

Nutrient Enrichment and Eutrophication on Fringing Coral Reefs of Bonaire and Curaçao, Netherlands Antilles

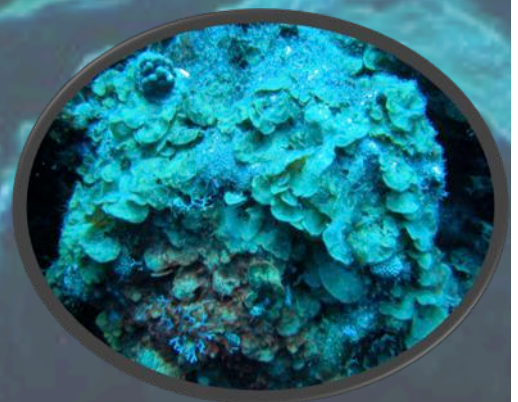
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Abstract - Land-based nutrient pollution is a major stressor on coral reef communities around the Caribbean region and globally. To assess the status of nutrient enrichment and eutrophication on Bonaire and Curacao's coral reefs, we conducted a comparative nutrient monitoring program that included seasonal sampling for nutrients (ammonium, nitrate, DIN, SRP, TDN, TDP), phytoplankton biomass (Chl *a*), stable nitrogen isotopes ($\delta^{15}\text{N}$) in reef macroalgae, and biotic cover (point count analysis of video transect data) of shallow and deep reef sites between March 2006 and June 2008. Ammonium dominated the DIN pool on both islands and the highest concentrations ($\sim 10 \mu\text{M}$) occurred on Bonaire's reef sites adjacent to the Cargill salt ponds. DIN concentrations averaged $> 1 \mu\text{M}$ on both shallow and deep reefs of both islands, indicating that these reefs are now above the DIN threshold noted to support expansion of algal turf, macroalgae and coral diseases. SRP concentrations averaged $\sim 0.1 \mu\text{M}$ on both islands, a level that also represents the SRP threshold for eutrophication on coral reefs. DON and DOP dominated the TDN and TDP pools; TDN/TDP ratios averaged 52 on Bonaire and 45 on Curacao, indicating strong P-limitation of algal growth. Mean Chl *a* concentrations were higher on Curacao ($0.25 \mu\text{g/l}$) than Bonaire ($0.19 \mu\text{g/l}$) and the highest Chl *a* concentrations on both islands occurred on reefs adjacent to urbanized, nutrient enriched areas. In contrast, low Chl *a* values of $\sim 0.05\text{-}0.1 \mu\text{g/l}$ occurred at the upstream reef sites and the offshore reference site, underscoring the importance of land-based nutrient enrichment to microbial growth and eutrophication on fringing reefs of both islands. The highest macroalgal $\delta^{15}\text{N}$ values ($> + 3 \text{ o/oo}$) occurred at the MegaPier and Piscadera Bay on Curacao, which reflects the highest watershed sewage nitrogen inputs of all reef sites in the study. The lower $\delta^{15}\text{N}$ ($< + 2 \text{ o/oo}$) values at the other reef sites reflect lower levels of sewage treatment as well as contributions from other nitrogen sources (nitrogen fixation, atmospheric inputs) that have lower source $\delta^{15}\text{N}$ values. Reefs on both islands were dominated ($\sim 75 \%$ cover) by benthic algae but showed distinct differences in algal composition; Bonaire's reefs had high cover of turf and low cover of macroalgae compared to the opposite pattern on Curacao. Our results suggest that the recent expansion of benthic algae and loss of coral cover on reefs in Bonaire and Curacao are not simply the result of top-down human pressures (e.g., overfishing) alone, but also reflect strong bottom-up effects from land-based nutrient pollution.

INTRODUCTION

Coral reefs globally are threatened by a variety of human-related impacts, including nutrient enrichment and eutrophication (Kinsey, 1988; MEA, 2005; UNEP 2006). Coral reefs are adapted to nutrient-poor (oligotrophic) tropical and subtropical waters and increases in the concentrations of nitrogen (N) and phosphorus (P) from human activities can cause myriad ecological effects (Smith et al. 1981; Bell 1992; NRC 2000). Nutrient pollution from sewage, urban stormwater, fertilizers, top soils, and fossil fuel combustion is a common thread that links an array of problems on coral reefs that include eutrophication, hypoxia, harmful algal blooms, coral diseases, decreased coral reproduction, and bioerosion (NRC 2000).

During the past several decades, coral reefs in the Caribbean region have experienced some of the greatest loss of coral cover worldwide. On many shallow reefs adjacent to expanding human populations, hermatypic (reef-forming) coral cover commonly averaged 70% or more in the 1970s, but by the year 2000 had decreased to ~ 7 % cover (Gardner et al. 2004). The reef corals have been largely replaced by algal blooms (some of which are harmful), which include frondose macroalgae (> 2 cm high), microfilamentous algal turfs (< 2 cm high), and crustose coralline algae (CCA; Littler and Littler 1984). This recent trend away from corals towards benthic algae has been widely attributed to “top-down” controls only, i.e. reduced grazing pressure as a result of overfishing and the die-off the long-spined urchin *Diadema antillarum* (Hughes 1994; Jackson 2001). An alternative hypothesis suggested that “bottom-up” forcing from nutrient enrichment and eutrophication was either a primary or contributing factor, depending on reef location and influence by human activities on local, regional and global scales (Lapointe 1997; Lapointe 1999).

The coral reefs of Bonaire and Curaçao are considered to be the best coral reefs remaining in the Caribbean region because of their relatively high coral cover and low cover of macroalgae. However, shallow reefs (< 30 m) off both Bonaire and Curaçao have changed dramatically since the 1970s, with significant decreases in coral cover and diversity compared to deep reefs (Bak and Nieuwland 1995; Bak et al. 2005). Steneck et al. (2007) related recent trends of increasing macroalgae to declining herbivory from parrotfish, increases in damselfish populations, and loss of large-bodied predators on Bonaire’s reefs. Although declining herbivory from parrotfish and other reef herbivores can result in increased macroalgae (Lewis 1986;

Carpenter 1988), nutrient enrichment, such as that associated with urbanization and sewage pollution, is also known to cause increases in reef macroalgae (Banner, 1974; Smith et al. 1981; Lapointe 1997), algal turfs (Hatcher and Larkum 1983; Vermeij et al. 2010) and CCA (Littler 1973). Nutrient enrichment and eutrophication, especially from sewage and agricultural runoff, have also been linked to increases in coral diseases and mortality (Bruno et al. 2003; Voss and Richardson 2006; Johnson et al. 2010).

To date, little is known about the role of land-based nutrient enrichment in the decline of the fringing coral reefs of Bonaire and Curaçao. In a one-year study, Gast et al. (1999) measured nutrient concentrations and microbial variables in eutrophied vs. non-eutrophied waters along the southern coast of Curaçao; they concluded that effects of sewage, groundwater discharge and urban runoff led to localized effects of nutrient enrichment on reefs adjacent to the urbanized area around Wilemstad, particularly in regards to elevated bacterial production at the impacted site. However, that study did not include analyses of benthic macroalgae and/or algal turfs, which are excellent “indicator species” of nutrient availability and could provide more robust spatial resolution of nutrient impacts to benthic reef communities. Not only do taxonomic shifts occur in benthic macroalgae as a result of land-based nutrient enrichment (Lapointe et al. 2010), but also analysis of nitrogen isotopes ($^{15}\text{N}/^{14}\text{N} = \delta^{15}\text{N}$) in macroalgae provides a cost-effective and objective means of quantifying spatial and temporal variability in sewage stress on coral reefs (Risk et al. 2009).

We hypothesized that the urban discharges of sewage and stormwater runoff on both Bonaire and Curaçao would be evident in elevated nutrient (DIN, SRP, TDN, TDP) and chlorophyll *a* concentrations at reefs adjacent to those inputs. Additionally, we hypothesized that patterns of $\delta^{15}\text{N}$ among macroalgae on fringing coral reefs of these islands would reflect the location(s) and source(s) of nitrogen inputs, with elevated values corresponding to sites impacted by sewage (Risk et al. 2009). Lastly, we hypothesized that the taxonomic structure of macroalgae (i.e. nutrient indicator species) would reflect sites most impacted by sewage.

MATERIALS AND METHODS

Study Area and Site Selection. The islands of Bonaire and Curaçao are located in the southern Caribbean approximately 70 km north of Venezuela. Both islands are part of the Kingdom of the Netherlands and considered an Overseas Territory by the European Union. Distinct differences between these two islands make for an interesting comparative study of land-based nutrient enrichment and reef health; some 150,000 people live on Curaçao, but only ~ 15,800 people live on Bonaire. Both islands contain biologically diverse fringing coral reefs, which begin at the shoreline and extend hundreds of meters from shore. On Bonaire, the reefs have received significant protection by establishment of the Bonaire Marine Park (BNMP) in 1979 and have had sustained management since 1991 by a local non-governmental agency STINAPA (Stichting Nationale Parken Nederlandse Antillean) Bonaire. Bonaire's economy is mainly based on tourism, which has long catered to SCUBA divers and snorkelers and is considered one of the best diving destinations in the world.

Ten reef sites on Bonaire (including Klein Bonaire) and nine reef sites on Curaçao extending along the leeward side of each island were chosen for the study (Fig. 1). The leeward fringing reefs on Bonaire and Curaçao are characterized by a ~ 50 m wide shallow terrace (7-12 m depth) that drops off to a seaward slope that varies from 45° to vertical (Bak 1975). The shallow (6 m) reefs were located on the terrace and deep (18 m) sites were located on the seaward drop off. On Bonaire, the ten reef sites included Red Slave (RS), Angel City (AC), 18th Palm (18th), Playa Lechi (PL), Front Porch (FP), Habitat Bonaire (HB), Karpata (Kar), and Playa Funchi (PF); two sites, Ebo's Special (ES) and South Bay (SB), were located on Klein Bonaire (Fig. 1). On Curaçao, the nine reef sites included East Point (EP), Fuik Bay (FB), Caracas Bay (CB), Jan Thiel (JT), Mega Pier (MP), Piscadera Bay (PB), Habitat Curaçao (HC), Sunset Waters (SW), and Watamula (W). In addition to the reef sites above, seawater samples were also collected from the Cargill salt ponds and Lac Bay on Bonaire and from Spanish Water and an open water site on Curaçao. These sites were chosen to represent a variety of coastal environments on the two islands, including sites adjacent to urbanized areas, industry (Cargill salt ponds), and relatively undeveloped coastlines.

Analysis of Seawater for DIN, SRP and Chl *a*. SCUBA divers collected seawater samples from the various reef sites seasonally between March 2006 and June 2008. Divers used clean, 0.25 liter HDPE Nalgene bottles to collect replicate ($n = 4$) seawater samples ~ 0.5 m off the bottom on the various shallow and deep reef sites. The water samples were held on ice in the dark in a cooler until return to shore where aliquots of the samples were filtered through a $0.7 \mu\text{m}$ GF/F filter and frozen. The samples were subsequently analyzed for ammonium (NH_4^+ -N), nitrate plus nitrite ($\text{NO}_3^- + \text{NO}_2^-$ -N), and SRP (PO_4^{3-} -P) at the Nutrient Analytical Services Laboratory (NASL), Chesapeake Biological Laboratory, University of Maryland System, Solomons, MD. The samples were analyzed on a Technicon Auto-Analyzer II (nitrate, SRP) or a Technicon TRAACS 800 (ammonium, nitrite). Detection limits were $0.21 \mu\text{M}$ for ammonium, $0.01 \mu\text{M}$ for nitrate plus nitrite, $0.01 \mu\text{M}$ for nitrite, and $0.02 \mu\text{M}$ for SRP, $2.06 \mu\text{M}$ for TDN and $0.05 \mu\text{M}$ for TDP (Keefe et al. 2004). Nitrogen to phosphorus ratios were computed both for the inorganic forms (DIN/DIP) and total dissolved forms (TDN/TDP). Salinity of the water samples was measured to ± 1.0 psu using a Bausch and Lomb refractometer. The GF/F glass fiber filters used for filtering the water samples (200 ml) were frozen and analyzed for chlorophyll *a* (Chl *a*) as a measure of phytoplankton biomass. The filters were extracted for 30 minutes using 10 ml of dimethyl sulfoxide and then with an added 15 ml of 90% acetone at 5°C overnight. The samples were measured fluorometrically before and after acidification for determination of Chl *a* and phaeopigment concentrations. Fluorescence measurements were made using a Turner Designs 10-000R fluorometer equipped with a infrared-sensitive photomultiplier and calibrated using pure Chl *a*.

Analysis of Macroalgae for $\delta^{15}\text{N}$. SCUBA divers collected replicate ($n = 2$) composite samples of the two most abundant macroalgae species from the various reef sites into nylon mesh bags. At least 3-6 separate plants were collected for each composite sample of each species to ensure representativeness. Following collection, the macroalgae were cleaned of debris and transferred to plastic Ziploc® plastic baggies and held in a cooler during transport to the lab. In the lab, the samples were identified, rinsed briefly (3-5 s) in deionized water to further remove debris. The plants were placed in aluminum drying dishes and dried in a lab oven at 65°C for 48 h. The dried macroalgae were ground to a fine powder using a mortar and pestle and stored in plastic

vials until analysis. Samples of dried, powdered macroalgae were analyzed for stable nitrogen isotope ratios ($\delta^{15}\text{N}$) at the Stable Isotope Biogeochemistry Laboratory at McMaster University, Hamilton, Canada, or the Stable Isotope Facility at University of California, Davis, CA, USA. The standard used for stable nitrogen isotope analysis was N_2 in air. $\delta^{15}\text{N}$ values, expressed as ‰, were calculated as $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, with R equal to $^{15}\text{N}/^{14}\text{N}$.

Quantification of Reef Biota. SCUBA divers used an underwater digital video camcorder (Sony TRV 900 in an Amphibico Navigator housing) to record imagery along two replicate 25 m long belt transects at each shallow and deep reef site. Divers obtained the imagery by holding the camcorder perpendicular to the reef surface (0.5 m off bottom, 0.5 m² image area) and slowly swimming along the transects to obtain clear, steady images. Fifteen frame-grabs, taken from equal time sequences along the video transects, were analyzed on a high resolution color monitor using Coral Point Count with Excel extensions (CPCe; Kohler and Gill 2006). This method provided a relatively unbiased estimate of the percent cover of hard corals, macroalgae (> 2 cm tall), algal turf (< 2 cm tall), sponges, and octocorals (Lapointe and Thacker, 2002).

