Benthic-pelagic coupling in a Caribbean reef lagoon affected by hurricane "Dolly"

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Abstract. In oligotrophic tropical coral reef environments tightly coupled benthic-pelagic material fluxes represent key biogeochemical processes sustaining high benthic productivity and overall ecosystem functioning. Tropical storms can severely impact the physico-chemical state of marine coastal ecosystems and are predicted to increase in intensity on global scale. Although tropical storms cause large-scale habitat devastation, there is only little information regarding their influence on ecosystem metabolism and benthic-pelagic coupling in coastal coral reef environments. Thus, this study investigates these processes in a typical Caribbean shallow water reef lagoon close to Puerto Morelos (Mexico) over the course of the tropical storm “Dolly” (2008). Pelagic and benthic lagoon metabolism were assessed by measuring oxygen fluxes along with dissolved organic carbon (DOC), particulate organic matter and chlorophyll *a* concentrations in lagoon waters. Our findings characterize the pelagic lagoon compartment as an overall heterotrophic environment, while the benthic community was generally net autotrophic. Tropical storm impact was clearly detectable by change in monitored lagoon water parameters and a significantly influence on pelagic and benthic lagoon metabolism, which responded rapidly (within 1-2 d) to storm-induced environmental change by increased pelagic and lowered benthic net primary production. Pelagic respiration was significantly increased (up to 11 d) following the later development of a phytoplankton bloom and concomitantly elevated DOC concentrations, while benthic respiration remained below pre-storm levels up to the end of the study period. These findings emphasize compartment-specific and rapid responses by reef lagoon communities with implications for the functioning of benthic-pelagic coupling affected by tropical storm disturbances.

Key words: Metabolism, Primary production, Respiration, Storm.

Introduction

Lagoons associated with tropical coral reefs represent important environments for benthic primary production and overall reef ecosystem metabolism (Boucher and Clavier 1990, Hatcher 1990). Tropical reef lagoons have been identified as major organic matter sinks, where in particular sandy sediments function as biocatalytical filter systems supporting benthic-pelagic coupling by efficient recycling of deposited nutrients (Koop and Larkum 1987, Wild et al. 2005). Concurrently, lagoonal benthic-pelagic coupling is controlled by high planktonic turnover rates for organic matter of benthic origin, resulting in significant and essential energy retention in oligotrophic reef ecosystem (Wild et al. 2008). Thus, benthic-pelagic coupling constitutes a range of key biogeochemical processes sustaining high benthic productivity and overall ecosystem functioning.

Recent climate modelling predicts the intensity of tropical storm events to increase significantly, while their actual global frequency may eventually decrease (Knutson et al. 2010). Nevertheless, intensity of North Atlantic storms affecting the Caribbean region is expected to increase coinciding with consistent frequency in near future climate scenarios (Webster et al. 2005). Conclusively, Caribbean reef lagoons will prospectively become the ones globally most intensively impacted by tropical storm events.

While the potential catastrophic mechanical impacts of tropical storms on coral reefs have been well described by previous studies (e.g. Harmelin-Vivien and Laboute 1986), our current understanding of their influence on metabolism and benthic-pelagic coupling in subtropical and tropical coastal habitats (Lawrence et al. 2004, Kolasinski et al. 2011) is still limited. Thus, the present study aims to investigate the influence of a tropical storm event on ecosystem metabolism and benthic-pelagic coupling in a regularly affected Caribbean reef lagoon. Benthic metabolism may likely exhibit changes resulting from intensive tropical storm impact, while such shifts may likewise be detectable within pelagic lagoon metabolism and benthic-pelagic coupling.

Material and Methods

Study site

This study was conducted during wet season (18 July to 1 August 2008) in an extensive, semi-enclosed Caribbean coral reef lagoon bordering the north–south orientated Mesoamerican barrier reef system near Puerto Morelos, Mexico (20° 52' 05.8''N, 86° 52' 03.0''W). All lab-based measurements were carried out locally in the facilities of the Institute of Marine Sciences and Limnology (ICML) operated by the National Autonomous University of Mexico (UNAM). The Puerto Morelos reef system can be divided into a front and rear reef featuring a reef crest and a reef lagoon framed by the coastline and the barrier reef at widths ranging from 0.2 to 1.5 km (Jordan et al. 1981). In the central parts of the lagoon, a maximum depth of 4 m is reached. Prevailing northwards current profiles in the lagoon average 0.1 m s^{-1} resulting in a mean residence time of 3 h for the entire lagoon water body under calm conditions, while during hurricane conditions residence time may decline to 0.3 h (Coronado et al. 2007). The dominant substrate of the lagoon sediments is calcareous sand, on which seagrass meadows cover most of the area together with scattered algae, minimal soft and hard coral growth (Haas et al. 2010).

