Baseline

Eutrophication threatens Caribbean seagrasses – An example from Curaçao and Bonaire

Laura L. Govers [a,*], Leon P.M. Lamers [b], Tjeerd J. Bouma [c], Jan H.F. de Brouwer [a,1], Marieke M. van Katwijk [a]

[a] Department of Environmental Science, Institute for Water and Wetland Research, Radboud University Nijmegen, Heyendaalseweg 135, 6525 AJ, Nijmegen, The Netherlands
[b] Department of Aquatic Ecology and Environmental Biology, Institute for Water and Wetland Research, Radboud University Nijmegen, Heyendaalseweg 135, 6525 AJ, Nijmegen, The Netherlands
[c] NIOZ Royal Netherlands Institute for Sea Research Yerseke, P.O. Box 140, 4400 AC, Yerseke, The Netherlands

A B S T R A C T

Seagrass beds are globally declining due to human activities in coastal areas. We here aimed to identify threats from eutrophication to the valuable seagrass beds of Curaçao and Bonaire in the Caribbean, which function as nursery habitats for commercial fish species. We documented surface- and porewater nutrient concentrations, and seagrass nutrient concentrations in 6 bays varying in nutrient loads. Water measurements only provided a momentary snapshot, due to timing, tidal stage, etc., but *Thalassia testudinum* nutrient concentrations indicated long-term nutrient loads. Nutrient levels in most bays did not raise any concern, but high leaf % *P* values of *Thalassia* in Piscadera Bay (∼0.31%) and Spanish Water Bay (∼0.21%) showed that seagrasses may be threatened by eutrophication, due to emergency overflow of waste water and coastal housing. We thus showed that seagrasses may be threatened and measures should be taken to prevent loss of these important nursery areas due to eutrophication.

© 2014 Elsevier Ltd. All rights reserved.

Seagrass beds are key coastal ecosystems, which support high biodiversity and provide important ecosystem services such as carbon sequestration, fisheries, and coastal protection (Christianen et al., 2013; Fourqurean et al., 2012; Heck et al., 2003). However, seagrass meadows are rapidly declining all over the world, due to increasing anthropogenic activities in coastal areas (Waycott et al., 2009). Human pressures on coastal areas in the Caribbean are also increasing, and factors like booming tourism, growing industries, oil drillings and spills, trace metal pollution and eutrophication threaten coastal ecosystems (Phillips, 1992; Short and Wyllie-Echeverria, 1996; Thorhaug et al., 1985).

An important stressor that has not been well studied in the Caribbean is eutrophication (but see Gast et al. (1999)). Eutrophication can potentially lead to degradation or complete disappearance of seagrass beds due to epiphyte overgrowth and/or light limitation (Burkholder et al., 2007; Kuenen and Debrot, 1995). We therefore aimed to identify and to quantify the effects of eutrophication on the seagrass beds of the Caribbean islands of Curaçao and Bonaire. On these islands, the seagrass beds form essential nursery habitats for many commercially important fish species

(Huijbers et al., 2013). However, seagrasses are present in bays with varying degrees of anthropogenic impacts (Debrot and Sybesma, 2000). Hence, we studied (1) the nutrient status of seagrasses in 6 bays on Curaçao and Bonaire, (2) the indicator value of seagrass leaf nutrient concentrations, and (3) possible threats of eutrophication in Curaçao and Bonaire bays.

Samples were collected in January 2010 on Curaçao (12°04′N, 68°51′W) and Bonaire (12°15′N, 68°28′), Netherlands Antilles. We sampled six different non-estuarine inland bays (50% of all bays with seagrass, which includes >90% of the total seagrass area) varying in anthropogenic disturbance levels (Table 1). The bays are dominated by mangrove (*Rhizophora mangle)* communities along the shores and by subtidal seagrass beds with turtle grass (*Thalassia testudinum*) and manatee grass (*Syringodium filiforme*). On Curaçao, we sampled Piscadera Bay, Spanish Water Bay, Boka Ascension Bay, Santa Anna Bay and Sint-Joris Bay, and on Bonaire Lac Bay (for more details, see Govers et al. (2014b)).

Sampling sites were maximally 10 m from the shore, and were reached either from the shore, or by boat. The bays were selected for their level of anthropogenic disturbance (Table 1). For each bay, samples were collected in gradients from the source of pollution to the bay mouth. At sites with seagrasses (Table 1), samples were taken in the seagrass bed; at sites without seagrass, porewater samples were taken from the bare sediment. More detailed information (date, tidal level, temperature, precipitation)

can be found in the supplements (Table S1). The distances between sampling points and key-point sources (residential areas, sewage pipes) were measured using the ruler tool in Google Earth^{tm}.

At each sampling site, a minimum of 10 shoots with below-ground biomass was manually sampled while snorkeling and pooled at depths between 0.5 and 2.5 m. All seagrass species present at a sampling site were collected. At each sampling site, two porewater samples were collected anaerobically, using 60 ml vacuum syringes connected to ceramic soil moisture samplers (Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands) placed in the top 7 cm of the soil. These duplicate porewater samples were subsequently pooled per sampling point. Surface water samples were collected similarly in the upper 5 cm of the water column. Samples were frozen on the day of sampling, for further analysis.

