Baseline surveys of Lac Bay benthic and fish communities, Bonaire

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Executive summary

Lac Bay, is a clear-water, 5 m deep shallow tropical lagoon of approximately 7 km^2 opening onto the wave- and wind-exposed east coast of the island of Bonaire, southern Caribbean. It contains the largest seagrass and algal beds of the island, and of the Caribbean Netherlands. Over the last decades land reclamation by mangroves in Lac has been expanding the surface of turbid, saline backwaters into the bay at an average rate of 2.34 ha per year. This process threatens the future habitat quality and critical ecological function the bay fulfills as the most important fish nursery habitat for Bonaire.

To help understand the changes taking place in the bay we here quantitatively document and describe the distribution of algal and seagrass beds along the environmental gradient from clear, open bay conditions to the turbid and isolated conditions of the inner mangrove pools. The percentage cover of principal benthic vegetation was estimated on 98 randomly chosen 4 m^2 survey plots distributed among three principal zones of the bay. Five main seagrass and algal communities were described that differ significantly in species composition, biotic density and gross distribution in the bay. The richest assemblages with highest biotic coverages occurred in high light-intensity and well-circulated shallow habitats that fringed the mangroves of the central bay area. Both landwards in through the mangrove channels and seawards of this zone, towards the deeper parts of the bay, both biotic diversity and cover decreased. Isolated mangrove pools had the lowest total cover, species richness and biodiversity of all habitats. Compared to the early 1990s, *Thalassia testudinum* no longer plays a role in the mangrove pool habitats of Lac but is only found in the central bay area and its margins. The lushest *Thalassia*-beds occur shallow where they are being encroached upon by *Halimeda* growth while the deeper *Thalassia*-beds are being massively invaded by the exotic seagrass *Halophila stipulacea*, first detected in 2010.

The fish community structure of the Lac habitats were investigated using visual census. We quantitatively sampled the fish species abundance, composition, and size-structures at a total of 139 sites distributed among nine different sub-habitats. Fish community variables differed consistently among habitats and were mainly influenced by the percent cover of seagrass vegetation or presence of mangrove-root structure. Mangrove fringe habitats were a premier habitat since multiple life stages of a variety of species showed highest densities there. Several reef fish species had a distribution pattern suggesting a unique step-wise post-settlement life cycle migration in which larger juveniles and/or subadults appear to move from the open bay environment (seagrass beds or bay mangrove fringe) to the interior mangrove fringes along mangrove pools, before later departing to the adult habitat of the coral reef. Particularly important among these was the IUCN red-listed rainbow parrotfish, *Scarus guacamaia* (NT), a prominent species in the bay.

In the case of the well-lit and well-circulated central bay habitat, the limiting factor to fish abundance and diversity appeared to be the paucity of three-dimensional shelter due to the predominance of the invasive seagrass *H. stipulacea* with small and short leaves. In the warm and hypersaline backwaters, physiological tolerance limits were likely a key factor. Our results indicate that maintenance of habitat connectivity and smaller-scale habitat diversity is a key management priority for ensuring secondary productivity of coastal marine habitats.

The valuable sea grass and mangrove habitats of Lac are essentially trapped in an enclosed bay.
As long-term mangrove expansion have been steadily reducing the net coverage of clear, well circulated open bay waters by an average of more than 2 hectares per year, the surface of shallow, muddy, stagnant, hypersaline backwaters has been increasing by an almost equal amount. These backwaters are unable to support either meaningful mangroves, seagrass or algal meadows, nor the key nursery species. Unchecked expansion of saline backwaters means that the most valuable nursery habitats will come under additional salinity stress and likely continue to decrease in coverage and quality at an accelerated rate. Consequently, the long-term biodiversity and ecosystem function of the bay is at stake

and management intervention is needed to stem further erosion of nursery habitat quality and ensure that a tipping-point is not reached beyond which recovery may be difficult or impossible.

To relieve the bay ecosystem of thermal and salinity stress caused by the shallow backwaters measures would need to be taken to help restore water depth, and circulation. The need to restore hydrology to stem mangrove forest mortality and further erosion of habitat quality was first pointed out by a team of experts in 1970, and is long due. Excavation of accumulated erosional and biogenic sediments as well as dredging to restore former feeder channels by removal of mangrove overgrowth (as already started by Stinapa) are among the measures that need to be taken. Such measures could also help alleviate the problem of eutrophication as documented for Lac in other studies. Finally, this work documents the alarmingly rapid invasion of the bay by the invasive seagrass *H. stipulacea*. Further studies are needed to assess the impacts that this species is having on the flora and fauna of the bay.

Contents

Terms of reference

The mangrove and seagrass lagoon of Lac Bay on Bonaire covers an area of roughly 700 ha. It is home to endangered green sea turtles, *Chelonia mydas*, and the Caribbean queen conch, *Strombus gigas*, and is an important roosting site for birds. Other endangered species include the threatened corals *Acropora palmata* and *A. cervicornis* and the rainbow parrotfish, *Scarus guacamaia* and some other IUCN vulnerable species. Based on its nature values this 7km^2 bay has been designated as a legally protected Ramsar site (Stinapa Bonaire 2003) and identified as a Birdlife International IBA (Important Bird Area) (Wells and Debrot 2008). The area falls under the management responsibility of the National Parks Foundation of Bonaire STINAPA Bonaire which tries to address several issues based on a 2009 management plan. Lac Bay is under increasing development pressure for recreational use and more-effective management is clearly necessary.

As a Ramsar area, several international obligations need to be met, including the documentation of changes, management according to wise use and regular reporting. Based on concerns about Lac and the international commitments, in 2010 the then Ministry of LNV, The Netherlands, commissioned IMARES to assess the situation (Debrot et al. 2010a) and come with a shortlist of action points (Debrot et al. 2010b) that address the principal information gaps. This ministry (today the Ministry of Economic Affairs, Agriculture and Innovation, or EL&I) continues to actively exercise its mandate with respect to the biodiversity of the Caribbean Netherlands and commissioned these studies.

Two of the identified information gaps were the need to quantitatively document and assess the current state of the seagrass and fish communities of the Lac ecosystem. These two important subjects are addressed separately in the two sections of this report.

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Section A:

The distribution of sea grass and algal beds in the changing seascapes of a tropical mangrove lagoon, Lac, Bonaire, Southern Caribbean

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Abstract

Lac Bay, is a clear-water, 5 m deep shallow tropical lagoon of approximately 7 km^2 opening onto the wave- and wind-exposed east coast of the island of Bonaire, southern Caribbean. It contains the largest seagrass and algal beds of the island. Over the last decades land reclamation by mangroves in Lac has been expanding the surface of turbid, saline backwaters into the bay at an average rate of 2.34 ha per year. This process threatens the future habitat quality and critical ecological function the bay fulfills as the most important fish nursery habitat for Bonaire.

To help understand the changes taking place in the bay we here quantitatively document and describe the distribution of algal and seagrass beds along the environmental gradient from clear, open bay conditions to the turbid and isolated conditions of the inner mangrove pools. The percentage cover of

principal benthic vegetation was estimated on 98 randomly chosen 4 m^2 survey plots distributed among three principal zones of the bay. Five main seagrass and algal communities were described that differ significantly in species composition, biotic density and gross distribution in the bay. The richest assemblages with highest biotic coverages occurred in high light-intensity and well-circulated shallow habitats that fringed the mangroves of the central bay area. Both landwards in through the mangrove channels and seawards of this zone, towards the deeper parts of the bay, both biotic diversity and cover decreased. Isolated mangrove pools had the lowest total cover, species richness and biodiversity of all habitats. Geographic position along the habitat gradient, salinity and substrate characteristics accounted for the most variation seen between the different benthic assemblages.

Compared to the early 1990s, *Thalassia testudinum* Banks ex König no longer plays a role in the mangrove pool habitats of Lac but is only found in the central bay area and its margins. The lushest *Thalassia*-beds occur shallow where they are being encroached upon by *Halimeda* growth while the deeper *Thalassia*-beds are being massively invaded by the exotic seagrass *Halophila stipulacea* (Forsskål) Ascherson, first detected in 2010. This invasive species was absent in the richest shallow assemblages dominated by *Thalassia* and *Halimeda* but has firmly invaded two disjunct seagrass assemblages with lower coverage of native species in the central bay area and the mangrove lagoonal habitat. The overall diversity of the assemblages described for Lac was lower than for assemblages described for the Spanish Water bay of Curaçao due to the total absence of hard substrates.

A.1 Introduction

Shallow-water marine ecosystems such as seagrass and algal meadows and mangroves provide habitat, nursery and feeding grounds for many fish (Parrish, 1989; Nagelkerken et al., 2000; Nagelkerken et al., 2000b; Laegdsgaard and Johnson, 2001) and invertebrate species (Haywood et al., 1995; Loneragan et al., 1998) and serve critical ecosystem functions (Gladstone, 2009; Nagelkerken, 2009). Waycott et al. (2009) document the alarming loss of seagrass communities worldwide. Seagrass and algal meadows are known to show great variability in appearance and structure due to such factors as depth, tidal regime and geomorphology. Such variability certainly also affects their function for different species and life-stages of organisms that use them, but few studies have described that variability or how it might affect ecological aspects. So while the discussion about the nursery function of such habitats continues (Blaber, 2007), the definition of such habitats also remains unsettled (Faunce and Layman, 2009) as do even the criteria by which to define them (Beck et al. 2001; Dahlgren et al., 2006; Sheaves et al., 2006). Yet the literature provides exceedingly few quantitative descriptions of seagrass beds.

In this study we provide quantitative assessment of seagrass and algal meadows for Lac Bay in Bonaire. Lac is an approximately 7 km^2 shallow lagoon in the southeast sector of Bonaire (Fig. 1). It is the largest lagoon of the island and contains by far the most extensive and important mangrove and seagrass habitats of Bonaire and the Caribbean Netherlands. Almost all other bays of the island are semi-enclosed and largely hypersaline in nature which makes them important for flamingos but largely unsuitable to significant seagrass and mangrove development.

The bay has been documented as a locally important habitat for the endangered queen conch (*Strombus gigas* Linnaeus) (Lott, 2000; Engel, 2008) and the protected green turtle, *Chelonia mydas* Linnaeus (Debrot et al., 2010) and furthermore functions as a valuable nursery habitat for many fish species (Van der Velde et al., 1992; Van Moorsel and Meijer, 1993; Nagelkerken et al., 2002). Based on its concentration of nature values, the bay has been designated as a legally protected Ramsar site and has also been identified as a regionally significant IBA (Important Bird Area) by Birdlife International (Wells and Debrot, 2008). The area is managed by the National Parks Foundation of Bonaire, STINAPA Bonaire, based on their recent management plan in which several issues are addressed. Nevertheless, Lac Bay is under increasing development pressure from recreational use and has been in long-term decline due to filling-in with sediments (e.g. Lott, 2001). Aerial and satellite maps of mangrove distribution dating back to 1961, show that the back of the bay is filling in relatively rapidly as the mangroves migrate seaward within the bay. Erdman and Scheffers (2006) found that free expansion of the mangroves in a seaward direction amounted to a growth of 81 ha of mangroves on the seaward margin (average: 2.34 ha per year) and a practically equal loss of mangrove surface area on the landside of the lagoon (of 82 ha) during a 35 year period up to 1996. In the process the net coverage of clear, well circulated open bay waters has declined by 81 ha while the surface of shallow, hyper-saline back-waters unable to support either mangroves, seagrass or algal meadows has grown by 82 ha. This process seriously threatens the long-term biodiversity and ecosystem function of the bay, but its exact causes and consequences are poorly understood. Additional problems include heavy recreational use, litter contamination, poaching of queen conch and eutrophication (Debrot et al., 2010a; Slijkerman et al., 2011). To address these issues and provide quantitative baseline data an action plan was recently outlined (Debrot et al., 2010b), which included the need for a baseline benthic community description as addressed in this study.

A quantitative description of the benthic seagrass and algal meadows distributed across the environmental gradient associated with the mangrove-driven land reclamation is a first critical step to help us to better understand how this dynamic process is affecting the distribution of benthic macro-flora (and –fauna) in the bay and provide insight into its mid- to long-term consequences to the various nursery habitats of the bay. Quantitative insights into such habitats are also critical for developing criteria with which to ultimately understand function. Therefore the principal objective of this study was to describe and compare the distribution of seagrass and algal meadows in terms of key community descriptors such as biotic cover, species richness and diversity as distributed along an environmental gradient in this tropical Caribbean bay, stretching from clear open bay waters adjacent to coral reefs to stagnant and saline mangrove pools. Several largely descriptive studies conducted on the fauna and flora of Lac (e.g. Wagenaar-Hummelinck and Roos, 1970; Hoek et al., 1972; Fransen, 1986; Van Moorsel and Meijer, 1993; Lott, 2000; Engel, 2008), provided background for some preliminary assessment of long-term changes occurring in the bay.

An additional point of interest was to assess the current status inside Lac of a recently discovered invasive seagrass, *Halophila stipulacea* (Forsskål) Ascherson. *This s*pecies is invasive in the Caribbean (Willette and Ambrose, 2009) and was first reported in Grenada in 2002 (Ruiz and Ballantine, 2004). *H. stipulacea* was not reported in the most recent seagrass assessment for Lac (Engel, 2008), but quite clearly showed high coverages in certain habitats of the bay.

A.2 Materials and methods

A.2.1 Study area

The lagoon of Lac Bay is located along the eastern coast of Bonaire and covers an area of somewhat more than 700 ha. The bay is largely 0-3 m deep and protected from the waves of the wind-exposed eastern coast by a shallow coral barrier. De Buisonjé (1974) points out that bays in the Leeward Dutch Caribbean were largely formed due to postglacial inundation of Pleistocene erosional valleys. The main channel connecting the bay to the luxuriant fringing reef is about 5 m deep. Likely related to overall sediment production and accumulation in the bay, the deepest part of the entrance to Lac Bay decreased in depth from 8 to the present 5 meters since 1949 (Lott, 2001). Lac is essentially a clear-water bay and horizontal Secchi visibility ranges from some 4.5 to more than 21 m in the central parts of the bay (Van Moorsel and Meijer, 1993). Hence, apart from the sediment-ridden murky back-waters, seagrass and algal development is not limited by light.

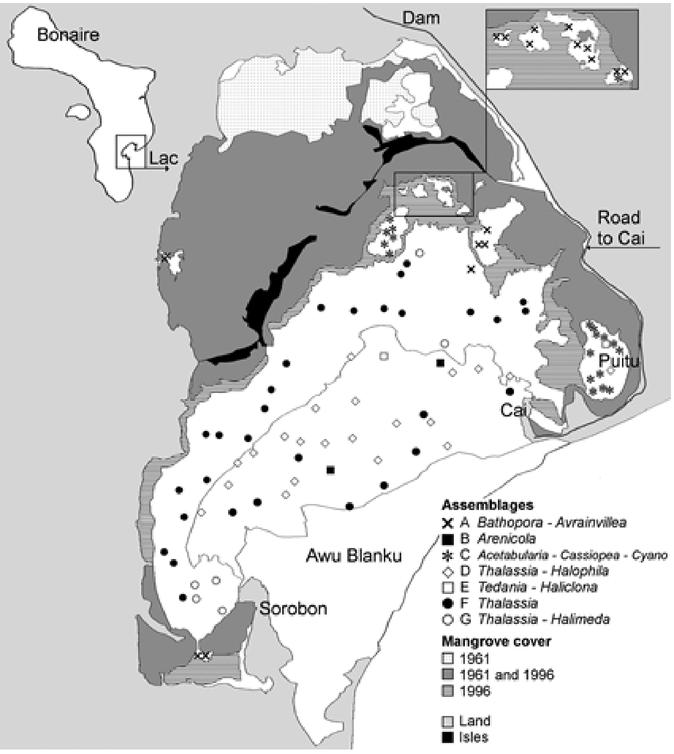

Fig. 1. The survey points for all distinguished assemblages in Lac and the extent of mangrove cover in 1961 and 1996 (modified after Erdmann and Scheffers, 2006).

The semidiurnal tidal amplitude in this part of the southern Caribbean averages about 30 cm (De Haan and Zaneveld, 1959), which, along with the shallow depth of large sections of the bay translate into reduced circulation. In Bonaire the average daily evaporation is 8.4 mm (De Freitas et al., 2005). This means that salt concentrations and water temperature can effectively build up in any shallow areas of the bay that have poor connection to open waters, whether it be due to accumulation of sediments in tidal channels or the narrowing of those channels due to mangrove growth. The consequence of these factors is a dynamic environmental gradient along which different benthic communities are found.

A.2.2 Sampling

Using satellite images from 2003, four principal habitat zones were distinguished: central bay, shallow, densely-vegetated bay border, “blue” mangrove pools and “dark” mangrove pools where the waters were discolored by mangrove tannins (Fig. 1). Sample plots were chosen using a random location generator. The minimum number of plots to be achieved per habitat was set at 15 plots each, but more sampling was achieved, with most extra sampling focused on the larger habitats (bay border and central bay habitats). The resulting number of plots per habitat was as follows: 18 in the dark mangrove pools, 20 in the blue mangrove pools, 30 in the bay border and 30 in the central bay. Each plot was visited for sampling once, between September and December 2011.