Statistical Analysis. Nutrient parameters (ammonium, nitrate, dissolved inorganic nitrogen (DIN = ammonium + nitrate), dissolved organic nitrogen (DON), total dissolved nitrogen (TDN = DIN + DON), SRP, dissolved organic phosphorus (DOP) and total dissolved phosphorus (TDP), Chl *a* data, and $\delta^{15}\text{N}$ values of macroalgal samples were tested for normality using the Shapiro-Wilk test. All parameters were non-normally distributed and thus log-transformed before statistical analyses. For each island, nutrient and planktonic Chl *a* concentrations for all sites combined were tested (t-tests) to assess potential differences between shallow and deep reefs. Analyses of variance (ANOVA) were used to test for nutrient and Chl *a* concentration differences among sites for each island, by reef depth. Additionally, for each island the $\delta^{15}\text{N}$ values were tested for inter-station differences using ANOVA, and for each individual station shallow reef versus deep reef $\delta^{15}\text{N}$ values were tested using t-tests. Statistical analyses were conducted using SAS (Schlottzauer and Littell 1987) with a significance level of $\alpha = 0.05$ utilized for significance.

RESULTS

Ammonium. Ammonium concentrations on Bonaire shallow reefs showed high variability, particularly at Stations RS, AC and 18th Palm (Table 1), with high maximum values at those three sites of 10.57, 6.11 and 3.85 μM , respectively. Those three sites had significantly higher ammonium concentrations than sites PL, FB and PF. Deep reefs on Bonaire had no significant differences ammonium among stations (Table 2), although maximum values were highest at RS (9.11 μM) and AC (6.11 μM). For all sites combined there were no significant differences in ammonium concentrations between shallow and deep reefs. Ammonium concentrations at shallow reefs on Curaçao ranged from 0.43-2.83 μM , with no significant differences between sites (Table 3). Likewise, deep reefs on Curaçao ranged from 0.49-3.08 μM , with no significant differences among sites (Table 4). For all sites combined there were no significant differences in ammonium concentrations between shallow and deep reefs.

Nitrate. Nitrate concentrations on Bonaire shallow reefs ranged from 0.45-1.57 μM , and did significantly vary among sites. Stations KAR, ES, HB, 18th Palm, PF and FP had significantly higher nitrate than Stations RS, AC, PL and SB (Table 1). Nitrate at the deep Bonaire reefs ranged from 0.51-1.92 μM , but did not significantly differ among sites (Table 2). The deep Bonaire reefs combined maintained significantly ($p = 0.002$) higher nitrate (mean of 0.57 ± 0.25 μM , median 0.51 μM) than the shallow reefs (mean of 0.49 ± 0.20 μM , median 0.45 μM). On Curaçao nitrate at the shallow reefs ranged from 0.48-3.13 μM , with significant station differences. Stations EP, MP, PB and JT had significantly higher nitrate than FB, CB, SW and WAT, with SPW and OW (the open water site) significantly lower than all the rest (Table 3). Nitrate at Curaçao deep reefs ranged from 0.52-2.75 μM , with no significant inter site differences (Table 4). As at Bonaire, the deep Curaçao reefs combined maintained significantly ($p = 0.01$) nitrate (mean of 0.60 ± 0.30 μM , median 0.52 μM) than the shallow reefs (mean of 0.54 ± 0.33 μM , median 0.48 μM).

Dissolved Inorganic Nitrogen (DIN). DIN concentrations at Bonaire ranged from 0.56-11.28 μM for the shallow reefs, and from 0.54-9.82 μM for the deep reefs (Tables 1 and 2). There were no significant concentration differences among stations for either shallow or deep reefs. DIN at the shallow Curaçao reefs ranged from 0.38-5.96 μM , with Station MP significantly

higher than Stations FB, SW, SPW and OW (Table 3). DIN at the Curaçao deep reefs ranged from 0.53-5.12 μM , with no significant differences among stations (Table 4). DIN composition at most stations was roughly equally comprised of ammonium and nitrate (Fig. 2). However, on Bonaire at Stations RS, AC and 18th Palm ammonium was clearly dominant (Fig. 2), likely due to salt works discharges.

Dissolved Organic Nitrogen (DON). DON showed wide variability among the Bonaire reefs, ranging from 6.05-65.28 μM at the shallow reefs, and from 4.99-39.03 μM at the deep reefs (Tables 1 and 2). DON among the Curaçao reefs were also highly variable (although not as much as the Bonaire sites), ranging from 2.25-36.53 μM at the shallow reefs, and from 3.83-24.10 μM at the deep reefs (Tables 3 and 4). Due to the high variability there were no significant DON differences among stations for either island.

Total Dissolved Nitrogen (TDN). TDN reflected the high variability displayed by the DON concentrations (Fig. 3). TDN at the Bonaire shallow reefs ranged from 6.75-66.86 μM at the shallow reefs and from 7.43-40.50 μM at the deep reefs (Tables 1 and 2). At Curaçao TDN ranged from 4.14-38.14 μM at the shallow reefs, and from 4.93-26.29 at the deep reefs (Tables 3 and 4). Again, there were no significant inter-station differences for either island due to the high variability. The DON fraction dominated TDN concentrations (Fig. 3), ranging on Bonaire shallow reefs from 61.9-97.7%, with an overall mean of 90.5% and median of 91.0%. TDN composition of the Bonaire deep reefs showed percent DON ranging from 55.1-96.4%, with a mean of 89.4% and a median of 90.7%. At Curaçao TDN at the shallow reefs ranged from 54.3-96.6% DON, with a mean of 88.5% and median of 89.6% DON. TDN at the deep reefs ranged from 61.0-96.5% DON, with a mean of 87.5 and median of 89.0% DON.

Soluble Reactive Phosphorus (SRP). SRP at the Bonaire reefs showed little variability, ranging among shallow reefs from 0.04-0.21 μM , and from 0.03-0.28 μM among deep reefs. There were no significant differences in SRP concentrations among either shallow or deep reefs, with station medians of 0.08-0.10 μM (Tables 1 and 2). On Curaçao shallow reefs SRP ranged from 0.05-0.20 μM , and at Curaçao deep reefs from 0.04-0.25 μM . There were no significant

differences in SRP concentration among either shallow or deep reefs at Curaçao, with station medians ranging from 0.08-0.09 μM (Tables 3 and 4).

Dissolved Organic Phosphorus (DOP). DOP at Bonaire shallow reefs ranged from 0.02-0.41 μM , and at the deep reefs from 0.03-0.58 μM , with no significant inter-station differences in concentration at either shallow or deep reefs (Tables 1 and 2). DOP at Curaçao shallow reefs ranged from 0.04-0.40 μM , and DOP at the deep reefs ranged from 0.05-0.66 μM . There were no significant inter-station differences for either the shallow or deep reefs (Tables 3 and 4).

Total Dissolved Phosphorus (TDP). At Bonaire, TDP at shallow reefs ranged from 0.11-1.41 μM , and TDP at deep reefs ranged from 0.12-0.86 μM . There were no significant TDP concentration differences among sites (Tables 1 and 2; Fig. 4). At Curaçao, TDP at shallow reefs ranged from 0.12-0.60 μM , and at deep reefs from 0.13-0.82 μM . Again, there were no significant differences in TDP concentrations among sites for either shallow or deep reefs (Tables 3 and 4). The majority of the TDP was in the organic form, although not to the extent that it was regarding TDN (Fig. 4). At the shallow Bonaire reefs the composition of TDP ranged from 9.9-85.8% DOP, with a mean of 62.7% and median of 64.3%. At the deep Bonaire reefs the DOP proportion of TDP ranged from 17.6-89.7%, with a mean of 63.7% and a median of 65.2% DOP. For the Curaçao shallow reefs the composition of TDP represented by DOP ranged from 25.4-85.9% DOP, with a mean of 61.0% and median of 60.8% DOP. For the Curaçao deep reefs the composition of TDP represented by DOP ranged from 26.1-85.3%, with a mean of 61.1% and median of 60.4% DOP.

DIN/SRP. For Bonaire shallow reefs DIN/SRP ratios were moderate, ranging from 4.6-113.9, with a mean of 14.4 and a median of 11.9 (Fig. 5). DIN/SRP ratios at the Bonaire deep reefs were likewise moderate, ranging from 5.4-86.2 with a mean of 15.2 and a median of 12.4. Ratios were highest at Stations RS and AC (Fig. 5). At Curaçao, DIN/SRP ratios were at relatively similar levels ranging at shallow reefs from 3.9-34.2, with a mean of 13.2 and a median of 12.1, with Stations MP, PB and HC having the highest ratios (Fig. 5). At the deep reefs DIN/SRP ranged from 3.8-51.8, with a mean of 14.1 and a median of 12.4.

TDN/TDP. Owing to the strong presence of organic nitrogen, the TDN/TDP ratios presented a much different story than the DIN/SRP ratios (Fig. 6). At Bonaire, the shallow reef TDN/TDP ratios ranged from 25.0-152.0 with a mean of 52.3 and 47.6. The deep reef TDN/TDP ratios ranged from 23.5-139.7 with a mean of 52.1 and a median of 47.2. The highest mean values were at the shallow HB and KAR reef sites. At Curaçao, the shallow reef TDN/TDP ratios ranged from 13.6-143.4, with a mean of 46.1 and a median of 41.2. Deep reefs at Curaçao had TDN/TDP ratios ranging from 21.4-94.7 with a mean of 43.8 and a median of 42.2. There was no consistent pattern of TDN/TDP ratios among shallow versus deep reefs, although for Curaçao stations MP and JT were both somewhat elevated (Fig. 6)

Chlorophyll *a*. Chl *a* was the planktonic nutrient response variable we measured in this investigation. For the shallow Bonaire reefs it ranged from 0.06-0.38 µg/L and for the deep reefs it ranged from 0.05-0.44 µg/L. There were no significant inter-station Chl *a* concentration differences for either shallow or deep reef sites on Bonaire (Tables 1 and 2; Fig. 7). For the Curaçao shallow reefs Chl *a* ranged from 0.05-0.99 µg/L, and concentrations significantly differed among stations into several tiers (Table 3). Stations MP and SPW were higher than all other sites (Fig. 7), followed by a second tier of Stations PB, FB and CB. A third tier consisted of HC, SW and JT. Watamula (WAT) did not differ from the second and third tiers. The final tier was EP and the open water site (OW), which had significantly lower Chl *a* than all other sites. Chl *a* at the deep Curaçao reefs ranged from 0.06-1.12 µg/L, and concentrations significantly differed among sites into three tiers (Table 4). Stations MP, HC and FB grouped into one tier followed by Stations PB, CB, SW and WAT, with Stations EP and JT having lower Chl *a* than all the other sites (Fig. 7).

Macroalgal $\delta^{15}\text{N}$ Values. The $\delta^{15}\text{N}$ values for the macroalgae on the Bonaire shallow reefs averaged 1.53 ± 0.57 o/oo, with a median of 1.40 o/oo and range of 0.24-2.72 o/oo. Values for the Bonaire deep reefs averaged 1.56 ± 0.53 o/oo with a median of 1.52 o/oo and range of 0.11-2.66 o/oo. There were no significant differences among stations for either the shallow or deep reefs on Bonaire. Likewise, there were no significant differences in macroalgal $\delta^{15}\text{N}$ values between the shallow and deep reefs at any site on Bonaire (Fig. 8). In contrast, the situation on

Curaçao showed a number of differences. The $\delta^{15}\text{N}$ values for macroalgae on the Curaçao shallow reefs averaged 2.03 ± 1.49 o/oo with a median of 1.54 o/oo and range of 0.21-7.51 o/oo. Values for the Curaçao deep reefs averaged 1.63 ± 0.97 o/oo with a median of 1.29 o/oo and range of 0.50-4.51 o/oo. Testing for differences in macroalgal $\delta^{15}\text{N}$ values among shallow reef stations revealed that values for Station MB were significantly greater than all other sites, and values for Station PB were greater than all sites except MP ($p < 0.0001$). For the deep Curaçao reefs $\delta^{15}\text{N}$ values for MP were again greater than all other sites, while Station PB $\delta^{15}\text{N}$ values were greater than most sites except Stations SW and HC (Fig. 8). Also, for these deep reefs $\delta^{15}\text{N}$ values for Station WAT were significantly lower than all sites except Station FB.

Testing for differences in macroalgal $\delta^{15}\text{N}$ values between depths for each station revealed significant differences at three stations, in each case the shallow reef macroalgae having $\delta^{15}\text{N}$ values greater than those of the deep reefs. At Station MP shallow reef macroalgal $\delta^{15}\text{N}$ values averaged 5.77 ± 0.89 o/oo with a median of 5.72 o/oo while the deep reefs at that site averaged 3.73 ± 0.53 o/oo with a median of 3.55 o/oo. At Station PB shallow reef macroalgal $\delta^{15}\text{N}$ values averaged 2.83 ± 0.43 o/oo with a median of 2.64 o/oo while at the deep reefs macroalgae averaged 2.00 ± 0.44 o/oo with a median of 2.04 o/oo. The other site showing significant depth differences was the site with the lowest overall $\delta^{15}\text{N}$ values, Station WAT. At this site $\delta^{15}\text{N}$ values averaged 1.33 ± 0.49 o/oo with a median of 1.22 o/oo at the shallow reef, while deep reef values averaged 0.80 ± 0.30 o/oo with a median of 0.77 o/oo (Fig. 8). Macroalgae collected for $\delta^{15}\text{N}$ analysis are identified in Table 6.

Biotic Cover on Fringing Reefs: The video transect analysis revealed some different patterns in biotic cover between reefs in Bonaire and Curaçao. Stony coral cover was similar on shallow reefs of Bonaire and Curaçao, averaging 15.42 % and 14.95 %, respectively; on deep reefs, however, stony coral cover averaged 31.12 % on Bonaire compared to 20.94 % on Curaçao (Fig. 9). Soft coral cover on shallow reefs averaged 8.96 % and 10.12 % on Bonaire and Curaçao, respectively, compared to lower values of 3.22% and 6.12% on deep reefs (Fig. 9). Macroalgae cover was lower on both shallow and deep reefs on Bonaire, 4.58% and 26.17%, respectively,

compared to 26.17% and 47.45%, respectively on Curaçao (Fig. 10). In contrast to macroalgae, turf cover was higher on both shallow and deep reefs in Bonaire, 70.01 and 40.53 %, respectively, compared to 48.20% and 24.96 %, respectively, on Curaçao (Fig. 11).