Seagrass samples were split up into roots, rhizomes, sheaths, and leaves, and all epiphytes were carefully removed using a scalpel. Subsequently, the samples were dried at 60 °C for 48 h, weighed (g DW) and ground. % C and % N of both leaves and rhizomes were determined with an elemental analyzer (Type NA 1500 Carlo Erba, Thermo Fisher Scientific Inc., USA), coupled online via an interface (Finnigan Conflo III) to a mass-spectrometer (Thermo Finnigan DeltaPlus, USA). Total concentration of phosphorous in seagrass tissue was measured with inductively-coupled-plasma emission spectrometry (IRIS Intrepid II, Thermo Electron Corporation, Franklin, MA, USA), after digestion with nitric acid, following Smolders et al. (2006) and as previously used for seagrass habitats by Govers et al. (2014a).

Porewater and surface water ammonium and ortho-phosphate concentrations were measured colorimetrically (Bran & Luebbe Autoanalyzer III, Seal Analytical, UK), using ammonium-molybdate and salicylate (Lamers et al., 1998). Nitrate was determined by sulphanilamide, after reduction of nitrate to nitrite in a Cadmium column and as previously used for tropical seagrass habitats by Christianen et al. (2012).

We additionally conducted a literature study to compare our *Thalassia* leaf nutrient concentrations to literature values for eutrophic and pristine *Thalassia* meadows (Table 4). References included in this table were found by using ISI Web of Science with the key words *Thalassia* AND nutrient[*], *T. testudinum* AND nutrient[*], *Thalassia hemprichii* AND nutrient[*] or the same key words with either nitrogen or phosphorus instead of nutrient[*].

Displayed values are means ± standard error (SE), the number of replicates for each bay is indicated in Table 1. To compare conditions between bays, we used a one-way ANOVA with a Tukey HSD post hoc test. Normality was tested prior to analysis with a Shapiro Wilk test and non-normal data were log-transformed prior to testing. To compare two different means (residential areas, literature values), we used an independent T-test. Correlations were tested with Pearson's correlation coefficient. Statistical tests were performed in IBM SPSS Statistics 19.0 and R 2.15.

Abiotic measurements such as surface water and porewater nutrient concentrations appeared to give a very limited indication of prevailing nutrient loads as we found no significant differences among bays (Table 2). However, surface water measurements indicated high nitrogen and phosphorus loads in St Anna Bay (13.64 and 1.83 μmol L^{-1} respectively) and Boka Ascension Bay (9.88 and 2.07 μmol L^{-1} respectively).

In contrast, tissue nutrient concentrations in *T. testudinum* tissue reflected nutrient loads accumulated over a longer period (Table 3). Leaf % N concentrations were highest in Piscadera Bay (2.16 ± 0.22% N) and lowest in Sint-Joris Bay and Lac Bay (1.66 ± 0.08% N and 1.78 ± 0.09% N respectively). Leaf %P was also highest in Piscadera Bay, (0.25 ± 0.03% P), and lowest in Lac Bay (0.17 ± 0.00% P). We therefore identified Piscadera Bay as the bay with the high nutrient loads, whereas Lac Bay and Sint Joris Bay had generally lower nutrient loads.

Mean leaf nutrient concentrations in Spanish Water Bay were not high compared to the other bays, possibly because of high mixing rates. However, when we looked at the effects of local eutrophication by coastal residential areas (Fig. 1d), we found a significance increase of >10% in *Thalassia* leaf % P in the vicinity (0–200 m) of residential areas (T-test, $P = 0.009$), compared to seagrass stands >350 m of residential areas (Fig. 1b). In addition, leaf % N also appeared to increase slightly (∼10%) near residential areas, but in contrast to % P, this increase was not significant ($P = 0.166$) (Fig. 1a). Increased nutrient availability near residential areas was also observed in the high macroalgal densities (*Halimeda* sp., see also (Kuenen and Debrot, 1995; Slijkerman et al., 2011)) in between *T. testudinum* (Fig. 1c) stands. In addition to the results of Spanish Water Bay, *T. testudinum* tissue nutrient concentrations seemed to indicate increased nutrient loads near the emergency overflow pipe (<500 m) of Piscadera Bay, as *Thalassia* leaf % N (2.6%) and % P (0.31%) were strongly elevated (indicated by grey triangles) compared to leaf nutrient concentrations near the bay mouth (1.9% N and 0.21% P) (Fig. 2) and compared to literature data for pristine *Thalassia* beds (Table 4). In contrast, *S. filiforme* did not display such an increase in leaf nutrient concentrations (i.e., 1.2% N and 0.18% P nearest to the emergence overflow pipe and 1.4% N and 0.19% P nearest to the bay mouth). No seagrass was sampled

Table 2
Porewater and surface water total nitrogen ($NH_4 + NO_3$) and PO_4 concentrations in μmol L^{-1}. Displayed data are means (# replicates in Table 1), and significant differences (ANOVA) are indicated by letters (a, b, etc.). However, as all results did not differ significantly, everything is indicated by the letter a.

