Sponges represent a major source of inorganic nitrogen in Florida Bay (U.S.A.)

Daniel R. Hoer [1*,a] **William Sharp,** [2] **Gabriel Delgado,** [2] **Niels L. Lindquist,** [3] **Christopher S. Martens** [1,3]

[1]Department of Marine Sciences, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina
[2]Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Marathon, Florida
[3]Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, North Carolina

Abstract

Florida Bay nutrient budgets have shown that the majority of existing and influent nitrogen (N) is in organic forms. Consequently, local remineralization processes have been found to regulate the supply of dissolved inorganic nitrogen (DIN). Sponges have dominated benthic animal biomass in Florida Bay and are known to influence local DIN concentrations through remineralization organic matter, yet the role of these organisms in local N budgets is largely unaddressed. We quantified the role of sponges in N cycling in Florida Bay during 2012–2013 by constructing an N budget for a sponge-rich basin. Surveys of sponge biomass conducted in Mystery Basin found sponges at 57 of the 59 assessed stations. Sponge population maxima reached 21 individuals m^{-2} and biomass contributions as high as 4.4 L_{sponge} m^{-2}. We estimated an average areal DIN contribution from total sponge biomass of 0.59 ± 0.28 mmol N m^{-2} d^{-1}. However, calculated fluxes from the 59 stations exhibited significant spatial variability associated with changes in the size and species composition of the sponge community; peak N fluxes reached 3.5 ± 0.9 mmol N m^{-2} d^{-1} in areas with large populations of high microbial abundance sponges. The average flux from the sponge community was the largest of the estimated sources of DIN to Mystery Basin, representing roughly half of the overall N sourcing. This N satisfied more than half of the demand by primary productivity. These results indicate that sponges are important sources of inorganic N to Florida Bay environments.

Florida Bay is an estuarine ecosystem bounded on the north by the Everglades wetlands, the south and east by the Florida Keys, and the Gulf of Mexico to the west (Fig. 1). The bay is generally shallow (typically < 3 m depth) and the water column is usually clear and oligotrophic (e.g., McNulty et al. 1972). Benthic communities are characterized by a diverse sponge population (e.g., Peterson et al. 2006), octocorals, small hard corals, seagrasses (primarily *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme*; Zieman et al. 1989), and macroalgae (calcareous green algae, including *Halimeda* spp. and *Penicillus* spp., and red drift algae, predominantly *Laurencia* spp.; Stevely et al. 2010). Primary productivity is dominated by extensive seagrass meadows and shows a trend of increasing phosphorus (P) limitation eastward of the broadly marine conditions in western Florida Bay where nitrogen (N) can be limiting (Fourqurean et al. 1993, Lavrentyev et al. 1998).

Bay-wide nutrient budgets constructed for this system (e.g., Rudnick et al. 1999; Boyer and Keller 2007) have shown that most nitrogen (N) and phosphorus (P) in the water column is in organic forms (Boyer et al. 1997; Boyer et al. 2006). The sources of these nutrients are similarly dominated by organic matter (as much as 90% of influent N from the Everglades is as dissolved organic nitrogen [DON]; Boyer et al. 1999; Childers et al. 2006). Consequently, local organic matter recycling processes have been found to regulate the supply of dissolved inorganic nitrogen (DIN) in many locations (Rudnick et al. 2005; Boyer and Keller 2007; Boyer et al. 2009).

Carbonate sand and mud banks subdivide the central bay into discrete basins which restrict physical exchange and lead to an enhanced role of local processes in chemical cycles (e.g., Fourqurean et al. 1993; Yarbro and Carlson 2008; Zhang and Fischer 2014). For example, the extensive seagrass beds in some of these basins have been highlighted as potentially important sites of DON remineralization (Yarbro and Carlson 2008). Sponges have also been shown to be important sources of recycled N through remineralization of dissolved and particulate organic matter in this and other environments (e.g., Corredor and Wilkinson 1988; Southwell et al. 2008; Hoer et al. 2018). The role of these organisms in Florida Bay N budgets has been posited to be significant (e.g., Boyer et al. 2005), they remain largely unaddressed.

An extensive biomass survey conducted throughout Florida Bay found sponge populations at 70% of 207 sites, with densities up to 22 individuals m^{-2} (Peterson et al. 2006). The communities

*Correspondence: dan.hoer@gmail.com

[a]Present address: Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts

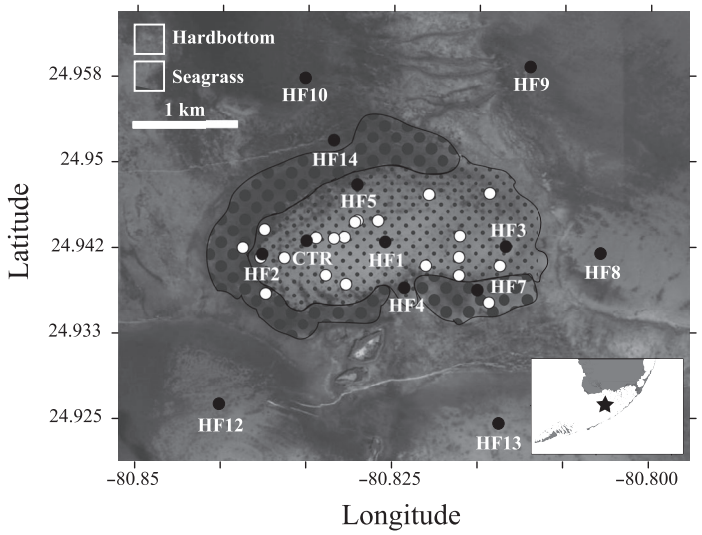

Fig. 1. ArcMap image of the study area showing the location of water quality collection sites as well as the areal extent of seagrass and hardbottom habitat types. The inset shows the study location (indicated with a black star) relative to peninsular Florida and the Florida Keys island chain. White circles indicate collections performed during August 2012 and labeled black circles were sampled in May 2013. SEASII-NO_x instrumentation was deployed at CTR during May 2013.

of these organisms were distributed heterogeneously throughout the bay and elevated sponge biomass and population densities were observed in the hardbottom habitats of the southern-central and western regions (Peterson et al. 2006). High sponge biomass has the potential to represent an important source of recycled N to Florida Bay, particularly considering the DIN release rates observed from 11 species common to this system (Hoer et al. 2018) and the role some of these species in the benthic nutrient budgets elsewhere (*Chondrilla nucula* and *Ircinia* sp.; Corredor and Wilkinson 1988; Diaz and Ward 1997; Southwell et al. 2008). Using sponge biomass data from the surveys conducted by Peterson et al. (2006), it was shown that the sponge community has the potential to produce a DIN flux of 15.3 ± 3.3 mmol N m^{-2} d^{-1} at a *C. nucula* dominated site in the northeastern corner of the bay (Hoer et al. 2018). Despite, and perhaps due to, the magnitude of this source of recycled N, this portion of the bay is generally severely P-limited (Fourqurean et al. 1993; Lavrentyev et al. 1998). Conversely, the western portion of the bay is often characterized by broadly marine conditions and is often N-limited (Fourqurean et al. 1993; Lavrentyev et al. 1998). We chose to test the role of sponge community N cycling in a sponge-rich site in west-central Florida Bay where the contributed DIN from organic matter remineralization may buffer N limitation from influent marine conditions.

Mystery Basin (24°56′36.6″N, 80°49′32.8″W) was selected for our experiments because its benthic community composition appeared to be representative of important sponge-rich sites throughout the N-limited areas of the bay. Like other basins in the bay, the restricted water exchange between Mystery Basin and surrounding waters was hypothesized to allow local processes to have a greater role in nitrogen cycling processes. Determination of DIN contributions from the abundant sponge biomass in Mystery Basin should also improve our ability to quantify their importance in the overall nitrogen budget of Florida Bay. We tested the role of sponges in Mystery Basin by first calculating the potential DIN contribution from sponges through combining species-specific biomass surveys with in situ, measured DIN release rates from 11 dominant species (Hoer et al. 2018). We then compared the magnitude of the calculated fluxes to other local sources and sinks of N. We hypothesized that the efflux of DIN associated with the sponge community would be a dominant source of NH_4^+ and $NO_2^- + NO_3^-$ and would be of critical importance to meeting the N demand from seagrass primary productivity (e.g., Fourqurean et al. 1993; Lavrentyev et al. 1998). Additionally, we hypothesized that the magnitude and relative importance of sponge DIN efflux vs. other sources and sinks would vary spatially as a result of varying sponge biomass and sponge community composition (i.e., relative abundance of particular species), and that these factors would contribute to locally visible changes in the quantity and speciation of water column DIN as either NH_4^+ or $NO_2^- + NO_3^-$ (henceforth NO_x^-).

Methods

Study area

Mystery Basin is located within the boundaries of the Everglades National Park, approximately 13 km north of Long Key, Florida. It is in the west-central portion of Florida Bay (Fig. 1; Boyer et al. 1997; Gibson et al. 2008), which tends toward marine conditions due to a dominant role of influent water from the Gulf of Mexico and only a minor contribution from Everglades discharge (Fourqurean et al. 1993; Boyer et al. 1997; Rudnick et al. 1999). The basin is within 10 km of five long-term (1991–2008) monitoring sites within the Southeast Environmental Research Center (SERC) water quality-monitoring network (SERC-FIU WQMN Program) which provides historical nutrient data for the surrounding geographic area. The central basin is characterized by a thin veneer (< 5 cm) of carbonate sediment overlying Pleistocene limestone hard grounds, and is populated by sponges, octocorals, small hard corals, seagrasses, and macroalgae common to the surrounding Florida Bay ecosystem. The sponge community in 2012 was roughly analogous to other sponge-rich sites throughout Florida Bay surveyed by Peterson et al. (2006). Mystery Basin is approximately elliptical (major axis: ~ 3 km, minor axis: ~ 2 km; Fig. 1) and has a < 2 m water column that is almost completely isolated from surrounding basins by seagrass-covered banks that shoal to depths less than 30 cm during low tides; the tide at this location is semidiurnal and characterized by a range of approximately 0.2 m (Rok et al. unpubl. data). The bank-attenuated water exchange leads to a

basin residence time between 7 and 14 d (Rok et al. unpubl.), which is approximately equal to the residence time of Rabbit Key Basin located immediately to the north (Hunt et al. 2005).