DISCUSSION

Inorganic Nutrient Concentrations: The results of this multi-year nutrient monitoring study provided several lines of evidence supporting the hypothesis that land-based nutrient pollution is significantly impacting coral reefs along the leeward coasts of Bonaire and Curaçao. Undisturbed Caribbean coral reefs typically have very low or undetectable ammonium concentrations ($< 0.2 \mu\text{M}$, Bell 1992; Lapointe and Smith 1987; Lapointe et al. 1993) and elevated concentrations can result from a variety of anthropogenic land-based sources and pathways, such as sewage outfalls, septic tanks, fertilizers, industrial effluents, agricultural runoff, reverse osmosis (RO) discharges, and atmospheric deposition (NRC 2000). The overall shallow reef mean ammonium concentration on Bonaire ($0.888 \mu\text{M}$) was 30% higher than that of Curaçao shallow reefs ($0.613 \mu\text{M}$) while the overall median ammonium at Bonaire shallow reefs ($0.611 \mu\text{M}$) was 20% higher than that of Curaçao ($0.494 \mu\text{M}$) (Table 5). The highest ammonium concentrations on Bonaire's reefs were higher than maximum values reported for other coral reefs in the Caribbean region. On several samplings unusually high ammonium concentrations (up to $\sim 10 \mu\text{M}$) occurred at shallow and deep reefs at RS and AC, which are adjacent to the Cargill salt ponds. High ammonium concentrations were also observed at 18th Palm, a reef site down-current from the salt ponds. These concentrations are similar to or higher than maximum ammonium concentrations reported for eutrophic coral reefs in the Florida Keys (Lapointe et al. 2007), Tobago (Lapointe et al. 2010), the Negril Marine Park, Jamaica (Lapointe and Thacker 2002; Lapointe et al. 2011), and Barbados (Tomascik and Sander 1985).

The elevated ammonium concentrations on Bonaire, especially those at RS and AC, likely result from land-based sources of pollution. Two grab samples collected from the Cargill salt ponds in June 2007 were analyzed for a variety of nutrient species and provided evidence that the salt ponds could be a source of elevated ammonium to adjacent reefs on Bonaire. Ammonium concentrations $>1,200 \mu\text{M}$ were measured in both diluted (10:1) and undiluted samples, suggesting that salt interference was not causing the high concentrations as an

analytical artifact. Surface water discharges from the salt works periodically occur, and potential submarine groundwater discharge of ammonium from the unlined ponds could also contribute. The affected reefs at both RS and AC had unusually abundant cyanobacterial coverage, a phenomenon that has been linked to elevated ammonium concentrations in eutrophic coral reef communities in the Florida Keys (Lapointe et al. 2004).

Periodically ammonium concentrations at or exceeding $1 \mu\text{M}$ were encountered at selected sites in both Bonaire and Curaçao. The widespread use of cesspits for sewage disposal on Bonaire and Curaçao would result in contamination groundwaters with ammonium and other contaminants, which would flow down-gradient and discharge into coastal waters (Lapointe et al. 1990). Discharges of surface waters polluted with sewage could also contribute. For example, the mean ammonium concentration in the tidal discharges of the South Negril River, Jamaica is $\sim 23.9 \mu\text{M}$ (Lapointe et al. 2011) and the Town Harbour, Curaçao is $\sim 40 \mu\text{M}$ (Gast et al. 1999), both of which are heavily polluted by sewage.

In contrast to ammonium, median nitrate concentrations (Table 5) were similar on Bonaire ($0.450 \mu\text{M}$) and Curaçao ($0.480 \mu\text{M}$) reefs and the highest nitrate concentrations consistently occurred on reefs in urbanized areas. The highest nitrate concentrations at Bonaire occurred on shallow and deep reefs at KAR, a reef site in close proximity to the reverse osmosis outfall used on this island for the production of potable water. On Curaçao, the highest nitrate concentrations occurred at MP, a reef site directly influenced by the Town Harbour tidal discharges that are influenced by untreated sewage, stormwater runoff, and industrial effluents from this urbanized area. Gast et al. (1999) also reported elevated nitrate concentrations on reefs off the Town Harbor, which they attributed to sewage pollution and other anthropogenic activities. Piscadera Bay, the nearest sampling site to MP also had comparatively high nitrate concentrations, as did JT and HC (Fig. 1; Table 3). Two grab samples collected in a hotel cistern on Bonaire had nitrate concentrations of $44 \mu\text{M}$, indicating that atmospheric deposition in this area could also contribute a considerable amount of biologically available nitrate.

Nitrate concentrations at the deep reefs on both islands were greater than nitrate concentrations at the shallow reefs (Tables 2 and 4). The reason for this pattern was not elucidated by this study. However, Gast et al. (1999) noted that nitrate inputs from the mainland could be reaching the deep reefs; possibly, submarine groundwater discharge delivers mainland derived nitrate more readily to the deeper reefs as opposed to the shallow reefs. Upwelling of

cold, nitrate-rich water does occur on some coral reefs in the Caribbean region (Lapointe et al. 2005) but the presence of such cold, deep water intrusions have not been reported for either Bonaire or Curaçao and was not evident during this study. Finally, sponges are well known to represent localized sources of nitrate enrichment on Caribbean reefs and, through filtration of particulate matter and subsequent bacterial nitrification, could contribute significantly to the nitrate pool in deep reef communities (Corredor et al. 1988).

The overall median DIN concentration at shallow reefs at Bonaire (1.111 μM) was similar to those at Curaçao (1.029 μM); both were at or above 1 μM , a concentration considered a threshold for eutrophication on coral reefs. Based on nutrient monitoring along eutrophication gradients in the Great Barrier Reef Lagoon, Kaneohe Bay, Hawaii, and Barbados, Bell (1992) suggested that a DIN concentration of 1 μM as a critical threshold for the demise of coral reefs from myriad effects of eutrophication. On the Belize Barrier Reef, Lapointe et al. (1993) studied a natural nutrient gradient from guano-rich Man-O-War Cay to undisturbed coral reefs at Curlew Cay and reported a similar DIN threshold concentration of 1 μM at which benthic algal overgrowth of coral reef communities occurred.

Organic Nutrient Concentrations: The total dissolved nitrogen pool at reefs on both islands was dominated by organic as opposed to inorganic nitrogen (approximately 90% organic). A similar situation occurs on the continental shelf of the Atlantic Ocean off shore of North Carolina. There TDN in both Onslow Bay (with no major riverine input) and Long Bay (with input from the Cape Fear River) is dominated to approximately 90% by DON (Dafner et al. 2007). In both that study and the present one DOP comprised the major portion of the TDP pool, although not to the extent that DON did with TDN. The presence of abundant organic N and P may or may not have an ecologically significant impact on phytoplankton or macroalgae. Labile organic N such as urea is known to stimulate phytoplankton production (Antia 1991; Mallin et al. 2004), is used in fertilizers and can become a pollutant in some circumstances (Glibert et al. 2008). However, if the DON (or DOP) is refractory it would be problematic for use as an algal nutrient. Our data did not address whether the organic nutrients were labile or refractory.

N/P Ratios and Potential Limiting Nutrients: Nutrient ratios are commonly used to estimate the primary nutrient limiting plant growth. For marine and freshwater algae, ratios > 30:1

indicate phosphorus limitation while ratios below 30:1 indicate nitrogen limitation (Rhee 1978; Lapointe 1987). Accordingly, the relatively low DIN/DIP ratios show a slight tendency for N limitation (Fig. 5). Phytoplankton Chl *a* was highest at some of the sites where DIN was also high, such as MP and PB on Curaçao, but in other locations elevated chlorophyll *a* may have also been influenced by physical factors (see section below). TDN/TDP ratios, in contrast, were far higher than the inorganic nutrient ratios and indicate strong P limitation (Fig. 6). Dodds (2003) has questioned the utility of the DIN/SRP ratio, especially at low ambient concentrations such as in this study, and points out that the DIN/SRP ratio is a weak surrogate for the TDN/TDP ratio. These arguments would suggest a primary importance of P rather than N-limitation in coastal waters of Bonaire and Curaçao. Nonetheless, the actual limiting nutrient in any given situation near these islands likely depends on how labile the organic fractions are.

Phytoplankton Biomass: The planktonic nutrient response variable, Chl *a*, showed significant elevation above background concentrations of $\sim 0.05 \mu\text{g/l}$ and averaged at or above the eutrophication threshold of $0.2 \mu\text{g/l}$ (Lapointe et al. 2007) at several stations on Curaçao that received elevated inorganic nitrogen, particularly at MP, PB and SPW. Station MP, as mentioned, receives sewage input from Harbour Bay (Gast et al. 1999) and is also located near where cruise ships anchor. As mentioned above, Station PB is located nearest to MP, and also receives elevated N loads from the surrounding watershed. Station SPW is not among the sites with the highest DIN concentrations; however, it represents a semi-enclosed area with less flushing than the seaward reefs; it is surrounded by development, and receives consequent septic and stormwater inputs. For Curaçao the sites with lowest Chl *a* were the open water reference site OW and East Point (EP) on the far southeastern and upstream end of the island, which both reflected background Chl *a* concentrations $< 0.1 \mu\text{g/l}$. Most of Bonaire reefs did not show as much evidence of elevated Chl *a* (Tables 1 and 2). However, the Bonaire stations with highest concentrations were PL, FP and HB, all of which are located in the most urbanized area of Bonaire -- Kralendijk (Fig. 1). The physical setting of those three reefs, along with nutrient inputs (Tables 1 and 2) from the urbanized watershed, may have made these locations more susceptible to phytoplankton biomass accumulation and eutrophication. For all stations combined, mean Chl *a* at the shallow reefs in Curaçao was 25% higher than at the shallow reefs in Bonaire, and median Chl *a* in Curaçao was 16% higher than in Bonaire (Table 5).

Macroalgae and $\delta^{15}\text{N}$ Values. The 55 species of benthic macroalgae sampled for $\delta^{15}\text{N}$ analysis in this study represented all three macroalgal Phyla, including the Rhodophyta (22 species), Chlorophyta (20 species) and Phaeophyta (13 species). The phaeophytes *Dictyota* spp. and *Lobophora variegata* were relatively abundant at many of the sampling sites, as were benthic blooms of cyanobacteria such as *Lyngbya* sp. and *Symploca hydroides*. Certain rhodophytes (*Acanthophora spicifera*, *Gracilaria tikvahiae*, *Hypnea* spp.) and chlorophytes (*Ulva* spp, *Chaetomorpha gracilis*) that are considered nutrient indicator species were also present at the more urbanized sites characterized by higher nutrient concentrations.

Overall, the $\delta^{15}\text{N}$ values of macroalgae on shallow/deep reefs on Bonaire (+1.53/1.56 o/oo) and Curaçao (+2.03/1.63 o/oo) were relatively low compared to higher values reported for shallow (+8.1 o/oo) and deep (+6.7o/oo) reefs in southeast Florida that experience much higher inputs of secondarily treated sewage with effluent values of + 8 - + 15 o/oo (Lapointe et al. 2005). The generally lower $\delta^{15}\text{N}$ values in macroalgae on Bonaire and Curaçao could result from the low levels of sewage treatment that would have lower $\delta^{15}\text{N}$ source values than treated sewage. Moreover, contributions from nitrogen fixation, atmospheric inputs, and oceanic sources would all have relatively low $\delta^{15}\text{N}$ values close to 0 o/oo (Lapointe et al. 2005). Nevertheless, the human fingerprint is apparent in the higher $\delta^{15}\text{N}$ values on Curaçao compared to Bonaire, as well as the higher values on shallow compared to deep reefs at MP and PB, reflecting greater sewage ^{15}N enrichment. Deep reefs at MP and PB were also higher than other sites on Curaçao, indicating that land-based sewage inputs were impacting both shallow and deep reefs in this urbanized area.

Phase-Shifts From Coral to Algae: Video transect monitoring of reef communities indicated that total benthic reef algae – the combination of algal turf and macroalgae -- now dominate the historically coral-dominated communities on both islands. Total benthic algal cover on shallow and deep reefs on Bonaire were 73.5 % and 63.5 %, respectively, compared to 74.4 % and 72.4 %, respectively, on Curaçao. Although the overall cover of benthic algae was similar on the two islands, the relative abundance of turf vs. macroalgae was quite different. Higher turf cover on Bonaire's reefs (up to 70 % on shallow reefs) could reflect, in part, overall higher grazing rates as

a result of reduced fishing pressure and increased grazing, especially by parrotfish, in the Bonaire Marine Park. Lapointe and Thacker (2002) noted how eutrophic Jamaican reefs with abundant but small parrotfish had higher macroalgal cover compared to the eutrophic reef communities at Looe Key in the Florida Keys, which has abundant populations of large-bodied parrotfish and a corresponding low cover of macroalgae but high cover of algal turf. The higher degree of nutrient loading and eutrophication on the more populated island of Curaçao, evidenced by overall higher Chl *a* and $\delta^{15}\text{N}$ values, could also contribute to the higher macroalgal cover in Curaçao (up to 47 % on deep reefs) compared to Bonaire.

Benthic algae have been replacing live coral cover more rapidly on reefs in < 30 m depths than on reefs > 40 m on these islands in recent decades (Bak et al. 2005). If such a pattern results from greater impacts of nutrient enrichment and eutrophication on shallow compared to deep reefs, then a spatial pattern of coral loss correlating with watershed nutrient enrichment should be evident. Indeed, the lowest hard coral cover on both islands occurred on reefs subject to elevated nutrients and/or Chl *a* from urban and/or industrial discharges. On Bonaire, for example, the lowest hard coral cover was on shallow reefs at HB (Habitat Bonaire; 1.17 %), FP (Front Porch; 1.5 %), RS (Red Slave, 4.68 %) and PL (Playa Lechi, 9.13 %). On Curaçao, the lowest coral cover was at HC (Habitat Curaçao, 4.35 %), MP (MegaPier, 5.93 %), CB (Caracas Bay, 6.60 %), and PB (Piscadera Bay, 10.76 %). The lowest coral cover at the Curaçao stations correlated with the highest macroalgae cover on shallow/deep reefs, which ranged from the highest at CB (43.31%/77.02%) > PB (25.97%/63.49%) > HC (35.13%/57.59%) > MP (32.17%/40.41%).

Although phase-shifts away from coral and towards algae on Caribbean reefs have been widely attributed to “top-down” controls from reduced grazing pressure as a result of overfishing and the *Diadema* die-off (Hughes, 1994; Jackson et al. 2001), the results of this study support a more complex hypothesis that includes simultaneous “bottom-up” effects of land-based nutrient pollution. The ecological effects of urbanization and land-based nutrient pollution have been known since the 1960s (Banner, 1974; Johannes 1975; Bell 1992), yet many coral reef biologists have not recognized the importance of bottom-up controls and favor more simple and less robust “top-down only” models (Lapointe 1999; Risk 1999). Our results indicate that improvements in sewage collection and treatment (including nutrient removal) and management of urban stormwater and industrial discharges could help moderate nutrient enrichment, algal blooms,

coral diseases and other biogeochemical processes that have been a primary factor in the loss of coral from fringing reefs in Bonaire and Curaçao.

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Figure 1. Bonaire and Curaçao study sites.