Bay	Porewater		Surface Water	
	Total N	PO$_4$	Total N	PO$_4$
Boka Ascension Bay	18.30^a	4.72^a	9.88^a	2.07^a
Lac Bay	25.11^a	2.16^a	4.35^a	0.62^a
Piscadera Bay	8.05^a	1.49^a	6.95^a	0.83^a
Santa Anna Bay	26.40^a	2.54^a	13.64^a	1.83^a
Sint Joris Bay	6.69^a	2.80^a	2.30^a	0.83^a
Spanish Water Bay	6.73^a	2.07^a	5.63^a	0.91^a

Table 1
Characteristics of the sampled bays on the islands of Curaçao and Bonaire with the number of sampling points per bay. Seagrass species abbreviations: Tt = *Thalassia testudinum*, Sf = *Syringodium filiforme*, Hw = *Halodule wrightii,* and Rm = *Ruppia maritima*.

Bay	Island	Surface (km^2)	Width bay mouth (m)	Seagrass species	Local disturbance	Total # sampling points	# Sampling points seagrass
Lac Bay	Bonaire	7.5	1600	Tt, Sf, Hw, Rm	Protected, light recreation	11	11
Piscadera Bay	Curaçao	0.75	90	Tt, Sf	Sewage discharge, boating	9	6
Spanish Water Bay	Curaçao	3	90	Tt, Sf, Hw, Rm	Domestic sewage, boating	14	14
Boka Ascension Bay	Curaçao	0.05	200	Tt, Sf, Hw	Plastic pollution, turtle grazing	3	3
Santa Anna Bay	Curaçao	4	230	None	Heavy industry; oil refinery	8	0
Sint Joris Bay	Curaçao	2.5	240	Tt	Some waste dumping	6	5

Table 3
Mean leaf nutrient concentrations of *Thalassia testudinum* in all sampled bays. Ratios are mol ratios. Significant differences between bays (ANOVA) are indicated by letters (a, b, etc.), as found by post hoc comparisons. The same letters indicate non-significant differences between groups; different letters indicate significant differences between groups.

Bay	% C	% N	% P	C:N	N:P	C:P	C:N:P
Boka Ascension Bay	30.84[a]	2.02[a]	0.18[ab]	18[a]	25[a]	451[abc]	451:18:01
Lac Bay	34.05[b]	1.78[ab]	0.17[a]	21[bc]	24[a]	524[c]	524:21:01
Piscadera Bay	34.88[b]	2.16[a]	0.25[c]	19[ab]	19[b]	366[a]	366:19:01
Sint Joris Bay	33.27[ab]	1.66[b]	0.18[ab]	24[c]	20[b]	476[cb]	476:24:01
Spanish Water Bay	33.93[b]	1.96[a]	0.19[b]	20[ab]	23[ab]	461[b]	461:20:01

Table 4
Literature overview of *Thalassia* sp. leaf nitrogen (% N) and phosphorus (% P) concentrations from eutrophic and pristine areas. Values were derived from tables and figures of the indicated references. The last lines indicate the range of leaf nutrient concentrations for both eutrophic and pristine areas. NA stands for not available.