In this study sessile macro-flora and –fauna is characterized as having a second shortest dimension of 1 cm or larger, taking into account the two-dimensional growth form of many algal taxa. Smaller flora and fauna like seagrass epiphytes were not taken into account. Taxa moving only when seriously disturbed such as upside-down jellyfish, *Cassiopeia* sp., were considered sessile. Survey plots were reached by boat or kayak using a Garmin GPS 12 XL device. At each survey plot the percentage cover per species was estimated using a 1 m^2 PVC quadrant divided into 100 10 x10 cm squares. If taxa occupied less than 1 percent, their presence was noted as 0.01 % cover. The sampling surface for community description was set at $4m^2$ based on the finding by Kuenen and Debrot (1995) that a sample surface of 3 m^2 (corresponding to three contiguous 1 m x 1 m quadrats) was sufficient to reach a 0.70 value for the Bray-Curtis similarity index in a range of seagrass communities in the Spanish Water Bay in Curaçao.

The percentage cover estimations were done by one of the two researchers performing this study, using SCUBA or snorkeling gear.

Most species could be readily identified in the field based on general identification guides and species lists for the bay. Identification was done up to the highest possible taxonomic level. Specimens of unknown taxa were collected in small plastic tubes with seawater and determined the same day using identification guides (Littler et al., 1989; Littler and Littler, 2000). If taxon identification was not possible the specimens were photographed and code-named. This name was used the rest of the research period. In December 2011 all unknown taxa were collected and fixed using a 4% formalin-seawater dilution. After 24 hours the specimens were transferred to a 90% ethanol dilution for identification in The Netherlands and deposition in the collections of Naturalis, Leiden, The Netherlands.

A.2.3 Abiotic variables

Several environmental variables were taken at every survey plot. Temperature was measured with a dive computer (Suunto Zoop) to one degree precision. Field measurements were obtained by correcting temperature measurements of the dive computer with temperature measurements of calibrated thermometer. Horizontal Secchi disk distance was taken at the surface as an indication of turbidity. The Secchi disk was hung on the boat at 0.5 m deep facing the sun, while a swimmer estimated the visibility using a line with every 0.1 m a distance marking. At each survey plot, water samples were collected in plastic bottles and afterwards salinity was measured in a laboratory using a YSI 556MPS salinity measuring device. Depth (± 0.3 m due to tidal influence) was measured using a weighted line with every 0.1 m a depth marking. The irradiance level at the bottom and at the surface were measured to calculate the percentage of light reaching the bottom of the survey plot. Irradiance measurements were done using a HOBO® Pendant Temperature/Light Data Logger (UA-002-64) and Waterproof Shuttle (U-DTW-1). All light measurements were taken between 10 am and 3 pm. Bottom measurements were taken 5-15 cm above the bottom, while surface measurements were taken 0-10 cm beneath the surface. Light measurements were collected in duplicate every 10 seconds during 100 seconds, resulting in 20 measurements per site for both bottom and surface. The sediment was divided in three categories: organic matter, silt and sand. For each category criteria were set in advance. Assessing the sediment composition was done by eye while moving a hand slowly 10 cm above the bottom. Organic matter was defined as particles of different size with plant or algae like material that was very easily disturbed by a moving hand. Silt was defined as very small particles of the same size that were easily disturbed by a moving hand. Sand was defined as small particles of the same size that were not easily disturbed by a moving hand. At some locations calcified *Halimeda* sediment was found, this consisted of remnants from the calcareous *Halimeda* algae.

A.2.4 Data analysis and assemblage description

All data was stored in Microsoft Excel 2007, except for the light measurements which were stored in HOBOware®-software. A cluster analysis of the plots based on percentage cover per taxon was performed to identify different biotic assemblages. Data were 4th root transformed to reduce dominance by abundant species and similarity between samples calculated using the Bray Curtis similarity coefficient. Hierarchical clustering used group average linkage. Assemblages were discerned using a variable stopping rule based on the SIMPROF analysis (Clarke et al., 2008) which uses permutation to test how likely it is that a group of samples forms a cluster by chance. Groups were discerned using a p value of 0.05. Visualization of the resulting assemblages was both through clustering and non-metric Multi-Dimensional Scaling (MDS). Differences between areas were tested for significance by the ANOSIM procedure (Clarke and Ainsworth, 1993) and PERMANOVA (Anderson, 2001; McArdle and Anderson, 2001). Homogeneity of multivariate dispersions was tested by the PERMDISP procedure (Anderson, 2006). The number of permutations used for all permutational testing was 999, except when mentioned otherwise. All multivariate analyses were performed with the statistical package Primer 6 (Clarke and Gorley, 2006). Identified assemblages were further compared in terms of (1) associated physical parameters, (2) the number of species, S; and (3) Shannon's index of diversity H' (Sodhi and Ehrlich, 2010). Overall comparisons were done by means of ANOVA, using log-transformation to normalize the data in certain instances as needed. Multiple comparisons discussed as "significant" below are only those in which 95% confidence limits showed no overlap between assemblages (ie. $p << 0.01$). Potential relationships between environmental variables and the biological communities were studied using the BIO-ENV procedure (Clarke and Ainsworth, 1993), which finds the correlation (Spearman rank) between the biological similarity matrix and a matrix formed by any combination of environmental variables. Significance was also tested using permutation (n=99).

For each plot biotic coverage, *S* and *H'* were calculated per 4 m^2. Not all specimens could be identified up to species level, which means species richness in this study is the mean number of taxa per 4 m^2. Percentage cover per taxonomic group and total biotic cover were calculated for each plot. For each assemblage, taxa were defined as “common” when occurring in 50-66% of the plots and taxa were defined as “typical” when occurring in >67% of the plots. Typical taxa having a mean cover of >30% were further defined as “dominant” (Kuenen and Debrot, 1995).

A.3 Results

A.3.1 General results

The GIS location of the survey plots of each assemblage distinguished are shown in Fig. 1. Lac displayed a strong zonation in habitats principally distributed along an environmental gradient from muddy, landlocked pools (in the northern portion of the sampling area) to open-water bay conditions (in the southern portion of the sampling area) and this was reflected not only in the biotic composition of the benthic assemblages found, but also in the associated physical habitat parameters. Seven significant biotic clusters were distinguished by the SIMPROF procedure ($P<0.05$), which were labeled A-G (see also Fig. 1). The seven assemblages distinguished were named after dominant and differentiating species present in the assemblages. The five main assemblages encountered were assemblages A, C, D, F, and G. In contrast, assemblages B and E were both found at only 2 of the 96 plots. No statistical contrasts or comparisons were done with the latter two assemblages, due to the low number of replicates.

Basic abiotic variables used to describe the sequence of habitats (and associated seagrass and algal meadows) can be found in Table 1. Comparison between the distinguished communities in terms of depth, Secchi-disk transparency, temperature and salinity using ANOVA demonstrated significant differences ($p < 0.01$) for all four of these parameters. Multiple comparisons noted as significant below are only those in which 95% confidence limits showed no overlap between habitat associated assemblages (i.e., $p < 0.01$).

Table 1 Mean abiotic variables (number of plots sampled, depth, horizontal Secchi disk depth, bottom irradiance, temperature, salinity and substrate type) per assemblage (±SD). nd = no data.

		A	B	C	D	E	F	G	
		Batophora-Avrainvillea	*Arenicola*	*Acetabularia–Cassiopeia-cyano*	*Thalassia-Halophila*	*Tedania - Haliclona*	*Thalassia*	*Thalassia-Halimeda*	Backwaters
N		18	2	19	21	2	30	6	23
Depth (m)		1.4±0.4	3.4±0.14	2.5±0.8	3.7±0.7	2.2±0.6	2.0±1.3	1.7±0.5	0.4±0.2
Horizontal SDD (m)		4.3±1.5	7.8±4.6	4.3±1.1	9.2±2.3	5.5±1.3	6.3±3.1	5.9±1.9	<0.4
Bottom irradiance (% of surface irradiance)		14.9±7.6	35.8±21.4	14.2±6.6	21.2±9.2	nd	44.3±22.9	26.4±7.7	12.2±4.8
Temperature (°C)		29.6±0.5	29.0±0.0	30.0-0.0	28.9±0.4	29.5±0.7	29.3±0.8	29.3±0.5	32.3±1.1
Salinity (ppt)		40.6±4.7	36.9±0.4	37.9±0.7	36.9±0.5	36.9±0.4	36.9±0.7	36.8±0.6	52.1±1.7
Substrate type (%)	organic matter	94.4±23.6	0.0±0.0	5.3±22.9	0±0.0	0±0.0	0±0.0	0±0.0	nd
	silt	5.6±23.6	25.0±0.0	81.6±26.1	20.0±19.2	50.0±35.4	27.6±16.8	28.6±26.7	nd

The most landward habitat zone sampled is referred to as the "backwaters". These were landlocked behind former islands and a wide mangrove forests in the north and especially northwestern landside quadrant of the Lac Bay. These areas were the shallowest of all habitats sampled, and also had highest salinities, and temperatures and transparencies of less than 40 cm. Temperature, salinity, depth and Secchi-disk transparency of the "back-waters" differed significantly with all other areas which had seagrass and/or algal communities ($p < 0.01$). The bottom consisted of a soupy brown terriginous and biogenic mud layer typically 40-80 cm deep, with in it dead remnants of a former mangrove forest. Apart from small bunches of *Batophora* attached just below the waterline on dead red mangrove trunks and surviving black mangrove (air roots), these adverse conditions did not allow development of sessile macrobenthic life. While sparse growth of *Ruppia maritima* was found along the shallow margins of the backwaters, these areas were generally devoid of seagrass and algal meadow development and they were consequently not sampled for community description.

Moving towards open bay waters, the next principal habitat encountered was that of the "dark mangrove pools". The water of these generally stagnant pools was brownish in color. In mangrove forests this is typically caused by leached tannins which are very abundant in mangrove tissues and humus. Salinities were the next highest of all habitats (40 ppt) and the sediment composition was 94% organic material. Average depth (1.4 ± 0.4) was a meter more than the backwaters. Conditions allowed limited development of some sparse and impoverished sessile benthic growth identified below as assemblage C. Temperatures in this assemblage were significantly higher than recorded in assemblages D and F ($p < 0.01$), which were found in the much better-circulated bay margin and central bay areas.

Moving seawards, the next habitat category was that of the "blue pools". These were on average yet another meter deeper (2.5 m) than the "dark pools" and salinities were lower than in the dark mangrove pools. In contrast to the dark mangrove pools, in the blue mangrove pools the water was not heavily discolored by tannins. With clearer waters but a rough meter more of depth, bottom light penetration was similar to that of the dark mangrove pool habitat. In contrast to dark mangrove pool habitat, the bottoms had little organic humus and were largely dominated by fine silt. The sessile benthic assemblage principally found here (assemblage A) was much better-developed with a more than 3 times higher sessile species richness and almost twice higher average benthic cover compared to the dark mangrove pools. Salinity in assemblage A differed significantly with that of assemblages C, D, F and G ($p < 0.01$).

The next habitat we refer to as the bay border", a shallow zone within the main bay waters, clearly distinguishable on aerial photographs as a band lining the mangroves. Average depths was generally 2 m or less and bottoms were dominated by calcareous sand ("42-71%) and/or *Halimeda* segments (0-29%). Temperature and salinity were generally similar to central bay conditions, but net bottom irradiance was significantly higher due to the shallower depths. Two principal assemblages were described for this habitat. These were assemblages F and G. Of these, assemblage F had the highest average biotic cover of the five principal communities described, while assemblage G had the highest sessile benthic species richness of all. This mosaic pattern of two main assemblages meant that the bay border zone had both the highest biotic cover and the principal concentration of species.

The final habitat sampled along this environmental gradient was that of the central bay area. Average depths were 3.7 m and water transparency was highest of all habitats. Nevertheless due to the greater depths, net bottom irradiance was generally lower than for instance shallow *Thalassia* fields in the bay borders. Substrates were principally fully calcareous sand and silt. The main assemblage for the central bay area was assemblage D. In terms of physical parameters, this assemblage contrasted with assemblages A, C and F especially in terms of the significantly higher transparency ($p < 0.01$).

Cluster analysis and non-metric Multi-Dimensional Scaling (MDS) gave very similar results. We show here the MDS plot (Fig. 2) because it gives a better spatial interpretation of the data and provides additional insight into environmental drivers. MDS analysis also shows that the distinguished clusters corresponded closely to the different habitat zones, and that the cluster dendrogram split well at a fixed similarity level of 25%. Both group tests (ANOSIM and PERMANOVA) indicate significant differences between the four main habitat zones sampled (p values respectively < 0.001 and equal to 0.001). Multivariate dispersions further appeared homogeneous (PERMDISP $p = 0.112$).

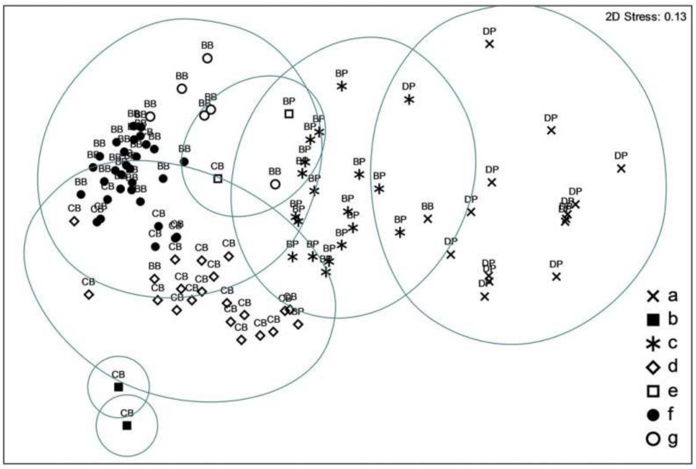

Fig. 2. Non-metric Multi-Dimensional Scaling graph showing a two dimensional representation of the samples based on Bray Curtis similarity. Symbols denote the 7 significantly different assemblages (labelled a to g, P< 0.05, using SIMPROF variable level cutting); ellipses enclose groups that exist when cutting at 75% dissimilarity (fixed level cutting), letters indicate the four different areas (BB, Bay Border; CB, Central Bay; BP, Blue Mangrove Pools; DP, Dark Mangrove Pools).

BIO_ENV gave the highest correlation (Rho= 0.532, p< 0.001) with the variables “latitude”, “salinity”, and “sand content”. The most stagnant mangrove pool habitats with highest salinity and silty or humus-rich substrate characteristics were all concentrated in the northern half of the sampling area, while the southern half of the sampling area only had stations with lower salinities and sandy bottoms.

A.3.2 Assemblage descriptions

Table 2 shows the specific taxa which were found in each assemblage. Mean biotic cover of each assemblage per taxon and in total is given in Table 3, while taxon richness per 4 m^2, is given in Table 4. Biotic cover, taxon richness and Shannon index of diversity of the assemblages are compared and contrasted in Fig. 3, 4 and 5, respectively. These tables and figures summarize the collected information and allow brief community descriptions.

Assemblage A, (*Batophora–Avrainvillea assemblage*), is described based on 18 plots: 17 plots in the dark mangrove pools and one plot in the bay border zone. The assemblage is found in shallow waters with a mean depth of 1.4 m and a bottom consisting mostly of organic matter (>94 %). The horizontal Secchi disc distance (SDD) was 4.3 m and mean temperature was 29.6 °C (Table 1). This *Batophora–Avrainvillea* assemblage is characterized by a saline environment (40.6 ppt) compared to open-water conditions (around 36 ppt; Froelich et al., 1978). Salinity in assemblage A was significantly higher (p < 0,01) than assemblages C, D, F and G, but also significantly lower than to backwater conditions. Plots in the *Batophora–Avrainvillea* assemblage had a low mean biotic cover of 2.9% (Fig. 3). The median total number of taxa per m^2 was 1.6, and was significantly lower than all other assemblages (Fig. 4), while the Shannon diversity index (0.27) was also significantly lower than most other assemblages, except assemblage D and F (Fig. 5). A typical taxon for this assemblage was the gree alga *Batophora oerstedii* Agardh. Other algal taxa were present on several plots but always in low quantities, except for the green alga *Avrainvillea nigricans* Decaisne which occurred in dense patches in a few plots.

Assemblage B (*Arenicola* assemblage) was a low-cover central bay alternate assemblage described on the basis of two plots, both situated in the central bay area (Fig. 1). The sediment was a mixture of sand (75%) and silt (25%). Mean depth of occurrence was 3.4 m, while mean salinity was 36.9 ppt. The mean temperature was 30 °C and the mean horizontal SDD was 7.8 m (Table 1). Biotic cover was low (<1%) and a mean number of 4 taxa per m^2 was found in this assemblage (Tables 3, 4). The Shannon diversity index was 1.12. The burrow worm *Arenicola cristata* Stimpson is a typical taxon for this assemblage. The sponge *Amphimedon compressa* Duchassaing & Michelotti, the green algae *Cladophora* cf. *liniformis* Kützing and the red algae *Acanthophora spicifera* (Vahl) Børgesen, *Amphiroa fragilissima* (Linnaeus) Lamouroux, *Ceramium* sp. and *Wrangelia argus* (Montagne) Montagne were also found in assemblage B.