Water column DIN and total dissolved nitrogen

Water samples for DIN measurements were taken at a total of 34 sites in and around Mystery Basin (Fig. 1) in August 2012 and May 2013 by divers using SCUBA. In addition to DIN measurements, total dissolved nitrogen (TDN) was also analyzed using the samples collected in May 2013. At each site, a water sample was collected in a 60 mL polypropylene syringe and filtered in-line at the point of collection. The filter (Whatman GF/F; ~ 0.7 μm nominal pore size) and 10 cm of small-diameter, high-density polyethylene tubing were attached to one arm of a polycarbonate three-way stopcock which was fitted directly to the syringe. The stopcock allowed isolation of collected water or discharge through the open third arm during rinsing. The length of attached tubing helped minimize contamination by allowing the collecting diver to be positioned down-current from the sampled water. A new, combusted (baked at 450°C for > 6 h), 25 mm GF/F was used for the filtration of each water sample. GF/Fs were selected due to their suitability for precombustion and use in prior studies of nutrient concentrations in Florida Bay (e.g., Boyer et al. 1997; Boyer et al. 2006; Gibson et al. 2008). During sample collection, the syringe, filter, and tubing were rinsed 3× with filtered target water and the rinsing volume was discharged. The fourth volume was slowly drawn into the syringe (< 2 mL s^{-1}) to ensure the collection was representative of the desired water mass, and the attached stopcock was closed to prevent accidental sample loss. The sample was returned to the surface and stored in a dark ice bath until transport to shore for subsampling and preservation (< 8 h from collection to shore-based processing). Samples were immediately divided for DIN (NH_4^+ and NO_x^-) as well as TDN analyses upon return to the laboratory provided by the Florida Fish and Wildlife Conservation Commission (FWC) located in Marathon, FL. TDN samples (20 mL volume) were put in sample-rinsed borosilicate glass scintillation vials; 100 μL of 50% H_3PO_4 was added, and the vials were stored at 4°C until subsequent analysis; DON was determined as the TDN content less DIN. Nitrate and nitrite (NO_x^-) samples (20 mL volume) were placed into sample-rinsed, borosilicate glass scintillation vials and immediately frozen and stored at −20°C until analysis. Ammonium (NH_4^+) samples (20 mL volume) were placed into sample-rinsed amber high-density polyethylene (HDPE) bottles. Ammonium samples were analyzed immediately upon return to the FWC shore laboratory to reduce the potential impact of degradation on sample integrity. For each location, the samples were collected in triplicate for quality assurance and control.

A single site near the center of Mystery Basin (Site ID: CTR; 24°56′30.84″N, 80°49′58.80″W; Fig. 1) was intensively sampled over a 3-d period (18–20 May 2013). During this time, a boat remained anchored at CTR, discrete water collections were performed using peristaltic pumps, and water column NO_x^- was analyzed in situ, in real-time via two deployed Spectrophotometric Elemental Analysis System autoanalyzers (SEASII-NO_x; Steimle et al. 2002; Adornato and Kaltenbacher 2005; Adornato et al. 2007; the latter includes detailed descriptions of similarly deployed instrumentation). Peristaltic pumps were set up to collect ambient water from two locations near the boat; one sample inlet was positioned near the bottommost SEASII-NO_x instrument which allowed discrete confirmation of in situ data. Inlets for peristaltic pump collection were approximately 0.15 m above bottom (mab) and target water was pumped through black HDPE tubing for shipboard collection. Sampling was performed four times daily, 08:00, 12:00, 17:00, and 22:00 h, in order to quantify diurnal variability in water quality parameters. The pumps ran constantly to prevent stagnation in the tubing and flow rates were set to 20 mL min^{-1} by adjusting pump speeds at the beginning of each sampled time to ensure accuracy in the delivered volumes. Samples were filtered using in-line 47 mm Whatman GF/Fs that were replaced and sample-rinsed prior to each collection. Samples for DIN and TDN were collected and stored in a dark ice bath until transport to shore for analysis or further preservation (< 24 h from collection to shore-based processing).

In addition to discrete peristaltic pump collections, the SEASII instruments obtained time-series NO_x^- concentrations at two different depths, 0.1 and 1.0 mab, in order to compare concentrations near the benthos with those near the surface. During analysis, each instrument sampled water from its respective depth and measured the combined concentrations of NO_3^- and NO_2^-, or NO_x^-, spectrophotometrically utilizing the Griess method (*see* Adornato et al. 2007). The instruments used 15 cm optical pathlengths which increased sensitivity and reduced the method detection limit to 25 nmol NO_x^- L^{-1} (determined by repeated analysis of standard solutions). Both SEASII-NO_x autoanalyzers were calibrated prior to and following deployment, and the accuracy of each instrument was checked daily with standards introduced in situ by divers on SCUBA. Buffer solution and premixed sulfanilamide/N(1-napthyl) ethylenediamine dihydrochloride reagents were attached to the instruments in darkened compounding bags (VitalMix 9316 and 9318) and these reagents were prepared and replaced daily.

Plastics that were used in sample collection and processing (peristaltic pump tubing, HDPE sample tubing, syringes, stopcocks, filter holders, and collection vial lids) were all soaked in a 0.1 mol L^{-1} HCl bath for > 12 h and triple rinsed with 18.2 MΩ type I water prior to use. Scintillation vials used for sample collection were acid washed, rinsed, and combusted. Amber HDPE sample bottles used for ammonium samples were acid washed and rinsed following the aforementioned protocol. Following the wash procedure, small aliquots of o-phthaladehyde working reagent were added to the bottles and

allowed to react for 24 h to ensure removal of any residual ammonium from the container. Prior to their use, the pretreatment solution was removed by triple rinsing with 18.2 MΩ type I water to ensure no residual reagent remained prior to sample or standard addition.

Laboratory sample analysis

Ammonium analyses were performed using the method of Holmes and Aminot (1999). Sampled volumes were reacted with 5 mL of o-phthaladehyde working reagent in amber, HDPE sample bottles and allowed to develop at room temperature for 2.5 h. After the incubation period, samples were analyzed using a Turner Designs TD-700 laboratory fluorometer equipped with an ammonium optical kit (Turner Designs 10-303). The method detection limit was determined to be 10 nmol L^{-1} by repeated standard measurements. Standards were prepared daily at the point of use by serial dilution of a purchased stock solution (Ricca Chemical Company 693-16), and analyzed with the prepared samples. Nitrate plus nitrite (NO_x^-) discrete samples were analyzed using SEASII-NO_x autoanalyzers configured for bench-top use. As with in situ analyses, NO_x^- was measured using 15 cm pathlengths and cadmium reduction of NO_3^- to NO_2^- followed by detection based on the Griess reaction. Standards for benchtop and in situ NO_x^- measurements were prepared by dilution of a purchased stock (SPEX Certiprep AS-NO39-2Y and ASNO29-2Y) and were analyzed daily with collected samples. TDN samples were analyzed with a Shimadzu TOC-L/TNM-L organic carbon and total nitrogen analyzer. Calibration curves were prepared from lab prepared stock solutions and were closely monitored during analysis. Standards were remade and rerun if the correlation coefficient was found to be less than 0.995, and standards were interspersed within samples to provide additional quality control.

Survey methodology

The boundary of Mystery Basin was operationally defined using satellite images in ArcMap (ESRI; Fig. 1) as the center of the bordering shoals, which surrounded the central hardbottom. Initial, qualitative assessments of the basin showed two apparently distinct substrata available for sponge colonization: seagrasses shoals that formed the border of the basin and carbonate hard grounds. Thus, sponge habitat in Mystery Basin was divided based on these distinctions to ensure that quantitative surveys accurately represented both putative habitats. The areal extent of each was then preliminarily identified and quantified from satellite images (Fig. 1). Brief assessments of points along established boundaries were subsequently conducted to confirm that the defined boundaries accurately represented both the chosen basin and the defined habitat type. Following field confirmation, a geo-referenced computer-generated grid of approximately 400, 100 m × 100 m squares was overlaid on the image of Mystery Basin and 59 sites were selected, randomly stratified by habitat type (39 hardbottom, 20 seagrass). The geographic coordinates of each site were defined as the centroid of the selected square. The surveys were completed from 13 July 2012 through 20 August 2013. Due to the observed spatial heterogeneity and variable organism size, a combination of sampling methods (belt transects and quadrats) was used to efficiently and accurately quantify the benthic community. At each chosen site, three 25 m × 2 m nonoverlapping transects were established haphazardly by divers using SCUBA. For each belt transect, divers identified, counted, and measured the dimensions (length [L], width [W], and height [H]) of all sponge biomass that was greater than 10 cm in its largest dimension. Sponges smaller than 10 cm were identified, counted, and measured within four 1 m^2 quadrats that were equidistantly spaced along the length of the transect. Sponge identifications were performed to the lowest taxonomic level possible and those which could not be identified in the field were photographed and collected for later identification in the lab. In each quadrat, seagrass and macroalgal distribution was also quantified using the Braun-Blanquet cover assessment method (Braun-Blanquet 1972). A score (0–6) was assigned to each species occurring within the quadrat based on its spatial coverage (Braun-Blanquet 1972; Fourqurean et al. 2001).

Species-specific, volumetric biomass was first estimated using morphometric measurements collected during field surveys and roughly approximating their geometry as a rectangular prism ($V = L \times W \times H$). This estimate was subsequently converted to a more accurate, displacement-based volume using direct measurements. Displacement-based, direct volumetric measurements were made on a subset of the surveyed taxa (15 of 23 identifiable species). These species were chosen due to their abundance, hypothesized ecological importance, or geometric complexity; the eight species that were not measured directly were the rarest of the surveyed species and were morphologically similar to a species for which a direct assessment was made. Harvested individuals representative of the 15 chosen species were placed in a water-filled container (19 L or 95 L, depending on sponge dimensions) and displacement was measured to the nearest milliliter. This process was replicated for 10–30 individuals to ensure a robust quantification and to characterize the spectrum of organism sizes observed in Mystery Basin. A regression was fit to the data using calculated volume ($L \times W \times H$) as the independent variable and measured displacement as the dependent variable in order to develop a predictive equation. This allowed more accurate species-specific biomass quantifications to be determined with the morphometric measurements obtained from field surveys. Biomass estimates for the eight species which were not harvested for displacement were approximated using the most morphologically similar taxa for which a regression was derived.

