Coral Reefs (2003) 22: 247–255
DOI 10.1007/s00338-003-0314-5

REPORT

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Measuring coral reef community metabolism using new benthic chamber technology

Received: 17 April 2002 / Accepted: 25 April 2003 / Published online: 26 July 2003

Abstract Accurate measurement of coral reef community metabolism is a necessity for process monitoring and in situ experimentation on coral reef health. Traditional methodologies used for these measurements are effective but limited by location and scale constraints. We present field trial results for a new benthic chamber system called the Submersible Habitat for Analyzing Reef Quality (SHARQ). This large, portable incubation system enables in situ measurement and experimentation on community-scale metabolism. Rates of photosynthesis, respiration, and calcification were measured using the SHARQ for a variety of coral reef substrate types on the reef flat of South Molokai, Hawaii, and in Biscayne National Park, Florida. Values for daily gross production, 24-h respiration, and net calcification ranged from 0.26 to 6.45 g O_2 m^{-2} day^{-1}, 1.96 to 8.10 g O_2 m^{-2} 24 h^{-1}, and 0.02 to 2.0 g $CaCO_3$ m^{-2} day^{-1}, respectively, for all substrate types. Field trials indicate that the SHARQ incubation chamber is an effective tool for in situ isolation of a water mass over a variety of benthic substrate types for process monitoring, experimentation, and other applications.

Keywords Reef metabolism · Benthic chamber · Calcification · Productivity

Introduction

Growing concerns for the decline of coral reef ecosystems have necessitated the enhancement and development of techniques for examining coral reef health and the impact of environmental perturbations. While traditional monitoring and characterization using descriptive assessment protocols provide valuable information on the current status and trends of coral reef health, this information provides little insight into the causes of change. Process monitoring and experimentation are required to understand the cause-and-effect relations between natural and anthropogenic stresses and changes in the health of coral reefs.

Measurement of coral metabolism has made it possible to characterize reef health in terms of fundamental coral reef processes such as photosynthesis, respiration, and calcification. This information enables geographic comparison of reefs in terms of system functionality (e.g., Kinsey 1983, 1985; Smith 1983). Community-scale measurements of metabolic and geochemical processes have generally been performed using a flow respirometry approach (Odum and Odum 1955; Smith 1973; Barnes 1983; Barnes and Devereux 1984; Gattuso et al. 1993). This technique measures spatial geochemical changes in the water column along transects (generally greater than 100 m) across the substrate at the upstream and downstream ends of each transect. Water circulation at the study site must be well characterized using current meters or other water-mass tracking techniques. This method assumes conservation of water mass along transects, and is limited to areas where unidirectional currents can be identified. Difficulties in accurately tracking the movement of water masses due to the complicated topography of coral reefs results in the potential for a large margin of error. Twenty-four-hour monitoring along transects is logistically difficult due to difficulties in navigating along transects during dark hours. Flow respirometry is also limited by the resolution of geochemical measurements. Water must reside over the substrate long enough for its chemistry to be affected by processes of interest. Faster water flow rates result in shorter residence times and require a higher resolution for geochemical measurements to detect smaller chemical changes. Slower flow rates increase residence time of water over the substrate; however, most benthic organisms alter their metabolism when

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flow rate decreases, producing an abnormal response (Carpenter et al. 1991). Structures resembling tunnels have been designed to divert water flow in a modified flow respirometry technique (Rogers 1979a). However, it is difficult to divert water flow over the long distances (hundreds of meters) typically required for accurate geochemical measurements. Additionally, investigations on the effects of environmental perturbations on reef communities have typically been limited to ecosystems in regions experiencing environmental stress or to laboratory-based experimentation requiring removal of organisms from their natural environment. Some large-scale laboratory experiments on coral metabolism have provided valuable information on the impact of various natural and anthropogenic stresses to coral reefs (Langdon et al. 2000). However, it is extremely costly and logistically difficult to replicate the complexities of natural systems, and few laboratories capable of accommodating complex systems exist.

In situ measurement and experimentation on the impact of environmental change to coral reef metabolism has also been problematic. Traditionally, in situ experiments on measuring metabolic and geochemical processes associated with benthic organisms have been performed using small (<0.5-m diameter, <4-l volume) incubation chambers constructed of rigid Plexiglas or acrylic glass (Rogers and Salesky 1981; Dodge et al. 1984; Kendall et al. 1984; Carpenter 1985; Morrissey 1985; Carpenter et al. 1991; Boucher et al. 1994). These chambers effectively isolate a small volume of water over individual or a few benthic organisms, enabling short-term incubation experiments. These small structures provide valuable information on processes associated with individual benthic species; however, accurate measurements of community-level responses cannot be achieved using this method. Additionally, these small structures are not versatile and cannot be adjusted for size or volume to accommodate variations in substrate topography. Rigid chambers have been limited in size due to difficulties in transporting and deploying larger chambers and in conforming and sealing them to the substrate.