Assemblage C, (*Acetabularia–Cassiopeia*–cyano assemblage), is described based on 18 plots in the blue mangrove pools and 1 plot in a dark mangrove pool. A mean depth of 2.5 m and a mean temperature 30 °C were measured. The horizontal SDD was 4.3 m. Mean salinity was high, 37.9 ppt, compared to open water conditions. Sediment type in this assemblage consisted mostly of silt (81.6%) with a smaller fraction of sand. The *Acetabularia–Cassiopeia*–cyano assemblage displayed a median biotic cover of 15%, median taxon richness of 6.6 and median Shannon index of diversity of 1.09. Among the assemblages described it compared low in terms of biotic cover (Fig. 3), but intermediate in terms of species richness (Fig. 4) and diversity (Fig. 5). A brown cyanobacterial growth, referred to as "Cyano brown" in this study, and the green algae *Acetabularia crenulata* Lamouroux are typical taxa for this assemblage. Less frequently observed, but still common taxa were the mangrove upside-down jellyfish *Cassiopeia xamanchana* Bigelow and the calcareous green algae *Halimeda incrassata* Lamouroux (Table 1).

*Table 2. Taxa present in Lac assemblages. * = present in at least one plot of the assemblage, C = common (present in more than 50% of the plots), T=typical (present in more than 66% of the plots) and D = dominant (typical taxon with a mean cover of 30% or more).*

		A	B	C	D	E	F	G
		Batophora-Avrainvillea	Arenicola	Acetabularia – Cassiopeia - cyano	Thalassia-Halophila	Tedania - Haliclona	Thalassia	Thalassia-Halimeda
Cyanobacteria	Cyano brown	*		T	T	C	*	*
Phaeophyceae	Dictyota cf. pulchella Lamouroux				*		*	*
	Dictyota sp. Lamouroux				*	C	*	C
Rhodophyceae	Acanthophora spicifera (Vahl) Børgesen		C	*	*	C	*	*
	Aglaothamnion cf. harveyi (Howe) Aponte, Ballantine & Norris				*		*	*
	Amphiroa fragilissima (Linnaeus) Lamouroux		C					
	Ceramium sp. Roth		C		*		*	
	Hypnea spinella (Agardh) Kütz			*	*	C	*	*
	Laurencia intricata Lamouroux				*			
	Wrangelia argus (Montagne) Montagne		C		*	C	*	
	Wrangelia bicuspidate Børgesen				*	C		
Chlorophyceae	Acetabularia crenulata Lamouroux			T	*			*
	Avrainvillea rawsonii (Dickie) Howe						*	
	Avrainvillea nigricans Decaisne	*		*	*	C	*	*
	Batophora oestedii Agardh	C		*				*
	Caulerpa cupressoides (West) Agardh					C	*	
	Caulerpa mexicana Sonder ex Kützing			*		C		
	Caulerpa racemosa (Forsskål) Agardh			*		C		
	Caulerpa sertularoides (Gmelin) Howe	*				C	*	*
	Chaetomorpha linium (Müller) Kützing			*	*			
	Cladophora cf. liniformis Kützing		C	*	*		*	
	Dictyosphaeria cavernosa (Forsskål) Børgesen						*	*
	Halimeda incrassata (Ellis) Lamouroux			C	*	C	C	T
	Halimeda opuntia (Linnaeus) Lamouroux			*			*	T
	Penicillus lamourouxii Decaisne			*	*		*	*
	Rhizoclonium cf. riparium (Roth) Harvey				*			
	Udotea flabellum Lamouroux				*		*	*
	Valonia ventricosa Agardh						*	C

		A	B	C	D	E	F	G
		Batophora-Avrainvillea	Arenicola	Acetabularia – Cassiopeia - cyano	Thalassia-Halophila	Tedania - Haliclona	Thalassia	Thalassia-Halimeda
Angiospermae	Halophila stipulacea (Forsskål) Ascherson			*	C			
	Ruppia maritima Linnaeus	*		*				
	Syringodium filliforme Kützing			*	*		*	
	Thalassia testudinum Banks ex König			*	T	C	D	T
Porifera	Amphimedon compressa Duchassaing & Michelotti		C					
	Chalinula molitba de Laubenfels			*			*	
	Chondrilla nucula Schmidt						*	
	Dysidea etheria de Laubenfels					C	*	*
	Haliclona tubifera George & Wilson						*	
	Haliclona twincayensis de Weerdt, Rützler & Smith			*	*	C	*	C
	Hyrtios proteus Duchassaing & Michelotti						*	
	Strongylamma baki van Soest				*			
	Tedania ignis Duchassaing & Michelotti			*	*	C	*	*
	Verongula rigida Esper						*	*
Cnidaria	Cassiopeia frondosa Pallas	*		*	*	C	*	
	Cassiopeia xamachana Bigelow	*		T	*			
	Condylactis gigantea Weinland				*		*	C
	Porites porites Pallas						*	
Mollusca	Strombus gigas Linnaeus				*	C	*	
	Pinna carnea Gmelin				*			
Annelida	Arenicola cristata Stimpson		C	*	T		C	*
	Eupolymnia sp.						*	
	Fanworm (Sabellidae)			*	*		*	T
Echinodermata	Holothuria mexicana Ludwig Diels						*	

Table 3. Mean biotic cover per m^2 (%), by taxon and in total, in each assemblage A-G, followed by 95% CL. Mean percentage cover and 95% confidence limits based on 4th root transformed values. For assemblages B and E, sample size was too low (N = 2) to permit meaningful confidence intervals.

	A	B	C	D	E	F	G
	Bathophora-Avrainvillea	*Arenicola*	*Acetabularia -Cassiopeia-cyano*	*Thalassia-Halophila*	*Tedania-Haliclona*	*Thalassia*	*Thalassia-Halimeda*
N	18	2	19	21	2	30	6
Actiniaria	0 (0,0)	0	0 (0,0)	0 (0,0)	0	0 (0,0)	0.01 (0,0.2)
Angiospermae	0 (0,0)	0	0.05 (0,0.4)	10.25 (2.3,30.5)	0.83	47.55 (40,56.2)	0.61 (0,7.8)
Bivalvia	0 (0,0)	0	0 (0,0)	0 (0,0)	0	0 (0,0)	0 (0,0)
Cassiopeidae	0.01 (0,0.1)	0	2.94 (1.9,4.4)	0 (0,0)	0.2	0 (0,0)	0 (0,0)
Chlorophyceae	2.19 (0.4,7.6)	0	4.15 (1.7,8.8)	0.05 (0,0.3)	21.57	1.59 (0.5,4.1)	32.85 (21.8,47.7)
Cyanobacteria	0 (0,0)	0	0.79 (0.1,2.6)	4.73 (1.5,11.5)	3.25	0.01 (0,0.1)	0.01 (0,0.7)
Gastropoda	0 (0,0)	0	0 (0,0)	0 (0,0)	0.03	0 (0,0)	0 (0,0)
Holothuroidea	0 (0,0)	0	0 (0,0)	0 (0,0)	0	0 (0,0)	0 (0,0)
Phaeophyceae	0 (0,0)	0	0 (0,0)	0 (0,0.1)	0.97	0 (0,0)	0.41 (0,4.8)
Polychaeta	0 (0,0)	0.01	0 (0,0)	0.01 (0,0)	0	0 (0,0)	0.01 (0,0.1)
Porifera	0 (0,0)	0	0 (0,0)	0.01 (0,0.1)	0.37	0.02 (0,0.1)	0.94 (0.5,1.7)
Rhodophyceae	0 (0,0)	0.15	0 (0,0.1)	0.13 (0,0.7)	6.83	0 (0,0)	0.03 (0,1.2)
Scleractinia	0 (0,0)	0	0 (0,0)	0 (0,0)	0	0 (0,0)	0 (0,0)
Total cover	2.84 (0.59,8.72)	0.21	14.96 (9.78,21.96)	46.05 (34.2,60.74)	49.6	58.68 (49.78,68.71)	42.14 (28.53,60.13)

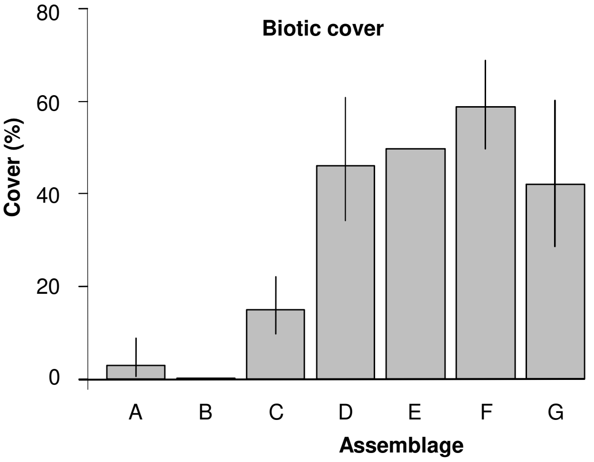

Fig. 3. Mean biotic cover (%) and 95% confidence limits based on 4th root transformed values for each assemblage.

Table 4. Mean richness (S), by taxon and in total, per 4 m^2, in each assemblage A-G, followed by 95% CL. Mean percentage cover and 95% confidence limits based on 4th root transformed values. For assemblages B and E, sample size was too low (N = 2) to permit meaningful confidence intervals.

	A	B	C	D	E	F	G
	Bathophora-Avrainvillea	*Arenicola*	*Acetabularia-Cassiopeia-cyano*	*Thalassia-Halophila*	*Tedania-Haliclona*	*Thalassia*	*Thalassia-Halimeda*
N	18	2	19	21	2	30	6
Actiniaria	0 (0,0)	0	0 (0,0)	0 (0,0)	0	0 (0,0)	0.06 (0,1.2)
Angiospermae	0 (0,0)	0	0.02 (0,0.2)	0.75 (0.3,1.7)	0.06	1.03 (1,1.1)	0.48 (0,2.4)
Bivalvia	0 (0,0)	0	0 (0,0)	0 (0,0)	0	0 (0,0)	0 (0,0)
Cassiopeidae	0.01 (0,0.1)	0	1.12 (1,1.3)	0 (0,0)	0.06	0 (0,0)	0 (0,0)
Chlorophyceae	1.06 (0.6,1.8)	0.06	2.7 (1.6,4.4)	0.11 (0,0.5)	4	0.67 (0.3,1.5)	4.1 (3.3,5.1)
Cyanobacteria	0 (0,0)	0	0.39 (0.1,1)	0.54 (0.2,1.1)	1	0 (0,0)	0.01 (0,0.5)
Gastropoda	0 (0,0)	0	0 (0,0)	0 (0,0)	0.06	0 (0,0)	0 (0,0)
Holothuroidea	0 (0,0)	0	0 (0,0)	0 (0,0)	0	0 (0,0)	0 (0,0)
Phaeophyceae	0 (0,0)	0	0 (0,0)	0 (0,0)	0.06	0 (0,0)	0.24 (0,2.4)
Polychaeta	0 (0,0)	1	0.06 (0,0.3)	0.7 (0.4,1.2)	0	0.08 (0,0.3)	0.56 (0,2.8)
Porifera	0 (0,0)	0.06	0.05 (0,0.3)	0.02 (0,0.2)	2.46	0.09 (0,0.4)	2 (1.2,3.3)
Rhodophyceae	0 (0,0)	1.8	0.01 (0,0.1)	0.11 (0,0.5)	2.46	0 (0,0)	0.02 (0,0.8)
Scleractinia	0 (0,0)	0	0 (0,0)	0 (0,0)	0	0 (0,0)	0 (0,0)
Total	1.59 (1.2,2.08)	3.9	6.56 (5.1,8.32)	5.71 (4.93,6.57)	11.87	4.65 (3.87,5.55)	10.21 (8.3,12.34)

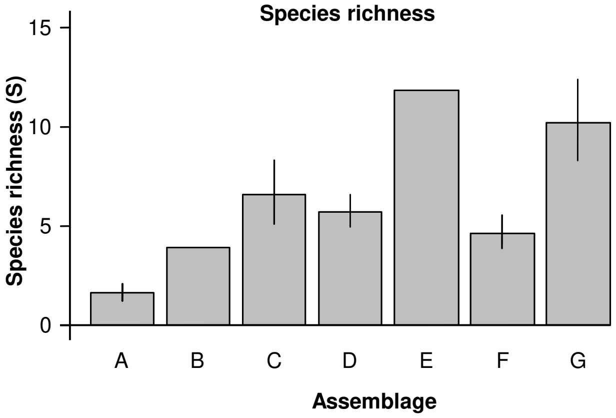

Fig. 4. Mean taxon richness (S) per 4 m^2 and 95% confidence limits based on 4th root transformed values for each assemblage.

Assemblage D, (*Thalassia-Halophila* assemblage), is described based on 19 plots located in the central bay, one plot located in the blue pool Puitu, and one plot located in the bay border. This assemblage was relatively deep (3.7 m) and and in clear waters (horizontal SDD = 9.2 m). The mean temperature was 28.9 °C and mean salinity was 36.9 ppt. The bottom consisted of sand (76%) and silt (24%). Mean total biotic cover was 46% (Table 3) and taxon richness was 5.7 (Table 4). The Shannon diversity index was 0.61. Hence, this assemblage was high in terms of coverage (Fig. 3), but intermediate in terms of both species richness and diversity (Figs. 4, 5).Typical taxa found in this assemblage were the burrow worm *A. cristata*, turtle grass *Thalassia testudinum* Banks ex König and “Cyano brown”. A common taxon was the non-native sea grass *Halophila stipulacea*.

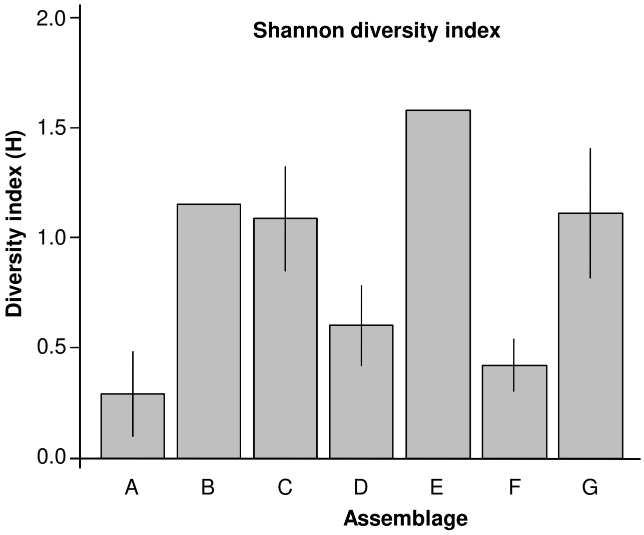

Fig. 5. Mean values of Shannon index of diversity (H’) per 4 m^2 and 95% confidence limits based on 4th root transformed values for each assemblage.

Assemblage E (*Tedania-Haliclona* assemblage) is an aberrantly high-cover sponge and species rich assemblage sporadically encountered in small patches in the generally poor blue pool and central bay habitats, and was represented by two plots; one in the central bay and one in the blue pool Puitu. Mean depth was 2.2 m and horizontal SDD was 5.5 m (Table 1). Mean temperature was 29.5 °C and mean salinity was 36.9 ppt. Assemblage E had an all-around high median biotic cover of 50% (high), a high taxon richness of 11.9, and a high diversity index of 1.58 (Figs. 3, 4, 5). Taxa for this assemblage were the fire sponge *Tedania ignis* Duchassaing & Michelotti and the sponge *Haliclona twincayensis* de Weerdt, Rützler & Smith, the green algae *Caulerpa sertularoides* (Gmelin) Howe and *H. incrassata* and the red algae *A. spicifera* (Table 2).

Assemblage F, (*Thalassia* assemblage), was described on the basis of 22 plots situated in the bay border and 8 in the central bay. Mean depth was 2 m and horizontal SDD was 6.3 m. Mean temperature was 29.3 °C and mean salinity was 36.9 ppt. The sediment type of the *Thalassia* assemblage consisted of sand (71%) and silt (29%). Plots in assemblage F displayed the highest median biotic cover of all (59%), but were notably low in terms of both median taxon richness (4.7) and diversity (0.44) (Figs. 4, 5). *T testudinum* dominated the benthic community and represented almost 35% of the total cover. Common taxa amongst the *Thalassia* were the burrow worm *A. cristata* and the calcareous green algae *H. incrassata*.

Assemblage G, (*Halimeda-Thalassia* assemblage), was found at 6 plots located in the bay border. It was a shallow (1.7 m) environment with a bottom consisting of a mixture of silt and sand, partly made up of remains of calcareous *Halimeda* algae. Horizontal SDD was 5.9, mean temperature was 29.3 °C and salinity was 36.8 ppt. Median total biotic cover was high (42%), median taxon richness was high (10.2), and diversity was also high 1.10. The (spatially) most closely associated assemblage (F) was similarly high in cover but notably lower in terms of both species richness and diversity (Fig. 4, 5). Typical taxa for this assemblage were *T. testudinum, H. incrassata*, *H. opuntia* Lamouroux and fan worms (*Polychaeta*). Common taxa were sea anemone *Condylactis gigantea* Weinland, the sponge *H. twincayensis*, the brown alga *Dictyota* sp. and the green alga *Valonia ventricosa* Agardh (Table 2).