Situated centrally on the so called Caribbean "hurricane belt", the region in radius of 50 km around the study site has been impacted by at least 35 major storm events since first records in 1857 (NOAA online archives) ranging in intensity from tropical storms to category 5 hurricanes (i.e. Beulah in 1967, Gilbert in 1988 and Wilma in 2005). This region thus qualifies for studies on the effects of regular tropical storm events on reef lagoon metabolism and benthic-pelagic coupling processes.

The period of the present study coincided with the tropical storm "Dolly", which made landfall ca. 20 km south of Puerto Morelos around noon on 20 July 2008 affecting the atmospheric conditions of the region for ca. 1.5 d, before passing the Yucatan peninsula and developing into a category 2 hurricane over the Gulf of Mexico (NOAA online archives). Consequently, our *in situ* and lab-based experimental measurements cover time periods shortly before (1-2 d), shortly after (1-4 d) and longer after (up to 11 d) the passage of "Dolly".

In situ temperature and light availability

Lagoon temperature and light availability were recorded throughout the study period using triplicate data loggers (Onset HOBO® Pendant UA-002-64) placed within 10 m distance around a referenced site (water depth 3 m, 1 min resolution). Light intensity data recorded in lux (lx) were subsequently converted to photosynthetically active radiation (PAR, µmol quanta m^{-2} s^{-1}, wavelength 400 to 700 nm) by approximation: 1 µmol quanta m^{-2} s^{-1} = 51.2 lx (Valiela 1984).

Seawater analyses

To investigate concentrations of particulate and dissolved compounds in lagoon waters, seawater samples (1.7 l, n = 4) were collected at the referenced site in 3 m water depth around noon time (12:00 – 13:00) on 10 d during the whole study period using pre-rinsed (HCl 10% and sampling seawater) glass bottles. Bottles were immediately transported to the laboratory and subsamples for dissolved organic carbon (DOC) analysis (10 ml, n = 4) were prepared by filtering through polyethersulfone membrane filters (0.2 µm pore size, VWR International) into pre-combusted (450°C, 4 h) brown glass vials, which were kept frozen at -20°C pending analysis. DOC concentrations were measured by high temperature catalytic oxidation using a Rosemount Dohrmann DC-190 total organic carbon (TOC) analyser. A TOC standard (ULTRA Scientific) was used to ensure analytical precision at < 3% of the certified value. Two subsamples (500 ml each) from each bottle were used for particulate organic carbon (POC) and particulate nitrogen (PN) analyses by filtration onto pre-combusted GF/F filters (Whatman, mesh-size: 0.7 µm). Subsequently, filters were dried for ≥ 48 h (40°C) and analysed using a Thermo™ NA 2500 elemental analyser (standards: atropine, cyclohexanone-2,4-dinitrophenylhydrazone; Thermo Quest; deviation < 3%). POC filters were exposed to a fuming HCl atmosphere for 24 h before measurements to remove particulate inorganic carbon. One subsample (500 ml) per bottle was likewise filtered for chlorophyll *a* (Chl *a*) analysis and stored frozen (-20°C) in the dark pending analysis. Chl *a* was extracted in the dark with 90% acetone (24 h, 4°C) and measured by spectro- fluorometry using a TD-700 fluorometer (Strickland and Parsons 1972). In addition, the initial O_2 concentration of each lagoon water sample was measured in parallel using an optode (Hach-Lange HQ 10, precision 0.01 mg l^{-1}, accuracy ± 0.05%).