In response to the need for improved accuracy in process monitoring and in situ experimentation associated with geochemical and metabolic changes in coral reef and other coastal ecosystems, we have constructed and implemented the Submersible Habitat for Analyzing Reef Quality (SHARQ). The SHARQ (US Patent #6,467,424 B1) is a large, portable incubation chamber designed to isolate the water mass overlying a section of coral reef or other substrate, enabling accurate, in situ measurement of changes in water chemistry over time (Fig. 1). This method is not limited by water current patterns. The large size of the incubation chamber enables geochemical measurements at the community scale. We present results from field trials of the SHARQ on coral reef substrates along the south coast of Molokai, Hawaii, and Biscayne National Park on the southeast coast of Florida, demonstrating its utility for monitoring and experimentation on coral reef processes.

Materials and methods

SHARQ construction

The SHARQ is constructed of a 4.9 (l)x2.4 (w)x1.2 (h)-m aluminum frame that disassembles into 2.4-m sections for transport. The frame is constructed by first assembling six 2.4-m sections, which comprise the 4.9x2.4-m frame base. Fourteen frame ribs are inserted into "t-fittings" on the base and into 90-degree fittings on the frame "spine." The frame can be constructed above water and

Fig. 1 The Submersible Habitat for Analyzing Reef Quality (SHARQ) is a large, portable benthic incubation chamber designed to isolate a mass of water over the underlying substrate. A flow-through analytical system enables continuous, 24-h monitoring of water chemistry resulting from benthic community processes

subsequently lowered into place on the substrate, or below water by SCUBA divers. A submersible pump (133 to 246 l min^{-1}), hose, and polyvinylchloride (PVC) arm (7.6 cm diameter) are mounted at the top centerline of the frame. This circulation system diverts flow down from the top of the incubation chamber at one end and back toward the opposite end. This system maintains turbulent flow inside the SHARQ, preventing water from becoming stagnated and from developing concentration gradients. A hose attachment at the top end of the PVC arm connects polyethylene hose used to carry water from within the incubation chamber (extracted from the circulation system) to the water's surface for analysis (outflow).

A clear, 3-mil vinyl tent fits over the frame and can be contoured to the substrate by laying sand bags around the perimeter. The tent body is 6.4 m in length and 4.9 m wide. A "bubble" port is attached to the top center of the tent and used to expel air trapped during SHARQ assembly. After SHARQ assembly is complete, a second polyethylene hose (inflow) is attached to this port and used to return water from the surface to the incubation chamber. The outflow and inflow water hoses are used to attach the SHARQ to a flow-through analytical system. This system pumps water out of the incubation chamber, through the analytical system (for pH, dissolved oxygen, salinity, and temperature measurements; removal of water samples; and injection of chemicals) and back into the chamber in a closed loop. Sand bags are laid on a 0.5-m seal-flap around the frame perimeter, overlapping end to end, to contour and weight the tent along the bottom, thus preventing leakage of water into or out of the tent. The flexible structure of the vinyl tent body allows oscillatory motion generated by waves to be translated through the tent structure to the water captured within the incubation system to mimic natural water movement.

The size (including length, width, and height), volume of the SHARQ, and flow rate of the circulation system can easily be adjusted by substituting smaller or larger frame components. Flow rate is easily adjusted by increasing or reducing flow using a ball valve on the PVC arm attachment for the circulation system hose or by changing water pump volume. The water mass inside the SHARQ can be isolated from the substrate by inserting a clear vinyl floor (6.1x3.7 m) between the substrate and frame base, thus completely isolating the volume of water from the rest of the water column and substrate.

The effects of clear vinyl sheeting on photosynthetically active radiation (PAR) were examined by measuring attenuation of PAR with water depth every 0.3 m to a depth of 8.5 m using a LiCor 4Π quantum sensor covered with a sleeve made from the same clear vinyl sheeting used to construct the tent and performing the same measurements with the sensor uncovered.

Minimum current velocities were measured inside the SHARQ incubation chamber deployed in approximately 1.5 m water depth. A Sontek acoustic doppler velocimeter was deployed in the center of the chamber approximately 15 cm above the seafloor. Current velocities were measured in x, y, and z coordinate directions every 1 min for 5 h. The smaller of two water pumps (133 l min^{-1}) typically used for the flow-through analytical system was activated during testing.

The volume of the SHARQ, the rate of water mixing in the incubation chamber, and the extent of water leakage were measured during SHARQ deployments. These measurements were accomplished by injecting a precisely known quantity of fluorescein dye into the incubation chamber through a sample port on the flow-through analytical system during dark hours. Fluorescein concentrations were monitored throughout the duration of experiments using a Model 10-AU Digital Fluorometer (Turner Designs). The water-mixing rate for consecutive SHARQ deployments was determined from the amount of time required to reach equilibrium dye concentrations after initial injection. The volume of the incubation chamber on various substrate types (including mud bottom, seagrass on sand, and patch reefs on sand) was calculated from dye dilution after equilibration was established. Over time, fluorescein dye binds to organic and carbonate material, and photodecays upon exposure to sunlight (Smart and Laidlaw 1977). Rates of water leakage from the SHARQ incubation chamber were determined by comparing dye concentrations corrected for theoretical decay by binding and photodecay to measured values. Values for absorption of dye to carbonate sediments (2% of total concentration) and organic material (17% of total concentration) (Smart and Laidlaw 1977) were used to calculate theoretical dye concentration decay due to absorption. An average minimum photochemical decay coefficient of 3.1×10^{-2} calculated from values of Smart and Laidlaw (1977) was used to determine theoretical concentration decay during light periods via $F = F1e^{-kt}$, where F1 is initial fluorescence, F is fluorescence at time t, e is the base of the natural logarithm, and k is the decay coefficient. Use of this photochemical decay coefficient for correction of dye curves is limited to water depth of approximately 1 m due to the dependency of the rate of photochemical decay on light intensity. This theoretical decay curve was then used to correct raw fluorescence data to show decreases in dye concentration associated with leakage of water into or out of the incubation chamber.

