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Trophic response of corals to large amplitude internal waves

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ABSTRACT: The trophic response of the scleractinian coral *Pocillopora meandrina* (Dana, 1846) to large amplitude internal waves (LAIW) was investigated in the Andaman Sea. Corals living on the western sides of the Similan Islands (Thailand) exposed to LAIW showed significantly higher biomass and protein content than sheltered corals on the eastern sides. LAIW-exposed corals were also more heterotrophic, displaying lower $\delta^{13}C$ ratios in their tissues and higher rates of survival in artificial darkness compared to sheltered counterparts. Heterotrophic nutrition in concert with photosynthesis leads to higher energy reserves in corals from LAIW-exposed reefs, making them more resilient to disturbance. As these differences in trophic status are due to LAIW-enhanced fluxes of organic matter, LAIW may play an important role in supporting coral metabolism and survival in these monsoon beaten reefs.

KEY WORDS: Large amplitude internal waves · Corals · Heterotrophic plasticity · Current regime · *Pocillopora meandrina* · Andaman Sea

INTRODUCTION

The trophic response of corals to natural and anthropogenic stressors has been addressed in several studies (Anthony 2000, Palardy et al. 2005, Anthony 2006, Rodrigues & Grottoli 2006, Borell et al. 2008, Palardy et al. 2008). Although most reef corals are functionally mainly photoautotrophic, deriving the bulk of their energy from photosynthesis (Franzisket 1969, Muscatine & Porter 1977), heterotrophy can supply 11 to 46% of the coral's daily carbon requirements (Houlbrèque & Ferrier-Pagès 2009), and >100% of daily carbon requirements in bleached corals (Palardy et al. 2008). Corals have been traditionally viewed as planktivores by virtue of their armature of tentacles and stinging nematocysts (Yonge 1930, Lewis & Price 1975). However, their diet comprises a much wider range of food including microphytoplankton (Glynn 1973), nano- and picoplankton (Ferrier-Pagès et al. 1998, Houlbrèque et al. 2004), bacteria (Sorokin 1973, Bak et al. 1998), dissolved organic matter (Sorokin 1973, Grover et al. 2008), detritus and organic matter laden sediments (Anthony 2000).

To detect and quantify the importance of photoauto- vs. heterotrophy in coral metabolism, stable isotopes have been established as a useful indicator (Muscatine et al. 1989, Grottoli 2002, Swart et al. 2005). The $\delta^{13}C$ ratio of the coral host tissue is the combined result of photosynthetically derived products and nutritional inputs from allochthonous sources (Muscatine et al. 1989). The ratio depends on the fractionation potential of the zooxanthellae, the consequential isotopic signature of their translocates, and the signature of heterotrophic carbon. The $\delta^{13}C$ ratio in corals is higher when photosynthetic rates are high and the internal carbon pool is depleted (Muscatine et al. 1989). It decreases with decreasing light at increasing depths in response to a decrease in photosynthesis and the increased proportionate heterotrophic uptake of isotopically lighter zooplankton and other oceanic particulate and dis-

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solved organic materials (Muscatine et al. 1989, Grottoli 2002).

Along with photosynthesis, heterotrophy enhances skeletal (Houlbrèque et al. 2003) and tissue growth (Ferrier-Pagès et al. 2003) by building up energy stores including lipids (Anthony 2006, Treignier et al. 2008) and proteins (Ferrier-Pagès et al. 2003, Houlbrèque et al. 2003). Heterotrophy has been shown to support coral photosynthesis (Grottoli 2002, Ferrier-Pagès et al. 2003, Borell et al. 2008) and resilience to stresses such as turbidity (Anthony 2006), warming (Borell et al. 2008) and bleaching (Grottoli et al. 2006, Palardy et al. 2008). Although active feeding does not generally constitute the dominant carbon source for zooxanthellate corals, it may reduce temporary energy deficits (Anthony 2000) so that corals with a high capability to heterotrophically assimilate carbon may be more effective in surviving multiple bleaching events and become dominant in future reefs (Grottoli et al. 2006).

The relative proportion of heterotrophy in coral metabolism may vary markedly between species (Grottoli et al. 2006), and has been documented in several studies. For example, Wellington (1982) observed that the branching coral *Pocillopora damicornis* grew independent of zooplankton supply, and was more markedly affected by shading than the massive coral *Pavona clavus*. Sebens & Johnson (1991) documented higher zooplankton capture rates by *Madracis decactis* with increasing current strength, but not by *Meandrina meandrites*. Rodrigues & Grottoli (2006) showed that the $\delta^{13}C$ ratios of *Montipora capitata* host tissue decreased when bleached because of increased heterotrophic feeding, while *Porites compressa* did not alter its nutrition. Moreover, Palardy et al. (2008) observed that the feeding response to one disturbance may vary significantly between different coral species.

The importance of heterotrophic feeding in coral metabolism may further vary between environments (Palardy et al. 2005). Decreasing light and photosynthesis (Muscatine et al. 1989, Palardy et al. 2008) have been shown to increase coral feeding in deep (Ferrier-Pagès et al. 1998, Palardy et al. 2005) and turbid environments (Anthony 2000, Anthony 2006). Coral feeding was also shown to be stimulated by high concentrations of dissolved organic matter (Houlbrèque et al. 2004) and zooplankton prey (Ferrier-Pagès et al. 1998, Ferrier-Pagès et al. 2003), and to be influenced by prey behavior (Palardy et al. 2005), coral feeding effort (Palardy et al. 2005, Palardy et al. 2008) and water currents (Sebens et al. 1998).

Internal waves are ubiquitous in the ocean (Jackson 2004) and propagate along the density interface (pycnocline) between warm surface and cold, nutrient-rich deep waters. Until now, these subsurface waves are poorly investigated as a source of ambient variability in coastal currents, turbidity and plankton (Pineda 1991, Leichter et al. 1996) and their potential effect on the trophic state of corals is virtually unexplored. The Andaman Sea features nonlinear internal waves of extraordinary amplitude, displacing the depth of the pycnocline by >80 m (Perry & Schimke 1965, Osborne & Burch 1980). Because these large amplitude internal waves (LAIW) are tidally generated, travel over long distances, and disintegrate into wave trains over shoaling bottoms (Vlasenko & Stashchuk 2007), reefs located in the swash area of LAIW are potentially subjected to frequent disturbances of the physico-chemical environment. So far, it is not known if and to what extent turbulent boluses generated by shoaling LAIW (Vlasenko & Stashchuk 2007) that advect cold, nutrient-rich waters upslope affect the trophic state of corals in LAIW environments.

Here, we combine observational data on the biomass, protein and stable isotope content of LAIW-exposed and -sheltered corals with *in situ* light-exclusion and transplantation experiments. The goal is to explore the role of LAIW on the trophic state of corals in response to the combined effect of increased currents (Sebens et al. 1998, Nakamura et al. 2003), fluxes of particulate matter (Anthony 2000) and plankton (Wellington 1982, Ferrier-Pagès et al. 1998, Ferrier-Pagès et al. 2003), along with lack of photosynthesis (Rodrigues & Grottoli 2006).

MATERIALS AND METHODS

Study site. The Similan Islands located 60 km off the west coast of Thailand consist of 9 granite islands (Fig. 1). The west sides (W) of the islands feature barren rock and scattered corals, the east sides (E) dense coral reefs (Chansang et al. 1999). The asymmetry in coral distribution corresponds to the western exposure of the islands to the swash zone of breaking LAIW generated near Sumatra and the Andaman-Nicobar islands (Jackson 2004, Vlasenko & Alpers 2005). Upslope propagating density intrusions emanate from near the shelf break (Vlasenko & Hutter 2002, Vlasenko & Stashchuk 2007) and are evident as frequent temperature drops and overall lower mean temperatures on the LAIW-exposed W sides (LAIW+) of the islands compared to the sheltered E sides (LAIW–) (G. M. Schmidt et al. unpubl.).

Coral sampling and experimental design. The scleractinian coral *Pocillopora meandrina* (Dana, 1846), which is a common species on both LAIW+ and LAIW– reefs of the Similan Islands (G. M. Schmidt et al. unpubl.), was chosen as the model organism for the study.

Coral fragments: To detect differences between sides (LAIW+ vs. LAIW–) and within sides of the differ-

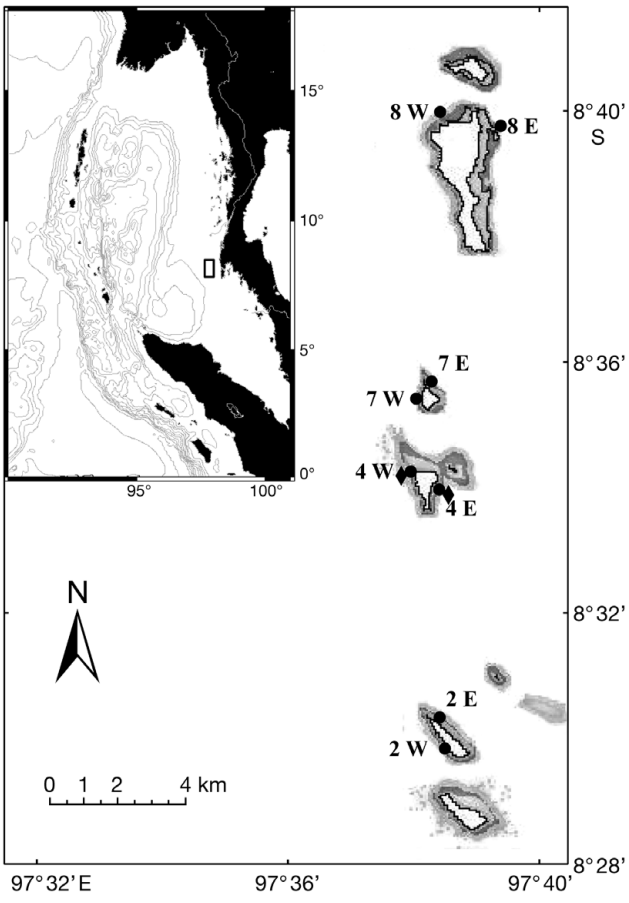

Fig. 1. The Similan Islands in the Andaman Sea off the coast of Thailand. Experimental sites (●) on the W (LAIW+) and E (LAIW–) of Island #4 (Koh Miang Island) are also locations of water and near-reef plankton sampling. (♦) Off-reef plankton sampling sites (on Island #4). Samples used for the multi-dimensional analysis were collected at all indicated reefs (2W, 2E, 4W, 4E, 7W, 7E, 8W, 8E). LAIW+/LAIW–: exposed/not exposed to large amplitude internal waves

ent islands (#2, 4, 7 and 8), fragments of *Pocillopora meandrina* (one per colony) were collected randomly (1 to 12 fragments per site). Collection was done at depths between 5 and 25 m from various LAIW+ (18 fragments) and LAIW– (21 fragments) reefs of the Similan Islands (Fig. 1) between 20 February and 24 March 2008. Fragments were placed in Ziploc bags (10 × 15 cm, max. 4 ml residual water) and transported to the laboratory for immediate processing.