Pelagic metabolism

Lagoon water samples (1500 ml; n = 4) were taken at the referenced site (3 m water depth) and processed within 1 h to determine pelagic metabolic activity (in terms of O_2 fluxes) conducting lab-based incubation experiments. Seawater incubations for net primary production were carried out using air-tight glass jars

(500 ml) submerged in a 500 l tank sustaining *in situ* temperature conditions by constant flow-through of freshly pumped lagoon water. Light conditions comparable to *in situ* levels were adjusted by prior measurements using data loggers and application of net clothing. Incubations lasted for 24 h in order to obtain representative rates of photosynthesis. Seawater respiration measurements were carried under the same conditions, except for using an opaque, submersed plastic foil preventing light penetration during incubations. Concentrations of dissolved O_2 were measured at the start and end of all incubations by optode and pelagic net primary production or respiration rates were determined by subtracting end from start values. Resulting O_2 concentration differences were normalized by incubation time. Seawater gross primary production rates were subsequently calculated for all incubations by adding a mean value derived from the measured respiration rates to the respective net primary production rates. To facilitate the display of temporal change in pelagic lagoon metabolism, results were pooled into 3 time periods ranging from 2 d before, 2-4 d after and 7-11 d after the storm event.

Benthic metabolism

Sediment samples representing a mixture of the 3 dominant local substrate types (i.e. sea grass, macroalgae and plain calcareous sand; Haas et al. 2010) were taken with a "mini-corer", which provided a defined sampling area (5.73 cm^2) and volume (3.4 ml). Samples were immediately transported to the lab and incubated with freshly sampled lagoon water to determine benthic net primary production and respiration rates (in terms of O_2 fluxes). Incubations and measurements were carried out as described above for pelagic metabolic activity. Resulting differences in O_2 concentrations were eventually normalized to the sampled sediment surface area and incubation time. As for pelagic metabolic rates, results were pooled into 3 time periods.

Sedimentation of particulate organic matter

To assess the amount and composition of POM reaching the seafloor, custom-made sediment traps were deployed for 24 h close to the referenced site (3 m water depth, n = 4) on 3 dates (2 d before, 1 d after and 11 d after the storm event. The opening of each trap contained a funnel, which was fixed at 7.5 cm above the substrate. At the end of the deployment period, the trap was closed with a lid *in situ* and transported to the lab. There, trap contents were processed immediately. Subsamples for POC, PN and Chl *a* content analysis were prepared as described above for seawater samples (filtered homogenized volume: 200 ml each). All content data were normalized by the trapping area defined by the diameter of the funnel and the duration of the deployment period.

Data analyses

Following analyses for preconditions of equal variances (Levene test) and normal distribution (Kolmogorov–Smirnov test), data were statistically analysed using parametric pair-wise t-tests or non-parametric Kruskal-Wallace (KW) and Wilcoxon-Mann-Whitney U-tests (MW) inside SPSS© software packages. Results were regarded as significant at $p<0.05$, unless stated differently.

Results

Temperature and light availability

Lagoon water temperature ranged from 29-32°C (2°C diel range) during the study period and was significantly influenced by the storm event (MW, $p<0.001$) decreasing rapidly by at least 3 units within a 12 h period and remaining constant at 29°C for at least 1.5 d (Fig. 1). PAR was likewise substantially reduced showing a rapid decline (51%) immediately after the onset of the storm (20 July) and significantly reduced (MW, $p<0.001$) rates (12% of study period mean) for the whole following day (Fig. 1).

Seawater analyses

All particulate (POC, PN and Chl *a*) and dissolved (DOC) organic parameters showed elevated concentrations in lagoon waters in response to the storm event (Fig. 2a,b). POC concentrations increased significantly (MW, $p=0.024$) by more than 6-times (PN (t-test, $p<0.001$) and Chl *a* (MW, $p<0.001$): ca. 3-times) during the storm (21 July) and showed a decline to pre-storm values after 2 d. As for PN, POC revealed a second significant 2-3-fold increase (t-test, $p<0.001$) after an additional 2 d time period (Fig. 2a). DOC concentrations increased by only 26% during the storm event (21 July), but continued to rise by more than 2-fold reaching a maximum 1 d after the storm (Fig. 2b). As for POC and PN, a subsequent rapid decline to pre-storm concentrations within 3 d was followed by a second substantial peak observed 7 d after the storm.