Study	Location	Species	% N	% P	Classification	Specifics	Reference
1	Florida, US	*Thalassia testudinum*	2.5	0.51	Eutrophic	Charlotte Habor	Fourqurean and Cai (2001)
2	Florida, US	*Thalassia testudinum*	2.14	0.16	Eutrophic	Near bird colony island	Fourqurean et al. (1992)
3	Panama	*Thalassia testudinum*	~2.4	0.26	Eutrophic	Agricultural runoff/erosion	Carruthers et al. (2005)
10	Florida, US	*Thalassia testudinum*	3.02	0.7	Eutrophic	Polluted bay	Campbell et al. (2012)
11	Bahamas	*Thalassia testudinum*	1.87–3.02	0.17–0.11	Eutrophic	Eutrophic (April/August)	Jensen et al. (1998)
13	Mexico	*Thalassia testudinum*	2.72	0.14	Eutrophic	Near a city	Gallegos et al. (1993)
14	China	*Thalassia hemprichii*	2.4	0.24	Eutrophic	Low intertidal	Zhang et al. (2014)
14	China	*Thalassia hemprichii*	2.8	0.28	Eutrophic	High intertidal	Zhang et al. (2014)
15	Indonesia	*Thalassia hemprichii*	1.68	0.49	Eutrophic	Close to river input	van Katwijk et al. (2011)
12	Florida, US	*Thalassia testudinum*	2.33	0.43	Eutrophic	PO_4 pollution	Rose and Dawes (1999)
13	Mexico	*Thalassia testudinum*	2.18	0.18	Pristine	Reef, oligotrophic	Gallegos et al. (1993)
1	Florida, US	*Thalassia testudinum*	2	0.1	Pristine	Florida Bay	Fourqurean and Cai (2001)
2	Florida, US	*Thalassia testudinum*	2.1	0.08	Pristine	>120 m From bird colony island	Fourqurean et al. (1992)
4	Bahamas	*Thalassia testudinum*	0.91–1.14	NA	Pristine	Tidal channel, mature leaves with epiphytes	Capone et al. (1979)
5	Barbados	*Thalassia testudinum*	2.29	0.157	Pristine	NA	Patriquin (1972)
6	Mexico	*Thalassia testudinum*	2.25	0.13	Pristine	Outer reef	Terrados et al. (2008)
7	Puerto Rico	*Thalassia testudinum*	2.4	0.14	Pristine	Surrounded by agricultural/urban land, but decoupled from watershed	Olsen and Valiela (2010)
8	Bahamas	*Thalassia testudinum*	1.88	0.073	pristine	Undisturbed tidal creeks with fringing mangroves	Allgeier et al. (2011)
9	Jamaica	*Thalassia testudinum*	1.44	NA	Pristine	No nitrogen rich upwelling	Peterson et al. (2012)
10	Florida, US	*Thalassia testudinum*	2.14	0.08	Pristine	Unpolluted bay	Campbell et al. (2012)
11	Bahamas	*Thalassia testudinum*	1.84–2.13	0.12–1.14	Pristine	Oligotrophic (April/August)	Jensen et al. (1998)
15	Indonesia	*Thalassia hemprichii*	2.28	0.1	pristine	Far away from river input	van Katwijk et al. (2011)
16	Indonesia	*Thalassia hemprichii*	2.04	NA	Pristine	Spermonde Archipelago	Vonk et al. (2008)
17	Indonesia	*Thalassia hemprichii*	1.9	0.14	Pristine	Spermonde Archipelago	Erftemeijer and Middelburg (1993)
18	Indonesia	*Thalassia hemprichii*	1.99	0.18	Pristine	Barang Lompo, 3rd leaf	Stapel and Hemminga (1997)
18	Indonesia	*Thalassia hemprichii*	1.99	0.16	Pristine	Gusung Tallang, 3rd leaf	Stapel and Hemminga (1997)
		Eutrophic	1.68–3.02	0.14–0.7			
		Pristine	0.91–2.4	0.073–0.18			

within a distance of 460 m from the emergency overflow pipe; as no seagrass was present this close to the outlet. In Santa Anna Bay, no seagrass was found, so this bay could not be included in the seagrass nutrient analysis.

Based on our literature study (Table 4), we found that *Thalassia* leaf nutrient concentrations are generally between 1.68–3.02% N and 0.14–0.7% P for systems that were marked as eutrophic (or polluted), and between 0.91–2.4% N and 0.073–0.18% P for pristine
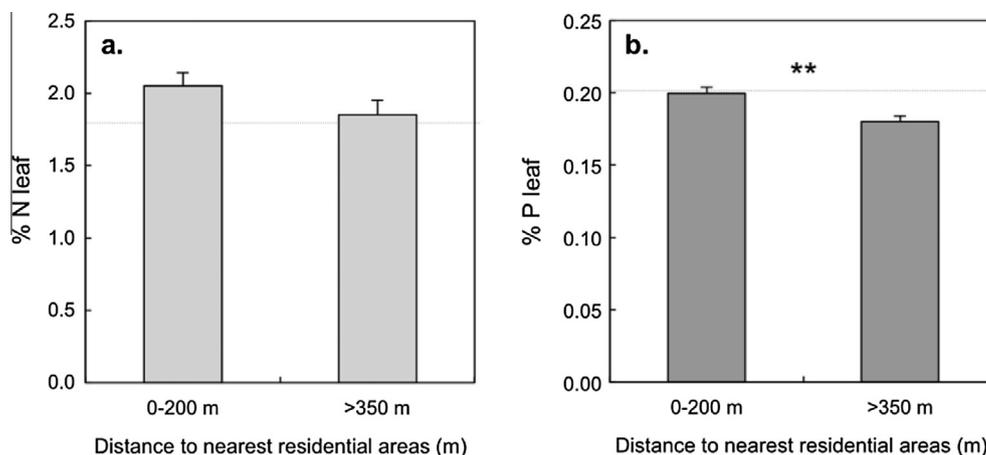
Fig. 1. Local eutrophication effects of residential areas on (a) leaf % N values and (b) leaf % P values of *Thalassia testudinum* in Spanish Water Bay. Dotted lines indicate the absolute limitation levels (1.8% N and 0.2% P) for seagrasses, as stated by Duarte (1990). **Indicates a significance level of $P < 0.01$ ($P = 0.009$). Displayed values are means and error bars present standard errors.
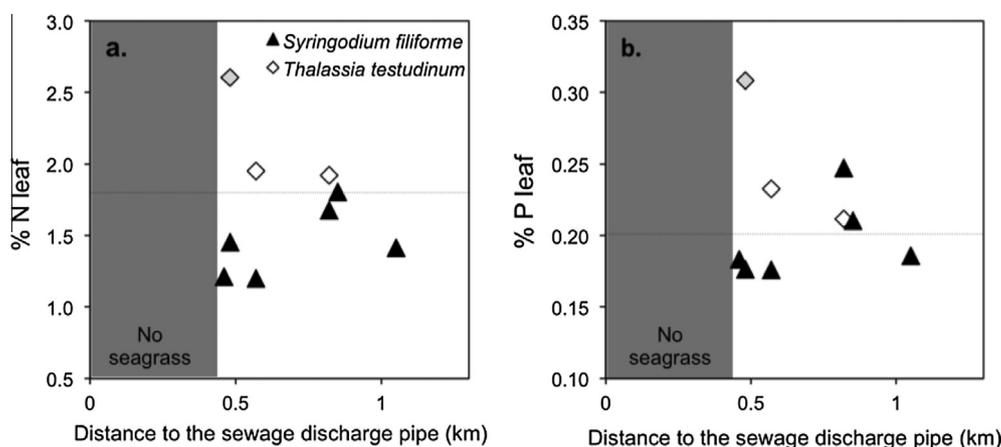