Light-exclusion experiment: The light-exclusion experiment (Fig. 2A) was conducted from 20 February to 24 March 2008. On each side of Koh Miang (Similan Island #4), 3 donor colonies of *Pocillopora meandrina* were collected at a depth of 20 m. From each colony, 21 fragments were clipped off and attached to 2 rails (control and experimental rail) made out of plastic wire by clamping the base of the fragment into cut out holes of the rail. Because branch spacing has an impact on flow patterns within the coral colony and, hence, on feeding capacity (Sebens et al. 1997), only single undivided branches were used in the experiment. Fragment-bearing rails were moored to a PVC frame and left on the reef to recover for 1 mo. At the onset of the experiment, triplicate start fragments (one per donor colony) were collected and the rails (each now bearing 10 fragments) placed in perspex flow pipes. A 3 × 2 stack of these flow pipes (Fig. 2A) was mounted on a rack equipped with a current vane. The vane allowed the setup to rotate freely around an iron rod anchored into the sediment (20 m depth), so that the upstream openings of the tubes (50 cm length, 10 cm diameter) were always facing into the current, ~1 m above the bottom. The drag of the chamber setup itself, as measured in repeat runs (n = 6) with fluorescent dye, was not found to have a significant effect on water velocity, reducing the ambient water flow by <5%. The upper row of translucent tubes held the control fragments (photosynthesis possible: PS+), while the lower row of tubes were shaded off with opaque foil (PS–), so that light levels near the fragments (measured with the light meter of a Diving-PAM) were below the compensation light intensity for photosynthesis (<5 µmol quanta m^{-2} s^{-1}). Sampling always took place before noon. Triplicate samples from controls and light-deprived fragments (1 fragment per tube) were collected at 6, 8, 10, 12, 14, 16, 20, 24, 28 and 32 d (LAIW–) or 33 d (LAIW+) after the onset of the experiments. Live fragments were placed into 10 × 15 cm Ziploc bags (max. 4 ml supernatant), transported to the laboratory and immediately processed. Dead fragments were recorded.

Transplantation experiment: Within the same timeframe (20 February to 24 March 2008), a cross-transplantation experiment (Fig. 2B) was conducted to detect changes in coral tissue composition due to transplantation. On each W (LAIW+) and E (LAIW–) Koh Miang reef, 3 additional donor colonies of *Pocillopora meandrina* were sampled. Sampling and fragment cultivation was identical to the light-exclusion experiment (but one fragment less on each rail). At experimental onset, triplicate start fragments (one per donor colony) were collected and the experimental rails (now each bearing 9 fragments) cross-transplanted between the W (LAIW+) and E (LAIW–) reefs. Rails transplanted from LAIW– to LAIW+ were subsequently exposed to higher flows of plankton, while rails transplanted in the opposite direction experienced lower food supplies compared to origin conditions. Control and cross-transplanted fragments were left anchored next to each other in the reef (20 m depth). Triplicate samples of control (Feed+) and feed-altered (transplanted from LAIW– to LAIW+: Feed++; transplanted from LAIW+

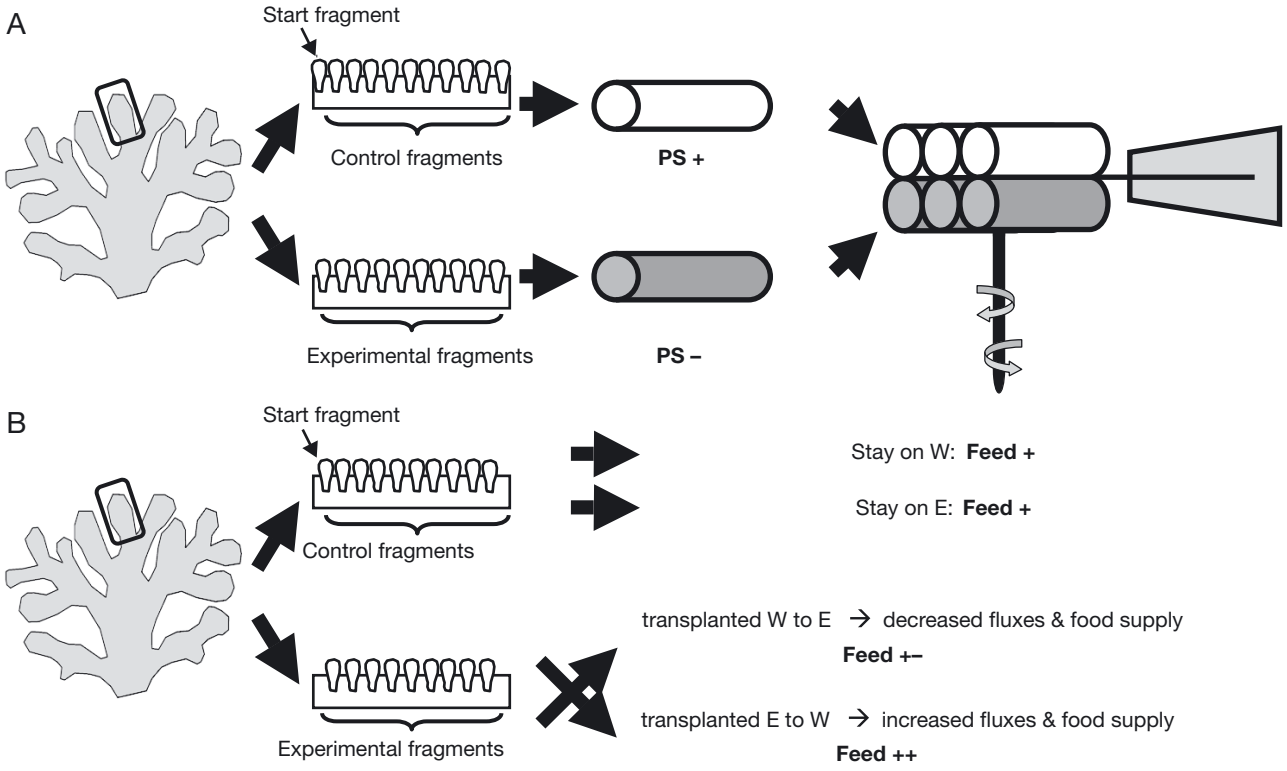

Fig. 2. Schematic representation of the experimental designs. (A) Light-exclusion experiment: 3 donor colonies per island side, each colony providing 21 fragments (1 start, 10 control and 10 light-deprived fragments); 1 chamber setup on each island side (W: LAIW+ and E: LAIW–) PS+/PS–: photosynthesis possible/not possible. (B) Transplantation experiment: 3 donor colonies per island side, each colony providing 20 fragments (1 start, 9 control and 9 transplanted fragments)

to LAIW–: Feed +–) fragments were then collected at 2, 4, 8, 12, 16, 20, 24, 28, 32 d (LAIW+) and 3, 5, 9, 13, 17, 21, 25, 29, 33 d (LAIW–) after the onset of the experiments. Collected fragments were placed into 10 × 15 cm Ziploc bags (max. 4 ml supernatant), transported to the laboratory and immediately processed.

Coral processing. For each fragment, the full set of parameters described below was analyzed. Coral tissue was removed from the skeleton using an airbrush and filtered seawater. After homogenization of the slurry, 6 ml aliquots were retained for zooxanthellae density counts and protein analysis, and 5 ml aliquots were GF/F (Whatman) filtered under 200 mm Hg vacuum (Millipore vacuum pump) and frozen for chlorophyll analysis.

Zooxanthellae densities: The total symbiont cell numbers were determined under a microscope (Leitz, 260× magnification) using a haemocytometer (Fuchs-Rosenthal). Concentrations were calculated on an areal basis as the mean of 6 replicate counts after correction for the homogenate volume and surface area of the coral fragment.

Chlorophyll a analysis: Chlorophyll was extracted by adding 90% acetone (~5 ml) to the thawed chlorophyll samples (Strickland & Parsons 1972); after cautious shaking, samples were incubated for 24 h at 4°C for chlorophyll extraction and centrifuged at high speed (10 000 × *g*, 30 s) to remove all particles in suspension before measurement (Szmant & Gassman 1990, Gardella & Edmunds 1999, Fitt et al. 2000). Chl *a* concentrations were determined spectrophotometrically (Shimadzu UV 1700, 1 nm slit) at 750 and 664 nm (Lorenzen 1967).

Protein content: Total protein content was determined based on Lowry et al. (1951) using a protein assay (DC Protein Assay Kit, Bio-Rad) and bovine serum albumin standards. Protein concentrations were measured spectrophotometrically (Shimadzu UV 1700, 1 nm slit) at 750 nm.

In the remaining slurry, zooxanthellae and host tissue were separated by centrifugation, and the host tissue was loaded (Millipore vacuum pump, ~100 mm Hg) on pre-combusted and pre-weighed GF/F (Whatman) filters and dried before further elemental and isotopic analyses (see below) (Muscatine et al. 1989, Grottoli et al. 2004, Swart et al. 2005). Fragment surface area was calculated using Simple Geometry (determining the geometric form that best resembles the

shape of the fragment and calculating its surface with respect to the geometric formula) to the nearest 0.05 mm and an approximation factor for *Pocillopora* as proposed by Naumann et al. (2009).

Total suspended matter, particulate and dissolved organic carbon. In the course of the experiment, during fragment collection and when possible once again in the afternoon, water samples (LAIW+: n = 19; LAIW–: n = 24) were taken close to the experimental setup by divers for subsequent analyses of total suspended matter (TSM), total particulate organic carbon (TPOC), and dissolved organic carbon (DOC). On several occasions, sampling occurred during LAIW passage, shortly before or after. Therefore, the temperature at the time of sampling was recorded (TidbiT v2, Onset, 1 min resolution and accuracy of <0.2°C). Water samples were taken with 1 l PE bottles, transported to the lab, filtered (Millipore vacuum pump, 200 mm Hg) on pre-combusted and pre-weighed GF/F (Whatman), dried for elemental analyses (see below) and weighed on a microbalance (Mettler, AT21 Comparator, 1 µg accuracy). Aliquots of the filtrates were transferred into pre-combusted glass vials and acidified with phosphoric acid (20%) to a pH of 2 before sealing and storage on ice. DOC concentrations were determined with a DOC/DIC analyzer (Rosemount DC-190) using a 10-point calibration with TOC standards (ULTRA Scientific).