The total sponge biomass for each survey technique (transects and quadrats) was determined for each species in Mystery Basin by taking the average of the surveyed displacement

(L_{sponge} m^{-2}) across both surveyed strata and assessing that value across the areal extent both habitats ($A_{hardbottom}$ + $A_{seagrass}$; m^2). The total biomass for each species was represented by weighted mean of the surveyed results from quadrats and transects which were evaluated separately (e.g., *Spheciospongia vesparium* biomass [10^6 L_{sponge}] was found to be 2.0 ± 0.42, 0.034 ± 0.007, and 1.9 ± 0.38 for the transects, quadrats, and the weighted mean, respectively; mean $\pm$ 1SE; Table 2). When calculating the weighted mean, the biomass from each survey technique was weighted based upon the area surveyed using that methodology (12 m^2 for quadrats and 150 m^2 for transects at each assessed location); the error of the weighted mean was calculated by the method of Baker and Nissim (1963). The error in all measures (transects, quadrats, and weighted mean) was extrapolated to the scale of the basin using the method of Krebs (1999). The transect data were not included in the weighted mean for small species which never satisfied the criteria for detection via this methodology (i.e., those that were never > 10 cm in the largest dimension; *Cinachyrella* sp., *C. nucula*, *Amphimedon viridis*, *Hyrtios* sp., and *Clione* sp.). Conversely, the weighted mean calculated for the species detected in belt transects reflects both utilized survey methodologies (Table 2); at some point during their lifetime, these organisms would be small enough to be counted in quadrats and therefore using this method did not preclude their detection, and the results from both methodologies were included in the corresponding weighted mean.

N sourcing to Mystery Basin

Rates of DIN release are only known for 11 of the 23 identifiable species surveyed in Mystery Basin (Hoer et al. 2018). Despite representing less than half of the observed species, these 11 represent approximately 97% of the sponge biomass in Mystery Basin. Nevertheless, these calculations should be considered the minimum N contribution from the sponge community as the remaining species contribute an unquantified amount of DIN. The areal flux of recycled N from each species (j_{sponge}; mmol N m^{-2} d^{-1}) was calculated as:

$$j_{sponge} = \frac{(V_{sponge} \times N_{sponge})}{A}$$

where V_{sponge} is the total surveyed volume of a sponge species in liters (L_{sponge}), N_{sponge} is the calculated DIN release rate for that species (μmol N d^{-1} $L_{sponge}{}^{-1}$; Hoer et al. 2018), and A is the total area of Mystery Basin (both habitat types; m^2). The sum of the fluxes from the 11 quantified species was extrapolated to A to determine the total N flux to Mystery Basin (mol N d^{-1}). Quantitative estimates of other important fluxes of N to and from the system (sediment–water exchange, rainfall, Everglades discharge, groundwater flux, N_2 fixation, and denitrification) were obtained through a review of published information on Florida Bay nutrient element sources, sinks, and cycling.

N demand from primary productivity

Seagrasses dominate primary production in Florida Bay and consequently represent the majority of photosynthetic N uptake in this environment (Zieman et al. 1989; Fourqurean and Robblee 1999). The species *Thalassia testudinum* dominated seagrass populations on the western margin of the bay, representing approximately 90% of total biomass, with *Halodule wrightii* and *Syringodium filiforme* representing the remaining 10% (Zieman et al. 1989; Fourqurean and Robblee 1999). Thick seagrass meadows in this region drive primary productivity at a rate of approximately 2.3 g dry weight m^{-2} d^{-1} for *Thalassia* alone (Zieman et al. 1989). This value was used to approximate benthic productivity for this species along the seagrass-covered shoals of Mystery Basin. With this rate assigned to *Thalassia*, the contributions of each of the other important species (*Halodule* and *Syringodium*) to overall seagrass biomass were obtained from the Braun-Blanquet rapid assessments performed during the sponge biomass surveys, and these proportions were used to calculate primary productivity relative to *Thalassia*. Species-specific C:N ratios (Fourqurean et al. 1992, Sprigger Bank, FCE LTER Data, Fourqurean 2011) were used in conjunction with the calculated productivity to obtain a photosynthetic N demand that was appropriately weighted for the locally relevant species in the seagrass community. Given that seagrasses can acquire N from the water column and sediment pore waters, this quantity of N demand was then adjusted by the factor predicted to be derived from water column sources. We applied the values calculated by Lee and Dunton (1999) for *Thalassia testudinum* (approximately 48% of the total N acquired comes from the water column) to all the observed species. While Lee and Dunton (1999) observed some seasonal variability, the value used herein (~ 48% from leaves) represents the approximate annual average.

Florida Bay is widely considered an oligotrophic system (Fourqurean et al. 1993; Boyer et al. 2006). Phytoplankton primary productivity per unit area is estimated to be approximately equal that found in the open ocean; surface water chlorophyll *a* concentrations in Rabbit Key Basin (directly north of our study site; SERC Site ID: 18) are similar to those found in surface-water samples from the Bermuda Atlantic Time-Series (BATS; bats_pigments.txt; batsftp.bios.edu). Therefore, we estimated net primary productivity values (mg C m^{-3} d^{-1}) using data from the surface (1–5 m depth) and 20 m stations of the BATS averaged from 1989 to 2011 (bats_production.dat; batsftp.bios.edu). BATS was selected as it provided a long temporal record of primary productivity data in the surface ocean that agreed with modeled and experimental results offshore of the Florida Keys (Yoder et al. 1983; Hofmann and Ambler 1988; Fiechter and Mooers 2007). The resultant average productivity was multiplied by the mean water depth in Mystery Basin (1.5 m; Rok et al. unpubl. data), and then converted to N demand using Redfield stoichiometry (C/N ~ 6.6; Redfield 1958).

In order to analyze the local importance of various fluxes in the N budget of this basin, a simple model was constructed and evaluated at each surveyed site:

$$N_{\text{flux}} = j_{\text{sponge}} + j_{\text{new}} + j_{\text{sed}} + \left(j_{\text{sg}} \times \text{BBCA}\right) - \left(j_{\text{wcpp}} + j_{\text{denitrification}} + \left[j_{\text{sgpp}} \times \text{BBCA}\right]\right)$$

where the flux at a given location (N_{flux}; mmol N m^{-2} d^{-1}) is equal to the sum of the sources of DIN: sponges (j_{sponge}), "new" N (e.g., rainfall, Everglades, N_2 fixation; j_{new}), sediment–water exchange (j_{sed}), and flux from seagrass sediments (j_{sg}) minus the N demand from removal processes (water column primary productivity [j_{wcpp}], denitrification [$j_{\text{denitrification}}$], and seagrass primary productivity [j_{sgpp}]). Both seagrass related fluxes (j_{sg} and j_{sgpp}) were scaled to the appropriate areal coverage in order to reflect an enhanced importance of these processes in more seagrass-rich habitats within the basin. This calculation was performed with a factor derived from the Braun-Blanquet density (BBCA) that was proportional to surveyed seagrass cover: densities (D_i; Fourqurean et al. 2001) between 0 and 0.1 were assigned a BBCA value of 0 (~ 0% cover), $0.1 < D_i \leq 1$ was assigned a value of 0.05 (~ 5% cover), $1 < D_i \leq 2$ was assigned a value of 0.25 (~ 25% cover), $2 < D_i \leq 3$ was assigned a value of 0.5 (~ 50% cover), $3 < D_i \leq 4$ was assigned a value of 0.75 (~ 75% cover), and $D_i > 4$ was assigned a value of 1 (~ 100% cover).

Contour plots of Mystery Basin

Contour plots were generated using MATLAB (R2019a; MathWorks) to analyze spatial trends in the collected data. A rectangular grid of 100 × 100 linearly spaced points was generated for Mystery Basin. This grid was bounded by the minimum and maximum values of the surveyed sites' geographic coordinates (decimal degrees of latitude and longitude represented the Y and X axes, respectively). The geo-referenced values (e.g., surveyed sponge biomass, modeled N flux, etc.) were plotted on this grid and a contour surface was generated by linear interpolation between the empirically determined values.

Results

Water column DIN and TDN

The water quality surveys conducted in Mystery Basin and the surrounding waters yielded NH_4^+ values ranging from 0.5 ± 0.4 to 2.9 ± 0.7 μmol L^{-1} and NO_x^- ranging from 0.4 ± 0.1 to 3.8 ± 0.7 μmol L^{-1} (Fig. 1; Table 1). There was broad comparability between the average values obtained inside and outside Mystery Basin, however, despite the comparability of the averages, the collected samples exhibited a high degree of spatial and temporal variability. In general, water collected from in hard ground habitats had higher concentrations of all DIN species (NH_4^+, NO_x^-, and total DIN) than those collected over seagrasses (unpaired *t*-test; $p < 0.02$), and the observed DIN concentrations were significantly elevated in May 2013 relative to observations in August 2012 (3.6 ± 1.5 μmol N L^{-1} and 1.5 ± 0.5 μmol N L^{-1} for 2013 and 2012, respectively; mean ± 1SD; unpaired *t*-test; $p < 0.01$). Ammonium was the dominant species of DIN found at all sampled locations, both inside and outside Mystery Basin (Inside: n = 28 paired collections; Wilcoxon signed rank test; $p < 0.001$; Outside: n = 7 paired collections; Wilcoxon signed rank test; $p < 0.01$).

The SEASII-NO_x instruments deployed at CTR yielded a 24-h time-series of NO_x^- determinations from 19 May to 20 May that comprised a total of ~13,000 individual concentration measurements. This time-series revealed relatively high NO_x^- concentrations inside the basin compared to surrounding waters (Fig. 2). The average concentration at 0.1 mab was 3.8 ± 0.7 μmol NO_x^- L^{-1} and 3.0 ± 0.5 μmol NO_x^- L^{-1} at 1.0 mab (mean ± 1SD). These time-series measurements agreed with contemporaneous discrete water collections (Fig. 2) and the overall average from discrete NO_x^- collections at CTR (2.6 ± 0.9 μmol NO_x^- L^{-1}; mean ± 1SD; n = 16; Table 1). Additionally, they indicate a degree of diurnal variability in NO_x^- concentrations where a minimum value is reached around

Table 1. Summarized DIN determinations from various sites within and surrounding Mystery Basin (Fig. 1). N species concentrations (NO_x^-, NH_4^+, total DIN, and TDN) are in μmol N L^{-1} and represent the mean ± 1SD. Number of collections (n) indicates the number of sites sampled for each habitat type (hardbottom or seagrass). For the CTR collections in May 2013, the n represents the number of discrete measurements made; CTR data are not included in the May 2013 hardbottom averages.

Date	Collections (n)	NO_x^-	NH_4^+	DIN	TDN	DON	Hardbottom/seagrass
Aug 2012	16	0.5 ± 0.2	1.1 ± 0.3	1.6 ± 0.5	—	—	Hardbottom
Aug 2012	5	0.4 ± 0.1	0.5 ± 0.4	1.0 ± 0.5	—	—	Seagrass
May 2013	CTR (SEASII; $n \approx 7300$)	3.0 ± 0.5	—	—	—	—	Hardbottom (1.0 mab)
May 2013	CTR (SEASII; $n \approx 6100$)	3.8 ± 0.7	—	—	—	—	Hardbottom (0.1 mab)
May 2013	CTR (n = 16)	2.6 ± 0.9	2.2 ± 0.9	4.8 ± 1.3	54 ± 8	50 ± 8	Hardbottom
May 2013	3	1.7 ± 0.3	2.9 ± 0.7	4.5 ± 0.9	60 ± 12	51 ± 12	Hardbottom
May 2013	3	0.6 ± 0.3	1.6 ± 0.7	2.1 ± 0.4	65 ± 22	61 ± 22	Seagrass
May 2013	3	0.8 ± 0.5	2.1 ± 0.5	2.9 ± 0.8	44 ± 2	38 ± 2	Hardbottom; outside MB
May 2013	4	0.4 ± 0.1	1.1 ± 0.3	1.4 ± 0.4	45 ± 2	42 ± 2	Seagrass; outside MB

MB, Mystery Basin.