Table 5. Plots per assemblage where H. stipulacea was found, mean H. stipulacea cover when present and highest H. stipulacea cover observed.

	C	D
	Blue pools	Central bay
Total plots	19	21
Plots with *H. stipulacea*	5	13
Mean *H. stipulacea* cover when present (%)	5.3	39.7
Highest *H. stipulacea* cover (%)	15.8	81.5

A.3.3 Invasive *Halophila* distribution

In Table 5, the assemblages where *Halophila stipulacea* was found are listed with mean and maximum *Halophila* cover values. *Halophila* was only found in two geographically disjunct sea grass communities, namely assemblage D, found in the relatively deep, clear central bay area, and assemblage C, found principally in the least stagnant lagoonal habitat (blue pools). It was not recorded in the shallower and more densely-vegetated *Thalassia* and *Halimeda-Thalassia* assemblages typical of the bay border, which lay between the zones with communities D and C. This may reflect a habitat preference (for cooler, deeper bay habitats of Lac), but may also reflect that the species is invading first into habitats with naturally lower biotic cover (and hence possibly lower competition for space). In the central bay assemblage D, it was found at 62% of plots. When present it typically had a high coverage level (avg. 39.7%, max. 82%). In the blue mangrove pools assemblage C, the species was found in a lower percentage of plots (26%) of plots, and when present also had a lower mean coverage (5.3%, max 16%) (Table 5).

A.4 Discussion

A.4.1 Drivers of assemblage structure

This study examined benthic macrophyte assemblages in four habitat zones of the non-estuarine Lac Bay: dark mangrove pools, blue mangrove pools, the bay border, and the central bay. Cluster analysis revealed that based on taxon composition, there were 5 principal assemblages. These assemblages occurred in almost perfect zonation, along the environmental gradient stretching from stagnant land-side backwaters to clear, deep, well-circulated open-bay waters, along a north to south gradient in the bay. Aside from salinity and substrate composition, depth, temperature and transparency also differed systematically along the north to south habitat gradient. Therefore, MDS results ordering assemblages along habitat dimensions with a strong geographic component was not surprising. BIO-ENV results further showed salinity and substrate characteristics were more strongly correlated to community structure than the parameters of temperature, transparency and depth.

Salinity is widely known to be a critical stressor to stenohaline marine benthic flora and fauna. Substrate characteristics form a critical determinant for both species requiring attachment to the substrate and for the presence or absence of filter feeders, and is considered the major controlling factor for distribution of benthic species (Levinton, 1982). Our results suggest that these factors also appear to be the principal factors structuring the biotic assemblages across the observed zones in Lac.

A.4.2 Comparison between Lac assemblage

One important “community” resulting from the processes that are occurring in the bay was not sampled for species composition as it was not considered to be either a sea grass or algal community. These are the turbid, saline backwater areas. The bottom of these areas was dominated by a thick, up to 80 cm layer of soupy silt upon which sporadic tufts of *Batophora* and/or *Ruppia maritima* Linnaeus were found.

Moving seawards from the turbid backwater areas, the first habitats encountered were the dark and blue mangrove pools. The dark and blue pool assemblages had a significant lower biotic cover than the central bay and *Thalassia* assemblages. The dark pool *Batophora–Avrainvillea assemblage*, had a lower total average cover than that of the blue pools (*Acetabularia–Cassiopeia–cyano assemblage*), but the difference was not major. However the difference between the dark and blue mangrove pools was significant in terms of both species richness and diversity (Figs. 4, 5). The mangrove pool habitat is formed as a result of expanding *Rhizophora mangle* Linnaeus trees. The dark mangrove pools are located further into the mangroves than blue mangrove pools and have a less direct connection to the bay.

Research elsewhere has shown that in mangrove systems, the reddish-brown discoloration of the water column is typically caused by decomposition of tannin-rich mangrove litter inside the mangrove forest. Phenolic tannic acids are toxic secondary plant metabolites that are important in the defense of plant tissues against herbivory. When they are released through decomposition into water they have important ecological effects and can inhibit bacterial decomposition (Kraus et al., 2003), phytoplankton productivity (Herrera-Silveira and Ramirez-Ramirez, 1996), meiofaunal development (Coull, 1999), even affect nutrient cycling (Maie, et al, 2008). Therefore, aside from salinity and sediment characteristics tannins may also contribute to the poor development of macrobenthic communities in these pools. A role for other factors such as higher temperatures, lower oxygen concentrations and reduced circulation which would limit the influx of larval stages and propagules, should not be excluded.

The highest biotic cover was found in the *Thalassia* assemblage, principally found in bay border plots but species richness and diversity were significantly lower than the physically most closely-associated *Halimeda-Thalassia* assemblage. On the other hand, the central bay *Thalassia-Halophila* (D) and (principally) bay border *Thalassia* (F) assemblages showed great resemblance to one-another in terms of community descriptors (cover, species richness and diversity), but did differ importantly in species composition. *Thalassia*, which was documented by Van Moorsel and Meijer (1993) as formerly being an important component of the benthic vegetation of the mangrove lagoons of Lac, now is no longer found in the lagoons but only in the bay borders and central bay area. In general ecological studies, all three of these communities would have easily been classified as “*Thalassia* seagrass beds”, but clearly differ in several important ways. In Lac, it appears that the shallowest *Thalassia* beds are being encroached by *Halimeda* while the deeper lying *Thalassia* fields are being encroached upon by the invasive seagrass *Halophila stipulacea*.

The assemblages B (*Arenicola* assemblage) and E (*Tedania-Haliclona* assemblage) were found at only two locations each but still deserve special notice. The barren central bay *Arenicola* assemblage basically amounted to barren patches dispersed principally among patches of assemblage D (*Thalassia-Halophila* assemblage). While only two such patches were sampled here, such barren areas may be representative for large parts of the Central bay area. Evidence of bioturbation were prominent at both plots sampled.

Assemblage E (*Tedania-Haliclona* assemblage) was notable for its higher diversity. Basically this assemblage occurred as small loose patches of structure in an otherwise flat and or barren seascape (“sponge patch reefs”) in relatively deep water where water movement was likely minimal and where coral patch reefs did not occur. The available structure created by such clumps also meant a concentration of fish species at such spots. While such spots were few and scattered, the structure and shelter possibility they provide may be significant to certain fish species.

A.4.3 Comparison with the sea grass communities of Spanish Water Bay Curaçao

In general, very few quantitative community descriptions are available for tropical sea grass and algal assemblages. The closest comparable study to ours is a similar study done for the Spanish Water, for the adjacent island of Curaçao (Kuenen and Debrot, 1995). The Spanish Water is an inland bay about half the size of Lac and possesses much more hard substrate and much stronger environmental contrasts in water transparency. In that study, the highest biodiversity was associated with communities on hard substrates. The Curaçao study documented a much higher total number of taxa (121) than we presently documented from Lac (52). We ascribe this principally to the lack of hard substrates in the Lac communities we sampled. Van Moorsel and Meijer (1993) have already pointed out the apparent low algal species richness of the marine meadows of Lac, and also ascribed this to the virtual absence of hard substrate throughout most of the bay. The barrier reef area of Lac (Awa Blanku) was not sampled by us but according to Van Moorsel and Meijer (1993) has greater algal diversity because of the presence of hard substrate. Other possible contributing factors may have been the lower total surface area sampled in the Lac study (392 versus 906 m^2) and the exclusion of fauna and flora that were between 0.5 and 1 cm in size (second shortest dimension of 1 cm or smaller versus 0.5 cm or smaller in the Spanish Water study).

Notwithstanding some differences that may be due to methods, some comparisons are useful. For instance, assemblage B and C in the Spanish Water were comparable with the *Halimeda-Thalassia* assemblage in Lac, a shallow bay border assemblage. All three assemblages were principally *Thalassia* beds mixed with *H. opuntia* and had a relatively high biotic cover (>44%). A notable difference was the presence of *H. incrassata* in relative high quantities in the *Halimeda-Thalassia* assemblage of Lac compared to the two similar Spanish Water assemblages. This may be due to the preference of this (psammophytic) species for growing in sediment as opposed to hard substrates (Van Tussenbroek and Van Dijk, 2007) which were not present in Lac but were present in the Spanish Water. Mean depth of the Lac *Halimeda-Thalassia* assemblage was comparable to assemblage C in the Spanish Water, but the substrate composition displays more similarities with assemblage B in the Spanish Water.

Assemblage D in the Spanish Water (Kuenen and Debrot, 1995) displayed some resemblance to the *Acetabularia–Cassiopeia*–cyano assemblage of the blue mangrove pool habitat in Lac. These assemblages were characterized by relatively high presence of *H. incrassata* and relatively low densities (or total lack) of *T. testudinum*. Biotic cover was of an average level (15-20%). Besides the taxa mentioned above, the benthic community consisted of a mix of mainly green algae and sponges. In the Spanish Water this community with depressed cover and diversity was found in deeper areas with less light (33.8% light levels).

Assemblage L in the Spanish Water was a typical sea grass meadow dominated by *T. testudinum*. The *Thalassia* assemblage of Lac was similar. This assemblage was situated in the Lac Bay border and central part of the bay. Both in Curaçao and Bonaire the *Thalassia* assemblages were characterized by an average depth of 1.5-2 m. This distinguishes them from the deep (3.7 m) central bay assemblage in Lac which was also characterized by the significant presence of *T. testudinum*. In the much more turbid Spanish Water, light penetration to such depths was simply too low to support any *Thalassia*. Biotic cover in *Thalassia*-fields was equally high and diversity values equally low in both Lac and the Spanish Water. However, biotic cover in the Lac *Thalassia* assemblage (62%) was significantly higher than in assemblage L in the Spanish Water (30%).

A.4.4 Comparison with past results for Lac

Wagenaar-Hummelinck and Roos (1970) provided the first description of the benthic communities of Lac in 1967. The sea grass taxa described in their study were also found in the present study, except *Halodule beaudettei* den Hartog (syn. *H. wrightii*) which they described from one location. More recent studies have not found *H. beaudettei* as widespread or abundant either (Van Moorsel and Meijer, 1993; Lott, 2000) but the species was observed by us in small amounts in shallow habitats of Sorobon (e.g. also Engel, 2008). According to Den Hartog (1967) the species is primarily a pioneer species). We also mention here the occurrence of *Syringodium filiforme* Kützing in Lac Bay. Studies by Engel (2007) have found *Syringodium* to be present in different areas of Lac but to be patchily distributed. In our study this seagrass was encountered in five plots. In the bay border and blue magrove lagoon habitats it was encountered once each at low densities, while in the central bay area it was encountered in three plots with total coverages of between 25 and 50%. A striking difference between findings by Wagenaar-Hummelinck and Roos (1970) and the present study concerns the starfish *Oreaster reticulatus* (Linnaeus) *O. reticulatus* occurred regularly in Lac's sea grass beds in 1967 (Wagenaar-Hummelinck and Roos, 1970), but was not seen during this research. Other studies on the benthic macrofauna in Lac reveal that *O. reticulates* was still present in 1993 and 1999 but almost disappeared in 2007, when only 2 individuals were found during extensive surveys in the bay (Van Moorsel and Meijer, 1993; Engel, 2008). Wagenaar-Hummelinck and Roos (1970) mentioned only four algal taxa, namely, *Halimeda opuntia, Avrainvillea nigricans, Acetabularia crenulata* and *Batophora oerstedii,* all of which we here can confirm to still be key species in various of the benthic assemblages described.

Van Moorsel and Meijer (1993) listed many additional algal taxa in their inventory which were not found in the present study. Most of these taxa were documented from their station "Secu di Sorobon" (Van Moorsel and Meijer, 1993), which is part of the backreef Awa Blanku area (Fig. 1). As our study focused on the benthic assemblages distributed along the environmental gradient associated with the mangrove expansion, we did no sampling in the Awa Blanku area.

Van den Hoek et al. (1972) and Van Moorsel and Meijer (1993) did some sampling in the mangrove pools of Lac. Both studies revealed the limited number of taxa in more isolated pools, compared to pools with a more open connection to the bay. This is corroborated by our results: blue pools were found to have a higher taxon richness than dark pools. *Avrainvillea nigricans* and *Batophora oerstedii* were found to be the most common taxa of the isolated (dark) mangrove pools both in the studies by Van den Hoek et al. (1972) and Van Moorsel and Meijer (1993) as well as in our study.

The main difference between the observations of Van den Hoek et al. (1972), Van Moorsel and Meijer (1993) and this study were the notably high densities of *T. testudinum* in some mangrove pools in 1972 and 1992, while at present, the identical mangrove pools have grown shut by mangroves and have a very low to no *T. testudinum* cover left. During the course of time the quality of the mangrove pool habitats has clearly declined.

A.4.5 The possible effects of *Halophila stipulacea*

In the Central bay *Thalassia-Halophila* assemblage the invasive sea grass *Halophila stipulacea* was found at 13 of the 21 plots. The mean cover in the plots where *Halophila* was found was 40%, but sometimes cover was as high as 80%. *H. stipulacea* was also found in five plots in the blue mangrove pool Puitu. The mean cover in these plots, which belong to the *Acetabularia-Cassiopeia*-cyano assemblage, was 5%. The species was not found in either the *Thalassia* or the *Halimeda-Thalassia* assemblages which showed the highest biotic cover and which in spatial context lay between the central bay and the blue pool habitats.

H. stipulacea was not reported in the sea grass characterization studies which had been done in Lac in 2000 and 2007 (Lott, 2000; Engel, 2008). This means that all *H. stipulacea* growth took place within the last four years. *H. stipulacea* originates from the Red Sea and East Africa and has been invasive in the Mediterranean Sea since the opening of the Suez Canal (Green and Short, 2003). The first report of *H. stipulacea* in the Caribbean was in Grenada in 2002 (Ruiz and Ballantine, 2004). In 2007 it was additionally found in Dominica and in St. Lucia (Willette and Ambrose, 2009), and has since been documented in Simpson Bay, St. Maarten (Debrot et al. 2011). In the Gazi Bay, Kenya, Coppejans et al. (1992) indicated that *H. stipulacea* behaved as a pioneer species. Bare sand and disrupted areas were quickly colonized by this fast growing sea grass, where after other sea grass and algal species can colonize the area. *T. testudinum* is the climax species of this ecosystem and stabilizes the bottom (Coppejans et al., 1992). According to our observations, *H. stipulacea* likewise seems to colonize principally low coverage assemblages. However, it remains to be seen if the same succession process will occur as in East Africa. It is also possible that *H. stipulacea* interferes with local sea grass succession or persistently invades existing sea grass beds (Willette and Ambrose, 2009), which in Lac mainly consist of *Thalassia* In Flamingo bay, Grenada, no other sea grass species were left after the invasion of *H. stipulacea*, while neighboring bays which had not been affected by *Halophila* were home to *Syringodium* and *Thalassia* (Ruiz and Ballantine, 2004). The authors suggest that it is possible that the other sea grass species were outcompeted by *H. stipulacea*. If *H. stipulacea* replaces other sea grass species it might result in an ultimate loss of *T. testudinum* cover, and a permanent change in species composition. Expansion of *H. stipulacea* might therefore have severe effects on the Lac biotopes. It will be interesting to see to what extent *Halophila* fulfills important ecosystem functions in terms of fish nursery functions, and habitat functions for the green turtle, *Chelonia mydas*, and the queen conch, *Strombus gigas*. Preliminary observations by sea turtle researchers in Lac suggest that *Halophila* is not being consumed by the green turtle (M. Nava, pers. comm.).

A.4.6 The process of land reclamation by mangroves in Lac

The large differences documented between communities across the mangrove forest are clearly caused and driven by the active process of land reclamation by the mangrove forest. The main results of this process are aptly captured by means of aerial photographs which accurately document the location and extent of mangrove coverage in the bay since 1961. The results show that the back of the bay is filling in relatively rapidly as the mangroves migrate seaward towards the coral barrier ridge that encloses the bay. In the process, the net coverage of clear, well-circulated open bay waters has declined by 81 ha while the surface of shallow muddy stagnant, hypersaline back-waters unable to support either mangroves and sea grass or nursery fish species has grown by 82 ha.

In most estuarine situations, such as in river deltas or along open coasts, expansion due to such succession processes in mangrove communities is not an ecological problem, as they have space to freely expand. However, Lac is an enclosed bay and, because of the very narrow and steep shelf area surrounding the volcanic island, it is also the only and limited area of the island with major sea grass and mangrove development can occur. If the process runs due course, the sea grass beds will likely first disappear, followed by the mangroves, ultimately converting the bay into a hypersaline salina. This process of land reclamation by the mangroves, may be caused or contributed to by a combination of sediment-dynamic processes such as input of terrigenous sediments due to run-off, organic leaf litter production by the mangroves themselves, accumulation of sand inside the bay which originates from the coral reef outside the bay, and endogenous sediment production, for instance by calcareous algae within the bay.