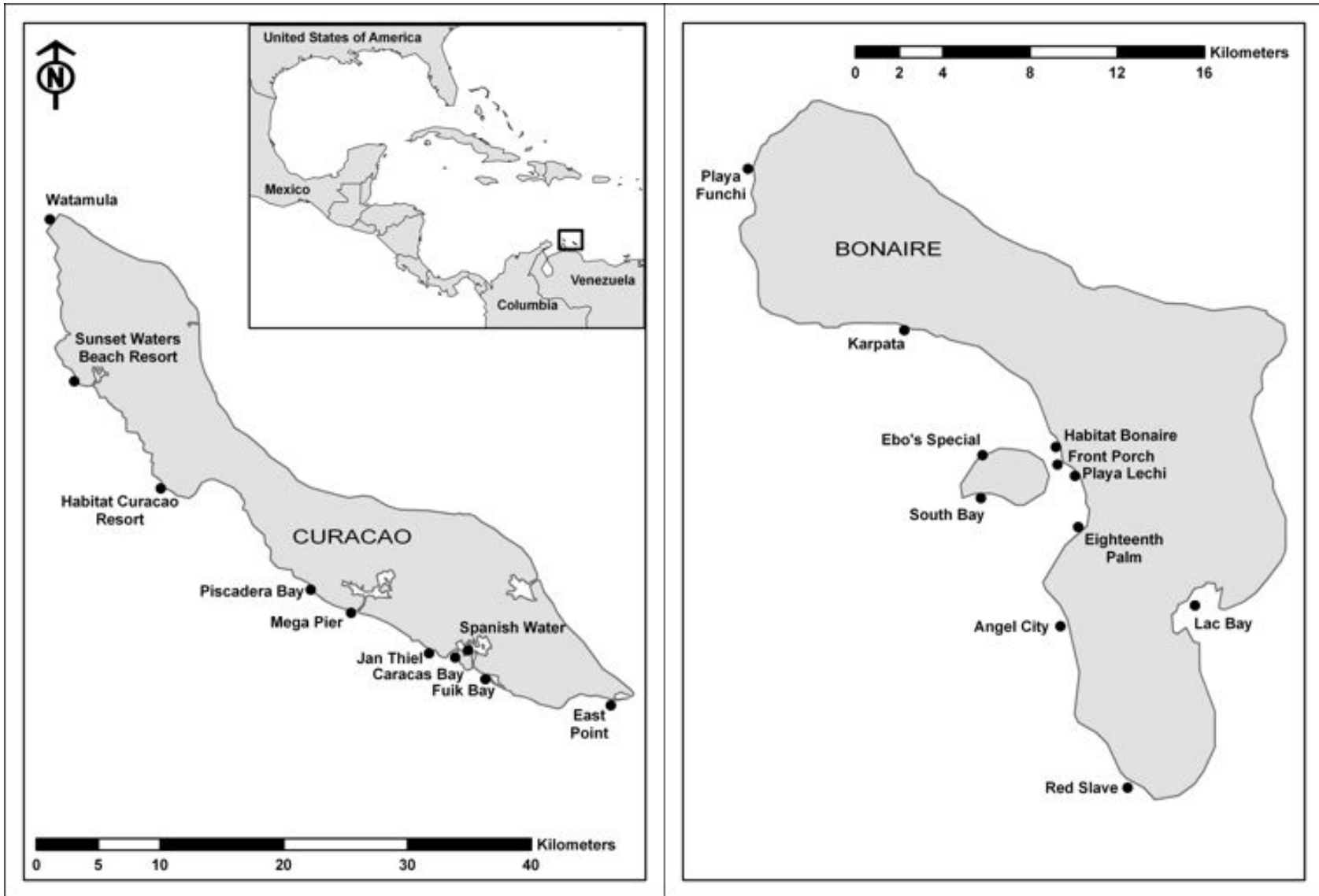


Figure 2a. Mean dissolved inorganic nitrogen composition at shallow sites in Bonaire and Curacao, 2006-2008

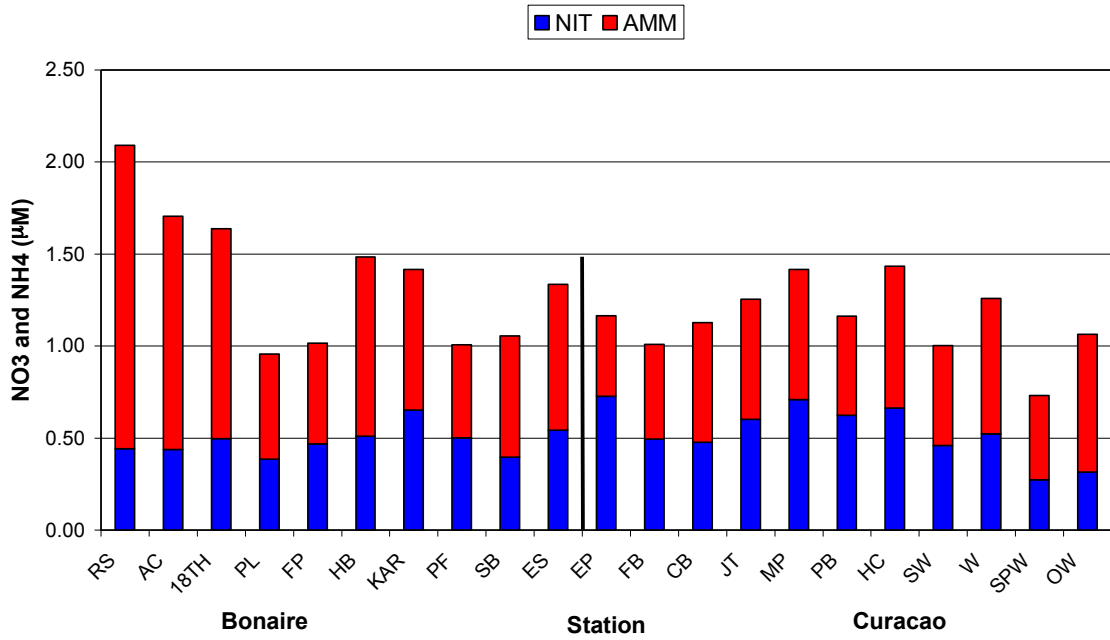


Figure 2b. Mean dissolved inorganic nitrogen composition at deep sites in Bonaire and Curacao, 2006-2008

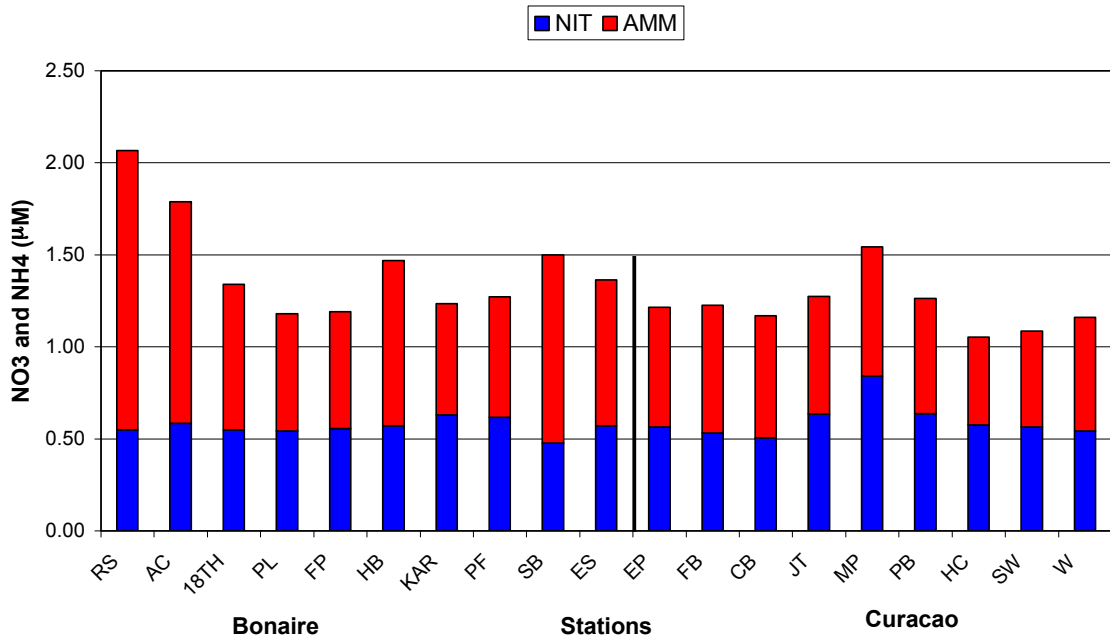


Figure 3a. Mean total dissolved nitrogen composition for shallow sites in Bonaire and Curacao, 2006-2008.

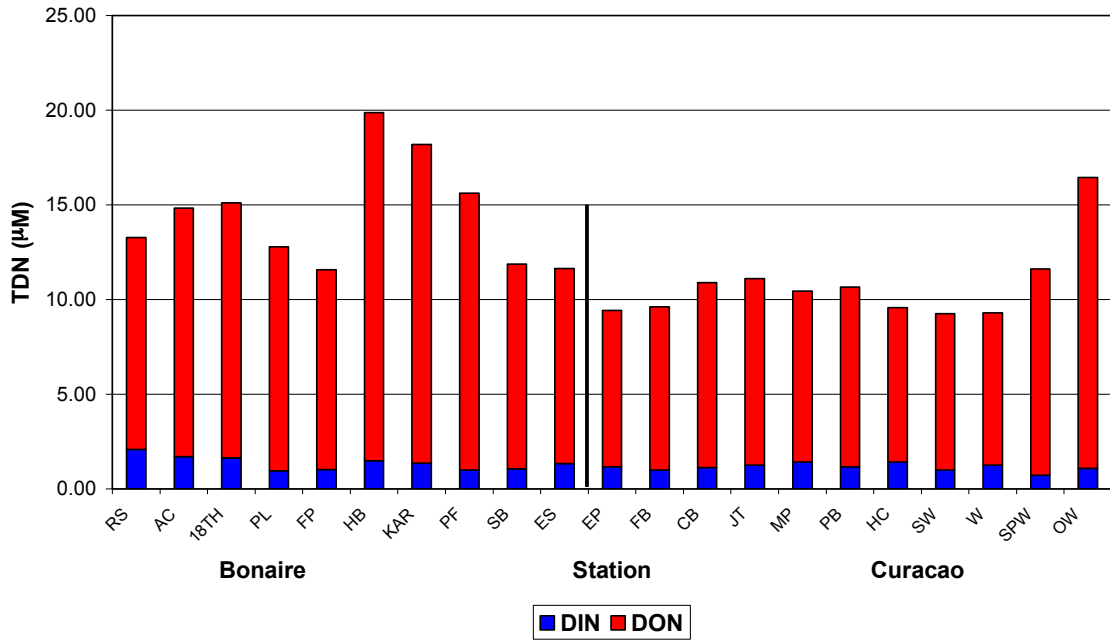


Figure 3b. Mean total dissolved nitrogen composition for deep sites in Bonaire and Curacao, 2006-2008

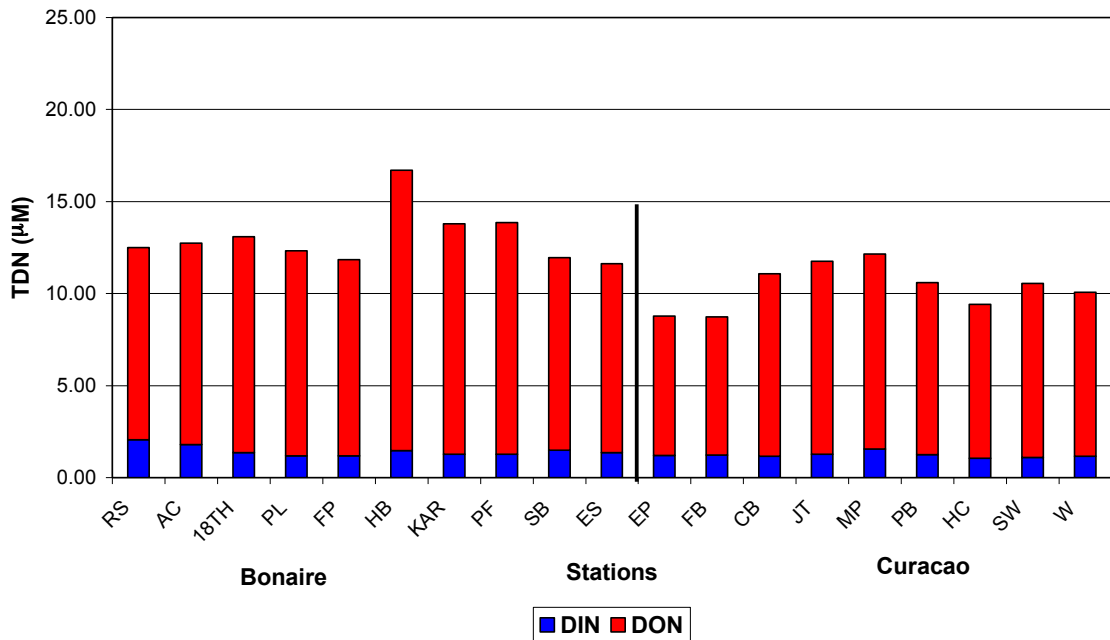


Figure 4a. Average total dissolved phosphorus composition at shallow sites in Bonaire and Curacao, 2006-2008

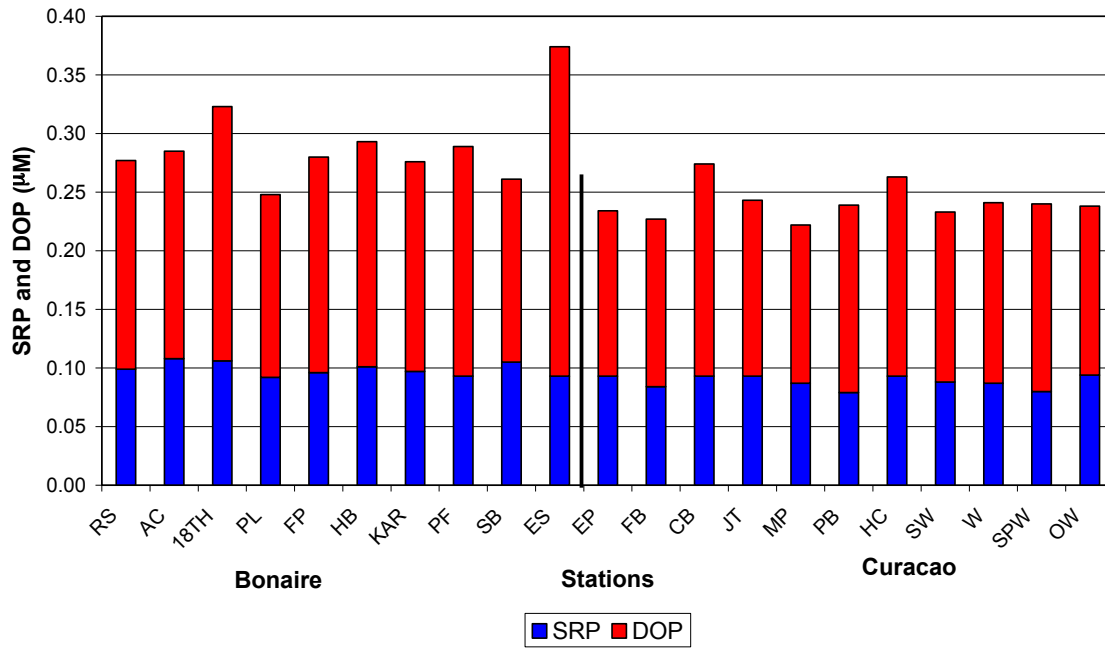


Figure 4b. Mean total dissolved phosphorus composition at deep sites in Bonaire and Curacao, 2006-2008