Dissolved O_2 concentrations decreased significantly with the onset of the storm (t-test, $p<0.001$) and continued to decline significantly (t-test, $p<0.001$) during its presence reaching levels 18% lower than pre-storm conditions (Fig. 2b). In the 2 d period following the storm, O_2 concentrations increased significantly (t-test, $p<0.001$) to greater than pre-storm values until a rapid decrease over 2 d was evident. After that, O_2 concentrations remained constant at intermediate levels ranging between pre-storm and in-storm conditions.

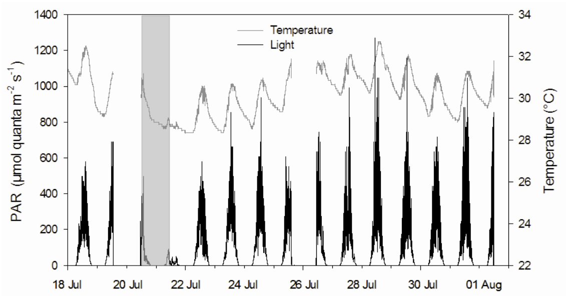

Figure 1: Seawater temperature and light availability at 3 m lagoon water depth during the study period. Light availability given as photosynthetically active radiation (PAR). Darkened bar indicates duration of tropical storm. Figure modified from Haas et al. (2010).

Pelagic metabolism

Pelagic net primary production was negative throughout the entire study period and influenced by the storm leading to a significant (t-test, p=0.012) increase shortly after the event (Fig. 3a). However, more than 1 wk later, values measured for pelagic net primary production decreased significantly below pre-storm levels (t-test, p=0.03). Pelagic respiration rates were significantly reduced by the event (t-test, p=0.014), but likewise increased significantly compared to pre-storm rates 1 wk after the event (t-test, p=0.027). Calculated rates for pelagic gross primary production were positive throughout the study periods and remained constant shortly after the storm event (Fig. 3a), while a significant decrease was detected more than 1 wk after as a result of increasing pelagic respiration (t-test, p=0.014).

Benthic metabolism

Benthic metabolism was significantly impacted following the storm, as benthic respiration rates decreased significantly shortly after (t-test, p=0.045) and remained constant at these levels for at least 11 d (Fig. 3b). Likewise, benthic net and gross primary production showed significant declines shortly after (t-test, p=0.013), with no significant indication for recovery to pre-storm conditions after 11 d (t-test, p=0.083, Fig. 3b).

Sedimentation of particulate organic matter

Sedimentation rates of POC, PN and Chl *a* showed no significant change during the particular deployment periods, ranging between: 4.5-4.9 mg POC (KW, p=0.4), 0.41-0.42 mg PN (KW, p=0.2) and 4.0-4.6 mg Chl *a* m^{-2} seafloor h^{-1} (KW, p=1.0).

Discussion

This study provides new information concerning the impact of tropical storms on benthic and pelagic reef lagoon metabolism, with implications for the functioning of benthic-pelagic coupling processes.

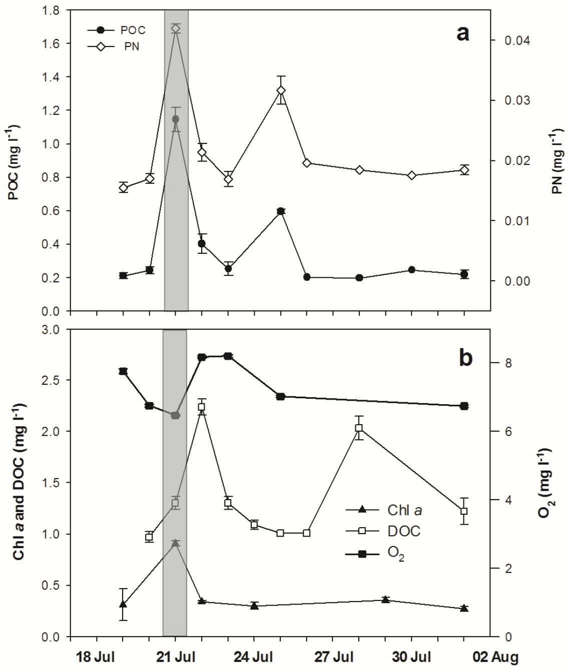

Figure 2: Concentrations of suspended particulate and dissolved compounds in lagoon waters. Panel a: Particulate organic carbon (POC) and nitrogen (PN); panel b: chlorophyll *a* (Chl *a*), dissolved organic carbon (DOC) and dissolved O_2. Values are mean ± SD.