Fig. 2. Distance analysis on the effects of a emergency overflow discharge pipe on (a) leaf % N and (b) leaf % P concentrations of *Thalassia testudinum* and *Syringodium filiforme* in Piscadera Bay. Dotted lines indicate the limitation levels (1.8% N and 0.2% P) for seagrasses, as stated by Duarte (1990). Displayed values are means and error bars present standard errors.

Thalassia beds. Although overlapping, both *Thalassia* leaf % N and leaf % P values differed significantly between eutrophic and pristine sites (*T*-tests, $P < 0.001$, $P = 0.007$ for % N and % P respectively).

Seagrass nutrient concentrations reflected nutrient loads over a longer period, which confirms previous work (Ferdie and Fourqurean, 2004; Udy and Dennison, 1997; van Katwijk et al., 2011). In contrast, abiotic parameters (surface and porewater nutrient concentrations) gave a very limited indication of prevailing nutrients loads, which agrees with earlier observations that such measurements only provide a momentary snapshot (Short and McRoy, 1984), affected by timing, tidal stage, terrestrial runoff, freshwater input, and rapid uptake of nutrients by plankton, seagrasses and macroalgae (van Katwijk et al., 2011). However, mean surface water total nitrogen ($>4 \, \mu mol \, L^{-1}$) and phosphate ($>0.6 \, \mu mol \, L^{-1}$) levels from most bays were well above the values indicated as eutrophic reef waters by Gast et al. (1999) and other coastal Caribbean lagoons (Carruthers et al., 2005; Olsen and Valiela, 2010; Peterson et al., 2012). Our values thus seem to indicate that nutrient levels can be above the threshold values for eutrophication for corals (Gast et al., 1999), and also hint at possible negative effects of high nutrient levels for seagrasses. Especially St Anna Bay (or Harbor Bay), where no seagrass can be found, displayed high

surface water nutrient levels, possibly, seagrasses have disappeared due to eutrophication in this heavily polluted bay (Gast et al., 1999). Yet, to gain a more complete picture of long-term nutrient loads in these bays, we mainly focused on the indicator value of seagrass tissue nutrient concentrations in this study.

We found that *Thalassia* leaf nutrient concentrations for pristine seagrass beds are generally between 0.91–2.4% N and 0.05–0.18% P, whereas leaf nutrient concentrations found in nutrient enriched systems are between 1.87–3.02% N and 0.14–0.70% P (Table 4). When comparing these literature values with our data, Lac Bay, St Joris Bay, and Boka Ascension Bay fall within the limits of oligotrophic/pristine systems for both nitrogen and phosphorus. In addition, *T. testudinum* leaf nitrogen concentrations also indicate limited nitrogen availability (<2.4% N) in the other bays. However, relatively low nitrogen concentrations may also be the result of the terrigenous sediments in these bays, which may promote nitrogen limitation in seagrasses, due to higher phosphorus availability in terrigenous than in carbonate sediments (Erftemeijer and Middelburg, 1993; Touchette and Burkholder, 2000). Or possibly, sea turtle grazing, such as in Boka Ascension Bay, may promote nutrient export, thereby lowering bay nutrient loads and protecting seagrasses from eutrophication effects (Christianen et al.,

2012). Total Phosphorus concentrations of both Piscadera Bay and Lac Bay may indicate excess phosphorus availability, based on comparison with literature data, which confirms the presence of point sources (coastal residencies and emergency overflow pipe) of eutrophication. Thus, our data, supported by our literature overview, show that *Thalassia* leaf nutrient concentrations (especially P) are commonly elevated in the vicinity of a nutrient source and can thus be used as bioindicator for nutrient pollution.