Measuring coral reef community metabolism

Field tests of the SHARQ system were performed on representative coral reef substrates located on the well-developed reef flat along the south coast of Molokai during 9 to 17 February 2000. The reef flat is shallow, ranging from 1.2 to 2 m, and highly turbid. Horizontal visibility rarely exceeded 5 m and was often less than 1.5 m. The reef flat is approximately 1 km wide and shows an onshore to offshore transition from coral rubble covered by terrigenous sediment and algal turf, to sand bottom and coral rubble, to sand bottom with small patch reefs up to the reef crest. Molokai reef-flat patch reefs are dominated by scleractinian corals (*Porites lobata*, *Porites compressa*, *Montipora capitata*, and *Pocillopora* sp.), several species of coralline algae, and *Halimeda discoidea*. The non-living components are covered with a veneer of brown filamentous algal growth. Temperature varied between 24.0 and 28.1 °C, salinity ranged from 33.2 to 35.6, and PAR ranged between 0 and 1,844 μEm^{-2} s^{-1} during field tests. Field tests were also performed on coral reef substrates in Biscayne National Park, Florida, during 27 June to 1 July 2000; 30 May to 2 June 2001; and 12 to 13 July 2002. The Biscayne patch reefs range from approximately 3 to 10 m in depth, and are dominated by octocorals, a variety of scleractinia (*Montastraea annularis*, *Porites astreoides*, *Acropora cervicornis*, *Siderastrea siderea*), several species of *Halimeda*, and coralline algae. Temperature varied between 27.3 and 30.2 °C, salinity ranged from 33.6 to 35.4, and PAR ranged between 0 and 2,333 μEm^{-2} s^{-1}.

Community metabolism (including photosynthesis, respiration, and calcification) associated with sand bottom, coral rubble encrusted with algal turf and coralline algae, 10% coral cover on sand, 22% coral cover on sand, 100% patch reef cover, and dense and sparse seagrass beds was measured by deploying the SHARQ incubation system on each substrate type for a minimum of 24 h. Percentage of coral cover within the SHARQ incubation chamber was determined by photoquads and by measuring the circumference of all coral colonies within the incubation chamber.

Total alkalinity (TA), dissolved oxygen, pH, salinity, and temperature of the water in the incubation chamber were measured and used to calculate community metabolism. Dissolved oxygen, pH, temperature, and salinity were measured continuously using a YSI dissolved oxygen meter and pressure-compensated field probe ($\pm$0.1 mg l^{-1}), Orion Ross pH electrode ($\pm$0.005 pH unit), salinity ($\pm$0.1 psu), and temperature probes ($\pm$0.1 °C). All probes were fitted into a PVC manifold attached to the flow-through analytical system of the SHARQ. Data were logged every 1 min during 24-h experiments. pH electrodes were calibrated using *Tris* seawater buffers prepared at an ionic strength of 0.7 and scaled to free-hydrogen-ion concentration scale (pH_T) (Millero 1996). Water samples for total alkalinity measurements were removed from a sampling port every 4 h. Total alkalinity ($\pm$4 μeq l^{-1}) was measured by Gran titration (Millero et al. 1993) using an automated titration system

calibrated with standard reference material (SRM) provided by Dr. F. Millero of the University of Miami. Salinity did not vary inside the incubation chamber during experiments; thus, total alkalinity was not normalized to salinity.

Metabolic parameters were calculated using procedures described in Kinsey (1978). Net calcification (C) was determined for six 4-h time periods within each 24-h incubation period (three during daylight hours and three during dark hours) using the alkalinity anomaly technique (Smith and Key 1975) such that $C = 0.5(\delta TA)$. Net photosynthesis (y) and respiration (r) were calculated from dissolved oxygen at 15-min intervals throughout 24-h incubation periods. Net metabolic rates per unit area of substrate (g O_2 m^{-2} 15 min^{-1}) were obtained from the concentration change (g O_2 m^{-3} 15 min^{-1}) from the beginning to end of each 15-min time period multiplied by the ratio of the volume (m^3) to surface area (m^2) of the incubation chamber. Diurnal curves of net photosynthesis (y) and respiration (r) were generated from an average of 84 data points per 24-h incubation period. Daily gross production (P) was calculated by integrating the metabolism curves from sunrise to sunset with respect to the rate of gross production (y + r). Twenty-four-hour respiration (R) was calculated from the mean rate of respiration measured during each incubation period. Incident PAR was measured less than 2 m above the water surface using a 2π LiCor quantum sensor and approximately 15 cm from the seafloor using a 4π LiCor quantum sensor during each deployment.