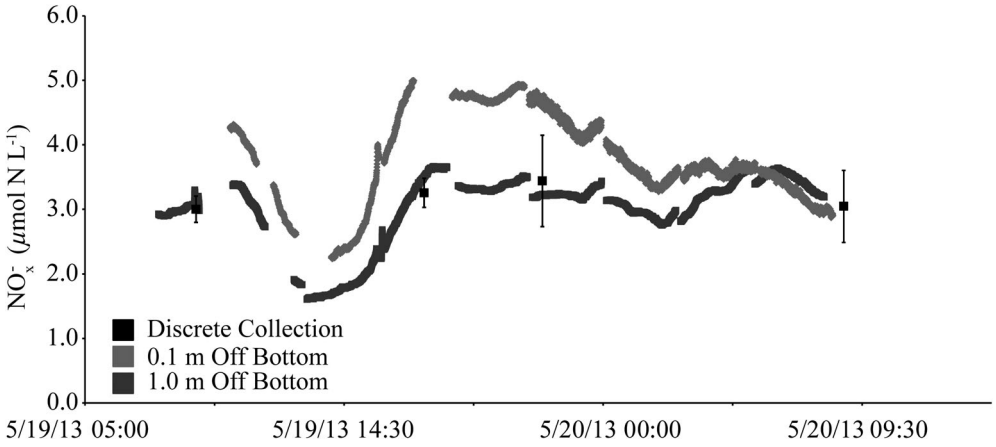

Fig. 2. Time-series data collected at CTR with discrete collections performed by peristaltic pump. Discrete collections represent the mean ± 1SD. Breaks in the data record are indicative of gaps where the instrument is programmed to obtain a new optical reference or instrument maintenance.

mid-day followed by a slow increase to a maximum around midnight (Fig. 2).

The May 2013 water quality survey generated a profile across the center of the basin that connected the presumed influent and effluent points (water mass flow in this area moves roughly north-northwest (NNW) to south-southeast (SSE); Hunt et al. 2005, Rok et al. unpubl. data). The transect, from HF10 to HF7 (Fig. 3), showed low DIN water at HF10 and HF14 near the entry into Mystery Basin from Rabbit Key Basin to the north-northwest (total DIN: 0.93 ± 0.04 and 1.8 ± 0.2 μmol N L^{-1} for HF10 and HF14, respectively), DIN content increased upon entering Mystery Basin from the NNW at HF5 (2.5 ± 0.1 μmol N L^{-1}), further increasing in central Mystery Basin near HF1 and CTR (5.5 ± 0.1 μmol N L^{-1} and 5.0 ± 1.7 μmol N L^{-1} for HF1 and CTR, respectively), before encountering lower DIN concentrations at HF4 and HF7 on the south-southeast shoal (1.7 ± 0.2 μmol N L^{-1} and 2.2 ± 0.2 μmol N L^{-1} for HF4 and HF7, respectively; Fig. 3). Site HF10 was located inside Rabbit Key Basin and its water column total DIN concentration was not significantly different than that observed there over the historical duration of SERC sampling in this location (1.35 ± 1.84 μmol N L^{-1}; n = 203; SERC Site ID: 18; unpaired t-test; $p > 0.5$). Conversely, the average water column DIN concentration observed inside Mystery Basin (all sites inside the basin; August 2012 and May 2013 collections) was significantly higher than the average DIN concentration observed in SERC sampling in Rabbit Key Basin (unpaired t-test; $p < 0.01$) as well as two other nearby SERC sites over their sampling duration periods (0.80 ± 0.81 μmol N L^{-1} and 1.24 ± 1.36 μmol N L^{-1};

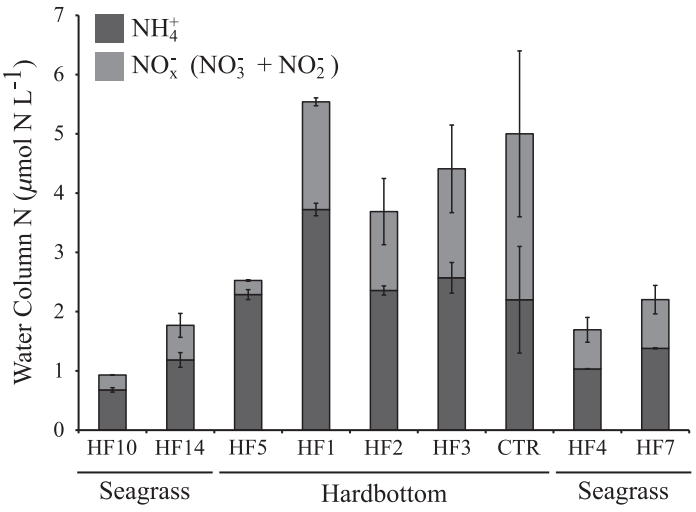

Fig. 3. Water column samples transecting Mystery Basin along the approximate trajectory of water transport into and out of the basin. Proximate site characterization is listed below the site IDs and the bars represent the mean of the sampled parameter. Error bars indicate ± 1SD.

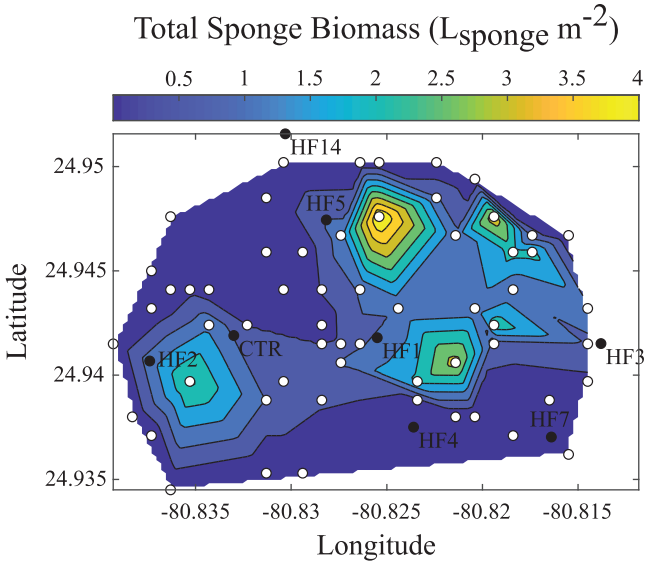

Fig. 4. Contour plot of surveyed sponge biomass in Mystery Basin. The white circles are the surveyed sites where the N flux model is evaluated, and the black circles are the eight site IDs which were sampled during the water quality survey.

n = 200 and 200; Site IDs: 27 and 28; Sprigger Bank and Old Dan Bank, respectively; unpaired t-test; $p < 0.05$).

TDN concentrations were only measured during the May 2013 sample collections and ranged from 56 ± 10 μmol N L^{-1} inside Mystery Basin (HF1–6 and CTR) to 45 ± 2 μmol N L^{-1} outside (HF8–14; mean ± 1SD), excluding two sites that were determined to be outliers (HF7 and HF10; 250 ± 80 μmol N L^{-1} and 210 ± 60 μmol N L^{-1}, respectively; mean ± 1SD; Table 1). DON represented the majority of available TDN in all sampled locations, but the calculated DON concentration did not differ between sites inside and sites outside the basin (unpaired t-test; $p > 0.05$). Inorganic N represented a larger proportion of TDN inside the basin as compared to outside (8.3% ± 2.2% inside and 5.0% ± 1.8% outside; mean ± 1SD; n = 21 and 6; unpaired t-test; $p < 0.005$; Table 1).

Sponge biomass survey

Sponges were found at 57 of the 59 surveyed sites across Mystery Basin and appeared to be the dominant heterotrophic biomass among the surveyed benthos. Population densities ranged from 0.08 to 21 individuals m^{-2} with biomass (volumetric displacement; L_{sponge}) averaging 0.70 ± 0.13 L_{sponge} m^{-2}, and as high as 4.4 L_{sponge} m^{-2} (Fig. 4; Table 2). The observed sponge density at the surveyed sites agreed with previous bay-wide quantifications (Peterson et al. 2006), which provided confirmation of the assumption that the Mystery Basin area was characterized by a biomass density that was representative of sponge-rich sites throughout the bay. The sponge population was diverse (23 identifiable species); however, the vast majority of the surveyed biomass was composed of six species: *S. vesparium*, *Ircinia felix*, *Geodia gibberosa*, *Cinachyrella* sp., *Haliclona magnifica*, and *Halichondria melanodocia* (Table 2). These species represented roughly 97% of surveyed biomass; *S. vesparium*, *I. felix*, and *G. gibberosa* alone comprise approximately 94% of the total (Table 2). Sponges were found to be heterogeneously distributed across the 59 stations. Hardbottom habitats particularly those in the eastern half of Mystery Basin exhibited large and diverse sponge populations (Fig. 4) that were predominantly composed of high microbial abundance (HMA) species (90% ± 23% HMA vs. 10% ± 23% low microbial abundance (LMA); mean ± 1SD). Dense seagrass meadow sites were characterized by smaller sponge biomass values and populations dominated by fewer species (e.g., primarily *C. nucula*; Fig. 4), and

Table 2. Total sponge biomass across both hardbottom and seagrass habitats in Mystery Basin (10^3 L_{sponge}). Values are shown for each utilized survey methodology (belt transect and 1 m^2 quadrat) and represent the mean ± 1SE in the calculated displacement.