We found a difference in nutrient accumulation in the leaves between a late and early successional seagrass species in the vicinity of a source of eutrophication (emergency overflow pipe, Piscadera Bay). In contrast to *T. testudinum*, the fast growing *S. filiforme* did not accumulate nutrients in the eutrophic bay, but seem to have used the extra nutrients for growth (pers. observations, Fig. S1). Leaf nutrient concentrations of the late successional *T. testudinum* were however >35% higher (0.31% P, 2.6% N) in vicinity of the overflow pipe than in plants near the bay mouth (0.21% P, 1.9% N). Christianen et al. (2011) found similar differences in leaf nutrient levels between an early successional and a late successional species, which might be explained by differences in growth strategy. An early successional species, such as *S. filiforme* generally shows higher production rates (Barber and Behrens, 1985) and shoot turn-over rates (2.0 yr^{-1}; Gallegos et al. (1994)), and is able take up nutrients faster than late successional species (Duarte, 1991; Rollon et al., 1998). In contrast, the late successional species *T. testudinum* is a slow growing species with low shoot turn-over rates (0.6 yr^{-1}; Gallegos et al. (1993)), which accumulates nutrients in the leaves (Carruthers et al., 2005; McGlathery et al., 1994). *T. testudinum* proved also to be a good indicator of point sources of eutrophication in Spanish Water Bay, as leaf % P was elevated in the vicinity of residential areas up to concentrations >0.18% which may be indicative of eutrophication according to literature values (Table 4). However, additional to leaf nutrient concentrations (% N, % P), nitrogen isotopic ratios would have provided even more detailed information on anthropogenic nutrient input in the studied bays (Mutchler et al., 2007; Schubert et al., 2013).

We conclude that that leaf nutrient values of *T. testudinum* may be used as bioindicator values for point sources of eutrophication. Additionally, we identified potential threats of eutrophication to seagrasses on Curaçao in Spanish water Bay (residential areas) and Piscadera Bay (emergency overflow discharge); nutrient levels in the other sampled bays did however not raise any concern yet. The seagrasses of Piscadera Bay have already retreated to the shallowest areas (<1 m, pers. observations) of the murky waters and are under threat of complete disappearance with a further increase of nutrient loads. Moreover, *T. testudinum* in Spanish Water Bay has been declining for some time (Kuenen and Debrot, 1995), and we are the first to suggest (leaf % P values) that this may be due to excess anthropogenic nutrient input by coastal residencies. This bay, with the largest seagrass area of Curaçao (Debrot et al., 1998; Kuenen and Debrot, 1995), highly contributes to coral reef fish populations by functioning as a nursery habitat (Huijbers et al., 2013). Possible disappearance of seagrasses due to eutrophication may therefore have serious consequences for the ecological and economical values of the coastal ecosystems of Curaçao. We have shown that some bays at Curaçao are subjected to excess nutrient inputs, which may already have contributed to seagrass loss and linked ecosystem services. We therefore hope that measures will be taken to prevent further loss of valuable seagrass beds due to eutrophication at Curaçao.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.marpolbul.2014.09.003.

References

Allgeier, J.E., Rosemond, A.D., Layman, C.A., 2011. Variation in nutrient limitation and seagrass nutrient content in Bahamian tidal creek ecosystems. J. Exp. Mar. Biol. Ecol. 407, 330–336.

Barber, B.J., Behrens, P.J., 1985. Effects of elevated temperature on seasonal *in situ* leaf productivity of *Thalassia testudinum* Banks ex König and *Syringodium filiforme* Kützing. Aquat. Bot. 22, 61–69.

Burkholder, J., Tomasko, D., Touchette, B., 2007. Seagrasses and eutrophication. J. Exp. Mar. Biol. Ecol. 350, 46–72.

Campbell, J.E., Yarbro, L.A., Fourqurean, J.W., 2012. Negative relationships between the nutrient and carbohydrate content of the seagrass *Thalassia testudinum*. Aquat. Bot. 99, 56–60.

Capone, D.G., Penhale, P.A., Oremland, R.S., Taylor, B.F., 1979. Relationship between productivity and N₂ (C₂H₂) fixation in a *Thalassia testudinum* community. Limnol. Oceanogr. 24, 117–125.

Carruthers, T.J.B., Barnes, P.A.G., Jacome, G.E., Fourqurean, J.W., 2005. Lagoon scale processes in a coastally influenced Caribbean system: implications for the seagrass *Thalassia testudinum*. Carib. J. Sci. 41, 441–455.

Christianen, M.J.A., van der Heide, T., Bouma, T.J., Roelofs, J.G.M., van Katwijk, M.M., Lamers, L.P.M., 2011. Limited toxicity of NH(x) pulses on an early and late successional tropical seagrass species: interactions with pH and light level. Aquat. Toxicol. 104, 73–79.

Christianen, M.J.A., Govers, L.L., Kiswara, W., Roelofs, J.G.M., Bouma, T.J., Lamers, L.P.M., van Katwijk, M.M., 2012. Marine megaherbivore grazing may increase seagrass resilience to high nutrient loads. J. Ecol. 100.