Plankton. Plankton sampling was carried out only during the day. Concomitant with each fragment sampling, near-reef zooplankton was collected by SCUBA push net tows (0.25 m diameter steel frame with a 55 µm mesh and 1 m sleeve), swimming along a 40 m swath along the 20 m isobath at 0.5 to 1 m above the bottom. Mean temperature during sampling was recorded (TidbiT v2, Onset, 1 min resolution and accuracy of <0.2°C) to determine LAIW impact at the time of sampling. Samples were transferred to the laboratory where they were separated into different size classes (55, 100, 150, 200 and 300 µm) over a fractionation tower. The different size classes were collected (Millipore vacuum pump, 200 mm Hg) on pre-combusted and pre-weighed GF/F (Whatman) filters and dried for 12 h at 40°C. The dry mass of the plankton was determined gravimetrically using a microbalance (Mettler, AT21 Comparator, 1 µg accuracy). Clogging was not a problem at the low volumes (8 m^3) fished. Filtered volume was calculated using the swimming distance and the cross-sectional area of the net opening, assuming 100% filtration efficiency (Smith et al. 1968).

Pump-sampled off-reef zooplankton was collected from a boat anchored at 35 m depth in front of the LAIW+ and LAIW– face of Koh Miang (Fig. 1), with the intake hose being located in mid-water 15 m above the bottom and equipped with a temperature logger (TidbiT v2, Onset, 1 min resolution and accuracy of <0.2°C). Sampling was conducted by boat at 15 min intervals for 4 h, simultaneously on both island sides in the afternoon of the 11th, 17th, 21st and 25th of March 2008. Water was pumped through a plastic tube (6 cm diameter, 245 l min^{-1}) and filtered for 5 min through a 50 µm plankton net. Samples were divided in half using a Folsom-splitter; one subsample was preserved in formalin (5%) for taxonomic identification (data presented elsewhere), the other was filtered (Millipore vacuum pump, 200 mm Hg) on pre-combusted and pre-weighed GF/F (Whatman) filters. The latter subsample was dried (12 h at 40°C) for mass determination (Mettler microbalance, AT21 Comparator, 1 µg accuracy) prior to elemental analysis. The pumped volume was determined by assessing the number of seconds it took to fill an 8 l container (3 trials each) to be able to relate plankton values to volume.

Visual inspection of the samples showed no detectable damage to the plankton using either of the sampling procedures.

Elemental and isotopic analyses of coral tissue, total suspended matter and plankton. The total carbon and nitrogen contents of the coral tissue, as well as the particulate organic carbon content of the TSM (TPOC) and plankton (POC) were determined using an elemental analyzer (NA2100 Protein) calibrated against an elemental CHNS standard (LECO). Stable carbon isotope ratios ($\delta^{13}C$) were measured in a gas isotope ratio mass spectrometer (Flash 1112 Analyzer) relative to Pee Dee Belemnite standard. For the organic content of TSM (TPOC) and plankton (POC), the samples were acidified with 0.1 M HCl prior to analyses until all inorganic carbon was removed. Coral samples did not require acidification as tissue was obtained without contamination from skeletal material.

Currents and fluxes. Autonomous upward-looking Acoustic Doppler Current Profilers (ADCP) were deployed during the experiment in the vicinity of the flow chamber setups (RDI Teledyne Workhorse Sentinel, 600 kHz and 300 kHz on the W and E of Koh Miang, respectively) to measure the 3-D current field at 1 m vertical and 1 min temporal resolution (accuracy of 0.3 to 0.5% of the water velocity ±0.3 to 0.5 cm s^{-1}). Data stored in the flash memory of the instruments were downloaded after the experiment, imported into Matlab (rdradcp.m by R. Pawlowicz, University of British Columbia, http://www2.ocgy.ubc.ca/~rich/), and analyzed. Mean daily fluxes of near-reef and off-reef plankton (total and POC), TSM, TPOC and DOC were calculated by multiplying their concentrations with the average daily current speeds during samplings (averaged across 12 h prior to 12 h post sampling time).

Temperature. To record LAIW incidences during the experiment, temperature loggers (TidbiT v2, Onset) were deployed near the experimental setup. Temperature was logged at 1 min temporal resolution (accuracy of <0.2°C over 0 to 50°C) and data downloaded using HOBOware 2.2.

Statistical analyses. Data sets were tested for normality of distribution and homogeneity of variances using Kolmogorov-Smirnov and Levene's tests, respectively, transformed if necessary and subjected to parametric or nonparametric statistical analyses (below), as appropriate.

To detect spatial differences between island sides and among sides of the different islands based on coral tissue composition (zooxanthellae numbers, chlorophyll content, tissue carbon and nitrogen, protein concentrations and isotopic composition), we performed a 2-factorial permutational MANOVA (PERMANOVA, Anderson et al. 2008) using PRIMER v6 multivariate statistical software (Clarke & Gorley 2006). The PERMANOVA allowed us to test for significant differences based on similarity (using Euclidean distance) between island side and island number (nested in island side). Data were log-transformed prior to analysis to account for differences in unit sizes. As sampling constraints led to an imbalanced data set over depth and sites, depth differences were 'regressed out' by treating depth as a covariate and removing possible depth effects before testing for site differences (Anderson et al. 2008, Mirto et al. 2010); the low and unevenly distributed number of data was then compensated for by running a large number (n = 9999) of permutations of the residuals (Gonzalez & Manly 1998, Anderson & Ter Braak 2003). The randomly collected reef fragments and the start fragments of both time series experiments were included in this analysis.

For the time series data gained from fragments that were subjected to the light-exclusion (Day 6 to Day 32/33) and transplantation (Day 2 to Day 32/33) experiments, we developed general linear models to test for the factors 'treatment' (i.e. control, light-deprivation or transplantation; nested within the respective side, fixed), 'colony' (nested within treatment, random) and 'day' (over treatment time, fixed) (Satterthwaite 1946). Prior to model application, the residuals of all time series (i.e. for each parameter and colony) were tested for autocorrelation (Ljung & Box 1978) on as many lags (2 to a max. of 33 d) as possible to ensure the effectual independence of the data, despite repeated samplings of the same colony or rack. Significant differences between treatments and sides were determined using the Fisher LSD post-hoc test.

Differences in mortality during the light-exclusion experiment were tested with a survival analysis. The survivorship functions (Kaplan Meier curves) of the W and E sides were compared using Cox's *F*-test.

Water and plankton samples as well as fluxes were statistically tested for LAIW-exposure using Student's *t*-tests. Size distributions of near-reef plankton weight, organic content and isotopic signatures were tested using 1-way ANOVA. Pearson's correlation analyses with temperature were conducted to reveal possible relations between LAIW passage and TSM, TPOC, DOC or plankton concentrations.

LAIW-related W (LAIW+) and E (LAIW–) current differences were analyzed using Student's *t*-test after Box-Cox transformation of the data. Pearson's correlation analyses between temperature and current velocity, followed by Student's *t*-tests, were conducted to examine correlations and their statistical significance.

RESULTS

Temperature, currents, plankton, TSM, TPOC and DOC fluxes

The temperature time series showed strong differences between the LAIW+ and LAIW– sides of Koh Miang (Fig. 3A). Although the modal values were similar ($\Delta T < 0.2$°C), the LAIW+ face showed a violent spiking, with temperature drops of up to >4°C occurring at subtidal frequencies indicative of the passage of internal waves. The temperature drops were associated with surges in current velocities (Fig. 3A,B, $p < 0.001$ for LAIW+ and LAIW–), so that the overall mean current velocity was 30% stronger on the LAIW+ than on the LAIW– side of the island (0.1008 ± 0.0004 vs. 0.0772 ± 0.0003 m s^{-1}, $p < 0.001$).

The stronger currents resulted in significantly higher ($p < 0.001$ for all) TSM, TPOC, DOC and plankton fluxes (Fig. 4) on the LAIW+ side of the island. The composition of the near-reef plankton was not different between the LAIW+ and LAIW– (Fig. S1) sides, and the concentrations alone (means ± SEs in Table S1) of both near- or off-reef plankton and POC (Figs. S1 & S2), as well as the TSM, TPOC or DOC (Fig. S3), showed no detectable differences between island sides ($p > 0.05$). Correlations with temperature were not significant for any of the parameters ($p > 0.05$) except for the offshore abundance of plankton individuals (not for off-reef POC), where the correlation was negative ($r^2 = 0.33$; $p < 0.05$) due to 2 sampling events that occurred exactly within LAIW incidents.

Coral tissue

Coral tissue compositions were significantly different between the LAIW-exposed and LAIW-sheltered sides of the Similan Islands, but not among the LAIW+ and