Species	Transect biomass (10^3 L_{sponge})	Quadrat biomass (10^3 L_{sponge})	Weighted mean (10^3 L_{sponge})
*S. vesparium**	2000 ± 410	34 ± 7.1	1900 ± 380
*I. felix**	1000 ± 220	78 ± 18	930 ± 210
*G. gibberosa**	510 ± 123	130 ± 10	480 ± 120
Cinachyrella sp.*,†	0	58 ± 5.4	58 ± 0.40
Haliclona magnifica	34 ± 8.5	25 ± 3.7	33 ± 7.8
*Halichondria melanodocia**	24 ± 8.0	94 ± 5.4	29 ± 7.4
Unidentified sponges	27 ± 13	42 ± 11	28 ± 12
Spongia sp.*	12 ± 3.7	9.3 ± 4.2	12 ± 3.4
Dysidea etheria	11 ± 3.2	19 ± 3.7	12 ± 3.0
Tedania ignis	9.9 ± 2.6	8.1 ± 1.9	9.7 ± 2.4
*Hippospongia lachne**	7.7 ± 2.5	1.9 ± 1.9	7.2 ± 2.3
Lissodendoryx stigmata	5.7 ± 1.5	3.6 ± 1.3	5.5 ± 1.4
*C. nucula**,†	0	5.1 ± 1.3	5.1 ± 0.1
Amphimedon viridis†	0	4.3 ± 2.8	4.3 ± 0.21
Haliclona sp.*	2.4 ± 0.98	27 ± 2.4	4.2 ± 0.92
Hyrtios sp.†	0	2.2 ± 0.54	2.2 ± 0.04
Ircinia strobilina	1.6 ± 0.82	0	1.5 ± 0.76
Tectitethya crypta	1.4 ± 0.70	2.3 ± 1.4	1.4 ± 0.66
Callyspongia sp.	0.49 ± 0.37	5.0 ± 0.77	0.83 ± 0.34
*Ircinia campana**	0.70 ± 0.70	0	0.65 ± 0.65
Aaptos lithophaga	0.61 ± 0.45	0	0.56 ± 0.42
Ircinia sp.	0	5.8 ± 4.5	0.43 ± 0.33
Niphates erecta	0.19 ± 0.12	1.0 ± 0.57	0.25 ± 0.12
Clione sp.†	0	0.24 ± 0.24	0.24 ± 0.02
Total biomass	**3600 ± 500**	**560 ± 27**	**3500 ± 450**

*Species which have measured DIN production rates.
†Species which were too small to be measured in transects and these data were excluded from the corresponding weighted mean.

these sites were more evenly split between HMA and LMA species (43% ± 46% HMA vs. 37% ± 45% LMA; mean ± 1SD).

Seagrass and macroalgal biomass

The results of the Braun-Blanquet cover assessment (BBCA) were used to calculate species density (D) for surveyed seagrass biomass following the method of Fourqurean et al. (2001). Seagrass was found at 55 of the 59 surveyed sites ($D \geq 0.1$; Fourqurean et al. 2001); *Thalassia testudinum* was encountered at all sites where seagrass was found. The other two observed species, *Halodule wrightii* and *Syringodium filiforme*, were found at 66% and 14% of the surveyed sites, respectively, and typically exhibited much lower densities than *Thalassia*. A fourth species, *Halophila engelmanni*, was observed in a single quadrat, yet exhibited a density less than the threshold assigned for determining the presence/absence of seagrass ($D \geq 0.1$; Fourqurean et al. 2001). The density of *Thalassia* encountered during surveys was greater than that of both *Halodule* and *Syringodium* combined, with the exception of a single site on the southwest shoal where *Halodule* was dominant. At the 20 sites in defined seagrass habitats, cumulative density was 75–100% cover ($D > 4$); *Thalassia* composed approximately 81% of this cumulative cover and *Halodule* and *Syringodium* contributed 17% and 2%, respectively. These relative abundances were used to calculate seagrass N demand.

Macroalgae biomass was also found throughout Mystery Basin during the BBCA, particularly in hardbottom sites where it often comprised the majority of surveyed macrophyte biomass. The observed macroalgae was dominated by red drift algae, predominantly *Laurencia* sp., with lesser contributions from calcareous green algae (*Halimeda* sp. and *Penicillus* sp.). Densities (D_i) were calculated for macroalgae in order to compare biomass with that of seagrasses. At 27 of the 59 surveyed sites, the sum of macroalgal species densities ($\Sigma D_{\text{macroalgae}}$) was greater than the sum of seagrass densities ($\Sigma D_{\text{seagrass}}$), and all of these sites were located in hardbottom habitats. Of these 27 sites, 23 were dominated by red drift algae and the remaining four by calcareous green algae. Furthermore, at most of these sites (23 of 27), the dominant type of algae (red drift, calcareous green) represented more than 50% of the total observed algae. Sites dominated by red drift algae demonstrated greater areal coverage (25–75% of quadrat area) than sites dominated by calcareous green algae (≤ 5%, one site showed ~ 25% coverage), yet due to the ephemeral biomass contribution resultant from the mobility of red drift algae, these quantifications are subject to considerable uncertainty.

Table 3. Nitrogen fluxes (mmol m^{-2} d^{-1}) for Florida Bay as well as the N budget for Mystery Basin (mol N d^{-1}). Sponge N efflux was determined from Mystery Basin biomass surveys and species-specific N release rates (Hoer et al. 2018). The remaining fluxes were calculated based upon published quantifications from Florida Bay or analogous environments ("Bare" Sediment; Great Barrier Reef, Australia). The areal nutrient fluxes were assessed across the appropriate habitat types (*see* Fig. 1). Reported values represent the mean ± 1SD.

	mmol N m^{-2} d^{-1}	mol N d^{-1}	References
I. Recycled N sources in FL Bay			
Sponge DIN flux (Mystery Basin biomass)	0.59 ± 0.28	2900 ± 1400	This study
Sediment-water flux (diffusive; seagrass beds)	0.36 ± 0.27	680 ± 510	Yarbro and Carlson (2008)
Sediment-water flux (diffusive; "bare" sediment)	0.04 ± 0.01	130 ± 30	Capone et al. (1992)
Total recycled N inputs	0.99 ± 0.39	3700 ± 1500	
II. New N inputs to FL Bay			
Rainfall	~ 0.06	~ 300	Prospero et al. (1996)
Everglades	~ 0.12	~ 400	Boyer and Keller (2007); Rudnick et al. (1999)
Groundwater discharge	< 0.3 ± 0.05	< 1500 ± 250	Boyer and Keller (2007); Corbett et al. (1999)
N_2 fixation (benthic algae)	~0.1	~500	Boyer and Keller (2007)
Total new N inputs	0.57 ± 0.06	2700 ± 250	
III. N demand—FL Bay net primary productivity			
Seagrasses (90% *Thalassia* sp.)	2.1 ± 0.2	4000 ± 400	Zieman et al. (1989); Fourqurean et al. (2001); FCE LTER
Phytoplankton	0.1 ± 0.07	510 ± 370	BATS NPP (0–20 m water depth, averaged from 1989 to 2011)
Minimum total N demand	2.2 ± 0.3	4510 ± 770	
IV. Nitrogen loss from FL Bay			
Benthic denitrification	~ 0.1	~ 500	Kemp et al. (2001)

A nitrogen budget for Mystery Basin

The available, species-specific sponge DIN release rates represented approximately 97% of the surveyed biomass in Mystery Basin (Hoer et al. 2018); remaining species without quantified DIN release rates were excluded from the N budget calculations thus making our estimate of sponge-released N a lower limit. The areal flux of DIN from the sponge community was 0.59 ± 0.28 mmol N m^{-2} d^{-1} (mean ± 1SD; Section I of Table 3; Fig. 5) was applied over the area of all habitat types (*A*) yielding a basin-wide contribution from the sponge community of 2900 ± 1400 mol N d^{-1} (mean ± 1SD; Section I of Table 3). The magnitude and speciation of the sponge DIN flux was spatially heterogeneous and largely dependent upon sponge biomass distribution and community composition (Fig. 6). The sponge DIN flux was dominated by HMA species (Fig. 5). In hardbottom sites, 88% ± 29% (mean ± 1SD) of the DIN flux was from HMA species, while LMA species contributed 12% ± 29% of the DIN (mean ± 1SD). Similarly, the N flux at seagrass sites was also predominantly from HMA species (79% ± 35% and 21% ± 29% for HMA and LMA, respectively; mean ± 1SD).

The previously measured DIN flux from sediment–water exchange in seagrass beds (0.36 ± 0.27 mmol N m^{-2} d^{-1}; Table 3; Yarbro and Carlson 2008) was applied exclusively to the seagrass dominated areas, and the flux from "bare" sediments (0.04 ± 0.01 mmol N m^{-2} d^{-1}; Table 3; Capone et al. 1992) was applied to the hardbottom habitats (Section I of Table 3). The remaining quantified N sources (Section II of Table 3) were applied to the area of all habitat types (*A*) to estimate N loading for each of these processes (summarized in Section II of Table 3). Benthic denitrification has been suggested to roughly balance with N_2 fixation in Florida Bay (Kemp et al. 2001), and this assumption was applied in our N budget for Mystery Basin. However, this generalized assumption ignores potential spatial and temporal variability (Kemp et al. 2001; Boyer and Keller 2007), and thus, represents an additional uncertainty.

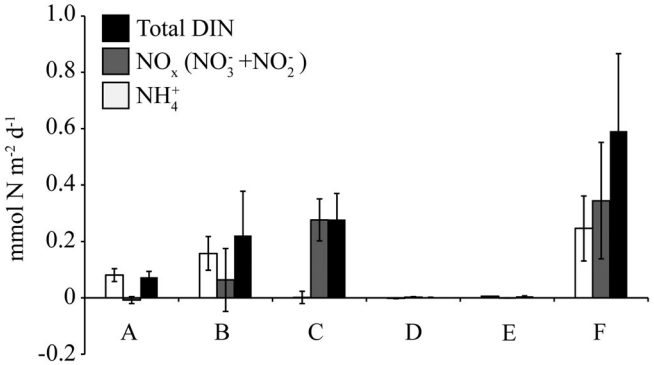

Fig. 5. Average NH_4^+, NO_x^-, and total DIN contributions from the sponge community in Mystery Basin. DIN fluxes are separated by species and arranged in descending order of biomass contribution (largest to smallest; from left to right): A. *S. vesparium*; B. *I. felix*; C. *G. gibberosa*; D. *Cinachyrella* sp.; E. *Halichondria melanodocia*; F. All surveyed species. Error bars are ±1SD. Of the most abundant species, the majority of DIN is contributed by HMA species (A–C).