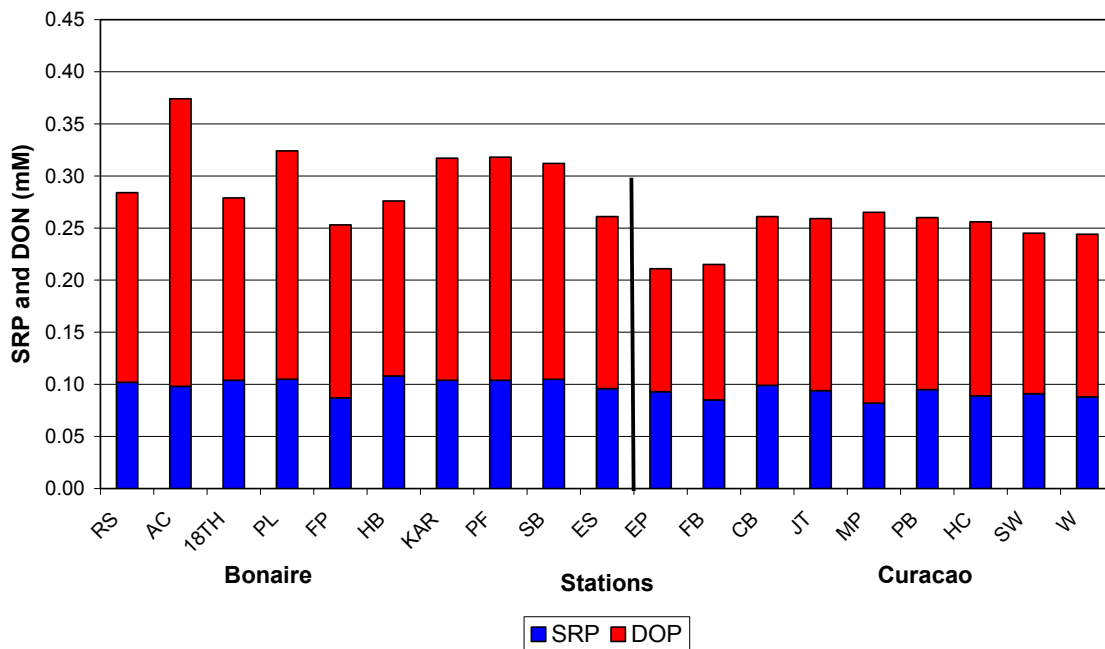


Figure 5a. Average dissolved inorganic nitrogen to soluble reactive phosphate ratios for shallow sites in Bonaire and Curacao, 2006-2008

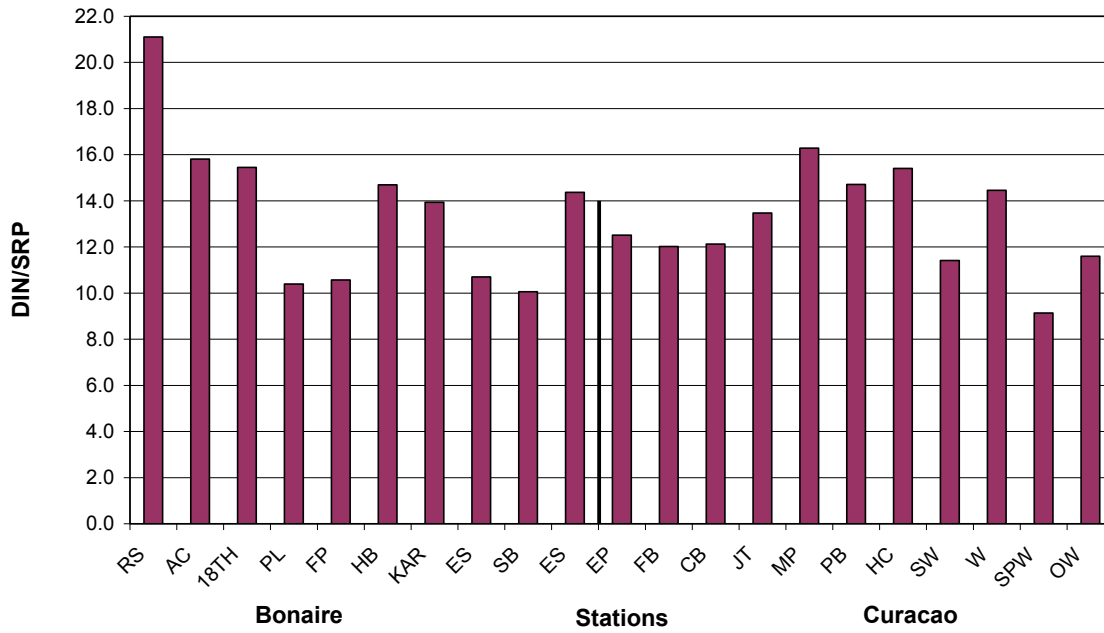


Figure 5b. Average dissolved inorganic nitrogen to soluble reactive phosphate ratios for deep sites in Bonaire and Curacao

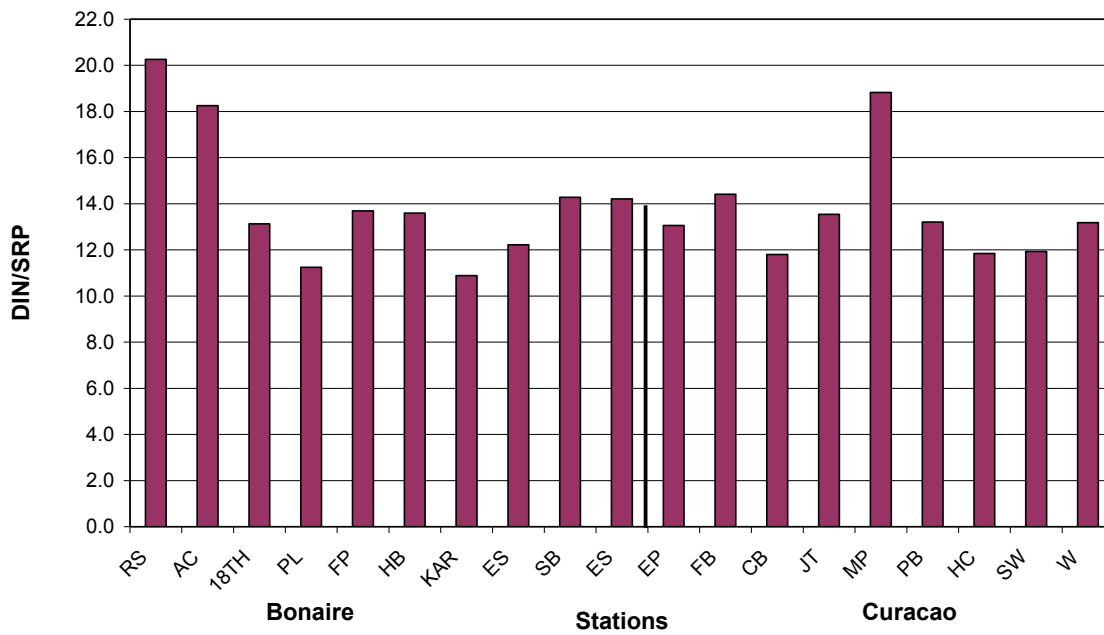


Figure 6a. Mean total dissolved nitrogen to total dissolved phosphorus ratios at shallow sites in Bonaire and Curacao, 2006-2008

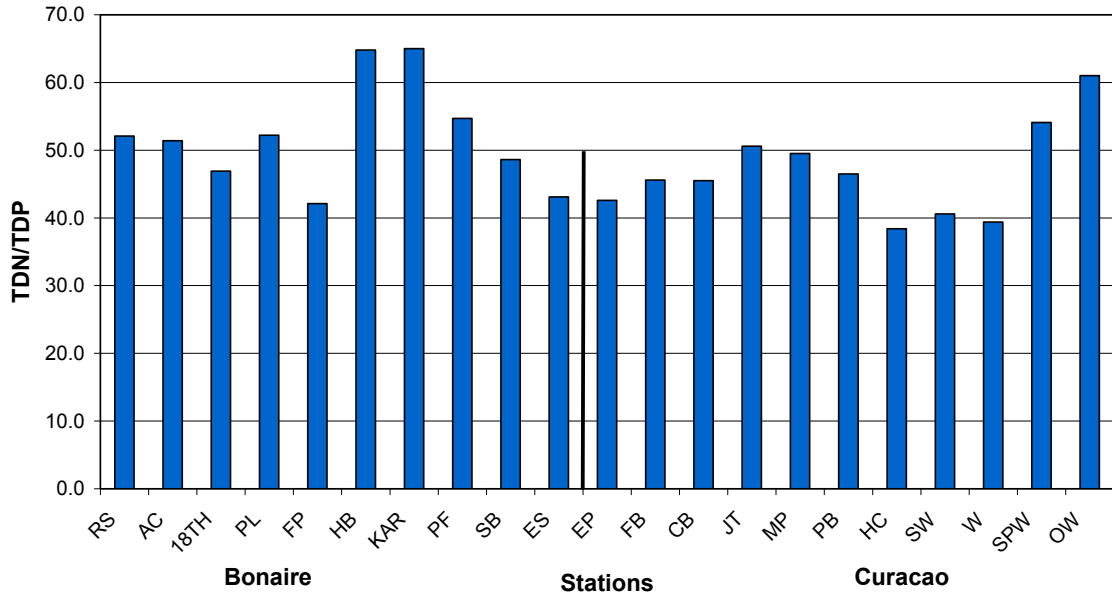


Figure 6b. Mean total dissolved nitrogen to total dissolved phosphorus ratios at deep sites in Bonaire and Curacao, 2006-2008

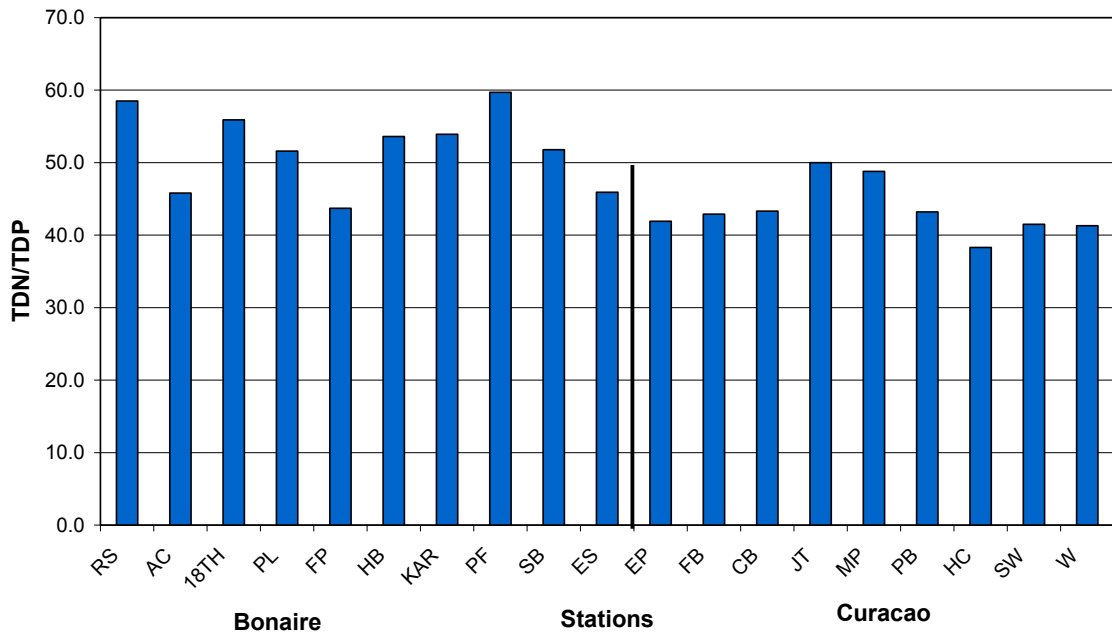


Figure 7a. Average chlorophyll a at shallow sites in Bonaire and Curacao, 2006-2008 (+ or - one standard deviation)

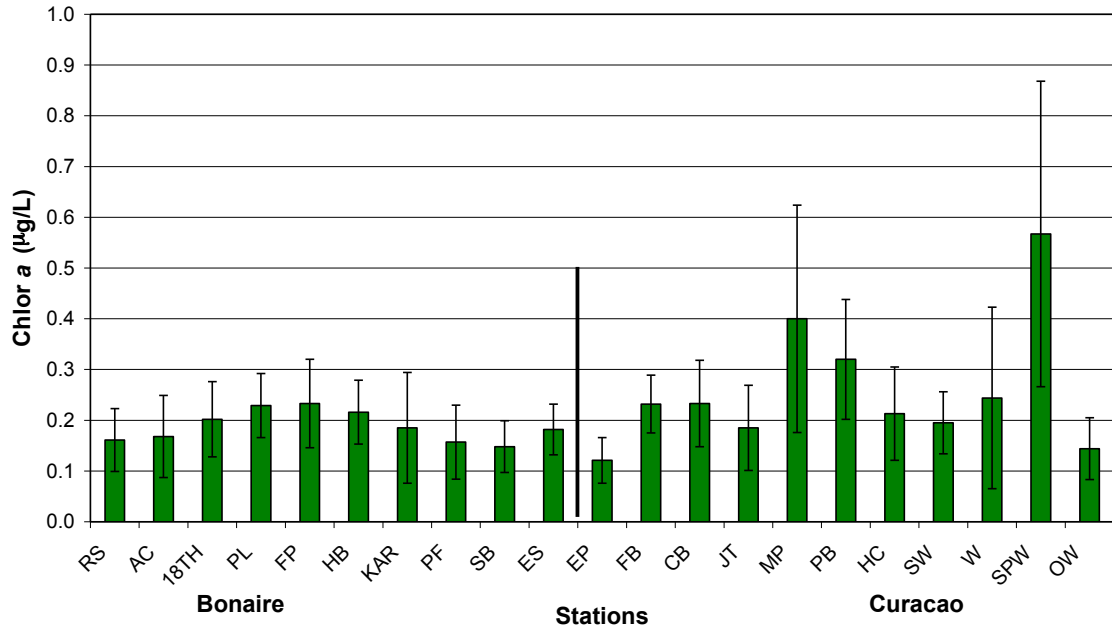


Figure 7b. Average chlorophyll a at deep sites in Bonaire and Curacao, 2006-2008 (+ or - one standard deviation)