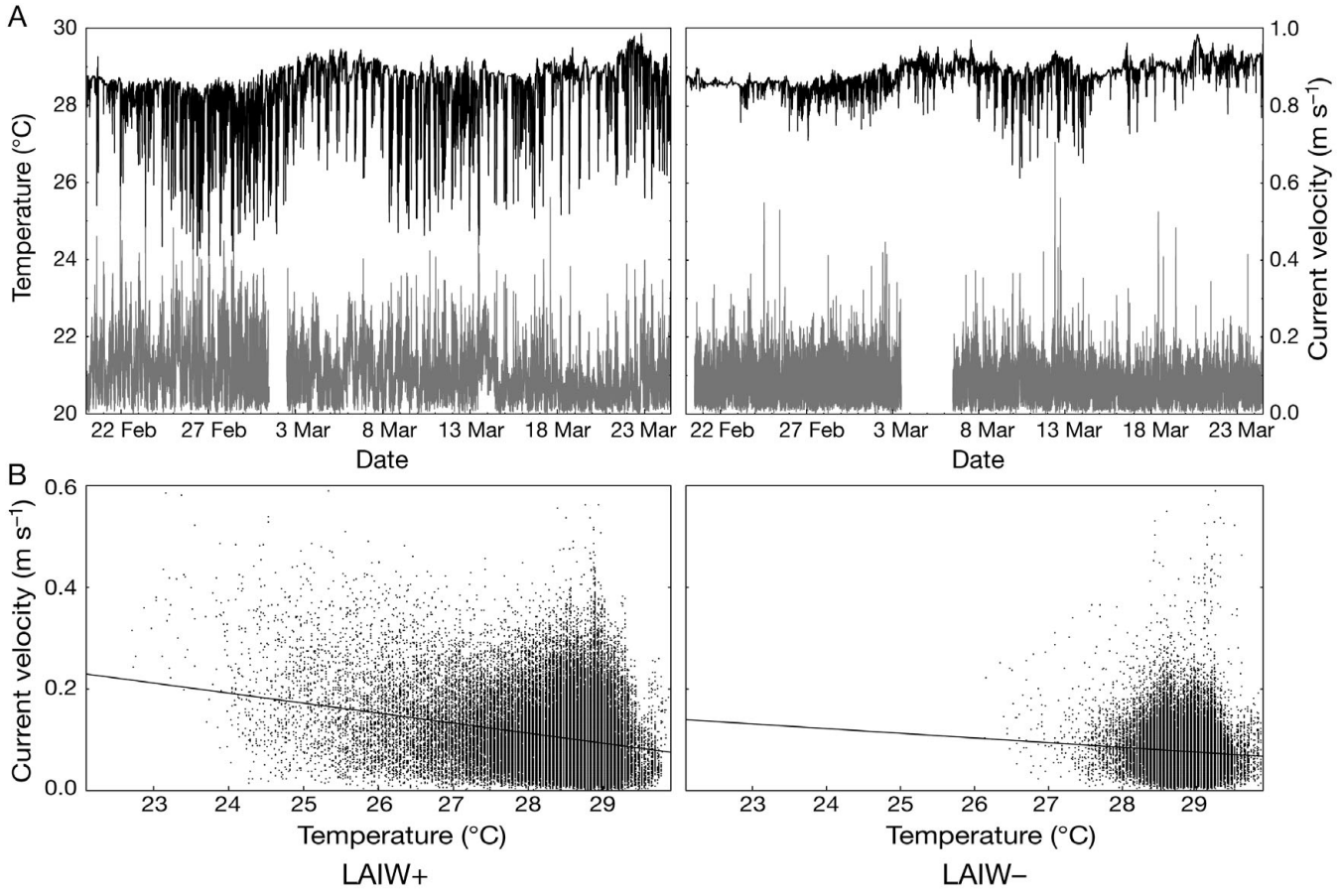

Fig. 3. Temperature and currents on the W (LAIW-exposed, left panels) and E (LAIW-sheltered, right panels) faces of Koh Miang. (A) Time series of temperature (black) and current velocity (gray) over the study period. Blank periods in the current data are due to recovery, cleaning and redeployment of the current meters. (B) Correlations between temperature and current velocity. Correlations are significant for both sides (both $p < 0.001$), but stronger for the W than for the E face ($r^2 = 0.06$ and 0.005, respectively)

LAIW– faces of the different islands (Table 1), as also illustrated in the multidimensional scaling (MDS) plot that showed overlap within but only little overlap between LAIW+ and LAIW– samples, respectively (Fig. 5).

In both experiments (Figs. 6 & 7), we were unable to detect bias due to repeated samplings from a limited number of donor colonies, i.e. we found no significant differences between the donor colonies and no trend over time (treat × day), whether in control or in experimental colonies (Tables 2 & 3).

In the light-exclusion experiment (Fig. 6), most tissue parameters were significantly higher for control corals (PS+) from the LAIW+ side of the island, compared to the LAIW– controls (Table 4). Zooxanthellae densities and chlorophyll concentrations were >40% higher, while tissue carbon, nitrogen and protein concentrations were >20% higher in LAIW-exposed corals (Fig. 6, Table 5). Only the differences in the carbon isotopic ratio of control host tissues were not significantly different between LAIW+ and LAIW– reefs (Tables 4 & 5). Under artificial darkness, ~80% of all zooxanthellae were lost on LAIW+ as well as on LAIW– corals and chl *a* decreased to a third of the original concentration on both sides (Fig. 6, Table 5). Moreover, losses in tissue carbon and nitrogen were

Table 1. Results of the 2-factorial (W vs. E and between Islands #2, 4, 7 and 8) PERMANOVA routine on the tissue composition of *Pocillopora meandrina* collected along the W and E sides of the different islands (nested within respective side) after removal of the covariate effect of depth. Tissue compositions of fragments from different islands do not show significant differences, while differences between the W and E sides are significant (*). df: degrees of freedom; SS: sum of squares; MS: mean square

Source of variance	df	SS	MS	*F*	p
Covariate: depth	1	0.802	0.8015	1.057	0.351
Side	1	7.878	7.878	3.129	0.032*
Island (side)	6	5.355	0.893	1.254	0.245
Residuals	42	29.9	0.712		
Total	50	43.935			

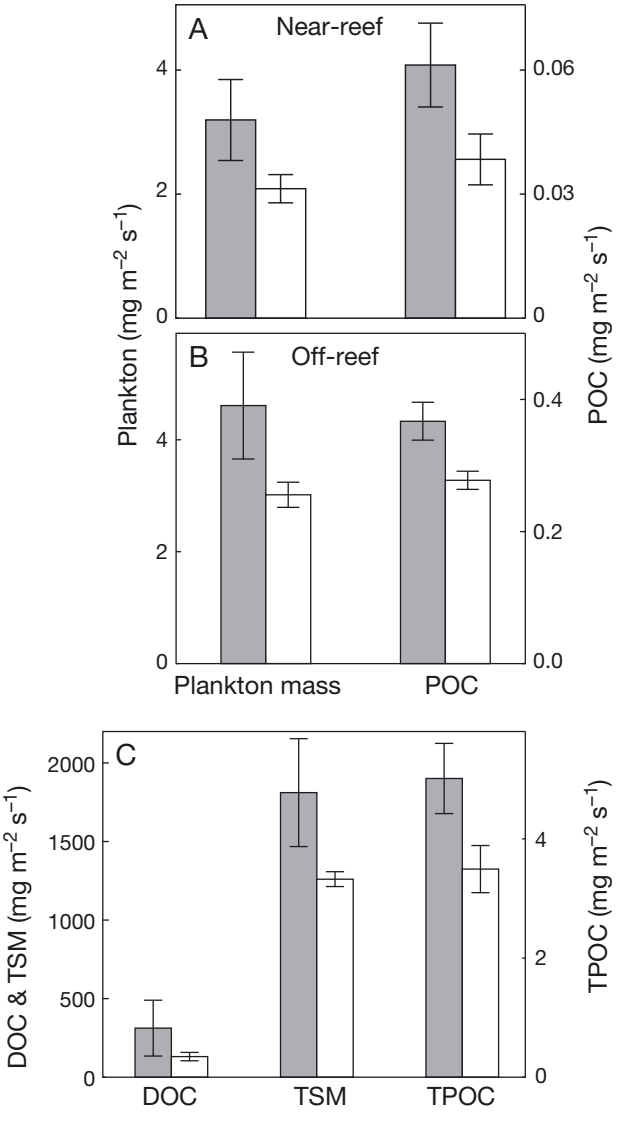

Fig. 4. Daily mean fluxes (±SE) of (A) near-reef plankton and its organic carbon fraction, (B) off-reef plankton and its organic carbon fraction, and (C) reef water dissolved organic carbon (DOC), total suspended matter (TSM) and total particulate organic carbon (TPOC) from LAIW+ (gray) and LAIW– (white) Koh Miang. All LAIW+ and LAIW– samples are significantly different

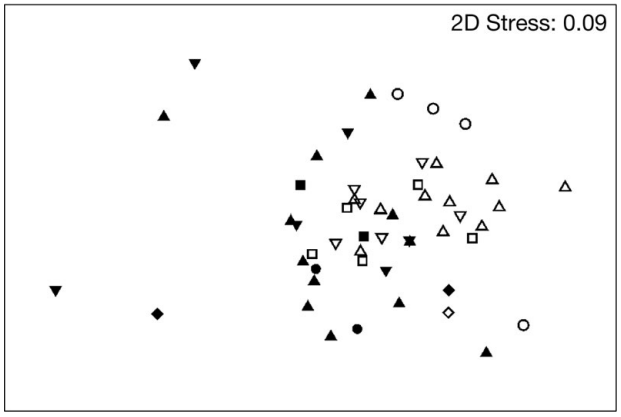

Fig. 5. MDS ordination of fragments from LAIW+ (n = 18 plus 6 start fragments from both experiments) and LAIW– (n = 21 plus 6 start fragments from both experiments) sides of all islands to illustrate the multi-dimensional similarities in coral tissue composition (in terms of zooxanthellae densities, chl *a*, tissue carbon and nitrogen contents, protein concentrations and isotopic carbon ratios) in a 2-D space. The Euclidean distance between 2 points represents their similarity. (■,□) Island #8; (●,○) Island #7; (▲,△) Island #4; (◆,◇) Island #2; (▼,▽) start fragments from the experimental setups. (◆,▼,▲,■,●) LAIW+ side fragments; (◇,▽,△,□,○) LAIW– side fragments. LAIW: large amplitude internal waves

>40%, while protein content was ~30% lower than in the control fragments in LAIW+ as well as LAIW– reefs (Fig. 6, Table 5). All depletions were significant when comparing controls and light-deprived fragments from both sides (Table 4). Although the protein content decreased on both sides, the decrease was less marked on the LAIW-exposed side, where protein levels of light-deprived fragments remained ~25% higher than their LAIW– counterparts and in the range of the LAIW– control fragments (Tables 4 & 5). During light exclusion (PS –), the LAIW– fragments changed their isotopic ratios only little (–0.28 ‰) (Fig. 6, Table 5), while the LAIW+ fragment ratios decreased significantly by –0.75 ‰. Consequently, light-deprived LAIW+ fragments differed significantly from light-deprived LAIW– fragments as well as from control fragments (PS +) from both sides (Fig. 6, Table 4).

LAIW-exposed corals also showed a much higher dark survival than LAIW-sheltered specimens (Fig. 8): all fragments survived well into the third week of the experiment, scarcely exceeding 10% total mortality at the end of the experiment. The LAIW– corals, in contrast, suffered heavy losses of ~40% of all light-deprived fragments. Mortality was already detected after 1 wk of the experiment and continued until total elimination of the fragments after 4 wk. Testing of the cumulative proportion of LAIW+ and LAIW– cases surviving up to the time of fragment collection (Fig. 8) showed that probabilities of survival were significantly higher for LAIW+ corals ($p < 0.001$).