From old maps (Wagenaar-Hummelink and Roos 1969) it is further clear that hypersaline waters were formerly only a minor part of the Lac system. Today such saline areas have grown in importance and it is therefore not surprising that the abundance of the West Indian flamingo, *Phoenicopterus ruber* Linnaeus, in Lac has grown from average daily counts of 10-35 birds, prior to the early 1990s to numbers typically well in excess of a 100 birds today (Van Moorsel and Meijer 1993). Due to their shallowness and poor circulation, these backwater areas are much more prone to produce hot, hypersaline conditions that cause stress to the nearby *Thalassia* and algal meadows. While seagrasses have the ability to osmoregulate, worldwide, salinity is a key factor affecting seagrass community structure and productivity (Short and Neckles, 1999; Trevathan et al., 2011; Sandoval-Gil et al., 2012). Hence, salinity and thermal stress caused by this new and growing habitat in Lac may also be partially responsible for the lower diversity and declining trends in certain taxa inside the bay, where our results indicate that salinity is a main driver of community structure inside Lac.

The process of land reclamation by the mangroves is likely greatly accelerated by the anthropogenic pressures in and around the bay and its catchment area. In a nearby example for Curaçao, studying sedimentary cores, Klosowska (2003) has shown that traditional agricultural land-use practices such as the felling of trees, clearing of fields and extensive livestock grazing were the cause of a highly elevated rate of filling in of the shallow lagoon of St. Michiel in Curaçao over the last centuries. The same processes are evident for Lac where a comparison of vegetation maps (De Freitas et al., 2005 versus Beers et al., 1997) shows that barren ground cover caused by excessive grazing by feral animals and poor land-use practices remains a much more persistent problem in Bonaire today than in Curaçao.

While more study is recommended on the various processes that contribute to the filling-in of Lac, this is certainly also contributed to by endogenous sediment production in the bay, not only by the mangroves, but also by the benthic seagrass and algal communities as described in this study. In this respect the calcareous green algae, notably *Halimeda* spp. can be directly implicated. Dense *Halimeda* algal fields are found in much of the bay, and much of the calcareous sand present in the lagoon is evidently made up of degraded *Halimeda* segments (Wagenaar-Hummelink and Roos, 1969; Lott, 2000).

A.4.7 The role of Halimeda

Halimeda algal communities have been more extensively described by Kuenen and Debrot (1995) for Curaçao and are principally comprised of *H. incrassata* and *H. opuntia*. In Curaçao these sand-producing green algae have led to filling-in of isolated sections of the eutrophic Spanish Water. For the early 1990s, Van Moorsel and Meijer (1993) discuss *Halimeda* banks in Lac as occurring in up to 3 m depths between the principal *Thalassia* fields of the central bay and the mangrove fringe. Many of these banks even displayed a groove and spur structure, reminiscent of coral reefs. The banks play a critical role in the seaward expansion of the mangroves and eventually develop into a mangrove barrier as mangrove propagules easily find footing in these shallow areas (Van Moorsel and Meijer 1993).

Worldwide *Halimeda* species figure among the principal producers of carbonate sediment and sand in tropical reefal environments (Freile et al., 1995; Rees et al., 2007; Van Tussenbroek and Van Dijk, 2007). Annual $CaCO_3$ production for *Halimeda* species can vary between 50 and 2323 g m^{-1} y^{-1}, but this was largely based on short-term studies. Van Tussenbroek and Van Dijk (2007) measured growth and turnover in *Halimeda incrassata* and documented average calcification rates at 815 g m^{-1} $y^{-1}$and an average turnover time of 30 days. Harney and Fletcher (2003) calculated average carbonate sediment production for a 12 km^2 tropical back reef at 0.53 kg m^{-1} y^{-1}. Freile et al. (1995) discuss *Halimeda* species as forming draperies and vines along reef slopes in the Bahamas.

Chazottes et al. (2008) point out that eutrophication leads to an increase in *Halimeda* and a change in sediment characteristics. As such *Halimeda* abundance may be an important indicator of eutrophication, which has recently been documented as a problem in Lac (Slijkerman et al., 2011). Due to calcification, *Halimeda* is also less palatable to herbivorous grazers and is even an important carrier of coral disease (Nugues et al., 2004).

In Lac Bay today, whereas *H. incrassata* forms meadows, *H. opuntia* typically forms mounds, overgrowing enveloping and excluding most other species including *Thalassia*. Encroachment by mangroves, combined with the growth of thick mounds of *Halimeda opuntia* in the various mangrove channels which formerly kept the northwest section of Lac vital, today means that many of these channels hardly function in terms of water exchange. In the past fishermen kept the channels open (Lott, 2001) and removed mangrove biomass for charcoal production, but this traditional use of the mangrove forest has stopped.

A.5 Conclusion

The valuable sea grass and mangrove habitats of Lac are essentially trapped in an enclosed bay. As shallow, warm and saline back-water habitat continues to increase in importance in the bay due to the process of land reclamation by mangroves, these current nursery habitats will come under additional salinity stress and likely continue to decrease in coverage and quality at an accelerated rate. If no measures are taken, the benthic communities can be expected to deteriorate along the sequence of communities we here described from the range of environmental conditions already present in the bay. To relieve the bay ecosystem of thermal and salinity stress caused by the shallow backwaters measures would need to be taken to help restore water depth, and circulation. Excavation of accumulated erosional and biogenic sediments as well as dredging to restore former feeder channels by removal of mangrove overgrowth (as already started by Stinapa) are among the measures that need to be taken. For Lac, the need to restore hydrology to stem mangrove forest mortality and further erosion of habitat quality was first pointed out by a team of experts in 1970 (Debrot et al. 2010a) and active measures are called for, following the simple restoration principles outlined by Lewis and Streever (2000) and Lewis (2005). Such measures could also help alleviate the problem of eutrophication as documented by Slijkerman et al., 2011). Finally, our study documents the alarmingly rapid invasion of the bay by the invasive seagrass, Halophila stipulacea. Further studies are needed to assess the impacts that this species may have on the flora and fauna of the bay.

Section B:

Fish species utilization of contrasting habitats distributed along an ocean-to-land environmental gradient in a tropical mangrove and seagrass lagoon

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Abstract

The fish community structure of a variety of interconnected habitats of the tropical lagoon of Lac in Bonaire, Dutch Caribbean, were investigated using visual census to test the degree to which these habitats provide a potentially disparate habitat function for fishes of different species and life stages. We quantitatively sampled the fish species abundance, composition, and size-structures at a total of 139 sites distributed among nine different sub-habitats that are common to mangrove and seagrass ecosystems. Fish community variables differed consistently among habitats and were mainly influenced by the percent cover of seagrass vegetation or presence of mangrove-root structure. Mangrove fringe habitats were a premier habitat since multiple life stages of a variety of species showed highest densities there. Several reef fish species had a distribution pattern suggesting a unique step-wise post-settlement

life cycle migration in which larger juveniles and/or subadults appear to move from the open bay environment (seagrass beds or bay mangrove fringe) to the interior mangrove fringes along mangrove pools, before later departing to the adult habitat of the coral reef. In the case of the well-lit and well-circulated central bay habitat, the limiting factor to fish abundance and diversity appeared to be the paucity of three-dimensional shelter due to the predominance of the invasive seagrass *Halophila stipulacea* with small and short leaves. In the warm and hypersaline backwaters, physiological tolerance limits were likely a key factor. Long-term changes driven by mangrove expansion into this non-estuarine lagoon have been steadily reducing the net coverage of clear bay waters, while the surface of shallow, muddy, stagnant and hypersaline backwaters has been increasing by an almost equal amount. The current study shows how this natural process of mangrove land reclamation could affect the nursery function within this tropical lagoons. Depending on local conditions, active measures may need to be considered to stem the deterioration of nursery habitat quality and ensure that a tipping-point is not reached beyond which ecological recovery may be difficult or impossible.

B.1 Introduction

Coastal marine ecosystems such as mangroves and seagrass beds provide important ecosystem services (Constanza et al., 1997; Gladstone, 2009). In particular, there has been an interest in the role they play as nurseries for fish and decapods (Heck et al., 2003; Sheridan and Hays, 2003; Nagelkerken, 2009). The presence of these habitats enhances the diversity, density and biomass of fish populations of nearby reef ecosystems (Nagelkerken et al., 2002, 2012; Dorenbosch et al., 2004; Mumby et al., 2004). Recent otolith and stable isotope studies on various reef fish species have provided direct evidence for the life-cycle migration of fishes from seagrass beds or mangroves to nearby reefs (Chittaro et al., 2004; Verweij et al., 2008; Nakamura et al., 2008) and provide strong support for this nursery role. High food abundance, low predation pressure through structure and shade, and a good environment to intercept fish larvae have been hypothesized to be the main drivers for the nursery function of seagrass beds and mangroves (Parrish, 1989; Laegdsgaard and Johnson, 2001; Verweij et al., 2006). However, the importance of enhanced food provisioning by nursery habitats has been recently disputed (Nakamura and Sano, 2005; Grol et al., 2008) and fish may actually trade-off growth for reduced predation risk (Grol et al., 2011; Kimirei et al., subm.).

While the nursery role of mangroves and seagrass beds has been acknowledged, much debate remains about the extent to which they fulfill this role (Blaber, 2007). Different views exist on the definition of a nursery habitat (Beck et al., 2001; Dahlgren et al., 2006; Sheaves et al., 2006; Nagelkerken et al., subm.) and studies have used different criteria to assign habitats as nurseries (Beck et al., 2001). Another issue that has led to confusion about the role that mangroves and seagrass beds play as juvenile habitats, is related to how the habitats themselves are defined (Faunce and Layman, 2009). Inshore vegetated habitats show great spatial variability in their appearance due to differences in bay geomorphology, tidal regime, seascape configuration, and presence of microhabitats. For example, mangrove fringes, inland mangrove forest, mangrove pools, mangrove tidal channels, mangrove creeks, and mangrove estuaries have all been referred to as 'mangrove habitat', yet they are likely to differ significantly in their fish communities and the advantages that they provide to associated fauna (Ewell et al., 1998; Rönnbäck et al., 1999; Blaber, 2007).

Nursery function is often evaluated at the level of complete habitat units (e.g. mangrove, seagrass, algal beds, patch reefs). Consequently, no distinction is made between the various types or microhabitats found within seagrass, mangrove or other vegetated habitats typical to bays and lagoons. Yet such insight is critically needed to better understand the consequences that various environmental and biotic processes have on the quality and distribution of fish habitats and their nursery function (Faunce and Layman, 2009). In the case of a many tropical lagoons, one such process of particular concern is that of active land reclamation by mangroves. Long-term observations documenting the loss of seagrass cover as such habitat becomes entrapped and isolated in the migrating mangrove forests in Lac, Bonaire (Debrot et al., submitted), demonstrate that this process negatively impacts the mangrove channel habitat, which has been found to be of special value to the larger juveniles of several fish species, and which energetically connects different microhabitats within the larger mangrove forest ecosystem (Blaber et al., 1985; Valentine-Rose et al., 2007; Sheaves, 2009).

A better understanding of how different species utilize smaller-scale habitats within coastal ecosystems throughout the different life-cycle stages can help us to also better understand how dynamic processes that affect the occurrence, hydrology, and geomorphology of vegetated habitats may affect their value to (commercially) important species of decapods and fish. Such studies provide insight into the mid- to long-term consequences of ongoing land reclamation by mangroves for the nursery function of mangroves and connected habitats, and into how habitat fragmentation or disruption of hydrological connectivity may affect mangrove fish communities. Therefore, the objective of this study was to compare and contrast the fish species composition, abundance, richness and diversity of an array of inshore fish habitats in a tropical Caribbean bay. These habitats stretched from seagrass beds in a clear-water open bay close to coral reefs to stagnant and saline backwaters found on the landside of the mangroves. To this end we quantitatively sampled fish communities at 139 sites distributed among nine distinguished bay habitats. We specifically tested the hypothesis that due to their unique environmental and biotic habitat characteristics, smaller-scale habitats that exist within major mangrove and seagrass ecosystems, will harbor dissimilar fish assemblages and play differential roles in the life-cycle of certain fish species.

B.2 Materials & methods

B.2.1 Study area

Lac Bay lagoon is located along the eastern coast of the Caribbean island of Bonaire (Fig. 1) and covers an area of somewhat more than 700 ha. It is a semi-enclosed non-estuarine bay, largely 0–3 m deep and protected from the waves of the wind-exposed eastern coast by a shallow coral barrier. The main channel connecting the bay to the fringing reef is about 5 m deep. Lac is essentially a clear-water marine bay and horizontal Secchi visibility ranges from some 4.5 to more than 21 m in the central parts of the bay (van Moorsel and Meijer, 1993). Hence, apart from the sediment-ridden murky backwaters, various levels of seagrass and macroalgal development are found throughout the Bay.

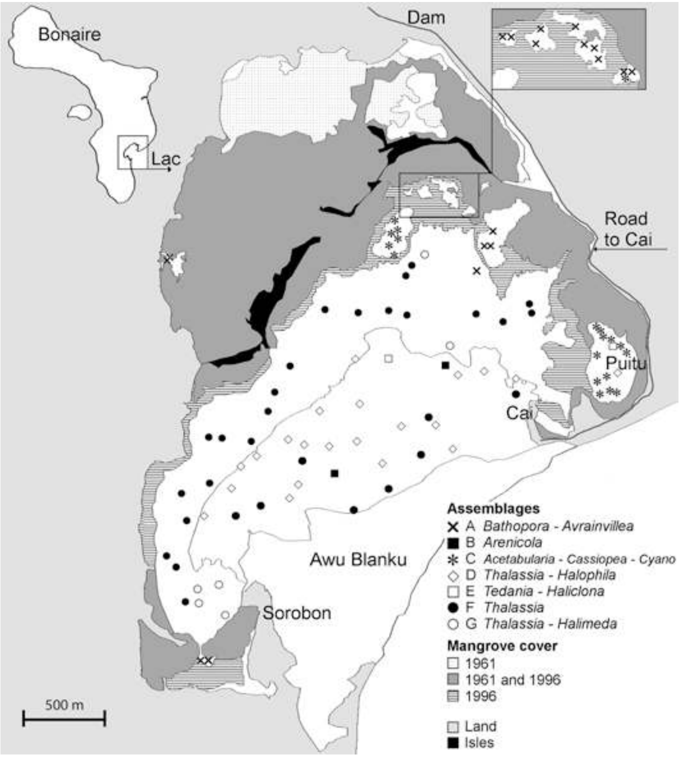

Fig. 1. Map of the study area in Lac, Bonaire, Southeastern Caribbean. Survey sites are indicated per habitat.

An analysis of cartographical maps dating back to 1866, aerial maps dating back to 1961 (Wagenaar-Hummelinck and Roos, 1969), and more recent satellite maps, shows that the north-western sector of Lac Bay as well as other bay margins have been filling in relatively rapidly due to mangrove expansion within the Bay. Comparing mangrove distribution between 1961 and 1996, it was found that the expansion of the mangroves during that period amounted to a growth of 81 ha of mangroves on the seaward margin (average: 2.34 ha per year) and a practically equal loss of mangrove surface area on the landside of the lagoon (of 82 ha) during the same period. In the process, the net coverage of clear, well circulated open bay waters declined by 81 ha, while the surface of shallow, muddy, stagnant, hypersaline backwaters grew by an almost equal amount (82 ha). The latter are unable to support functional mangroves, seagrass or algal meadows. Consequently, this process may seriously threaten the long-term biodiversity and ecosystem function of the bay, even though its exact causes and consequences are poorly understood.

In most estuarine situations, such as in river deltas opening onto unobstructed coastlines, expansion due to such successional processes in mangrove communities is not an ecological problem, as they have space to freely expand. However, Lac is a semi- enclosed bay, and because of the very narrow and steep shelf area surrounding the volcanic island, it is also the only and limited area of the island allowing substantial seagrass and mangrove development. From old cartographical maps dating back to 1866 it is further clear that hypersaline waters were formerly only a minor part of the Lac system (Wagenaar-Hummelink and Roos, 1969). Today such saline areas have grown in surface area.

The semidiurnal tidal amplitude in this part of the southern Caribbean averages about 30 cm (de Haan and Zaneveld, 1959), which, along with the shallow depth of large sections of the Bay translate into low circulation. This means that salt concentrations and water temperature can effectively build up in any shallow areas of the Bay that have obstructed connection to the Bay's open waters, whether it be due to accumulation of sediments in tidal channels or the narrowing of those channels due to mangrove growth. The result of these factors is a dynamic environmental gradient along which different benthic "seagrass" communities are found but which are not necessarily of equal value to the species that depend on these habitats. Current total coverage of mangroves in the bay amounts to about 238 hectares. As is the case with the seagrass beds, different mangrove prop root habitats can be distinguished, depending on their position along the environmental gradient stretching from bay shorelines, through the mangrove channel systems out into open bay waters.

Based on its nature values the Bay has been legally designated as a Ramsar site (since 1980) and has also been identified as an IUCN IBA (Important Bird Area) (Wells and Debrot, 2008). The area is managed by the National Parks Foundation of Bonaire, STINAPA Bonaire, based on their recent management plan in which several issues are addressed. The main management tool used is the zoning of recreational activities and a moratorium on the fishing of queen conch, *Strombus gigas*. Aside from spearfishing, which is prohibited, fishing activity is not restricted or regulated. Nevertheless, artisanal subsistence fishing pressure, showed a declining trend from 1987 to 1992 (van Moorsel and Meijer, 1993), and has continued to decline in the last 20 years. For instance, whereas in 1992, van Moorsel and Meijer still documented some 36 small open fishing boats at Lac, today that number averages six (Debrot et al., 2012). Van Moorsel and Meijer (1993) further indicated that whereas Lac formerly had the highest density of fish traps in Bonaire, today this kind of fishery has all but disappeared from the bay. The use of gillnets has also shown a dramatic drop since former times (van Moorsel and Meijer, 1993). So traditional subsistence fishing activity by means of several gear types in Lac has greatly declined, most likely due to the growth of dive-tourism and greater emphasis on more-profitable sources of income. As such, Lac can be considered a relatively pristine tropical lagoon, ideal to study natural fish habitat utilization patterns with little bias from human disturbances.