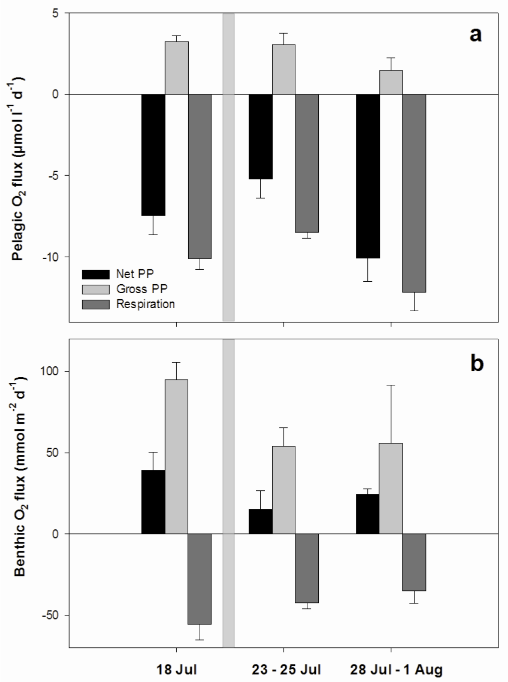

Figure 3: Pelagic and benthic reef lagoon metabolism. Panel a: pelagic- and panel b: benthic primary production (net, gross) and respiration rates. Values are mean ± SD. Elongated grey bars indicate the instance of the storm event. PP = primary production. Dates indicate measurement periods before (18 Jul), shortly after (22-25 Jul) and more than 1 wk after the storm event (28-01 Aug).

Our findings indicate that the metabolism of both lagoon compartments is significantly affected by storm-induced changes in key environmental parameters. The most drastic changes clearly being increased water column turbidity and rapid decline in seawater temperature. Increased turbidity indicated by elevated POM concentrations during the storm, together with complete daytime cloud cover (M. Naumann pers. observ.), caused a distinct decrease in PAR lasting for up to 2 d and coinciding with a temperature decline of 3°C.

Benthic lagoon metabolism was severely affected by these rapid environmental shifts, as evident by the early decline in benthic primary production, which was still detectable by lowered net and gross primary production rates after up to 11 d. Nevertheless, benthic metabolism remained net autotrophic during the entire study period, likely due to the relatively short duration of the event and swift PAR as well as temperature re-adjustment to pre-storm conditions after storm passage. This is supported by our measurements of seawater O_2 concentrations, showing a rapid increase immediately after the event.

Pelagic metabolism was likewise stimulated shortly after the storm, as revealed by increased net primary production rates, possibly as a consequence of inorganic nutrients leaching from storm-induced lagoon sediment mixing and/or enhanced influx from oceanic waters (Ullman and Sanstrom 1987). This may further explain our findings of increased DOC concentrations in lagoon waters 1 d after the storm as a potential indication for DOC release by planktonic primary producers. However, for this time period we fail to link the subsequent decrease in DOC to any significant positive response by benthic and/or pelagic community respiration, which may suggest a loosely linked microbial loop, known from subtropical oligotrophic lagoon environments (Rochelle-Newall et al. 2008). The rapid decline of DOC concentrations shortly after the storm may possibly also result from the export of this material by the potential increase of exchange rates of the lagoon water body during storm events (residence time: 0.3 h, Coronado et al. 2007) compared to calm atmospheric conditions (3 h).

Further, our findings suggest that benthic-pelagic coupling may be strongly affected by the above storm-induced changes in lagoon water residence times. During and shortly after the storm event those may have weakened benthic-pelagic coupling through rapid export of POM and dissolved nutrients. This is supported by peaks in POC and PN concentrations 4 d after the storm, which indicate the presence of a phytoplankton bloom likely responsible for the subsequent increase in DOC concentrations. After the reestablishment of calm atmospheric conditions (4-11 d after), we thus suppose a tight benthic-pelagic coupling process initiated by the continuing inorganic nutrient release from storm-induced sediment mixing, elevating DOC concentrations by phytoplankton release or decay, thus providing a substrate for the subsequently observed increase in pelagic respiration. This biogeochemical pathway may represent a focal issue for follow-up lagoon ecosystem studies.

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