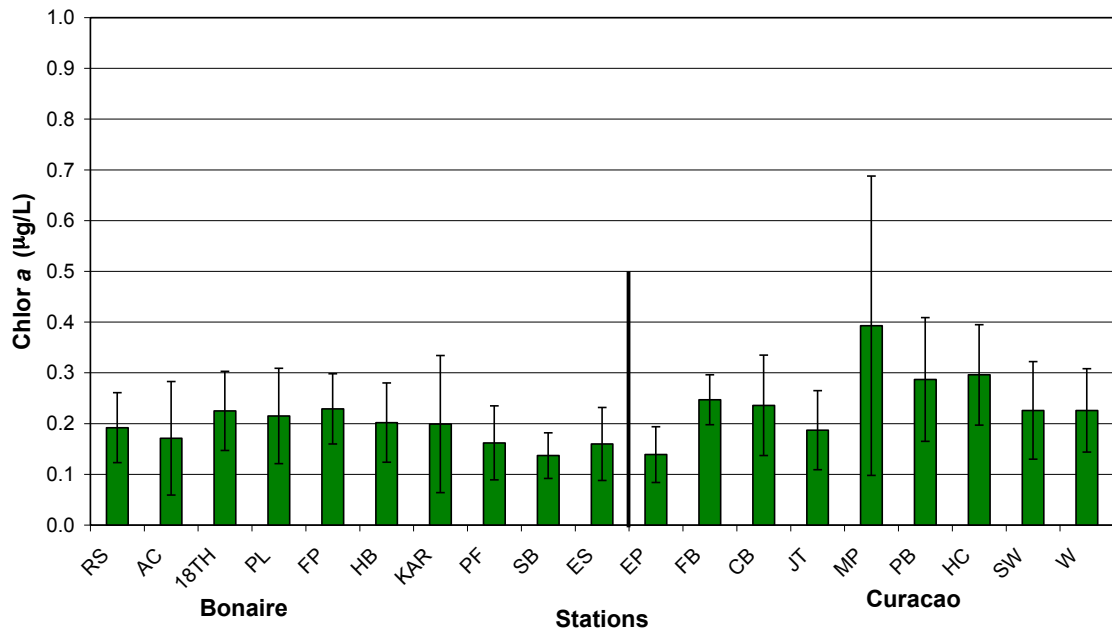


Figure 8a. Average $\delta^{15}\text{N}$ values for macroalgae on shallow reefs in Bonaire and Curacao, 2006-2008 (+ or - one standard deviation)

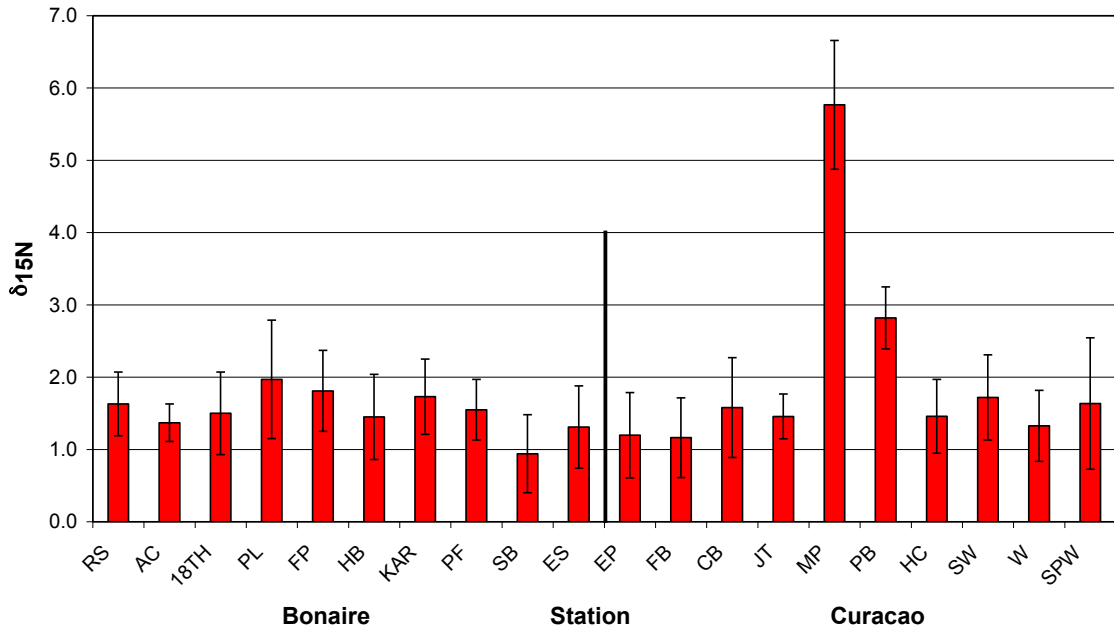


Figure 8b. Average $\delta^{15}\text{N}$ values for macroalgae on deep reefs in Bonaire and Curacao, 2006-2008 (+ or - one standard deviation)

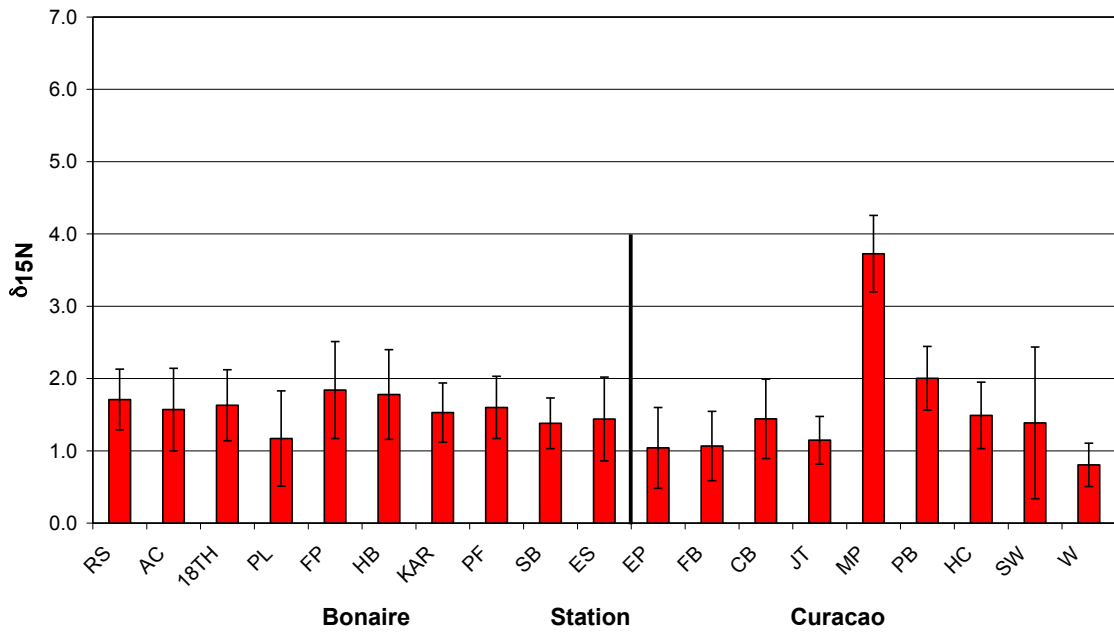


Figure 9a. Percent benthic cover of soft and stony corals at shallow sites in Bonaire and Curaçao, 2006-2008.

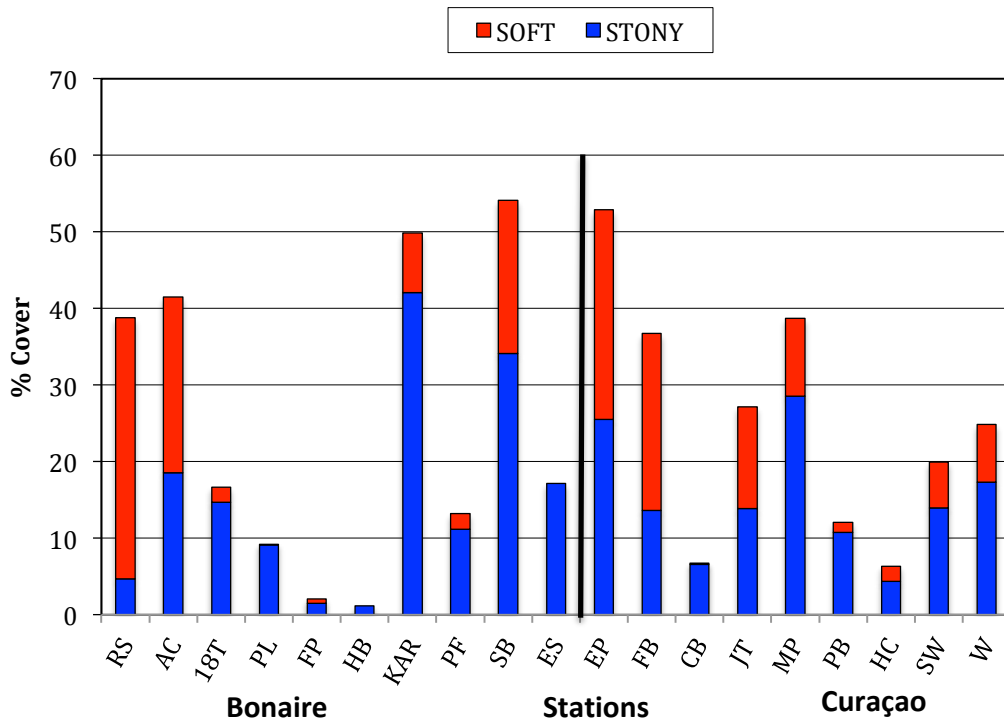


Figure 9b. Percent benthic cover of soft and stony corals at deep sites in Bonaire and Curaçao, 2006-2008.

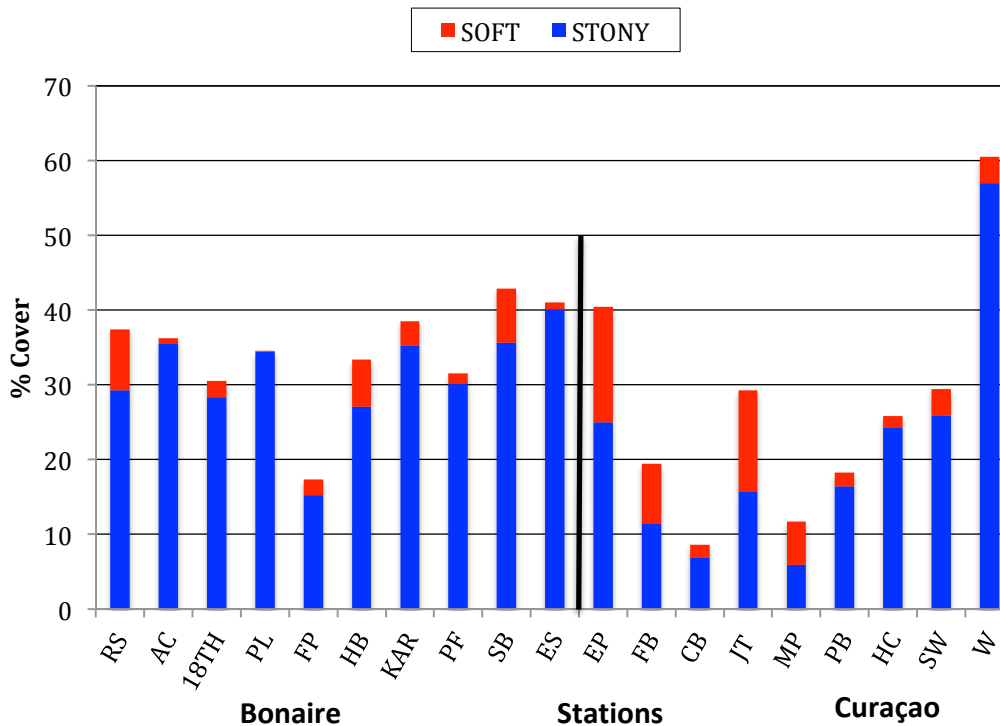


Figure 10a. Percent benthic cover of macroalgae at shallow sites in Bonaire and Curaçao, 2006-2008.

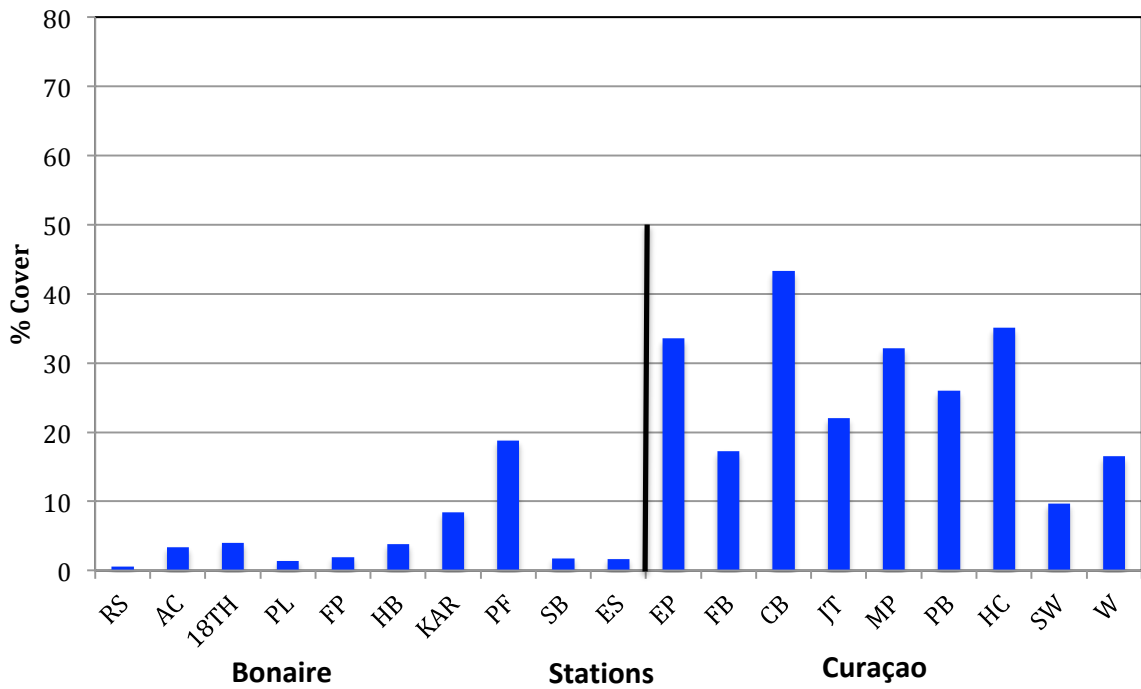


Figure 10b. Percent benthic cover of macroalgae at deep sites in Bonaire and Curaçao, 2006-2008.