B.2.2 Habitat types

Nine different habitat types were studied in the Bay (in contrast to only two by Nagelkerken et al., 2000), consisting of three sub-habitats in each of three main habitat types (i.e., seagrass bed, mangrove pools, and mangrove fringes). All data collection and sampling of fish communities took place between September and December of 2011. For the seagrass beds (Fig. 1), we identified the following sub-habitats: (1) “central bay” habitat reflecting study sites that were located in the deeper-water parts of Lac and had relatively low cover of seagrass (Table 1); (2) “*Thalassia*” habitat which was predominantly found in the shallower zone between the mangrove fringe and the central bay and was characterized by a relatively high cover of seagrass. However, eight of the sites for this habitat were located in deeper-waters of the bay (Fig. 1); (3) “*Thalassia/Halimeda*” habitat which was dominated by macroalgae, especially *Halimeda* sp. It was predominantly located in the shallower “bay border” zone between the central bay and mangrove fringe.

Mangrove pools were open water pools fringed by mangroves and were found throughout the mangrove forest of Lac. For this study we identified three sub-habitats: (4) “blue pools” which are mangrove pools that appear blue on satellite images. Their sparse macroflora consisted principally of a brown cyanobacteria and the green algae *Acetabularia crenulata* (Debrot et al., subm.). The upside-down jellyfish, *Cassiopeia* sp. was especially common. Notable was that average depth in these pools was deeper than in the average *Thalassia* or *Thalassia/Halimeda* habitats sampled (Table 1).; (5) “dark pools”, which appear as dark pools on satellite images. These had an even lower vegetation cover, mainly consisting of the green macroalgae *Batophora* and *Avrainvillea*. Dark pools were located more land-inwards than and were shallower than the blue pools (Fig. 1, Table 1); (6) “backwaters”, resulting from the death of mangrove trees at the landward margins of the Bay. These were large, muddy, barren areas inundated with hypersaline water.

Table 1. Number of survey sites (N) and mean depth, temperature, salinity, horizontal Secchi disk depth (SDD) and percentage biotic cover per habitat. nd= no data.

	Central bay	*Thalassia*	*Thalassia/-Halimeda*	Blue pools	Dark pools	Mangroves	Mangroves	Mangroves dark pools	Backwaters
N	19	31	6	19	19	15	15	15	23
Abiotic variables:									
Depth (m)	3.7 ± 0.7	2.0 ± 1.3	1.7 ± 0.6	2.6 ± 0.8	1.4 ± 0.4	0.9 ± 0.2	1.1 ± 0.2	1.0 ± 0.5	0.4 ± 0.2
Temperature (°C)	28.8 ± 0.4	29.3 ± 0.8	29.3 ± 0.5	30.0 ± 0.0	29.6 ± 0.5	29.1 ± 0.8	29.6 ± 0.5	29.3 ± 0.6	32.3 ± 1.1
Salinity (ppt)	36.8 ± 0.4	36.9 ± 0.7	36.9 ± 0.6	37.8 ± 0.5	40.6 ± 4.6	36.9 ± 0.6	36.4 ± 0.9	37.1 ± 0.8	52.1 ± 1.7
Horizontal SDD (m)	7.7 ± 1.7	4.7 ± 1.6	6.2 ± 1.8	4.4 ± 1.2	4.3 ± 1.4	nd	nd	nd	< 0.4
Percentage cover:									
Sponges	0.3 ± 0.5	0.3 ± 0.7	1.0 ± 0.5	0.1 ± 0.1	0.0 ± 0.0	nd	nd	nd	nd
Macroalgae	3.6 ± 6.1	7.0 ± 8.9	37.2 ± 12.3	12.5 ± 16.9	11.3 ± 20.1	nd	nd	nd	nd
Seagrasses	35.1 ± 32.2	51.4 ± 20	4.8 ± 10.3	1.7 ± 3.9	0.0 ± 0.1	nd	nd	nd	nd
Other cover	12.2 ± 10.7	3.7 ± 13.1	1.0 ± 2.0	7.6 ± 5.3	0.5 ± 1.1	nd	nd	nd	nd
Bare substrate	48.8 ± 27.7	37.6 ± 20.4	56.0 ± 16.1	78.2 ± 18.7	88.2 ± 20.1	nd	nd	nd	nd

The third main habitat type consisted of mangrove fringes and was subdivided into the sub-habitats: (7) mangrove fringes along the open bay water; (8) interior mangrove fringes along the blue pools; and (8) interior mangrove fringes along the dark pools.

Physico-chemical variables were measured at each survey site to help define habitat differences. Temperature was measured with a dive computer (Suunto Zoop) with an accuracy of one degree Celcius. Field measurements were obtained by correcting temperature measurements of the dive computer with temperature measurements of a calibrated thermometer. Horizontal Secchi-disk distance was taken at the surface to measure water clarity. The Secchi disk was hung at a water depth of 0.5 m facing the sun, while a swimmer estimated the visibility using a marked line with a 0.1 m accuracy. At each survey site, water samples were collected to measure salinity using a YSI 556MPS salinity measuring device. Water depth (± 0.3 m due to tidal influence) was measured using a weighted marked line (0.10 m accuracy).

The measured values of abiotic variables supported the distinctiveness of the three sub-habitats within each main habitat(Table 1). Comparison between the distinguished communities in terms of depth, Secchi-disk transparency, temperature and salinity using ANOVA demonstrated significant differences ($p < 0.01$) for all four of these parameters. Multiple comparisons highlighted as “significant” are only those in which 95% confidence limits showed no overlap between habitat-associated assemblages (i.e., $p << 0.01$). For instance, water temperature, salinity, depth and Secchi-disk transparency of the backwaters differed significantly from all other habitats ($p << 0.01$). Water depth decreased across the different habitat types from 3.7 m in the central bay, to 1.7-2.0 m on the *Thalassia* and *Thalassia/Halimeda* beds and 1.4-2.6 m in the mangrove pools, to around 1 m along the mangrove fringes, and to 0.4 m in the mangrove backwaters. Mean temperature ranged between 28.8 and 30.0 °C, except for the backwaters where it reached 32.3 °C. Temperatures in the blue pool habitats were significantly higher than recorded in the central bay ($p << 0.01$), while salinity in dark pools differed significantly with that of the central bay, *Thalassia,* and *Thalassia/Halimeda* beds ($p < 0.01$). Mean salinity in all habitat types, except the more saline backwaters, ranged between 36.4 and 40.6 ppt., but habitats situated more land-inward general had a higher salinity and water temperature than the open bay habitats. Water transparency in the central bay habitat was significantly higher than in both the blue and dark pools and the shallower and more turbulent *Thalassia* beds ($p << 0.01$).

B.2.3 Site selection

The number of replicates for each of the three sub-habitats of mangrove fringes was set at 15. The further selection of the visual survey sites in the mangroves was based on water depth (>0.5 m) and visibility (>2 m horizontal Secchi-disk visibility), thus making sure visual census was possible. A minimum distance between replicate transects was set at 25 m per site. For the other habitat categories, sites were chosen using a random location generator without a priori knowledge of the specific vegetation present at each sampling site (Fig. 1). Here, the minimum number of sites to be achieved per habitat type was set at 15 each, but more sampling was deemed necessary, especially in the larger zones (bay border and central bay habitats). Quantification of benthic cover at these sites was subsequently used to distinguish the different types of seagrass beds as described earlier.

B.2.4 Faunal assessment

In each sub-habitat, except for the backwaters where sampling was done using a cast net, size-frequency data of all the encountered fish species were collected using a visual census technique (Nagelkerken et al., 2000). The 139 preselected visual survey sites were reached by boat or kayak using a Garmin GPS 12 XL device. During each visit, underwater visibility was first measured as horizontal Secchi-disk distance and the site was surveyed on a different day if the visibility was <2 m. At each site a 25 m transect line was anchored onto the bottom with two iron poles. A delay of 15 min was used between placing the transect line and surveying the site; this appeared sufficient to restore the initial fish communities (personal observation). For the mangrove fringe sites, a 25-m transect line was laid out parallel to the mangrove fringe. Fish swimming inside the mangroves within one meter of the transect line were identified and counted via visual census, covering an area of 25 m^2 per transect. In all other sub-habitats all fishes swimming within one meter at each side of the transect line were counted, covering an area of 50 m^2 per transect. At some mangrove sites where the substrate was easily disturbed and would reduce the visibility to less than two meter, the data were collected immediately while laying out the transect line.

Faunal assessments were done using SCUBA for water deeper than 1 m or snorkeling gear for shallower sites. Visual census is subject to differences in estimation of sizes and numbers between observers (Nagelkerken et al., 2000b). To minimize these differences, size estimation was regularly practiced with the use of fish-shaped objects of known size placed on the sea bottom. Prior to data collection, test transects were practiced by both observers until size estimates were similar between both divers. Size estimation was done within size classes of 5 cm total length. Schools smaller than 10 fish were counted. In the case of larger groups of fish, numbers were estimated in a manifold of 10, or even 100 in case of bigger schools. As the backwaters were too shallow and visibility was too low to perform meaningful visual censuses, a cast net was used instead to assess the fish diversity in this habitat (i.e. presence/absence). The net had a mesh size of 5mm and a radius of 2 m. At 23 randomly chosen sites the net was thrown 2-4 times, resulting in a total of 50 throws.

Fish identification was practiced prior to the surveys by diving and snorkeling at the survey area. Unknown species were photographed and identified using Humann and DeLoach (1994). At the start of the true surveys, all fish in Lac could easily be identified at first sight by both observers. However, the silver jenny *Eucinostomus gula* and the slender mojarra *E. jonesi* could not be distinguished in the field and were grouped together as a single taxon. For small schooling baitfish species such as scads (*Selar crumenophthalmus*) and species belonging to the families Atherinidae (silversides), Clupeidae (herrings and sardines) and Engraulidae (anchovies), only their presence was noted but no counts were made. Cryptic species like Blenniidae and Gobiidae were not taken into account in this study.

Table 2. Mean density per 100 m^2 of all encountered fish species per sub-habitat. P = present (not counted), - = absent. Total densities per fish family per sub-habitat are given in the rows with the family names.

Spec. No.	Family/ Species, common name	Central Bay	*Thalassia*	*Thalassia/ Halimeda*	Blue pools	Dark pools	Mangroves bay	Mangroves blue pools	Mangroves dark pools	Back-waters
	Acanthuridae									
1	*Acanthurus chirurgus*, doctorfish	0.9 ± 3.3	0.8 ± 2.1	-	-	-	-	3.5 ± 8.0	-	-
	Atherinidae									
2	*Atherinomorus stipes*, hardhead silverside	-	-	-	-	-	P	P	P	P
	Carangidae	**3.9**	**6.7**	**0**	**1.2**	**0.1**	**0.3**	**1.6**	**2.7**	
3	*Caranx crysos*, blue runner	3.9 ± 7.7	6.6 ± 19.8	-	1.2 ± 3.5	-	0.3 ± 1	1.6 ± 6.2	-	-
4	*Caranx latus*, horse-eye jack	-	-	-	-	0.1 ± 0.5	-	-	2.7 ± 10.3	-
5	*Caranx ruber*, bar jack	-	0.1 ± 0.5	-	-	-	-	-	-	-
6	*Selar crumenophthalmus*, bigeye scad	-	-	-	-	P	-	-	P	-
	Centropomidae									
7	*Centropomus undecimalis*, common snook	-	-	-	-	-	-	-	0.5 ± 2.1	-
	Chaetodontidae									
8	*Chaetodon capistratus*, foureye butterflyfish	0.3 ± 1.4	0.2 ± 0.8	0.3 ± 0.8	0.1 ± 0.5	-	3.5 ± 4.7	-	0.3 ± 1.0	-
	Cyprinodontidae									
9	*Cyprinodon dearborni*	-	-	-	-	-	-	-	P	P
	Diodontidae									
10	*Chilomycterus schoepfi*, striped burrfish	-	0.1 ± 0.4	-	-	-	-	-	-	-
	Elopidae									
11	*Elops saurus*, ladyfish	-	-	-	-	-	-	-	-	P
	Gerreidae	**3**	**0.4**	**2.6**	**0.9**	**6.7**	**29.5**	**51.7**	**57.3**	
12	*Diapterus auratus*, Irish pompano	-	-	-	-	-	0.5 ± 2.1	0.5 ± 1.4	0.5 ± 1.4	P
13	*Eucinostomus* spp., other mojarras	2.9 ± 12.4	0.3 ± 1.2	2.3 ± 5.7	0.3 ± 1.4	3.3 ± 8.5	19.7 ± 22.7	38.4 ± 68.1	19.2 ± 33.6	P
14	*Gerres cinereus*, yellowfin mojarra	0.1 ± 0.5	0.1 ± 0.5	0.3 ± 0.8	0.6 ± 1.3	3.4 ± 5.8	9.3 ± 10.5	12.8 ± 14.7	37.6 ± 28.0	P
	Haemulidae	**4.3**	**4.8**	**0**	**0**	**0**	**19.7**	**16.3**	**0.8**	
15	*Anisotremus surinamensis*, black margate	0.1 ± 0.5	1.2 ± 6.1	-	-	-	-	-	-	-
16	*Haemulon flavolineatum*, French grunt	4.2 ± 18.4	1.3 ± 7.2	-	-	-	18.4 ± 32.0	14.4 ± 51.4	-	-
17	*Haemulon sciurus*, bluestriped grunt	-	2.3 ± 5.3	-	-	-	1.3 ± 3.3	1.9 ± 3.0	0.8 ± 1.7	-
	Labridae	**3.5**	**12.1**	**12.3**	**0**	**0**	**0.5**	**0**	**0**	
18	*Halichoeres bivittatus*, slippery dick	2.4 ± 4.8	11.9 ± 23.9	12 ± 16.1	-	-	0.5 ± 1.4	-	-	-
19	*Serranus tigrinus*, harlequin bass	0.1 ± 0.5	-	-	-	-	-	-	-	-
20	*Thalassoma bifasciatum*, bluehead wrasse	-	-	0.3 ± 0.8	-	-	-	-	-	-
21	*Xyrichthys martinicensus*, rosy razorfish	0.9 ± 4.1	0.1 ± 0.4	-	-	-	-	-	-	-
22	*Xyrichthys splendens*, green razorfish	0.1 ± 0.5	0.1 ± 0.7	-	-	-	-	-	-	-
	Lutjanidae	**0.3**	**19.7**	**3**	**5**	**2.9**	**33.6**	**60.8**	**25.6**	
23	*Lutjanus apodus*, schoolmaster	-	1.4 ± 2.7	-	1.4 ± 2.6	0.4 ± 1.4	22.1 ± 15.0	23.5 ± 17.4	7.5 ± 8.7	-
24	*Lutjanus cyanopterus*, Cubera snapper	-	-	-	-	-	0.3 ± 1.0	0.5 ± 2.1	0.5 ± 1.4	-
25	*Lutjanus griseus*, grey snapper	-	14.6 ± 23.7	3.0 ± 3.9	3.6 ± 7.5	2.5 ± 9.2	10.9 ± 17.0	36.8 ± 40.3	17.6 ± 19.6	-
26	*Lutjanus mahogoni*, mahogany snapper	-	0.1 ± 0.4	-	-	-	-	-	-	-
27	*Ocyurus chrysurus*, yellowtail snapper	0.3 ± 1.0	3.6 ± 6.2	-	-	-	0.3 ± 1.0	-	-	-
	Mugilidae									
28	*Mugil curema*, white mullet	-	-	-	-	-	-	-	-	P
	Mullidae	**0**	**0.2**	**0**	**0**	**0**	**0.5**	**0.3**	**0**	
29	*Mulloidichtys martinicus*, yellow goatfish	-	-	-	-	-	0.5 ± 2.1	0.3 ± 1.0	-	-
30	*Pseudupeneus maculatus*, spotted goatfish	-	0.2 ± 0.8	-	-	-	-	-	-	-
	Ostraciidae	**0.6**	**0.1**	**0**	**0**	**0**	**1**	**0.3**	**0**	
31	*Lactophrys bicaudalis*, spotted trunkfish	-	-	-	-	-	0.5 ± 1.4	-	-	-
32	*Lactophrys triqueter*, smooth trunkfish	0.6 ± 1.9	0.1 ± 0.5	-	-	-	0.5 ± 1.4	0.3 ± 1	-	-
	Pomacentridae	**0.3**	**2.8**	**3.3**	**0**	**0**	**9.9**	**0**	**0**	
33	*Abudefduf saxatilis*, sergeant major	-	-	-	-	-	2.4 ± 5.8	-	-	-
34	*Microspathodon chrysurus*, yellowtail damsel	-	0.1 ± 0.5	-	-	-	-	-	-	-
35	*Stegastes diencaeus*, longfin damselfish	-	0.1 ± 0.5	-	-	-	0.3 ± 1.0	-	-	-
36	*Stegastes leucostictus*, beaugregory	0.3 ± 0.7	2.6 ± 4.7	3.3 ± 4.1	-	-	7.2 ± 15.1	-	-	-