Results and discussion

SHARQ specifications

Field trials indicate that the SHARQ incubation chamber is an effective tool for in situ isolation of a water mass over a variety of benthic substrate types for process monitoring and experimentation. Results of tests on the effect of the clear vinyl sheeting used to construct the SHARQ on attenuation of PAR indicate that no difference in PAR attenuation occurs between sleeved and unsleeved sensor data below a depth of 0.9 m (Fig. 2). Clear vinyl sheeting reduces PAR by 29% at 0.3 m, 21% at 0.6 m, and 4% at 0.9 m water depth relative to measurements taken using an unsleeved sensor. PAR attenuation due to vinyl sheeting was not detected below 1.0 m depth.

Preliminary results of current meter measurements inside the incubation chamber indicate that water flow is primarily oscillatory when deployed in water depths that are impacted by waves. Figure 3 shows velocity data collected from the center of the incubation chamber approximately 15 cm above the seafloor in the z-coordinate direction. The z-coordinate lies parallel to the length of the chamber along the spine. Current velocities near the chamber floor reach up to 6 cm s^{-1}. In this particular example, the primary wave influence on the seafloor was from wave sets with a frequency of approximately 40 s. Similar oscillatory patterns are also observed in vertical (y-coordinate) and width-parallel (x-coordinate) data sets. Visual observations show that movement of seagrass (and other benthos) inside the chamber mimics movement of benthos located outside the chamber. Calculated current velocities of water exiting the PVC arm of the circulation system are 50 cm s^{-1} at a pump flow-rate of 133 l min^{-1} and 93 cm s^{-1} at a pump volume of 246 l min^{-1} based on a PVC arm diameter of 7.5 cm. Current velocities measured near the center floor of the chamber represent minimum velocities. Visual observation of dye injections into the chamber while deployed at depths that exceed wave influence indicate turbulent flow. Flow characteristics are highly influenced by the topography of the substrate within the chamber and will vary from location to location.

Andrews and Pickard (1990) report water current velocities ranging from 5 to 144 cm s^{-1} in various reef environments. Ogston et al. (2003) reports that current velocities on the Molokai reef flat are primarily wind-driven and reach maximum speeds of approximately 15 cm s^{-1} with peak tidal currents of 3 to 5 cm s^{-1}. Current velocities inside the SHARQ incubation chamber are within the range of velocities measured for many reef environments. Additional current-meter studies are required to characterize flow in greater detail.

The average volume of the SHARQ (determined by fluorescein dye injections) assembled using a frame length and width of 4.9x2.4 m at heights of 0.6 m for three consecutive deployments on "flat" mud bottom is $3{,}975 \pm 47$ l (or 1.2%). Volume varied depending on substrate topography, but is consistent between replicate deployments on the same substrate (Table 1). For replicate deployments, percent error has not exceeded 3.7%. Water mixing rates ranged from 12 to 14 min at a SHARQ-enclosure height of 0.6 m and a water pumping rate of 133 l min^{-1}, 24 to 30 min at a height of 1.2 m and a water pumping rate of 133 l min^{-1}. Water-mixing rates at each height are reduced by approximately half the time when using a water pumping rate of 246 l min^{-1}.

Graphical results of raw fluorescence data typically show a slight linear decrease in fluorescein concentrations through dark hours consistent with rates of dye adsorption to sediments and organic material, and exponential decrease during light hours due to photochemical decay of fluorescein (Fig. 4). Repetitive dye injections during experiments performed at different depths indicate that the measured rate of photochemical decay can only be predicted using the coefficients reported by Smart and Laidlaw (1977) for depths of approximately 1 m or less. In Fig. 4, the measured rate of photodecay deviates from the theoretical decay curve due to attenuated light at a water depth of approximately 8 m during this experiment. Theoretical dye concentrations calculated from dye absorption are representative of raw fluorescence data. Dye concentrations corrected for adsorption generally show a horizontal linear trend when no leakage of water from the incubation chamber occurs.

No significant leakage occurred from the incubation system during Biscayne National Park experiments, or during experiments on sand or patch reefs on the Molokai reef flat despite significant wave pulse due to swells. However, leakage was observed during the experiment on coral rubble through periods of significant wave