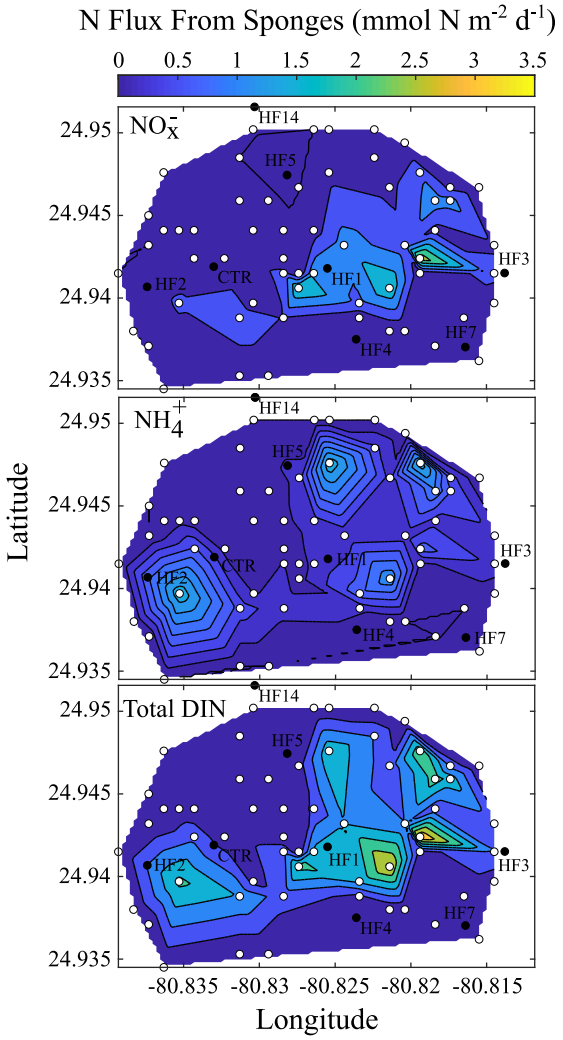

Fig. 6. Contour plots of NH_4^+, NO_x^-, and total DIN contributions from the sponge community in Mystery Basin. The white circles are the surveyed sites where the N flux model is evaluated, and the black circles are the eight site IDs which were sampled during the water quality survey.

The total N demand from primary productivity is calculated to be 2.2 ± 0.2 mmol N m^{-2} d^{-1} (Section III of Table 3); most of the N demand associated with primary productivity is by seagrasses (2.1 ± 0.2 mmol N m^{-2} d^{-1}) with a minor additional demand from phytoplankton (0.13 ± 0.09 mmol N m^{-2} d^{-1}; Section III of Table 3).

Discussion

Mystery Basin nitrogen budget

The spatial variability in our N budget (Fig. 7) illustrates the local importance of net N demand along the shoaling seagrass beds in contrast to net DIN input from sponges throughout the central hardbottom habitat. The modeled N fluxes range

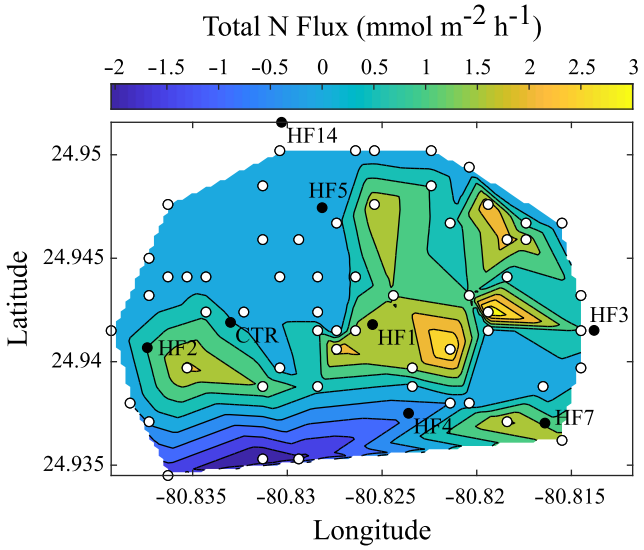

Fig. 7. Contour plot of the calculated N flux model used to determine local importance of N sources and sinks throughout Mystery Basin. The white circles are the surveyed sites where the N flux model is evaluated, and the black circles are the eight site IDs which were sampled during the water quality survey.

from a net uptake of 2.1 ± 0.1 mmol m^{-2} d^{-1} (mean ± 1SD) in dense seagrass meadows with minimal sponge coverage to a net input of 3.5 ± 0.9 mmol m^{-2} d^{-1} (mean ± 1SD) from sponge-rich hardbottom environments in the central and eastern areas of the basin where demand from photosynthesis is minimal.

Our estimate of total N demand by primary producers does not include a contribution from macroalgal biomass due to the observed ephemeral nature of the dominant species (e.g., red drift algae), particularly in hardbottom habitats. Therefore, our calculated total N demand by primary producers is likely to be an underestimate. Despite this, it is similar to that determined by remote sensing measurements in dense seagrass communities on the Grand Bahama Banks (3.5 ± 1.3 mmol N m^{-2} d^{-1}; mean ± 1SD; Dierssen et al. 2010) as well as in macrophyte-dominated systems (5 ± 2 mmol N m^{-2} d^{-1}; mean ± 1SD; reviewed by Gattuso et al. 1998). The ecosystems surveyed by Gattuso et al. (1998) span from the Chesapeake Bay (U.S.A.) to tropical reefs in the Pacific Ocean. These estimates may not be as representative of the conditions in Florida Bay due to this more panoptic view of N demand from primary productivity.

Our results indicate that the collective DIN efflux from the sponge community is the largest of the estimated sources of N to the water column of Mystery Basin (Table 3). Sponge remineralized DIN represents a minimum of 45% ± 24% of the total DIN sources to the basin or roughly half of the calculated demand from primary productivity (Table 3). Localized, site-specific sponge community fluxes were the largest source of N at 60% of the surveyed locations within the basin. The calculated peaks in sponge community DIN efflux in Mystery Basin often did not correlate with sponge biomass maxima (Figs. 4, 6) because of variable community composition and the correspondingly variable rates of DIN production dependent on the constituent species. The sponge community in hardbottom habitats was composed mostly of HMA sponge species (~ 90% of sponge biomass in hard ground were HMA species), which are often associated with concentrated DIN in their effluent plumes (e.g., Hoer et al. 2018). Unsurprisingly, the DIN from the sponge community was predominantly sourced from HMA species (~ 88% of N from HMAs compared to ~ 12% from LMAs). However, locally elevated sponge biomass in Mystery Basin was often characterized by dominant populations of *S. vesparium*, which, counter to many HMA species, contributes very little DIN per unit of sponge biomass (Hoer et al. 2018). Peaks in DIN flux were generally associated with large *G. gibberosa* populations, which exhibit a much higher rate of DIN production, largely as NO_x^- (Hoer et al. 2018). Sponge species that exhibit similarly high rates of DIN production per unit biomass have been shown to dominate DIN fluxes in other environments (e.g., Corredor and Wilkinson 1988; Diaz and Ward 1997; Southwell et al. 2008). While several sponge species found frequently in Florida Bay have the capacity to generate benthic fluxes on those scales, the role of sponges in the broader Florida Bay ecosystem will be locally variable based upon community biomass, species composition, and the microbial population associated with the present species. Consequently, quantifying their impact on the N cycle at specific locations throughout Florida Bay and in other habitats globally will necessitate high spatial resolution in sponge biomass quantification.

The calculated, average flux from the sponge community in Mystery Basin (0.59 ± 0.28 mmol N m^{-2} d^{-1}; Table 3) should be considered a minimum estimate; N release rates have not been measured for approximately 3% of the surveyed population, plus the sponge communities living on the shallow shoals bordering the tested site could have been underestimated during biomass surveys. These seagrass-covered banks frequently harbored large populations of *C. nucula*, a species that is often found growing attached to seagrass blades in Florida Bay and elsewhere (e.g., Corredor and Wilkinson 1988; Diaz and Ward 1997; Stevely et al. 2010). Despite direct observations of these populations, the shoaling sill habitats featuring dense seagrass meadows were exceedingly difficult to survey as they are only overlain by a thin layer of water, typically < 0.3 m at high tide. Our inability to accurately quantify the DIN flux from the sill habitat's *C. nucula* population has likely led to an underestimation of the DIN flux from the basin's total sponge community (Corredor and Wilkinson 1988; Diaz and Ward 1997; Hoer et al. 2018).

Our results support the conclusions of previous work in other environments which showed the potential for the sponge community to supply a large proportion of the water column DIN

reservoir (e.g., Corredor and Wilkinson 1988; Southwell et al. 2008; Keesing et al. 2013). The calculated flux is of similar magnitude to that observed on the western coast of Australia (0.35–0.63 mmol m^{-2} d^{-1}; Keesing et al. 2013); however, it is lower than the average flux from other communities in the Caribbean and Mediterranean (e.g., Corredor and Wilkinson 1988; Jiménez and Ribes 2007; Southwell et al. 2008). The differences between the average areal fluxes observed for this and other systems are most likely due to varying sponge community density and species composition. However, the surveyed area in Mystery Basin is larger than those in previous surveys and our data reveal that the average, calculated sponge community flux is heterogeneously distributed (Fig. 6). Localized peaks in DIN efflux (3.5 ± 0.9 mmol N m^{-2} d^{-1}; Fig. 6) were of the same magnitude as values calculated from lower biomass densities found at sites in the Caribbean and Mediterranean (0.12–1.5 mmol N m^{-2} d^{-1}, Diaz and Ward 1997; ~ 2.5 mmol N m^{-2} d^{-1}, Jiménez and Ribes 2007).

Impact of sponge N efflux

We hypothesize that sponge N efflux leads to the locally elevated DIN concentrations observed in central Mystery Basin, and further contend that the impact of sponges is amplified by bank-attenuated physical water exchange in basin settings and throughout the bay due to the shallow water column. The shoal-damped exchange in Mystery Basin results in moderate water retention relative to other basins in central Florida Bay (Hunt et al. 2005); modeling advective flux using data from in situ water level loggers yielded a water column residence time between 7 and 14 d for this site (Rok et al. unpubl. data). Conversely, species-specific sponge pumping rates measured at various sites in Florida Bay (N. Lindquist et al. unpubl. data) suggest an average total basin filtration time by the sponge community of 8 h. This filtration rate is dominated by *S. vesparium*; using the surveyed biomass of *S. vesparium* alone and pumping rates for this species (average of Lynch and Phlips 2000, 0.069 L_{sw} L_{sponge}^{-1} s^{-1}, Weisz et al. 2008, 0.176 L_{sw} L_{sponge}^{-1} s^{-1}, Lindquist et al. unpubl., 0.092 L_{sw} L_{sponge}^{-1} s^{-1}; 0.112 L_{sw} L_{sponge}^{-1} s^{-1}) yields a 10 h turnover time for the full volume of Mystery Basin.

Given the range in water residence times, the same parcel of water would be expected to be filtered more than 20 times by the sponge population while remaining within Mystery Basin. The large particle filtration rate and the associated heterotrophic processes mediated by the sponge community have been suggested to exert significant grazing pressure on overlying waters by Peterson et al. (2006). We suspect that the local variability in DIN concentrations that we observe in Mystery Basin results from rapid overturn in labile organic matter by heterogeneously distributed sponge biomass. These impacts are likely to be enhanced in times when advective mixing is suppressed, thereby allowing local processes to dominate.