Spec. No.	Family/ Species, common name	Central Bay	*Thalassia*	*Thalassia/ Halimeda*	Blue pools	Dark pools	Mangroves bay	Mangroves blue pools	Mangroves dark pools	Back-waters
	Scaridae	**9.1**	**131**	**73.7**	**0.1**	**0.2**	**252.8**	**21.6**	**23.9**	
37	*Cryptotomus roseus*, bluelip parrotfish	0.1 ± 0.5	0.1 ± 0.7	2.7 ± 3.0	-	-	-	-	-	-
38	*Scarus coeruleus*, blue parrotfish	-	-	0.3 ± 0.8	-	-	-	-	1.3 ± 5.2	-
39	*Scarus guacamaia*, rainbow parrotfish	-	0.1 ± 0.7	-	-	0.2 ± 0.9	34.7 ± 56.9	19.2 ± 28.6	22.1 ± 43.5	-
40	*Scarus iseri*, striped parrotfish	5.4 ± 11.2	118.8 ±143.6	66.7±163.3	-	-	195.2±311.9	2.4 ± 6.7	-	-
41	*Sparisoma aurofrenatum*, redband parrotfish	0.1 ± 0.5	0.1 ± 0.4	-	-	-	-	-	-	-
42	*Sparisoma radians*, bucktooth parrotfish	3.5 ± 7.3	11.0 ± 14.3	4.0 ± 4.6	0.1 ± 0.5	-	18.4 ± 35.1	-	-	-
43	*Sparisoma rubripinne*, yellowtail parrotfish	-	-	-	-	-	-	-	0.5 ± 2.1	-
44	*Sparisoma viride*, stoplight parrotfish	-	0.9 ± 1.8	-	-	-	4.5 ± 6.6	-	-	-
	Sphyraenidae									
45	*Sphyraena barracuda*, great barracuda	-	-	-	-	0.1 ± 0.5	2.4 ± 2.5	2.9 ± 2.8	1.3 ± 2.5	-

B.2.5 Data analysis

Various fish community structure variables were investigated: fish density, total number of fish species *S* (per 50 m^2), and Shannon's index of diversity *H'* (Sodhi and Ehrlich, 2010). To compare *S* and *H'* of the mangrove transects (25 m^2) with the other transects (50 m^2), each mangrove transect was combined with the nearest other mangrove transect of the same habitat into a single 50 m^2 sample.

Similarity in fish assemblage structure among habitats was analyzed using the program PRIMER (Clarke and Warwick, 2001). To incorporate spatial differences in the Bay among study sites, fish densities were averaged across sites that were located close to one another, for each of the sub-habitats separately. This resulted into the following higher-order mean values per sub-habitat and represented replicates for statistical analysis in PRIMER: two replicates for blue pools (reflecting the two sampled pools; Fig. 1), four replicates for dark pools (reflecting the three isolated pools, and averaging the four small connected pools shown as an inset at the northeastern part of the bay as a fourth replicate), two replicates for mangrove fringes along the two blue pools, three replicates for mangrove fringes along the dark pools (two isolated dark pools and the average for the smaller connected dark pools in the northeast), one replicate for mangrove fringes along the bay border, one replicate for the *Thalassia*/*Halimeda* sites, two replicates for *Thalassia* beds (separating seagrass sites along the Bay border at an average water depth of 0.7–2.8 m vs. those at greater depths of 2.9–5.0 m in the central portion of the Bay), and two replicates for the low-seagrass-cover central bay sites (located at a mean water depth of 2.6–2.8 m vs. 3.0–5.2 m).

All data were fourth-root transformed and Bray-Curtis similarity coefficients were calculated among the sub-habitats, using the statistical software package PRIMER (Clarke and Warwick, 2001). The resulting similarity matrix was used to generate a non-metric multi-dimensional scaling plot. Differences in fish community structure among habitats as well as sub-habitats were tested using a 1-way ANOSIM. CLUSTER analysis based on group averages was then used to generate clusters consisting of sub-habitats that showed 40% similarity in assemblage structure. Additionally, the RELATE-procedure (a non-parametric analogue of the Mantel test) was used to test the relationship (Spearman rank) between the resemblance matrices of the fish density data and benthic cover data at the level of sub-habitats, but excluding the three mangrove fringe habitats as no benthic cover data were collected there (see Table 1). Likewise, potential relationships between environmental variables (standardized by subtracting the mean and dividing by the standard deviation for that variable) and the fish community structure of these sub-habitats were studied using the BIO-ENV procedure (Clarke and Warwick 2001), which calculates the correlation (Spearman rank) between the similarity matrices of the biological (Bray-Curtis) and environmental (Euclidean) data. All significancies for the above tests were calculated on the basis of 999 permutations.

B.3 Results

B.3.1 Fish communities

Total fish density was highest in the mangroves fringing the bay, with an average of 350 fish per 100 m^2 (Fig. 2a). Statistically, this did not differ from the fish densities in mangroves fringing the blue or dark pools nor the *Thalassia* or *Thalassia/Halimeda* habitats. However, the mean fish density in all three mangrove fringe habitats and the *Thalassia* habitat was significantly higher than that in the central bay and the two mangrove pool habitats. Mean species richness showed a similar trend to that of fish densities (Fig. 2b). On average, there were 12 (± 2.8) species found per 50 m^2 in the mangroves fringing the bay, which is significantly higher than that for the central bay, blue pool and dark pool habitats. Compared to the latter three habitats, the *Thalassia* habitat and mangroves fringing the blue and dark pools also had a significantly higher species richness. The Shannon index for diversity was highest in the three mangrove fringe habitats, and differed significantly from that in the central bay, and blue and dark pool habitats, but not from the *Thalassia* and *Thalassia/Halimeda* habitats (Fig. 2c). Fish density, species richness and diversity in the central bay habitat was low, notwithstanding relatively high levels of biotic (seagrass) cover (> 50%).

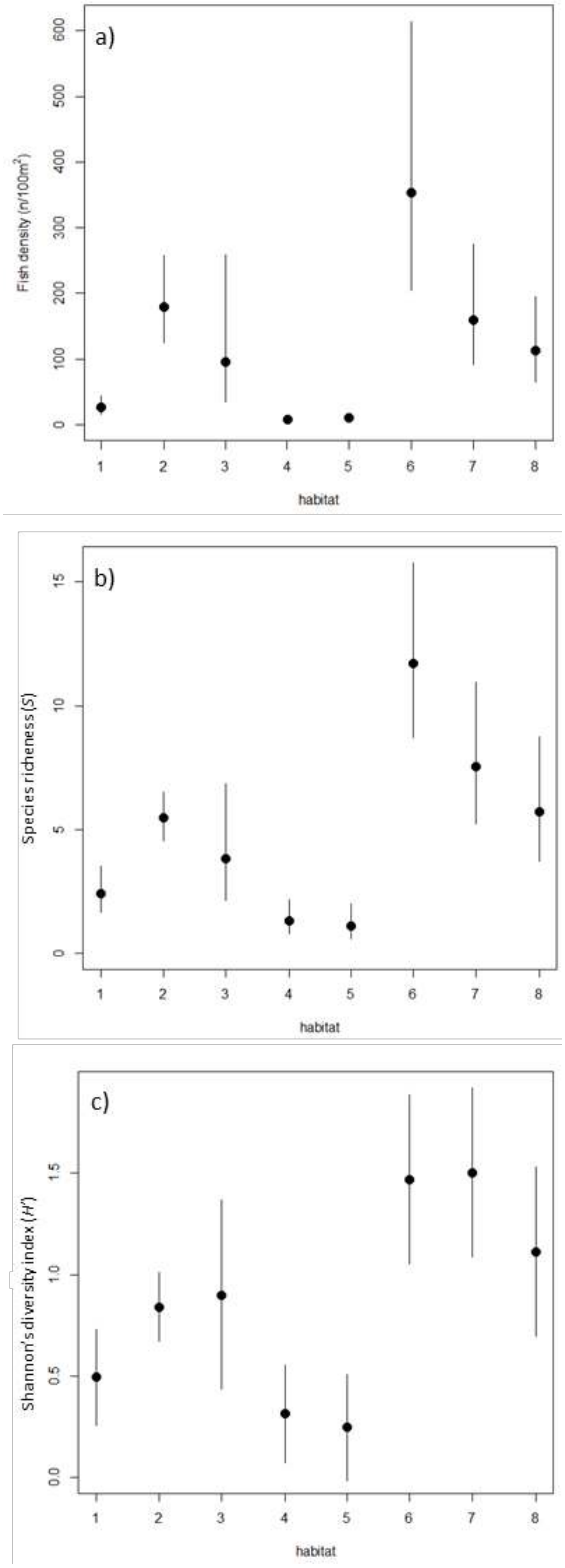

Fig. 2. Mean (± 95% confidence interval) (a) fish density per 100 m^2, (b) species richness (S) per 50 m^2, and (c) Shannon's diversity index (H') per 50 m^2 in each sub-habitat (1: central bay; 2: Thalassia beds; 3: Thalassia/Halimeda beds; 4: blue pools; 5: dark pools; 6: mangrove fringe bay; 7: mangrove fringe blue pools; 8: mangrove fringe dark pools).

Table 3. Relative abundance (%) of 10 common (density ≥ 2.3 100 m^{-2} in at least one sub-habitat) nursery species in each sub-habitat.

Species, common name	Central bay	*Thalassia*	*Thalassia/ Halimeda*	Blue pools	Dark pools	Mangroves bay	Mangroves blue pools	Mangroves dark pools
Acanthurus chirurgus, doctorfish	3.4	0.4					2.2	
Chaetodon capistratus, foureye butterflyfish	1.1	0.1	0.3	1.4		1		0.3
Haemulon flavolineatum, French grunt	16	0.7				5.2	9.1	
Haemulon sciurus, bluestriped grunt		1.3				0.4	1.2	0.7
Lutjanus apodus, schoolmaster		0.8		19.2	4	6.2	14.8	6.7
Lutjanus griseus, grey snapper		8.2	3.2	49.3	25	3.1	23.1	15.7
Ocyurus chrysurus, yellowtail snapper	1.1	2				0.1		
Scarus guacamaia, rainbow parrotfish		0.1			2	9.8	12.1	19.7
Scarus iseri, striped parrotfish	20.6	66.4	70.1			55.2	1.5	
Sphyraena barracuda, great barracuda					1	0.7	1.8	1.2
Total	42.2	80	73.6	69.9	32	81.7	65.8	44.3

Fish community structure differed significantly (ANOSIM, global R = 0.57, p = 0.001) among the three main habitat types (pools vs. mangroves: R = 0.60, p = 0.002; pools vs. seagrass: R = 0.50, p = 0.015; mangroves vs. seagrass: R = 0.69, p = 0.004). No significant differences were found, however, among the sub-habitats (R = 0.50, p > 0.057), although blue pools and dark pools formed separate clusters at 40% similarity (Fig. 3). On average, the shallower central bay sites showed more similarity in their community structure to that of the dark pool sites than to that of the other seagrass-harboring sites (Fig. 3). There was a high resemblance (RELATE, R = 0.706, p = 0.005) among the ordination of the sub-habitats based on their fish communities vs. their benthic communities (seagrasses, macroalgae, sponges, corals, etc.). Seagrass cover was the single best environmental factor that explained differences in fish communities among all sub-habitats in which benthic cover was quantified (BEST, R = 0.45, p = 0.01). Addition of the second and third best explanatory variables, water depth and temperature, only increased the global R to 0.461 and therefore did not play an important role.

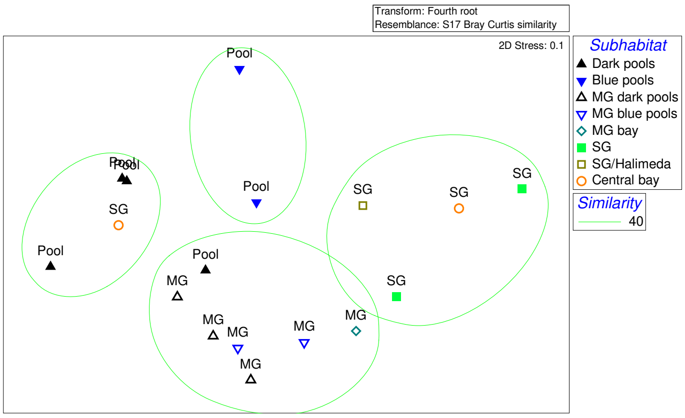

Fig. 3. Non-metric multi-dimensional scaling plot for fish densities in different sub-habitats belonging to mangrove (MG), seagrass (SG; incl. central bay) and mangrove pool (Pools) main habitats. Clusters showing 40% similarity in community structure (ellipses) are overlaid onto the sub-habitats.

The three most abundant species in the central bay habitat were the herbivorous *Scarus iseri,* the benthivorous *Haemulon flavolineatum* and the piscivorous *Caranx crysos* (Table 2). High densities were also found for *E. jonesi/gula, Halichoeres bivittatus* and the parrotfish *Sparisoma radians*. In the *Thalassia* and *Thalassia/Halimeda* habitats, *S. iseri* represented 66 and 70%, respectively, of all fish that were encountered. Other abundant species were *H. bivittatus, S. radians* and *Lutjanus griseus*. Members of the Gerreidae were almost absent in these two habitats. The three mangrove fringe habitats showed notable differences in the abundances of certain species. In the mangroves fringing the bay, the parrotfish *S. iseri* and *Scarus guacamaia* were the most abundant species with a relative abundance of 55 and 10%, respectively. However, *S. guacamaia* was also abundant in the mangroves fringing the blue and dark pools, whereas *S. iseri* was (nearly) absent in these two habitats. For the Gerreidae and the snappers *L. apodus* and *L. griseus,* the mangroves fringing the two pool types were notably important habitats. The blue and dark pools were mainly inhabited by species belonging to the Gerreidae and Lutjanidae. The backwater habitat, which was sampled with a cast net, showed the exclusive presence of *Elops saurus* and *Mugil curema*. Other species collected here were *Cyprinodon dearborni*, *Atherinomorus stipes* and three species of Gerreidae. These species were also observed in the mangrove fringe habitats.

B.3.2 Ontogenetic habitat use by nursery species

Ontogeny refers to the study of how particular aspects of the ecology and biology of a species change as it develops through different stages of its life-cycle. Nursery species were defined as reef fish species whose juveniles use bay habitats as nursery areas and whose adults use primarily reef habitats (sensu Nagelkerken et al., 2000b). Of 17 Caribbean documented nursery species, 12 were observed in Lac Bay. The distribution of nursery species varied across sub-habitats (Table 3), with some species occurring predominantly in seagrass sub-habitats (*Ocyurus chrysurus*), some mainly in mangrove fringe and mangrove pool habitats (*Lutjanus* spp., *S. guacamaia*, *Sphyraena barracuda*), some being absent from pool habitats (*Haemulon* spp., *S. iseri*), or some occurring across a range of sub-habitats (*C. capistratus*). The nursery species *Lutjanus mahogoni* and *Scarus coeruleus* were only observed in one sub-habitat (Table 3), and therefore their habitat utilization patterns could not be evaluated.

Table 4. Mean length at first maturity (L_m) for 10 common nursery species. Data are from Bouchon –Navaro et al. (2006), Faunce and Serafy (2007), Faunce and Serafy (2008), Martinez-Andrade (2003), Mateo and Tobias (2001), Munro (1983) and Xavier et al. (2012). nd = no data.

Species	L_m (cm)
Acanthurus chirurgus	14
Chaetodon capistratus	7
Haemulon flavolineatum	18.8
Haemuleon sciurus	22
Lutjanus apodus	25.8
Lutjanus griseus	19
Ocyurus chrysurus	32.3-42.1
Scarus guacamaia	nd
Scarus iseri	15.9
Sphyraena barracuda	58

Juveniles of *Acanthurus chirurgus* mainly used the central bay and *Thalassia* habitats, while adult-sized fish (see mean length at first maturity L_m in Table 4) were observed in the mangrove fringes of the blue pools (Fig. 4). All observed size classes of *Chaetodon capistratus* mainly used the mangroves fringing the bay. L_m in this species is 7 cm (Table 4), which makes it difficult to conclude if the observed fish in the size class 5-10 cm were large juveniles or adults. The L_m for *H. flavolineatum* is 18.8 cm, so most encountered individuals were juveniles. The mangrove fringes of the bay and blue pools were the main daytime habitat for this species, while the central bay harbored only large individuals. *Haemulon sciurus* was encountered in all mangrove fringe sub-habitats and in the *Thalassia* beds. Most individuals were observed in the size class 15-20 cm, which can be regarded as large juveniles as the L_m of this species is 22 cm. Adults were mainly observed in the mangroves fringing the Bay. The snappers *L. apodus* and *L. griseus* were both found in large numbers. Almost all individuals of *L. apodus* could be regarded as juveniles (Fig. 4), because they were smaller than the L_m of 25.8 cm (Table 4). Many of the observed *L. griseus* (Fig. 5) were also juveniles (L_m= 19 cm), although adult-sized fish were also regularly observed in Lac. Juveniles of both species mainly used the mangrove fringes of the bay, dark and blue pools. Larger juvenile *L. griseus* (10-20 cm) also used the *Thalassia* habitat while adult-sized *L. griseus* mainly utilized the mangrove fringes of the blue and dark pools. For *O. chrysurus*, the L_m is >32.3 cm. Therefore, all observed individuals were juveniles and *Thalassia* beds were their most important habitat. *Scarus iseri* juveniles, all which were smaller than L_m=15.9 cm, were mainly observed in the mangroves fringing the bay, and in the *Thalassia* and *Thalassia-Halimeda* habitats (Fig. 5). For the parrotfish *S. guacamaia* no L_m data could be found. However, body coloration indicated that all observed individuals were juveniles. The different mangrove fringe habitats were clearly very important for this species, because they were not observed in any other habitat. The larger size-classes of this species (>20 cm) were found predominantly in the mangroves of the blue and dark pools (Fig. 5). Finally, *Sphyraena barracuda* individuals were found in all size classes up to 60 cm and with an L_m of 58 cm almost all of them were juveniles. Small juveniles of 0-20 cm were mainly found in mangroves fringing the bay, while larger juveniles of 20-50 cm mainly used the mangrove fringes along the blue and the dark pools.