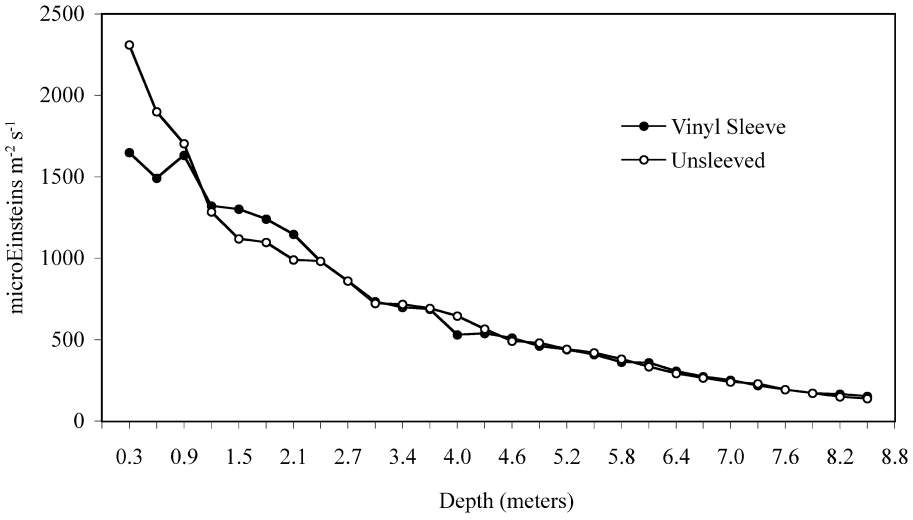

Fig. 2 Attenuation of photosynthetically active radiation (PAR) by the clear vinyl sheeting used to construct the SHARQ. No attenuation is observed below 1 m water depth

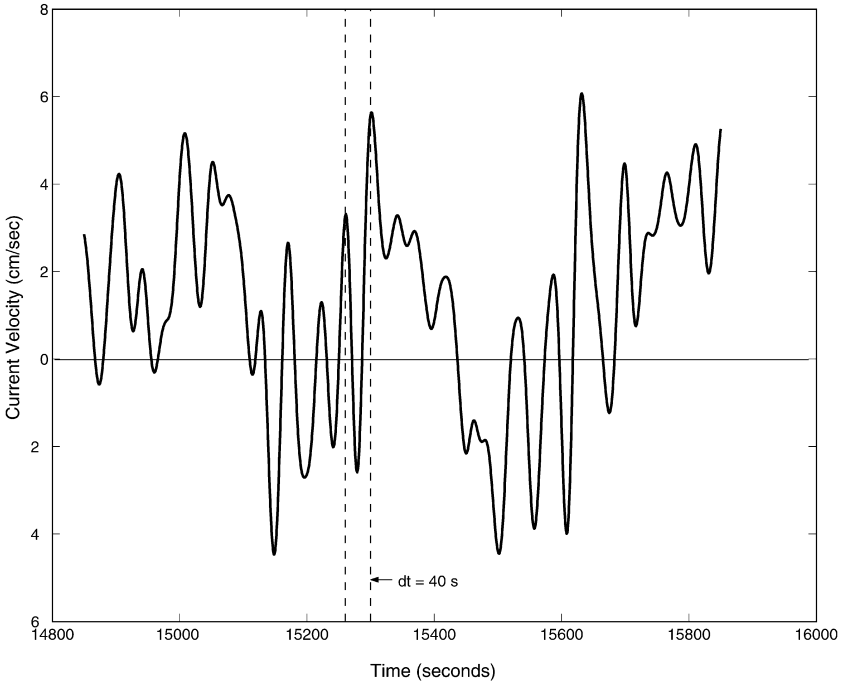

Fig. 3 Current velocity data from inside the SHARQ measured along the z-coordinate axis, parallel to the length of the incubation chamber. *Dotted lines* indicate spacing between wave sets generating oscillatory current flow, with complete oscillation occurring at a frequency of approximately 40 s

pulse, presumably due to pumping of water through the coarse rubble as the chamber flexed with passing waves.

Coral reef community metabolism

The SHARQ system enables continuous measurement of chemical changes associated with community-level benthic processes and accurate determination of metabolic parameters throughout 24-h time periods. Diurnal curves of community metabolism for all substrate types are similar to classical metabolism curves presented in March and Smith (1978) and Kinsey (1978). Figure 5 shows a typical curve generated for a patch reef in Biscayne Bay with approximately 10% coral cover. Net rates of production were calculated at 15-min intervals (the approximate rate of mixing in the incubation chamber) to generate robust data sets from which to derive daily gross production rates via data set integration. While the rate of respiration in this example approaches constancy during the night, many data sets show variable rates of respiration during dark hours. Respiration rates of many marine organisms begin to decrease at dissolved oxygen values below 20% of air saturation (e.g. Giese 1962; Eriksen and Iversen 1997). However, dissolved oxygen did not decrease below 20% of ambient oxygen saturation during any of the experiments. Twenty-four respiration rates were derived from the mean respiration rate from each data set.

Metabolic parameters including net calcification, daily gross production, 24-h respiration, calcification/dissolution (C/D) ratios, gross daily production/24-h

Table 1 Repetitive volume measurements of the SHARQ system from fluorescein dye injections. *SD* Standard deviation

Substrate Type	Frame lxwxh	Volume 1 (liters)	Volume 2 (liters)	Volume 3 (liters)	Average (liters)	SD (liters)	Percent error
Mud bottom	4.9×2.4×0.6	3,935	4,027	3,964	3,975	47	1.2
Seagrass on sand	4.9×2.4×1.2	9,806	9,307	–	9,557	352	3.7
Patch reef	4.9×2.4×1.2	10,797	10,950	–	10,874	108	0.99