The hypothesized local impacts of the sponge population were particularly pronounced in our May 2013 samples transecting Mystery Basin along the approximate trajectory of advective water transport from HF10 to HF7 (Fig. 3). These transect results also reflect the predicted local importance of modeled N sources and sinks to overall water column DIN (Fig. 7). The greatest sponge-mediated organic matter remineralization occurs in the central part of the basin (Fig. 7) and corresponding samples exhibit elevated DIN concentrations (HF1, HF2, HF3, CTR; Fig. 3). By contrast, locations where N demand from primary productivity by shoaling seagrass habitats is expected to be greatest (Fig. 7) show lower water column DIN concentrations (HF10, HF14, HF4, HF4; Fig. 3). While physical mixing and exchange with surrounding basins featuring less sponge biomass might be limited by shoals, it is probable that the nutrient demand at these more protected locations will be partially satisfied by pulsed input of DIN-enriched water in response to tidal or wind-driven mixing.

DIN comprises a larger fraction of water column TDN in Mystery Basin (8.3% inside as compared to 5.0% outside) potentially due to sponge remineralization processes. The chemical speciation of water column DIN did not directly correlate with that predicted for effluent N from the total sponge community at our Mystery Basin stations (e.g., Fig. 7), yet an increased proportion of total DIN as NO_x^- was observed at several locations within Mystery Basin (Fig. 3). Ammonium has been shown to characterize the majority of water column DIN in Florida Bay (e.g., Lavrentyev et al. 1998; Boyer et al. 1999; Gardner and McCarthy 2009), and continuation of this trend at sites in Mystery Basin would be expected given that the presumed DIN sources to this environment were largely NH_4^+-based (roughly 60% of total, nonsponge DIN input is as NH_4^+; i.e., rainfall, groundwater discharge, sediment/water exchange, etc.). However, we calculate that 60% of DIN from the sponge community is supplied as NO_x^- (Fig. 5); this enhanced delivery of oxidized N by sponges may contribute to DIN chemical speciation differences between habitats with and without sponges. The dominance of NO_x^- in sponge-supplied DIN is unsurprising given that the N released by sponges is primarily from HMA species, and NO_x^- is the dominant N species in the effluent plume of this clade (e.g., Hoer et al. 2018).

Uncertainties in N budget parameters

The calculated N budget for Mystery Basin includes best estimates for a variety of contributing sources and sinks, and provides a means to comparatively analyze the potential importance of sponges as a significant yet unrecognized input of recycled N to Florida Bay. The addition of N from sponge-mediated organic matter remineralization to the calculated budget results in an approximate balance between known sources and sinks (Table 3). However, this apparent balance should be viewed cautiously due to uncertainties in the estimates of several nitrogen inputs. The flux of N from

groundwater discharge utilized in the budget (Table 3) was based upon an average seepage rates for basins in the middle of FL Bay and interstitial DIN concentrations measured at eastern sites closer to the Florida Keys island chain (Corbett et al. 1999). We do consider these seepage rates plausible for Mystery Basin as similar rates have been observed in Rabbit Key Basin directly north of our stations (Corbett et al. 2000). However, the DIN concentrations of seepage waters in Mystery Basin are unknown. In any case, the DIN input from sponges is at least twice the theoretical maximum "new" DIN input from groundwater discharge (Table 3). The local flux of N, mostly as DON from the Everglades is subject to similar uncertainty, as it was obtained from a bay-wide estimate of TDN discharge assessed evenly across the spatial extent of FL Bay (2220 km^2; Rudnick et al. 1999).

The exclusion of macroalgal primary productivity as a N sink represents a considerable source of uncertainty in the calculated uptake flux at sites where primary productivity of these organisms likely outweighed that of seagrasses (27 of 59 surveyed sites). At these locations, the macroalgal biomass was dominated by red drift algae (primarily *Laurencia* sp.), and this biomass is susceptible to physical transport (Madden et al. 2009). Conversely, the contribution of the most abundant attached species (calcareous green algae) at these sites was significantly lower and represented typically ≤ 5% coverage, even at locations featuring dense populations. Due to the uncertainty in the areal coverage of the dominant, drift alga, the N demand from these organisms is excluded. Improved quantification of N uptake by these drifting organisms would greatly improve the accuracy of the N uptake by photosynthesis. Furthermore, the observed diurnal variability in NO_x^- in Mystery Basin (Fig. 2) demonstrates a temporal aspect of the N budget that is not well captured by the present budget.

Temporal variability in sponge DIN input

The N contribution from the sponge community is expected to exhibit significant temporal variability. Similar to the other N fluxes taken from the literature and discussed above, the rate of DIN release from the sponge population exhibits short-term temporal variability on the scale of days to weeks (e.g., Southwell et al. 2008), a factor not directly accounted for in the present budget (Table 3). The rates of species-specific N release presented here were measured over many months and cannot account for any temporally dynamic behavior (Hoer et al. 2018). The nature of any temporal variability in N efflux from the species we studied is unknown. Future work would be well informed by time-series studies to elucidate the temporal dependence of these processes.

In addition, the Florida Bay ecosystem is also subject to dramatic long-term variability including the near-total eradication of sponge populations during large-scale phytoplankton blooms (Butler et al. 1995; Peterson et al. 2006; Stevely et al. 2010) including a 2013–2014 event that occurred in Mystery Basin and the surrounding areas following our field study. These blooms appear to have become a recurring phenomenon in central Florida Bay (e.g., Butler et al. 1995; Fourqurean and Robblee 1999; Stevely et al. 2010), including after hurricanes, and have the potential to quickly decimate dominant sponge populations as has been postulated in past bloom events (Butler et al. 1995; Wall et al. 2012). Yet, despite temporal overlap, a direct, causal link between blooming *Synechococcus* and sponge mortality remains unknown (Butler et al. 1995; Lynch and Phlips 2000; Peterson et al. 2006). Based upon our estimates of their N contribution, major sponge biomass losses should significantly alter the nitrogen budget of surrounding waters, particularly basins with limited exchange across shallow sills.

Conclusions

Our results indicate a potentially dominant role for sponges in the N budgets of shallow coastal ecosystems where they frequently dominate benthic biomass. Sponge-mediated N release in Mystery Basin provides 0.59 ± 0.28 mmol N m^{-2} d^{-1} representing a minimum of $45\% \pm 24\%$ of the total N sources to Mystery Basin and providing roughly half of the calculated N demand by primary producers. The spatially heterogeneous sponge biomass within Florida Bay may contribute to some of the variability observed in water column DIN at the ecosystem scale. Additional comparative assessments with other environments within the bay with differing sponge densities and community compositions could provide evidence as to the importance of sponge-recycled N to the overall N budgets in this ecosystem.

The major source of the recycled DIN from sponges is likely the result of remineralization of labile particulate organic matter (e.g., Hoer et al. 2018), although remineralization of dissolved organic N may be conducted by a limited number of sponge species. The role of DON remineralization in DIN release is still unknown. The importance of the sponge source should increase toward the western edge of Florida Bay where N is generally the limiting nutrient for primary production. Loss of sponge biomass resulting from *Synechococcus* sp. phytoplankton blooms or other disturbing force may lead to significant alterations in local nutrient cycling.

References

Adornato, L., and E. Kaltenbacher. 2005. Continuous in situ determinations of nitrite at nanomolar concentrations. Deep-Sea Res. Part I Oceanogr. Res. Pap. **52**: 543–551. doi: 10.1016/j.dsr.2004.11.008

Adornato, L. R., E. A. Kaltenbacher, D. R. Greenhow, and R. H. Byrne. 2007. High-resolution in situ analysis of nitrate and phosphate in the oligotrophic ocean. Environ. Sci. Technol. **41**: 4045–4052. doi:10.1021/es0700855

Baker, R. W. R., and J. A. Nissim. 1963. Expressions for combining standard errors of two groups and for sequential standard error. Nature **198**: 1020–1020. doi:10.1038/1981020a0

Boyer, J. N., J. W. Fourqurean, and R. D. Jones. 1997. Spatial characterization of water quality in Florida Bay and Whitewater Bay by multivariate analyses: zones of similar influence. Estuaries **20**: 743.

Boyer, J. N., J. W. Fourqurean, and R. D. Jones. 1999. Seasonal and long-term trends in the water quality of Florida Bay (1989-1997). Estuaries **22**: 417. doi:10.2307/1353208

Boyer, J. N., B. Peterson, and D. Mir-Gonzalez. 2005. Water quality monitoring and analysis for the Florida Keys National Wildlife Refuge. Final report. US Fish & Wildlife Services Agreement #401812M584. SERC Tech Report T-244.

Boyer, J. N., S. K. Dailey, P. J. Gibson, M. T. Rogers, and D. Mir-Gonzalez. 2006. The role of dissolved organic matter bioavailability in promoting phytoplankton blooms in Florida Bay. Hydrobiologia **569**: 71–85. doi:10.1007/s10750-006-0123-2

Boyer, J. N., and B. Keller. 2007. Nutrient dynamics, p. 55–76. *In* J. H. Hunt and W. Nuttle [eds.], Florida Bay. Science program: A synthesis of research on Florida Bay. Fish and Wildlife Research Institute Technical Report TR-11. Florida Fish and Wildlife Research Institute.

Boyer, J. N., C. R. Kelble, P. B. Ortner, and D. T. Rudnick. 2009. Phytoplankton bloom status: Chlorophyll a biomass as an indicator of water quality condition in the southern estuaries of Florida, USA. Ecol. Indic. **9**: 56–67. doi:10.1016/j.ecolind.2008.11.013

Braun-Blanquet, J. 1972. Plant sociology: The study of plant communities. Hafner.