Christianen, M.J.A., Van Belzen, J., Herman, P.M.J., van Katwijk, M.M., Lamers, L.P.M., Van Leent, P.J.M., Bouma, T.J., 2013. Low-canopy seagrass beds still provide important coastal protection services. PLoS One 8, e62413.

Debrot, A.O., Sybesma, J., 2000. The Dutch Antilles. In: Sheppard, C.R.C. (Ed.), Seas at the Millennium: An Environmental Evaluation. Elsevier, Amsterdam.

Debrot, A.O., Kuenen, M.M.C.E., Dekker, K., 1998. Recent declines in the coral fauna of the Spaanse Water, Curaçao, Netherlands Antilles. Bull. Mar. Sci. 63, 571–580.

Duarte, C.M., 1990. Seagrass nutrient content. Mar. Ecol. – Progr. Ser. 67, 201–207.

Duarte, C.M., 1991. Allometric scaling of seagrass form and productivity. Mar. Ecol. Prog. Ser. 77, 289–300.

Erftemeijer, P.L.A., Middelburg, J.J., 1993. Sediment–nutrient interactions in tropical seagrass beds – a comparison between a terrigenous and a carbonate sedimentary environment in South Sulawesi (Indonesia). Mar. Ecol. Prog. Ser. 102, 187–198.

Ferdie, M., Fourqurean, J., 2004. Responses of seagrass communities to fertilization along a gradient of relative availability of nitrogen and phosphorus in a carbonate environment. Limnol. Oceanogr. 49, 2082–2094.

Fourqurean, J.W., Cai, Y., 2001. Arsenic and phosphorus in seagrass leaves from the Gulf of Mexico. Aquat. Bot. 71, 247–258.

Fourqurean, J.W., Zieman, J.C., Powell, G.V.N., 1992. Phosphorus limitation of primary production in Florida Bay – evidence from C–N–P ratios of the dominant seagrass *Thalassia testudinum*. Limnol. Oceanogr. 37, 162–171.

Fourqurean, J.W., Duarte, C.M., Kennedy, H., Marba, N., Holmer, M., Angel Mateo, M., Apostolaki, E.T., Kendrick, G.A., Krause-Jensen, D., MCGlathery, K.J., Serrano, O., 2012. Seagrass ecosystens as a globally significant carbon stock. Nat. Geosci. 5, 505–509.

Gallegos, M.E., Merino, M., Marba, N., Duarte, C.M., 1993. Biomass and dynamic of *Thalassia testudinum* in the Mexican Caribbean: elucidating rhizome growth. Mar. Ecol. Prog. Ser. 95, 185–192.

Gallegos, M.E., Merino, M., Rodriguez, A., Marba, N., Duarte, C.M., 1994. Growth patterns and demography of pioneer Caribbean seagrasses *Halodule wrightii* and *Syringodium filiforme*. Mar. Ecol. Prog. Ser. 109, 99–104.

Gast, G.J., Jonkers, P.J., Van Duyl, F.C., Bak, R.P.M., 1999. Bacteria, flagellates and nutrients in island fringing coral reef waters: influence of the ocean, the reef and eutrophication. Bull. Mar. Sci. 65, 523–538.

Govers, L.L., de Brouwer, J.H.F., Suykerbuyk, W., Bouma, T.J., Lamers, L.P.M., Smolders, A.J.P., van Katwijk, M.M., 2014a. Toxic effects of increased sediment nutrient and organic matter loading on the seagrass *Zostera noltii*. Aquat. Toxicol. 155, 253–260.

Govers, L.L., Lamers, L.P.M., Bouma, T.J., Eygensteyn, J., de Brouwer, J.H.F., Hendriks, A.J., Huijbers, C.M., van Katwijk, M.M., 2014b. Seagrasses as indicators for coastal trace metal pollution: a global meta-analysis serving as a benchmark, and a Caribbean case study. Environ. Pollut., http://dx.doi.org/10.1016/j.envpol.2014.08.028.

Heck, K.L., Hays, G., Orth, R.J., 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar. Ecol. – Progr. Ser. 253, 123–136.

Huijbers, C.M., Nagelkerken, I., Debrot, A.O., Jongejans, E., 2013. Geographic coupling of juvenile and adult habitat shapes spatial population dynamics of a coral reef fish. Ecology 94, 1859–1870.

Jensen, H.S., McGlathery, K.J., Marino, R., Howarth, R.W., 1998. Forms and availability of sediment phosphorus in carbonate sand of bermuda seagrass beds. Limnol. Oceanogr. 43, 799–810.

Kuenen, M., Debrot, A.O., 1995. A quantitative study of the seagrass and algal meadows of the Spaanse water, Curacao, the Netherlands Antilles. Aquat. Bot. 51, 291–310.

Lamers, L.P.M., Tomassen, H.B.M., Roelofs, J.G.M., 1998. Sulfate-induced eutrophication and phytotoxicity in freshwater wetlands. Environ. Sci. Technol. 32, 199–205.