In the transplantation experiment (Fig. 7), acclimatization to the new environment was rapid and occurred within the first few days after transplantation. All transplanted corals did not differ in tissue composition from control corals of their new environment (Fig. 7, Table 6). However, differences between the transplanted corals and their corresponding control colonies from the same donor colony (control corals from the other island side)

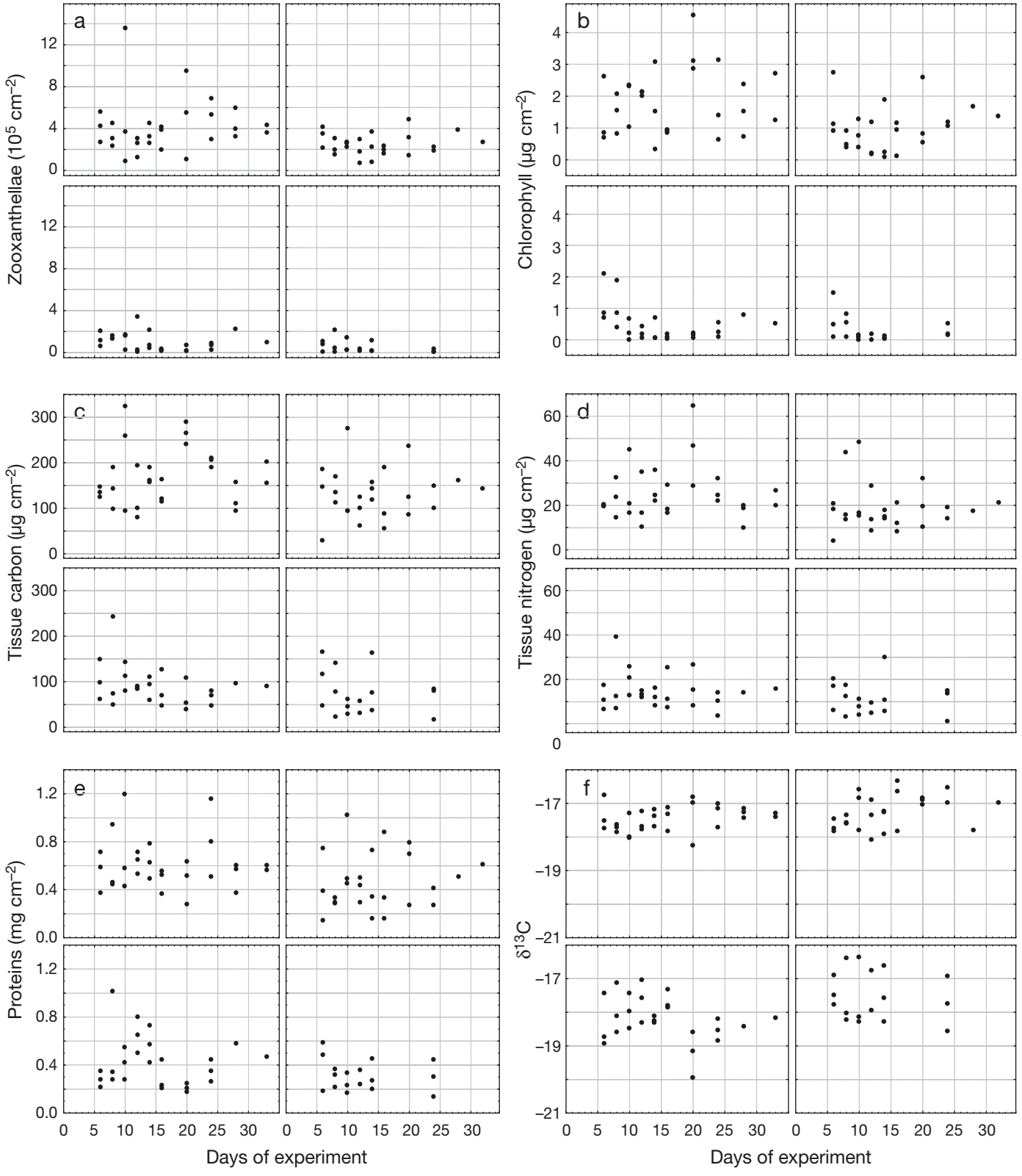

Fig. 6. Time-series of all tissue parameters. (a) Zooxanthellae densities, (b) chl content, (c) tissue carbon content, (d) tissue nitrogen content, (e) protein concentrations and (f) isotopic carbon ratios, measured in controls and light-deprived fragments from the W (LAIW+) and E (LAIW–) over the experimental period. Upper left: PS + (LAIW+); upper right: PS + (LAIW–); lower left: PS – (LAIW+); lower right: PS – (LAIW–). LAIW: large amplitude internal waves

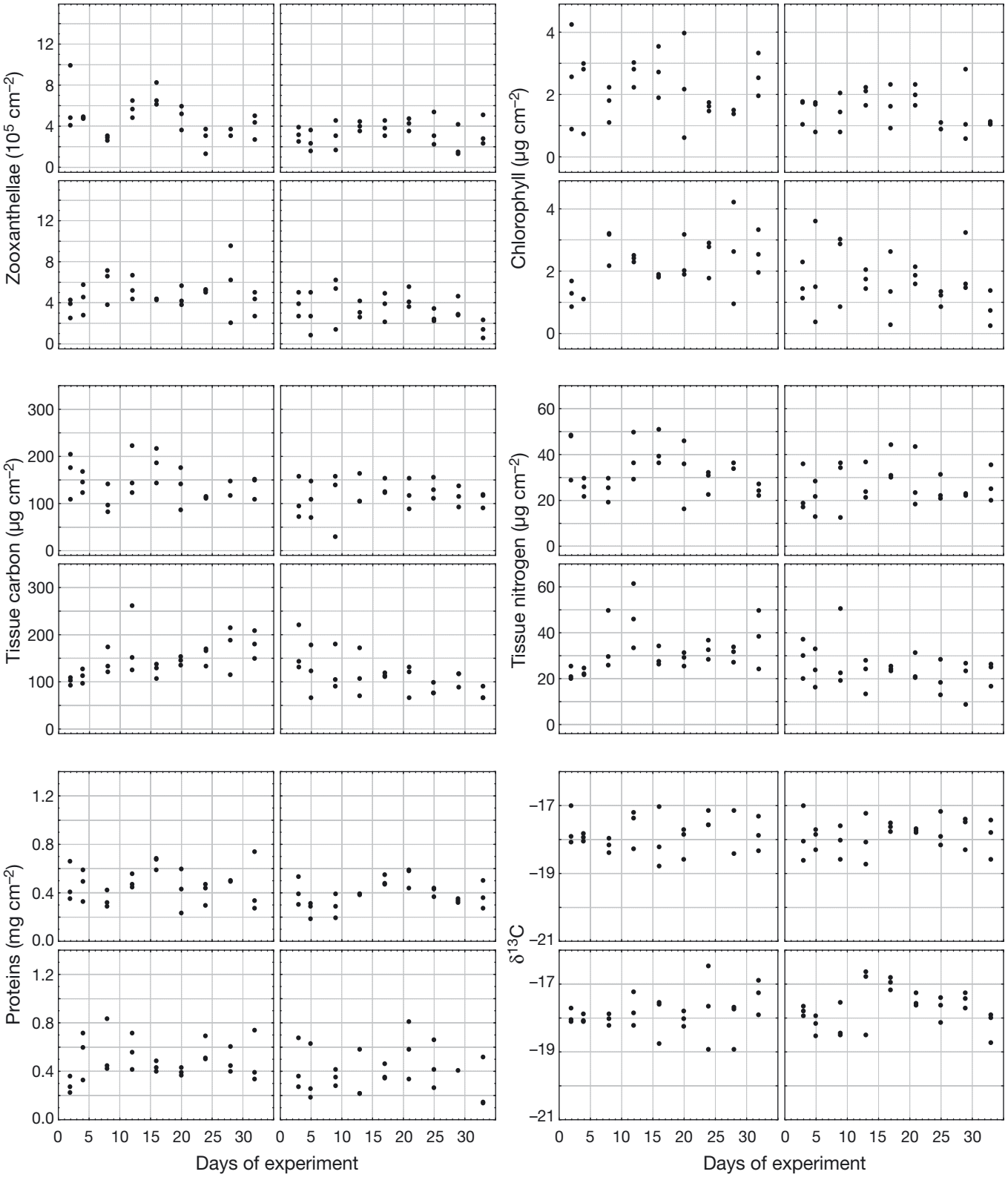

Fig. 7. Time-series of all tissue parameters. (a) Zooxanthellae densities, (b) chlorophyll content, (c) tissue carbon content, (d) tissue nitrogen content, (e) protein concentrations and (f) isotopic carbon ratios, measured in controls and feed-altered fragments from the W (LAIW+) and E (LAIW–) over the experimental period. Upper left: Feed+ (LAIW+); upper right: Feed+ (LAIW–); lower left: Feed++ (transplanted from LAIW– to LAIW+); lower right: Feed+– (transplanted from LAIW+ to LAIW–)

Table 2. Analysis of spatio-temporal variation in tissue parameters in *Pocillopora meandrina* fragments collected in a time series during a light-exclusion experiment. Compared are time series of control and light-deprived fragments exposed (LAIW+) or sheltered (LAIW–) from large amplitude internal waves (LAIW). df: degrees of freedom; MS: mean square; (*) significant p-values; ns: not significant

Source of variance		df	MS	*F*	p
Zooxanthellae cm^{-2}					
Intercept	Fixed	1	7.443×10^{11}	31.616	*
Treat (Side)	Fixed	2	1.702×10^{11}	6.618	*
Colony (Treat)	Random	4	1.419×10^{10}	0.552	ns
Treat × Day	Fixed	2	1.654×10^{10}	0.643	ns
Error		87	2.572×10^{10}		
Chl *a* (µg cm^{-2})					
Intercept	Fixed	1	14.865	29.184	*
Treat (Side)	Fixed	2	4.695	8.911	*
Colony (Treat)	Random	4	0.434	0.824	ns
Treat × Day	Fixed	2	0.914	1.735	ns
Error		87	0.527		
Tissue carbon (µg cm^{-2})					
Intercept	Fixed	1	261382.101	100.716	*
Treat (Side)	Fixed	2	11151.604	3.911	*
Colony (Treat)	Random	4	1497.650	0.525	ns
Treat × Day	Fixed	2	2853.269	1.001	ns
Error		87	2850.995		
Tissue nitrogen (µg cm^{-2})					
Intercept	Fixed	1	5964.492	64.522	*
Treat (Side)	Fixed	2	384.813	4.036	*
Colony (Treat)	Random	4	80.013	0.839	ns
Treat × Day	Fixed	2	7.389	0.078	ns
Error		87	95.337		
Protein (mg cm^{-2})					
Intercept	Fixed	1	3.857	95.532	*
Treat (Side)	Fixed	2	0.201	4.605	*
Colony (Treat)	Random	4	0.026	0.602	ns
Treat × Day	Fixed	2	0.008	0.190	ns
Error		87	0.044		
δ^{13}C (‰)					
Intercept	Fixed	1	5596.603	18468.703	*
Treat (Side)	Fixed	2	2.189	7.359	*
Colony (Treat)	Random	4	0.327	1.100	ns
Treat × Day	Fixed	2	1.064	3.577	ns
Error		87	0.297		

and between controls from LAIW+ and LAIW– were obvious. Zooxanthellae densities and chl *a* concentrations were both ~30 % higher, while tissue carbon and nitrogen contents were ~20 % elevated in LAIW+ corals compared to the significantly lower concentrations in LAIW– corals (Fig. 7, Tables 5 & 6). The corals that were transplanted from the LAIW– to the feed-enriched LAIW+ side (Feed++) ended up being significantly enriched in protein content (Fig. 7, Table 6) compared to the LAIW– controls or the fragments that were transplanted to the LAIW– side (Feed +–). Although the differences between LAIW+ control (Feed+) and LAIW– control (Feed+) or feed-deprived (Feed+–) corals were marginally insignificant (Table 6), protein content was ~20 % higher in the LAIW+ controls (Fig. 7, Table 5).