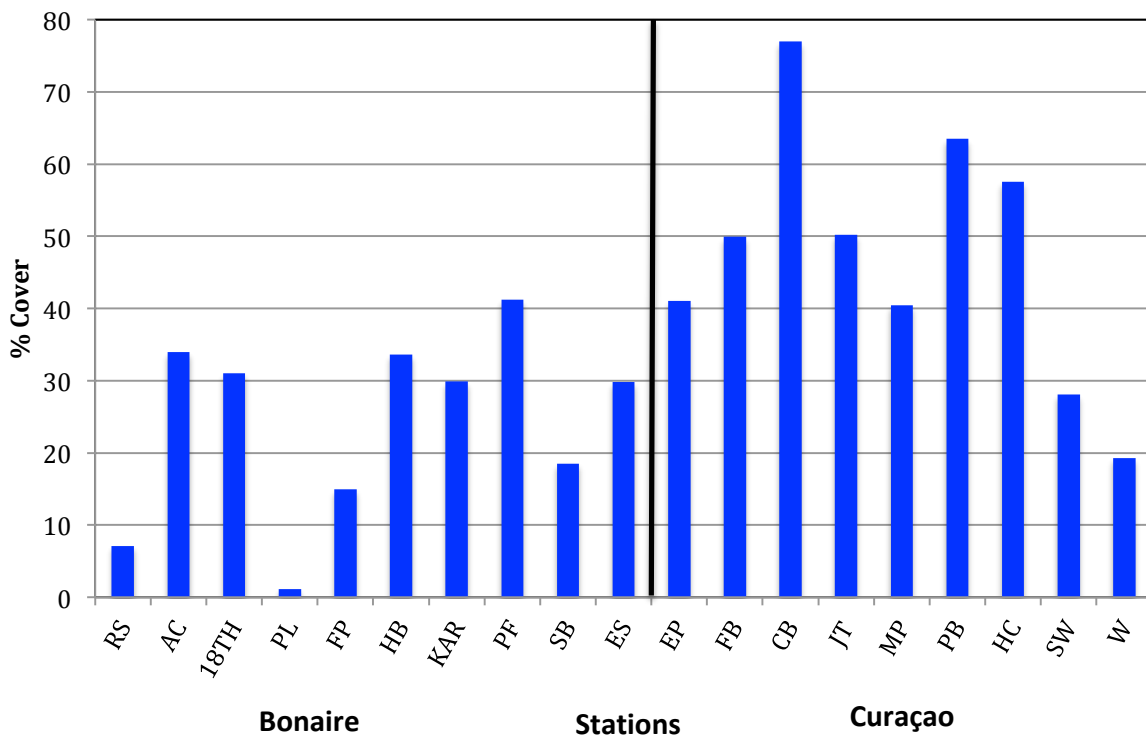


Figure 11a. Percent benthic cover of turf algae at shallow sites in Bonaire and Curaçao, 2006-2008.

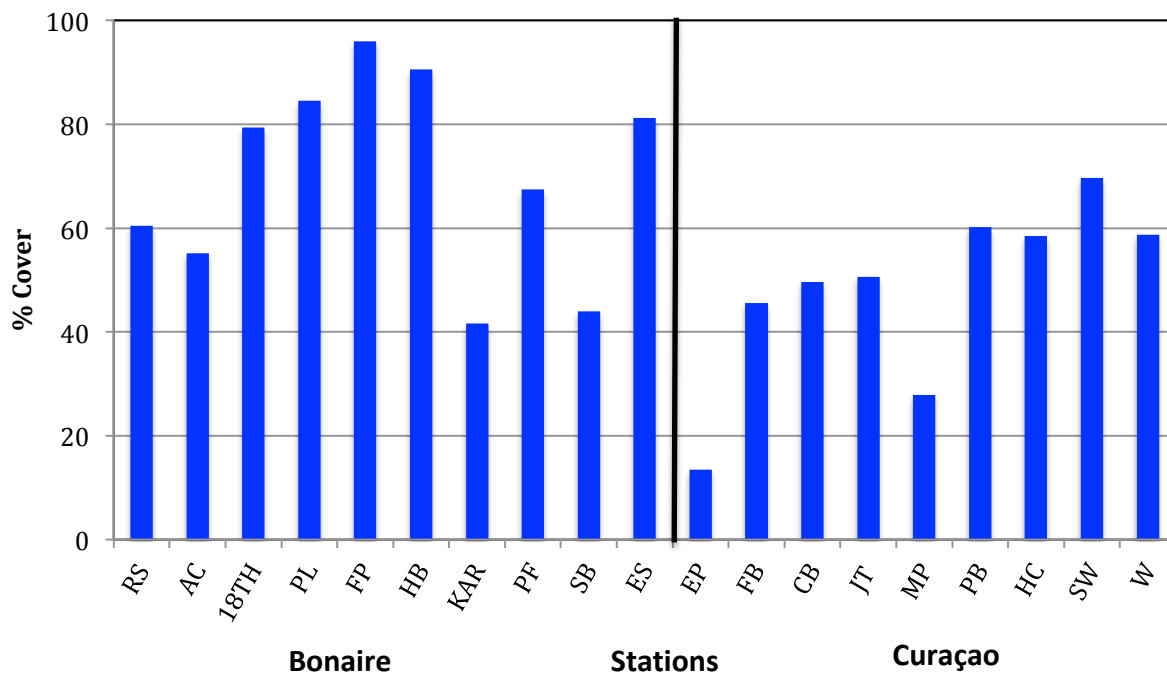
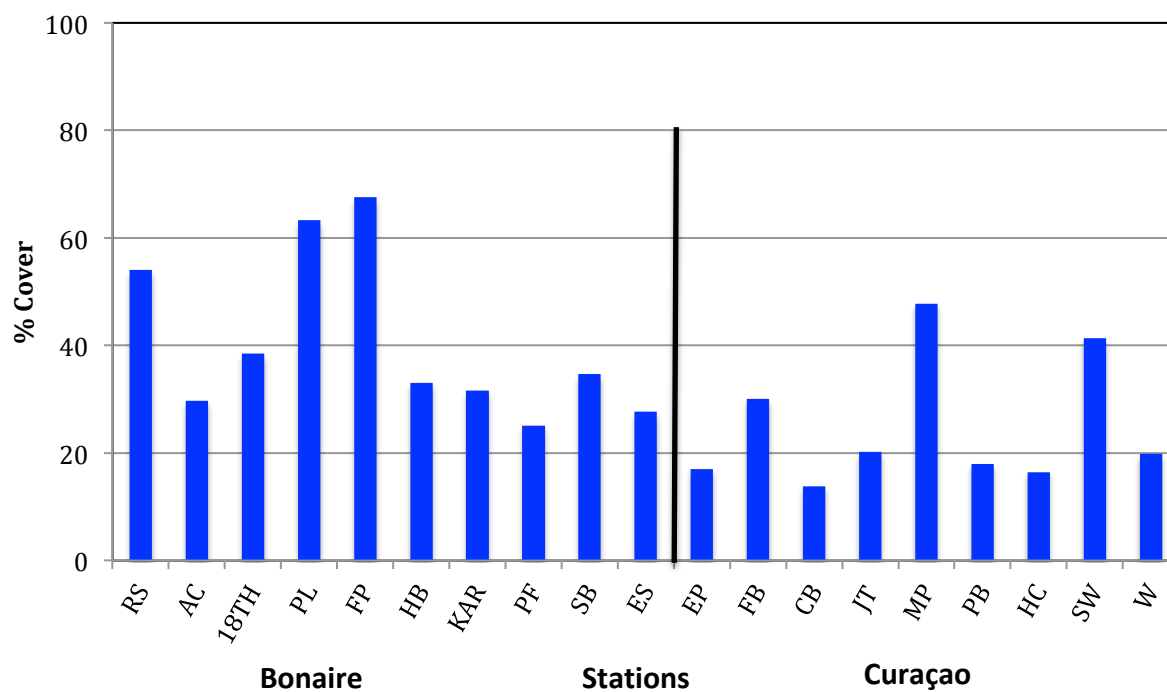


Figure 11b. Percent benthic cover of turf algae at deep sites in Bonaire and Curaçao, 2006-2008.



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Table 1. Nutrient and chlorophyll *a* concentrations at Bonaire shallow reefs, 2006-2008, data as mean \pm standard deviation / median.*

	Station									
	RS	AC	18 th	PL	FP	HB	KAR	PF	SB	ES
NH ₄ ⁺	1.65 \pm 2.83 0.89	1.27 \pm 1.59 0.75	1.14 \pm 1.07 0.66	0.57 \pm 0.21 0.54	0.55 \pm 0.23 0.49	0.97 \pm 0.59 0.70	0.76 \pm 0.38 0.66	0.51 \pm 0.27 0.42	0.66 \pm 0.22 0.66	0.79 \pm 0.64 0.58
NO ₃ ⁻	0.44 \pm 0.15 0.43	0.44 \pm 0.07 0.45	0.50 \pm 0.13 0.45	0.39 \pm 0.11 0.39	0.47 \pm 0.14 0.46	0.51 \pm 0.26 0.43	0.65 \pm 0.37 0.57	0.50 \pm 0.19 0.47	0.40 \pm 0.11 0.37	0.54 \pm 0.14 0.53
DIN	2.09 \pm 2.92 1.21	1.71 \pm 1.60 1.19	1.64 \pm 1.14 1.19	0.96 \pm 0.29 0.87	1.02 \pm 0.32 1.04	1.48 \pm 0.83 1.11	1.35 \pm 0.43 1.24	1.01 \pm 0.31 1.05	1.06 \pm 0.29 1.06	1.34 \pm 0.75 1.07
DON	11.20 \pm 3.61 10.44	13.13 \pm 5.87 10.95	13.47 \pm 5.55 11.73	11.82 \pm 5.83 11.15	10.57 \pm 2.39 10.65	18.39 \pm 12.6 15.24	16.85 \pm 15.7 12.51	14.61 \pm 8.29 12.59	10.82 \pm 2.33 10.45	10.30 \pm 1.83 10.21
TDN	13.29 \pm 6.34 11.82	14.84 \pm 6.03 12.54	15.11 \pm 6.40 12.61	12.78 \pm 5.48 12.09	11.58 \pm 2.57 11.86	19.88 \pm 13.4 16.50	18.20 \pm 15.8 13.86	15.62 \pm 8.32 13.61	11.88 \pm 2.40 11.50	11.44 \pm 1.95 11.21
SRP	0.10 \pm 0.02 0.10	0.11 \pm 0.03 0.10	0.11 \pm 0.03 0.10	0.09 \pm 0.04 0.10	0.10 \pm 0.02 0.09	0.10 \pm 0.04 0.10	0.10 \pm 0.03 0.09	0.09 \pm 0.03 0.09	0.11 \pm 0.03 0.10	0.09 \pm 0.04 0.08
DOP	0.18 \pm 0.07 0.20	0.18 \pm 0.07 0.17	0.22 \pm 0.05 0.20	0.16 \pm 0.06 0.15	0.18 \pm 0.06 0.19	0.19 \pm 0.07 0.17	0.18 \pm 0.09 0.18	0.20 \pm 0.04 0.21	0.16 \pm 0.08 0.16	0.28 \pm 0.36 0.19
TDP	0.28 \pm 0.07 0.31	0.28 \pm 0.06 0.27	0.32 \pm 0.06 0.33	0.25 \pm 0.06 0.24	0.28 \pm 0.05 0.29	0.29 \pm 0.09 0.27	0.28 \pm 0.10 0.29	0.29 \pm 0.04 0.29	0.26 \pm 0.08 0.26	0.37 \pm 0.33 0.27
Chl <i>a</i>	0.16 \pm 0.06 0.19	0.17 \pm 0.08 0.18	0.20 \pm 0.07 0.18	0.23 \pm 0.06 0.24	0.23 \pm 0.09 0.23	0.22 \pm 0.06 0.23	0.19 \pm 0.11 0.13	0.16 \pm 0.07 0.15	0.15 \pm 0.05 0.15	0.18 \pm 0.05 0.18

*RS = Red Slave, AC = Angel City, 18th = Eighteenth Palm, PL = Playa Lechi, FP = Front Porch, HB = Habitat Bonaire, KAR = Karpata, PF = Playa Funchi, SB = South Bay, ES = Ebo's Special

Table 2. Nutrient and chlorophyll *a* concentrations at Bonaire deep reefs, 2006-2008, data as mean \pm standard deviation / median.*

	Station									
	RS	AC	18 th	PL	FP	HB	KAR	PF	SB	ES
NH ₄ ⁺	1.52 \pm 2.42 0.84	1.21 \pm 1.62 0.52	0.79 \pm 0.55 0.58	0.64 \pm 0.33 0.48	0.63 \pm 0.30 0.52	0.90 \pm 0.58 0.75	0.60 \pm 0.31 0.55	0.65 \pm 0.32 0.63	1.02 \pm 0.56 1.00	0.79 \pm 0.78 0.63
NO ₃ ⁻	0.55 \pm 0.22 0.50	0.58 \pm 0.21 0.56	0.55 \pm 0.12 0.54	0.54 \pm 0.44 0.44	0.56 \pm 0.14 0.58	0.57 \pm 0.23 0.53	0.63 \pm 0.46 0.47	0.62 \pm 0.25 0.59	0.48 \pm 0.14 0.48	0.57 \pm 0.10 0.58
DIN	2.07 \pm 2.49 1.40	1.79 \pm 1.62 1.34	1.37 \pm 0.62 1.20	1.18 \pm 0.51 0.96	1.19 \pm 0.34 1.17	1.47 \pm 0.57 1.20	1.27 \pm 0.57 1.11	1.27 \pm 0.36 1.29	1.50 \pm 0.58 1.42	1.36 \pm 0.74 1.23
DON	13.25 \pm 5.06 12.21	14.39 \pm 7.58 11.64	14.52 \pm 7.03 11.31	11.31 \pm 3.55 9.46	10.32 \pm 2.53 9.83	12.56 \pm 4.75 11.12	14.22 \pm 7.44 11.93	15.74 \pm 8.82 12.39	14.30 \pm 8.03 12.44	10.18 \pm 2.57 10.32
TDN	15.31 \pm 5.63 13.86	16.18 \pm 7.63 14.54	15.89 \pm 7.57 12.64	12.38 \pm 3.76 10.93	11.51 \pm 2.83 11.11	14.02 \pm 4.85 12.40	15.38 \pm 7.97 12.79	17.01 \pm 8.92 13.68	15.80 \pm 8.16 13.47	11.54 \pm 2.25 11.54
SRP	0.10 \pm 0.02 0.11	0.10 \pm 0.03 0.10	0.10 \pm 0.03 0.10	0.11 \pm 0.06 0.09	0.09 \pm 0.02 0.10	0.11 \pm 0.04 0.10	0.10 \pm 0.03 0.10	0.10 \pm 0.03 0.10	0.11 \pm 0.04 0.09	0.10 \pm 0.02 0.10
DOP	0.17 \pm 0.05 0.16	0.27 \pm 0.23 0.20	0.18 \pm 0.05 0.17	0.20 \pm 0.14 0.19	0.19 \pm 0.08 0.17	0.16 \pm 0.06 0.15	0.22 \pm 0.11 0.21	0.20 \pm 0.05 0.18	0.20 \pm 0.04 0.19	0.17 \pm 0.06 0.18
TDP	0.27 \pm 0.06 0.27	0.36 \pm 0.20 0.31	0.28 \pm 0.07 0.25	0.31 \pm 0.19 0.28	0.27 \pm 0.08 0.27	0.26 \pm 0.04 0.25	0.31 \pm 0.09 0.31	0.30 \pm 0.08 0.28	0.30 \pm 0.07 0.28	0.26 \pm 0.06 0.26
Chl <i>a</i>	0.19 \pm 0.07 0.20	0.17 \pm 0.11 0.19	0.23 \pm 0.08 0.23	0.22 \pm 0.09 0.22	0.23 \pm 0.07 0.22	0.20 \pm 0.08 0.20	0.20 \pm 0.14 0.13	0.16 \pm 0.07 0.17	0.14 \pm 0.05 0.14	0.16 \pm 0.07 0.14