McGlathery, K.J., Marino, R., Howarth, R.W., 1994. Variable rates of phosphate uptake by shallow marine carbonate sediments: mechanisms and ecological significance. Biogeochemistry 25, 127–146.

Mutchler, T., Dunton, K.H., Townsend-Small, A., Frederiksen, S., Rasser, M.K., 2007. Isotopic and elemental indicators of nutrient sources and status of coastal habitats in the Caribbean Sea, Yucatan Peninsula, Mexico. Estuar. Coast. Shelf Sci. 74, 449–457.

Olsen, Y.S., Valiela, I., 2010. Effect of sediment nutrient enrichment and grazing on turtle grass *Thalassia testudinum* in Jobos Bay, Puerto Rico. Estuaries Coasts 33, 769–783.

Patriquin, D.G., 1972. The origin of nitrogen and phosphorus for growth of the marine angiosperm *Thalassia testudinum*. Mar. Biol. 15, 34–46.

Peterson, B.J., Stubler, A.D., Wall, C.C., Gobler, C.J., 2012. Nitrogen-rich groundwater intrusion affects productivity, but not herbivory, of the tropical seagrass *Thalassia testudinum*. Aquatic Biology 15, 1–9.

Phillips, R.C., 1992. The seagrass ecosystem and resources in Latin America. In: Seeliger, U. (Ed.), Coastal Plant Communities of Latin America. Academic Press, San Diego, California.

Rollon, R.N., Van Steveninck, E.D.D., van Vierssen, W., Fortes, M.D., 1998. Contrasting recolonization strategies in multi-species seagrass meadows. Mar. Pollut. Bull. 37, 450–459.

Rose, C.D., Dawes, C.J., 1999. Effects of community structure on the seagrass *Thalassia testudinum*. Mar. Ecol. Prog. Ser. 184, 83–95.

Schubert, P.R., Karez, R., Reusch, T.B.H., Dierking, J., 2013. Isotopic signatures of eelgrass (*Zostera marina* L.) as bioindicator of anthropogenic nutrient input in the western Baltic Sea. Mar. Pollut. Bull. 72, 64–70.

Short, F.T., McRoy, L.P., 1984. Nitrogen uptake by leaves and roots of the seagrass *Zostera marina* L. Bot. Mar. 27, 547–555.

Short, F.T., Wyllie-Echeverria, S., 1996. Natural and human-induced disturbances of seagrasses. Environ. Conserv. 23, 17–27.

Slijkerman, D.M.E., Peachey, R.B.J., Hausmann, P.S., Meesters, H.W.G., 2011. Eutrophication status of Lac, Bonaire, Durch Caribbean, inlcuding proposals for measures. IMARES Wageningen UR.

Smolders, A.J.P., Moonen, M., Zwaga, K., Lucassen, E., Lamers, L.P.M., Roelofs, J.G.M., 2006. Changes in pore water chemistry of desiccating freshwater sediments with different sulphur contents. Geoderma 132, 372–383.

Stapel, J., Hemminga, M.A., 1997. Nutrient resorption from seagrass leaves. Mar. Biol. 128, 197–206.

Terrados, J., Ramírez-García, P., Hernández-Martínez, Ó., Pedraza, K., Quiroz, A., 2008. State of *Thalassia testudinum* Banks ex König meadows in the Veracruz Reef System, Veracruz, México. Aquat. Bot. 88, 17–26.

Thorhaug, A., Miller, B., Jupp, B., Booker, F., 1985. Effects of a variety of impacts on seagrass restoration in Jamaica. Mar. Pollut. Bull. 16, 355–360.

Touchette, B.W., Burkholder, J.M., 2000. Review of nitrogen and phosphorus metabolism in seagrasses. J. Exp. Mar. Biol. Ecol. 250, 133–167.

Udy, J.W., Dennison, W.C., 1997. Growth an physiological responses of three seagrass species to elevated nutrients in Moreton Bay, Australia. J. Exp. Mar. Biol. Ecol. 217, 253–277.

van Katwijk, M.M., van der Welle, M.E.W., Lucassen, E.C.H.E.T., Vonk, J.A., Christianen, M.J.A., Kiswara, W., al Hakim, I.I., Arifin, A., Bouma, T.J., Roelofs, J.G.M., Lamers, L.P.M., 2011. Early warning indicators for river nutrient and sediment loads in tropical seagrass beds: a benchmark from a near-pristine archipelago in Indonesia. Mar. Pollut. Bull. 62, 1512–1520.

Vonk, J.A., Christianen, M.J.A., Stapel, J., 2008. Redefining the trophic importance of seagrasses for faunal in tropical Indo-Pacific meadows. Estuar. Coast. Shelf Sci. 79, 653–660.

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. 106, 12377–12381.

Zhang, J., Huang, X., Jiang, Z., 2014. Physiological responses of the seagrass *Thalassia hemprichii* (Ehrenb.) Aschers as indicators of nutrient loading. Mar. Pollut. Bull. 83, 508–515.