Table 3. Analysis of spatio-temporal variation in tissue parameters in *Pocillopora meandrina* fragments collected in a time series during a transplantation experiment. Compared are time series of control fragments that were exposed to (LAIW+) or sheltered from (LAIW–) large amplitude internal waves (LAIW) and of fragments that were transplanted into higher (from LAIW– to LAIW+) or decreased (from LAIW+ to LAIW–) water fluxes, respectively. df: degrees of freedom; MS: mean square; (*) significant p-values; ns: not significant

Source of variance		df	MS	*F*	p
Zooxanthellae cm^{-2}					
Intercept	Fixed	1	5.315×10^{12}	236.297	*
Treat (Side)	Fixed	2	2.540×10^{11}	10.676	*
Colony (Treat)	Random	4	1.980×10^{10}	0.795	ns
Treat × Day	Fixed	2	2.300×10^{10}	0.965	ns
Error		97	2.379×10^{10}		
Chl *a* (µg cm^{-2})					
Intercept	Fixed	1	100.587	156.618	*
Treat (Side)	Fixed	2	5.619	8.131	*
Colony (Treat)	Random	4	0.503	0.728	ns
Treat × Day	Fixed	2	0.224	0.324	ns
Error		94	0.691		
Tissue carbon (µg cm^{-2})					
Intercept	Fixed	1	483775.133	366.965	*
Treat (Side)	Fixed	2	11456.002	7.881	*
Colony (Treat)	Random	4	943.407	0.649	ns
Treat × Day	Fixed	2	78.897	0.054	ns
Error		97	1453.670		
Tissue nitrogen (µg cm^{-2})					
Intercept	Fixed	1	23834.669	219.450	*
Treat (Side)	Fixed	2	643.984	7.905	*
Colony (Treat)	Random	4	183.810	2.256	ns
Treat × Day	Fixed	2	9.424	0.116	ns
Error		97	81.461		
Protein (mg cm^{-2})					
Intercept	Fixed	1	4.878	240.621	*
Treat (Side)	Fixed	2	0.090	4.067	*
Colony (Treat)	Random	4	0.015	0.674	ns
Treat × Day	Fixed	2	0.004	0.195	ns
Error		97	0.022		
δ^{13}C (‰)					
Intercept	Fixed	1	9132.298	37651.938	*
Treat (Side)	Fixed	2	0.199	0.722	ns
Colony (Treat)	Random	4	0.149	0.541	ns
Treat × Day	Fixed	2	0.259	0.938	ns
Error		95	0.276		

DISCUSSION

Introduction of upwelled subthermocline water into reef communities and the possible effects on water quality (Andrews & Gentien 1982, Leichter et al. 1996, Leichter et al. 2007), biodiversity (Cortés 1997), coral growth (Leichter & Genovese 2006) and feeding (Palardy et al. 2005) have been addressed in previous studies. Here, we compare reefs growing around an island chain that is unilaterally exposed to temperature oscillations more severe and frequent than previously reported in other areas (Leichter et al. 1996, Leichter &

Table 4. Significance levels of Fisher LSD tests for fragments of *Pocillopora meandrina* from the light-exclusion experiment. (○,●) LAIW– side, (□,■) LAIW+ island side colonies. (●,■) Light-deprived (PS–) data sets, (○,□) (control (PS+) sets. *Significant differences

		○ PS +	● PS –	□ PS +
Zooxanthellae cm^{-2}				
●	PS –	0.000*		
□	PS +	0.000*	0.000*	
■	PS –	0.001*	0.360	0.000*
Chl *a* (µg cm^{-2})				
●	PS –	0.004*		
□	PS +	0.000*	0.000*	
■	PS –	0.015*	0.461	0.000*
Tissue carbon (µg cm^{-2})				
●	PS –	0.001*		
□	PS +	0.010*	0.000*	
■	PS –	0.008*	0.309	0.000*
Tissue nitrogen (µg cm^{-2})				
●	PS –	0.016*		
□	PS +	0.016*	0.000*	
■	PS –	0.137	0.262	0.000*
Protein (mg cm^{-2})				
●	PS –	0.026*		
□	PS +	0.013*	0.000*	
■	PS –	0.530	0.088	0.002*
δ^{13}C (‰)				
●	PS –	0.113		
□	PS +	0.183	0.657	
■	PS –	0.000*	0.000*	0.000*

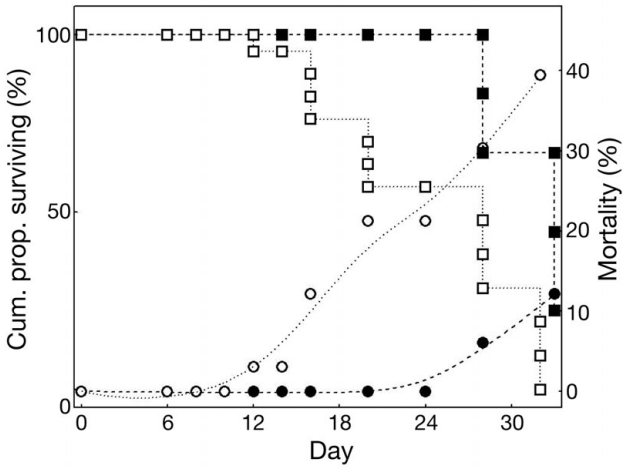

Fig. 8. Survival analysis of *Pocillopora meandrina* in the light-exclusion experiment. Kaplan Meier cumulative proportion survival curves (left *y*-axis,) of corals from LAIW+ (■) and LAIW– (□) reefs of Koh Miang over the experimental period (*x*-axis), showing the cumulative proportion of living light-deprived corals per sampling. The right *y*-axis displays the percent mortality of all light-deprived corals from LAIW+ (●) and LAIW– (○) reefs of Koh Miang over the experimental period. Control corals are not shown

Genovese 2006) and among the highest so far observed (Sheppard 2009). Given the proximity of the W (LAIW+) and E (LAIW–) sides of the islands (<200 m), the differences in the physical oceanographic parameters between the 2 island sides are striking. Variability in temperature and currents (this study), and also in oxygen, pH and nutrient concentrations (G. M. Schmidt et al. unpubl.) are much more pronounced on LAIW-exposed reefs compared to their sheltered counterparts, resulting in lower mean temperatures, stronger mean current velocities (Fig. 3) and increased input of corrosive, nutrient-rich deep water.

We demonstrated that despite the disparities in tissue composition of *Pocillopora meandrina* between LAIW+ and LAIW– reefs, the average amount and stable isotope composition of the plankton and the TSM are similar (see supplement at www.int-res.com/articles/suppl/m412p113_supp.pdf). The TSM, TPOC (near- and off-reef), DOC and near-reef plankton con-

Table 5. *Pocillopora meandrina*. Tissue parameters, means ± SE (n), measured in control (PS+) and light-deprived (PS–) fragments from the W (LAIW+) and the E (LAIW–) during the light-exclusion experiment, and in control (Feed+) and transplanted (from LAIW– to LAIW+: Feed++; from LAIW+ to LAIW–: Feed+–) fragments from the W (LAIW+) and the E (LAIW–) during the transplantation experiment. Missing data are due to mortality (light-exclusion experiment) or sample loss during analysis (transplantation experiment); 1 control fragment (LAIW+) from the transplantation experiment (colony 2, Day 28) was lost

		Zooxanthellae cm^{-2}	Chl *a* (µg cm^{-2})	Tissue carbon (µg cm^{-2})	Tissue nitrogen (µg cm^{-2})	Protein (mg cm^{-2})	δ^{13}C (‰)
Light-exclusion experiment							
LAIW+	PS +	412205 ± 47578 (29)	1.80 ± 0.19 (29)	169.08 ± 11.60 (29)	25.22 ± 2.17 (29)	0.60 ± 0.04 (29)	–17.46 ± 0.07 (29)
	PS –	95454 ± 16679 (26)	0.45 ± 0.10 (26)	90.44 ± 8.24 (26)	14.54 ± 1.51 (26)	0.42 ± 0.04 (26)	–18.21 ± 0.13 (26)
LAIW–	PS +	247178 ± 20270 (25)	0.96 ± 0.14 (25)	130.88 ± 10.97 (25)	18.64 ± 2.03 (25)	0.46 ± 0.05 (25)	–17.26 ± 0.10 (25)
	PS –	49383 ± 14237 (17)	0.29 ± 0.09 (17)	73.38 ± 11.43 (17)	11.10 ± 1.79 (17)		
Transplantation experiment							
LAIW+	Feed +	463338 ± 36475 (26)	2.21 ± 0.19 (26)	141.52 ± 7.41 (26)	32.36 ± 1.93 (26)	0.46 ± 0.03 (26)	–17.85 ± 0.10 (26)
	Feed ++	475997 ± 30455 (27)	2.24 ± 0.16 (25)	145.26 ± 7.69 (27)	31.58 ± 1.92 (27)	0.48 ± 0.03 (27)	–17.89 ± 0.10 (27)
LAIW–	Feed +	330515 ± 22089 (27)	1.51 ± 0.11 (26)	116.89 ± 6.18 (27)	26.19 ± 1.64 (27)	0.39 ± 0.02 (27)	–17.87 ± 0.09 (27)
	Feed +–	328249 ± 28513 (27)	1.62 ± 0.17 (27)	111.94 ± 7.64 (27)	23.89 ± 1.59 (27)	0.39 ± 0.04 (25)	–17.71 ± 0.11 (27)

Table 6. Significance levels of Fisher LSD tests for fragments of *Pocillopora meandrina* from the transplantation experiment. (○,●) Donor colonies from the LAIW– side, (□,■) donor colonies from the LAIW+ side colonies. (●,■) Fragments exposed to LAIW (LAIW+), (○,□) fragments cultivated on the sheltered LAIW– side. *Significant differences

		○ Feed +	□ Feed +–	■ Feed +
Zooxanthellae cm^{-2}				
□	Feed +–	0.958		
■	Feed +	0.002*	0.002*	
●	Feed ++	0.001*	0.001*	0.766
Chl *a* (µg cm^{-2})				
□	Feed +–	0.619		
■	Feed +	0.003*	0.011*	
●	Feed ++	0.002*	0.009*	0.908
Tissue carbon (µg cm^{-2})				
□	Feed +–	0.634		
■	Feed +	0.021*	0.006*	
●	Feed ++	0.007*	0.002*	0.722
Tissue nitrogen (µg cm^{-2})				
□	Feed +–	0.352		
■	Feed +	0.015*	0.001*	
●	Feed ++	0.031*	0.002*	0.754
Protein (mg cm^{-2})				
□	Feed +–	0.898		
■	Feed +	0.068	0.096	
●	Feed ++	0.025*	0.038*	0.685
δ^{13}C (‰)				
□	Feed +–	0.283		
■	Feed +	0.887	0.356	
●	Feed ++	0.868	0.216	0.760

centrations are not dependent on LAIW impact; however, upwelled water seems to be depleted in plankton. The lack of difference in the biological and chemical oceanographic parameters appears at odds with the pronounced differences in the physical oceanographic variables, suggesting that processes other than mixing are involved.