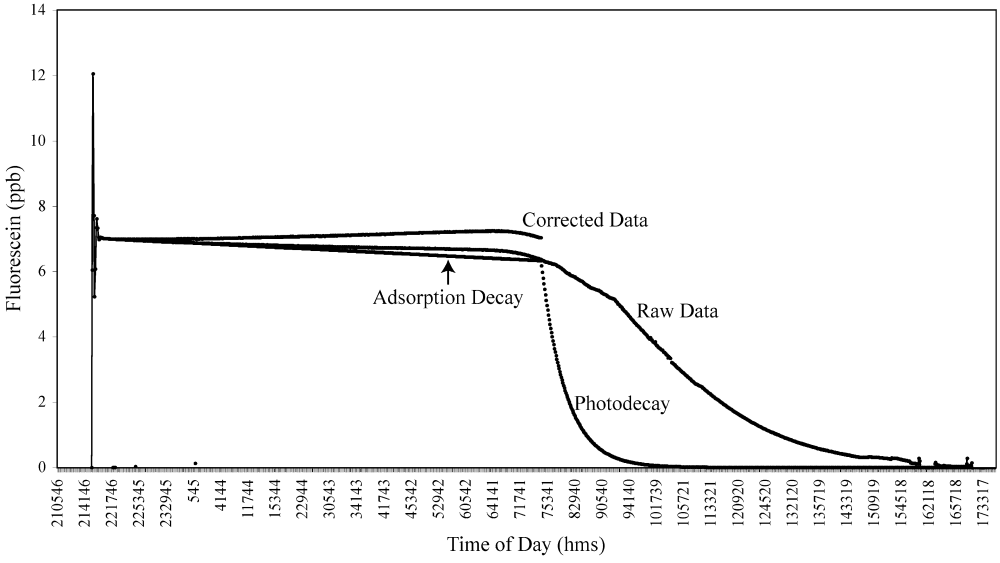

Fig. 4 Fluorescein dye injections are used to calculate the volume of the incubation chamber, equilibration rate, and whether or not the chamber is leaking. Raw data were corrected for decay by adsorption to organics and photodegradation

respiration (P/R) ratios, and the correlation between irradiance and the rate of net production are shown in Table 2. Rates of daily gross production and 24-h respiration for all substrate types ranged from 0.26 to 6.45 g O_2 $m^{-2}day^{-1}$ and 1.96 to 8.10 g O_2 m^{-2} 24 h^{-1}, respectively. Lowest P values were associated with sand bottom, while highest values were associated with patch reefs and seagrass beds from Biscayne Bay. Lowest rates of R were associated with seagrass beds and sand bottom, while highest rates were associated with patch reefs. Sparse seagrass beds (primarily consisting of less than 20% *Thalassia* sp. on carbonate sand) showed the highest P/R ratios, ranging from 0.8 to 1.2. Dense seagrass beds (primarily consisting of mixed *Syringodium* sp. and *Thalassia* sp. with no substrate visible between blades) had P/R ratios similar to patch reefs, ranging from approximately 0.8 to 0.9. Sand bottom in Hawaii showed the lowest P/R ratio of approximately 0.1. Average P/R ratios for patch reefs, dense seagrass beds, and sparse seagrass beds are approximately 0.8, 0.9, and 1.1, respectively. Photosynthetic and respiratory quotients were not determined for this study.

Measured rates of metabolism for these experiments fall within the range of values determined for similar benthic habitats using leaf-marking techniques, ^{14}C uptake experiments (Zieman et al. 1989; Fourqurean et al. 2001), and flow respirometry (Smith 1983; Kinsey 1983, 1985). Fourqurean et al. (2001) measured areal productivity rates for *Thalassia testudinum* seagrass beds in south Florida ranging from 0.05 to 3.29 g dw (dry weight) m^{-2} day^{-1} with a yearly mean of 0.70 g dw m^{-2} day^{-1}. Conversion of these areal productivity values to net photosynthesis assuming a leaf carbon content of 40% (Zieman 1982) results in rates ranging from 0.05 to 3.52 g O_2 m^{-2} day^{-1} with an average of 0.75 g O_2 m^{-2} day^{-1}. Zieman et al. (1989) measured similar values for areal productivity for *Thalassia* ranging from 0.05 to 3.42 g dw m^{-2} day^{-1} with a mean of 0.97 g dw m^{-2} day^{-1}. Conversion of these values results in net productivity rates of 0.05 to 3.65 g O_2 m^{-2} day^{-1} with an average of 1.04 g O_2 m^{-2} day^{-1}. Daily net photosynthesis (g O_2 m^{-2} day^{-1}) for *Thalassia* and mixed *Thalassia* and *Syringodium* seagrass beds from Biscayne Bay was calculated by integrating metabolism curves from sunrise to sunset with respect to the rate of net photosynthesis (y). Daily net photosynthesis values range from 0.66 to 1.82 g O_2 m^{-2} day^{-1} with an average of 1.27 g O_2 m^{-2} day^{-1}. These values are consistent with previously reported values described above.