Butler, M. J., and others. 1995. Cascading disturbances in Florida Bay, USA: Cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobsters *Panulirus argus*. Mar. Ecol. Prog. Ser. **129**: 119–125. doi:10.3354/meps129119

Capone, D. G., S. E. Dunham, S. G. Horrigan, and L. E. Duguay. 1992. Microbial nitrogen transformations in unconsolidated coral reef sediments. Mar. Ecol. Prog. Ser. **80**: 75–88. doi:10.3354/meps080075

Childers, D. L., J. N. Boyer, S. E. Davis, C. J. Madden, D. T. Rudnick, and F. H. Sklar. 2006. Relating precipitation and water management to nutrient concentrations in the oligotrophic upside-down estuaries of the Florida Everglades. Limnol. Oceanogr. **51**: 602–616. doi:10.4319/lo.2006.51.1_part_2.0602

Corbett, D. R., J. Chanton, W. Burnett, K. Dillon, C. Rutkowski, and J. W. Fourqurean. 1999. Patterns of groundwater discharge into Florida Bay. Limnol. Oceanogr. **44**: 1045–1055. doi:10.4319/lo.1999.44.4.1045

Corbett, D. R., K. Dillon, W. Burnett, and J. Chanton. 2000. Estimating the groundwater contribution into Florida Bay via natural tracers, ^{222}Rn and CH_4. Limnol. Oceanogr. **45**: 1546–1557. doi:10.4319/lo.2000.45.7.1546

Corredor, J., and C. Wilkinson. 1988. Nitrate release by Caribbean reef sponges. Limnol. Oceanogr. **33**: 114–120. doi:10.4319/lo.1988.33.1.0114

Diaz, M., and B. Ward. 1997. Sponge-mediated nitrification in tropical benthic communities. Mar. Ecol. Prog. Ser. **156**: 97–107. doi:10.3354/meps156097

Dierssen, H. M., R. C. Zimmerman, L. A. Drake, and D. Burdige. 2010. Benthic ecology from space: Optics and net primary production in seagrass and benthic algae across the Great Bahama Bank. Mar. Ecol. Prog. Ser. **411**: 1–15. doi:10.3354/meps08665

Fiechter, J., and C. N. K. Mooers. 2007. Primary production associated with the Florida Current along the East Florida Shelf: Weekly to seasonal variability from mesoscale-resolution biophysical simulations. J. Geophys. Res. Ocean. **112**: 1–21.

Fourqurean, J. 2011. Florida Bay Nutrient Data, Everglades National Park (FCE), South Florida from August 2008 to present. environmental data initiative; [accessed 2017 November 10]. Available from https://doi.org/10.6073/pasta/5f7a209d1a0fc5042258fb254a6996bb

Fourqurean, J. W., J. C. Zieman, and G. V. N. Powell. 1992. Relationships between porewater nutrients and seagrasses in a subtropical carbonate environment. Mar. Biol. **114**: 57–65.

Fourqurean, J. W., R. Jones, and J. Zieman. 1993. Processes influencing water column nutrient characteristics and phosphorus limitation of phytoplankton biomass in Florida Bay, FL, USA: Inferences from spatial distributions. Estuar. Coast. Shelf Sci. **36**: 295–314. doi:10.1006/ecss.1993.1018

Fourqurean, J. W., and M. B. Robblee. 1999. Florida Bay: A history of recent ecological changes. Estuaries **22**: 345. doi:10.2307/1353203

Fourqurean, J. W., A. Willsie, C. D. Rose, and L. M. Rutten. 2001. Spatial and temporal pattern in seagrass community composition and productivity in South Florida. Mar. Biol. **138**: 341–354. doi:10.1007/s002270000448

Gardner, W. S., and M. J. McCarthy. 2009. Nitrogen dynamics at the sediment-water interface in shallow, sub-tropical Florida Bay: Why denitrification efficiency may decrease with increased eutrophication. Biogeochemistry **95**: 185–198. doi:10.1007/s10533-009-9329-5

Gattuso, J.-P., M. Frankignoulle, and R. Wollast. 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. Annu. Rev. Ecol. Syst. **29**: 405–434. doi:10.1146/annurev.ecolsys.29.1.405

Gibson, P. J., J. N. Boyer, and N. P. Smith. 2008. Nutrient mass flux between Florida Bay and the Florida Keys National Marine Sanctuary. Estuaries Coast. **31**: 21–32. doi:10.1007/s12237-007-9032-5

Hoer, D. R., J. P. Tommerdahl, N. L. Lindquist, and C. S. Martens. 2018. Dissolved inorganic nitrogen fluxes from common Florida Bay (U.S.A.) sponges. Limnol. Oceanogr. **63**: 2563–2578. doi:10.1002/lno.10960

Hofmann, E. E., and J. W. Ambler. 1988. Plankton dynamics on the outer southeastern U.S. continental shelf. Part II: A time-dependent biological model. J. Mar. Res. **46**: 883–917.

Holmes, R., and A. Aminot. 1999. A simple and precise method for measuring ammonium in marine and freshwater ecosystems. Can. J. Fish. **56**: 1801–1808. doi:10.1139/f99-128

Hunt, M., D. Rudnick, J. VanArman, and D. Swift. 2005. Appendix C. Technical documentation to support development of minimum flows and levels for Florida Bay. Produced by the Watershed Management and Water Supply Departments for the South Florida Water Management District.

Jiménez, E., and M. Ribes. 2007. Sponges as a source of dissolved inorganic nitrogen: Nitrification mediated by temperate sponges. Limnol. Oceanogr. **52**: 948–958. doi:10.4319/lo.2007.52.3.0948

Keesing, J. K., J. Strzelecki, J. Fromont, and D. Thomson. 2013. Sponges as important sources of nitrate on an oligotrophic continental shelf. Limnol. Oceanogr. **58**: 1947–1958. doi:10.4319/lo.2013.58.6.1947

Kemp, W. M., J. Cornwell, M. Owens, L. Pride, E. Haberkern, and J. Davis. 2001. Role of benthic communities in the cycling and balance of nitrogen in Florida Bay. Final report to the U.S. Environmental Protection Agency Region 4.

Krebs, C. J. 1999. Ecological methodology, 2nd ed. Addison-Welsey Longman.

Lavrentyev, P. J., H. A. Bootsma, T. H. Johengen, J. F. Cavaletto, and W. S. Gardner. 1998. Microbial plankton response to resource limitation: Insights from the community structure and seston stoichiometry in Florida Bay, USA. Mar. Ecol. Prog. Ser. **165**: 45–57. doi:10.3354/meps165045

Lee, K., and K. H. Dunton. 1999. Inorganic nitrogen acquisition in the seagrass *Thalassia testudinum*: Development of a whole-plant nitrogen budget. Limnol. Oceanogr. **44**: 1204–1215. doi:10.4319/lo.1999.44.5.1204

Lynch, T. C., and E. J. Phlips. 2000. Filtration of the bloom-forming cyanobacteria *Synechococcus* by three sponge species from Florida Bay, U.S.A. Bull. Mar. Sci. **67**: 923–936.

Madden, C. J., D. T. Rudnick, A. A. McDonald, K. M. Cunniff, and J. W. Fourqurean. 2009. Ecological indicators for assessing and communicating seagrass status and trends in Florida Bay. Ecol. Indic. **9**: 68–82. doi:10.1016/j.ecolind.2009.02.004

McNulty, J. K., W. N. Lindall, Jr., and J. E. Sykes. 1972. Cooperative Gulf of Mexico estuarine inventory and study, Florida: Phase I, area description. NOAA technical report NMFS CIRC- 368.

Peterson, B., C. Chester, F. Jochem, and J. Fourqurean. 2006. Potential role of sponge communities in controlling phytoplankton blooms in Florida Bay. Mar. Ecol. Prog. Ser. **328**: 93–103. doi:10.3354/meps328093

Prospero, J. M., and others. 1996. Atmospheric deposition of nutrients to the North Atlantic Basin. Biogeochemistry **35**: 27–73. doi:10.1007/BF02179824

Redfield, B. C. 1958. The biological control of chemical factors in the environment. Am. Sci. **46**: 205–221.

Rudnick, D., Z. Chen, D. Childers, and T. Fontaine. 1999. Phosphorus and nitrogen inputs to Florida Bay: The importance of the Everglades watershed. Estuaries **22**: 398–416. doi:10.2307/1353207

Rudnick, D. T., P. B. Ortner, J. A. Browder, and S. M. Davis. 2005. A conceptual ecological model of Florida Bay. Wetlands **25**: 870–883. doi:10.1672/0277-5212(2005)025[0870:ACEMOF]2.0.CO;2

SERC-FIU WQMN Program. Data were provided by the SERC-FIU Water Quality Monitoring Network which is supported by SFWMD/SERC Cooperative Agreement #4600000352 as well as EPA Agreement #X7-96410603-3.

Southwell, M., J. Weisz, C. Martens, and N. L. Lindquist. 2008. In situ fluxes of dissolved inorganic nitrogen from the sponge community on Conch Reef, Key Largo, Florida. Limnol. Oceanogr. **53**: 986–996. doi:10.4319/lo.2008.53.3.0986

Steimle, E., E. Kaltenbacher, and R. Byrne. 2002. In situ nitrite measurements using a compact spectrophotometric analysis system. Mar. Chem. **77**: 255–262. doi:10.1016/S0304-4203(02)00003-8

Stevely, J. M., D. E. Sweat, T. M. Bert, C. Sim-Smith, and M. Kelly. 2010. Commercial bath sponge (spongia and hippospongia) and total sponge community abundance and biomass estimates in the Florida Middle and Upper Keys, USA. Proc. 61st Gulf Caribb. Fish. Inst. 62.

Wall, C. C., B. S. Rodgers, C. J. Gobler, and B. J. Peterson. 2012. Responses of loggerhead sponges *Spechiospongia vesparium* during harmful cyanobacterial blooms in a subtropical lagoon. Mar. Ecol. Prog. Ser. **451**: 31–43. doi:10.3354/meps09537

Weisz, J. B., N. Lindquist, and C. S. Martens. 2008. Do associated microbial abundances impact marine demosponge pumping rates and tissue densities? Oecologia **155**: 367–376. doi:10.1007/s00442-007-0910-0

Yarbro, L. A., and P. R. Carlson. 2008. Community oxygen and nutrient fluxes in seagrass beds of Florida Bay, USA. Estuaries Coast. **31**: 877–897. doi:10.1007/s12237-008-9071-6

Yoder, J. A., L. P. Atkinson, S. Stephen Bishop, E. E. Hofmann, and T. N. Lee. 1983. Effect of upwelling on phytoplankton productivity of the outer southeastern United States continental shelf. Cont. Shelf Res. **1**: 385–404.

Zhang, J.-Z., and C. J. Fischer. 2014. Carbon dynamics of Florida Bay: Spatiotemporal patterns and biological control. Environ. Sci. Technol. **48**: 9161–9169. doi:10.1021/es500510z

Zieman, J. C., J. W. Fourqurean, and R. L. Iverson. 1989. Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. Bull. Mar. Sci. **44**: 292–311.

Acknowledgments

We would like to thank John Hunt and the rest of the scientists and staff at the Florida Fish and Wildlife Conservation Commission South Florida Regional Laboratory in Marathon, Florida for facilitating field work in Florida Bay. We would also like to thank Howard Mendlovitz, Jake Tommerdahl, and Meredith Kintzing for their assistance in the field. The presented research was conducted under Everglades National Park permit number EVER-2012-SCI-0024. Financial support was provided to C.S.M. and N.L.L. from NSF Chemical Oceanography grant OCE-1132155.

Conflict of Interest

None declared.

Submitted 06 May 2019
Revised 29 September 2019
Accepted 31 October 2019

Associate editor: Ronnie Glud