Previous studies showed that internal waves could act as a 'plankton pump' supplying phyto- and zooplankton to benthic communities (Witman et al. 1993, Leichter et al. 1998), thus fuelling growth rates of corals (Leichter & Genovese 2006). In the Andaman Sea, which features a pronounced oxygen minimum zone (OMZ) below the surface mixed layer, the concentration of plankton depends on the depth of the upwelled water. Below the surface mixed layer and the thermocline, the concentrations of phyto- and zooplankton decrease dramatically along with declines in oxygen concentrations (Madhu et al. 2003, Nielsen et al. 2004), leading to lower zooplankton concentrations in cold (<3°C relative to modal temperature) upwelled water. During periods of weak or intermittent upwelling, enrichment and depletion of nutrients due to upwelling/mixing and primary production, respectively, may even out (Kinsey 1988, Cushing 1989). Increased current strength increases nutrient uptake by corals (Hearn et al. 2001) and fuels zooxanthellae primary production (Szmant 2002), which has further been shown to be highest in cooler water with temperatures of 23 to 26°C (Al-Horani 2005). Strong currents enhance photosynthesis and calcification by altering the thickness of the boundary layer over the coral tissue and increasing gas exchange (Dennison & Barnes 1988). Current-induced turbulence may also mitigate the negative effects of low-oxygen water on coral metabolism (Shashar et al. 1993), where turbulence may be further enhanced by coral tentacle expansion (Patterson 1992) during feeding (Sebens & DeRiemer 1977). Currents are also indispensable for corals (Sebens et al. 1998) since they are passive suspension-feeders whose prey capture potential rises with increasing current strength (Sebens & Johnson 1991). The survival probability of corals exposed to high temperatures (Nakamura & van Woesik 2001), as well as the rates and time of recovery after bleaching are positively influenced by increased water flow (Nakamura et al. 2003).

Low temperature may further affect coral metabolism in various ways. Saxby et al. (2003) observed a decrease in photosynthetic performance in waters <20°C and other studies showed that slowed polyp contraction decreased the feeding activity of corals on zooplankton during upwelling periods (Palardy et al. 2005) and in cold water (Johannes & Tepley 1974).

Moreover, 'corrosive' low-pH water (Feely et al. 2008), which is another LAIW-distinctive feature (Schmidt et al. subm.), is known to alter trophic pathways by diverting energy from energy consuming calcification into somatic growth (Fine & Tchernov 2007).

Because the LAIW-induced unfavorable conditions in terms of temperature, oxygen and pH persist only for some minutes (Fig. 3), it is difficult to assess their potential impact on coral status over days and weeks. It is also difficult to discern antagonistic effects, e.g negative temperature effects, from possibly positive nutrient effects on coral photosynthesis. Antagonistic effects may also affect coral feeding, where the positive effects of enhanced plankton supply may be offset by possible negative effects of polyp retraction (Johannes & Tepley 1974).

As sampling was limited to daytime hours for logistic reasons, both the nocturnal feeding habit of the corals (Lewis & Price 1975, Muscatine & Porter 1977, Sebens & DeRiemer 1977) and the nocturnal emergence of demersal zooplankton (Porter & Porter 1977, Yahel et al. 2005) may have introduced a bias in our analysis with respect to coral feeding. The potential feeding bias is likely to have been mitigated in our experiment where light-deprived fragments were subjected to constant darkness and feeding was presumed to take place at any time. The plankton bias, on the other

hand, may have affected only the sheltered E Similan reef, given the lack of a coral framework on the LAIW-exposed W side of the island and the observation that the concentration of demersal zooplankton increases with the complexity of the reef substrate (Porter & Porter 1977).

In artificial darkness, LAIW-exposed *Pocillopora meandrina* was able to subsist exclusively by heterotrophy and on energy reserves (Fig. 6). The sharp drop in zooxanthellae numbers and chl *a* concentrations illustrates the capacity of the light-deprived corals to rapidly adapt metabolically to the lack of phototrophy, in contrast to the LAIW-sheltered corals from E Koh Miang that eventually all died (Fig. 8). The concomitant decrease in the surviving corals' tissue carbon, nitrogen and total protein concentrations (Fig. 6) is reminiscent of the declines in tissue carbon (Szmant & Gassman 1990) and lipid concentrations (Grottoli et al. 2004) that have been reported for bleached corals and attributed to the consumption of energy reserves when photosynthetic contribution to coral metabolism was reduced. Moreover, the higher protein concentrations despite eroding differences in tissue biomass between the light-deprived LAIW+ and LAIW– corals indicates a sustained supply of protein-rich plankton food in the LAIW-exposed reef, as heterotrophic carbon has been found to be incorporated into cnidarians mainly as protein (Bachar et al. 2007). This is further corroborated by the stable isotope data showing $\delta^{13}C$ depletion for light-deprived LAIW-exposed corals only (Fig. 6), which is similar in magnitude to the depletion reported for vigorously feeding *Montipora capitata* during and after bleaching (Rodrigues & Grottoli 2006). Strong water flows not only enhance food supply (Sebens et al. 1998), but also prevent a steady-state boundary layer from forming over the coral surface, hence increasing suspension feeding of particulate and adsorption of dissolved organic material (Helmuth & Sebens 1993), eventually resulting in longer and higher survival during periods of deprived phototrophy compared to LAIW-unaffected corals.

Acclimatization to LAIW-exposure and -shelter as well as to the accompanying altered food provision was rapid and resulted in increased zooxanthellae numbers, chl *a* content, tissue carbon, nitrogen, and protein when exposed to LAIW, and in their decrease when transplanted out of LAIW impact (Fig. 7). While upward changes in zooxanthellae numbers and chl *a* content might be the combined result of increased nutrient availability (Szmant 2002), currents (Dennison & Barnes 1988, Hearn et al. 2001) and overall lower mean temperatures (Al-Horani 2005), our results suggest that the higher energy reserves are the consequence of heterotrophic nutrition acting in combination with photosynthesis (Borell et al. 2008). Previous reports of feeding experiments showed that fed corals exhibited higher levels of protein than starved ones (Ferrier-Pagès et al. 2003, Borell et al. 2008) and lipid levels were increased when corals were kept under low light conditions and fed with zooplankton (Treignier et al. 2008). The higher tissue carbon, nitrogen and protein concentrations in our study may thus indicate higher heterotrophic input and larger energy stores in LAIW exposed corals.

Our results show that heterotrophic plasticity and the trophic status of a coral may vary intraspecifically depending on its environment, particularly the water flow (Skirving & Guinotte 2001) and food supply regimes. LAIW-enhanced supplies of food may be crucial for coral resilience to stress and survival during periods of reduced or inactivated photosynthesis, as are known to occur after coral bleaching events (Brown 1997, Hoegh-Guldberg 1999). *Pocillopora meandrina* rapidly adapts to changing environmental conditions, but may only have limited heterotrophic plasticity, as indicated by the lack of change in its isotopic carbon composition in the sheltered LAIW– corals. The potential of plasticity, however, is enhanced when food supply is increased by increasing current strength as shown for the LAIW+ coral fragments. Because other coral genera may be more efficient feeders than *Pocillopra* (Palardy et al. 2005, Palardy et al. 2008), it is likely that different species may acclimatize variously to LAIW influences. In the absence of genetic data, however, we can only speculate on whether such profound differences may reflect adaptation or acclimatization to LAIW.

As LAIW are ubiquitous in the ocean, particularly in tectonically active areas such as South East Asia that feature a rich underwater topography, strong density stratification and tidal currents, LAIW may play an important yet unexplored role in the capacity of corals to adapt to a changing marine environment.

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LITERATURE CITED

Al-Horani FA (2005) Effects of changing seawater temperature on the photosynthesis and calcification in the scleractinian coral *Galaxea fascicularis*, measured with O_2, Ca^{2+} and pH microsensors. Sci Mar 69:347–354

Anderson MJ, Ter Braak CJF (2002) Permutation tests for multi-factorial analysis of variance. J Statist Comput Simulation 73:85–113

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth

Andrews JC, 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 KR (2000) Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). Coral Reefs 19:59–67

Anthony KRN (2006) Enhanced energy status of corals on coastal, high-turbidity reefs. Mar Ecol Prog Ser 319:111–116

Bachar A, Achituv Y, Pasternak Z, Dubinsky Z (2007) Autotrophy versus heterotrophy: the origin of carbon determines its fate in a symbiotic sea anemone. J Exp Mar Biol Ecol 349:295–298

Bak R, Joenje M, de Jong I, Lambrechts D, Nieuwland G (1998) Bacterial suspension feeding by coral reef benthic organisms. Mar Ecol Prog Ser 175:285–288

Borell E, Yuliantri A, Bischof K, Richter C (2008) The effect of heterotrophy on photosynthesis and tissue composition of two scleractinian corals under elevated temperature. J Exp Mar Biol Ecol 364:116–123

Brown BE (1997) Coral bleaching: causes and consequences. Coral Reefs 16:S129–S138

Chansang H, Satapoomin U, Poovachiranon S (1999) Maps of coral reefs in Thai waters, Andaman Sea, Vol 2. Coral Reef Resource Management Project, Department of Fisheries, Bangkok, p 198

Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth

Cortés J (1997) Biology and geology of eastern Pacific coral reefs. Coral Reefs 16(Suppl):S39–S46

Cushing DH (1989) A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. J Plankton Res 11:1–13

Dennison WC, Barnes DJ (1988) Effect of water motion on coral photosynthesis and calcification. J Exp Mar Biol Ecol 115:67–77

Feely RA, Sabine CL, Hernandez-Ayon M, Ianson D, Hales B (2008) Evidence for upwelling of corrosive 'acidified' water onto the continental shelf. Science 320:1490–1492

Ferrier-Pagès C, Allemand D, Gattuso J, Jaubert J, Rassoulzadegan F (1998) Microheterotrophy in the zooxanthellate coral *Stylophora pistillata*: effects of light and ciliate density. Limnol Oceanogr 43:1639–1648

Ferrier-Pagès C, Witting J, Tambutté E, Sebens KP (2003) Effect of natural zooplankton feeding on the tissue and skeletal growth of the scleractinian coral *Stylophora pistillata.* Coral Reefs 22:229–240

Fine M, Tchernov D (2007) Scleractinian coral species survive and recover from decalcification. Science 315:1811