*RS = Red Slave, AC = Angel City, 18th = Eighteenth Palm, PL = Playa Lechi, FP = Front Porch, HB = Habitat Bonaire, KAR = Karpata, PF = Playa Funchi, SB = South Bay, ES = Ebo's Special

Table 3. Nutrient and chlorophyll *a* concentrations at Curaçao shallow reefs, 2006-2008, data as mean \pm standard deviation / median.*

	Station										
	EP	FB	CB	JT	MP	PB	HC	SW	WAT	SPW	OW
NH ₄ ⁺	0.44 \pm 0.21 0.36	0.52 \pm 0.30 0.48	0.65 \pm 0.32 0.65	0.65 \pm 0.33 0.58	0.71 \pm 0.22 0.63	0.54 \pm 0.27 0.49	0.77 \pm 0.66 0.80	0.54 \pm 0.30 0.45	0.74 \pm 0.78 0.35	0.46 \pm 0.18 0.44	0.75 \pm 0.70 0.42
NO ₃ ⁻	0.73 \pm 0.21 0.75	0.49 \pm 0.12 0.50	0.48 \pm 0.36 0.38	0.60 \pm 0.24 0.56	0.71 \pm 0.33 0.62	0.63 \pm 0.36 0.50	0.66 \pm 0.72 0.52	0.46 \pm 0.13 0.47	0.52 \pm 0.15 0.53	0.27 \pm 0.11 0.25	0.32 \pm 0.19 0.26
DIN	1.16 \pm 0.31 1.20	1.01 \pm 0.37 0.99	1.13 \pm 0.42 1.00	1.25 \pm 0.52 1.07	1.42 \pm 0.44 1.29	1.16 \pm 0.44 1.08	1.43 \pm 1.33 1.13	1.00 \pm 0.39 0.90	1.26 \pm 0.84 0.80	0.73 \pm 0.22 0.65	1.09 \pm 0.66 0.88
DON	8.25 \pm 2.51 8.66	8.60 \pm 3.56 7.72	9.77 \pm 9.87 8.56	9.86 \pm 4.11 9.10	9.04 \pm 2.75 8.77	9.51 \pm 3.43 8.52	8.14 \pm 3.27 8.09	8.24 \pm 3.12 7.33	8.03 \pm 2.97 7.57	10.88 \pm 3.14 10.75	15.36 \pm 11.72 9.52
TDN	9.42 \pm 2.44 9.79	9.82 \pm 3.87 8.50	10.63 \pm 4.73 9.14	11.02 \pm 4.32 10.00	10.46 \pm 3.06 10.00	10.67 \pm 3.66 9.43	9.57 \pm 2.76 8.93	9.25 \pm 3.25 8.36	9.29 \pm 3.39 8.33	11.61 \pm 3.20 11.75	16.46 \pm 12.28 10.40
SRP	0.09 \pm 0.03 0.09	0.08 \pm 0.03 0.08	0.09 \pm 0.03 0.09	0.09 \pm 0.02 0.09	0.09 \pm 0.02 0.08	0.08 \pm 0.01 0.08	0.09 \pm 0.03 0.09	0.09 \pm 0.02 0.08	0.09 \pm 0.02 0.09	0.08 \pm 0.02 0.08	0.09 \pm 0.03 0.09
DOP	0.14 \pm 0.05 0.13	0.14 \pm 0.09 0.10	0.18 \pm 0.09 0.16	0.15 \pm 0.05 0.15	0.14 \pm 0.06 0.11	0.16 \pm 0.07 0.16	0.17 \pm 0.08 0.16	0.15 \pm 0.08 0.12	0.15 \pm 0.08 0.15	0.16 \pm 0.07 0.17	0.14 \pm 0.07 0.12
TDP	0.23 \pm 0.07 0.24	0.23 \pm 0.08 0.19	0.27 \pm 0.11 0.25	0.24 \pm 0.06 0.24	0.22 \pm 0.06 0.22	0.24 \pm 0.07 0.24	0.26 \pm 0.09 0.26	0.23 \pm 0.08 0.20	0.24 \pm 0.08 0.25	0.24 \pm 0.07 0.23	0.23 \pm 0.07 0.23
Chl <i>a</i>	0.12 \pm 0.05 0.11	0.23 \pm 0.06 0.24	0.23 \pm 0.09 0.22	0.19 \pm 0.08 0.18	0.40 \pm 0.21 0.36	0.32 \pm 0.12 0.28	0.21 \pm 0.09 0.22	0.20 \pm 0.06 0.21	0.24 \pm 0.18 0.18	0.57 \pm 0.30 0.46	0.14 \pm 0.06 0.14

* EP = East Point, FB = Fuik Bay, CB = Caracas Bay, JT = Jan Theil, MP = Mega Pier, PB = Piscadera Bay, HC = Habitat Curaçao, SW = Sunset Waters, WAT = Watamula, SPW = Spanish Water, OW = open water

Table 4. Nutrient and chlorophyll *a* concentrations at Curaçao deep reefs, 2006-2008, data as mean \pm standard deviation / median.*

	Station								
	EP	FB	CB	JT	MP	PB	HC	SW	WAT
NH ₄ ⁺	0.65 \pm 0.63 0.47	0.69 \pm 0.81 0.41	0.66 \pm 0.37 0.53	0.64 \pm 0.40 0.56	0.70 \pm 0.60 0.63	0.63 \pm 0.46 0.60	0.48 \pm 0.23 0.43	0.52 \pm 0.30 0.46	0.62 \pm 0.43 0.40
NO ₃ ⁻	0.56 \pm 0.18 0.54	0.53 \pm 0.23 0.44	0.51 \pm 0.27 0.45	0.63 \pm 0.26 0.63	0.84 \pm 0.62 0.79	0.64 \pm 0.24 0.59	0.58 \pm 0.13 0.54	0.56 \pm 0.19 0.53	0.54 \pm 0.17 0.50
DIN	1.21 \pm 0.72 1.10	1.23 \pm 0.81 0.85	1.17 \pm 0.52 1.04	1.27 \pm 0.51 1.33	1.54 \pm 1.18 1.40	1.26 \pm 0.47 1.27	1.05 \pm 0.27 0.97	1.09 \pm 0.44 0.98	1.16 \pm 0.46 1.00
DON	7.56 \pm 2.34 7.16	7.50 \pm 2.17 7.02	9.92 \pm 4.49 8.52	10.49 \pm 4.69 9.49	10.60 \pm 3.98 10.64	9.34 \pm 4.72 7.98	8.36 \pm 2.40 7.81	9.46 \pm 4.94 7.99	8.91 \pm 4.69 6.34
TDN	8.77 \pm 2.74 7.96	8.72 \pm 2.23 8.34	11.09 \pm 4.76 9.22	11.74 \pm 4.97 10.79	12.15 \pm 4.30 13.07	10.60 \pm 4.63 9.21	9.41 \pm 2.56 8.65	10.54 \pm 5.31 8.93	10.07 \pm 4.66 7.47
SRP	0.09 \pm 0.03 0.09	0.09 \pm 0.02 0.09	0.10 \pm 0.04 0.09	0.09 \pm 0.02 0.09	0.08 \pm 0.01 0.08	0.10 \pm 0.04 0.09	0.09 \pm 0.05 0.08	0.09 \pm 0.03 0.08	0.09 \pm 0.02 0.09
DOP	0.12 \pm 0.05 0.11	0.13 \pm 0.06 0.12	0.16 \pm 0.06 0.15	0.17 \pm 0.07 0.15	0.18 \pm 0.10 0.16	0.17 \pm 0.15 0.13	0.17 \pm 0.05 0.17	0.15 \pm 0.07 0.14	0.16 \pm 0.09 0.15
TDP	0.21 \pm 0.05 0.21	0.22 \pm 0.06 0.22	0.26 \pm 0.09 0.24	0.26 \pm 0.09 0.24	0.26 \pm 0.10 0.23	0.26 \pm 0.16 0.22	0.26 \pm 0.08 0.25	0.25 \pm 0.09 0.22	0.24 \pm 0.09 0.24
Chl <i>a</i>	0.14 \pm 0.06 0.12	0.25 \pm 0.05 0.23	0.24 \pm 0.10 0.23	0.19 \pm 0.08 0.15	0.39 \pm 0.30 0.29	0.29 \pm 0.12 0.26	0.30 \pm 0.10 0.32	0.23 \pm 0.10 0.23	0.23 \pm 0.08 0.24

* EP = East Point, FB = Fuik Bay, CB = Caracas Bay, JT = Jan Theil, MP = Mega Pier, PB = Piscadera Bay, HC = Habitat Curaçao, SW = Sunset Waters, WAT = Watamula

Table 5. Inorganic nutrient and chlorophyll *a* concentrations at Bonaire and Curaçao shallow and deep reefs, 2006-2008, all stations combined, data as mean \pm standard deviation / median, range.

	Bonaire		Curaçao	
	Shallow	Deep	Shallow	Deep
NH ₄ ⁺	0.89 \pm 1.16 0.61, 0.20-10.57	0.88 \pm 1.03 0.63, 0.20-9.11	0.61 \pm 0.43 0.49, 0.20-2.83	0.62 \pm 0.49 0.49, 0.20-3.08
NO ₃ ⁻	0.49 \pm 0.20 0.45, 0.20-1.57	0.57 \pm 0.25 0.51, 0.24-1.92	0.54 \pm 0.33 0.48, 0.14-3.13	0.60 \pm 0.30 0.52, 0.21-2.75
DIN	1.37 \pm 1.21 1.12, 0.56-11.28	1.45 \pm 1.07 1.23, 0.54-9.81	1.16 \pm 0.62 1.03, 0.38-5.96	1.22 \pm 0.65 1.08, 0.53-5.51
SRP	0.10 \pm 0.03 0.10, 0.04-0.21	0.10 \pm 0.04 0.10, 0.03-0.28	0.09 \pm 0.02 0.08, 0.05-0.20	0.09 \pm 0.03 0.08, 0.04-0.26
Chl <i>a</i>	0.19 \pm 0.08 0.19, 0.06-0.38	0.19 \pm 0.09 0.18, 0.05-0.44	0.25 \pm 0.18 0.22, 0.05-0.99	0.25 \pm 0.15 0.23, 0.06-1.12

Table 6. Macroalgae collected from deep and shallow reefs on Bonaire and Curaçao for $\delta^{15}\text{N}$ analysis between March 2006 and June 2008.

Taxa	Bonaire		Curaçao	
	Shallow	Deep	Shallow	Deep
Rhodophyta				
<i>Gracilaria tikvahiae</i>	X			
<i>Gracilaria mammalaris</i>			X	
<i>Acanthophora spicifera</i>	X		X	
<i>Digenia simplex</i>	X		X	
<i>Laurencia obtusa</i>	X		X	
<i>Laurencia papillosa</i>			X	
<i>Ceramium sp.</i>			X	
<i>Hydrocoleum coccineum</i>	X		X	
<i>Dasya sp.</i>	X	X		
<i>Dasya spinuligara</i>	X		X	
<i>Amphiroa sp.</i>	X			
<i>Amphiroa fragillissima</i>		X		
<i>Hypnea cervicornis</i>	X			
<i>Hypnea sp.</i>	X			
<i>Galaxaura marginata</i>	X	X	X	X
<i>Galaxaura sp.</i>	X			
<i>Wrangelia penicillata</i>	X	X		
<i>Cryptonemia sp.</i>	X			
<i>Cryptonemia crenulata</i>	X			
<i>Jania adhaerens</i>	X	X	X	
<i>Jania capillaceae</i>	X	X		
<i>Martensia pavona</i>	X			
Phaeophyta				
<i>Dictyota bartraysiana</i>	X	X		
<i>Dictyota pinnatifida</i>	X	X		
<i>Dictyota crispata</i>	X	X		
<i>Dictyota pulchella</i>	X	X	X	X
<i>Dictyota guineensis</i>	X			
<i>Dictyota cervicornis</i>			X	
<i>Dictyota martensii</i>	X			
<i>Dictyota sp.</i>	X			
<i>Lobophora variegata</i>	X	X	X	X
<i>Styopodium zonale</i>	X		X	
<i>Padina sp.</i>	X	X		
<i>Padina pavona</i>		X	X	
<i>Sargassum hystrix</i>				X

Table 6. Continued

Taxa	Bonaire		Curaçao	
	Shallow	Deep	Shallow	Deep
Chlorophyta				
<i>Ulva lactuca</i>			X	
<i>Ulva chaetomorphoides</i>	X			
<i>Ulva</i> sp.	X			
<i>Chaetomorpha gracilis</i>			X	
<i>Boodeleopsis verticillata</i>		X		
<i>Halimeda copiosa</i>	X		X	X
<i>Halimeda opuntia</i>	X		X	X
<i>Halimeda opuntia</i> v <i>triloba</i>	X			
<i>Halimeda tuna</i>	X			
<i>Halimeda cryptica</i>	X			
<i>Halimeda discoidea</i>	X			
<i>Halimeda incrassata</i>			X	
<i>Halimeda gracilis</i>	X			
<i>Anadyomene</i> sp.				
<i>Udotea cyathiformis</i>	X			
<i>Udotea occidentalis</i>	X			
<i>Caulerpa racemosa</i>	X		X	
<i>Caulerpa sertularioides</i>	X			
<i>Caulerpa serrulata</i>	X		X	
<i>Caulerpa mexicana</i>			X	
Cyanophyta				
<i>Lyngbya</i> sp.	X			
<i>Symploca hydroides</i>	X	X	X	