Kinsey (1985) reviews gross primary production rates and P/R ratios measured using flow respirometry for a variety of coral reef environments. Daily gross production values reported in this review range from 6.1 to 16.0 g O_2 m^{-2} day^{-1} with a P/R of 1 for complete Pacific reef systems, and 10.7 to 51.0 g O_2 m^{-2} day^{-1} for Pacific reef-flat coral/algal zones with a P/R ranging from 0.7 to 1.6. Rogers (1979b) reports slightly lower P and P/R values for San Cristobal reef in the Caribbean of 5.4 g O_2 m^{-2} day^{-1} and 0.7, respectively. Daily gross

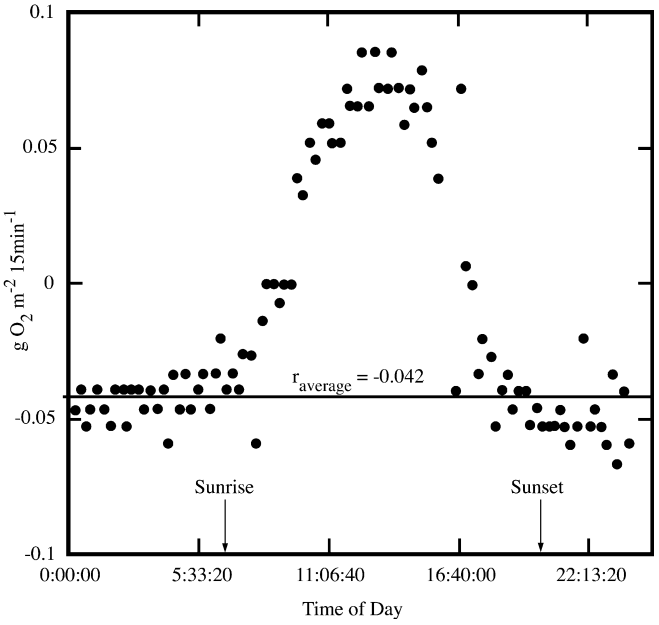

Fig. 5 Diurnal metabolic curve generated from measured rates of net photosynthesis (y) and respiration (r) for a patch reef in Biscayne Bay with approximately 10% coral cover. Metabolic rates were calculated at 15-min intervals throughout the incubation period. $r_{average}$ Average rate of respiration (g O_2 m^{-2} 15 min^{-1}) from which 24-h respiration (*R*) was calculated

production and P/R values for the South Molokai reef flat and Biscayne Patch reefs in this study range from 2.4 to 6.5 g O_2 m^{-2} day^{-1} and 0.6 to 0.9 (Table 2), respectively. Lowest P values are associated with the Molokai reef flat, an area that is highly impacted by terrigenous sediment influx (Ogston et al. 2003). Higher P values associated with Biscayne Bay patch reefs are more similar to those reported for the San Cristobal reef system (Rogers 1979b).

Net calcification values range from 0.02 g $CaCO_3$ m^{-2} day^{-1} associated with sand bottom to greater than 2 g $CaCO_3$ m^{-2} day^{-1} associated with patch reefs (Table 2). The average net calcification rate for Molokai and Biscayne patch reefs was 1.12 g $CaCO_3$ m^{-2} day^{-1}. Note that during daylight hours, calcification dominated over dissolution of carbonate sediment. However, dissolution exceeded calcification during dark hours on all substrates except one Biscayne patch reef (labeled FL Patch Reef Top, 02/06/01 in Table 2). Dissolution during the night ranged from 0.28 to 1.77 g $CaCO_3$ m^{-2} - $night^{-1}$. Patch reefs generally showed the highest calcification:dissolution (C:D) ratios ranging from 0.43 to 4.10. Average C:D ratios for patch reefs, dense seagrass beds, sparse seagrass beds (excluding an anomalously high C:D ratio for a sparse seagrass bed examined on 30/05/01), coral rubble, and sand bottom are 1.6, 0.6, 0.4, 0.2, and 0.7, respectively. Molokai reef flat substrates showed the highest rates of carbonate sediment dissolution. This may result from the high content of high-magnesian calcite in Molokai carbonate sand (40%) relative to Biscayne Bay carbonate sand (24%) (Enos 1977). High-magnesian calcite is more soluble than calcite or aragonite (Weyl 1967; Plummer and Mackenzie 1974).

Table 2 Metabolic parameters for representative substrate types of the Biscayne Bay, Florida (*F*), reef tract and South Molokai, Hawaii (*HI*), reef flat. *C* Net calcification (positive values) or dissolution (negative values); *LRE* linear regression equation describing the correlation between *y* (rate of net photosynthesis) and irradiance, where *y* = g O_2 m^{-2} 15 min^{-1}, *m* is the slope of the line in scientific notation where *e* is exponent, *x* = microEin m^{-2} s^{-1}, *b* is the y intercept, and *me*−5 = mx10^{-5}; *Corr*. correlation coefficient, *R*, for reported LRE; *P* daily gross production (g O_2 m^{-2}), integration of metabolism curve with respect to *y* + *r* from sunrise to sunset; *R* 24-h respiration (g O_2 m^{-2}) calculated from the average night-time respiration rate; *P*/*R* ratio of daily gross production to 24-h respiration; *C*/*D* ratio of net calcification during day to net dissolution during night; *n* number of net photosynthesis and respiration data points collected and used to generate each metabolism curve; *nd* no data available; *na* not applicable