Fitt WK, McFarland F, Warner M, Chilcoat G (2000) Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. Limnol Oceanogr 45:677–685

Franzisket L (1969) Riffkorallen können autotroph leben. Naturwissenschaften 56:144

Gardella DJ, Edmunds PJ (1999) The oxygen microenvironment adjacent to the tissue of the scleractinian *Dichocoenia stokesii* and its effects on symbiont metabolism. Mar Biol 135:289–295

Glynn P (1973) Ecology of a Caribbean coral reef. The Porites reef-flat biotope: Part II. Plankton community with evidence for depletion. Mar Biol 22:1–21

Gonzalez L, Manly BFJ (1998) Analysis of variance by randomization with small data sets. Environmetrics 9:53?65

Grottoli AG (2002) Effect of light and brine shrimp on skeletal $\delta^{13}C$ in the Hawaiian coral *Porites compressa*: a tank experiment. Geochim Cosmochim Acta 66:1955–1967

Grottoli AG, Rodrigues LJ, Juarez C (2004) Lipids and stable carbon isotopes in two species of Hawaiian corals, *Porites compressa* and *Montipora verrucosa*, following a bleaching event. Mar Biol 145:621–631

Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440: 1186–1189

Grover R, Maguer J, Allemand D, Ferrier-Pagès C (2008) Uptake of dissolved free amino acids by the scleractinian coral *Stylophora pistillata.* J Exp Biol 211:860–865

Hearn C, Atkinson M, Falter J (2001) A physical derivation of nutrient-uptake rates in coral reefs: effects of roughness and waves. Coral Reefs 20:347–356

Helmuth B, Sebens KP (1993) The influence of colony morphology and orientation to flow on particle capture by the scleractinian coral *Agaricia agaricites* (Linnaeus). J Exp Mar Biol Ecol 165:251–278

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50:839–866

Houlbrèque F, Ferrier-Pagès C (2009) Heterotrophy in tropical scleractinian corals. Biol Rev Camb Philos Soc 84:1–17

Houlbrèque F, Tambutté E, Ferrier-Pagès C (2003) Effect of zooplankton availability on the rates of photosynthesis, and tissue and skeletal growth in the scleractinian coral *Stylophora pistillata.* J Exp Mar Biol Ecol 296:145–166

Houlbrèque F, Tambutté E, Richard C, Ferrier-Pagès C (2004) Importance of a micro-diet for scleractinian corals. Mar Ecol Prog Ser 282:151–160

Jackson CR (2004) An atlas of internal solitary-like waves and their properties, 2nd edn. Global Ocean Associates, Rockville, MD, p 560

Johannes RE, Tepley L (1974) Examination of feeding of the reef coral *Porites lobata in situ* using time lapse photography. Proc 2nd Int Coral Reef Symp 1:127–131

Kinsey DW (1988) Coral reef system response to some natural and anthropogenic stresses. Galaxea 7:113–128

Leichter JJ, Shellenbarger G, Genovese SJ, Wing SR (1998) Breaking internal waves on a Florida (USA) coral reef: a plankton pump at work? Mar Ecol Prog Ser 166:83–97

Leichter JJ, Genovese SJ (2006) Intermittent upwelling and subsidized growth of the scleractinian coral *Madracis mirabilis* on the deep fore-reef slope of Discovery Bay, Jamaica. Mar Ecol Prog Ser 316:95–103

Leichter JJ, Wing SR, Miller SL, Denny MW (1996) Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. Limnol Oceanogr 41: 1490–1501

Leichter JJ, Paytan A, Wankel S, Hanson K, Miller SL, Altabet MA (2007) Nitrogen and oxygen isotopic signatures of subsurface nitrate seaward of the Florida Keys reef tract. Limnol Oceanogr 52:1258–1267

Lewis JB, Price WS (1975) Feeding mechanisms and feeding strategies of Atlantic reef corals. J Zool 276:527–545

Ljung GM, Box GEP (1978) On a measure of lack of fit in time series models. Biometrika 65:297–303

Lorenzen CJ (1967) Determination of chlorophyll and pheopigments: spectrophotometric equations. Limnol Oceanogr 12:343–346

Lowry OH, Rosebrough NJ, Farr AL, Randall RJ (1951) Protein measurement with the Folin phenol reagent. J Biol Chem 193:265–275

Madhu NV, Jyothibabu R, Ramu K, Sunil V, Gopalakrishnan TC, Nair KKC (2003) Vertical distribution of mesozooplankton biomass in relation to oxygen minimum layer in the Andaman Sea. Indian J Fish 50:533–538

Mirto S, Bianchelli S, Gambi C, Krzelj M and others (2010) Fish-farm impact on metazoan meiofauna in the Mediterranean Sea: analysis of regional vs. habitat effects. Mar Environ Res 69:38–47

Muscatine L, Porter JW (1977) Reef corals: mutualistic symbioses adapted to nutrient-poor environments. Bioscience 27:454–460

Muscatine L, Porter JW, Kaplan IR (1989) Resource partitioning by reef corals as determined from stable isotope composition. Mar Biol 100:185–193

Nakamura T, van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar Ecol Prog Ser 212:301–304

Nakamura T, Yamasaki H, van Woesik R (2003) Water flow facilitates recovery from bleaching in the coral *Stylophora pistillata*. Mar Ecol Prog Ser 256:287–291

Naumann M, Niggl W, Laforsch C, Glaser C, Wild C (2009) Coral surface area quantification–evaluation of established techniques by comparison with computer tomography. Coral Reefs 28:109–117

Nielsen TG, Bjørnsen PK, Boonruang P, Fryd M and others (2004) Hydrography, bacteria and protist communities across the continental shelf and shelf slope of the Andaman Sea (NE Indian Ocean). Mar Ecol Prog Ser 274: 69–86

Osborne AR, Burch TI (1980) Internal solitons in the Andaman Sea. Science 208:451–460

Palardy JE, Grottoli AG, Matthews KA (2005) Effects of upwelling, depth, morphology and polyp size on feeding in three species of Panamanian corals. Mar Ecol Prog Ser 300:79–89

Palardy JE, Rodrigues LJ, Grottoli AG (2008) The importance of zooplankton to the daily metabolic carbon requirements of healthy and bleached corals at two depths. J Exp Mar Biol Ecol 367:180–188

Patterson MR (1992) A chemical engineering view of cnidarian symbioses. Am Zool 32:566–582

Perry RB, Schimke GR (1965) Large-amplitude internal waves observed off the Northwest coast of Sumatra. J Geophys Res 70:2319–2324

Pineda J (1991) Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. Science 253:548–551

Porter JW, Porter KG (1977) Quantitative sampling of demersal plankton migrating from different coral reef substrates. Limnol Oceanogr 22:553–556

Rodrigues LJ, Grottoli AG (2006) Calcification rate and the stable carbon, oxygen, and nitrogen isotopes in the skeleton, host tissue, and zooxanthellae of bleached and recovering Hawaiian corals. Geochim Cosmochim Acta 70: 2781–2789

Satterthwaite FE (1946) An approximate distribution of estimates of variance components. Biom Bull 2:110–114

Saxby T, Dennison WC, Hoegh-Guldberg O (2003) Photosynthetic response of the coral *Montipora digitata* to cold temperature stress. Mar Ecol Prog Ser 248:85–97

Sebens KP, DeRiemer K (1977) Diel cycles of expansion and contraction in coral reef anthozoans. Mar Biol 43:247–256

Sebens KP, Johnson AS (1991) Effects of water movement on prey capture and distribution of reef corals. Hydrobiologia 226:91–101

Sebens KP, Witting J, 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

Sebens KP, Grace SP, Helmuth B, Maney E Jr, Miles J (1998) Water flow and prey capture by three scleractinian corals, *Madracis mirabilis, Montastrea cavernosa* and *Porites porites* in a field enclosure. Mar Biol 131:347–360

Shashar N, Cohen Y, Loya Y (1993) Extreme diel fluxes of oxygen in diffusive boundary layers surrounding stony corals. Biol Bull 185:455–461

Sheppard C (2009) Large temperature plunges recorded by data loggers at different depths on an Indian Ocean atoll: comparison with satellite data and relevance to coral refuges. Coral Reefs 28:399–403

Skirving W, Guinotte J (2001) The sea surface temperature story on the Great Barrier Reef during the coral bleaching event of 1998. In: Wolanski E (ed) Oceanographic processes of coral reefs: physical and biological links in the Great Barrier Reef. CRC Press, Boca Raton, FL, p 301–310

Smith PE, Counts RC, Clutter RI (1968) Changes in filtering efficiency of plankton nets due to clogging under tow. ICES J Mar Sci 32:232–248

Sorokin YI (1973) On the feeding of some scleractinian corals with bacteria and dissolved organic matter. Limnol Oceanogr 18:380–385

Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis, 2nd edn. Fish Res Board Can Bull 167

Swart PK, Saied A, Lamb K (2005) Temporal and spatial variation in the $\delta^{15}N$ and $\delta^{13}C$ of coral tissue and zooxanthellae in *Montastrea faveolata* collected from the Florida reef tract. Limnol Oceanogr 50:1049–1058

Szmant A (2002) Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries 25:743–766

Szmant A, Gassman NJ (1990) The effects of prolonged 'bleaching' on the tissue biomass and reproduction of the reef coral *Montastrea annularis.* Coral Reefs 8: 217–224

Treignier C, Grover R, Ferrier-Pagès C, Tolosa I (2008) Effect of light and feeding on the fatty acid and sterol composition of zooxanthellae and host tissue isolated from the scleractinian coral *Turbinaria reniformis.* Limnol Oceanogr 53:2702–2710

Vlasenko V, Alpers W (2005) Generation of secondary internal waves by the interaction of an internal solitary wave with an underwater bank. J Geophys Res 110. doi:10.1029/2004JC002467

Vlasenko V, Hutter K (2002) Numerical experiments on the breaking of solitary internal waves over a slope-shelf topography. J Phys Oceanogr 32:1779–1793

Vlasenko V, Stashchuk N (2007) Three-dimensional shoaling of large-amplitude internal waves. J Geophys Res 112. doi:10.1029/2007JC004107

Wellington GM (1982) An experimental analysis of the effects of light and zooplankton on coral zonation. Oecologia 52: 311–320

Witman JD, Leichter JJ, Genovese SJ, Brooks DA (1993) Pulsed phytoplankton supply to the rocky subtidal zone: influence of internal waves. Proc Natl Acad Sci 90: 1686–1690

Yahel R, Yahel G, Genin A (2005) Near-bottom depletion of zooplankton over coral reefs: I: diurnal dynamics and size distribution. Coral Reefs 24:75–85

Yonge CM (1930) Studies on the physiology of corals. I. Feeding mechanisms and food. Scientific Reports on the Great Barrier Reef Expedition 1928–29 1:1–57

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