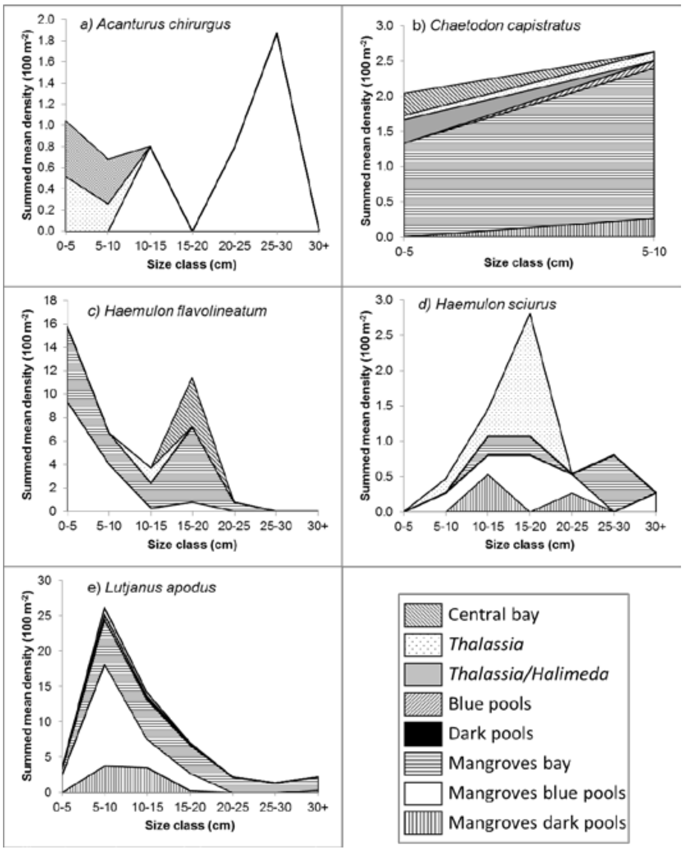

Fig. 4. Summed mean densities per habitat for 5 common nursery species: a) Acanthurus chirurgus, b) Chaetodon capistratus, c) Haemulon flavolineatum, d) H. sciurus, and e) Lutjanus apodus.

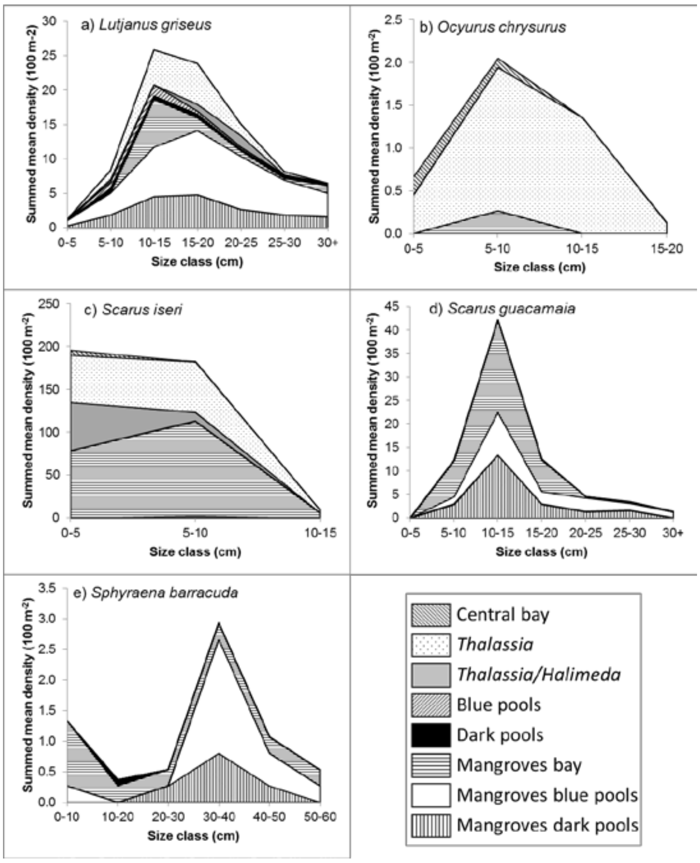

Fig. 5. Summed mean densities per habitat for 5 common nursery species: a) L. griseus, *b)* Ocyurus chrysurus*, c)* S. iseri*, d)* Scarus guacamaia*, and e)* Sphyraena barracuda*.*

B.4 Discussion

B.4.1 Drivers of fish assemblage structure

The present study shows that distinct lagoon habitats present in this tropical mangrove and seagrass bay are used differently and therefore likely serve different habitat functions for the various fish species. The largest difference in community variables (density, species richness, species diversity, and assemblage structure) was found between three major lagoon habitat types: seagrass habitats, mangrove-fringe habitats, and mangrove-pool habitats. Sub-habitats that occur within these three major habitat types also showed some unique properties, albeit with smaller-scale differences. The strongest predictor variable explaining differences in fish communities among sub-habitats (excluding mangrove fringe habitats) was presence of seagrass vegetation. Cover of bottom vegetation (seagrass and macroalgae) decreased from the seagrass beds, to the seagrass/*Halimeda* beds, to the central bay habitat, to the low-cover and almost barren mangrove pools and backwaters. Fish density, species richness, and diversity followed a similar decreasing trend across these sub-habitats. A decrease in bottom vegetation cover results in less shelter and feeding opportunities, which are the two factors that appear to be main drivers for use of these sub-habitats by juveniles of many reef fishes (Laegdsgaard and Johnson, 2001; Verweij et al., 2006). Mangrove fringes did not have much bottom vegetation cover but provided ample shaded structure with their complex prop-root matrix. Previous studies have shown the attractiveness of dark and structure-rich mangrove prop-roots habitats to many nursery fish species (Cocheret de la Morinière et al., 2004; Verweij et al., 2006; Nagelkerken and Faunce, 2008; Nagelkerken et al., 2010), explaining why mangrove fringes around pools that were isolated from the open bay water still showed fish densities nearly as high as those of the mangroves fringing the open bay. The low fish density in the central bay habitat, notwithstanding relatively high seagrass cover levels is interesting and may have to do with the different species of seagrass that it harbors (*Halophila stipulacea*) compared to the other sub-habitats (*Thalassia testudinum*). *H. stipulacea* has recently invaded the Caribbean (Ruiz and Ballantine, 1984) and due to its much shorter and smaller leaves compared to *T. testudinum* fish are more exposed to piscivores. This is further supported by the fact that the central bay sites that harbored some *T. testudinum* in addition to *H. stipulacea* showed a fish community similar to that of the seagrass bed sub-habitat, whereas the central bay sites that harbored *H. stipulacea* alone showed a reduced fish community similar to that of the barren blue and dark pool habitats (Fig. 2).

Even though the mangroves fringing the dark and blue pools were situated inside the pools, both sub-habitats appear to be functionally disconnected in terms of fish habitat usage, at least during daytime. The dark, structure-rich mangrove fringes harbored high densities of nocturnally active nursery species of Lutjanidae, Haemulidae and some other reef species (presumably for shelter; Verweij et al., 2006), and high densities of diurnally active species of Gerreidae (presumably for feeding; Verweij et al., 2006). Individuals of nursery species may have strayed into the adjacent open pool areas as these were among the few species observed in that habitat. Backwater habitat, with high salinities and lacking adjacent mangrove fringe habitat indeed showed complete absence of juvenile reef fish species and only presence of some bay species like Gerreidae. While it is unknown how the mangrove pool habitats are used at night, it is possible that they function as night-time foraging areas for fish sheltering in adjacent mangroves, just as is commonly observed for fish undertaking nocturnal feeding migrations from mangroves to adjacent seagrass beds (Ogden and Erlich, 1977; Verweij and Nagelkerken, 2007). It is clear that distance to the open bay played a relatively small role in explaining the above patterns, as mangrove fringes located far away from the open bay area also harbored high fish abundances.

In contrast to what was observed for the mangrove fringe vs. unvegetated pool habitats, juxtaposition of two vegetated habitats may result in increased habitat connectivity and higher species abundance and richness at their borders (Nagelkerken et al., 2001; Dorenbosch et al., 2006). Mangroves fringing the open bay showed highest values for fish density and species richness of all habitats studied. Their occurrence next to seagrass beds with high vegetation cover is likely to create edge effects that result in increased fish density and species richness. Such edge effects have also been observed among other types of vegetated habitats, such as patch reef–seagrass ecotones (Dorenbosch et al., 2005; Tuya et al., 2011) and provide a transition area for movement between two habitat, while providing benefits (shelter, food, etc.) from both habitats at small spatial scales. Fishes that feed in seagrass beds during daytime (Robblee and Zieman, 1984) have the advantage of increased protection from predation in directly adjacent mangroves when attacked by larger predators roaming in the open waters of the bay. Furthermore, many nocturnally-active species undertake foraging migrations at night from mangroves to seagrass beds (Ogden and Ehrlich, 1977; Nagelkerken et al., 2000a), so mangroves that are located close to seagrass foraging areas will likely be more favorable to fish species. The deeper, central bay seagrass beds may have had lower fish density, species richness and diversity in part because of this effect.

Land reclamation by mangroves is a natural process occurring over timescales of decades to centuries (Bingham 2001). The present study shows that this could potentially have negative effects on the nursery function of marine embayments. As discussed in the study area description, over the last 35 years, land reclamation by mangroves in Lac has been expanding into the bay at an average rate of 2.34 ha per year and has formed hypersaline and warm habitats with bare substratum land-inwards of the mangroves. Although sampling methods used in the backwater areas differed from the visual census used in the other habitats, the results indicate convincingly that the backwaters are inhabited by totally different fish species than the other habitats, and nursery reef-fish species were not found there at all. The ongoing bay-ward mangrove extension has lead to transformation of open bay habitats (*Thalassia* and *Thalassia*/*Halimeda* beds) with high fish abundance and diversity into depauperate mangrove pools (see Fig. 1) with very low fish abundance/diversity. This process especially affects nursery fish species, which are preferably associated with mangrove/seagrass vegetation. However, mangrove extension has also lead to an increase in mangrove fringe area with rich fish communities, and this may have (partially) offset the loss of habitat harboring bottom vegetation.

B.4.2 Ontogenetic habitat use

Four of the nursery fish species (*Acanthurus chirurgus*, *L. griseus*, *S. guacamaia* and *S. barracuda*) had distribution patterns suggesting a step-wise post settlement life cycle migration (Cocheret de la Morinière et al., 2002; Nagelkerken et al., 2000b) from open water habitats to more isolated inland habitats, before moving to the coral reef (Nagelkerken et al., 2000b, c). For these species, small juveniles predominated in seagrass and/or mangrove fringe habitats in the bay, while larger juveniles and/or subadults predominated deeper in the mangrove system (fringes along the blue and dark pools). Our focus on sub-habitats provides a more detailed insight into potential habitat shifts compared to earlier studies that regarded mangrove and seagrass habitats as single habitat units (e.g., Nakamura et al., 2008; Cocheret de la Morinière et al., 2002; Nagelkerken et al., 2000b). Usage of land-inward mangrove habitats at greater distances from the adult reef habitat could perhaps be driven by factors such as increased feeding opportunities in areas that are less accessible to other reef species. While the exact reasons are not known, it shows that the variety of niches that occur in the mangrove ecosystem are all occupied by certain life stages of various fish species.

Ontogenetic habitat shifts from open water mangrove fringes to interior mangrove fringes was not the norm for all nursery fish species. Smaller juveniles of *H. flavolineatum*, *H. sciurus* and *L. apodus* also occurred in mangrove fringes along the two pool habitats, but for the largest individuals of these species, the mangroves fringing the open bay were more important, suggesting a movement from the interior mangroves towards the open bay. The apparently contrasting strategies in ontogenetic movements suggests that different life stages of various nursery species have adapted to occupy contrasting non-reef habitats, probably in a way to minimize competition for resources among life-stages and species (Nagelkerken et al., 2006).

Juvenile *O. chrysurus* were mainly encountered in the *Thalassia* beds. This confirms results of earlier studies that indicate their dependence on seagrass beds (Robblee and Zieman, 1984; Nagelkerken et al., 2000; Verweij et al., 2008), although there are also studies which suggest the preference of juvenile *O. chrysurus* for mangrove fringes (Nagelkerken 2007). *Scarus iseri* showed a similar pattern of habitat usage as in other studies (Cocheret de la Morinière et al., 2002), occurring in seagrass as well as mangrove habitats, while *C. capistratus* was most abundant in mangroves as was the case elsewhere (Nagelkerken et al., 2000b).

During our surveys no groupers were recorded during count nor seen outside of the counts. In the past, up until the early 1990s various grouper species had been documented for the bay, among which *Epinephelus itajara, Mycteroperca rubra, Epinephelus guttatus, Epinephelus striatus,* and *Epinephelus adscencionis* (van Moorsel and Meijer, 1993). While the nursery function of non-reef habitats like mangroves and or algal beds for several species of large groupers like *E. itajara* (Frias-Torres, 2006; Koenig et al., 2007) and *E. striatus* (Eggleston, 1995; Dahlgren and Eggleston, 2000) has been known for some time, most of these species have largely disappeared from the waters of the island due to overfishing in the past and have not since recovered (Debrot and Criens, 2005). Nurse sharks which were formerly regularly encountered in the mangrove creeks of Lac (van Moorsel and Meijer (1993) were also not observed in this study.

Since first being observed on the reefs of the island in October 2009, the invasive lionfish (*Pterois volitans/miles*) has developed into a major problem on the reefs of Bonaire (Debrot et al., 2011). The species was not observed in our transects, nor anywhere else in the seagrass or mangrove habitats studied. However, during separate dives to isolated coral heads in the central bay area, lionfish were seen on numerous occasions. As the lionfish has been abundant for some time already on the fringing reefs of the island, it would appear that somehow the bay habitats are not being selected by the lionfish. However, Barbour et al. (2010) have found that the lionfish can also invade mangrove areas.

B.5 Conclusions

Our results indicate that the spatial setting of various habitat types within a shallow-water seascape has important consequences for the way in which these habitats are used by fishes during their ontogeny. While mangroves fringing open waters had highest overall fish densities and species diversity likely due to edge effects and complex shaded structure, the various vegetated sub-habitats all played a unique role for different size-classes of different fish species. The results suggest that maintenance of habitat connectivity and smaller-scale habitat diversity is a key management priority for ensuring secondary productivity of coastal marine habitats.

The central bay and blue pool habitats were hardly used as a juvenile habitat by reef fish, while in the more isolated dark pools and backwaters, nursery species were almost totally absent. In the case of the central bay habitat, the limiting factor likely was the low degree of three-dimensional shelter offered by an invasive seagrass species , while in the isolated, dark pools and warm and hypersaline backwaters, physiological tolerance limits were likely the most important factors.

Long-term changes driven by mangrove expansion into this non-estuarine lagoon have been steadily reducing the net coverage of clear, well circulated open bay waters by an average of more than 2 hectares per year, while the surface of shallow, muddy, stagnant, hypersaline backwaters has been increasing by an almost equal amount. These backwaters are unable to support either meaningful mangroves, seagrass or algal meadows. Consequently, the long-term biodiversity and ecosystem function of the bay could be at stake and management action is needed to stem further erosion of nursery habitat quality and ensure that a tipping-point is not reached beyond which recovery may be difficult or impossible.

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Quality assurance

IMARES utilises an ISO 9001:2008 certified quality management system (certificate number: 57846-2009-AQ-NLD-RvA). This certificate is valid until 15 December 2012. The organisation has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Environmental Division has NEN-EN-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 27 March 2013 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation.

Justification

Report C129/12
Project Number: 430.87010.03

The scientific quality of this report has been peer reviewed by a colleague scientist and the head of the department of IMARES.

Approved: Dr. D.M.E. Slijkerman
Scientist

Signature: Diana M

Date: November, 2012

Approved: F.C. Groenendijk, MSc.
Head of Department

Signature:

Date: 6 December, 2012