Substrate description	Date	Hours of sunlight	C (g $CaCO_3$ m^{-2})		LRE y = mx + b m/b	Corr.	P	R	P/R	C/D	*n*
			Day	Night							
HI patch reef 22%	16/02/00	11.4	2.06	–1.77	8.386e–5/–0.04698	0.95	2.80	4.44	0.63	1.20	75
HI patch reef 10%	15/02/00	11.4	0.56	–1.30	6.241e–5/–0.03795	0.90	2.40	2.74	0.88	0.43	81
FL patch reef 10%	29/06/00	13.8	0.61	–0.54	nd	nd	3.23	4.01	0.81	1.13	94
FL patch reef top	30/06/00	13.8	2.33	–0.57	nd	nd	6.45	8.08	0.80	4.10	88
FL patch reef top	02/06/01	13.6	0.47	0.35	4.678e–4/–0.15657	0.98	6.41	8.10	0.79	na	96
FL heterogeneous	31/05/01	13.6	0.70	–0.74	nd	nd	4.23	5.31	0.80	0.95	96
FL dense seagrass	30/05/01	13.6	0.25	–0.28	1.140e–4/–0.02307	0.82	2.53	2.89	0.83	0.88	83
FL dense seagrass	31/05/01	13.6	0.45	–0.49	1.140e–4/–0.02307	0.82	3.09	3.51	0.88	0.92	93
FL dense seagrass	01/06/01	13.6	0.10	–0.50	1.140e–4/–0.02307	0.82	3.60	4.02	0.90	0.20	86
FL dense seagrass	02/06/01	13.6	0.19	–0.50	1.140e–4/–0.02307	0.82	2.29	2.86	0.80	0.38	73
FL sparse seagrass	27/06/00	13.8	0.34	–0.64	nd	nd	2.97	3.56	0.83	0.53	76
FL sparse seagrass	28/06/00	13.8	0.23	–0.65	nd	nd	3.64	3.34	1.09	0.35	89
FL sparse seagrass	30/05/01	13.6	0.97	–0.35	9.108e–5/–0.00868	0.75	3.08	2.50	1.23	2.73	83
FL sparse seagrass	12/07/02	13.6	0.21	–0.33	1.386e–4/–0.00854	0.97	3.16	2.68	1.18	0.64	87
HI coral rubble	13/02/00	11.4	0.34	–1.41	5.804e–5/–0.02296	0.95	2.72	2.79	0.97	0.24	81
HI sand bottom	09/02/00	11.4	0.02	–0.33	2.158e–5/–0.02374	0.87	0.26	2.62	0.10	0.06	52
FL sand bottom	12/07/02	13.6	0.411	–0.30	7.385e–5/–0.00914	0.93	1.76	1.96	0.90	1.37	95

Smith's (1983) review of calcification rates for a variety of Pacific reef-flat environments reports calcification rates ranging from 0.3 to 12 kg $CaCO_3$ m^{-2} - $year^{-1}$. Seasonal calcification rates were not measured for Biscayne and Molokai patch reefs in this study. However, preliminary estimates based on an average calcification rate of 1.12 g $CaCO_3$ m^{-2} day^{-1} for patch reefs result in a yearly production rate of 0.41 kg $CaCO_3$ m^{-2}. This estimate suggests that calcification rates associated with patch reefs measured in this study fall within the range of values previously measured for reef systems using flow respirometry techniques.

Results of this study have demonstrated the utility of the SHARQ system for use as a monitoring tool for fundamental benthic habitat processes. The SHARQ also provides a mechanism for in situ alteration of environmental variables (including, but not limited to, nutrients, salinity, turbidity, pH, pCO_2, and contaminants) and investigations of reef responses to environmental stress. In situ investigations using the SHARQ incubation system to examine the effects of elevated CO_2 on coral reef metabolism have been performed on the Molokai reef flat. The SHARQ has been used to naturally elevate CO_2 levels in situ by trapping respired CO_2 (Halley and Yates 2000), and has also been coupled with equilibration chambers located in-line with the flow-through analytical system that enabled injection of CO_2 gas and equilibration of seawater overlying the enclosed substrate. These preliminary experiments indicate that the SHARQ is an effective tool for in situ alteration of environmental parameters and experimentation.

Experiments using the SHARQ have been performed on relatively short time scales (days to 2 weeks) due to the manual collection of water samples from sample ports of the flow-through analytical system that required maintenance of a surface platform. However, the SHARQ can be utilized in conjunction with deployable, automated multimeters, dispensing with the need to maintain a surface platform. This will enable experiments to be performed over longer time periods (weeks to months) with minimal maintenance of the system.

Acknowledgments This research was funded by the US Geological Survey, Geological Discipline, Coastal and Marine Geology Program. We gratefully acknowledge Richard Curry, Research Coordinator of Biscayne National Park, for field and logistical support. We extend sincere gratitude to Captain Barry Denton and First Mate Randy Miglowski, the crew of the support vessel Winning Ticket, for assistance with Biscayne field expeditions. We thank Jerry Johnson, Smiley Kahue, Lyndon DelaCruz, and Roland Moran for technical and logistical assistance during Molokai field expeditions.

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