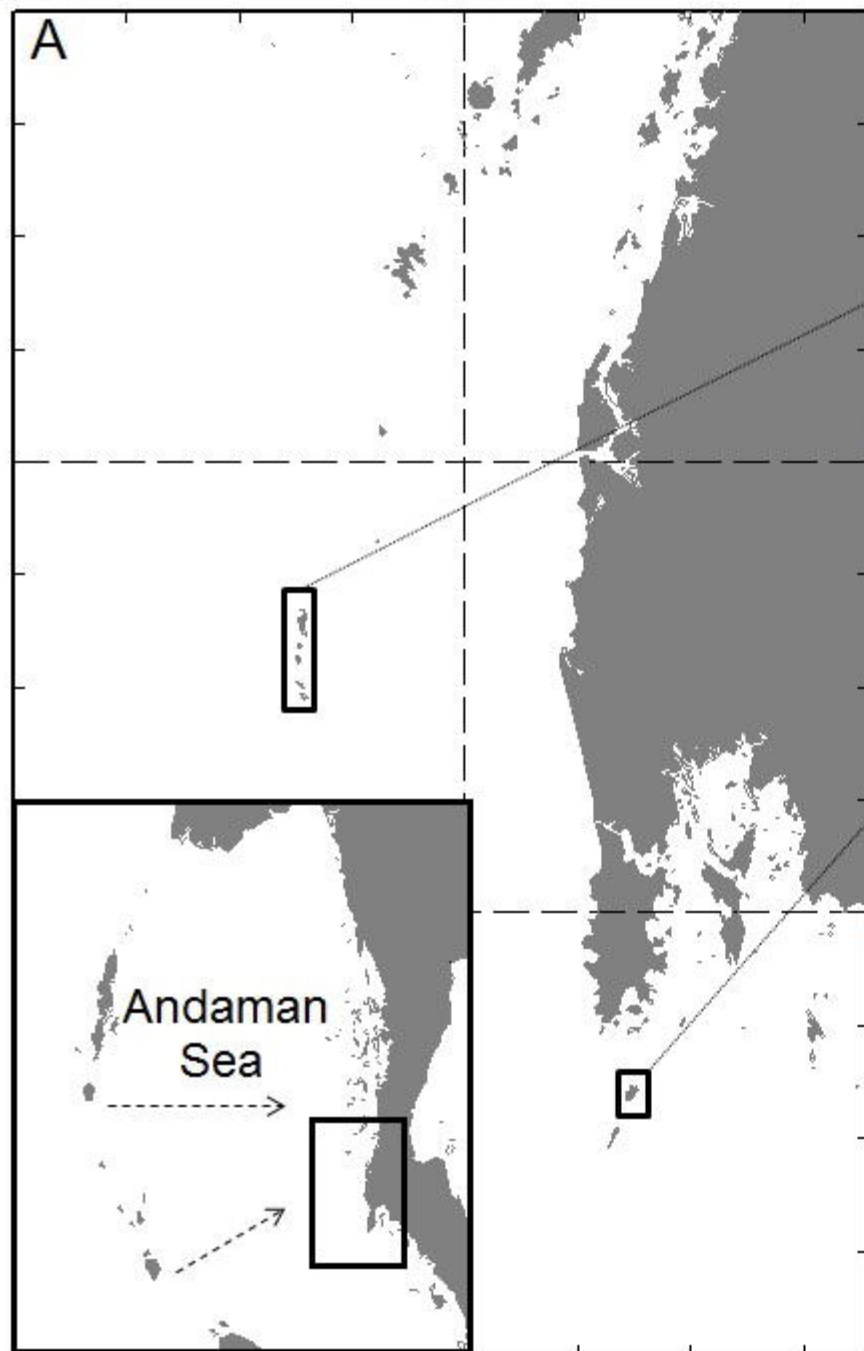
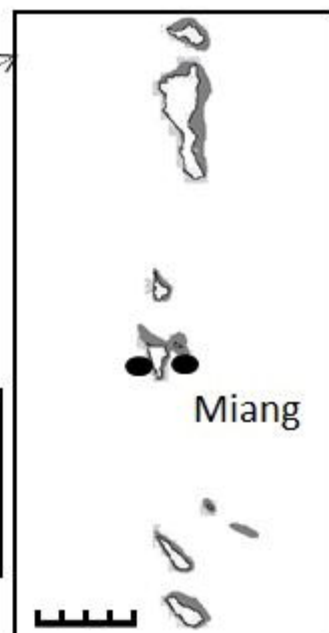
Fig. 5. Maximum quantum yield of photosystem II (F_v/F_m) of *Symbiodinium* within *Porites lutea* across two temperatures and between two sides of nubbin origin (W = west and E = east). Vertical lines represent standard error. Control temp. \pm SD: 29.11 ± 0.62 °C; LAIW

Temp.: 19.48 ± 0.56 °C. Letters on top of the bars represent Tukey's honestly significant difference (HSD) groups ($\alpha \leq 0.05$).

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. (W) Response of the nubbins originated from the west island sides and (E) response of the nubbins originated from the east sides. Black: control temp. \pm S.D. = 29.11 ± 0.62 °C; Grey: LAIW Temp. = 19.48 ± 0.56 °C. Vertical lines = standard error.

97° E

98° E

**B****C**